Status Survey and Conservation Action Plan

Canids: Foxes, Wolves, Jackals and Dogs

Edited by Claudio Sillero-Zubiri, Michael Hoffmann
and David W. Macdonald

IUCN/SSC Canid Specialist Group

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The Canid Specialist Group is the world's chief body of scientific and practical expertise on the status and conservation of all species of the Canidae, advising the IUCN Species Survival Commission. The CSG has its base at the Wildlife Conservation Research Unit (WildCRU) and is composed of more than 100 experts, representing over 30 countries (and with experience in many more), serving as honorary advisors.

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Species Survival Commission

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BORN FREE FOUNDATION

PEOPLE'S TRUST FOR ENDANGERED SPECIES

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IUCN – The World Conservation Union
2004

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Cover photo: Male Blanford's fox (*Vulpes cana*). Many fox species can be easily identified by large ears that have developed to enable the animals to pick up the minute rustlings of small prey, and to help dissipate heat in hot climates. Jebel Hafit, Al Ain, Abu Dhabi, United Arab Emirates, 1998. Photo: Chris and Tilde Stuart.

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Foreword

As humans usurp more and more of the Earth, and the natural world continues to shrink, carnivores will bear a disproportionate toll of the effects. This is because carnivores tend to have larger home ranges, more extensive movements, and longer dispersal distances than their prey, so their spatial requirements bring them into greater contact with humans. Furthermore, carnivores tend to conflict directly with human interests because of the proclivity of many of them to kill animals that humans use themselves.

Canids form one of the most prominent families of carnivores, with 36 interesting taxa in 13 genera that occur throughout most of the world. Foxes, dholes, dingoes, wolves, jackals, coyotes and various dogs comprise the family, and they find human-raised livestock irresistible prey. As a family, canids occupy every continent except Antarctica. The grey wolf, alone, was originally the most widely distributed terrestrial mammal; its successor to the throne is another successful canid, the red fox. Thus, canids have borne a high proportion of the conflict between humans and carnivores. The more prolific and adaptable canids, like the jackal and coyote, have fared well despite this competition, while the more specialised members of the family, like the Ethiopian wolf, have become threatened with extinction.

However, whatever the past or present status of a particular canid species, we can be sure that the future will present new problems as human populations grow, intrude on natural habitat, and convert more of the Earth to their own liking. Whether the issue is habitat loss, direct competition, or disease spread (both from canids to humans as with rabies, or from human sources to canids, such as canine parvovirus from domestic dogs to wolves), increasing human pressure means that canids face an uncertain future.

Fortunately, some humans have taken notice and have decided to assess the situation systematically. Through the World Conservation Union's (IUCN) Species Survival Commission, the Canid Specialist Group has developed this Action Plan for Canid Conservation. Editors Claudio Sillero-Zubiri, Michael Hoffmann and David Macdonald have assembled here an impressive collection of information about all living canid species and the conservation problems they face. From genetics to diseases, conflict resolution to reintroduction, this Canid Action Plan not only covers the basics, but also addresses the most pressing issues for canid conservation in a comprehensive manner.

Perusing this wealth of well-organised and important information is enough to give one hope that, despite the many problems canids face, this mobilisation of information and planning will help ensure the survival of all these intriguing species that comprise the family Canidae.

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Eight-week old island fox pup (*Urocyon littoralis*). Santa Rosa Island, California, USA, 2001.

Don Jones

Acknowledgements

This book has grown from the deliberations of the IUCN/SSC Canid Specialist Group, during many gatherings since the Group was formed in 1981. This exchange of ideas culminated in September 2001 with the Canid Biology and Conservation Conference at Oxford, where many of the ideas presented in this volume were discussed. We owe our gratitude to each of the 88 authors that contributed to this volume (Appendix 3), most of whom are members of the Canid Specialist Group. The Group is supported by an army of affiliates around the world, whose efforts have produced the data on which this action plan are based (see Appendix 4). Our gratitude goes to all that generously corresponded with us, reviewed manuscripts or assisted with data.

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The production of this action plan has involved much hard work and generosity by many people and organisations, and it is hoped that this support will also facilitate its implementation.

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Executive Summary

The new Canid Action Plan synthesises the current knowledge on the biology, ecology and status of all wild canid species, and outlines the conservation actions and projects needed to secure their long-term survival. Aiming at conservation biologists, ecologists, local conservation officials, administrators, educators, and all others dealing with canids in their jobs, the authors aspire to stimulate the conservation of all canids by highlighting problems, debating priorities and suggesting action.

The 36 taxa of wild canids that comprise the family Canidae, ranging in size from the tiny fennec fox to the mighty grey wolf, and found in every continent except Antarctica, are special. They are special because they have, as perceived friend or foe, preoccupied the imaginations of mankind for millennia; because the breadth of their adaptations makes them enthralling to science; and because the contradictory facets of their relations with people perplex the conservationist. The increase in numbers of people, the spread of settlement, and the exploitation of natural resources of previously little-disturbed wild lands, together with persecution, are threatening some of these canids with extinction. The possibility that we are heedlessly, perhaps needlessly, mismanaging many of them is saddening; the probability that our negligence will force several more to extinction should fill us with bottomless dismay. It demands action, and that is why we have compiled this new Canid Action Plan.

Following a short introduction and a chapter on phylogeny, classification, and evolutionary ecology of the Canidae (Part 1), Part 2 provides the latest information on the distribution, biology and conservation status of each species, organised by geographical region. The accounts also list current field projects, and their contact details are provided in an appendix. The Canid Specialist Group's members are active worldwide. Nine of the 36 taxa covered are threatened (3 Critically Endangered, 3 Endangered and 3 Vulnerable), and one is considered Near Threatened. Six species (7%) were listed as Data Deficient, and 20 (56%) species as Least Concern (Appendix 1). The threatened canids are:

- Darwin's fox (CR). Until recently, known only from the Island of Chiloé (Chile) until rediscovered 600km away in the coastal mountains, where domestic dogs threaten them with disease or direct attack.
- Red wolf (CR). Currently the subject of taxonomic debate, red wolves were declared Extinct in the Wild by 1980, but have been reintroduced into eastern North Carolina, where they are now locally common. Hybridisation with coyotes is the primary threat.
- Island fox (CR). Restricted to the six largest of the eight California Channel Islands, each island population is considered a separate subspecies, and four have declined precipitously. Threats include hyperpredation by golden eagles and the introduction of canine diseases.
- Ethiopian wolf (EN). Less than 500 individuals remain, confined to eight locations in the Ethiopian Highlands. Previously listed as Critically Endangered, continuous loss of habitat due to high-altitude subsistence agriculture remains the major threat, along with disease (particularly rabies).
- African wild dog (EN). Formerly distributed throughout sub-Saharan Africa, excluding rainforests, wild dogs have disappeared from 25 of the former 39 range states. More than half of the mortality recorded among adults is caused directly by human activity.
- Dhole (EN). Formerly distributed across Asia, dholes have undergone widespread decline and are threatened by depletion of their prey base, habitat loss, persecution, competition and disease.
- Dingo (VU). Austronesian people transported the dingo from Asia to Australia and other islands in between 1,000 and 5,000 years ago. Pure dingoes occur only as remnant populations in central and northern Australia and in Thailand, and they are threatened by cross-breeding with domestic dogs.
- Bush dog (VU). Despite a supposedly widespread distribution in South American forests, this species is perceived as rare, and threatened by habitat conversion and human encroachment.
- Blanford's fox (VU). Present in arid mountainous regions of the Middle East and north-eastern Egypt eastwards to Afghanistan, where human development could pose a threat.

In contrast to the threats faced by threatened canids, several species are thriving in human-dominated landscapes and incur the loathing of farmers and hunters alike. Red foxes are notoriously successful in urban settings, and coyotes, golden jackals, crab-eating and kit foxes seem able to thrive amidst human settlements. Management prompted by rabies control, fur harvest, and livestock predation leads to the slaughter of hundreds of thousands of canids annually.

Part 3 of the Plan considers nine major issues in canid conservation, namely canid society, conservation genetics, assessing and managing diseases, management of canids near people, impact of exploitation and trade, survey and census techniques, captive conservation, reintroduction and meta-population management, and conservation education.

Part 4 is arguably the most important section. It includes a chapter on the need for setting priorities and measuring success in canid conservation, and the detailed Action Plan for canid conservation into the 21st century. Although we have sought to refine and consolidate these entries, they represent the views of the many experts around the world who suggested them, who debated them in our workshops and in the forum of our international congress, hosted by the WildCRU in Oxford in September 2001. The list of proposed projects makes no claim to be comprehensive, but it is the result of extremely wide consultation. The plan itself, together with the databases concerning existing members and research projects, are all available on the web at http://www.canids.org. The Action Plan was prepared in parallel with our edited monograph entitled *The Biology and Conservation of Wild Canids* (Oxford University Press, 2004) which contains comprehensive reviews of the science underpinning this Action Plan, together with 14 case studies of wild canid biology.

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PART 1

Overview

Chapter 1

Introduction

C. Sillero-Zubiri and D.W. Macdonald

Canids: Foxes, Wolves, Jackals and Dogs Status Survey and Conservation Action Plan consists of a review of 36 wild canids, of which at least nine are threatened with extinction: island fox (*Urocyon littoralis*), Darwin's fox (*Pseudalopex fulvipes*), red wolf (*Canis rufus*), Ethiopian wolf (*C. simensis*), African wild dog (*Lycaon pictus*), dhole (*Cuon alpinus*), bush dog (*Speothos venaticus*), Blanford's fox (*Vulpes cana*) and dingo (*Canis lupus dingo*). In contrast, other species such as side-striped jackals (*Canis adustus*) and fennec foxes (*Vulpes zerda*) are widespread but rare (or certainly not common) throughout their range. Our knowledge of many of the remaining species (e.g., short-eared fox, *Atelocynus microtis*, and pale fox, *Vulpes pallida*), is too poor to determine how serious are the threats they face – although the snippets of information available offer little cause for optimism.

On the other hand, many wild canids are too common for their own good (e.g., red fox, *Vulpes vulpes*, culpeo, *Pseudalopex culpaeus*, golden jackal, *Canis aureus* and coyote, *C. latrans*), and thus are involved in often controversial wildlife management issues (such as rabies transmission, predation on livestock, sport hunting, fur trade).

The canids are a fascinating family biologically (studies of them have been at the forefront of half a century of research that has revolutionised understanding of evolutionary biology and behavioural ecology) and they also pose particular challenges to conservation – the topic of this Action Plan. These two topics – the biology and conservation of wild canids – are the subject matter of our monograph on this family (Macdonald and Sillero-Zubiri 2004a), and many of the points that we touch on briefly in this Introduction are fully elaborated therein.

1.1 Canid diversity

The number of species contained within the family Canidae is a point of some contention, and Clutton-Brock *et al*. (1976), Wozencraft (1989, 1993) and Ginsberg and Macdonald (1990) argue for between 34 and 37 distinct species, to which the recognition of *Canis lycaon* (see Wilson *et al*. (2000) would add another. In this plan, we recognise 35 full canid species, although we discuss also a 36th taxon, the dingo (*Canis lupus dingo*), which we consider a subspecies of the grey wolf (*Canis lupus*).

Canids range in size from Blanford's (*Vulpes cana*) and fennec foxes, which can weigh less than 1kg, to the grey wolf exceeding 60kg. Their distributions may be highly restricted – almost the entire Darwin's fox population occurs only on one island (Yankhe *et al*. 1996), and some unusual subspecies occur on one island each, such as island foxes or Mednyi Arctic foxes (*Alopex lagopus semenovi* – Wayne *et al*. 1991; Goltsman *et al*. 1996),


Love Dalén

Juvenile female Arctic fox lying on the den at dawn. Helags Mountains, Northern Sweden, August 2002.

whereas other species span several continents – about 70 million km² in the case of the red fox (Lloyd 1980). Their diets range from omnivory (with, at times, almost exclusive emphasis on frugivory or insectivory) to strict carnivory – and they glean these livings in habitats ranging from deserts to icefields, from mountain to swamp or grassland, and from rain forest to urban 'jungle' (Macdonald and Sillero-Zubiri 2004b). To do this they may travel home ranges as small as 0.5km² (island fox – Roemer *et al*. 2001) or as large and non-defensible as 2,000km² in African wild dogs (Frame *et al*. 1979).

Geographical variability in body size can be explained to some degree by differences in availability of food, with small canids (e.g., fennec fox) usually associated with arid and poor habitats in which only a small body mass can be supported year round, whereas large canids (e.g., Ethiopian wolf and African wild dog) are often associated with habitats in which prey is abundant. The maned wolf (*Chrysocyon brachyurus*), unusual in its social organisation for a large canid, lives in South American savannas and feeds largely on rodents and fruit (Dietz 1985). Geffen *et al*. (1996) suggest that low food availability probably constrains both the maned wolf's group and litter size (which is low at 2.2).

1.2 Patterns of distribution of the Canidae

The contemporary Canidae are the most widespread family of extant Carnivora, with at least one species present in all continents except Antarctica. A quick perusal of the ranges of all canid species (Macdonald and Sillero-Zubiri 2004b) indicated that over the last century the geographical ranges of seven species have increased, eight have decreased and nine have remained stable. The kaleidoscope of species diversity has changed: there are places where the grey wolf and the red fox have been replaced by what amounts to their 'ecological average', the coyote (once confined to mainly arid areas in western North America and now found in every state, province and country north of Panama – Moore and Parker 1992; Reid 1997; Bekoff and Gese 2003).

Many Canidae have distributions that span at least a whole continent. Red foxes and grey wolves have the most extensive natural range of any land mammal (with the exception of humans and perhaps some commensal rodents). Red foxes are the only canid present on five continents, recorded in a total of 83 countries. Grey wolves occur naturally in North America, Europe and Asia, their range spanning 62 countries. Two species are present on three continents, namely the golden jackal and Arctic fox (*Alopex lagopus*). And two other, the red fox and dingo have reached Australia and Oceania with assistance from mankind.

At least 155 of the 192 countries across the globe have canids (81%), with Sudan the country with the highest number of species (10 species), followed by USA (9 species) and Ethiopia (8 species). Those countries that do not host any canid species are island states (e.g., Caribbean islands, Madagascar, Malta, most Australasian islands).

Africa, Asia and South America support the greatest diversity with more than 10 canid species each. Red foxes are sympatric with 14 other canids (from three geographical regions), golden jackals with 13 (from two regions) and grey wolves with 11 (from three regions). Within any one location, however, canid diversity is usually limited to one to five species.

There are five canid species endemic to a single country. Not surprisingly, most are also threatened (red wolf, Ethiopian wolf, Darwin's fox, island fox and hoary fox – *Pseudalopex vetulus*), with the Sechuran fox (*P. sechurae*) a near-endemic to Peru. Of the two continents with the highest species diversity, South America harbours nine species (out of 11 species present) confined entirely to south of Panama, while Africa has eight endemics (of 13 species present). Of 12 canid species found in Asia, only two are restricted to that continent.

Although the genera *Canis* and *Vulpes* are both found in North America, Europe, Africa, and Asia (and were introduced by man to Australia), of the remaining eight genera six are restricted to one continent: *Chrysocyon*, *Otocyon*, *Pseudalopex*, *Speothos* (South America), *Cuon* (Asia), *Lycaon* (Africa); *Urocyon* is restricted to North and South America, whereas *Nyctereutes*, formerly restricted to Asia, has been introduced to Europe.

1.3 The Canid Action Plan

The Canid Action Plan is one in a series of such plans fostered by the World Conservation Union (IUCN) and written by members of the Species Survival Commission (SSC)'s Specialist Groups. The Canid Action Plan is the product of the deliberations of the Canid Specialist Group (CSG), itself one of more than 120 groups of specialists with a taxonomic focus on conservation under the aegis of SSC. The CSG has classified 36 living wild canid taxa and assigned a conservation status to each based on evaluated risk using the IUCN Red List Categories and Criteria: version 3.1 (IUCN 2001).

As its name implies, The Canid Action Plan aspires to identify important actions and to plan for their implementation. One way of doing this has been to canvass the views of the international community of canid specialists on the latest knowledge and status of each species, the threats they face, the questions that must be answered and the actions that must be taken to ameliorate these threats.

Paradoxically, the preparation of this Canid Action Plan has been a unique experience precisely because we have done it before! That conundrum is explained because in 1990 the CSG published the first Canid Action Plan, compiled by Joshua Ginsberg and David Macdonald. A particularly fascinating aspect of preparing the current plan has been that it afforded us the opportunity, for the first time, to take stock of how things had changed and what had been achieved in the intervening 14 years. We will return below (section 1.4) to some lessons learnt from this longer perspective, but first we summarise the main features of this, the second Canid Action Plan:

- This publication is an entirely new compilation of information on canids, reviewing exhaustively the salient advances in science relevant to canid conservation biology, and the most up-to-date information on status and distribution for each species.
- The classifications, and the proposed actions and plans, collated in this publication have been produced by the most systematic methods currently in use. To classify the 36 taxa we have used version 3.1 of the IUCN's Red List Categories and Criteria, and to generate candidate actions we have taken advantage of electronic communication to canvass a vast and internationally dispersed body of experts for their suggestions.
- The plan includes text written by 88 contributors and reviewed by more than 90 additional referees.
- The plan includes a comprehensive list of current projects and researchers.
- The entire plan will be available on the internet (http://www.canids.org), offering the facility for regular updates.

The authors of action plans have a clear remit: to provide current and accurate information that will help individuals, institutions, and governments to make educated decisions with the aim of ensuring the long-term survival of the species in question. To succeed in this objective, the authors of an action plan must first collect, collate, and synthesise the information available on the status, abundance, and distribution of the taxon under consideration. Only then can priorities be established and a plan for action developed.

Some other IUCN Action Plans have organised their contents on a regional basis, and some are further divided into regional reports, providing a level of detail at country level that is enviable. However, such an approach is not appropriate for the canids, and we have opted to organise the canid action plan differently. The reasons for this are several and stem from the basic biology of carnivores. First, carnivore species occur at lower densities than their prey; second, at any one location, the diversity of carnivore species is usually rather low, while third, the geographic ranges of many species are rather large. These traits of canid distribution are not just regional, but global. In deciding how to present our information we were impressed by the generalisation that the status of a particular canid species appears to be remarkably consistent throughout its range.

Thus, given the wide geographical ranges of many canid species, and their relatively low species diversity, a country-by-country analysis of status, abundance, and distribution seemed to us unjustifiable and potentially repetitive. Worse, it would be unworkable, insofar as information on the status of many canids remains sparse. For most countries, one simply could not write detailed reports because detailed information is unavailable. Nonetheless, policies often have a regional focus. Many people involved in biological conservation are shifting their attention from a species-oriented to an ecosystem-oriented approach. Therefore, in what we hope is a sensible and utilitarian compromise between the realities of canid biology, the limitations of the data, and the necessity for a geographical framework, we have organised this second Canid Action Plan by species status accounts listed under relevant geographic regions. The regions reflect, in broad terms, the biogeographical distribution of Canidae.

1.4 The longer view

Fifteen years have passed since the team preparing the first Canid Action Plan was at work and the publication of this second Plan. Those years have witnessed a continuing and exponential growth in understanding of, and enthusiasm for, conservation biology. Theory, far more abundant than data in 1990, has proliferated yet faster, and with dazzling sophistication in the meantime. For the canids as a whole, empirical knowledge has, if anything, fallen yet further behind – the corsac fox, the small-eared dog and the Indian fox are still as unknown as they were in 1990 – but the situation is partly saved because the intervening years have seen the publication of some wonderful field studies (and 14 of these are highlighted as case studies in Macdonald and Sillero-Zubiri 2004a). Despite the gaps, therefore, a great deal more is known now than then. Against that background, revisiting the first plan while working on this second one has caused us to ask what has changed. Some things have not.

Foremost amongst the things that have not changed are the inherent natures of wild canids and of people – natures that all too often throw us into conflict. Thus, it is still true that the fox trotting across your field of view may be, simultaneously, a resource for the trapper, a health hazard to the rabies official, a quarry to the huntsman, a subject to the photographer, vermin to the poultry farmer, and a joy to behold to the aesthete. What is more, it is still true that their judgements are neither right nor wrong according to some self-appointed prophet – each could argue a case, but would do so using incommensurable currencies (how are we to equate units of jobs versus units of cultural heritage versus units of suffering versus money, etc.?). Again and again, scientific judgement trips over ethical judgement. In the Introduction to the first Canid

Action Plan we wrote of the challenge of untangling these issues as the prerequisite to resolving them – it remains no less a challenge now.

Science has been helpful. For example, the oral vaccination of foxes against rabies was *avant garde* in the 1980s, but is *de rigour* now. On the other hand, alternative, and often non-lethal, approaches to resolving conflicts with canids that we vaunted expectantly in 1990 – such as aversive conditioning or sophisticated repellents – have still not really materialised (although the scope is great; see Sillero-Zubiri *et al.* (2004)). On the other hand, appreciation of the human dimension to conservation biology has advanced hugely, and the processes and outcomes associated with the reintroduction of wolves to Yellowstone illustrate the new deal. In this vein, exciting, collaborative, often community-based projects are developing, and the trial introduction of African wild dogs to a consortia of adjoining South African game ranches is a case in point: the question is whether some way can be found to ensure that the profit from ecotourists attracted by the wild dogs will outweigh the losses caused by their depredations on valuable antelope – the research is underway and the answer may be some years in coming, but it is exciting that the question is at least being both asked and tackled.

In 1990 we wrote that the very opportunism and mobility that is the hallmark of success for many members of the dog family is also responsible for throwing them into conflict with people. This conflict involves, first, competition between man and canids through depredations on game and domestic stock; and, second, canids as victims of, and often vectors for, several zoonoses, of which rabies is undeniably the most notable. In addition to rabies, there are several other pathogens of direct (e.g., leishmaniasis) and indirect (e.g., sarcoptic mange) concern to man, the latter threatening the fur trade, the former threatening life. The traditional response to perceived problems of predation and disease has been to attempt to reduce canid numbers by killing them. This time-honoured approach had, and still has, two notable drawbacks: it tends to throw different factions into conflict (e.g., fur traders object to their commodity being blasted by irate shot-gun-toting stockmen, and those concerned with animal welfare object to both groups killing canids); and it may not work (either because the problem was merely perceived but not real, or because the solution was inappropriate). The issues raised by predation and disease are biologically and economically complicated. Data on both topics are more revealing nowadays, and Part 3 of this Action Plan considers these continuing realities within a much more secure framework of ideas than was available in the first edition.

Our intention remains to identify problems common to many canids, real and imaginary, to seek some indication of their magnitudes, and to evaluate the effectiveness of existing solutions and the practicability of novel ones, all from the point of view of species conservation. Perhaps the most clear-cut change in attitude is that disease has become accepted as a two-faced demon in canid conservation: not only is infectious disease a scourge of populous canids, and thus a threat to mankind and his domestic stock, but it is also a threat to rare canids themselves – sometimes because numerous canids threaten them (uncommon Blanford's foxes might succumb to rabies transmitted by abundant red foxes), but more commonly because rare wild canids (Ethiopian wolves, African wild dogs, island foxes) are decimated by diseases of domestic dogs. Happily, this realisation has fostered productive links between biologists, veterinarians, public health officials and community development experts. This is the sort of interdisciplinarity that we hailed as necessary in 1990, and which is now widely becoming familiar – but there is still a long way to go.

1.5 Structure of the Action Plan

The arrangement of species sections within chapters follows a regional approach. Each of the world's canid species has been assigned to one of seven regional chapters (Chapters 3–9). The structure of each geographically organised chapter is explained in the Introduction of Part 2 "Species Status Accounts".

Our approach was to seek more than one author for each entry and then to support them with a team of reviewers. The reviewers were selected, where possible, to span the geographic region covered by the species in question. The final entry, therefore, combines the expertise of the authors, reviewers and editors in what we believe are the most comprehensive accounts available. A first step in this process, however, was to agree which species are to be recognised, and by which names are we to refer to them. Therefore, in Chapter 2 there is a discussion of canid taxonomy, and the classification used in this publication is explained. Although the Action Plan does not attempt to analyse conservation priorities at the level of subspecies (with the exception of the dingo, herein considered a subspecies of the grey wolf), each species account includes a list of recognised subspecies for those who wish to pursue questions of taxonomy and biogeography.

Foxes, wolves, and jackals have much in common, both in their biology, their relationships with man and their conservation challenges. Hence, following the geographical chapters, in Part 3 we present nine chapters on topics almost universally relevant to the conservation of the Canidae as a whole. The topics are sociobiology, genetics, diseases, management of canids near people, trade, research techniques, captive breeding, reintroduction, conservation policies, and conservation education.

Finally, Part 4 represents the true 'action' component of the plan, an 'Action Plan for Canid Conservation in the

21st century', introduced by a short chapter on the increasing need in conservation biology for setting priorities and measuring success (Chapter 19). In chapter 20 we list the projects and actions that we believe are priorities for canid conservation over the next 10 years. These are presented in a simple summary form. Given that canids are present throughout the world, and that many of the range countries do not have appropriate scientific and conservation infrastructure, we have attempted to identify the most needed projects and actions to improve the conservation status of canid species, rather than present a "wish" list of projects per country as other IUCN action plans have done. We aim to achieve a realistic list of projects and actions that would have a good chance of being implemented within a decade. Thus the projects/actions focus on the threatened species, and are organised into two sections; a) general projects/actions affecting all species, and b) projects/actions listed under relevant species. The process of assembling these proposals was revealing, as was the nature of the proposals themselves – we feel certain generalisations emerge from them, and we have discussed these at length in Macdonald and Sillero-Zubiri (2004c).

During the three years or so that it has taken to produce this Action Plan we received many reports from CSG members and other canid enthusiasts. We received standardised questionnaire forms providing information on the distribution and status of wild canids at country level. Such information was made available to the authors of each species' account. The second Canid Action Plan could not have been completed without the help of these correspondents, and we have tried to represent their views accurately. Many of our correspondents have emphasised the potential usefulness of a register of conservation and research projects dealing with canids and those people involved with canid research. This has prompted the CSG to develop a web-based Canid Project Database (http://www.canids.org/database/ – see Appendix 5). This directory is by no means complete, and we encourage readers to submit information on those projects that are not yet covered by the database.

1.6 Limitations of this Action Plan

The structure we have imposed upon this second edition of the Canid Action Plan has suited our purpose, but it has drawbacks. For example, by making our focus regional and global, we have largely ignored aspects of conservation at the level of subspecies or of local populations. In defence of this, we would argue that, for the most part, patterns of extinction are regional: a succession of subpopulations disappears, survivors become fragmented, and local extirpations start the slippery slide to extinction. In addition, for many species such as the short-eared dog (*Atelocynos microtis*) or the pale fox (*Vulpes pallida*), data are so inadequate that the available materials swiftly determined the scope of our accounts.

The nomination of priorities also lures us into an imponderable mirage dividing biology and ethics. It may be tempting to seek criteria on which to decide whether it is more important to save the Ethiopian wolf than the red wolf. But both are irreplaceable. We might be able to guess the order in which threatened canid species will go extinct, but we have tried not to place relative value on the loss of one versus another. Nonetheless, as funds and time are limited, we have tried to focus our action planning on those species most threatened with imminent extinction, and secondly those for which more data are needed in order to make judgement.

1.7 The Canid Specialist Group

The Canid Specialist Group (CSG) is the world's chief body of scientific and practical expertise on the status and conservation of all species of the Canidae (wolf, jackal and fox family), advising the Species Survival Commission (SSC) of the World Conservation Union (IUCN). The CSG is based at the Wildlife Conservation Research Unit (WildCRU), Oxford University, UK (http://www.wildcru.org).

The CSG is composed of more than 100 experts, representing over 30 countries (and with experience in many more). These people serve as honorary advisors to the CSG in their personal capacities, but bring with them the experience and the knowledge gained in their professional careers. CSG membership is rapidly expanding and is open to anybody actively involved in canid conservation and research. There is a separate Wolf Specialist Group concerned specifically with grey and red wolves.

The Mission of the CSG is to promote the long-term conservation of all Canid species throughout their ranges

Objectives:

- Compile, synthesise and disseminate information on the conservation of all canids across their range, with particular emphasis on species that are threatened or rare.
- Provide technical information and advice on all matters concerning wild canids, including their status in the wild; their biology and natural history; the threats they face and their conservation requirements to the following:
  a) range state government agencies;
  b) national and international NGOs, including potential funding bodies;
  c) inter-governmental organisations (e.g., IUCN, CITES);
  d) field projects concerned with canid conservation.

- Promote and catalyse conservation activities on behalf of wild canids, prioritising and coordinating efforts of researchers and conservationists worldwide.
- Fundraise for canid research and conservation and undertake research directly when necessary or appropriate.
- Improve management of the common and sometimes troublesome species.
- Build capacity through the exchange of ideas, information, and technical expertise among the members of the Group.

CSG functions and activities

- Liaison between field biologists, wildlife managers, governments, NGOs and sponsors on any topic concerning the conservation of canid species.
- Compilation, synthesis and dissemination of canid related information.
- Development of the *Canid Conservation Database*, an updated list of references and information on current research and conservation projects.
- Hold regular meetings of CSG members alongside international conferences.
- Serve as the IUCN Red List Authority for the Canidae, responsible to evaluate the category of threat of all canids.
- Regionalised approach – A global network with Regional Section Chairs for: Sub-Saharan Africa; North Africa and Middle East; North and Central Asia; South Asia and Australasia; Europe; North and Central America; South America.
- Species Working Groups – Bringing together the experts of a particular species: African wild dog; Arctic fox; Ethiopian wolf; dhole; island fox, kit fox and swift fox.
- Topical Working Groups – Addressing specific problems across species: Disease and Epidemiology; Ecology and Research; Genetics; Harvesting and Pest Control; International Policy; Re-introduction and Translocation.

Chapter 2

Phylogeny, Classification, and Evolutionary Ecology of the Canidae[1]

Wang Xiaoming, R.H. Tedford, B. Van Valkenburgh, and R.K. Wayne

The family Canidae belongs to the order Carnivora, a large group of mostly predatory mammals characterised by their common possession of a pair of carnassial teeth (upper fourth premolar and lower first molar) that are modified to maximise efficiency for shearing skins, tendons, and muscles in their preys. Canids are characterised by an inflated entotympanic bulla (bony chamber enclosing the middle ear region) that is divided by a partial septum along the entotympanic and ectotympanic suture. Other features characteristic of canids are the loss of a stapedial artery and the medial position of the internal carotid artery that is situated between the entotympanic and petrosal for most of its course and contained within the rostral entotympanic anteriorly (Wang and Tedford 1994). These basicranial characteristics have remained more or less stable throughout the history of canids, allowing easy identification in the fossil record when these structures are preserved.

2.1 Phylogeny from morphological and palaeontological perspective

There are three major groups (subfamilies) in the family Canidae: Hesperocyoninae, Borophaginae and Caninae (Tedford 1978) (Figures 2.1, 2.2). Of these, two are represented by fossil forms only. The Hesperocyoninae is the most ancient group of all canids, and its basal member, *Hesperocyon*, gave rise to the two more advanced subfamilies, Borophaginae and Caninae (Wang 1994). A major evolutionary transformation involves the modification of the talonid heels on the lower carnassial tooth (first lower molar), which changes from that of a trenchant, blade-like condition in the Hesperocyoninae to that of a basined condition enclosed by two cusps in the Borophaginae and Caninae (Figure 2.3). Mainly due to their common possession of this basined talonid, the Borophaginae and Caninae are hypothesised to share a common ancestry. Along with a more quadrate upper first molar with a large hypocone on the inner corner of the tooth, the basined talonid establishes an ancestral state from which all subsequent forms were derived. Such a dental pattern has proved to be very versatile and can readily be adapted toward either a highly carnivorous or a less carnivorous type of dentition, both of which were repeatedly employed by both Borophaginae and Caninae.

The extinct Borophaginae was the first major group of canids to demonstrate the viability of a basined talonid and achieved the greatest morphological breadth and taxonomical diversity within the North American continent (Wang *et al.* 1999). Toward the less predaceous end of the morphological spectrum, it sports highly omnivorous forms that parallel similar adaptations by living Procyonidae (the raccoon family). Toward the more predaceous end, on the other hand, the Borophaginae is well known for its tendencies to develop strong bone-crushing dentitions that parallel the habits of living Hyaenidae (the hyaena family).

The subfamily Caninae started with *Leptocyon*, an ancestral species the size of a small fox. Besides sharing a bicuspid talonid of M1 and a quadrate M1 with the borophagines, *Leptocyon* is also characterised by a slender rostrum and elongated lower jaw, and correspondingly narrow and slim premolars, features that are inherited in all subsequent canines. It first appeared in the early Oligocene (Orellan, 34–32 million years before present [BP]) and persisted through the late Miocene (Clarendonian, 12–9 million years BP). Throughout its long existence (no other canid genus had as long a duration), facing intense competition from the larger and diverse hesperocyonines and borophagines, *Leptocyon* generally remained small in size and low in diversity, never having more than two or three species at a time.

By the latest Miocene (Hemphillian, 9–5 million years BP), fox-sized niches are widely available in North America, left open by extinctions of all small borophagines. The true fox clade, Tribe Vulpini, emerges at this time and undergoes a modest diversification to initiate primitive species of both *Vulpes* and *Urocyon* (and their extinct relatives). The North American Pliocene record of *Vulpes* is quite poor. Fragmentary materials from early Blancan indicate the presence of a swift fox (*Vulpes velox*) in the Great Plains. *Vulpes* species were widespread and diverse in Eurasia during the Pliocene (see Qiu and Tedford 1990), resulting from an immigration event independent from

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[1] This paper is adapted from Wang, X., Tedford, R.H., Van Valkenburgh, B. and Wayne, R.K. 2004. Evolutionary history, molecular systematics, and evolutionary ecology of Canidae. Pp. 38–54 in D.W. Macdonald and C. Sillero-Zubiri (eds). *Biology and conservation of wild canids*, Oxford University Press, Oxford, UK.

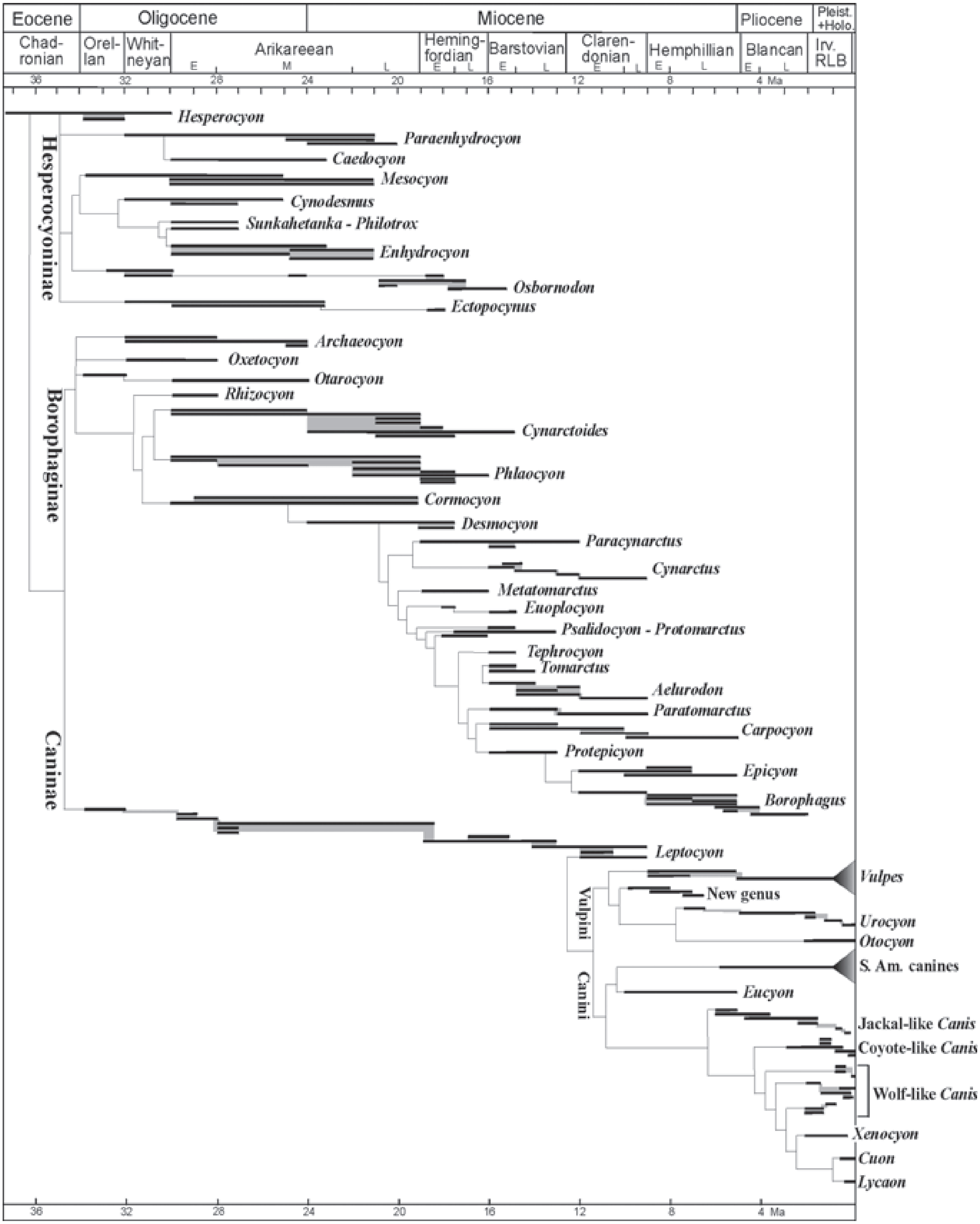
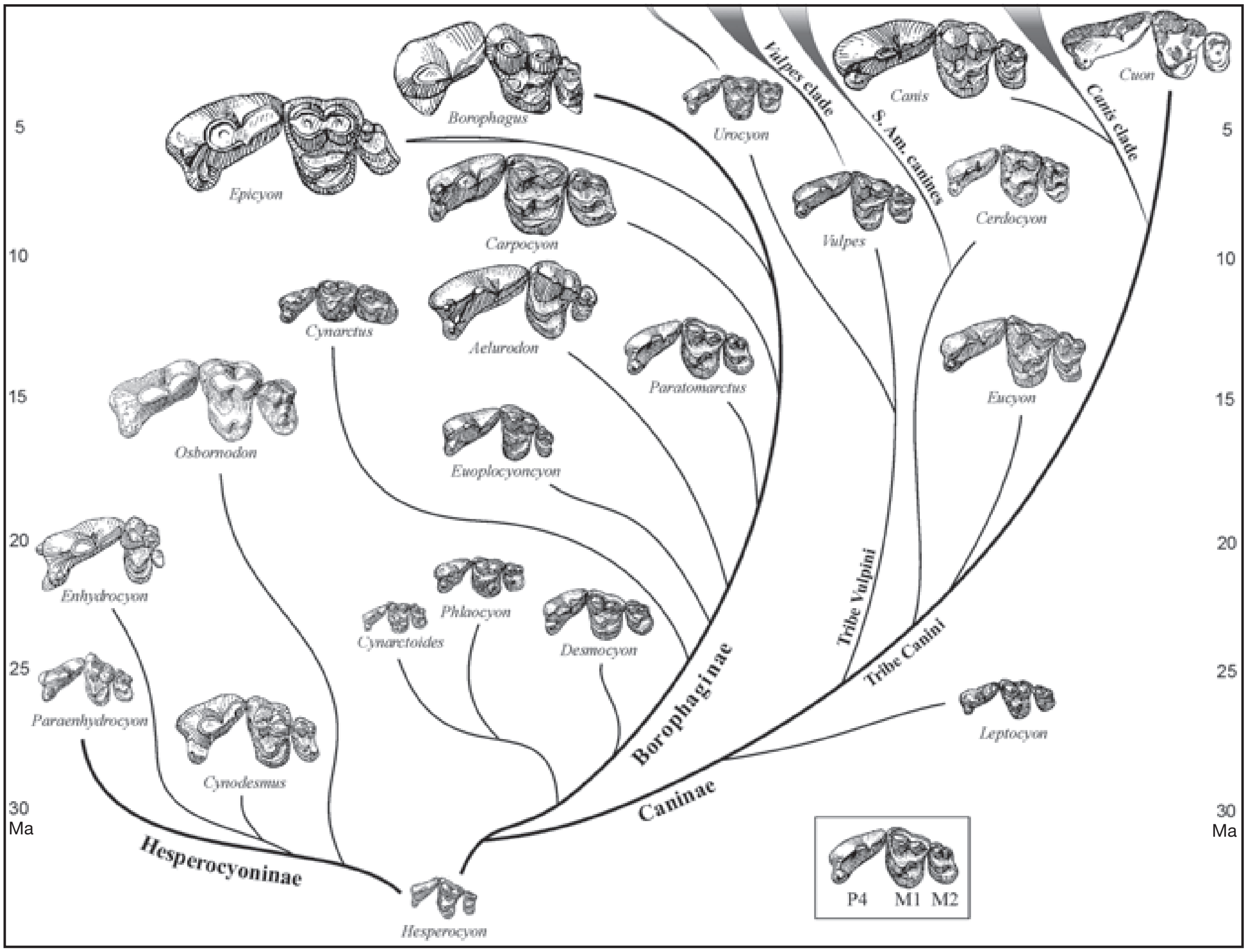


Figure 2.1. Simplified phylogenetic relationships of canids at the generic level.
Species ranges are indicated by individual bars enclosed within grey rectangles, detailed relationships among species in a genus is not shown. Relationships for the Hesperocyoninae is modified from Wang (1994: fig. 65), that for the Borophaginae from Wang *et al.* (1999: fig. 141), and that for the Caninae from unpublished data by Tedford, Wang, and Taylor.

Figure 2.2. Dental evolution of representative canids as shown in upper cheek teeth (P4-M2).
Generally the most derived species in each genus is chosen to enhance a sense of dental diversity. Species in the Hesperocyoninae are: *Hesperocyon gregarius*; *Paraenhydrocyon josephi*; *Cynodesmus martini*; *Enhydrocyon crassidens*; and *Osbornodon fricki*. Species in the Borophaginae are: *Cynarctoides acridens*; *Phlaocyon marslandensis*; *Desmocyon thomsoni*; *Cynarctus crucidens*; *Euoplocyon brachygnathus*; *Aelurodon stirtoni*; *Paratomarctus temerarius*; *Carpocyon webbi*; *Epicyon haydeni*; and *Borophagus diversidens*. Species in the Caninae are: *Leptocyon gregorii*; *Vulpes stenognathus*; *Urocyon minicephalus*; *Cerdocyon thous*; *Eucyon davisi*; *Canis dirus*; and *Cuon alpinus*. All teeth are scaled to be proportional to their sizes.



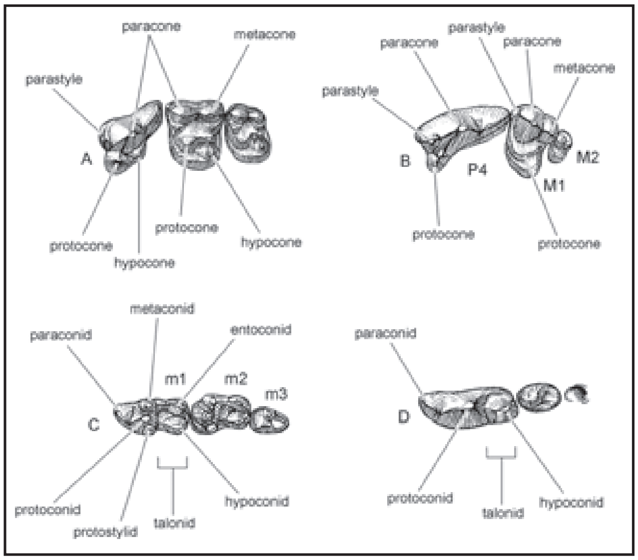


Figure 2.3. Hypercarnivorous (B, *Aelurodon* and D, *Euoplocyon*) and hypocarnivorous (A, *Phlaocyon* and C, *Cynarctus*) dentitions.
In hypercarnivorous forms, the upper cheek teeth (B) tend to emphasise the shearing part of the dentition with an elongated and narrow P4, an enlarged parastyle on a transversely elongated M1, and a reduced M2. On the lower teeth (D), hypercarnivory is exemplified by a trenchant talonid due to the increased size and height of the hypoconid at the expense of the entoconid (reduced to a narrow and low ridge), accompanied by the enlargement of the protoconid at the expense of the metaconid (completely lost in *Euoplocyon*) and the elongation of the trigonid at the expense of the talonid. In hypocarnivorous forms, on the other hand, the upper teeth (A) emphasise the grinding part of the dentition with a shortened and broadened P4 (sometimes with a hypocone along the lingual border), a reduced parastyle on a quadrate M1 that has additional cusps (e.g., a conical hypocone along the internal cingulum) and cuspules, and an enlarged M2. The lower teeth (C) in hypocarnivorous forms possess a basined (bicuspid) talonid on m1 enclosed on either side by the hypoconid and entoconid that are approximately equal in size. Other signs of hypocarnivory on the lower teeth include widened lower molars, enlarged metaconids, and additional cuspules such as a protostylid.

that of the *Canis* clade. Red fox (*Vulpes vulpes*) and Arctic fox (*Alopex lagopus*) appeared in North America only in the late Pleistocene, evidently as a result of immigration back to the New World.

Preferring more wooded areas, the gray fox (*Urocyon*) has remained in southern North America and Central America. Records of the gray fox clade have a more or less continuous presence in North America throughout its existence, with intermediate forms leading to the living species *U. cinereoargenteus*. Morphologically, the living African bat-eared fox (*Otocyon megalotis*) is closest to the *Urocyon* clade, although molecular evidence suggests that the bat-eared fox lies at the base of the fox clade or even lower (Geffen *et al.* 1992; Wayne *et al.* 1997). If the morphological evidence is correct, then the bat-eared fox must represent a Pliocene immigration event to the Old World independent of other foxes.

Advanced members of the Caninae, Tribe Canini, first occur in the medial Miocene (Clarendonian) in the form of a transitional taxon *Eucyon*. As a jackal-sized canid, *Eucyon* is mostly distinguished from the Vulpini in an expanded paroccipital process and enlarged mastoid process, and in the consistent presence of a frontal sinus. The latter character initiates a series of transformations in the Tribe Canini culminating in the elaborate development of the sinuses and a domed skull in the grey wolf (*Canis lupus*). By the late Miocene, species of *Eucyon* have appeared in Europe (Rook 1992) and by the early Pliocene in Asia (Tedford and Qiu 1996). The North American records all predate the European ones, suggesting a westward dispersal of this form.

Arising from about the same phylogenetic level as *Eucyon* is the South American clade. Morphological and molecular evidence generally agrees that living South American canids, the most diverse group of canids on a single continent, belong to a natural group of their own. The South American canids are united by morphological characters such as a long palatine, a large angular process of the jaw with a widened scar for attachment of the inferior branch of the medial pterygoid muscle, and a relatively long base of the coronoid process (Tedford *et al.* 1995). By late Hemphillian and early Blancan, certain fragmentary materials from southern United States and Mexico indicate that the earliest taxa assignable to *Cerdocyon* (Torres and Ferrusquía-Villafranca 1981) and *Chrysocyon* occur in North America. The presence of these derived taxa in the North American late Miocene predicts that ancestral stocks of many of the South American canids may have been present in southern North America or Central America. They appear in the South American fossil record shortly after the formation of the Isthmus of Panama in the Pliocene, around three million years BP (Berta 1987). The earliest records are *Pseudalopex* and its close relative *Protocyon*, an extinct large hypercarnivore, from the Pliocene (Uquian, around 2.5–1.5 million years BP) of Argentina. By the late Pleistocene (Lujanian, 300,000–10,000 years BP), most living species or their close relatives have emerged, along with the extinct North American dire wolf (*Canis dirus*). By the end of the Pleistocene, all large, hypercarnivorous canids of South America (*Protocyon*, *Theriodictis*) as well as *Canis dirus* had become extinct.

The *Canis*-*Lycaon* clade within the Tribe Canini, the most derived group in terms of large size and hypercarnivory, arose near the Miocene-Pliocene boundary between 6 and 5 million years BP in North America. A series of jackal-sized ancestral species of *Canis* thrived in the early Pliocene (early Blancan), such as *C. ferox*, *C. lepophagus*, and other undescribed species. At about the same time, first records of canids begin to appear in the European late Neogene: *Canis cipio* in the late Miocene of Spain (Crusafont-Pairó 1950), *Eucyon monticinensis* in the late Miocene of Italy (Rook 1992), the earliest raccoon-dog (*Nyctereutes donnezani*), and the jackal-sized *Canis adoxus* in the early Pliocene of France (Martin 1973; Ginsburg 1999). The enigmatic *C. cipio*, only represented by parts of the upper and lower dentition at a single locality, may represent a form at the *Eucyon* level of differentiation rather than truly a species of *Canis*.

The next phase of *Canis* evolution is difficult to track. The newly arrived *Canis* in Eurasia underwent an extensive radiation and range expansion in the late Pliocene and Pleistocene, resulting in multiple, closely related species in Europe, Africa and Asia. To compound this problem, the highly cursorial wolf-like *Canis* species apparently belong to a circum-arctic fauna that undergoes expansions and contractions with the fluctuating climates. Hypercarnivorous adaptations are common in the crown-group of species especially in the Eurasian middle latitudes and Africa. For the first time in canid history, phylogenetic studies cannot be satisfactorily performed on forms from any single continent because of their Holarctic distribution and faunal intermingling between the New and Old Worlds. Nevertheless, some clades are localised in different parts of the Holarctic. The vulpines' major centre of radiation was in the Old World. For the canines, North America remained a centre through the Pliocene producing the coyote (*Canis latrans*) as an endemic form. The wolves, dhole (*Cuon alpinus*), African wild dog (*Lycaon pictus*) and fossil relatives are the products of the Eurasian and African continents. During the Pleistocene, elements of the larger canid fauna invaded mid-latitude North America – the last invasion of which was the appearance of the grey wolf south of the glacial ice sheets in the late Pleistocene (about 100,000 years BP).

A comprehensive systematic revision of North American fossil canines by Tedford *et al.* (in prep.) is near completion, which forms the basis of much of the above summary. As part of the above revision, the phylogenetic framework as derived from living genera was published by

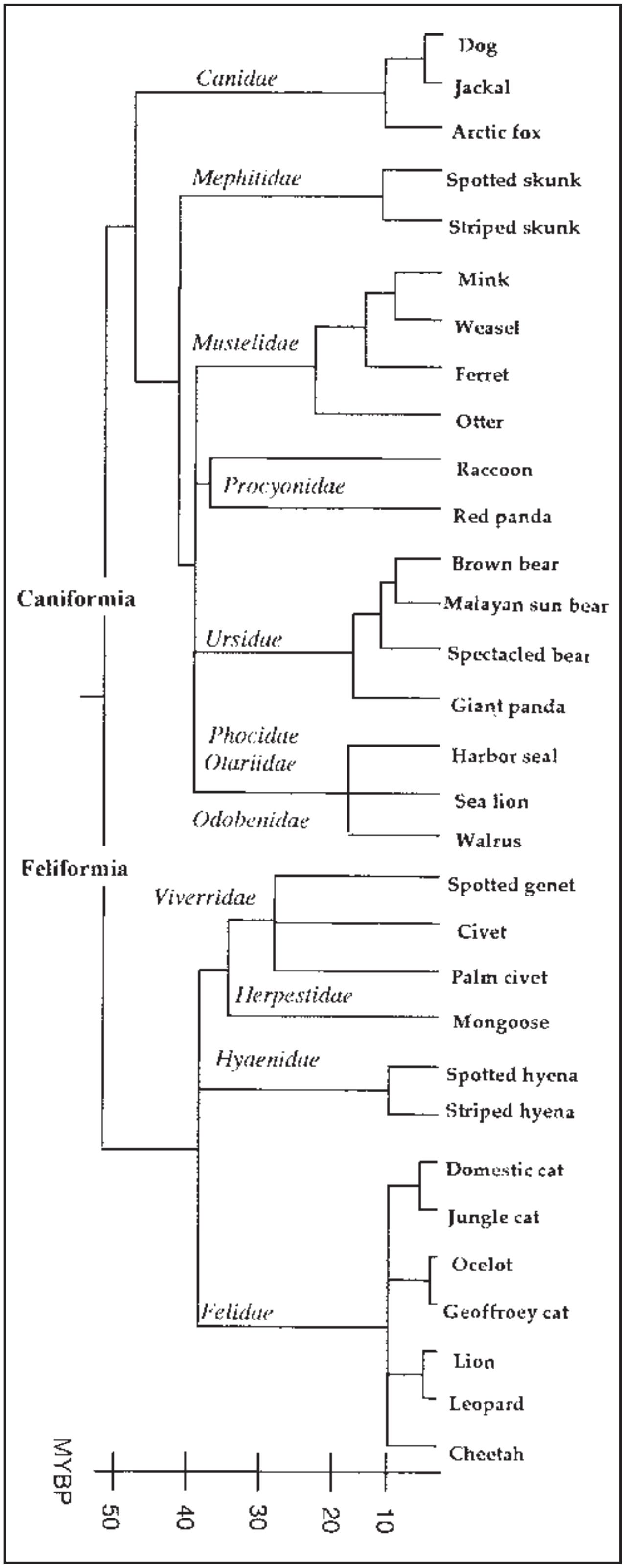
Tedford *et al.* (1995). Nowak (1979) monographed the Quaternary *Canis* of North America; Berta (1981, 1987, 1988) did the most recent phylogenetic analysis of the South American canids; Rook (1992, 1994) and Rook and Torre (1996a, 1996b) partially summarised the Eurasian canids. The African canid records are relatively poorly understood and recent discoveries promise to significantly advance our knowledge in that continent (L. Werdelin pers. comm.).

2.2 Molecular phylogeny

The ancient divergence of dogs from other carnivores is reaffirmed by molecular data. DNA-DNA hybridisation of single copy DNA clearly shows them as the first divergence in the suborder Caniformia that includes pinnipeds, bears, weasel and raccoon-like carnivores (Figure 2.4). This basal placement is further supported by mitochondrial DNA (mtDNA) sequence studies (Vrana *et al.* 1994; Slattery and O'Brien 1995; Flynn and Nedbal 1998). Based on molecular clock calculations, the divergence time was estimated as 50 million years BP (Wayne *et al.* 1989). This value is consistent with the first appearance of the family in the Eocene, although it is somewhat more ancient than the date of 40 million years suggested by the fossil record (see above). Considering that first appearance dates generally postdate actual divergence dates because of the incompleteness of the record (e.g., Marshall 1977), the agreement between fossil and molecular dates is surprisingly good.

Evolutionary relationships within the family Canidae have been reconstructed using comparative karyology, allozyme electrophoresis, mtDNA protein coding sequence data, and, most recently, supertree method (Wayne and O'Brien 1987; Wayne *et al.* 1987a, 1987b, 1997; Bininda-Emonds *et al.* 1999). Further, relationships at the genus level have been studied with mtDNA control region sequencing (a non-coding, hypervariable segment of about 1200 years BP in the mitochondrial genome) and microsatellite loci (hypervariable single copy nuclear repeat loci) (Geffen *et al.* 1992; Bruford and Wayne 1993; Girman *et al.* 1993; Gottelli *et al.* 1994; Vilà *et al.* 1997, 1999). The protein-coding gene phylogeny, which is largely consistent with trees based on other genetic approaches, shows that the wolf genus *Canis* is a monophyletic group that also includes the dhole or Asian wild dog. The grey wolf, coyote and Ethiopian Wolf or Simien Jackal (*Canis simensis*) form a monophyletic group, with the golden jackal (*C. aureus*) as the most likely sister taxon (Figure 2.5). The black-backed (*C. mesomelas*) and side-striped jackals (*C. adustus*) are sister taxa, but they do not form a monophyletic group with the golden jackal and Ethiopian wolf. Basal to *Canis* and *Cuon* are the African wild dog and a clade consisting of two South American canids, the

Figure 2.4. Relationship of carnivores based on DNA hybridisation data (Wayne *et al.* 1989).
Family and suborder groupings are indicated. Time scale in millions of year before present (MYBP) is based on comparisons of DNA sequence divergence to first appearance times in the fossil record.



bush dog (*Speothos venaticus*) and the maned wolf (*Chrysocyon brachyurus*). Consequently, although the African wild dog preys on large game as does the grey wolf and dhole, it is not closely related to either species but is sister to the clade containing these species. This phylogeny implies that the trenchant-heeled carnassial now found only in *Speothos, Cuon* and *Lycaon,* evolved at least twice or was primitive and lost in other wolf-like canids and the maned wolf.

The South American canids do not form a monophyletic group. *Speothos* and *Chrysocyon* are sister taxa that group with the wolf-like canids rather than the South American foxes. The large sequence divergence between the bush dog and maned wolf and between these taxa and the South American foxes suggests that they diverged from each other 7–6 million years BP, well before the Panamanian land bridge formed about 3–2 million years BP. Thus, three canid invasions of South America are required to explain the phylogenetic distribution of the extant species. These invasions are today survived by the bush dog, maned wolf, and the South American foxes. Further, within the South American foxes, divergence values between crab-eating fox (*Cerdocyon thous*), the short-eared dog (*Atelocynus microtis*) and other South American foxes, suggest they may have diverged before the opening of the Panamanian land bridge as well (Wayne *et al*. 1997).

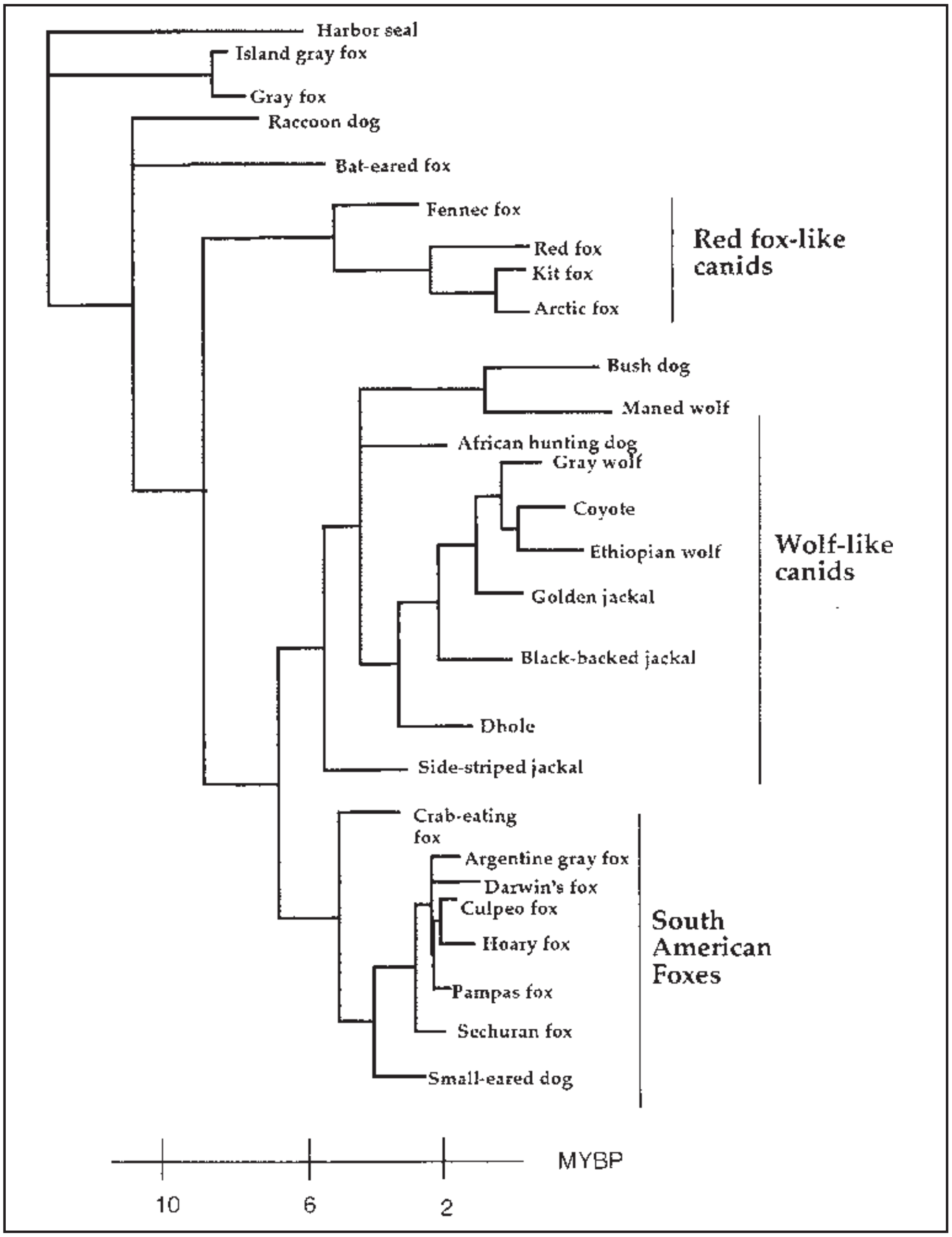
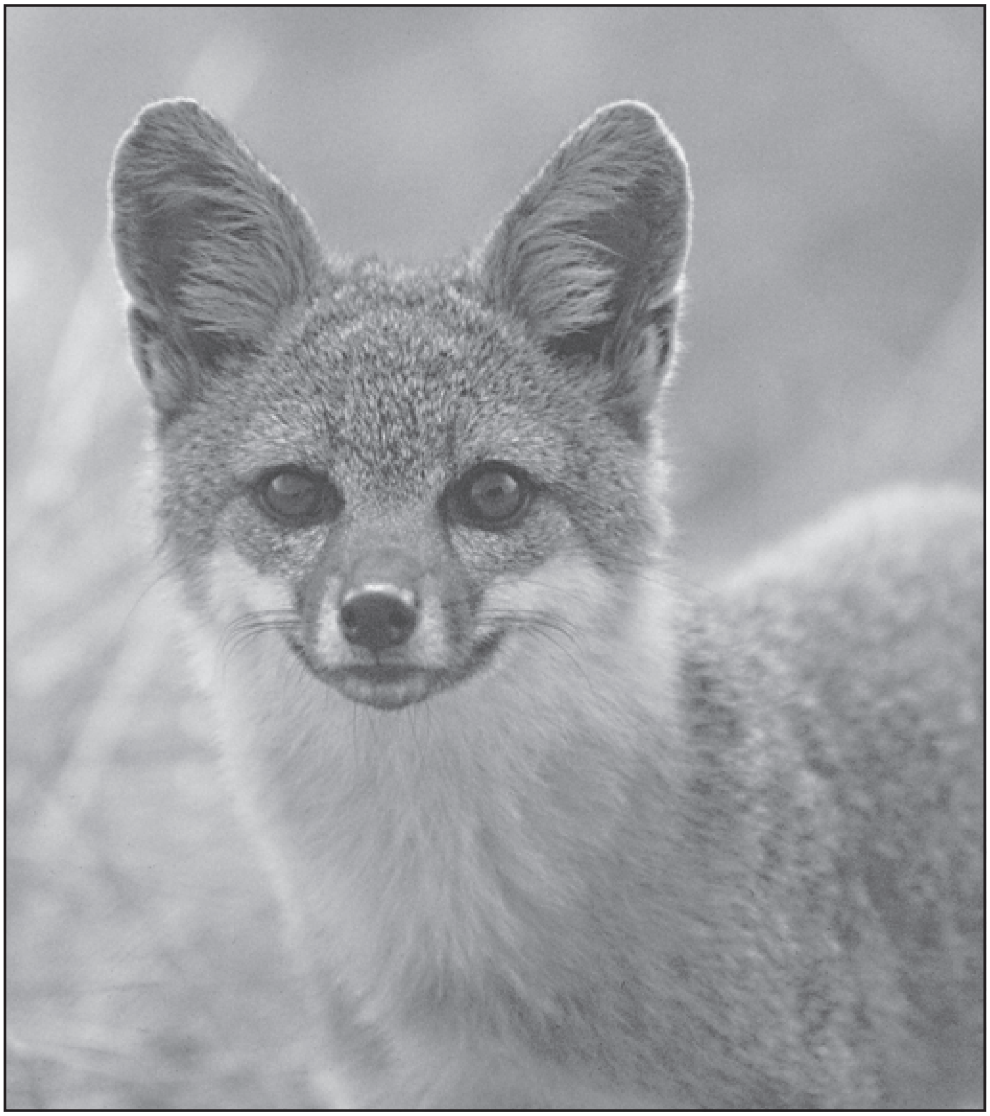


Figure 2.5. Consensus tree of 26 canid species based on analysis of 2,001 bp of DNA sequence from mitochondrial protein coding genes (Wayne *et al*. 1997). See Geffen *et al*. (1992) for a more detailed analysis of the Red-fox like canids. Time scale in millions of year before present (MYBP) is based on comparisons of DNA sequence divergence to first appearance times in the fossil record.



Yearling male island fox prior to dispersal from natal area. Fraser Point, Santa Cruz Island, California, USA, 1993.

Gary Roemer

The fossil record supports the hypothesis that the crab-eating fox had its origin outside of South America as the genus has been described from late Miocene deposits of North America (6–3 million years BP) (Berta 1984, 1987, see above). Consequently, only the foxes of the genus *Pseudalopex*, *Lycalopex* and perhaps *Atelocynus*, appear to have a South American origin. Further, the generic distinction given to *Pseudalopex* and *Lycalopex* does not reflect much genetic differentiation, and in the absence of appreciable morphologic differences, the genetic data suggest these species should be assigned to a single genus.

A fourth grouping in the tree consists of other fox-like taxa, including *Alopex* and *Vulpes* (here considered to include the fennec fox, *Vulpes zerda*, sometimes included in the genus *Fennecus*) (Figure 2.5) (Geffen *et al.* 1992; Mercure *et al.* 1993; Wayne *et al.* 1997). The Arctic fox is a close sister to the kit fox (*Vulpes macrotis*) and both share the same unique karyotype (Wayne *et al.* 1987a). Finally, *Otocyon*, *Nyctereutes*, and *Urocyon* appear basal to other canids in all molecular and karyological trees (Wayne *et al.* 1987a). The first two taxa are monospecific whereas the third includes the island fox (*Urocyon littoralis*) and the gray fox (*U. cinereoargenteus*). The three genera diverged early in the history of the family, approximately 12–8 million years BP as suggested by molecular clock extrapolations.

In sum, the living Canidae is divided into five distinct groupings. These include the wolf-like canids, which consists of the coyote, grey wolf, Ethiopian wolf, jackals, dhole and African wild dog. This clade is associated with a group containing bush dog and maned wolf in some trees and, further, this larger grouping is associated with the South American foxes (Wayne *et al.* 1997). The red fox group is a fourth independent clade containing *Alopex* and *Vulpes* (including the fennec fox). Finally, three lineages have long distinct evolutionary histories and are survived today by the raccoon dog, bat-eared fox and island and gray fox. Assuming an approximate molecular clock, the origin of the modern Canidae begins about 12–10 million years BP and is followed by the divergence of wolf and fox-like canids about 6 million years BP. The South American canids are not a monophyletic group and likely owe their origin to three separate invasions. This group included the maned wolf, bush dog, crab-eating fox and the other South American canids that diverged from each other about 6–3 million years BP.

2.3 Evolutionary ecology

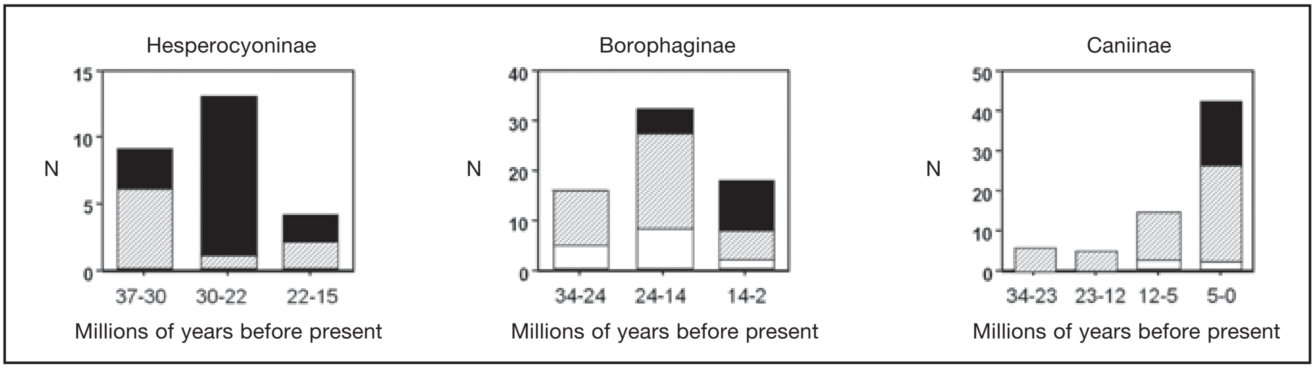
2.3.1 Iterative evolution of hypercarnivory

One of the most remarkable features of canid history is their repeated tendency to evolve both hypocarnivorous and hypercarnivorous forms. As noted above, hypercarnivorous species evolved within each subfamily, and hypocarnivorous species evolved within two of the three (all but the Hesperocyoninae). Hypocarnivory was most fully expressed in the Borophaginae, where at least 15 species showed a tendency towards a dentition similar to that of living raccoons (Wang *et al*. 1999). Among the Caninae, the tendency has not been quite as strong, with only a single lineage, *Nyctereutes*, developing a markedly hypocarnivorous dentition. However, all three subfamilies include multiple species of apparent hypercarnivores with enhanced cutting blades on their carnassials, reduced grinding molars, and enlarged canines and lateral incisors. When and why did hypercarnivory evolve within each subfamily?

In two of the three subfamilies, Hesperocyoninae and Caninae, the evolution of hypercarnivory appears to have occurred at least partly in response to a reduced diversity of other hypercarnivorous taxa. The Hesperocyoninae evolved hypercarnivory early in their history (Figures 2.1, 2.2, 2.6) and the most advanced forms appear in the early Miocene (about 24–20 million years BP) at a time when the two previously dominant carnivorous families had vanished. These two families were the Nimravidae, an extinct group of saber-tooth cat-like forms, and the Hyaenodontidae, a group of somewhat dog-like predators included in the extinct order Creodonta. The nimravids and hyaenodontids dominated the North American guild of large, predatory mammals in the late Eocene to mid-Oligocene (37–29 million years BP), but faded rapidly in the late Oligocene, and were extinct in North America by about 25 million years BP (Van Valkenburgh 1991, 1994). During most of their reign, hesperocyonines existed at low diversity and small (fox-size) body size, but as the hyaenodontids and nimravids declined in the late Oligocene, the early canids seem to have radiated to replace them. Most of these hypercarnivorous canids were jackal-size (less than 10kg), with only the last surviving species, *Osbornodon fricki*, reaching the size of a small wolf (Wang 1994). In the early Miocene, large hypercarnivores emigrated from the Old World in the form of hemicyonine bears (Ursidae) and temnocyonine bear-dogs (Amphicyonidae). The subsequent decline to extinction of the hesperocyonines might have been a result of competition with these new predators (Van Valkenburgh 1991, 2001).

Hypercarnivory appears late in the history of the Caninae and represents at least several independent radiations in South America, North America, and the Old World (Figures 2.1, 2.6). As was true of the hesperocyonine example, the South American radiation of large hypercarnivorous canids occurred at a time (2.5–0.01 million years BP) when cat-like predators were rare or absent. It followed the elevation of the Panamanian land bridge around 3–2 million years BP that allowed immigration between the previously separated continents. The canids that first entered South America found a

Figure 2.6. Iterative evolution of large hypercarnivores.
Number (N) of hypocarnivorous (white), mesocarnivorous (grey), and large (>20kg) hypercarnivorous (black) species over time in each of the three subfamilies. The few hesperocyonine species with trenchant-heeled carnassials estimated to have been less than 20kg in mass were assigned to the mesocarnivorous category because they are assumed not have taken prey as large or larger than themselves. For the Hesperocyoninae and Borophaginae, their stratigraphic ranges were broken into thirds; for the Caninae, four time divisions were used because of the large number of species appearing in the past five million years. Species were assigned to dietary categories and body mass was estimated on the basis of dental morphology as described in Van Valkenburgh (1991) and Wang *et al*. (1999).



depauperate predator community, consisting of one bear-like procyonid carnivoran, three species of carnivorous didelphid marsupials, one of which was the size of a coyote, and a gigantic, predaceous ground bird (Marshall 1977). With the possible exception of the rare ground bird, none of these species was a specialised hypercarnivore. Between 2.5 million and 10,000 years BP, 16 new species of canids appeared in South America, at least seven of which had trenchant-heeled carnassials and clearly were adapted for hypercarnivory (Berta 1988; Van Valkenburgh 1991). They represent three different endemic genera: *Theriodictis*, *Protocyon* and *Speothos*. In addition, there were three large wolf-like species of *Canis* in South America, *C. gezi*, *C. nehringi*, and *C. dirus*, all of which were probably hypercarnivorous but retained a bicuspid heel on their carnassials. Of these only the dire wolf, *C. dirus*, evolved in North America. All but one of these ten hypercarnivorous canids of South America went extinct at the end of the Pleistocene (Van Valkenburgh 1991). The sole survivor, the bush dog, is rarely sighted.

In the Old World, the evolution of hypercarnivorous canines occurred within the last four million years and did not coincide with an absence of cats. Large cats, both the sabertooth and conical tooth forms, are present throughout the Plio-Pleistocene when the highly carnivorous species of *Canis*, *Cuon*, *Lycaon* and *Xenocyon* appear (Turner and Antón 1996). However, their evolution might be a response to the decline of another group of hypercarnivores, wolf-like hyaenids. Hyaenids were the dominant dog-like predators of the Old World Miocene, reaching a diversity of 22 species between 9 and 5 million years BP, but then declining dramatically to just five species by about 4 million years BP (Werdelin and Turner 1996). Their decline may have opened up ecospace for the large canids and favoured the evolution of hypercarnivory.

The remaining episode of hypercarnivory in canids occurred in the Borophaginae between 15 and 4 million years BP (Van Valkenburgh *et al.* 2003). As was true of the Caninae, the hypercarnivorous species do not evolve early in the subfamily's history. Instead, they appear in the latter half of the subfamily's lifespan and only become prevalent in the last third (mid to late Miocene; Figures 2.1, 2.6). In the late Miocene, borophagine canids were the dominant dog-like predators of North America, having replaced the amphicyonids and hemicyonine bears that had themselves replaced the hesperocyonines some 10 million years earlier (Van Valkenburgh 1999). In the case of the Borophaginae, the evolution of hypercarnivory appears more gradual than in the other two subfamilies, and is not easily ascribed to opportunistic and rapid evolution into empty ecospace.

In all three subfamilies, there is a pattern of greater hypercarnivory and increasing body size with time (Figure 2.6). Even in the Hesperocyoninae, where hypercarnivory evolves very early, large species with the most specialised meat-eating dentitions appear later (Wang 1994). This directional trend toward the evolution of large, hypercarnivorous forms is apparent in other groups of dog-like carnivores, such as the amphicyonids (Viranta 1996) and hyaenids (Werdelin and Solounias 1991; Werdelin and Turner 1996), and may be a fundamental feature of carnivore evolution. The likely cause is the prevalence of interspecific competition among large, sympatric predators. Interspecific competition tends to be more intense among large carnivores because prey are often difficult to capture and can represent a sizeable quantity of food that is worthy of stealing and defending. Competition appears to be a motive for much intraguild predation because the victim often is not eaten (Johnson *et al.* 1996; Palomares and Caro 1999; Van Valkenburgh 2001). Larger carnivores tend to dominate smaller ones and so selection should favour the evolution of large body size. Large body size in turn selects for a highly carnivorous diet because of energetic considerations. As shown by Carbone *et al.* (1999), almost all extant carnivores that weigh more than 21kg take prey as large as or larger than themselves. Using an energetic model, they demonstrated that large body size brings with it constraints on foraging time and energetic return. Large carnivores cannot sustain themselves on relatively small prey because they would expend more energy in hunting than they would acquire. By taking prey as large as, or larger than, themselves, they achieve a greater return for a given foraging bout. Killing and consuming large prey is best done with a hypercarnivorous dentition and so the evolution of large body size and hypercarnivory are linked. Of course, this does not preclude the evolution of hypercarnivory at sizes less than 21kg but it seems relatively rare. It has occurred in the Canidae as evidenced by the hesperocyonines and the extant Arctic fox and kit fox. However, the two extant foxes do not have trenchant-heeled carnassials despite their highly carnivorous diets (Van Valkenburgh and Koepfli 1993).

Returning to the questions of when and why hypercarnivory evolves among canids, it seems that *when* and *why* are intertwined. That is, because of intraguild competition and predation, selection favours the evolution of larger size in canids and as a consequence, hypercarnivory. However, *when* this occurs is largely a function of other members of the predator guild. In the case of the Hesperocyoninae, it occurred relatively early in their history because previously dominant large hypercarnivores were in decline or already extinct. In the case of the Borophaginae and Caninae, it did not occur until much later because other clades held the large hypercarnivorous roles for much of the Miocene. In all these examples, it appears as though the rise of large hypercarnivorous canids reflects opportunistic replacement rather than competitive displacement of formerly dominant taxa (Van Valkenburgh 1999).

2.3.2 The last one million years

All of the canids that are extant today evolved prior to the late Pleistocene extinction event approximately 11,000 years BP. The same could be said of most, if not all, extant carnivores. In the New World, the end-Pleistocene event removed numerous large mammals, including both herbivores (e.g., camels, horses, proboscideans) and carnivores (e.g., sabertooth cat, dire wolf, short-faced bear). In the Old World, many of the ecological equivalents of these species disappeared earlier, around 500,000 years BP (Turner and Antón 1996). Consequently, all extant carnivore species evolved under very different ecological circumstances than exist at present. For example, the grey wolf today is considered the top predator in much of the Holarctic, but it has only held this position for the last 10,000–11,000 years. For hundreds of thousands of years prior to that time, the wolf coexisted with 11 species of predator as large as, or larger than, itself (Figure 2.7). Now only the puma (*Puma concolor*), American or Asiatic black bears (*Ursus americanus* and *U. thibetanus*) and grizzly bear (*U. arctos*) remain, and wolves are usually dominant over the first two species at least (Van Valkenburgh 2001). Thus, for most of its existence, the grey wolf was a mesopredator rather than a top predator, and so its morphology and behaviour should be viewed from that perspective. Given the greater diversity and probable greater abundance of predators in the past, interspecific competition was likely more intense than at present. Higher tooth fracture frequencies in late Pleistocene North American predators provide indirect evidence of heavy carcass utilisation and strong food competition at that time (Van Valkenburgh and Hertel 1993). Intense food competition would favour group defence of kills and higher levels of interspecific aggression. Perhaps the sociality of the wolf and the tendency of some carnivores to kill but not eat smaller predators are remnant behaviours from a more turbulent past.

The only canid to go extinct in North America by the late Pleistocene was the dire wolf. The grey wolf, coyote, and several foxes survived. In addition to the dire wolf, two bears and three cats went extinct, all of which were very large (Figure 2.7). By examining the 'winners' and 'losers' in the late Pleistocene we are able to learn about the causes of current predator declines. Examination of the loser species reveals that they tended to be the more specialised members of their clades, they were larger (Figure 2.7) and tended to be more dentally specialised for hypercarnivory (Van Valkenburgh and Hertel 1998). Remarkably, two of the species that went extinct, the dire wolf and sabertooth cat (*Smilodon fatalis*), are five times more common in the Rancho La Brea tar pit deposits than the next most common carnivore, the coyote. This suggests that the dire wolf and sabertooth cat were dominant predators at this time, comparable to the numerically dominant African lion (*Panthera leo*) and spotted hyaena (*Crocuta crocuta*) of extant African ecosystems. The extinction of the apparently successful dire wolf and sabertooth cat implies there was a major perturbation to the ecosystem in the late Pleistocene. Their demise and that of the other large hypercarnivores suggests that large prey biomass dropped to extremely low levels. Supporting this are the parallel extinctions of ten of the 27 species of raptors and vultures (Van Valkenburgh and Hertel 1998).

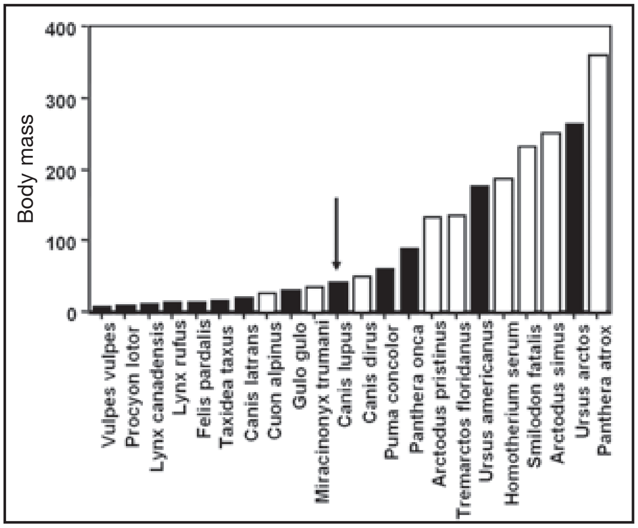


Figure 2.7. North American Pleistocene carnivorans arranged by body mass.
Black bars represent extant species, and white bars represent extinct species. Arrow indicates the grey wolf (*Canis lupus*). Data from Van Valkenburgh and Hertel (1998).

In the late Pleistocene, the largest meat-eaters, both avian and mammalian, were the most vulnerable. Looking at the case today, of the three large hypercarnivorous canids, the dhole, grey wolf and African wild dog, both the dhole and the wild dog are Endangered. Among living canids in general, species that appear to be most at risk tend to be insular (Darwin's fox, island fox) or restricted to limited habitats (Ethiopian wolf), or just very poorly known species (e.g., short-eared dog, bush dog). Indeed, it is a bit difficult to answer the question of which of the living species are most threatened because we have so little information on many of the smaller taxa. Nevertheless, it does seem that by the Late Pleistocene extinction is not a good analog for what is happening at present, at least in terms of who is most vulnerable. Then, it was the largest, most abundant, and most carnivorous. Now it seems more often to be smaller mesocarnivores that are at risk due to small population size exacerbated by habitat loss. In both the late Pleistocene and at present, the hand of humanity looms large as a cause of predator declines. Initially, the damage was largely due to overhunting of both prey and predator, and to this we have added significant habitat loss. Survivors of the current crisis are likely to be both dietary and habitat generalists, such as the coyote and the black-backed jackal.

2.4 History of canid classification

Caroli Linnaeus (1758) listed four genera, *Canis*, *Hyaena*, *Vulpes*, and *Alopex*, under the heading *Canis*, an informal category between genus and order (family level classification was not used then). Besides the misplaced *Hyaena*, Linnaeus's basic concept of canids has endured to the present time. By the late 1800s, the family Canidae had stabilised to include most of what are presently regarded as species of canids (e.g., Mivart 1890a, 1890b). The late 1800s and early 1900s was also a time of explosive growth of the number of fossil canids. However, the fragmentary nature of most of the fossil forms became a major source of confusion in canid classification. As a result, a much broader concept of the Canidae was often adopted to accommodate a wide range of forms that do not neatly fit into existing categories. Thus, fossil forms such as amphicyonid bear-dogs, certain basal arctoids, and hyaenoid 'dogs' frequently became mixed with real canids (e.g., Zittel 1893; Trouessart 1897; Matthew 1930). This is primarily caused by an over reliance on the evolutionarily highly repetitive dental patterns, i.e., dental morphologies that evolved multiple times in independent lineages. Such a broadened concept of Canidae was still seen in Simpson's classification of mammals (Simpson 1945), in which numerous primitive arctoids as well as whole groups of amphicyonids were still considered canid. Simpson, however, was keenly aware that the rich fossil records only serve to compound the problems and much remained to be done to sort out the complexity. The legacy of Simpson's classification was still felt in the 1970s, when one of his peculiar group, the subfamily Simocyoninae (a mixed bag of highly predaceous carnivorans), was still being circulated (Stains 1974).

Shortly after Simpson's influential classification, students of Carnivora began to gain increasing appreciation of the importance of morphologies in the middle ear region (bones around and behind the ear drums) (Hough 1948; Hunt 1974). The recognition that different groups of carnivores tend to have a unique pattern of middle ear region greatly enhanced our ability to discriminate members of various families of Carnivora. Focusing on the ear bones, many of the forms previously considered canid have now been allocated to other groups. The Canidae thus defined attains a greater degree of uniformity in morphology and consistency with phylogeny (Wang and Tedford 1994). McKenna and Bell's (1997) latest revision of Simpson's (1945) classification largely reflects these results. Throughout this period of waxing and waning of the scope of fossil canids during the past 100 years, the content of living species of canids, however, has remained largely stable.

Recent advances in the last 30 years in systematic practices favour approaches that evaluate characters in a historical perspective to guard against rampant parallelisms in evolution, in contrast to phenetic approaches that evaluate overall similarities only. Numerical taxonomic analysis of living canids by Clutton-Brock *et al.* (1976) was based on a large number (666 characters) of quantitative measurements of skull and body proportions, skin colours, and a few dental characters. The few qualitative characters were also treated in a phenetic way (i.e., lacking polarity determination) and were easily overwhelmed by a large number of other phenotypic characters. Not surprisingly, the dendrograms derived from their cluster analysis (Clutton-Brock *et al.* 1976; Figure 8) bear little resemblance to those derived from phylogenetic analyses (both morphological and molecular) discussed above and are inappropriate to be the basis for classification. Similar caution should be exercised regarding attempts to introduce hybridisation data into the canid classification by Van Gelder (1978), a result that also lacks a phylogenetic basis.

2.5 Classification of the living Canidae

As discussed above, the classification of living Canidae amounts to the classification of a subset of the subfamily Caninae since two ancient subfamilies, the Hesperocyoninae and Borophaginae, were long extinct (see Wang and Tedford 1994; Wang *et al.* 1999 for their classifications). Within the Caninae, genera and species that are exclusively in the fossil record are not discussed here. At the generic level, at least six genera are represented by extinct forms only and are not further discussed: *Leptocyon*, *Eucyon*, *Protocyon*, *Theriodictis*, *Norcyon*, and *Xenocyon*. At the species level, many fossil species are included under common generic names that may or may not be ancestral to living species. For example, large numbers of fossil species of *Canis* are recognised throughout Eurasia and North America. While these extinct forms may shed light in the history of modern species, they are not further discussed here since we are dealing with classification of living forms without attempt to elucidate detailed relationships between species.

As can be seen from the above sections, there are parts of phylogenetic hypotheses that are consistent between morphological and molecular evidences, and there are parts that are not. Such conflicts are the results of our inability to unambiguously discriminate noise from true signal. In other words, true genealogical relationships can be overshadowed by superficial similarities due to evolutionary tendencies of parallelism. Such conflicts are likely to continue for a long time and our classification (Table 2.1) largely follows that of Wozencraft (1993). See Ginsberg and Macdonald (1990) for a list of subspecies.

Table 2.1. Classification of living Canidae (subfamily Caninae) followed by the Canid Specialist Group, modified from that by Wozencraft (1993).
A total of 36 living taxa, excluding the recently extinct (†) Falkland (Malvinas) Island fox *Dusicyon australis*. The Australian dingo is included as distinct subspecies of the grey wolf. *Vulpes macrotis* and *V. velox* treated as separate species. *Pseudalopex fulvipes* given full specific status. A proposal to split *Nyctereutes procyonoides* into two distinct species was rejected at the CBC conference in September 2001.

Alopex lagopus	Arctic fox
Atelocynus microtis	Short-eared dog
Canis adustus	Side-striped jackal
Canis aureus	Golden jackal
Canis lupus dingo	Dingo
Canis lupus	Grey wolf
Canis latrans	Coyote
Canis mesomelas	Black-backed jackal
Canis rufus	Red wolf
Canis simensis	Ethiopian wolf
Cerdocyon thous	Crab-eating fox
Chrysocyon brachyurus	Maned wolf
Cuon alpinus	Dhole
Dusicyon australis	Falkland Island fox †
Lycaon pictus	African wild dog
Nyctereutes procyonoides	Raccoon dog
Otocyon megalotis	Bat-eared fox
Pseudalopex culpaeus	Culpeo
Pseudalopex fulvipes	Darwin's fox
Pseudalopex griseus	Chilla
Pseudalopex gymnocercus	Pampas fox
Pseudalopex sechurae	Sechuran fox
Pseudalopex vetulus	Hoary fox
Speothos venaticus	Bush dog
Urocyon cinereoargenteus	Gray fox
Urocyon littoralis	Island fox
Vulpes bengalensis	Indian fox
Vulpes cana	Blanford's fox
Vulpes chama	Cape fox
Vulpes corsac	Corsac
Vulpes ferrilata	Tibetan fox
Vulpes macrotis	Kit fox
Vulpes pallida	Pale fox
Vulpes rueppellii	Rüppell's fox
Vulpes velox	Swift fox
Vulpes vulpes	Red fox
Vulpes zerda	Fennec fox

2.5.1 Genus or species of controversial taxonomic status

The following discussions of selected taxa involve controversial cases of taxonomy that were discussed during the Canid Biology and Conservation Conference held in the Department of Zoology at Oxford University during September 2001.

Canis rufus Audubon and Bachman, 1851

The systematic status of the red wolf in the south-eastern United States has become increasingly contentious. Current theories of origin range from it being a small distinct wolf species with an ancient ancestry going back to the Pleistocene or a more recent hybrid between the grey wolf and coyote. Additionally, other alternative scenarios have been suggested. The wide-ranging issues cannot be adequately explored in this chapter, although they mainly involve evidence from a palaeontological, morphological, morphometric, molecular, and conservation perspective (Paradiso and Nowak 1971; Wayne and Jenks 1991; Nowak 1992; Phillips and Henry 1992; Roy *et al.* 1994; Wilson *et al.* 2000; Nowak 2002). Palaeontological and morphological approaches suffer from a poor fossil record, especially those from the high latitudes of Eurasia and North America where wolves were presumed to have radiated from, and of recent samples of confidently identified museum specimens. Additional difficulties are encountered in attempts to resolve relationships among the early members of *Canis* (Tedford *et al.* in prep.). Yet, Nowak (2002) reaffirmed his earlier conviction that a distinct red wolf-like form can be traced back to the late Pleistocene based on multivariate analysis. The debate in the last ten years has not brought about a convergence, and it is not wise to legislate the debate at this time.

Lycalopex vs. Pseudalopex

Debate about the proper usage of *Lycalopex vs. Pseudalopex* for certain South American foxes, particularly regarding the hoary fox (*vetulus*), has been going on for many years (e.g., Cabrera 1931; Osgood 1934; Langguth 1975; Berta 1987, 1988; Tedford *et al.* 1995). The controversy focuses on the question of whether or not *vetulus* should be placed under the monotypic *Lycalopex* or included under *Pseudalopex*, along with various other small foxes. The ultimate solution lies in the determination of whether *vetulus* represents a unique lineage distinct from other species of *Pseudalopex*. However, the primitive morphology of the small foxes is a major hindrance to a clear resolution of their relationships. The key to resolving this problem may lie in a detailed species-level phylogenetic analysis. Until that is done, it is still a matter of opinion which generic name is the most appropriate.

Pseudalopex fulvipes Martin, 1837

Osgood (1943) argued that the dark-coloured fox from southern Chiloé Island off the southern coast of Chile (and first collected by Charles Darwin) is morphologically distinct. Cabrera (1957) followed Osgood's conclusion, whereas Langguth (1969) presented data for its inclusion in *Pseudalopex griseus*, its mainland counterpart in Chile and Argentina, a conclusion also followed by Wozencraft (1993). However, mtDNA sequencing studies clearly established that the taxon has a mainland distribution, reaffirming earlier reports, and showed that sequences from the Darwin's fox defined a distinct clade (Yahnke *et al*. 1996). Consequently, rather than representing an island form of *griseus*, Darwin's fox is genetically distinct from the South American gray fox and was, until recently, sympatric with this species at one or more mainland localities. Hence, it should be considered a separate species, *Pseudalopex fulvipes.*

New Guinea singing dog

Preliminary sequencing studies showed that the New Guinea singing dog has mtDNA sequences identical to the dingo (*Canis lupus dingo*), which is classified within a clade of dog sequences distinct from grey wolves (Vilà *et al*. 1997; Wayne *et al*. 1997; Leonard *et al*. 2002). Contrary to one report (Koler-Matznick *et al*. 2003), sequencing studies rule out an ancestry with dholes and the African wild dog, and clearly assign it to the domestic dog, which is sister to the grey wolf (Vilà *et al*. 1997; Wayne *et al*. 1997; Leonard *et al*. 2002). Given the current evidence, we feel there is little justification for assigning specific or subspecific status.

PART 2

Species Status Accounts

Edited by M. Hoffmann and C. Sillero-Zubiri

Species Status Accounts: an Introduction

M. Hoffmann and C. Sillero-Zubiri

The species accounts represent the core of the Action Plan. Each species account consists of a detailed entry summarising the information available on the biology, abundance, population trends and threats facing the species.

Some readers may balk at the amount of information presented for each species. Ordinarily, species action plans restrict the amount of information they include on basic ecology and behaviour and emphasise the sections on conservation, abundance, threats and so on. This is still very much the policy followed here; however, the viewpoint of the editors was that the conservation, status and threats facing a species cannot be viewed independently of a species' biology. Much of the information contained within the pages of this action plan has never appeared in published form before, and certainly never in such a summarised format. We believe that the inclusion of basic life-history information in this plan is crucial to fostering a clearer understanding of the sections on conservation and status, and that this information will, in itself, serve as an important reference for future canid biologists. For this reason, the editors have sought to ensure that this action plan represents a detailed summary of all aspects of a species' life history, without sacrificing on the real "meat and bones" of the plan.

Each species account has been prepared by one or more contributors, at the invitation of the editors. We have endeavoured to draw on the expertise of biologists and naturalists from many countries and, as far as possible, those with first-hand experience and knowledge of the species concerned. The species accounts are based primarily on published information (i.e., from books and journals), supplemented as far as possible with reliable unpublished material and personal observations from the author's own studies or other sources. The use of grey literature has been strongly recommended, and authors were also encouraged to correspond with other colleagues likely to have unpublished material or to be able to contribute unpublished data. Accounts on African canids benefited from our linking in with the *Mammals of Africa* project, being edited by Jonathan Kingdon, David Happold and Tom Butynski. For the most part, the information contained in the species accounts is derived from free-living populations. Occasionally, this has been supplemented by information from captivity (for example, details of longevity which often are not available for wild populations); for other species that have never been studied in the wild, information on captive animals has been consulted more extensively where available. Each profile was reviewed by two or more appropriate reviewers, either chosen by the authors or suggested by the editors.

Regional sections

To respect evolutionary affiliations and facilitate access to the reader, we follow a biogeographical approach (*sensu* Sclater and Sclater 1899), with species accounts listed under the relevant regional regions.

Thus, we have organised the species accounts in seven chapters that follow the major biogeographical regions recognised for mammals by Wallace (1876). For the sake of convenience, the names of the biogeographical regions are paired with the relevant geographical regions covered by the Canid Specialist Group's Regional Sections (Table 1). The Ethiopian region is divided into two distinct groups of species. Those species that occur in more than one such region are included in the region that encompasses the largest area of the species' range.

Table 1. Biogeographical regions are paired with the relevant geographical regions covered by the CSG Regional Sections.

Biogeographical Region	CSG Regional Section
Neotropical (up to south Mexico)	South America/North and Central America
Nearctic	North and Central America
Palearctic Ethiopian	Europe/North and Central Asia Sub-Saharan Africa
Ethiopian	North Africa and Middle East
Oriental (south of the Himalaya)	South Asia and Australasia
Australasian	South Asia and Australasia

Outline of accounts

Because of the inconsistencies inherent in multi-author projects, the editors have requested authors to adhere to a strict set of guidelines in the compilation of the species accounts. While every effort has been made to make all species accounts conform to the same general structure and content, some idiosyncrasies remain evident. Far from detracting from the quality of the plan, we believe this only serves to make the plan a more interesting read! As far as possible then, and where available data allow, species accounts use the following format.

Preferred English name

Where more than one English name is commonly used, the preferred name appears.

Scientific name (authority and year)

The currently accepted scientific name of the species is followed by the details of the author and the year in which the species was described. The latter appears in brackets where it is now included in a genus other than that in which the original author placed it.

IUCN Red List Category

The current (2003) Red List ranking, as assessed by the Canid Specialist Group using version 3.1 of the criteria (IUCN 2001). For information on the categories of canid species assessed by the Canid Specialist Group in 1996 see Appendix 1.

Author(s)

The names of the author(s) responsible for researching and compiling the species account.

Other names

These include further English names, French, German, Spanish, Italian, Portuguese, and other names for any major language (and listed alphabetically). Names under indigenous languages are those in use in localised areas. The indigenous language is given, followed by the names used in that language and the country in which the indigenous language is used.

Taxonomy

This begins with the type species and description. This is the full and original citation of the species name, followed by the type locality. This information largely follows Wozencraft (1993), although in some cases the authors or editors have seen cause to deviate from this rule.

The taxonomy of the Family Canidae is dealt with in Chapter 2 of this volume. Within the species accounts, this section is used where the taxonomy of a species requires clarification, particularly where recent studies may have challenged the accepted nomenclature of certain species. These are discussed here as relevant. Details of chromosome number are provided where available.

Description

The purpose of this section is to provide the reader with adequate information to identify the species. As far as possible, the description of a given species is based on live specimens and includes details of general appearance, followed with a detailed description beginning with the head, body, legs, feet and tail. This section includes notes on pelage characteristics (i.e., colour, length, variation in different parts of the body, pattern, areas of bare skin), and special attention is given to diagnostic features and the relative size of ears, eyes, muzzle, tail, etc. In addition, unique or characteristic cranial and dental features are noted, as well as the dental formula of adults (i/i-c/c-p/p-m/m = total number of teeth).

Body measurements General body measurements are given separately in a table. These are either from previously published or unpublished sources and provide general morphometric data from a particular region within the range of the species.

HB	Head-Body length
T	Tail
E	Ear
SH	Shoulder height
WT	Weight

Subspecies The number of currently accepted subspecies is given here (followed by the source), with details of their geographical range. Where relevant, details important for diagnosis are provided. If no subspecies are currently recognised, the species is regarded as monotypic.

Similar species The common name and scientific name of any similar species with which the current species could be confused, followed by details of how each similar species differs from the species being described (i.e., any description is for the similar species, not the one under the heading).

Current distribution

The geographical range of the species, described from west to east, and from north to south. Range extensions or reductions, reintroductions and introductions, and disagreements about the range of a species are discussed here. The ranges of rare species or those with a very restricted distribution (e.g., Ethiopian wolf) are described in more precise terms. The spelling of geographical names follows that given in *The Times Atlas* (2003). Where information pertaining to the historical range of a species exists, the distribution is given in two separate headings, namely historical distribution and current distribution:

Historical distribution Includes details and references for known historical data; evidence for assumed former range such as museum specimens, palaeontological and/or archaeological evidence, cave paintings and so on.

Current distribution The distribution of the species as currently understood.

Range countries A list of the range countries from which a species is known to occur (and listed alphabetically), followed by the most important sources from which this information is derived. Possible, but unknown, occurrences are indicated by (?).

Distribution map

Each species account includes a map of distribution. The present distribution of the species is shadowed in a map of suitable scale. If the historic distribution of the species is known and differs significantly from present, it may be shown shaded in a lighter grain. Reliable single sightings within the last 10 years outside those areas are marked with crosses (X). Areas where species may be present but sightings unconfirmed are marked with a question mark (?).

Relative abundance

A general indication of abundance in the habitat, including details of density and frequency of observations whenever that is available. Whenever possible, a table is presented with site-specific populations/relative abundance and population trend, summarised for each of its range states. Quantitative population estimates are usually obtained from total counts, ground surveys, questionnaire surveys and informed guesses by knowledgeable observers. Population abundance is indicated by: abundant (A), common (C), uncommon (U), rare (R), vagrant (V), present but abundance unknown (x), presence not confirmed (?), absent (-), extinct (Ex), probably extinct (Ex?). Population trends are indicated by: increasing (I), stable (S), decreasing (D), unknown (?).

Habitat

The preferred habitat and range of habitats, including details of rainfall, altitude and seasonal shifts in habitat. Details of any association with a specific plant, terrain, water availability, and so on, are also mentioned.

Food and foraging behaviour

This section is divided into three subheadings:

Food Preferred food items; range of prey consumed; variation in diet in different ecosystems.

Foraging behaviour Location of food; time when foraging occurs, including notes on activity; whether solitary or group hunters; sex/age differences in foraging; nomadic movements in relation to food availability; scavenging; food caching; how the species kills and handles its prey.

Damage to livestock or game Whether species preys on domestic stock or impact on wild game, and associated economic significance.

Adaptations

Morphological (e.g., proportions, shape, dental structure), physiological (e.g., water metabolism, temperature regulation, moult), and behavioural (e.g., huddling, allo-suckling) adaptations that show how a species uniquely interacts with its environment.

Social behaviour

Details of group structure, group size and composition, home range, territorial behaviour, greeting or agonistic behaviour, use of secretions and vocalisations.

Reproduction and denning behaviour

Physiological and morphological characteristics related to reproduction, including: spermatogenesis and details of oestrous cycle; courtship and mating behaviour; length of gestation; time of birth, including peaks of births and relationship to rainfall or food availability; litter size; birth weight and size; spacing of litters; pup development, and time to weaning and sexual maturity; behaviour of young; presence of helpers. This section may be supplemented with information from captive animals. This section also includes details of dens and burrows, such as location, type, structure, use of bedding material and so on.

Competition

Details of those species with which the current species is known to compete for food, dens or other resources.

Mortality and pathogens

This section is divided into six subheadings:

Natural sources of mortality Sources of mortality that can be regarded as being natural (i.e., outside of the influence of man); for example, effects of major predators on populations, starvation, death of young animals during dispersal and so on.

Persecution Sources of mortality, with the exception of hunting and trapping for fur, which can be attributed to anthropogenic factors. For example, persecution of animals due to their preying on livestock and/or game, the capture of animals for the pet trade, and so on.

Hunting and trapping for fur The impact of the fur trade as a mortality factor in the species, including details of the quantities of animals affected by hunting or harvesting; fur harvests and yields; peak years in the fur trade; fur prices; exports and imports.

Road kills The impact of road traffic on populations, including information, where available, of numbers of animals killed.

Pathogens and parasites Effects of pathogens and parasites on populations; susceptibility to particular diseases, pathogens and parasites (endo- and ectoparasites); the importance of the species as a vector or reservoir of diseases of domestic stock and humans.

Longevity The known or estimated longevity of the species. Where data from the wild are not available, this is supplemented by known records from captive animals.

Historical perspective

The species' importance in culture; traditional uses; conservation measures taken in the past.

Conservation status

This section is divided into six subheadings:

Threats The most important tangible and potential threats the species faces for its immediate or long-term survival.

Commercial use Present human use and influence (e.g., fur trade, pet trade); international demand and marketing.

Occurrence in protected areas The species' known occurrence in protected areas within the normal distribution range of the species. This section is not intended to provide an exhaustive listing of protected areas from which a particular species is known to occur, although we have attempted to be as comprehensive as possible for threatened species (e.g., dhole). For other species, such as black-backed jackal, we list only a few of the larger and better-known protected areas. The lack of adequate survey data means that our knowledge of the occurrence of some species in protected areas is poor (e.g., pale fox). In some accounts, this information is arranged according to country, in others it is presented in a more generalised manner. A useful resource for readers, and one that is set to improve over coming years, is the ICE Biological Inventory Database (http://www.ice.ucdavis/bioinventory/bioinventory.html), which features a searchable interface enabling users to find information on the occurrence of species in protected areas across the globe.

Protection status CITES listing; threat status in national or regional Red Data books.

Current legal protection Any protection status that is legally enacted or enforced for the express aim of protecting a species, including national legislation; whether hunting and trade are prohibited or regulated; legal protection; and legal status as problem animal.

Conservation measures taken International treaties and conventions; traditional protection due to cultural reasons; establishment of protected areas; action plans; vaccination trials; other specific actions being undertaken or completed.

Occurrence in captivity

Notes on whether the species is kept in captivity, and how successfully they breed in captive conditions. As far as possible, these have been checked with ISIS (International Species Information System based in Minnesota, USA, http://www.isis.org) and the International Zoo Yearbooks (Published by The Zoological Society of London as a service to zoos around the world since 1960). Captive breeding programmes, which have as their aim reintroduction of the species to areas in the wild, are discussed here.

Current or planned research projects

A list of research projects currently being conducted on the species, including brief details of the project, its coordinators and their institutional affiliations. Future projects are also listed.

Gaps in knowledge

Obvious gaps in our knowledge of the species that must receive priority in the next 10 years in order to improve our understanding of the respective species.

Core literature

A list of specific references that represent major works for the species. General references are not given unless they represent the primary source of information. Full citations of all references mentioned in the text are provided in the **References** section.

Reviewer(s)

The names of the reviewers responsible for reviewing and commenting on the species account.

Editor(s)

The names of the editors responsible for editing and ensuring the comprehensive nature of the species account.

Chapter 3

South America (Neotropical)

3.1 Short-eared dog
Atelocynus microtis (Sclater, 1883)
Data Deficient (2004)

M.R.P. Leite Pitman and R.S.R. Williams

Other names

English: short-eared fox, small-eared dog, small-eared zorro; **French:** renard à petites oreilles; **German:** kurzohriger hund; **Portuguese:** cachorro-do-mato-de-orelhas-curtas; **Spanish:** perro de monte; perro de orejas cortas, zorro negro, zorro ojizarco; **Indigenous names:** Ayoreo: divequena; Chiquitano: nomensarixi; Guarayo: cuachi yaguar; More: quinamco; Ninim, Moseten: achuj jhirith; Siriono: ecoijok; Tsimane: achuj foij (Bolivia); Kaiabi: awara (Brazil); Yucuna: uálaca; Huitoto: urúbui; Yebá masá o Barasana: búyaíro; Bora: wipe; Okaima: juhxuutsoonna; Carijona: karejuqué (Colombia); Achuar: kuap yawa; Cofán: tsampi'su ain; Huaorani: babei guinta; Quechua: sacha alcu, jujunda, puma; Iona-Secoya: wë yai (Ecuador); Guarani: aguerau (Paraguay); Amarakaeri: huiwa toto; Matsiguenga: machit; Quechua: monte alcu; Shipibo: caman ino; Cashinaua: kama, kama inu; Amahuaca: kama, shindokama; Sharanahua: padoshoinca (Peru).

Taxonomy

Canis microtis Sclater, 1883. Proc. Zool. Soc. Lond., 1882:631 [1983]. Type locality: "Amazons", restricted by Hershkovitz (1961) to "south bank of the Rio Amazonas, Pará, Brazil."

Atelocynus is a monotypic genus. The species *A. microtis* has been placed in the genus *Lycalopex* (Studer 1905), *Cerdocyon* (Pocock 1914), *Dusicyon* (Osgood 1934; Clutton-Brock *et al*. 1976), and *Atelocynus* (Cabrera 1931; Languth 1975; Stains 1975). Van Gelder (1978) considered *Atelocynus* a subgenus of *Canis*. Berta's (1987) phylogenetic analysis showed *Atelocynus microtis* to be a distinct taxon most closely related to another monotypic Amazonian canid genus, *Speothos*, and this hypothesis is now widely accepted (Wozencraft 1993; Nowak 1999).

Chromosome number: 2n=76 (Wurster and Benirschke 1968). The only individual studied was a female and the karyotype included 36 pairs of acro- or subacrocentric autosomes and one pair of large submetracentric chromosomes, probably X-chromosomes.

Description

The short-eared dog is a medium-sized canid, averaging about 10kg as an adult (Table 3.1.1). According to Hershkovitz (1961), a captive adult female was a third larger than a captive adult male. The animal's head is fox-like, with a long, slender muzzle and rounded, relatively short ears. The pelt colour can range from black to brown to rufous grey. Pelage is often darkest in a dorsal line from the head to the tail. However, various colour patterns are observed in different individuals, and it is not clear whether colour varies with age, habitat, or moult; in

M.R.P. Leite Pitman and M. Swarner

Adult male short-eared dog, taken by automatic camera. Alto Purus, Peruvian Amazon, 2002.

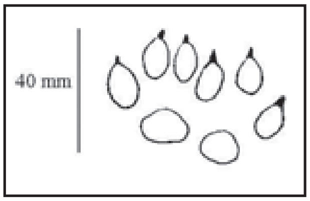
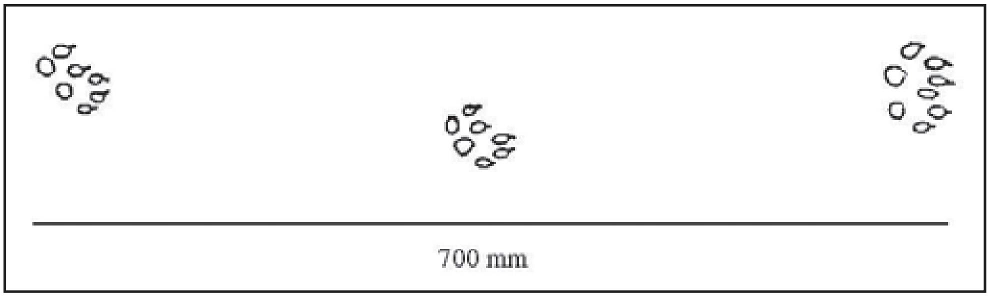


Figure 3.1.1. Footprint of adult short-eared dog recorded in Cocha Cashu, Peru (Leite 2000).

Figure 3.1.2. Tracks of adult short-eared dog in Cocha Cashu, Peru (Leite 2000).



Cocha Cashu Biological Station, Madre de Dios, Peru, both reddish and black individuals have been observed (Leite 2000). A complete moult lasting three weeks was observed in July 1960, when a captive animal was transported from Colombia to a zoo in the United States. During the moult, large flakes of orange-brown oily exudates appeared with the falling hairs. A subsequent moult was observed in March (Hershkovitz 1961; A. Gardner pers. comm.). The tail is bushy, particularly in comparison to the short pelage on the rest of the body, with a dark mid-dorsal band of thick erectile hairs and light-coloured underside.

The nasals are short; the forehead slightly convex; the frontal sinus small; the presphenoid very narrow with lateral wings and large bulla. The dental formula is 3/3-1/1-4/4-2/3=42. The lower third incisor is short and not caniniform. The upper canines are distinctively long, their tips projecting outside the closed mouth for about 50mm. The upper molars are narrow for their length (Hershkovitz 1961; Berta 1986).

Table 3.1.1. Combined body measurements for the short-eared dog from across the species' range (Nowak 1999).

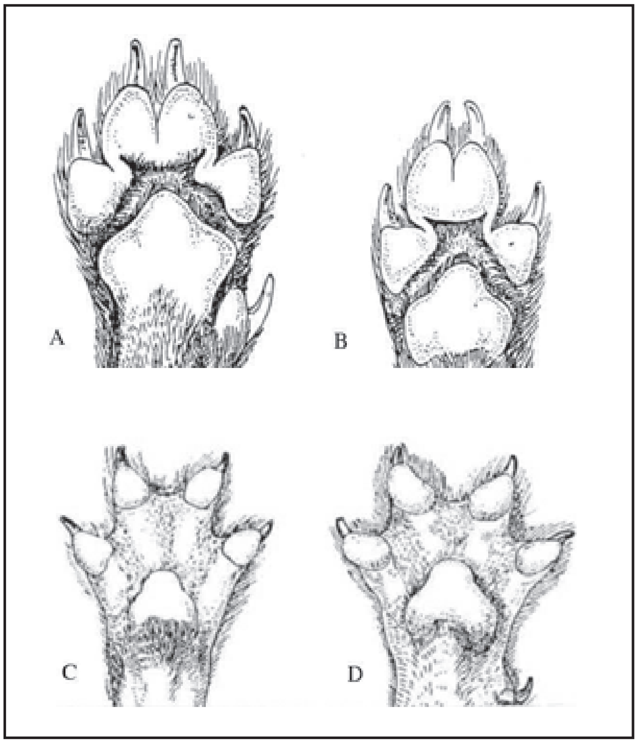
HB	720–1,000mm
T	250–350mm
E	34–52mm
SH	356mm
WT	9–10kg

Subspecies Monotypic (Berta 1986).

Similar species Only one other species of wild dog is known to inhabit lowland Amazonian forest, namely the bush dog (*Speothos venaticus*). Confusing the two species is unlikely due to unambiguous physical and behavioural differences. Bush dogs are smaller, light-coloured, with a very short muzzle, legs, and tail; they live in packs and are seldom seen alone. Tracks may be distinguished by the bush dog's conspicuous interdigital membrane, with the middle toes fused, whereas the short-eared dog's interdigital membrane is only partial (Figures 3.1.1, 3.1.2, 3.1.3). The bush dog's stride is also shorter, and its tracks and pads larger than those of the short-eared dog.

Two additional species of wild canids whose ranges border Amazonia, the crab-eating fox (*Cerdocyon thous*) and the culpeo (*Pseudalopex culpaeus*), as well as domestic dogs, could potentially be mistaken for the short-eared dog, but none of these have the combination of a slender, long snout, short ears, and a bushy tail. Tayras (*Eira barbara*) are also brownish and have bushy tails, but differ in their much smaller ears, yellowish throat and mostly arboreal habits. The jaguarundi (*Herpailurus yaguarondi*), which is sometimes similar in colour, is smaller, more delicate, and has a very slender tail (Emmons and Feer 1990).

Figure 3.1.3. Comparison of bush dog and short-eared dog feet, based on dried skins (Pocock 1914).
A and B – Right fore foot and hind foot of bush-dog.
C and D – Right hind foot and fore foot of short-eared dog.



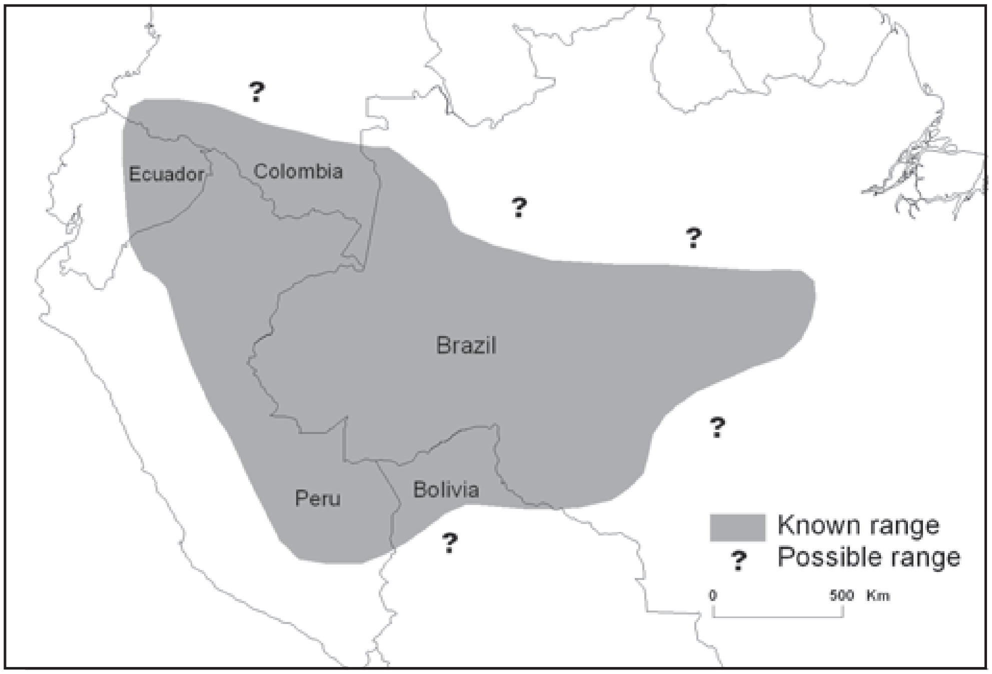


Figure 3.1.4. Current distribution of the short-eared dog.

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Current distribution

The short-eared dog has been found in scattered sites from Colombia to Bolivia and Ecuador to Brazil (Figure 3.1.4). Its presence in Venezuela was suggested by Hershkovitz (1961) but never confirmed. Various distributional hypotheses for the species have been published, suggesting the presence of the species throughout the entire Amazonian lowland forest region, as well as Andean forests in Ecuador and savannah regions (Emmons and Feer 1990, 1997; Tirira 1999).

For this study, we rechecked museum specimens and carried out an extensive survey of field biologists doing long-term research in the species' putative range, constructing a new distributional map based only on specimens of proven origin and incontrovertible field sightings. Our results suggest a much smaller distribution range, limited to western lowland Amazonia. The northernmost record is in Mitú, Colombia, at 1°15'57"N, 70°13'19"W (Hershkovitz 1961), the southernmost on the west bank of the river Heath, Pampas del Heath, north-west Bolivia, at 12°57'S, 68°53'W (M. Romo pers. comm.). The easternmost record is from the vicinity of Itaituba, Brazil, at 4°20'S, 56°41'W (M. De Vivo pers. comm.), and the westernmost in the Rio Santiago, Peru, at 4°37'S, 77°55'W (Museum of Vertebrate Biology, University of California, Berkeley, collected 1979). Unfortunately, there is no information on the continuity of the species' distribution within its extent of occurrence; the absence of records from large areas suggests that its distribution may not be continuous throughout its range.

Range countries Bolivia, Brazil, Colombia, Ecuador, Peru (M.R.P. Leite unpubl.).

Relative abundance

The short-eared dog is notoriously rare, and sightings are uncommon across its range. However, this may not always have been the case. The first biologists to study the species found it relatively easy to trap during mammal surveys around Balta, Amazonian Peru, in 1969 (A.L. Gardner and J.L. Patton pers. comm.). Grimwood (1969) reported collecting specimens around the same time in Peru's Manu basin (now Manu National Park), suggesting that the species was also relatively common in that area.

Following these reports, the species went practically unrecorded in the Peruvian Amazon until 1987, despite intensive, long-term field surveys of mammals in the intervening years (Terborgh *et al.* 1984; Jason and Emmons 1990; Woodman *et al.* 1991; Pacheco *et al.* 1993, 1995). Even Louise Emmons, who carried out long-term projects monitoring and trapping ocelots (*Leopardus pardalis*) and other mammals at the Cocha Cashu Biological Station in Manu, never saw or trapped the short-eared dog (L. Emmons pers. comm.). For whatever reason, the species appears to have temporarily vanished from the region between 1970 and 1987.

Over the last decade, it appears that the species may be recovering in southern Peru and eastern Ecuador, with increasing numbers of sightings in recent years at both sites. Between 1987 and 1999, biologists working in the Peruvian department of Madre de Dios, mostly in the vicinity of Cocha Cashu Biological Station, have reported 15 encounters with the short-eared dog (M.R.P. Leite *et al.* unpubl.).

Estimated populations/relative abundance and population trends In an ongoing field study initiated at

Cocha Cashu in 2000, Leite and colleagues have sighted and followed five individuals in an area of 10km^2, giving an estimated density of 0.5 individuals/km^2. However, far too little is known about the species to extrapolate this estimate (itself preliminary) to the rest of the species' range. For the time being, the short-eared dog must be considered extremely rare throughout its range and certainly one of the rarest carnivores wherever it occurs.

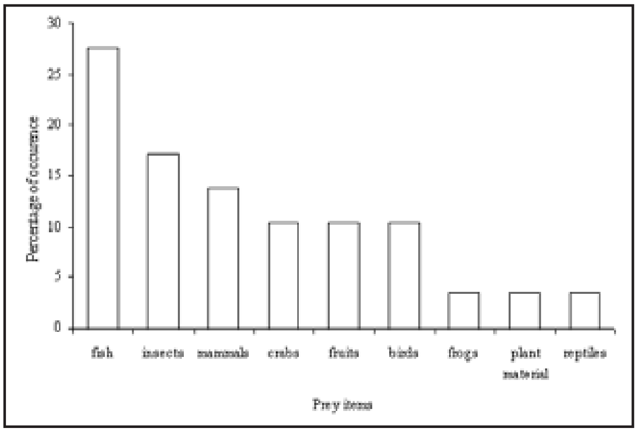
Habitat

The short-eared dog favours undisturbed rainforest in the Amazonian lowlands. The species has been recorded in a wide variety of lowland habitats, including terra firme forest, swamp forest, stands of bamboo, and primary succession along rivers (M.R.P. Leite unpubl.). At Cocha Cashu, sightings and tracks of the species are strongly associated with rivers and creeks, and there are five reliable reports of short-eared dogs swimming in rivers. Records are very rare in areas with significant human disturbance, i.e., near towns or in agricultural areas. It is unclear whether the short-eared dog is able to utilise habitats outside wet lowland forests. One sighting in Rondonia, Brazil, was in lowland forest bordering savannah (M. Messias pers. comm.). Another, at the highest elevation yet documented for the species, was at 1,200m a.s.l. in the Ecuadorean Andes, in a transitional zone between lowland forest and cloud forest (Pitman 2002). Two specimens collected in 1930 are allegedly from even higher elevations in the same region – above 2,000m on Volcan Pichincha and Antisana (near Quito) – but the absence of any other reports from these well-studied areas leads us to believe that these represent mislabelled specimens.

Food and foraging behaviour

Food An ongoing study of the short-eared dog's diet, based on scat samples collected at Cocha Cashu since 2000 (M.R.P. Leite unpubl.), shows the species to be a generalist carnivore (Figure 3.1.5). Fish appear to be the most important item in their diet (present in 28% of samples; n=21). Defler and Santacruz (1994) had previously suggested that fish form part of the short-eared dog's diet, based on the discovery of a cestode (*Diphyllobothrium latum*) in a museum specimen's intestine (the parasite requires a fish as its intermediate host). Insects (mainly Coleoptera) were the second most important item in their diet (17% of samples), while mammal remains (agoutis, marsupials and small rodents) were present in 13% of the scats collected in Cocha Cashu. This corroborates earlier anecdotal evidence that small rodents, agoutis (*Dasyprocta* spp.), pacas (*Agouti paca*), and acouchis (*Myoprocta* spp.) are important components of the diet (Peres 1992; Defler and Santacruz 1994).

Figure 3.1.5. Frequency of occurrence of various prey items in 21 scat samples from Cocha Cashu, Peru (Leite 2000).



The remains of fruits, including *Borismenia japurensis*, *Strychnos asperula*, *Unonopsis floribunda*, *Pouteria procera*, *Sciadotenia toxifera*, *Socratea exorrhiza*, *Astrocaryum murumuru*, *Euterpe precatoria*, *Trattinnickia* sp., and various Cucurbitaceae and Moraceae were found in 10% of samples. Fruits of the palm *Euterpe precatoria* were found germinating in two scats. Defler and Santacruz (1994) report short-eared dogs eating fallen *Brosimum* fruits and the Cofan Indians of Ecuador report them being attracted to fallen bananas (R. Borman pers. comm.).

Close to 4% of droppings contained the remains of frogs, including *Osteocephalus taurinus* (see below). Parker and Bailey (1990) reported seeing a short-eared dog with a frog in its mouth in Madidi National Park in Bolivia. Crabs (10.3% of samples), birds (10.3%), reptiles (3.4%) and vegetable fibre (3.4%) were other components of the diet at Cocha Cashu.

Foraging behaviour The short-eared dog has been reported hunting alone and in pairs (Peres 1992; M.R.P. Leite unpubl.). Y. Campos (pers. comm.) described two adults hunting either a fish or a frog in a water hole in Ecuador; Peres (1992) observed an individual hunting a rodent (*Proechmys* sp.). M.R.P. Leite (unpubl.) observed an adult chasing a squirrel on the ground, and found a small waterhole where another adult had apparently killed, but not eaten, dozens of frogs (*Osteocephalus taurinus*).

Both diurnal and nocturnal activity patterns have been observed. Field reports (n=30) appear to indicate a diurnal or at least partly diurnal animal, with 95% of the observations made in daylight hours. However, the species has also been photographed at night walking on trails of Madidi National Park, Bolivia (R. Wallace pers. comm.), and one animal was captured swimming after a paca, in a river at 03:00 in Colombia (Defler and Santacruz 1994).

Damage to livestock or game A. Salas (pers. comm.) has documented a wild short-eared dog eating chickens near Tambopata National Reserve, Peru, and P. Santos *et al.* (unpubl.) reported two captive individuals in Brazil also killing poultry.

Adaptations

There is evidence, including the partial interdigital membrane, sleek, thick coat, and sightings on rivers, to suggest that the short-eared dog may be at least partly aquatic (Berta 1986). The short limbs (though not so short as those of the bush dog) likely facilitate movement in dense forests (Hershkovitz 1961).

Social behaviour

The short-eared dog is mainly solitary, although observations have been made of two adult animals walking together in October in Peru and between January and March in Ecuador (M.R.P. Leite unpubl.; Y. Campos pers. comm.). Since 2000, three individuals of adult size have been observed to use a 1.6km stretch of white sandy beach near Cocha Cashu, where two latrines are used infrequently by both short-eared dogs and river otters (*Lontra longicaudis*).

According to Hershkovitz (1961) and A.L. Gardner (pers. comm.), most observations of wild and captive individuals indicate that the species is very docile around humans, with the exceptions of a captive male in the Schönbrunner Zoo and a female in the Brookfield Zoo, which growled, snarled and attempted to bite when frightened. In addition, when a Brazilian hunting party with six domestic dogs found a pair of short-eared dogs with two puppies, "the mother protected the babies fiercely, having attacked one of the domestic dogs." Another female and two puppies were sufficiently docile to allow them to be carried in a basket with no attempt being made to bite the hunters (P. Santos *et al.* unpubl.). Hershkovitz (1961) and A.L. Gardner (pers. comm.) reported a strong musky odour in males for both wild and captive animals, this being hardly noticeable in females.

Reproduction and denning behaviour

Based on the fresh carcass of a three- or four-month-old juvenile found in September 2000 at Cocha Cashu Biological Station, short-eared dogs give birth in May or June in Peru. Breeding time is not known precisely, but pups have been found throughout the range in April to May, June, September, and November to December, suggesting that parturition occurs in the dry season.

Three dens have been found inside hollow logs, one of them containing two adults and two pups, another, the female and two pups (Defler and Santacruz 1994; P. Santos *et al.* unpubl.). Another den, containing three pups, was found in a paca burrow (M.R.P. Leite unpubl.). At Cocha Cashu Biological Station, the short-eared dog was found also to use several paca burrows along the steep banks of a creek.

Competition

Considering the short-eared dog's generalist diet, it is likely that all medium-sized sympatric carnivores, frugivorous monkeys, rodents, and ungulates, are competitors to some extent. Paca dens seem to be used often by short-eared dogs.

Mortality and pathogens

Natural sources of mortality Very little is known. Ocelot tracks found around the corpse of a dead juvenile in Cocha Cashu suggest it is a possible predator. Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are also potential predators.

Persecution There are only a few reports of the short-eared dog being hunted by man. In one case, the species was reportedly killed and eaten by the Yora indigenous people of Peru (Museum of Vertebrate Zoology, Berkeley, California MVZ No.: 181288 Accn No.: 12921). In another, A. Salas (pers. comm.) reported that villagers injured a male short-eared dog (which subsequently died) as it was killing chickens in the Tambopata river region, Peru. A recently captured and radio-collared animal was shot and killed by a hunter in the Alto Purus region of south-eastern Peru. The hunter claimed it was mistakenly shot.

Hunting and trapping for fur There are no known reports of the species being hunted or trapped for its fur.

Road kills The species avoids developed areas, and there are no known cases of road kills, so the impact of vehicles on population numbers is probably minimal.

Pathogens and parasites To date, no diseases have been reported in wild short-eared dogs. Common viral diseases such as canine distemper virus and canine parvovirus are widespread among domestic dogs in South America, even in the most pristine areas of the Amazon (Leite Pitman *et al.* 2003). Domestic dogs are kept throughout the region as pets or hunting companions and occur in a feral state around villages. Since potentially all wild canid species are susceptible to distemper, it is feasible that epidemics could occur, decimating or even locally eliminating populations of wild canids. P. Santos *et al.* (unpubl.) report the death of a captive, one year-old short-eared dog by canine distemper virus, and the possible death of another captive individual by the same means. These and other infectious diseases may represent a serious threat to wild populations of Neotropical canids. For example, one hypothesis to explain why this species largely disappeared from the Peruvian Amazon during the 1970s and 1980s (see Relative abundance) is that epidemics started by domestic dogs decimated the population over large areas. Clearly, the current and potential impacts of these diseases require further study.

The cestode, *Diphyllobothrium latum,* was found as an intestinal parasite of the short-eared dog (Defler and

Santacruz 1994). This tapeworm can cause pernicious anaemia and occasionally death in domestic dogs, as it competes with the host for vitamin B12.

Longevity Most captive animals survive for less than a year, with the exception of two animals that lived for nine years (Anon. 2000) and eleven years (Jones 1982). There is no data on longevity in the wild.

Historical perspective

The short-eared dog generally is poorly known by indigenous peoples of the Amazon basin and is not known to hold any special significance for them. Several Huaorani in Ecuador stated that it was one of the animals they did not hunt, but they could not offer a clear reason. The Amarakaeri indigenous people of Peru call the short-eared dog "huiwa toto", meaning solitary devil, and believe that it will attack men by biting their testicles (M. Swarner pers. comm.).

Conservation status

Threats Diseases from domestic dogs (see above) and habitat loss. There are no reports of widespread persecution of the species. An ongoing distribution survey (M.R.P. Leite unpubl.) suggests that the short-eared dog is rare throughout its range and threatened by the large-scale forest conversion underway in Amazonia.

Commercial use Reports of commercial use are scattered and few. In some cases, wild individuals have been captured for pets and occasionally for sale to local people and zoos.

Occurrence in protected areas The short-eared dog is likely to occur in most protected areas that encompass large tracts of undisturbed forest in western Amazonia. During the last decade, its presence has been confirmed in the following protected areas:

- *Bolivia*: Madidi National Park, Tahuamanu Ecological Reserve and Estación Biologica Beni;
- *Brazil*: Guajara Mirim State Park, Cristalino Reserve. The species has never been reported from Xingu National Park, Amanã Reserve, Mamirauá Reserve, Jaú National Park and Serra do Divisor National Park, but sightings close to these areas suggest the species is present at very low densities (M.R.P. Leite unpubl.);
- *Ecuador*: Yasuní National Park, Reserva Ecologica Cofanes de Bermejo and the Cuyabeno Wildlife Reserve;
- *Peru*: Manu National Park, Tambopata National Reserve, Alto Purus Reserved Zone, and Manu Wildlife Research Center.

Protection status CITES – not listed.
The species is on the Brazilian list of endangered species (see: www.ibama.gov.br/fauna/extincao.htm) and on the preliminary list of Colombian endangered species (Rodriguez 1998).

Current legal protection Protected by law in Brazil. Recently removed from the list of protected species in Peru.

Conservation measures taken Although protected on paper in some Amazonian countries, this has not yet been backed up by specific conservation action.

Occurrence in captivity

No short-eared dogs are known to be currently held in captivity, and only a dozen confirmed records of captive animals exist. The first recorded captive short-eared dog (eventually the holotype) was kept at the Zoological Society of London late in the 19th century (Sclater 1883). At around the same time, two males were kept at the Zoological Gardens of Para, Brazil, and in 1933 another one was present in the Schönbrunner Tiergarten, Germany (Hershkovitz 1961). Since then, individuals have been held in several U.S. zoos (including the Lincoln Park Zoo, the National Zoo, the Brookfield Zoo, the Oklahoma City Zoo, and the San Antonio Zoo), mostly during the 1960s and 1970s. Over the last decade, sporadic reports of captive animals have come from Peru (Pucallpa and Puerto Maldonado), Colombia (Medellin), Ecuador (Quito), and Brazil (Canaria and Itaboca in the Amazon).

Current or planned research projects

M.R.P. Leite (Duke University Center for Tropical Conservation, USA) is conducting an ongoing research programme on the ecology and conservation of the short-eared dog at Cocha Cashu Biological Station and the Alto Purus Reserved Zone, in south-eastern Peru. The project is currently seeking funding to establish a domestic dog vaccination programme in the Amazonian protected areas of Peru and to expand field work to other sites within the species' range, including western Brazil, Ecuador, Bolivia, Colombia, and northern Peru.

Gaps in knowledge

The biology, pathology, and ecology of the species are virtually unknown. Especially lacking is any estimate of population density and an understanding of the species' habitat requirements.

Core literature

Berta 1986; Defler and Santacruz 1994; Leite 2000; Peres 1992.

Reviewers: Annalisa Berta, Orin Courtenay, Louise Emmons, Alfred Gardner, James Patton, Pedro Santos, Matthew Swarner, John Terborgh. **Editors:** Claudio Sillero-Zubiri, Michael Hoffmann.

3.2 Crab-eating fox
Cerdocyon thous (Linnaeus, 1766)
Least Concern (2004)

O. Courtenay and L. Maffei

Other names

English: crab-eating zorro, common zorro, common fox, savannah fox, forest fox; **French**: renard crabier, chien des bois (Guyana); **German:** maikong, waldfüchse; **Italian:** volpe sciacallo; **Portuguese:** raposa, raposão, cachorro-do-mato, lobinho, graxaim, graxaim-do-mato, mata virgem, lobete, guancito, fusquinho, rabo fofo (Brazil); **Spanish:** zorro cangrejero, zorro carbonero, zorro de monte (Argentina); zorro de monte, zorro, zorro patas negras (Bolivia); zorro, lobo, zorro-lobo, perro-zorro, zorro-perro, zorro perruno, zorra baya, perro sabanero, perro de monte (Colombia); zorro perro (Uruguay); zorro común, zorro de monte, zorro sabanero (Venezuela); **Indigenous names:** Izoceno-Guarani: aguara (Bolivia). Guarani: aguará chai (Argentina); Guarani: aguara'i (Uruguay); Nações do Parque Indígena do Xingu (Kuikuro, Matipú, Naruótu, and Kalapalo people): sorokokusge; Ualapiti: tsunakatirre; Mehinaku and Uaurá: uáu; Suiá: roptó; Tumai: auaraí; Kamaiurá: uarain; Auetí: tovait; Xavante: waptsã'uwa (Brazil). Namo: guahibo; Oá: desano piratapuya, tukano; Perupa: chaké, yuko, yupa; Uá-kua: chimila; Yu: puinave; Fo/Fu: chibcha, muyska; Vescura: tunebo; Aguari/Awari: piaroa; Macadwimi: cubeo; Taimi: cuna; Gagaru: arhuaco; Maktu: kogui; Uá-kua: chimila; Uarir: wayú; Kiisoué: chimila (Colombia).

Taxonomy

Canis thous Linnaeus, 1766. Syst. Nat., 12th ed., 1:60. Type locality: "Surinamo" [Surinam].

Placed in genus *Cerdocyon* by Hamilton-Smith (1839), Cabrera (1931), Langguth (1975), Stains (1975) and Berta (1987). Placed in genus *Dusicyon* by Clutton-Brock *et al*. (1976), subgenus *Dusicyon* (*Cerdocyon*) by Osgood (1934), and subgenus *Canis* (*Cerdocyon*) by Van Gelder (1978).

Chromosome number: 2n=74 (Wurster-Hill 1973).

Description

A medium-sized (5–7kg) canid (Table 3.2.1), tail moderately bushy, often with black tip and dark at base. No sexual dimorphism. Rostrum long and pointed, head relatively short and narrow. Pelage generally dark grey to black along dorsum down to midline; midline to ventrum including legs grey or black, sometimes with yellow to

Table 3.2.1. Combined body measurements for the crab-eating fox from Brazil: Marajó (Pará state, n=28), São Miguel (Minas Gerais, n=5), Baturité (Ceará, n=3) (Courtenay *et al*. 1996, O. Courtenay unpubl.); Cuiabá, Chapada dos Guimarães, Poconé, Barra do Bugres, Jangada (Matto Grosso, n=26), Vila Boa (Goais, n=1) Altinópolis (São Paulo, n=1) (J. Dalponte unpubl.); Venezuela: Masaguaral (Guarico state, n=10) (Sunquist *et al*. 1989); various (data represent mean values of n=11–44 specimens from five different regions) (Bisbal 1988); Argentina: Sierras de Mal Abrigo (Colonia, n=6) (Cravino *et al*. 2000). Cranial and dental measurements are found in Berta (1982), Bisbal (1988), and Courtenay *et al*. (1996).

HB	658mm (570–775) n=61
T	310mm (220–410) n=52
HF	136mm (125–147) n=50
SH	368mm (330–415) n=34
E	69mm (55–86) n=47
WT	5.7kg (4.5–8.5) n=52

Adriano Gambarini

Crab-eating fox. Emas National Park, Goias, Brazil, 2002.

orange flecks; neck and underparts cream to buff white. Pelage notably bristly and coarse. Substantial inter- and intra-population pelage colour variation including dark to almost black (e.g., northern Venezuela, Amazonia, central Brazil), silver grey (e.g., Venezuelan llanos), and light grey-yellow rufous (e.g., Ceará, Brazil). Continuous black dorsal line from neck to tail tip variably present. The dental formula is 3/3-1/1-4/4-1/2=44.

Subspecies Five subspecies are recognised (Cabrera 1931, 1958; Berta 1982).

- *C. t. thous* (south-eastern Venezuela, Guyana, Surinam, French Guiana, northern Brazil)
- *C. t. azarae* (north-eastern and central Brazil)
- *C. t. entrerianus* (south Brazil, Bolivia, Uruguay, Paraguay, Argentina)
- *C. t. aquilus* (north Venezuela, Colombia)
- *C. t. germanus* (Bogotá region, Colombia)

Similar species Pampas fox (*Pseudalopex gymnocercus*): sympatric in southern Brazil, Bolivia, Uruguay, Paraguay and Argentina; similar build and weight (4–7kg); bushier tail, pelage mixed grey, with variable dark band running along dorsum; ears, neck, lower legs, and tail yellow to rufous. Culpeo (*Pseudalopex culpaeus*): sympatric in Bolivia and possibly Colombia; larger, sexually dimorphic (6–13kg); bushy coat, distinct reddish to agouti on head, limbs, and orange tinge on belly. Hoary fox (*P. vetulus*): sympatric in Brazil; smaller (2.5–4kg), less robust; pelage woolly not bristly; rostrum length shorter relative to rostrum width in *C. thous* (e.g., RL:RW ratio: *P. vetulus* 2.1 vs *C. thous* 2.5; Courtenay *et al*. 1996); confusion only likely with lighter pelage varieties of the crab-eating fox, or near melanic forms of the hoary fox. Short-eared dog (*Atelocynus microtis*): possible sympatry in undisturbed areas in lowland Amazonian forest of Brazil, Bolivia, Colombia and Venezuela; weight similar (6.5–7.5kg); rostrum long and narrow; small rounded ears; tail bushy relative to body pelage which is short; colour variable. Gray fox (*Urocyon cinereoargenteus*): sympatric in Colombia and north-west Venezuela; weight similar (3–7kg); distinct reddish pelage on shoulders, ears, legs, and ventrum below neck. Bush dog (*Speothos venaticus*): sympatric throughout most of range; similar weight (5–7kg), but much more robust with substantially shorter legs and tail, thicker neck, and broader head; brown to tawny. Tayra (*Eira barbara*): sympatric throughout most of range; weight similar (2.7–7kg); glossy brown to black over body with contrasting grey yellow brown head and neck; tail long, two-thirds of body length; ears small and round. Jaguarundi (*Felis yagouaroundi*): sympatric throughout most of range; weight similar (4.5–9kg); fur short and silky; legs short; body slender; tail relatively long; head and ears relatively small; silky black to tawny pelage.

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Figure 3.2.1. Current distribution of the crab-eating fox.

Current distribution

The species is relatively common throughout its range from the coastal and montane regions in northern Colombia and Venezuela, south to the province of Entreríos, Argentina (35°S); and from the eastern Andean foothills (up to 2,000m) in Bolivia and Argentina (67°W) to the Atlantic forests of east Brazil to the western coast of Colombia (1°N) (Figure 3.2.1). Its known central distribution in lowland Amazon forest is limited to areas north-east of the Rio Amazon and Rio Negro (2°S, 61°W), south-east of the Rio Amazon and Rio Araguaia (2°S, 51°W), and south of Rio Beni, Bolivia (11°S).

Few records exist in Suriname and Guyana. Recent records in French Guyana (Hansen and Richard-Hansen 2000) have yet to be confirmed (F. Catzeflis pers. comm.). The previous citation of its occurrence in Peru (Pacheco *et al*. 1995) has since been retracted by the authors (D. Cossios pers. comm.).

Historical distribution Not dissimilar to current. Fossils found in deposits dating to the late Pleistocene (Lujanian 300,000–10,000 years before present) to Recent, in Lagoa Santa Caves, Minas Gerais, Brazil (Berta 1987).

Range countries Argentina, Colombia, Bolivia, Brazil, French Guiana(?), Guyana, Paraguay, Suriname, Uruguay, Venezuela (Cabrera 1958; Berta 1982).

Relative abundance

No precise estimates of population sizes are available, but populations generally are considered stable.

Estimated populations/relative abundance and population trends Average densities include 0.55 animals per km^2 (range: 0.273–0.769, n=7 territorial groups) in the savannah/scrub mosaic of Marajó, Brazil (Courtenay 1998); 4/km^2 in the Venezuelan llanos (Eisenberg *et al.* 1979), and 1/km^2 in dry forest in Santa Cruz, Bolivia (Maffei and Taber 2003). F. Michalski (pers. comm.) estimates <100 individuals in Ipanema National Forest (São Paulo) and Lami Ecological Reserve (Rio Grande do Sul), Brazil, and Hill *et al.* (1997) indicate high relative encounter rates in the Mbaracayu Forest Reserve, Paraguay. There is little documentation for Suriname, French Guiana, and periphery areas of lowland Amazon forest.

Habitat

Occupies most habitats including marshland, savannah, cerrado, caatinga, chaco-cerrado-caatinga transitions, scrubland, woodlands, dry and semi-deciduous forests, gallery forest, Atlantic forest, Araucaria forest, isolated savannah within lowland Amazon forest, and montane forest. Records up to 3,000m a.s.l. Readily adapts to deforestation, agricultural and horticultural development (e.g., sugarcane, eucalyptus, melon, pineapples) and habitats in regeneration. In the arid Chaco regions of Bolivia, Paraguay, and Argentina, confined to woodland edge; more open areas used by the Pampas fox.

Vegetative habitats generally utilised in proportion to abundance, varying with social status and climatic season. Radio-tagged foxes in seasonally flooded savannas of Marajó, Brazil, predominated in wooded savannah (34%) and regeneration scrub (31%); low-lying savannah was “avoided”, and areas of wooded savannah “preferred”, more by senior than junior foxes and more in the wet season than dry season (Macdonald and Courtenay 1996). In the central llanos of Venezuela, fox home ranges similarly shift to higher ground in response to seasonal flooding, though are generally located in open palm savannah (68% of sightings) and closed habitats (shrub, woodlands, deciduous forest, 32%) (Brady 1979; Sunquist *et al.* 1989). In Minas Gerais, Brazil, two radio-tagged foxes (1 male, 1 female) in different territories were observed most often at the interface of livestock pasture and gallery forest (“vereidas”) (82%) and in eucalyptus/agricultural plantations (8%) (O. Courtenay unpubl.). Eighty-eight crab-eating fox specimens collected by the Smithsonian Venezuelan Project were taken from prairie and pasture (49%), deciduous and thorn forest (19%), evergreen forest (17%), and marshes, croplands and gardens (15%) (Handley 1976 as cited in Cordero-Rodríguez and Nassar 1999).

Food and foraging behaviour

Food Omnivorous, including fruit, vertebrates, insects, amphibians, crustaceans, birds, and carrion. An opportunistic predator; dietary components (and their relative frequency) at any one location varies according to availability, climatic season, and probably social status. In areas of human disturbance, a large proportion of the diet may comprise foods such as cultivated fruits, domestic fowl and refuse.

In the Venezuelan llanos, 104 stomach contents from four different locations comprised in percent volume: small mammals (26%), fruit (24%), amphibians (13%), insects (11%); the dry season diet was predominantly small mammals, reptiles and amphibians, with insect and fruit becoming more frequent in the wet season (Brady 1979; Eisenberg *et al.* 1979; Bisbal and Ojasti 1980; Motta-Junior *et al.* 1994). In one Venezuelan location, land crabs (*Dilocarcinus*) were the most frequent stomach content dietary item (frequency 33%, volume 17%) in the rainy season (Bisbal and Ojasti 1980), and in the wetlands of Laguna Ibera (Corrientes), Argentina, aquatic birds were identified in 87% of 23 fox scats collected in the vicinity of the bird’s breeding colony (Parera 1996). Vertebrates were the most frequently encountered food item (69%) of 74 prey items identified in 22 scats collected at elevations of >2,600m in the eastern Colombian Andes (Delgado-V in press), but the least favoured food item (15%) in faeces collected from the lowland wooded savannahs of Marajó, Brazil, where cultivated and wild fruit (57%) and insects (86%) were more frequently encountered (Macdonald and Courtenay 1996). In Barlovento, Miranda state, Venezuela, the percentage volume of identifiable food items in nine fox stomachs was vegetable remains (80%), vertebrates (11%), and insects (5%) (Cordero-Rodríguez and Nassar 1999), whereas in Campinas, Brazil, the stomach contents of 19 road-killed foxes contained, by percent volume, fruit (44%), birds (17%), mammals (20%), arthropods (2%), fish (<1%), and amphibians (1%) (Facure and Monteiro-Filho 1996).

Foraging behaviour Crab-eating foxes are primarily nocturnal and crepuscular. They hunt individually, but most commonly as pairs; 1–3 adult-sized offspring may accompany them. Cooperative hunting apparently is rare, but was observed by a single pair in Masaguaral (Brady 1979). They will tolerate close proximity when foraging on concentrated, easily available food items such as turtle eggs, fruit, insects (e.g., termites), and sizeable carrion (e.g., goat carcass) (Montgomery and Lubin 1978; Brady 1979; O. Courtenay unpubl.). The young start to hunt with the parents at about six weeks old.

Hunting strategies include spring-pouncing to capture vertebrates, ground-level lateral head movements to snatch insects, and directional manoeuvres in chase of land crabs. Prior to consumption, Marajó foxes treat some food items (e.g., toads, eggs) with a series of shoulder blows with face up-turned. In the same region, foxes search for and consume small stones from specific open gravel sites presumably as a source of minerals (O. Courtenay pers. obs.). Foxes cache food items but do not regularly urine mark them (Brady 1979).

Crab-eating foxes probably act as seed dispersers of a range of wild and cultivated plant species, as indicated by the presence of germinating seeds in their scats. Examples include ”tusca” (*Acacia aroma*) and ”tala” (*Celtis tala*) in Chaco Serrano de Tucumán, Argentina (R. Varela pers. comm.), “butia” palm (*Butia capitata*) in Uruguay (Paz *et al*. 1995, R. Rodríguez-Mazzini and B. Espinosa pers. comm.), hovenia (*Hovenia dulcis*) in the Iguacu National Park (D. Rode pers. comm.), figs (*Ficus* spp.) in south-eastern Brazil (Motta-Junior *et al*. 1994), guava (*Psidium guineense*) in Maraca Ecological Station (M.R.P. Leite Pitman pers. comm.), and “miri” (*Humiria balsamifera*) and cashew (*Anacardium occidentale*) in Amazon Brazil (Macdonald and Courtenay 1996).

Damage to livestock or game Reports of poultry raiding by the crab-eating fox are widespread; however, there is no evidence that foxes represent a significant predator of lambs or cause of economic loss to farmers in wool-producing countries. In Colonia, Uruguay, predation by foxes (crab-eating fox and Pampas fox) contributed only 2.9% of the lamb mortality rate (0.4% of viable lamb mortality) (Cravino *et al*. 1997). Similarly, in Rio Grande do Sul, Brazil, only 1.9% of 1,468 lambs born in two months on six properties succumbed to fox predation, though foxes appeared to account for 57% of the 49 predatory attacks (Dotto *et al*. 2001). Sheep remains were identified in the stomach contents of 7% (1/14) crab-eating fox and 48.5% (16/33) Pampas fox examined in Rio Grande do Sul (M. Fabian pers. comm.). In Colonia 17% (1/6) crab-eating fox and 32% (5/16) Pampas fox examined had sheep remains in the stomach contents (Cravino *et al*. 2000: appendix 2).

The crab-eating fox predates incubating eggs of loggerhead sea turtles (*Caretta caretta*), hawksbill (*Eretmochelys imbricata*), olive ridley (*Lepidochelys olivacea*), and green turtles (*Chelonia mydas*) on Brazilian beaches including Praia do Forte, Bahia (Santos *et al*. 2000).

Adaptations

Crab-eating foxes are among the most versatile of canids, as evidenced by their ability to use a variety of habitat types and to exploit a number of different food sources.

Social behaviour

Monogamous. Social groups comprise a breeding pair and 1–5 offspring (older than one year). Family members travel around their home ranges usually in pairs or, if offspring are present, in loosely knit family groups. Separated foxes maintain contact by long distance, high-pitched, bird-like trill vocalisations. In Marajó, Brazil, territorial breeding pairs were located <100m apart on a mean 54% (n=7) of occasions during the period of activity, whereas close proximity of breeding adults and their adult-sized offspring varied from 7.2% to 93.3% between given pairings (Macdonald and Courtenay 1996).

Reported home range sizes are based on a variety of estimation techniques: in Marajó, Brazil, adult foxes occupied stable territories of 5.3km^2 (range=0.5–10.4km^2; n=21; restricted polygon estimates (RP); Macdonald and Courtenay 1996). In pasture/eucalyptus habitats in Minas Gerais, Brazil, an adult male’s range was 2.2km^2 (RP; O. Courtenay unpubl.); and in dry forest in Santa Cruz, Bolivia, an adult female and two adult males occupied mean home ranges of 2.2km^2 (range=1.1–2.8km^2; minimum convex polygon estimates (MCP); Maffei and Taber 2003). In the central Venezuelan llanos (Masaguaral), Brady (1979) reported a joint home range size of 1.0km^2 for an adult M/F fox pair (convex polygon estimate CP); a more recent study of three adult foxes and three adult fox pairs in the same site (Sunquist *et al*. 1989) showed dry season home ranges (mean=0.7km^{2}a; range=0.5–1.0km^2) to be generally larger than wet season home ranges (mean=0.7km^2; range=0.3–1.0km^2; MCP). Shrinkage of fox range sizes in the wet season is thought to be in response to changes in availability of dry fox habitats and/or prey density, a phenomenon also observed in Marajó Island, Brazil (Macdonald and Courtenay 1996).

Dispersing offspring established territories adjoining or adjacent to their natal range, an average distance between range centres of 2.4km (range=1.9–2.9km; n=4) (Macdonald and Courtenay 1996). Post dispersal, these foxes interacted amicably with kin members both inside and outside their natal range. Four male foxes returned to their natal range 3–13 months after their dispersal, in two cases following the death of their mate and in one case after breeding (Macdonald and Courtenay 1996).

Group latrines are not usual features of crab-eating fox society; however, a latrine comprising >72 scats visited by at least four adult-sized individuals was observed in Maraca Ecological Station, Brazil (M.R.P. Leite Pitman pers. comm.). Brady (1979) also reports the use of scat latrines located near resting sites.

Reproduction and denning behaviour

In the wild, litters are produced once per breeding year, with litters observed in September/October in Marajó (n=6 litters; Macdonald and Courtenay 1996); June in Minas Gerais, Brazil (n=2; O. Courtenay unpubl.); December in Brasilia district (F. Rodrigues pers. comm.); between December and February in the Venezuelan llanos, with lactating females seen in June (Montgomery and Lubin 1978, Brady 1979), and year round (estimated in January, May, July, and October) in Barlovento, state of Miranda, Venezuela, with lactating foxes recorded in August (Cordero-Rodríguez and Nassar 1999). A pregnant female was caught in July in south-eastern Brazil (K. Facure and A. Giaretta pers. comm.), and a pair with three cubs approximately three months old were seen in late November in Ipanema National Forest (SP) indicating parturition in August (F. Michalski pers. comm.). On emergence at 2–3 months, the mean litter size is 2.6 (range=2–3; n=6), with a male:female sex ratio of 5:1 (Macdonald and Courtenay 1996). It is not known whether the presence of a dominant female inhibits ovulation in subordinate females.

In captivity, births have been recorded in January, February, March, June and October, and foxes may breed twice annually at intervals of 7–8 months (Coimbra-Filho 1966; Brady 1978). The mean litter size is 4.5 (range=3–6; n=6) with male:female sex ratios of 3:6 (n=2 litters; Biben 1982) and 10:8 (range=5:1 to 1:4; n=4 litters; Brady 1978). The gestation period is 56 days (range=52–59 days), and neonatal weight 120–160g (Brady 1978).

Cub rearing is the responsibility of both breeding adults. Additional helpers have not been observed directly in the wild. However, the strong social affiliations between adults and dispersed returning offspring during subsequent breeding periods are strongly suggestive of sibling helpers (Macdonald and Courtenay 1996). In captivity, both sexes bring solid food (they do not regurgitate) to the young who consume solids from day 16–20 (Biben 1982, 1983; Brady 1978). The milk teeth start to erupt at day 14. Cubs first leave the den around day 28, but more regularly from day 45 when 1–1.5kg, at which time they develop the adult pelage. Lactation lasts for approximately 90 days (Brady 1978). Post-weaning dependency lasts for up to five months until sexual maturity which occurs at approximately nine months (Brady 1978). Offspring disperse when 18–24 months old (*cf*. Brady 1979), which in Marajó is between August and December.

Crab-eating foxes do not regularly excavate burrows, but rest above ground in dense undergrowth (including when rearing cubs), but occasionally adopt abandoned burrows of other animals such as armadillos (Brady 1979; Macdonald and Courtenay 1996; R. Cunha de Paula pers. comm.).

Competition

Potential competitors include the similarly sized hoary fox (2.5–4kg), Pampas fox (4–7kg), and larger-sized maned wolf (*Chrysocyon brachyurus*) (20–33kg). Interspecific divergence in dietary composition appears to allow these canid species to coexist (Juarez and Marinho 2002). Interspecific competition is unlikely to affect conservation status.

Mortality and pathogens

Natural sources of mortality One radio-tagged crab-eating fox was located inside the belly of a green anaconda (*Eunectes murinus*) in Emas National Park, Brazil (Jácomo and Silveira 1998), and an ocelot (*Leopardus pardalis*) was seen feeding on a carcass of this fox in Iguacu National Park (Crawshaw 1995). Domestic dogs are known to chase and kill foxes (Brady 1979), and cause cub deaths when dens are located in peri-urban areas. Likely natural predators include caimans (*Caiman yacare* and *C. latirostris*), jaguar (*Panthera onca*) and puma (*Puma concolor*), though no cases have been reported.

Persecution The fox is perceived as a pest of poultry throughout much of its range (and in Uruguay as a predator of lambs), and they are thus shot, trapped, and poisoned indiscriminately (Cravino *et al*. 1997). In Marajó, 83% of 12 fox deaths between 1988 and 1991 were due to local hunters (Macdonald and Courtenay 1996). The mortality rate in the Marajó population was 0.325 per year (95% C.L. 0.180–0.587), corresponding to a mean life expectancy of 3.1 years (95% C.L. 1.70–5.56). This is reflected in a young population with 57% of the population aged =12 months (1988–1989, n=25; 1994–1995, n=37), and high population replacement (turnover) rate of 0.84 per year (Courtenay 1998).

Hunting and trapping for fur Young foxes are often taken as pets, and at least one hunting household in Marajó, Brazil, admitted to consuming a fox on one occasion. Heavy trapping occurred in dry forest regions in Bolivia before the early 1980s when single pelts were worth US$30 (L. Maffei pers. obs.).

Road kills In north-eastern São Paulo state, Brazil, 29 deaths (male:female ratio of 1:1.5) were recorded along 13,500km of surveyed road between January 1981 and December 1983; the ratio of crab-eating to hoary fox carcasses was about 10:1 (J. Dalponte and J. Tavares-Filho unpubl.; see also Dalponte and Courtenay this volume).

Pathogens and parasites The effect of pathogen infection on population status has been rarely monitored; there are currently no reports of population declines. Rabies was confirmed in 18 foxes in Ceará, Brazil between 1980 and 1986, 11 of which were from the same region and within a six month period (Barros *et al*. 1989). Two confirmed fatal cases of canine distemper virus (CDV) were passively detected in crab-eating foxes, both in Brazil, including one male from Santa Genebra forest (Universidade de Campinas, Sao Paulo state) in 1989 (M.R.P. Leite Pitman pers. comm.), and one male in Lami Biological Reserve (Rio Grande do Sul) in 1999 (R. Printes pers. comm.). Domestic dogs were the suspected source of infection in both cases. By contrast, serological and clinical screening of 37 foxes that had substantial contact with domestic dogs with past exposure to CDV and canine parvovirus (CPV) in Marajó, Brazil, revealed no serological or clinical evidence of infection (Courtenay *et al*. 2001). Similarly, there was no evidence of alopecia consistent with scabies infection in 16 animals observed in the Gran Chaco, Bolivia, despite 20% (19/94) of the sympatric Pampas fox presenting confirmed or suspected infection with *Sarcoptes scabiei* (S. Deem pers. comm.).

The involvement of the crab-eating fox in the epidemiology of the protozoan parasite *Leishmania infantum* causing human and canine leishmaniasis has been the subject of extensive field studies in Marajó, Brazil (Courtenay *et al*. 1994, 2002; Courtenay 1998). Foxes with confirmed infection do not usually suffer infection-related mortality and are rarely infectious; thus it is unlikely that they are maintenance reservoirs in the absence of infectious domestic dogs (the known disease reservoir). Evidence suggests that infection spills over into foxes from infected sympatric dog populations (Courtenay *et al*. 2001, 2002). Hoary foxes have reportedly been infected with *L. infantum* and the rabies virus in Ceará, Brazil (Deane 1956; Barros *et al*. 1989); however, these animals were probably misidentified crab-eating foxes (Courtenay *et al*. 1996).

In captivity, crab-eating fox deaths have been attributed to infanticide, scabies, echinococcus infection, pulmonary disease, ectoparasites (scabies and fleas), and meningitis (Brady 1978; J. Cartes pers. comm.). Other documented parasites of free-ranging animals include *Hepatozoon canis* (Alencar *et al*. 1997) and various species of fleas (Cerqueira *et al*. 2000) and lice (Hopkins 1949, in Clutton-Brock *et al*. 1976).

Longevity The oldest recorded free-ranging fox was 9.2 years old, captured in Marajó, Brazil (O. Courtenay pers. obs.).

Historical perspective

The crab-eating fox is sometimes tamed as pets by indigenous and rural people (C. Baltzinger pers. comm.); there is limited talisman use, e.g., farmers in Ceará, Brazil, pin fox tails to animal sheds to warn off rabid bats (O. Courtenay pers. obs.).

Conservation status

Threats Potential threat of spill-over pathogenic infection from domestic dogs. In the Serra da Canastra National Park, Brazil, crab-eating foxes raid human refuse dumps in close company with unvaccinated domestic dogs along park boundaries (R. Cunha de Paula pers. comm.).

Commercial use No direct commercial value as furbearer due to the unsuitability of the fur which is coarse and short; however, pelts are sometimes traded as those of the South American grey fox in Argentina, and as those of the latter species and the Pampas fox in Uruguay (Cravino *et al*. 1997; A. Farias pers. comm.). Current illegal trade is small as the probable consequence of low fur prices; in Paraguay, for example, no illegal fox pelts were confiscated from 1995 to 2000 (J. Cartes pers. comm.).

Occurrence in protected areas Occurs in a large number of protected and unprotected areas across its geographical range.

Protection status CITES – Appendix II.

In Argentina, the crab-eating fox was considered "not endangered" by the 1983 Fauna and Flora National Direction (resolution 144), and its exploitation and commercial use was forbidden in 1987 (A. Novaro pers. comm.; A. Farias pers. comm.); currently listed as "potentially vulnerable" in the recent Argentine Red Data Book (Diaz and Ojeda 2000). In Bolivia, it is considered common and is, therefore, excluded from the Bolivian Red Data Book (Ergueta and Morales 1996), as it is from the Brazilian (Biodiversitas 1998) and Colombian (Rodríguez 1998) lists of threatened species.

Current legal protection There is no specific protective legislation for this species in any country, though hunting wildlife is officially forbidden in most countries. Generally, there is no specific pest regulatory legislation for the crab-eating fox, but it is strongly disliked locally as a pest of livestock (poultry and lambs) leading to illegal hunting and consequential sales of pelts. In some countries, pest control is limited by specific quotas (without official bounties), although the system is often ignored, abused, or not reinforced (J. Carvino pers. comm.; A. Soutullo pers. comm.). In Uruguay, hunting permits have not been issued since 1989 on the basis that lamb predation by foxes is negligible (Cravino *et al*. 1997, 2000).

Conservation measures taken Nothing proposed. No protection required.

Occurrence in captivity

Present in many zoos and private collections throughout South America where it generally breeds well and offspring survival rates are high.

Current or planned research projects

R. de Paula (Associação Pró-Carnívoros, São Paulo, Brazil) is studying the interactions between wild and domestic canids in Serra da Canastra National Park, Brazil.

C. Costa and O. Courtenay (Federal University of Piauí, Brazil and University of Warwick, UK) are conducting epidemiological studies on the role of the crab-eating fox in the transmission of zoonotic leishmaniasis.

J. Dalponte, E. Lima and R. Jorge (Serviço Social do Comércio/Fundação Pró-Natureza, Brazil) are investigating the diet and parasites of sympatric carnivores in Reserva Particular do Patrimônio Natural do Serviço Social do Comércio, Pantanal, Mato Grosso, Brazil.

L. Silveira and J. Marinho-Filho (Brasilia University, Brazil) are studying the ecology of sympatric carnivores in Emas National Park, Goias, Brazil.

S. Marques and T. da Santos (Furnas Centrais Elétricas, Brazil) are conducting radio-telemetry studies on the crab-eating fox and hoary fox in Guimarães region of Mato Grosso, Brazil.

Gaps in knowledge

Little is known of population status, particularly in lowland Amazon forest. The significance of infection and disease in population regulation, and behavioural ecology in the context of resource dispersion, are of interest.

Core literature

Berta 1982, 1987; Brady 1978, 1979; Courtenay *et al*. 1994, 1996, 2001, 2002; Macdonald and Courtenay 1996; Maffei and Taber 2003; Montgomery and Lubin 1978; Sunquist *et al*. 1989.

Reviewers: Julio Dalponte, Carlos A. Delgado-V, M. Renata P. Leite Pitman, Mauro Lucherini, Anibal Parera. **Editors:** Michael Hoffmann, Claudio Sillero-Zubiri.

3.3 Maned wolf
Chrysocyon brachyurus (Illiger, 1815)
Near Threatened (2004)

M. Rodden, F. Rodrigues and S. Bestelmeyer

Other names

French: loup à crinière; **German:** mähnenwolf; **Portuguese:** lobo guará, guará; **Spanish:** aguará guazú (Argentina), lobo de crin, borochi (Bolivia).

Taxonomy

Canis brachyurus Illiger, 1815. Abh. Phys. Klasse K. Pruess. Akad. Wiss., 1804–1811 :121. Type locality: not specified, but later listed by Cabrera (1958) as "los Esteros del Paraguay".

The species was originally placed in the genus *Canis*, but is now widely included in the genus *Chrysocyon* (Langguth 1975; Stains 1975; Van Gelder 1978; Berta 1987; Wozencraft 1993).

Chromosome number is 2n=76, very close to that of *Canis* (2n=78). A comparison of chromosome morphology and banding patterns suggest that the maned wolf and grey wolf (*Canis lupus*) share a common wolf-like ancestor (Wayne *et al.* 1987a).

Description

The maned wolf is hard to confuse with any other canid due to its long, thin legs, long reddish orange fur and large ears. The English common name comes from the mane-like strip of black fur running from the back of the head to the shoulders, averaging 470mm in length. Muzzle black, throat white, inner ears white, forelegs black and most of distal part of hindlegs black. An average of 44% of the tail length is white at the distal end, but the amount varies between individuals (from 17–66% of the tail length). No under fur present. The adult dental formula is 3/3-1/1-4/4-2/3=42. See table 3.3.1 below for body measurements.

Table 3.3.1. Combined body measurements for the maned wolf from Serra da Canastra National Park, Brazil (Dietz 1984), Emas National Park, Brazil (Silveira 1999; Bestelmeyer 2000) and Águas Emendadas Ecological Station, Brazil (F. Rodrigues unpubl.).

HB	1,058mm (950–1150) n=23
T	446mm (380–500) n=22
E	163mm (135–200) n=23
WT	25.0kg (20.5–30) n=16

Rogerio Cunha

Adult female maned wolf. Serra da Canastra National Park, Minas Gerias State, Brazil, 2001.

Figure 3.3.1. Current distribution of the maned wolf.

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Subspecies Monotypic (Dietz 1984).

Similar species Juveniles could possibly be confused with the crab-eating fox (*Cerdocyon thous*) because of their similar black and grey colouring.

Current distribution

The maned wolf inhabits the grasslands and scrub forest of central South America from the mouth of the Parnaiba River in north-eastern Brazil, south through the Chaco of Paraguay into Rio Grande do Sul State, Brazil, and west to the Pampas del Heath in Peru (Dietz 1985) (Figure 3.3.1. Beccaceci (1992a) found evidence of maned wolves in Argentina as far south as the 30th parallel, and a sighting in the province of Santiago del Estero was recently reported (Richard *et al.* 1999). They probably range into northern Uruguay. Their presence in this country was confirmed through a specimen trapped in 1990 (Mones and Olazarri 1990), but there have not been any reports of sightings since that date (S. Gonzalez pers. comm.).

Range countries Argentina, Bolivia, Brazil, Paraguay, Peru, Uruguay (Dietz 1985; Mones and Olazarri 1990; Beccaceci 1992a).

Relative abundance

With their primarily solitary habits and large home ranges (see Social behaviour), maned wolves are found in low densities throughout the range. In some areas of central Brazil, they appear to be more common, but increasing habitat fragmentation may threaten the viability of wild populations (Table 3.3.2).

Estimated populations/relative abundance and population trends

Table 3.3.2. The status of maned wolves in various range countries. (Population trend: D=declining, ?=unknown, Ex=extinct).

Country	Population size	Trend
Argentina	1,000?	D?
Bolivia	>1,000	?
Brazil	?	?
Peru	?	?
Paraguay	?	?
Uruguay	Ex?	?

Habitat

Maned wolves favour tall grasslands, shrub habitats, woodland with an open canopy (cerrado), and wet fields (which may be seasonally flooded). Some evidence indicates that they may prefer areas with low to medium shrub density (Bestelmeyer 2000). Maned wolves are also seen in lands under cultivation for agriculture and pasture. Daytime resting areas include gallery forests (Dietz 1984), cerrado and marshy areas near rivers (Bestelmeyer 2000; F. Rodrigues unpubl.). There is some evidence that they can utilise cultivated land for hunting and resting (A.

Jácomo and L. Silveira unpubl.), but additional studies are essential in order to quantify how well the species tolerates intensive agricultural activity.

Food and foraging behaviour

Food Omnivorous, consuming principally fruits and small- to medium-sized vertebrates. Numerous authors (Dietz 1984; Carvalho and Vasconcellos 1995; Motta-Júnior *et al*. 1996; Azevedo and Gastal 1997; Motta-Júnior 1997; Rodrigues *et al*. 1998; Jácomo 1999; Santos 1999; Silveira 1999; Juarez and Marinho 2002; Rodrigues 2002) have investigated the diet of the maned wolf. These studies have all found a wide variety of plant and animal material in the diet, with about 50% of the diet comprising plant material and 50% animal matter (Table 3.3.3). The fruit *Solanum lycocarpum* grows throughout much of the range and is a primary food source; other important items include small mammals (*Caviidae, Muridae, Echimydae*) and armadillos, other fruits (*Annonaceae, Myrtaceae, Palmae, Bromeliaceae*, and others), birds (*Tinamidae, Emberizidae* and others), reptiles and arthropods. Although the frequency of plant and animal items found in faecal samples is approximately equal (Table 3.3.2), the biomass of animal items is usually greater than that of plant items (Motta-Júnior *et al*. 1996; Santos 1999; Rodrigues 2002). Certain items, such as rodents and *Solanum,* are consumed year round, but the diet varies with food availability. At least occasionally, pampas deer (*Ozotoceros bezoarticus*) are also consumed (Bestelmeyer and Westbrook 1998). In Jácomo's (1999) study, deer appeared in 2.4% of 1,673 samples analysed.

Foraging behaviour Nocturnal and crepuscular, maned wolves may forage for up to eight consecutive hours, feeding on everything they can catch and every ripe fruit they detect (Bestelmeyer 2000; L. Silveira and A. Jácomo unpubl.). Strategies for hunting animal prey include: 1) stalking prey with a final pounce; 2) digging after burrowing animals; 3) leaping into the air to capture flying birds and insects, and 4) sprinting after fleeing deer. Approximately 21% of all hunting attempts end with the successful capture of prey, and the strategies do not differ in their success rates (Bestelmeyer 2000). Beccaceci (1992a) and C. Silva (unpubl.) recorded maned wolves feeding on coypus (*Myocastor coypus*) that were caught in traps set by hunters. L. Silveira and A. Jácomo (unpubl.) observed maned wolves scavenging opportunistically on road-kill carcasses.

Damage to livestock and game The maned wolf has been known to prey on domestic animals, especially chickens (Dietz 1984). However, poultry remains were found in only 0.6–1.4% of analysed scat samples (Dietz 1984; Motta-Júnior *et al*. 1996; Rodrigues 2002).

Adaptations

The maned wolf's long legs, large ears and pacing gait are considered adaptations for standing in and moving above tall grasses to hear small prey below. The long legs also enable maned wolves to run swiftly, at least occasionally tracking down fleeing pampas deer (Bestelmeyer and Westbrook 1998).

Table 3.3.3. Frequency of classes of food items in the maned wolf's diet in 11 places of the Cerrado of Brazil. (1) Juarez and Marinho 2002; (2) Dietz 1984; (3) Motta-Júnior *et al*. 1996; (4) – Motta-Júnior 1997; (5) Azevedo and Gastal 1997; (6) Jácomo 1999; (7) Silveira 1999; (8) Santos 1999; (9) Carvalho and Vasconcellos 1995; (10) Rodrigues 2002.

	Locality										
Items	**Faz. Rio Pratudão/ BA (1)**	**P.N.S. da Canastra/ MG (2)**	**Faz. Água Limpa/ DF (3)**	**E.E. de Jataí/ SP (4)**	**Faz. Salto e Ponte/ MG (4)**	**Campus da UFSC AR/ SP (4)**	**APA Gama-Cab Veado/ DF (5)**	**P.N. Emas/ GO (6, 7)**	**Faz São Luis/ MG (8)**	**Santa Bárbara/ SP (9)**	**Águas Emendadas E.E./ DF (10)**
Solanum lycocarpum	31.9	32.6	25.7	15.6	31.0	24.4	23.1	18.0	29.3	32.3	27.4
Miscellaneous fruit	9.4	7.3	9.2	14.7	2.8	10.2	10.7	36.3	7.8	6.3	24.2
Grass	9.4	11.1	11.8	14.3	20.0	12.8	13.8	3.2	17.2	9.4	8.2
Subtotal – vegetable	**50.7**	**51.0**	**46.7**	**44.6**	**53.8**	**47.4**	**47.6**	**57.5**	**54.3**	**48.0**	**59.8**
Arthropods	3.6	5.7	2.0	5.5	2.1	5.1	23.1	1.6	12.1	7.3	5.8
Reptiles	1.6	0.3	2.6	3.4	4.8	1.3	–	3.1	1.8	–	0.1
Birds	8.4	12.0	13.8	8.4	10.4	7.7	10.7	11.1	11.1	12.5	10.1
Eggs	–	–	–	–	–	–	3.1	0.2	–	–	0.4
Rodents & marsupials	33.0	26.6	25.0	32.1	27.5	34.6	15.4	24.0	14.1	29.2	16.7
Armadillos	1.6	3.1	9.2	2.9	–	1.3	–	2.1	6.3	1.0	6.7
Other mammals	1.0	0.7	0.7	2.1	1.4	1.3	–	0.2	0.5	–	0.5
Other vertebrates	–	0.6	–	1.0	–	1.3	–	–	0.3	2.1	–
Subtotal – animal	**49.2**	**49.0**	**53.3**	**55.4**	**46.2**	**52.6**	**52.3**	**42.3**	**46.2**	**52.1**	**40.3**
No. of occurrences	191	2,056	304	237	145	78	65	4,540	396	96	901
No. samples	70	740	104	61	46	21	20	1,673	150	?	328

Social behaviour

Maned wolves appear to be facultatively monogamous. Pairs are not often seen together, although researchers have observed pairs resting, hunting and travelling together.

Dietz (1984) found that home ranges of pairs in Serra da Canastra National Park varied between 21.7 and 30.0km² (average 25.2 ± 4.4km²; n=3 pairs). The home ranges of individuals studied in other areas are larger, ranging from 15.6–104.9km² (average 57.0 ± 34.3km², n=5) in Águas Emendadas Ecological Station (Rodrigues 2002) and 4.7–79.5km² (average 49.0 ± 31.8km², n=5) in Emas National Park (Silveira 1999). Home range boundaries appear stable over time and are defended against adjacent pairs, although there may be overlap at the edge of the home range (Rodrigues 2002). Males and females do not differ in their rates of scent marking. Termite mounds are preferentially used as urine-marking sites, and more marks are placed on the upwind side of objects than on the downwind side (Bestelmeyer 2000). Floater individuals without territories appear to move along territory boundaries (Dietz 1984) and do not scent mark (Bestelmeyer 2000).

The most frequently heard vocalisation is the roar-bark, a loud vocalisation that has been heard during all times of the day and night and at all times of the year (Brady 1981; Bestelmeyer 2000; L. Silveira and A. Jácomo unpubl.).

Reproduction and denning behaviour

Female maned wolves enter oestrus once per year, for approximately five days. Peak breeding season is from April to June. There are numerous published accounts of breeding behaviour in captivity, but little information is available from wild populations (Silveira 1968; Encke 1971; Brady and Ditton 1979; Bartmann and Nordhoff 1984; Dietz 1984; Rodden *et al*. 1996; Bestelmeyer 2000). In captivity, the frequency of vocalisations (roar-bark) and scent marking increases during the weeks prior to mating (Brady 1981), and the amount of time a pair spends in close proximity increases significantly during the oestrous period. Courtship is characterised by frequent approaches, mutual anogenital investigation, and playful interactions. Mounting may occur frequently during oestrus; successful breeding includes a copulatory tie that may last several minutes. In Emas National Park, Brazil, a breeding pair observed at night for approximately 3.5 hours foraged together and vocalised frequently whenever one partner was out of sight. The male marked with urine or faeces wherever the female marked. A breeding display lasting 10 minutes included a two-minute copulatory tie. After copulation, the pair continued to forage together (L. Silveira and A. Jácomo unpubl.).

Gestation length is approximately 65 days, with the majority of births occurring from June to September, during the dry season. One female gave birth to three pups in a bed of tall marsh grass. At 45 days of age the pups had not yet left the den and weighed 2.0kg (female) and 2.25kg (males) (L. Silveira and A. Jácomo unpubl.). All dens found in the wild have been above ground, gaining shelter from natural features such as the canopies of shrubs, rock crevices, gullies, and dry mounds in marshy, tall-grass areas.

In captivity, an analysis of 361 births indicated that parturition peaks in June (winter), and the average litter size is 3 (range=1–7; Maia and Gouveia 2002). Birth weights average 390–456g (n=8). In captive animals, nursing bouts begin to decline after the first month, and weaning is complete by around 15 weeks. Pups begin consuming solids regurgitated by the parents at around four weeks of age; regurgitation has been recorded up to seven months after birth (Brady and Ditton 1979). Females with 7–14-week-old pups have been observed hunting for continuous periods of eight hours over 3km from their den sites and pups (Bestelmeyer 2000; F. Rodrigues unpubl.). Pups stay in the mother's home range for approximately one year, when they begin to disperse. Juveniles attain sexual maturity at around the same time, but usually do not reproduce until the second year.

One of the many unknown aspects of maned wolf behaviour is the role the male plays in rearing pups. Pups have been seen accompanied by two adults (Dietz 1984), and a female with pups was seen accompanied by a male many times (F. Rodrigues unpubl.). In captivity, males increase pup survival rates and are frequently observed regurgitating to pups and grooming pups (Bestelmeyer 2000). Nonetheless, direct confirmation of male parental care in the wild is still lacking.

Competition

No direct competition has been observed with other carnivores sharing maned wolves' primary habitat, including the bush dog (*Speothos venaticus*), crab-eating fox (*Cerdocyon thous*), hoary fox (*Pseudalopex vetulus*), pampas fox (*P. gymnocercus*), puma (*Puma concolor*), jaguar (*Panthera onca*), pampas cat (*Oncifelis colocolo*), jaguarundi (*Herpailurus yaguarondi*), crab-eating raccoon (*Procyon cancrivorus*), hog-nosed skunk (*Conepatus semistriatus*), and grison (*Galictus cuja* and *G. vittata*). The diet of the maned wolf significantly overlaps with that of the crab-eating fox, and to a lesser extent with that of the smaller hoary fox (Silveira 1999; Juarez and Marinho 2002). However, maned wolves can take larger prey than either fox species (Bestelmeyer and Westbrook 1998; Silveira 1999; Juarez and Marinho 2002). Evidence from northern Argentina indicates that the maned wolf and pampas fox may eat many of the same food items (L. Soler pers. comm.). Packs of domestic dogs may also compete for prey with maned wolves.

Mortality and pathogens

Natural sources of mortality Because of its size, other carnivores do not usually prey upon the maned wolf, although there is a record of predation by a puma (M. Reis pers. comm.). In areas inhabited by humans, domestic dogs have been observed pursuing and killing maned wolves (A. Hass pers. comm.; F. Rodrigues unpubl.; and see also Threats).

Persecution Maned wolves are not viewed as a serious threat to livestock, although they may occasionally be shot when caught raiding chicken pens. Diet studies indicate that domestic chickens have little importance in their diet, but this relationship needs to be studied more thoroughly.

Hunting and trapping for fur The pelt of the maned wolf is of no value to the fur trade.

Road kills Road kills are one of the main causes of mortality of maned wolves, especially for young individuals and sub-adults (Beccaceci 1992a; Vieira 1996; Silveira 1999; Rodrigues 2002; L. Soler pers. comm.). Road kills on highways are responsible for mortality of approximately half of the annual production of pups in some reserves (Rodrigues 2002).

Pathogens and parasites The giant kidney worm, *Dioctophyma renale*, which infects wild and captive maned wolves in South America, is considered a serious health threat (Matera *et al.* 1968; Beccaceci 1990). Beccaceci (1992b) found evidence of tuberculosis in a wild specimen, and hemo-parasites have also been recorded (F. Vinci pers. comm.).

In captivity, maned wolves are susceptible to typical canine viruses, including canine distemper, parvovirus, rabies, and adenovirus. Infectious diseases and digestive disorders are among the main causes of death among pups 31–120 days old (Maia and Gouveia 2002). Ovarian tumours are frequently found in adult females (Munson and Montali 1991). Cystinuria, a metabolic disease of the renal system, is prevalent in both captive and wild maned wolves, although its impact on wild populations is not known (Bush and Bovee 1978; Bovee *et al.* 1981; Mussart and Coppo 1999).

Longevity In captivity, maned wolves may live up to 16 years. To the best of our knowledge, there is no information available for longevity in the wild.

Historical perspective

Throughout its range, attitudes towards the maned wolf range from tolerance to fear and dislike. Native folklore and superstitions contribute to the attitudes of local people. For example, in Brazil certain parts of the maned wolf are used in local medicines to cure bronchitis and kidney disease or as a treatment for snakebite. Other body parts are believed to bring good luck (C. Silva pers. comm.). In Bolivia, cowboys believe that sitting on the pelt of a maned wolf will protect them from bad luck (L. Sainz pers. comm.).

Although it is one of the largest carnivores in the grasslands, the species is apparently not well known to a large segment of the population. In a study of visitors at Brasilia Zoo, which is surrounded by cerrado, 32% of 30 adults and 30 children surveyed did not recognise the maned wolf when shown a photograph of the animal (Bizerril and Andrade 1999).

Conservation status

Threats The most significant threat to maned wolf populations is the drastic reduction of habitat, especially due to conversion to agricultural land (Fonseca *et al.* 1994). The cerrado has been reduced to about 20% of its preserved original area (Myers *et al.* 2000), and only 1.5% of it is currently protected (Ratter *et al.* 1997). In addition, habitat fragmentation causes isolation of sub-populations. Many maned wolves are killed on the nation's roads. Highways border many of the Conservation Units of the Brazilian cerrado, and drivers often do not respect speed limits. Reserves close to urban areas often have problems with domestic dogs. These dogs pursue and may kill maned wolves and can also be an important source of disease. Domestic dogs also possibly compete with the maned wolf for food. Interactions with humans also pose a threat to the maned wolf. Diseases, such as those mentioned above, can be important causes of mortality in the wild, but there is very little information available about the health of wild populations. In areas where there are domestic dogs, the problem is certainly greater.

Commercial use None. Indications are that the use of maned wolf parts for medicinal purposes does not involve any sort of large-scale commercial transactions and is confined to native folk medicine (see Historical perspective).

Occurrence in protected areas

— *Argentina*: Chaco National Park, Mburucuyá National Park, Iberá Provincial Reserve, San Juan de Poriahú, San Alonso Private Reserves, Río Pilcomayo National Park, El Bagual Private Reserve, Campo Bouvier, La Esmeralda Reserve, and possibly La Loca Provincial Reserve;

— *Bolivia*: Estación Biológica del Beni, Parque Nacional Noel Kempff Mercado, Parque Nacional and Area Natural de Manejo Integrado Otuquis and San Matías, Parque Nacional Madidi. May occur in Parque Nacional Kaa Iya del Gran Chaco and Territorio Indígena & Parque Nacional Isiboro Sécure;

— *Brazil*: occurs in the following National Parks: Brasília, Emas, Chapada dos Veadeiros, Araguaia, Serra da Canastra, Grande Sertão Veredas, Serra do Cipó,

Chapada dos Guimarães, Serra da Bodoquena, Ilha Grande, Aparados da Serra, Serra Geral, São Joaquim, Serra da Bocaina, Itatiaia. Ecological Reserve Roncador, Ecological Stations Águas Emendadas, Uruçuí-Una, Serra das Araras, Pirapitinga and Taiamã. State Parks: Ibitipoca, Itacolomi, Nascentes do Rio Taquari, Caracol, Iatapuã, Turvo, Cerrado, Vila Velha;
— *Paraguay*: Mbaracayu Forest Biosphere Reserve;
— *Peru*: Pampas del Heath?

Protection status CITES – Appendix II.
Protected in Argentina (classified as Endangered on the Red List); and included on the list of threatened animals in Brazil (Bernardes *et al.* 1990).

Current legal protection Hunting is prohibited in Brazil, Paraguay and Bolivia. Maned wolves are protected by law in many parts of their range, but enforcement is frequently problematic. Included in the United States Endangered Species list.

Conservation measures taken We are not aware of any conservation actions specific to the maned wolf. However, they are the beneficiaries of broader attempts to protect the cerrado (for example, recent actions to reduce the impact of road kills in Brasilia).

Occurrence in captivity

Records of captive maned wolves have been kept in an International Studbook, which was maintained by the University of Heidelberg from 1973 to 1978, and since 1979 by Frankfurt Zoo, Germany. As of 31 December 2003, 146 institutions reported a total of 431 maned wolves in captivity, including 208 males and 222 females. Cooperative breeding programmes exist among zoos in Europe, North and South America, and there has been considerable research on reproductive behaviour and physiology, nutrition, diseases and other husbandry issues. There are no known reintroduction projects currently underway. Individuals are sometimes kept as pets or in private collections.

Current or planned research projects

In Brazil, there are several ecological studies underway, investigating aspects such as home range, feeding ecology, behaviour and reproductive behaviour, including studies by: F. Rodrigues, Rogério Cunha and Eduardo Eizirik (Associação Pró-Carnívoros), Adriana Hass (CNPq) and F. Vinci (União de Ensino do Planalto Central) in Serra da Canastra National Park; F. Rodrigues (Associação Pró-Carnívoros) in Distrito Federal; A. Jácomo and L. Silveira (Associação Pró-Carnívoros) in Goiás; J. Carlos Motta-Júnior (Universidade de São Paulo) in São Paulo and Minas Gerais; L. Fernando Silva (Fundação ZooBotânica de Belo Horizonte) in Minas Gerais; J. Eduardo Mantovani (Instituto Nacional de Pesquisas Espaciais) in São Paulo; C. Silva (Instituto Brasileiro de Meio Ambiente) in Paraná.

Studies of genetic variability are being done by J. Roberto Moreira (Centro Nacional de Recursos Genéticos / Empresa Brasileira de Agropecuária) and M. Nazaré Clautau (Universidade de Brasília). J. Roberto Moreira is also revising the distribution of the species in Brazil.

In Argentina, A. Soria and S. Heinonen Fortabat (Delegación A.P.N.) have been conducting surveys of maned wolves in three National Parks: Pilcomayo, Chaco, and Mburucuyá. L. Soler (HUELLAS, and Grupo de Ecología Comportamental de Mamíferos, GECM) has proposed a study in the Mburucuyá National Park in the province of Corrientes, to examine habitat use and availability and to census the carnivore species utilising the park and surrounding areas. The attitudes of local people will be a major focus of the study. Although HUELLAS and Oikoveva (a French NGO) are providing partial funding, additional support is being sought. S. Gonzalez (División Citogenética, Universidad de la República Oriental del Uruguay) and M. Beccaceci (Universidad del Salvador) have also proposed a study of the genetic variability of wild populations in Argentina.

In Bolivia, additional studies of canid ecology in eastern Bolivia have been proposed (L. Emmons, Smithsonian National Museum of Natural History, and L. Sainz, Museo de Historia Natural Noel Kempff Mercado).

A captive study of maned wolf nutritional requirements (M. Allen and S. Childs), supported by the American Zoo and Aquarium Association's Maned Wolf Species Survival Planâ, the National Zoological Park, and Purina Mills, is underway. A second captive study focusing on the modes of inheritance of cystinuria, is supported by the AZA MWSSP, University of Pennsylvania, and Morris Animal Foundation (J. Kehler and P. Henthorn, University of Pennsylvania).

Gaps in knowledge

Population surveys throughout the species' range are needed. The impact of human encroachment on suitable habitat is not clearly understood, and the suitability of agricultural land as maned wolf habitat needs to be investigated. The impact of disease processes on wild populations is not well understood.

Core literature

Bestelmeyer 2000; Brady and Ditton 1979; Dietz 1984, 1985; Jácomo 1999; Motta-Junior *et al.* 1996; Silveira 1999.

Reviewers: Marcelo Beccaceci, Otávio Borges Maia, James Dietz, Louise Emmons, Anah Jácomo, Leandro Silveira, Lucía Soler. **Editors:** Michael Hoffmann, Claudio Sillero-Zubiri.

3.4 Culpeo
Pseudalopex culpaeus (Molina, 1782)
Least Concern (2004)

J.E. Jiménez and A.J. Novaro

Other names

English: Andean fox; **French:** Culpeau; **German:** Andenfuchs; **Spanish:** zorro colorado (Argentina); zorro Andino (Bolivia, Peru); zorro culpeo (Chile); lobo Andino (Ecuador); **Indigenous names:** Aymara: khamake (Peru, Bolivia, Chile); Mapuche: culpem (Chile, Argentina); Quechua: atoj (Peru).

According to Molina (1782 cited in Osgood 1943: 64) the name culpeo derives from the Mapuche word 'culpem' that means 'madness', because individuals expose themselves to hunters that easily kill them.

Taxonomy

Canis culpaeus Molina, 1782. Sagg. Stor. Nat. Chile, p. 293. Type locality: "Chili" restricted by Cabrera (1931) to the "Santiago Province" (*c.*71°00'W, 33°30'S; Osgood 1943, Novaro 1997a).

Due to their wide range in distribution, high phenetic variability and scarcity of material, the taxonomy of the South American canids has been a topic of much debate. During the last three decades, Clutton-Brock *et al.* (1976) and Wozencraft (1989) placed the culpeo in the genus *Dusicyon*, Langguth (1975) and Van Gelder (1978) in *Canis*, while Berta (1987), Wozencraft (1993) and Tedford *et al.* (1995) considered it as *Pseudalopex*. Finally, Zunino *et al.* (1995) proposed use of the genus *Lycalopex*. As a result, the taxonomic status of the culpeo is still unresolved (Novaro 1997a).

The culpeo separated from their closest relative, the chilla (*P. griseus*) between 250,000 and 500,000 years ago. Morphological evolution of these foxes, relative to other species, has been faster than genetic changes (Wayne *et al.* 1989). In fact, in both species, some populations within species are genetically more distinct than populations between species (Yahnke *et al.* 1996).

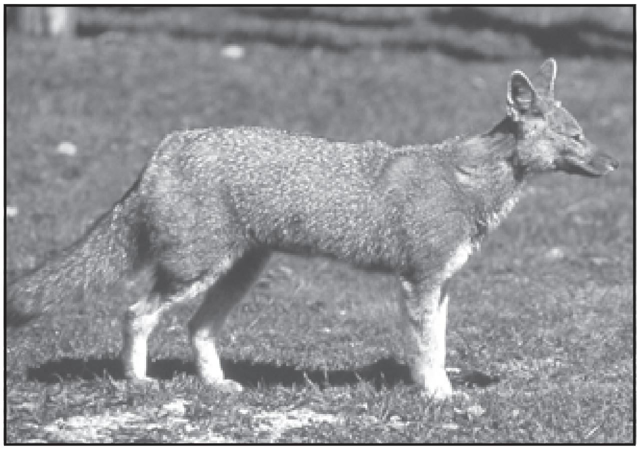
Chromosome number: 2n=74 (Vitullo and Zuleta 1992).

Description

The culpeo is the largest fox in the genus (Novaro 1997a; Table 3.4.1) and among South American canids, is only smaller than the maned wolf (*Chrysocyon brachyurus*). The head is broad and the muzzle is wide, which gives the culpeo a strong appearance. The species is dimorphic, males being larger and on average 1.5 times heavier than females (Johnson and Franklin 1994a; Travaini *et al.* 2000). It has a white to light tawny chin and body underparts. Dorsal parts of the head, including the ears and neck, as well as legs and flanks are tawny or rufous. The rump is darker, ranging in colour from tawny to dark

Table 3.4.1. Body measurements for the culpeo.

	Peru highlands (B.D. Patterson pers. comm.)	**Salar de Punta Negra** (highland desert, northern Chile) (M. Parada pers. comm.)	**Reserva Nacional Las Chinchillas** (matorral, north central Chile) (J.E. Jiménez unpubl.)	**Neuquén** (steppe, north Patagonia, Argentina) (A.J. Novaro unpubl.)	**Parque Nacional Torres del Paine** (steppe, south Patagonia, Chile) (W.E. Johnson pers. comm..)
HB male	700mm (613–752) n=6	715mm (660–790) n=8	586mm (545–635) n=6	879mm (810–925) n=11	729mm (445–840) n=6
HB female	680mm (675–685) n=2	641mm (490–705) n=8	675mm (610–720) n=4	832.3mm (765–890) n=15	756mm (742–770) n=4
T male	354mm (305–408) n=6	380mm (350–415) n=8	381mm (360–415) n=6	452mm (425–493) n=11	433mm (400–465) n=6
T female	360mm (340–380) n=2	362mm (310–400) n=8	355mm (340–370) n=4	414mm (370–450) n=15	397mm (380–410) n=4
HF male	163mm (153–175) n=6	156mm (144–170) n=10	149mm (145–152) n=6	173mm (160–184) n=9	174mm (165–180) n=6
HF female	152mm (149–155) n=2	150mm (137–157) n=8	139mm (130–145) n=4	162mm (145–177) n=13	155mm (148–160) n=4
E male	94mm (90–98) n=6	110mm n=1	84mm (79–88) n=6	89mm (82–95) n=11	91mm (85–96) n=6
E female	88mm (85–90) n=2	90mm n=1	83mm (79–87) n=4	82mm (75–90) n=15	83mm (78–88) n=4
WT male		6.5kg (5.4–8.6) n=10	4.0kg (3.4–4.9) n=3	11.0kg (8.5–12.3) n=11	10.5kg (7.3–13.8) n=6
WT female		5.4kg (4.6–6.8) n=9	4.6kg (3.9–5.1) n=4	8.5kg (7.4–10.0) n=15	7.8kg (6.8–9.0) n=4



Enrique Couve Montané

Culpeo, age and sex unknown. Magallanes, southern Chile.

grey, according to the subspecies. The tail is long and bushy of grey colour with a black tip and a dark dorsal patch near its base. Feet and legs are bright tawny with no black (Osgood 1943). Specimens from northern ranges (i.e., *P. c. andina*) are lighter in colour (Osgood 1943; J.E. Jiménez pers. obs.). Compared to the chilla, culpeos have longer canines and shorter second molars (Wayne *et al.* 1989). The dental formula is 3/3-1/1-4/4-2/3=42 (Novaro 1997a).

Subspecies Six subspecies are recognised (Cabrera 1931).
— *P. c. andina* (altiplano)
— *P. c. culpaeus* (central Chile and west central Argentina)
— *P. c. lycoides* (island of Tierra del Fuego)
— *P. c. magellanica* (Magallanes and Patagonia)
— *P. c. reissii* (Andes of Ecuador)
— *P. c. smithersi* (mountains of Córdoba, Argentina)

Similar species Chilla (*P. griseus*): sympatric in Chile and northern, western, and southern Argentina; smaller, with dark chin and dark patch on the thighs. Pampas fox (*P. gymnocercus*): closest in size to the culpeo, but apparently not sympatric with it. Crab-eating fox (*Cerdocyon thous*): sympatric in southern Bolivia (L. Maffei pers. comm.); smaller with darker coat.

Current distribution

The culpeo is distributed along the Andes and hilly regions of South America from Nariño Province of Colombia in the north (Jiménez *et al.* 1995) to Tierra del Fuego in the south (Markham 1971; Redford and Eisenberg 1992) (Figure 3.4.1). It ranges down to the Pacific shoreline in the desert of northern Chile (Mann 1945; J.E. Jiménez pers. obs.), south to about Valdivia (Osgood 1943), and then again in Magallanes. On the eastern slopes of the Andes, the culpeo is found in Argentina from Jujuy Province in the North, reaching the Atlantic shoreline from Río Negro and southwards. This extended eastward distribution is relatively recent and was apparently favoured by sheep ranching (Crespo and De Carlo 1963; Novaro 1997a). See also Relative Abundance.

Range countries Argentina, Bolivia, Chile, Colombia, Ecuador, Peru (Cabrera 1958; Novaro 1997a).

Relative abundance

Due to conflicts with humans (i.e., preying upon poultry and livestock; Crespo and De Carlo 1963; Bellati and von Thüngen 1990) and because of its value as a furbearer, the culpeo has been persecuted throughout its range for many decades (Jiménez 1993; Novaro 1995). Thus, current population numbers may be the result of past and present hunting pressure and food availability. The introduction of exotic prey species such as European hares (*Lepus europaeus*) and rabbits, as well as small-sized livestock into Chile and Argentina *c.* 100 years ago, probably led to increases in the distribution and abundance of culpeos, and facilitated their expansion towards the lowlands in eastern Argentina (Crespo and De Carlo 1963; Crespo 1975; Jiménez 1993; Jaksic 1998; Novaro *et al.* 2000a). Currently, culpeos range over a much wider area in

Figure 3.4.1. Current distribution of the culpeo.

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Patagonia than previously. Likewise, in several areas of the desert of northern Chile, recent mining activities provide the culpeo with resources such as food, water, and shelter that were in much shorter supply in the past, and hence have changed their local distribution and abundance (J.E. Jiménez pers. obs.).

Culpeos appear to withstand intense hunting levels as shown by fur harvest data from Argentina and still maintain viable regional populations (Novaro 1995). Culpeo populations that are harvested intensively may maintain viable levels through immigration from neighbouring unexploited areas that act as refugia (Novaro 1995). The culpeo population in Neuquén Province in north-west Patagonia for example, appears to function as a source-sink system in areas where cattle and sheep ranches are intermixed (Novaro 1997b). Cattle ranches where no hunting occurs supply disperser foxes that repopulate sheep ranches with intense hunting. Changes in sex ratio may be another mechanism that allows culpeo populations to withstand intense hunting (Novaro 1995). Furthermore, large litter size and early maturity (Crespo and De Carlo 1963) could explain the culpeo's high resilience to hunting.

When hunting pressure is reduced, culpeo populations usually can recover quickly (Crespo and De Carlo 1963). This increase was observed at the Chinchilla National Reserve (Jiménez 1993) and at Fray Jorge National Park (Meserve *et al*. 1987; Salvatori *et al*. 1999), both in north central Chile. Culpeo densities also have increased in many areas of Argentine Patagonia following the reduction of fur prices and hunting pressure in the late 1980s and early 1990s (Novaro 1997b; A.J. Novaro and M.C. Funes unpubl.). An exception to this response is the culpeo population in Tierra del Fuego, where they are still declining in spite of several years of reduced hunting pressure (N. Loekemeyer and A. Iriarte pers. comm.).

Estimated populations/relative abundance and population trends Estimates from intensive trapping by Crespo and De Carlo (1963) provided a density of 0.7 individuals/km² for north-west Patagonia, Argentina. Thirty years later, Novaro *et al*. (2000b), using line transects, reported densities of 0.2–1.3 individuals/km² for the same area. In north central Chile, the ecological density of culpeos in ravines is 2.6 individuals/km², whereas the crude density (throughout the study site) is 0.3 individuals/km² (Jiménez 1993). In Torres del Paine, a crude density of 1.3 individuals/km² was reported based on sightings (J. Rau pers. comm.). Interestingly, a later estimate for the same area, based on telemetry, rendered an ecological density of 1.2 individuals/km² (Johnson 1992, in Jiménez 1993).

Based on radio telemetry, sightings and abundance of faeces, Salvatori *et al*. (1999) concluded that culpeos respond numerically to a decline in the availability of their prey in north central Chile. Earlier, based on abundance of faeces, Jaksic *et al*. (1993) reached the same conclusion for the same culpeo population. In contrast, culpeos (not distinguished from sympatric chillas) did not show a numerical or a functional response during a decline of their main prey at another site in north central Chile (Jaksic *et al*. 1992).

Habitat

Throughout its wide distribution, the culpeo uses many habitat types ranging from rugged and mountain terrain up to the tree line, deep valleys and open deserts, scrubby pampas, sclerophyllous matorral, to broad-leaved temperate southern beech forest in the south. The culpeo uses all the range of habitat moisture gradients from the driest desert to the broad-leaved rainforest. In the Andes of Peru, Chile, Bolivia, and Argentina, the culpeo reaches elevations of up to 4,800m a.s.l. (Redford and Eisenberg 1992; Romo 1995; A.J. Novaro *et al*. unpubl.; J.E. Jiménez pers. obs.). Redford and Eisenberg (1992) placed the culpeo in the coldest and driest environments of South America relative to other South American canids.

Food and foraging behaviour

Food Trophic ecology is perhaps the best-studied aspect of culpeo biology (Medel and Jaksic 1988; Jaksic 1997). The culpeo diet, based mainly on faecal analysis, has been described for northern Chile (Marquet *et al*. 1993), north central Chile (Meserve *et al*. 1987; Jaksic *et al*. 1993; Jiménez 1993), central Chile (Yáñez and Jaksic 1978; Jaksic *et al*. 1980; Simonetti 1986; Iriarte *et al*. 1989; Ebensperger *et al*. 1991), northern Argentine Patagonia (Crespo and De Carlo 1963; Crespo 1975; Novaro *et al*. 2000a), southern Patagonia (Yáñez and Rau 1980; Jaksic *et al*. 1983; Johnson 1992; Johnson and Franklin 1994b), and Tierra del Fuego (Jaksic and Yáñez 1983; Jaksic *et al*. 1983). Most of these studies are from areas where only culpeo foxes are present, given that their faeces cannot be easily distinguished from those of the chilla (Jiménez *et al*. 1996a; but see Capurro *et al*. 1997).

Their main prey ranges from wild ungulates in Peru, European hares and domestic sheep in northern Patagonia, hares in southern Patagonia, small mammals and European rabbits (*Oryctolagus cuniculus*) in central Chile and Tierra del Fuego, to small mammals, ungulates, and insects in the highlands of northern Chile. Other vertebrates such as lizards, birds, and insects, make up a small component of this fox's diet. Although it is an opportunistic predator, the culpeo is considered more carnivorous and a consumer of larger mammalian prey than the other South American foxes (Crespo 1975; Langguth 1975; Redford and Eisenberg 1992). When seasonality was examined, almost all studies found differences in diet composition, likely in response to prey availability. In Argentine Patagonia, culpeos prey on hares more than would be expected from their availability (Novaro *et al.* 2000a) and selected among rodent species for those that may be more vulnerable (Corley *et al.* 1995). Culpeos in central Chile select the largest small mammals available (Meserve *et al.* 1987; Iriarte *et al.* 1989; Jaksic *et al.* 1993).

Although the bulk of the diet is made up of animal prey, it is often described as a consumer of fruits and berries and is, therefore, considered a disperser of a variety of seed species (Yáñez and Jaksic 1978; Jaksic *et al.* 1980; Bustamante *et al.* 1992; Castro *et al.* 1994; Leon-Lobos and Kalin-Arroyo 1994). Highest fruit consumption occurs when small mammals are the least abundant and vice versa (Castro *et al.* 1994).

Foraging behaviour Culpeos appear to be solitary foragers (W. Johnson pers. comm.). Culpeo foraging may be influenced by the nocturnal activity of its main prey (Iriarte *et al.* 1989; Johnson and Franklin 1994a) but also by persecution. In Argentina, highland Peru, (where it is intensively persecuted), the Chilean desert and Magallanes, the culpeo has an almost completely nocturnal activity pattern (Crespo and De Carlo 1963; Crespo 1975; Johnson 1992; Novaro 1997b; M. Parada unpubl.). This contrasts with the diurnal activity patterns in north central Chile (Jiménez 1993; Salvatori *et al.* 1999), where it is protected. The reason for the nocturnal activity in Magallanes is perhaps because they are hunted in the surrounding areas. Culpeos have been recorded moving linear distances of about 7km in Fray Jorge National Park (Salvatori *et al.* 1999) and north-west Patagonia (A.J. Novaro *et al.* unpubl.), but movements three times as large have been documented for desert-dwelling foxes in northern Chile (M. Parada pers. comm.). This high variability is likely associated with the spatial distribution and abundance of its food and water sources.

Damage to livestock and game Bellati and von Thüngen (1990) indicate that foxes, mainly culpeos, are involved in predation of lambs during parturition and account for 60% of the attacks by predators in Patagonia. Lamb mortality by foxes ranges from 5–40%, but it may be mainly compensatory (Bellati and von Thüngen 1990). Up to 83% of the biomass of the culpeo diet in some areas is from exotic mammals, mainly from European hares and sheep, but most of the sheep could be taken as carrion (Crespo and De Carlo 1963; Miller and Rottmann 1976; Novaro *et al.* 2000a). Offending individuals attack the throat, the neck, or the scapular area on the back of their victims. A collared juvenile culpeo (weighing 3.6kg) attacked and killed a 24kg goat by biting and hanging from the throat (J.E. Jiménez pers. obs.).

Adaptations

The culpeo has the smallest molars of all South American foxes, which reflects its highly carnivorous diet (Kraglievich 1930). Its relatively longer canines also indicate carnivory (Wayne *et al.* 1989).

Culpeo fur quality changes between seasons (Osgood 1943), becoming longer and denser during the winter (Crespo and De Carlo 1963). The increase in body size towards the south (Jiménez *et al.* 1995) and to higher elevations (Miller and Rottmann 1976; J.E. Jiménez unpubl.) may be the result of a bio-energetic adaptation to lower temperatures and harsher conditions.

Social behaviour

Culpeos seem to be solitary foxes. Spatial studies throughout their range indicate that they have inter- and intra-sexually non-overlapping home ranges (Johnson 1992; Jiménez 1993; Salvatori *et al.* 1999; M. Parada pers. comm.). Small areas of spatial overlap occur at sites of human refuse, but foxes still segregate temporally (Salvatori *et al.* 1999). Females are apparently more spatially intolerant than males in the wild (Salvatori *et al.* 1999) as well as in captivity.

In north central Chile, home ranges of females averaged 8.9km^2 and were 2.5 times larger than those of males (Salvatori *et al.* 1999). In contrast, culpeo home ranges in Torres del Paine were only 4.5km^2 in size and similar for males and females (Johnson and Franklin 1994a). Desert-dwelling culpeos show high variability in home range size, ranging from 10km^2 for culpeos living in ravines to 800km^2 for foxes associated with highland salt flats and lakes (M. Parada unpubl.).

Reproduction and denning behaviour

In the Patagonian steppe of Argentina, male culpeos produce sperm between June and mid-October (early winter to early spring). Females are monoestrous and mating occurs from the beginning of August through October (Crespo and De Carlo 1963). Gestation is 58 days. Based on embryo counts, Crespo and De Carlo (1963) estimated a mean litter size of 5.2 (range=3–8). At birth pups weight *c.*170g and reach up to 13kg when adults. Juveniles reach adult size within seven months and can reproduce during the first year. Although the sex ratio of 253 individuals was skewed in favour of males in the Neuquén population (Crespo and De Carlo 1963), some 30 years later the sex ratio approached parity, as expected for intensively hunted populations (Novaro 1995).

Competition

For evidence of potential competition between culpeo and chilla, please refer to the corresponding section of the latter species account.

In the steppe of Argentina, Crespo (1975) proposed that an increase in food availability through the introduction of sheep and hares may have relaxed potential competition between culpeos and other carnivores such as chilla, little grisons (*Galictis cuja*), mountain cats (*Oncifelis* *colocolo*), and Geoffroy's cats (*O. geoffroyi*). A study in the same region indicates that culpeos, chillas, Geoffroy's cats, and pumas (*Puma concolor*), all select European hares as one of their main prey items. Hares undergo periods of low abundance, when competition may be intense and consumption of native prey may increase (Novaro *et al*. 2000a).

Ebensperger *et al*. (1991) found that in central Chile, despite an eight-fold body mass difference, culpeos prey on similar prey and in similar proportions to little grisons, suggesting potential competition for food. In contrast, a study of a carnivore community in highland Peru shows that sympatric predators such as culpeos, pumas, and mountain cats feed on similar prey items, but in very different proportions, rendering different mean prey sizes (Romo 1995).

Mortality and pathogens

Natural sources of mortality Crespo and De Carlo (1963) state that with the exception of pumas, the culpeo lacks natural enemies.

Persecution One of the prime causes of mortality in the species has been persecution by farmers through hunting and trapping because of their reputation for preying on lambs; they are also controlled by using strychnine (Bellati and von Thüngen 1990; Novaro 1995). See Relative Abundance.

Hunting and trapping for fur Until the early 1990s the main cause of mortality was hunting and trapping for fur (Miller and Rottmann 1976; Novaro 1995). During 1986, in excess of 2,100 fox skins (culpeo and chilla) were exported from Chile (Iriarte *et al*. 1997). An average of 4,600 culpeo pelts were exported annually from Argentina between 1976 and 1982, with a peak of 8,524 in 1977. Legal exports declined to an average of approximately 1,000 between 1983 and 1996 with peaks of 2,421 in 1990 and 4,745 in 1996 and have been negligible since 1997 (Novaro 1995; Dirección de Fauna y Flora Silvestres and M. Elisetch pers. comm.). See Relative Abundance.

Road kills Road kills occur frequently in Neuquén, Argentina (A.J. Novaro pers. obs.).

Pathogens and parasites In central Chile, one culpeo tested for *Trypanosoma cruzi*, the protozoan of Chagas disease, gave negative results (Jiménez and Lorca 1990).

Stein *et al*. (1994) found a low prevalence of the nematodes *Physolaptera clausa*, *Toxascaris leonina*, and *Protospirula numidica* in the 129 culpeos examined from Argentine Patagonia. In addition, in culpeos from the same general area, the cestode *Echinoccocus patagonicus* and the tick *Toxocara canis* were reported (Crespo and De Carlo 1963). In Peru, culpeos had *Taenia hydiatigena* and *T. multiceps* (Moro *et al*. 1998). In Chile, a *Taenia* sp. was also found in the intestine (Medel and Jaksic 1988) and adults of *Linguatula serrata* were detected in the trachea of culpeos (Alvarez 1960 in Medel and Jaksic 1988).

Longevity The oldest wild-caught individual based on cementum annuli was 11 years old (Novaro 1997b).

Historical perspective

Remains of the prey of culpeo (in the form of faeces and large bones) complicate studies by archaeologists at rock shelters that were co-used by humans in the past (Mondini 2000).

Conservation status

Threats Main threats to culpeos have been hunting for fur and persecution to reduce predation on livestock and poultry. Habitat loss does not appear to be an important threat to this species. Predation by feral and domestic dogs may be important in some areas (Novaro 1997b).

Commercial use This has usually taken the form of hunting and trapping for fur, although trade has decreased in the last decade. See Hunting and trapping for fur; see also Relative Abundance.

Occurrence in protected areas

- — In Chile, the culpeo occurs in 38 protected areas distributed throughout the country, encompassing all the habitats where it can be found. However, only 14% are large enough to support viable populations.
- — In Argentina, the species occurs in 12 national parks and several provincial reserves, the majority of which probably support viable populations.
- — In Peru, culpeos occur in 13 protected areas (D. Cossios pers. comm.).

Protection status CITES – Appendix II

Current legal protection In Chile, the species is considered as "Insufficiently Known" and the subspecies *P. c. lycoides* is considered as "Endangered" by Glade (1993). According to Cofré and Marquet (1999), the culpeo is not in need of immediate conservation action. Hunting has been banned since 1980, although law enforcement is not strict.

The Argentine legislation about culpeos is contradictory. Culpeos were considered "Endangered" by a 1983 decree of the Argentine Wildlife Board (Dirección de Fauna y Flora Silvestre), due to the numbers of culpeo pelts traded during the 1970s and early 1980s. Trade at the national level and export of culpeo pelts, however, was legal during that entire period and currently remains legal. The culpeo's endangered status has never been revised in spite of marked changes in the fur trade and reports from monitoring programmes (see Relative Abundance). The Tierra del Fuego population has been legally protected since 1985 (N. Loekemeyer pers. comm.).

In Peru, the culpeo is not considered endangered and culpeo hunting may be legal if a management plan is approved by the government (D. Cossios pers. comm.). In Bolivia, although the fur export was banned in 1986, the species is not protected (Tarifa 1996; L. Pacheco pers. comm.).

Conservation measures taken The Argentine Wildlife Board is starting to develop a management plan for canids that will include the culpeo (V. Lichtschein and M. Eliseth pers. comm.). Five regional workshops that included wildlife agency officials from provincial governments, wildlife traders, conservationists, and scientists have been held in Argentine Patagonia during recent years (the last one in 2002) to coordinate efforts to manage culpeo populations in a sustainable manner and reduce sheep predation. Similarly, in Chile, two national carnivore workshops have been organised by the Livestock and Agricultural Bureau during recent years. These were aimed at presenting new findings on the natural history of canids, including culpeos, and wildlife-livestock issues and to discuss ways of improving our knowledge and better protecting Chilean carnivore populations.

Occurrence in captivity

The culpeo is common in zoos throughout Chile and Argentina.

Current or planned research projects

In Chile, the culpeo is one of three species being studied in Nahuelbuta National Park as part of a doctoral dissertation by E. McMahon (University of Massachusetts, USA).

Ongoing research at Salar de Punta Negra in the highland desert of northern Chile (conducted by Minera Escondida and Chile's Forest Service) has been focusing on culpeo ecology and its impact on flamingo reproduction. The monitoring programme, which has been running since 1986, includes examining the diet and a study of movement patterns using satellite and standard telemetry.

There are two other long-term monitoring projects in north central Chile at Fray Jorge and at Aucó, led, respectively, by P. Meserve (Northern Illinois University, USA) and F. Jaksic (Universidad Católica de Chile). In addition, researchers from Universidad Austral de Chile are studying the ecology of culpeos on Tierra del Fuego (M. Briones pers. comm.).

Biologists from Córdoba University in central Argentina are conducting a study of the diet and prey availability of the little-known *P. c. smithersi* population of Pampa de Achala (M. Pía and S. López pers. comm.).

In Neuquén Province, A.J. Novaro (Centro de Ecología Aplicada del Neuquén, Argentina), is in charge of an ongoing project investigating the role of culpeos in regulating European hare populations.

Throughout Argentine Patagonia, researchers from several agencies have been evaluating population trends of culpeos and other carnivores using standardised scent-stations and other methods since 1989 (A.J. Novaro and M.C. Funes of Centro de Ecología Aplicada del Neuquén, C. Chehebar of Parques Nacionales, A. Travaini of Universidad Austral, and N. Loeckemeyer of Dirección de Recursos Naturales of Tierra del Fuego).

Gaps in knowledge

1. It appears that conservation measures (e.g., hunting and trapping regulations) to protect culpeos are not effective to prevent poaching. There is a need for science-based information to aid management decisions and formulation of conservation regulations.
2. Studies on and long-term monitoring of population dynamics are needed to manage culpeos as a furbearer species. Given the wide distributional range of the species, research that encompasses the entire range of variability of the species is required. This is also true with regards to the genetic makeup of the species, especially as concerns the status of the currently recognised subspecies.
3. It is essential to develop means of making sheep-ranching activities compatible with sympatric wildlife including culpeos. Research aimed at better understanding culpeo behaviour as a sheep predator combined with sheep husbandry could help in decreasing the impact of predation. Bounty systems to kill culpeos are still in place in some Argentine provinces to reduce predation on sheep. This control system has proven to be widely ineffective with other carnivores. Research is needed to determine whether sheep predation is carried out only by certain individuals as is the case with coyotes (*Canis latrans*), in which case selective removal may be a more effective system of control (J. Bellati pers. comm.).
4. A study is urgently needed to determine the causes of decline of the Tierra del Fuego population and measures to reverse it.

Core literature

Crespo and De Carlo 1963; Jiménez 1993; Jiménez *et al.* 1996b; Johnson 1992; Johnson and Franklin 1994a,b; Medel and Jaksic 1988; Novaro 1997a,b; Novaro *et al.* 2000a; Salvatori *et al.* 1999.

Reviewers: Elise McMahon, Warren E. Johnson, Fabián M. Jaksic. **Editors:** Claudio Sillero-Zubiri, Michael Hoffmann.

3.5 Darwin's fox
Pseudalopex fulvipes (Martin, 1837)
Critically Endangered – CR: C2a(ii) (2004)

J.E. Jiménez and E. McMahon

Other names

Spanish: zorro de Darwin, zorro de Chiloé, zorro chilote; **Indigenous names:** Huilliche: payneguru (i.e., blue fox) (Chile).

Taxonomy

Vulpes fulvipes Martin, 1837. Proc. Zool. Soc. Lond., p.11. Type locality: near the mouth of San Pedro Channel on the southern end of Chiloé Island, Chile (*c.* 73°45'W, 43°20'S; Osgood 1943).

Until recently the Darwin's fox was known only from the Island of Chiloé. Its taxonomic status was uncertain and confusing, mainly due to a paucity of museum material from which to make an accurate taxonomic assessment. It has been considered alternatively as an island form of the chilla (*P. griseus*) (Langguth 1969; Clutton-Brock *et al.* 1976; Pine *et al.* 1979; Corbet and Hill 1980; Honacki *et al.* 1982; Redford and Eisenberg 1992; Wozencraft 1993) or as a distinct species (Martin 1837; Osgood 1943; Cabrera 1958; Miller *et al.* 1983; Tamayo *et al.* 1987).

However, the discovery of a mainland population in sympatry with the chilla (Medel *et al.* 1990), and the analysis of mitochondrial DNA of the three Chilean foxes (i.e., including culpeo *P. culpaeus*), provides strong evidence for considering the Darwin's fox as a legitimate species (Yahnke *et al.* 1996). This study found that: (1) Darwin's fox separated from the chilla 275,000 to 667,000 years ago; (2) the mainland population is a relict population (and not a founder group that escaped from captivity as has been suggested; Medel *et al.* 1990) and was probably distributed over a larger area in south central Chile; and (3) the mainland stock separated from the island stock about 15,000 years ago. In other words, current populations of Darwin's fox are relicts of a former, more widely distributed species (Yahnke 1995; Yahnke *et al.* 1996). Yahnke (1995), based on pelage coloration, found some similarities between the Darwin's fox and the Sechuran fox (*P. sechurae*) from the coastal desert of Perú (2,000km to the north), supporting Osgood's (1943) speculations of a phylogenetic relationship.

Chromosome number is not known.

Description

Darwin's fox is a small, stout fox possessing an elongated body and short legs (Table 3.5.1). Its muzzle is short and thin and extends into a rather rounded forehead. The agouti hair on the torso is a mixture of grey and black that contributes to its dark appearance. It has rufous markings on the ears and along the legs below the knees and elbows (i.e., *fulvipes*). White markings are found under the chin, along the lower mandible, on the under belly and on the upper and inner part of the legs. The tail is dark grey, relatively short and quite bushy, a useful diagnostic character for distinguishing this species from congenerics (Novaro 1997). Compared to the chilla, the skull is shorter and the auditory bulla smaller, but the dentition is heavier (Osgood 1943). Dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Monotypic.

Table 3.5.1. Body measurements for Darwin's fox.

	Chiloé Island (J.E. Jiménez unpubl.)	**Nahuelbuta National Park** (E. McMahon unpubl.).
HB male	540mm (525–557) n=6	538mm (482–561) n=9
HB female	514mm (480–550) n=9	522mm (495–591) n=7
T male	224mm (195–240) n=7	220mm (195–255) n=9
T female	219mm (175–250) n=9	221mm (199–235) n=7
HF male	107mm (99–111) n=7	110mm (101–117) n=9
HF female	103mm (93–110.5) n=9	105mm (101–114) n=7
E male	67mm (61–75) n=6	69mm (62–81) n=5
E female	64mm (52–71) n=9	60mm (56–66) n=3
WT male	3.26kg (2.8–3.95) n=7	2.44kg (1.9–2.8) n=9
WT female	2.91kg (2.55–3.7) n=9	2.26kg (1.8–2.5) n=7

Darwin's foxes. Radio-collared ~four-year-old male with five-month-old male pups. Parque Nacional Nahuelbuta, Chile, 2000.

Elise McMahon

Similar species Sechuran fox (*P. sechurae*): smaller in size; inhabits open areas and sandy coastal deserts of Perú. Chilla (*P. griseus*): larger in size, with longer legs and lighter colour; sympatric only in Nahuelbuta National Park.

Current distribution

Darwin's fox is endemic to Chile (Figure 3.5.1). It has a disjunct distribution with two populations: one found in the forests of Chiloé Island (42°S, 74°W), and another on the coastal mountains in Nahuelbuta National Park of mainland Chile (37°45'S, 73°00'W).

There are few records for the species. Charles Darwin collected the first specimen in 1834 from the south-eastern end of Chiloé Island. Osgood (1943) later captured it at the mouth of the Inio River, on the southern shore of the same island. On the Pacific shore of Chiloé, the species has been trapped on Playa Tricolor (in June 1999; J.E. Jiménez pers. obs.) and intensively monitored since November 2001 at Ahuenco; on the Cordillera del Piuché, the fox has been monitored since 1989 (Jiménez *et al.* 1990). On the northern part of Chiloé Island, one fox was captured in November 1999 and at Tepuhueico, on the central part, two adults were observed in June 2002 (J.E. Jiménez pers. obs.). On the north-western part of the same island, a local recently killed a female and her two cubs; and there have been additional sightings in the same area (C. Muñoz pers. comm.). Thus, Darwin's fox occurs on most of Chiloé Island (about 200km long x 62km wide), especially where forest remains, with the exception of the most populated areas on the eastern and north-eastern parts.

Figure 3.5.1. Current distribution of Darwin's fox.

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On mainland Chile, Jaime Jiménez has observed a small population since 1975 in Nahuelbuta National Park; this population was first reported to science in the early 1990s (Medel *et al.* 1990). It appears that Darwin's foxes are restricted to the park and the native forest surrounding the park (McMahon *et al.* 1999). This park, only 68.3km² in size, is a small habitat island of highland forest surrounded by degraded farmlands and plantations of exotic trees (Greer 1966). This population is located about 600km north of the island population and, to date, no other populations have been found in the remaining forest in between (W.E. Johnson pers. comm.).

Range countries Chile (Osgood 1943).

Relative abundance

Darwin's fox was reported to be scarce and restricted to the southern end of Chiloé Island (Osgood 1943). The comparison of such older accounts (reporting the scarcity of Darwin's fox), with recent repeated observations, conveys the impression that the Darwin's fox has increased in abundance, although this might simply be a sampling bias.

Estimated populations/relative abundance and population trends Yahnke *et al.* (1996) speculated that 500 foxes live on the Island of Chiloé. Based on home range estimates of six foxes, and considering their extensive range overlaps (42–99%) Jiménez (2000) calculated that the ecological density of the Darwin's fox is 0.95 individuals/km² at the Piruquina study site (*c.* 9km²) on Chiloé. Although difficult to estimate the overall density on the island, the species is rare on the northern part and around towns on the north-eastern and eastern part of Chiloé. Otherwise, the species is fairly common for a wild canid in forested environments, especially on the mountain terrain and lowland beaches on the Pacific Ocean side.

Table 3.5.2. The status of Darwin's fox populations in Chile (Trend: I=increasing, S=stable, D=declining, ?=Unknown).

	Protected areas		Other areas		Total	
Region	Population size	Trend	Population size	Trend	Population size	Trend
Mainland	~78	?	10	D	<100	?
Chiloe Island	250	S	250	D	500	S

Based on intensive captures in Nahuelbuta National Park, E. McMahon (unpubl.) estimated a density of 1.14 individuals/km^2 and extrapolated an abundance of 78 individuals in this isolated population. This estimate is similar to the figure of 50 foxes given by Cofré and Marquet (1999). This number is quite small considering it is the only known mainland population. Nevertheless, the mainland population appears to have increased in numbers since 1986, apparently as a response to a decrease in chillas (Jaksic *et al*. 1990). Recent quantitative information (Table 3.5.2) does not agree with a previous study that reported that the Darwin's fox was about twice as abundant on Chiloé as in Nahuelbuta (Jiménez *et al*. 1990).

Habitat

Darwin's fox is generally believed to be a forest obligate species found only in southern temperate rainforests (Jaksic *et al*. 1990; Medel *et al*. 1990). Recent research on Chiloé, based on trapping and telemetry data on a disturbance gradient, indicates that, in decreasing order, foxes use old-growth forest followed by secondary forest followed by pastures and openings (Jiménez 2000). Although variable among individuals, about 70% of their home ranges comprised old-growth forest. However, compared with the amount available, foxes preferred secondary forest and avoided old growth. Selection of openings varied among individuals. The forest is of Valdivian type, comprising a few native conifers and several species of broad-leaved evergreen species, and dominated by fruit-bearing trees of the Mirtaceae family. This forest is dense, with different strata and very moist all year round (Jiménez *et al*. 1990).

On the Pacific coast of Chiloé, Darwin's fox lives in a fragmented environment of coastal sand dunes mixed with dense evergreen forest. On the northern part of the island, Darwin's fox uses a relatively flat, but fragmented landscape of broad-leaf forest and dairy cow pastures. Research on the mainland population supports the notion of the species using primarily dense forest (Jaksic *et al*. 1990; Jiménez *et al*. 1990). Capture and telemetry data indicate that animals are found in dense *Araucaria*-*Nothofagus* forest, open *Nothofagus* forest and open pasture with decreasing frequency (McMahon *et al*. 1999). The forest comprises mainly monkey-puzzle trees (*Araucaria araucaria*) and five species of southern beech (*Nothofagus* spp.), one of which is non-deciduous.

Food and foraging behaviour

Food Darwin's fox is omnivorous, has a broad diet spectrum, and is highly opportunistic; these traits facilitate its survival in a prey-poor and highly fluctuating environment (such as Nahuelbuta and Chiloé; Jaksic *et al*. 1990; Jiménez *et al*. 1990). It changes its diet as the availability of food items changes in the environment, which renders marked seasonal changes. Based on faecal analysis, Jiménez *et al*. (1990) reported that the mainland population ate mainly small mammals, reptiles, insects, birds, and arachnids (in that order of importance). The proportions of these prey classes fluctuated strongly among seasons. More recently, analysis of faeces of trapped foxes indicated that, by number, insects were the most abundant prey in the diet, followed by small mammals and reptiles (although small mammals constituted most of the diet biomass). Berries were also included in the diet, showing up in *c*. 20% of the faeces.

On the mainland, Darwin's foxes rely heavily on the seeds of monkey-puzzle trees from March to May (E. McMahon unpubl.). During the summer months, droppings are filled with insect remains and seeds. Further content and genetic analysis of scats collected in Nahuelbuta National Park over a four-year period will provide more detailed information on seasonal fluctuations in diet and the dietary separation between the Darwin's fox and the other carnivores in the system.

On Chiloé, during the warm season insects were the most abundant in the diet by number, followed by amphibians, mammals, birds and reptiles (Jiménez *et al*. 1990); 49% of faeces had seeds. A recent dietary study of three different fox populations on the island found that in the summer, foxes fed mainly on insects, which were replaced by small mammals during the winter (J. Jiménez and J. Rau unpubl.). During late summer and fall, the diet was comprised almost entirely of fruits of Mirtaceae trees. Armesto *et al*. (1987) speculated that foxes could be considered a key species because of their role in dispersing seeds of forest species. An ongoing experiment indicates that at least for one tree species (*Amomyrtus luma*), a high percentage of seeds collected from faeces germinate under field conditions. A small amount of the diet consists of carrion, as evidenced by the remains (e.g., hair) of sheep, pigs, cattle, and horse in faeces.

Foraging behaviour Our telemetry data indicate that up to four foxes may concentrate on a carcass for a few days, but that they are otherwise solitary hunters. Jiménez *et al*. (1990) stated that foxes would scavenge opportunistically. Local settlers reported that lone Darwin's foxes would kill Southern pudu deer (*Pudu puda*) (about 10kg in weight) by biting their ankles and then the throat. They have been observed hunting ducks in a marsh during midday in the coastal range at Playa Ahuenco (October 2000; J.E. Jiménez pers. obs.). In addition, coastal foxes feed on shellfish and shorebirds, and up to nine individuals have been observed feeding on large brown algae on the beach. In Nahuelbuta National Park, where the Darwin's fox is sympatric with the chilla, McMahon (2002) has found that Darwin's fox forage in habitats rich in small mammals mainly at night, when the larger chilla is less active. Daytime activity of the Darwin's fox seems to be concentrated in forested areas where they may feed on reptiles, amphibians, and forest-floor dwelling birds species such as the tapaculos (Rhinocryptids).

Damage to livestock or game On Chiloé, foxes are well known for killing poultry and raiding garbage dumps, apparently with little fear of people and dogs to the point that they enter houses at night in search for food (J.E. Jiménez pers. obs.). In the farmlands surrounding Nahuelbuta National Park, interviews with the local farmers indicate that Darwin's foxes are not involved in livestock or poultry predation (E. McMahon unpubl.).

Adaptations

Small size and short limbs and tail appear to be adaptations for living in the dense forest understorey. Short extremities and compact body shape might also serve to decrease heat loss in cold and wet environments (Allen's rule) such as those favoured by Darwin's fox. The dark pigmentation pattern of the body corresponds with subsistence in a moisture-saturated environment (conforming to Gloger's rule). Dark coloration might also serve as camouflage in the dark environment close to the forest floor. The fox has been observed swimming across a river in excess of 15m wide on Chiloé. This aquatic ability might enable the Darwin's fox to move and disperse in a landscape where water bodies are a common landscape feature.

Social behaviour

Telemetric information on Chiloé indicates that when not breeding, Darwin's foxes are solitary carnivores (J.E. Jiménez unpubl.). They would, however, congregate at a food source when faced with concentrated resources (e.g., carcasses and seaweed stranded on beaches). A pair appears to be the standard unit during the breeding season. In the island population, home ranges are about 1.6km² for males and 1.5km² for females (J. Jiménez and J. Rau unpubl.). Given the very large range overlaps among neighbouring foxes, and that individuals share their home range with an average of 4.7 males and 3.3 females, the Darwin's fox appears to be a non-territorial species (Jiménez 2000).

On the mainland, pairs persist throughout the year, often being found within close proximity (E. McMahon unpubl.). Pairs have been known to share their home range with offspring from previous years. All family members associate closely with each other, showing very little aggressive behaviour between the parents and yearling offspring. Although one family has been observed for over three years, we have not seen any evidence of older siblings serving as helpers to new litters. Two yearling male siblings have been observed foraging and frolicking together (E. McMahon pers. obs.). Other known pairs (n=4) have juvenile males and females using their home range. Telemetry results from the mainland population indicate that there are groups of individuals with overlapping home ranges. However, there is little overlap between groups.

The maintenance of a large family group may be influenced by a paucity of suitable territories for potentially dispersing juveniles. Dispersal appears to be delayed and may be opportunistic such as in the case of one female, monitored since first captured as a yearling. She remained in association with her putative family group until three years of age, when she dispersed into an adjoining area with an adult male who had lost his mate. In another case, two males marked and radio-collared as pups, dispersed from their familial home range at two years of age. Their dispersal was six months post the death of their mother and coincided with the breeding season and the arrival of an adult female who subsequently paired with their father (E. McMahon unpubl.).

Reproduction and denning behaviour

On the mainland, lactating females have been caught in October (austral spring) and pups have been documented leaving the den area and venturing out with both parents in December (austral summer) (E. McMahon unpubl.). Litter size is estimated to be 2–3 pups based on observations of parents with litters and capture data. Weaning occurs in February. During weaning, the female spends relatively less time with the pups and a greater portion of their interactions are antagonistic, whereas the male spends more time playing with and grooming the pups (E. McMahon pers. obs.). Jaksic *et al*. (1990) described a den as a rock cavity (2m deep, 1.8m wide, and 0.7m high), located in *Araucaria*-*Nothofagus* forest with a bamboo understorey.

On Chiloé, reproduction occurs at least between October and January, when lactating females have been found. A small pup was found denning in a rotten and hollow log on the ground in late December (J.E. Jiménez pers. obs.). During mating, males and females are together for a few days. During the few weeks after parturition occurs, females do not move much and appear to stay in the den.

Competition

The only other terrestrial carnivores that live on Chiloé Island are the kod-kod or guiña (*Oncifelis guigna*), the hog-nosed skunk (*Conepatus chinga*), and the little grison (*Galictis cuja*). However, there are no data to support potential competition of these carnivores with the fox. The sympatric rufous-legged owl (*Strix rufipes*) is another potential competitor of Darwin's fox for small mammal prey.

The mainland population overlaps geographically with six carnivore species. These include the puma (*Puma concolor*), the culpeo and the chilla, the guiña, the hog-nosed skunk and the grison. The first three carnivores are larger and represent not only potential competitors, but also potential predators. Preliminary results of the current investigation of the ecological overlap between Darwin's fox and the chilla indicate that they exhibit some degree of overlap in home ranges and activity patterns (E. McMahon unpubl.). Clearly, the potential exists for competition between these two species.

It appears that when in sympatry with other carnivores, such as on the mainland, Darwin's fox moves into the open forest/grassy areas mainly at night, when the small mammals are active and when the grey fox is less active (E. McMahon pers. obs.). Thus, nocturnal behaviour may be related to avoidance of competitors as well as potential predators.

Mortality and pathogens

Natural sources of mortality In Nahuelbuta National Park, puma, culpeo, and chilla are all potential predators of the Darwin's fox. The larger culpeo has also been trapped in the same area as the Darwin's fox, but based on telemetry data, these individuals were passing through the area and therefore less likely to be serious competitors. Of the 29 radio-collared foxes we have followed over four years, there have been five mortalities attributed to larger carnivores, of which one was a puma. This latter fox had a home range adjacent to the park and was often in open patchy habitat. However, the main habitat of the Darwin's fox includes extremely dense undergrowth, which may prohibit serious pursuit by pumas (E. McMahon pers. obs.).

In Nahuelbuta National Park, survival rates of radio-collared juvenile and adult Darwin's foxes are 84% for females and 93% for males. Analysis of cause-specific mortality rate for the mainland population indicates that 74% of mortalities are due to natural causes while 26% are human caused (McMahon 2002).

Persecution Aside from reports by locals that they kill Darwin's foxes because they eat their poultry, and individuals killed by dogs, no other mortality causes have been detected on the island. On the mainland, radio-telemetry data and interviews with local people support the idea that the Darwin's fox does not venture far enough outside the park and forested area surrounding the park to be considered a nuisance by farmers.

Hunting and trapping for fur Although this fox is easily and repeatedly trapped, there is no known hunting or trapping for its fur.

Road kills In Nahuelbuta National Park, an adult, lactating female was killed by a tourist in the parking lot of the park's main attraction (McMahon 2002). Some foxes have become habituated to people by constant and unrestricted feeding by park visitors. These foxes spend much of their time under vehicles in the parking lot and are at risk of being killed by visitor's cars. Foxes have been observed climbing into visitor's cars, and there have been reports from CONAF park rangers of visitor's attempting to leave the park with Darwin's foxes in their vehicles. This lack of supervision over tourists who feed and thereby encourage foxes to spend time in the parking lot is thought to be one of the main conservation concerns for this mainland population.

Pathogens and parasites No pathogens or parasites have been reported for the Darwin's fox.

Longevity In Nahuelbuta National Park, an adult male estimated to be three years old at capture has been monitored since 1998, making him now seven years of age. We have been following another male estimated to be 6–7 years old and a female who is five years old (McMahon 2002).

Historical perspective

No information available.

Conservation status

Threats and conservation measures taken Although the species is protected in Nahuelbuta National Park, substantial mortality sources exist when foxes move to lower, unprotected private areas in search of milder conditions during the winter. Some foxes even breed in these areas. This is one of the reasons why it is recommended that this park be expanded to secure buffer areas for the foxes that use these unprotected ranges (McMahon *et al.* 1999).

The presence of dogs in the park may be the greatest conservation threat in the form of potential vectors of disease or direct attack. There is a common practice to have unleashed dogs both on Chiloé and in Nahuelbuta; these have been caught within foxes' ranges in the forest. Although dogs are prohibited in the national park, visitors are often allowed in with their dogs that are then let loose in the park. There has been one documented account of a visitor's dog attacking a female fox while she was nursing her two pups (E. McMahon pers. obs.). In addition, local dogs from the surrounding farms are often brought in by their owners in search of their cattle or while gathering *Araucaria* seeds in the autumn. Park rangers even maintain dogs within the park, and the park administrator's dog killed a guiña in the park. Being relatively naive towards people and their dogs is seen as non-adaptive behaviour in this species' interactions with humans.

The island population appears to be relatively safe by being protected in Chiloé National Park. This 430km² protected area encompasses most of the still untouched rainforest of the island. Although the park appears to have a sizeable fox population, foxes also live in the surrounding areas, where substantial forest cover remains. These latter areas are vulnerable and continuously subjected to logging, forest fragmentation, and poaching by locals. In addition, being naive towards people places the foxes at risk when in contact with humans. If current relaxed attitudes continue in Nahuelbuta National Park, Chiloé National Park may be the only long-term safe area for the Darwin's fox.

Commercial use None. However, captive animals have been kept illegally as pets on Chiloé Island (Jiménez pers. obs).

Occurrence in protected areas Nahuelbuta National Park (IX Administrative Region) protects the mainland population in *c.* 68km^2; Chiloé National Park (X Admistrative Region) protects the island population in *c.* 430km^2.

Protection status CITES – Appendix II
The conservation status in Chile is 'rare' on the mainland and 'vulnerable' on Chiloé Island (Glade 1993). More recently, Cofré and Marquet (1999) considered the Darwin's fox as 'critical', assigning it the second most urgent conservation priority among Chilean terrestrial mammals. Spotorno (1995) reported that the mainland population is vulnerable and its future survival uncertain if current environmental trends continue.

Current legal protection Protected by Chilean law since 1929 (Iriarte and Jaksic 1986), but enforcement is not always possible and some poaching occurs.

Occurrence in captivity

The Temuco Zoo held a male and a female until their release in October 2000 on Chiloé. No known specimens are kept elsewhere.

Current or planned research projects

J.E. Jiménez (Universidad de Los Lagos, Osorno, Chile) has studied the Darwin's fox since 1989 on Chiloé. He is currently conducting a study on the ecology of the species and the effects of forest fragmentation on the behaviour and habitat use of Darwin's fox. In 2001, he began an outreach programme with local farmers to help protect the species. In August 2002, a three-year Darwin Initiative to focus on the conservation of the Chiloé population was initiated by J.E. Jiménez and S.M. Funk. It is addressing questions on the ecology, genetic structure, spatial modelling of distribution and abundance, and an assessment of risks of disease transmission by dogs, in addition to having a strong education programme with local people.

E. McMahon (University of Massachusetts, Amherst, USA) has been studying the behavioural ecology of the Darwin's fox in Nahuelbuta National Park since 1998. One aspect of this study is an investigation of interspecific interactions with sympatric chillas, culpeos, and guiñas. A further initiative concerns conservation education in the local schools involving both children and their parents.

E. McMahon (University of Massachusetts) has conducted a study on disease and parasites affecting the Darwin's fox in the mainland population since January 2002. Since potential interaction with domestic dogs appears to be one of the primary conservation threats to the mainland population, a study is planned to determine the presence of rabies, parvovirus, and distemper in the dogs living in the area surrounding the park.

E. McMahon (University of Massachusetts) and W.E. Johnson (National Cancer Institute, Maryland, USA) will be examining levels of inbreeding in the mainland population and conducting further investigation of the phylogenetic relationships between the Darwin's fox and other South American canids.

Gaps in knowledge

A high priority would be to conduct intensive searches for other populations between Nahuelbuta and Chiloé. There are many remote pockets that are little explored where isolated populations could still be found.

The behavioural ecology of a forest-specialist or forest-dependent species is of utmost interest. Research topics to be explored include: social behaviour (e.g., tolerance to conspecifics), large home range overlaps, presence of helpers, and small litter sizes. In addition, little is known as concerns population dynamics, dispersal behaviour, and metapopulation structure.

Genetic aspects, including levels of inbreeding and inbreeding depression, and past population bottlenecks, are little known and important for future management.

Impacts of and resilience to human-related disturbances, the effects of free-ranging dogs, the foxes ecological naiveté to people, and forest disappearance and fragmentation are all of interest for fox survival. The impact of habitat loss (through forest conversion) on fox populations is also of interest. At least in Chiloé, habitat disturbance *per se* seems to play little, if any, role in population dynamics. On the mainland, however, fragmentation might increase risk of predation by other native predators.

Considering the potential disease threat posed by domestic dogs, an investigation into diseases and pathogens (and other allied mortality causes) is crucial.

If Darwin's fox is so closely related to the Sechuran fox of southern Perú as the circumstantial evidence suggests, then how did the two species diverge and became separated? These two ranges have been separated by the Atacama Desert for a long time. Exploring this question, in connection with other puzzling biogeographical patterns, could provide evidence to better understand canid speciation and species interactions.

Core literature

Jaksic *et al.* 1990; Jiménez *et al.* 1990; Medel *et al.* 1990; Yahnke *et al.* 1996.

Reviewers: Fabián M. Jaksic, Warren E. Johnson. **Editors:** Claudio Sillero-Zubiri, Michael Hoffmann.

3.6 Chilla
Pseudalopex griseus (Gray, 1837)
Least Concern (2004)

R. González del Solar and J. Rau

Other names

English: South American grey fox, Argentinean grey fox, grey zorro; **French:** renard gris; **German:** Patagonischen fuchs; **Spanish**: zorro gris, zorro gris chico, zorro gris Patagónico (Argentina); zorro gris, zorro chico, zorro chilla, zorro de la pampa (Chile); **Indigenous names:** Araucano/Mapuche: ngürü, nuru, n'rú (Argentina/Chile); Puelche: yeshgai (Argentina); Quechua: atój (Argentina/Peru).

Taxonomy

Vulpes griseus Gray, 1837. Mag. Nat. Hist. [Charlesworth's], 1:578. Type locality: "Magellan", listed in Cabrera (1958) as "Costa del Estrecho de Magallanes" [Chile].

The Darwin's fox (*Pseudalopex fulvipes*) was first deemed an island form of *P. griseus* (Osgood 1943; Clutton-Brock *et al*. 1976; Honacki *et al*. 1982). More recently, however, the discovery of sympatric populations of *P. fulvipes* and *P. griseus* on the Chilean mainland (Medel *et al*. 1990), and studies using metachromatic and genetic (see Yahnke *et al*. 1996) analyses support the recognition of *P. fulvipes* as a species. The Pampas fox (*P. gymnocercus*) has recently been suggested to be conspecific with *P. griseus* on the basis of a craniometric and pelage characters analysis (Zunino *et al*. 1995). These authors conclude that *P. gymnocercus* and *P. griseus* are clinal variations of one single species, namely *Lycalopex gymnocercus*.

Chromosome number is 2n=74; fundamental number is FN=76. Somatic karyotype of the female constituted by 36 pairs of acrocentric chromosomes. The X chromosome is metacentric, and the Y chromosome is a micro-chromosome (Gallardo and Formas 1975).

Description

A small fox-like canid with body measurements as shown in Table 3.6.1. Head rufescent, flecked with white. Large ears. Chin with well-marked black spot. Coat brindled grey, made up of agouti guard hairs with pale underfur.

Table 3.6.1. Body measurements for the chilla.

	Tucumán, Argentina (Mares *et al*. 1996).	**Parque Nacional Nahuelbuta**, Chile (E. McMahon pers. comm.).	**Parque Nacional Torres del Paine**, Chile (Johnson and Franklin 1994c).	**Reserva Nacional Las Chinchillas**, Chile (Jiménez 1993, Jiménez *et al*. 1995).
HB male	520mm (501–540) n=2			
HB female	566mm (562–570) n=2	579mm (515–660) n=14		
T male	337mm (328–347) n=2			
T female	319mm (317–322) n=2	283mm (115–330) n=14		
HF male	128mm (125–131) n=2			
HF female	122mm (120–124) n=2	130mm (118–145) n=14		
E male	75mm (70–81) n=2			
E female	81mm (80–82) n=2	84mm (55–169) n=8		
WT male			4.0 ± 0.1 (SE) kg, n=23	
WT female		3.5kg (2.5–5.0) n=14	3.3 ± 0.1 (SE) kg, n=21	2.5 ± 0.9 (SE) kg, n=16

Rafael González del Solar

Chilla, age and sex unknown. Parque Nacional Talampaya, La Rioja, Argentina.

Thighs crossed by a black patch. Legs and feet pale tawny. Underparts pale grey. Tail long and bushy, with dorsal line and tip black. Tail's underside presents a mixed pale tawny and black pattern (Osgood 1943; Clutton-Brock *et al.* 1976).

The cranium is small, lacking an interparietal crest. Teeth widely separated. The dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Four subspecies are recognised (Osgood 1943).

— *P. g. domeykoanus* (I Region to IX Region, Chile; southern Peru). Dentition weaker than *P. g. griseus*; pelage paler than *P. g. maullinicus*.

— *P. g. gracilis* (Western Argentina [Monte desert], from Santiago del Estero Province to west Río Negro Province).

— *P. g. maullinicus* (Southern temperate forests of Argentina and Chile, and in the latter from VIII Region to XI Region). Dentition weaker than *P. g. griseus*; pelage darker than *P. g. domeykoanus*.

— *P. g. griseus* (Argentinean and Chilean Patagonia, south from Río Negro to Magellan's Strait in the former, and in the steppes from east XI Region to XII Region in the latter; introduced in Tierra del Fuego).

Similar species Culpeo (*P. culpaeus*): generally larger; chin whitish; cranium with interparietal crest; relatively longer canines and relatively shorter molars. Pampas fox (*P. gymnocercus*): more robust; pelage more uniformly grey (less rufescent). Darwin's fox (*Pseudalopex fulvipes*): smaller; pelage darker brown; deeper and richer shaded rufescent areas on head, ears and legs; tail not bushy.

Current distribution

Widespread in plains and mountains on both sides of the Andes (Figure 3.6.1), from northern Chile (17°S) down to Tierra del Fuego (54°S).

In Argentina, they occur in the western and southern arid and semi-arid regions of the country, from *c.* 23°S (Jujuy and Salta) to Tierra del Fuego, and from the eastern foothills of the Andes mountain range to meridian 66°W, reaching the Atlantic coast (*c.* 63°W) south from Río Negro. Present in the following provinces: Jujuy (Jayat *et al.* 1999), Salta (Mares *et al.* 1996), Tucumán, Catamarca, Santiago del Estero, La Rioja, San Juan, Mendoza, west of San Luis, Neuquén, west of La Pampa, Río Negro, Chubut, Santa Cruz, and Tierra del Fuego (Osgood 1943; Olrog and Lucero 1981).

Widespread in Chile from the I Administrative Region (Atacama Province) in the north, south to the Strait of Magellan (XII Administrative Region, Magallanes Province), and Tierra del Fuego (Medel and Jaksic 1988; Marquet *et al.* 1993), and from the western foothills of the Andes mountain range to the Pacific coast (71–73°W). They were introduced to Tierra del Fuego in 1951 in an attempt to control rabbit (*Oryctolagus cuniculus*) infestation (Jaksic and Yáñez 1983).

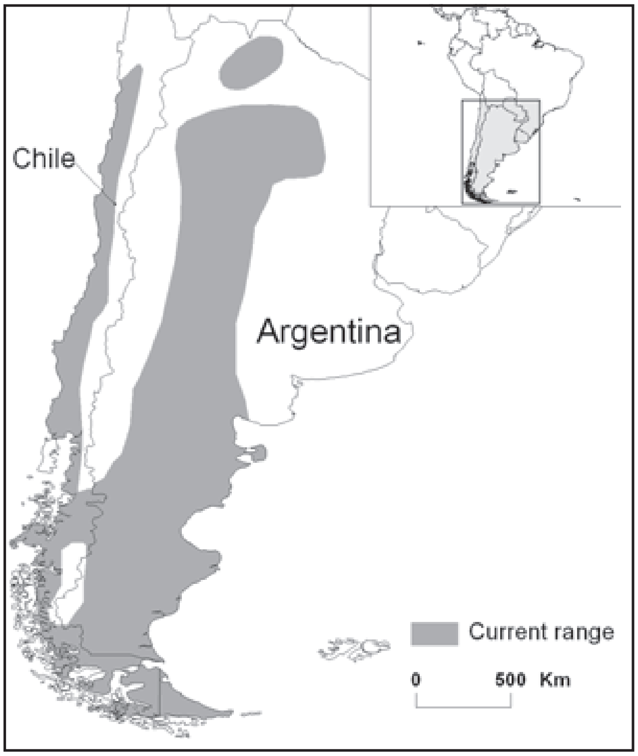


Figure 3.6.1. Current distribution of the chilla.

Other populations have been reported to exist in some of the southern Atlantic islands, including Malvinas/Falkland (Olrog and Lucero 1981), but this requires confirmation. Their presence in Peru is uncertain.

Range countries Argentina, Chile, Peru (?) (Osgood 1943; Olrog and Lucero 1981; Jayat *et al.* 1999).

Relative abundance

In Argentina, Olrog and Lucero (1981) considered chillas to be "locally common". In the latter country, relative abundance of chillas has been evaluated mainly through the scent stations technique. Autumn data collected in Pilcaniyeu (Río Negro) from 1983 to 1989, as well as winter data collected in Patagonia from 1989 to 2000 (A. Novaro and M. Funes unpubl.) and in north-eastern Mendoza from 1993 to 1997 (F. Videla *et al.* unpubl., R. González del Solar *et al.* unpubl.), suggest that populations are essentially stable in the southern half of Argentina where habitat is more favourable. They are reported to have expanded their distribution in Tierra del Fuego since their introduction (A. Novaro pers. comm.). J. Bellati (pers. comm.) estimated in 1996 an ecological density of one chilla/km^2 in Tierra del Fuego. Their status in the northern half of the country is unknown.

Estimated populations/relative abundance and population trends In Chile, chillas are considered frequent in the northernmost and northern regions (1 individual detected weekly); scarce (1 individual detected monthly) in central Chile; frequent-common (common: 1–5 individuals detected daily) in southern Chile; and common-abundant (abundant: >5 individuals detected daily) in southernmost Chile. The species became very abundant around Bahía Inútil (Tierra del Fuego) in the areas where it was first released in 1951 (Jaksic and Yáñez 1983). Despite having been overexploited for their fur in the past, chillas seem not to be decreasing in number (J. Jiménez pers. comm.).

In Chile, a mean ecological density of 3.3 chillas/km^2 was reported for the core area of Parque Nacional Torres del Paine, which is particularly safe and rich in resources for chillas. However, a much lower crude density (1.3 foxes/km^2) resulted when the former figure was extrapolated to the whole park. The density of foxes in Parque Nacional Torres del Paine, however, is likely to be higher than in most other Chilean populations, since the park is located in a particularly productive area. Three different density estimates resulted from the use of three different techniques for a site similar to Parque Nacional Torres del Paine (Durán *et al.* 1985). The most conservative of these estimates is 1.3 foxes/km^2 – a result similar to that of Johnson and Franklin (1994a) – and the highest 2.3 foxes/km^2, a figure that was deemed an overestimation (probably caused by methodological problems) by different authors (see Johnson and Franklin 1994a). In Reserva Nacional Las Chinchillas, the minimum abundance estimate (absolute density) over the entire reserve was 0.43 foxes/km^2, while the ecological density was 2.04 grey foxes/km^2 (Jiménez 1993).

In north-eastern Mendoza (Argentina), visitation indices progressively decrease from summer to winter, suggesting that the population suffers a decline during the cold season (R. González del Solar unpubl.). A similar pattern was found in Chile's Bosque Experimental San Martín (Martínez *et al.* 1993).

Habitat

The chilla occurs in steppes, "pampas" (grasslands), and "matorral" (scrublands) (Olrog and Lucero 1981). They generally inhabit plains and low mountains, but they have been reported to occur as high as 3,500–4,000m a.s.l. (see Marquet *et al.* 1993; Jayat *et al.* 1999). Although chillas occur in a variety of habitats, they prefer shrubby open areas. In central Chile, they hunt more commonly in flat, open patches of low height (1–2m) scrub than in areas with dense vegetation or ravines. Yet, they do visit ravines, apparently in search of fruit (Jaksic *et al.* 1980; Jiménez *et al.* 1996b). In southern Chile (Parque Nacional Nahuelbuta), chillas also prefer open areas to those more dense patches where Darwin's foxes occur (Jaksic *et al.* 1990; Jiménez *et al.* 1990; Medel *et al.* 1990). Durán *et al.* (1985) found that in Chilean Patagonia, their typical habitat was the shrubby steppe composed of "coirón" (*Festuca* spp., *Stipa* spp.) and "ñires" (*Nothofagus antarctica*), and that burning and destruction of forests in order to augment the land for sheep farming seems to have been advantageous for chillas. A similar preference was detected in Parque Nacional Torres del Paine, where 58% of the 12 monitored individuals used matorral shrubland or *Nothofagus* thicket habitat within their home ranges, more than was expected (Johnson and Franklin 1994c). In the north-eastern Mendoza desert (Argentina), these foxes seem to prefer the lower levels of the shrubby sand dunes that characterise the landscape or the valleys among dunes rather than their higher sections (R. González del Solar unpubl.).

Chillas are tolerant to very different climatic regimes from remarkably hot and dry areas, such as the Atacama coastal desert in northern Chile (less than 2mm average annual rainfall, 22°C mean annual temperature), to the humid regions of the temperate Valdivian forest (2,000mm average annual rainfall, 12°C mean annual temperature) and the cold Tierra del Fuego (*c.* 400mm average annual rainfall, 7°C mean annual temperature).

Food and foraging behaviour

Food Chillas are omnivorous generalists, feeding on a variety of food types including mammals, arthropods, birds, reptiles, fruit, and carrion (Medel and Jaksic 1988). Fruits ingested include berries of *Cryptocarya alba* and *Lithraea caustica* in Chile (Yáñez and Jaksic 1978; Jaksic *et al.* 1980), pods of *Prosopis* spp., and the berry-like fruits of *Prosopanche americana* and of several Cactaceae in Argentina (González del Solar *et al.* 1997, unpubl.).

A tendency to carnivory, however, is apparent, since vertebrates, especially rodents, are reported to be the most important prey in most studies. Small mammals were the most important vertebrate prey in most sites in the Chilean matorral (Yáñez and Jaksic 1978; Jaksic *et al.* 1980; Simonetti *et al.* 1984; Marquet *et al.* 1993; Jiménez *et al.* 1996b) and in the temperate rainforests of southern Chile (Martínez *et al.* 1993; Rau *et al.* 1995). Different situations have been found elsewhere. In Reserva Malleco (temperate forest of southern Chile), rodents and insects were similarly represented (R. Figueroa and E. Corales pers. comm.), whereas in Parque Nacional Torres del Paine, the European hare (*Lepus europaeus*) was the most represented vertebrate prey, followed by artiodactyl carrion and akodontine rodents (Johnson and Franklin 1994b). In Argentina's Patagonian steppe (Neuquén), artiodactyl carrion was the most important food item in 42 stomachs collected in winter (representing 62% of biomass ingested), followed by hares and cricetine rodents (Novaro *et al.* 2000). Similar results emerged from Argentina's southern Patagonia (Chubut), where carrion was followed by birds, rodents, and fruit (S. Saba pers. comm.). Finally, in two studies conducted in Tierra del Fuego, invertebrates were followed by ungulates (reportedly carrion), birds, and rodents (Jaksic *et al*. 1983).

In the harshest habitats of its distribution range, the diet of the chilla includes increasingly higher proportions of non-mammal food as small mammal availability decreases (Yáñez and Jaksic 1978). For example, lizards (44% minimum number of individuals) were the most consumed vertebrate prey in winter, the season of lowest small mammal availability in coastal northern Chile (Simonetti *et al*. 1984). In central Chile, where small mammal availability decreases towards autumn, berries appeared in 52% of the droppings (n=127) collected in that season; while in spring, when small mammal availability is the highest, berries were present in only 18% of the faeces (n=62; Jaksic *et al*. 1980). In north-eastern Mendoza (Argentinean Monte desert), fruit (61% annual mean of weight of remains [MWR]) was represented in 35% of faeces (n=116), followed by small mammals (19% frequency of occurrence [FO], 15% MWR) – mostly the murid (*Eligmodontia typus*). Small mammal consumption decreased from autumn (28% MWR) to summer (8% MWR), while fruit consumption simultaneously increased from 59% to 71% (MWR) (González del Solar *et al*. 1997).

Chillas might favour species richness in terrestrial ecosystems by acting as key predators to competitor rodents (J. Rau unpubl.). Chillas may also have an influence on vegetation structure by restricting the low-scale spatial distribution of rodents (e.g., *Octodon degus*) through predation (Martínez *et al*. 1993), and through seed dispersal (Yáñez and Jaksic 1978; Campos and Ojeda 1997; R. González del Solar unpubl.).

Foraging behaviour Feeding behaviour appears to be rather selective in certain areas (Martínez *et al*. 1993; Novaro *et al*. 2000a) and more or less opportunistic in others (Jaksic *et al*. 1980, 1983; Simonetti *et al*. 1984). Foraging occurs mostly in open areas (Jaksic *et al*. 1980; Jiménez *et al*. 1996b). Although hunting groups of up to 4–5 individuals have been reported, grey foxes mostly hunt solitarily except perhaps at the end of the breeding season, when juveniles may join the parents in the search for food. In Parque Nacional Torres del Paine, the most common foraging behaviour consists of "slow walking, with abrupt, irregular turns through the low (<500 mm) vegetation", while "prey appear to be located by sound, sight, and smell, with the fox's ears often turned forward and back in response to sound and the muzzle turned upward sniffing into the breeze" (Johnson and Franklin 1994a). Mice are captured with a sudden leap or by rapidly digging holes (40–100mm deep, 20–40mm wide). Scavenging is common, as well as defecation on and around guanaco (*Lama guanicoe*) and goat (*Capra hircus*) carcasses (Johnson and Franklin 1994a; R. González del Solar *et al*. unpubl.). Caching behaviour has also been reported (Johnson and Franklin 1994a).

Direct observation reports suggest that chillas are crepuscular, although they can be commonly seen in daylight (Greer 1965; R. González del Solar pers. obs.). Data from radio-collared individuals showed that they were primarily nocturnal in Parque Nacional Torres del Paine, although having a greater mean daily activity rate in summer and autumn than culpeos (Johnson and Franklin 1994c). Radio-tracking data from Reserva Nacional Las Chinchillas showed that foxes were active day and night (Jiménez 1993). As inferred from their prey, they would be most active in late afternoon and night (Yáñez and Jaksic 1978; Jaksic *et al*. 1980; R. González del Solar *et al*. unpubl.).

Damage to livestock or game The chilla has been considered a voracious predator of livestock, poultry and game (Yáñez and Jaksic 1978). In north-eastern Mendoza (Argentina), local breeders claim important goat losses due to grey fox predation. Despite this, dietary studies suggest that the remains of domestic animals found in faeces (R. González del Solar e*t al*. unpubl.) and stomachs are not only scarce but probably come from carrion, since such remains are often associated with larvae of Diptera (e.g., Calliphoridae) that usually occur in rotten carcasses (Jaksic *et al*. 1983). Furthermore, it is unlikely that one individual of such a small canid would be able to kill a healthy adult goat or sheep. A different situation concerns newly-born livestock. Predation on lambs has been observed in Reserva Nacional Las Chinchillas (Chilean matorral), where an individual fox was seen distracting a ewe while another robbed its lamb (J.E. Jiménez pers. comm.).

Adaptations

The chilla has relatively short canines and relatively long second molars, traits that suggest a tendency to include less meat and more plant and insect food in its diet (Wayne *et al*. 1989).

Social behaviour

The basic component of social organisation in Parque Nacional Torres del Paine is the breeding monogamous pair, accompanied by occasional female helpers, male dispersal, and occasional polygyny (Johnson and Franklin 1994a). Solitary individuals were seen from March to July (94% mean monthly visual observations), while pairs comprised 42% of sightings during August. Male and female of the pair maintained an exclusive home range year-round, which did not overlap with home ranges of neighbouring grey fox pairs. Intraspecific interactions displayed were few and usually aggressive. Individual home range sizes (n=23) varied between 2.0 ± 0.2km^2 (minimum convex polygon) and 2.9 ± 0.3km^2 (95% harmonic mean) (Johnson and Franklin 1994a, b, c).

Reproduction and denning behaviour

Mating occurs in August and September, and the gestation period is 53–58 days (Johnson and Franklin 1994a). In Parque Nacional Torres del Paine, mating takes place mainly in August, and 4–6 pups are born in October. Dens are located in a variety of natural and man-made places such as a hole at the base of a shrub or in culverts under a dirt road, and may be changed to a new location during the nursing period. During the first 3–4 days, the mother rarely leaves the den; during this period the male provisions her with food. Pups are cared for by both parents on an approximately equal time basis. Young foxes start to emerge from the den when they are about one month old, and start to disperse (8–65km) around 5–6 months later, i.e., at 6–7 months of age (Johnson and Franklin 1994a). Therefore, lactation lasts 4–5 months as inferred from the time when radio-tracked adults in Parque Nacional Torres del Paine were last seen with their pups (Johnson and Franklin 1994a). Age of sexual maturity is uncertain but believed to be about one year.

Two interesting phenomena concerning breeding behaviour may occur: combined litters (associated with polygyny) and the presence of female helpers. Both phenomena seem to be related to higher food availability and the possibility to raise larger litters, since an extra female would contribute by bringing more food to the den, increasing anti-predator vigilance, and/or substituting for the other female if she dies during the breeding period (Johnson and Franklin 1994a).

Competition

Interspecific competition has been suggested as a potential mechanism for explaining the distribution patterns of the chilla and the culpeo, since populations of these species coexist in a large section of their geographical distribution, consume similar vertebrate prey items, and have similar activity patterns (Fuentes and Jaksic 1979; Jiménez 1993; Johnson and Franklin 1994b, 1994c; Jiménez *et al*. 1996b). Chillas and culpeos are allopatric in northern Chile and central Argentina, whereas they are sympatric in the southern regions of both countries (Johnson and Franklin 1994b; Jiménez *et al*. 1996b; Novaro *et al*. 2000a), and in north-western Argentina (Jayat *et al*. 1999).

Fuentes and Jaksic (1979) attempted to explain this pattern of distribution in terms of character displacement of body size and altitudinal habitat partitioning (niche complementarity hypothesis). According to these authors, the similar size of both species in central Chile would be due to the chillas tending to use lower and more open habitats, while culpeos would usually occupy higher lands or more densely vegetated areas such as ravines. In the southern part of the country (south of 33°S, Reserva Nacional Las Chinchillas and Parque Nacional Torres del Paine), the rather homogeneous topographic profile would preclude habitat segregation by altitude, causing foxes to diverge in body size (culpeo: 7–12kg, chilla: 3–4kg) and partition food resources in order to lessen interspecific competition.

Other authors (Jiménez 1993; Johnson and Franklin 1994b, c) have suggested that culpeo and chilla distributions are an effect of different energy requirements and interspecific interference. Small size and lower energetic needs would allow chillas to exploit a broader spectrum of less optimal food categories and inhabit poorer habitats, from which culpeos would be excluded because of their higher energetic needs. When in sympatry, chillas would be excluded from the richest patches by culpeos, which are larger and more aggressive.

The Darwin's fox is also thought to be a potential competitor of the chilla, since initial data on the ecology of sympatric populations of these foxes suggest that they exhibit similar activity patterns, a high degree of overlap in home range and habitat use, and considerable overlap in their diets (E. McMahon pers. comm.).

Mortality and pathogens

Natural sources of mortality Little known. A culpeo was reported to attack and kill a chilla at Parque Nacional Nahuelbuta (Jiménez *et al*. 1996b). In Parque Nacional Torres del Paine, five out of 11 radio-tracked individuals lost during the study died from natural causes, and one unmarked individual was killed, but not eaten, by a puma (*Puma concolor*) (Johnson and Franklin 1994a).

Persecution Chillas are hunted on the belief that they are voracious predators of small livestock, poultry and game. The usual means are shooting, dogs, poison, snares, and foothold traps. Hunting occurs despite foxes being protected by legal regulations (Johnson and Franklin 1994a; R. González del Solar pers. obs.). Domestic dogs may also kill chillas. Around 45% of the mortality documented by Johnson and Franklin (1994a) in Parque Nacional Torres del Paine resulted from either poaching or dog attacks.

Hunting and trapping for fur Chillas have been heavily hunted for their pelts in the past (Ojeda and Mares 1982; Iriarte and Jaksic 1986), and are still hunted (though apparently with much less intensity) in Chilean and Argentinean Patagonia.

Ojeda and Mares (1982) report that 5,789,011 pelts were legally exported from Argentina generically labelled as "zorro gris" (grey fox) from 1972 to 1979. In 1979 the total amount of exports reached US$40,877,042, at US$39 per skin. At about the same time (1978), a hunter would receive US$8 for a skin in Salta Province (Ojeda and Mares 1982). From 1976 to 1979, the approximate annual number of pelts reported to have been exported ranged from 700,000 to 1,200,000. However, these extremely high numbers are difficult to interpret, and it is unlikely that the chilla was as heavily hunted as previously thought. Official reports on exports appear to have labelled as "grey fox" pelts corresponding to three different species, namely the chilla, the crab-eating fox (*Cerdocyon thous*), and, particularly, the Pampas fox (Ojeda and Mares 1982). On the other hand, available data do not include illegal exports or internal commerce. In any case, the legal exports of chilla pelts markedly decreased from 1980 onwards. During the 1980 to 1986 period, annual exports – mostly to Germany – averaged 100,000, reaching 300,000 pelts in some years. The fox-fur market experienced another decline in the late 1980s and early 1990s, plunging from about 100,000 pelts exported in 1987 to approximately 33,000 in 1990. The number of pelts commercialised through the Fine Fur Auctions Office of Río Negro Province also decreased from about 9,000 pelts in 1988 to about 1,000 in 1991, at a rate of roughly one half per year. Whether the cause of this trend was a decline in fox populations, decreased demand for their fur, or simply the failure of the country's administration to cope with the black market is unknown. The continued decline of fox-pelt exports – even when foxes are still heavily hunted in some regions of the country – could also be linked to the particular exchange rate between domestic and foreign currency, which makes exporting goods a barely profitable alternative. In 1996, there was a brief reactivation of the fox-fur market due to commerce with Russia, but during the 1997 to 1999 period the national exports reached an annual average of only 8,000 fox (*Pseudalopex* spp.) pelts (A. Novaro and M. Funes pers. comm.; but see also illegal exports from Chile, below). The current price of a skin at Río Gallegos (Santa Cruz Province) is US$ 2–3 (A. Iriarte pers. comm.).

In Chile, there are official reports on pelt exports since 1910; however, available data correspond to voluntary declaration of legal exports, leaving aside unreported legal exports and illegal trade. Besides, as in the case of Argentina, the significance of the internal commerce is unknown. From 1926 to 1946, fox pelts were the principal native wildlife item being exported from the country, even though no hunting or commercialisation was permitted since 1929. Between 1939 and 1944 the average amount of skins exported was *c.* 24,000 every five years (see details in Iriarte and Jaksic 1986). Chilla pelts, more valuable than those of culpeo, comprised *c.* 90% of the total exports. In 1939, about 1,000 skins, plausibly including a few culpeos, were reported as being brought to market in Punta Arenas, southernmost Chile (Osgood 1943). From 1945 to 1949 (9,692 skins) until 1955 to 1959 (2,845 skins), the exports decreased dramatically, exhibiting a new increase (an average of *c.* 14,000 pelts per five-year period) during the 1960 to 1974 interval, and a final decline from 1975 to 1984 (Iriarte and Jaksic 1986). The numbers of fox skins exported from Chile are consistently lower than those reported from Argentina, even when the area of each country is considered. For the period 1970 to 1979 (see information above for Argentina), a total of 12,846 fox skins (*Pseudalopex* spp.) were exported (see Iriarte and Jaksic 1986). The ban on chilla hunting was lifted for two years in the mid-1980s, on the basis of density estimates obtained from southernmost Chile (Durán *et al.* 1985). New regulations allowed a limited harvest of 10,000 individuals in Chile, and this was never completed, perhaps due to the difficulty in capturing enough individuals (Johnson and Franklin 1994b, Iriarte 2000). From 1985 to 1995, the chilla was the third most exported Chilean wild mammal (3,630 skins; Iriarte 2000). Illegal exports are estimated at 10,000–15,000 skins/year, especially from Magallanes Region (southernmost Chile) to Río Gallegos (southernmost Argentina). Between 1991 and 1994, a total of 996 chilla pelts or individuals were confiscated by the SAG, the Chilean Bureau of Livestock and Agriculture (Iriarte 2000). In 1996, 8,500 pelts were exported to Argentina (A. Iriarte pers. comm.).

Road kills Little data available, but frequently observed in Mendoza (Argentina), especially in summer (R. González del Solar pers. obs.).

Pathogens and parasites Stein *et al.* (1994) report the presence of nematodes in most of the stomachs (n=22) collected in Neuquén (Argentina) and suggested that the high prevalence of *Physaloptera clausa* (present in 68% of the sample), and the lower prevalence of *Toxascaris leonina* (23%) and *Protospirura numidica criceticola* (9%) may be a result of characteristics of diet and the intermediate vectors of the parasites.

Different gastrointestinal parasites were found in 63% of 22 stomachs obtained in the coastal steppe of Chubut (Argentina), during 1996 (S. Saba pers. comm.). Nematodes were present in 100% of the infected stomachs, cestodes in 14%, and acanthocephalans in 14%. Proglotides of *Echinococcus* spp. were found in the anus and faeces of a chilla captured in Reserva Nacional Las Chinchillas (J.E. Jiménez pers. comm.). Chagas' trypanosomes (*Trypanosoma cruzi*) were absent from the blood samples of two foxes captured at the same site (Jiménez and Lorca 1990).

Longevity Longevity is unknown in the wild. Individuals of undetermined age lived a maximum of five years in the Chilean National Zoo (G. González pers. comm.).

Historical perspective

In ancient times, chillas were used as food by some Argentinean aboriginal groups such as Matacos and Mocovíes, but this was not a common practice among other indigenous groups or among the "criollo" people (the offspring of European immigrants born in Argentinean territory), who only ate fox meat under extreme circumstances. Several aboriginal groups, such as Onas, Yámanas, and Tehuelches, used foxes' pelts to make clothes of different sorts. With the arrival of the Europeans and the emergence of criollos, pelts began to be used as currency. In general, the relation between chillas and human beings has been conflictive, especially from the settling of small-livestock breeders onwards. Traditionally, Argentinean peasants have deemed foxes to be a nuisance or even a menace for poultry, sheep, goat, and game. Chillas were even considered a pest some 20 years ago in areas of Argentina, where there are still occasional attempts to legalise commerce in fox pelts and their status as a pest. For example, in 1999, small-livestock breeders' pressure led the Office for Natural Resources of Mendoza to partially lift the ban, allowing breeders to kill those individual foxes demonstrably causing trouble to them (González del Solar *et al.* 1997, unpubl.).

Argentinean indigenous folklore regards "Juan" (or "Don Juan") the fox (*Pseudalopex* spp., *Cerdocyon*), as representing shrewdness and generally challenging the authoritarian power of his rich uncle the jaguar (*Panthera onca*). However, far from being the perfect hero, Juan is selfish and never tries to unite with other weak animals. Moreover, Juan sometimes tries to deceive other small animals (e.g., the armadillo *Chaetophractus* spp.), aiming to rob them of their food or females. But, more often than not, the fox ends up fooled by his supposed victims.

Conservation status

Threats The main threat to chilla populations in the past was commercial hunting. However, inferences on the historical rate of chilla extraction are difficult, since official pelt-export reports apparently have conflated data corresponding to different species. Hunting intensity has apparently declined in recent years (see Commercial use). Illegal trapping still occurs in some regions of Chile and Argentina, mainly related to controlling predation on small livestock and apparently not as intensively as in the past (A. Iriarte pers. comm.).

Commercial use Hunted for its pelt in Argentina and Chile (see Hunting and trapping for fur).

Occurrence in protected areas

- *Argentina:* Uncertain. Present in at least six protected areas in central west Argentina: Parque Nacional Talampaya, Parque Nacional Ischigualasto, Reserva Provincial Bosque Telteca, Parque Nacional Las Quijadas, Man and Biosphere Reserve of Ñacuñán, Reserva Porvincial La Payunia;
- *Chile:* present in 30 Wildlife Protected Areas (WPA) from a total of 49 surveyed. However, 40% of those 30 WPAs are smaller than the 115km^2 needed to sustain a minimum viable population (500 individuals). Estimates of local extinctions in WPAs from central Chile reach 50% (see Simonetti and Mella 1997). The most important Chilean WPAs in which chillas occur include: Parque Nacional Lauca, Parque Nacional Puyehue, Parque Nacional Vicente Pérez Rosales, Parque Nacional Torres del Paine.

Protection status CITES – Appendix II.

Current legal protection Resolution 144/83 of the former National Secretary of Natural Resources and Sustainable Development of Argentina categorises this species as "In Danger". Chillas are totally protected in Mendoza, Catamarca, and San Luis, while in the continental provinces of Patagonia and in Tierra del Fuego, hunting and fur trading are legal (A. Novaro and M. Funes pers. comm.).

In Chile, the passing of the 1972 furbearer's protection law appears to have curtailed the exports of pelts (Iriarte and Jaksic 1986; Iriarte 2000; but see above). Currently, all Chilean populations are protected by law N° 19,473 [1996], except for those from Tierra del Fuego (XII Region), where a maximum of 10 individuals/day/hunter are allowed from May 1 to July 31 (A. Iriarte pers. comm.).

Conservation measures taken Efforts are being made in Argentina to concentrate the relevant biological, legal and commercial information on the species in an attempt to design a plan for sustainable use and conservation (A. Novaro and M. Funes pers. comm.).

Occurrence in captivity

Chillas occur in many zoos of Argentina and Chile, but details of breeding in captivity are not known.

Current or planned research projects

A. Novaro and M. Funes (Centro de Ecología Aplicada del Neuquén, Neuquén, Argentina) have been coordinating an ongoing survey of Patagonian carnivores in Argentina since 1992. The programme includes annual surveys of chilla population trends and periodic meetings attended by specialists, government officials, and pelt-market entrepreneurs.

R. González del Solar, S. Puig and F. Videla (Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina) are conducting a dietary study on the species in the Argentinean central Monte desert.

J. Rau (Universidad de Los Lagos, Osorno, Chile) and A. Muñoz-Pedreros (Universidad Católica de Temuco, Temuco, Chile) are also involved in a dietary study in the Araucania Region (southern Chile), and at the time of writing, were finishing their analysis of a large sample of chilla droppings.

A. Mangione and B. Núñez (Universidad Nacional de San Luis, San Luis, Argentina) are carrying out research on the nutritional ecology of chillas.

F. Jaksic (Universidad Católica de Chile, Santiago, Chile), J. Jiménez. (Universidad de Los Lagos, Osorno, Chile) and collaborators have conducted monitoring of chilla food habits since 1987 in Reserva Nacional Las Chinchillas.

E. McMahon (University of Massachusetts, Amherst, USA) is coordinating a study of niche relationships among the three Chilean foxes (*P. griseus*, *P. culpaeus* and *P. fulvipes*) at Parque Nacional Nahuelbuta.

Gaps in knowledge

The need for a deeper understanding of the biology of the chilla has been repeatedly emphasised by Argentine as well as by Chilean studies (e.g., Johnson and Franklin 1994b; González del Solar *et al.* 1997). Reliable information is needed especially with regard to those biological aspects required for population management leading to sustainable use and conservation: population-dynamics, incidence of parasites and other diseases, and research on the role of chillas in small-livestock mortality.

Core literature

Campos and Ojeda 1996; Durán *et al.* 1985; González del Solar *et al.* 1997; Jaksic *et al.* 1980; Johnson and Franklin 1994a, b, c; Medel and Jaksic 1988; Rau *et al.* 1995.

Reviewers: Fabián Jaksic, Jaime Jiménez, Mauro Lucherini, Andrés Novaro. **Editors:** Claudio Sillero-Zubiri, Michael Hoffmann.

3.7 Pampas fox
Pseudalopex gymnocercus
(G. Fischer, 1814)
Least Concern (2004)

M. Lucherini, M. Pessino and A.A. Farias

Other names

English: Azara's fox, Azara's zorro; **French:** renard d'Azara; **German:** Pampasfuchs; **Italian:** volpe Azara, volpe grigia delle Pampas; **Portuguese:** graxaim do campo, cachorro do campo, rasposa do mato; **Spanish:** zorro pampeano (Argentina); zorro de patas amarillas (Bolivia); zorro de Azara, zorro Pampa, zorro del país, zorro de campo (Uruguay); **Indigenous names:** Guaraní: aguara cha'I (Argentina, Paraguay); Mapuche: ngürü (Argentina); Quechua: atój (Argentina, Bolivia).

Taxonomy

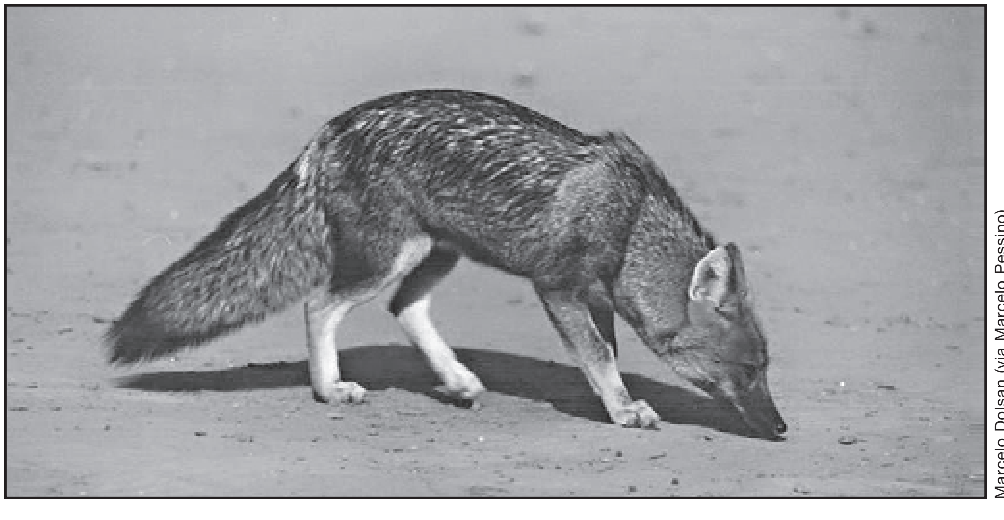
Procyon gymnocercus G. Fischer, 1814. Zoognosia, 3: xi, 178. Type locality: "Paraguay", restricted by Cabrera (1958) to "a los alrededores de Asunción" [Paraguay, *c.* 25°S, 57°W].

The taxonomic status of the Pampas fox and other related species is controversial. This canid was first included in the genus *Canis* by Linnaeus (1758) and in *Pseudalopex* by Burmeister (1854). However, it was treated as *Dusicyon* by Cabrera (1958) and then by Langguth (1969), who gave *Pseudalopex* subgeneric rank. Later, Langguth (1975) and Van Gelder (1978) placed *Pseudalopex* as a subgenus of *Canis*, excluding *Dusicyon australis*. Clutton-Brock *et al.* (1976) included all these taxa and *Pseudalopex vetulus* in *Dusicyon*. However, Berta (1988) gave full generic recognition to *Pseudalopex*, arguing that the species falling into this genus (*culpaeus*, *griseus, gymnocercus*, *sechurae*, and *vetulus*) share derived features that support a single origin for those taxa, separated from other genera now extinct and more closely related with *Dusicyon australis*. Recently, Zunino *et al.* (1995) proposed that *P. griseus* and *P. gymnocercus* represent clinal variants of *Lycalopex gymnocercus*. They considered *Lycalopex* as the valid genus name because it would have been used by Burmeister two years earlier. Chromosome analyses carried out by Gallardo and Formas (1975), and Vitullo and Zuleta (1992) supported this proposal (see Wozencraft 1993 and Zunino *et al.* 1995 for detailed comments).

Chromosome number: 2n=74 (Wayne *et al.* 1987).

Description

A medium-sized South American fox, smaller than the culpeo (*P. culpaeus*). The head, somewhat triangular in shape, is reddish with a pale grey to white ventral surface.



Marcelo Dolsan (via Marcelo Pessino)

Adult Pampas fox, thought to be male. Lihuel Calel National Park, La Pampa, Argentina, 2001.

Table 3.7.1. Body measurements for the Pampas fox.

	La Pampa province, Argentina (Crespo 1971)	**Buenos Aires province,** Argentina (E. Luengos Vidal and M. Lucherini unpubl.)	**Colonia Department**, Uruguay (Cravino *et al.* 2000).
HB male	648mm (597–700) n=10	660mm (620–740) n=20	
HB female	621mm (535–683) n=16	630mm (505–720) n=18	
T male	352mm (320–365) n=10	342mm (280–380) n=24	
T female	319mm (270–356) n=16	325mm (250–410) n=20	
HF male	140mm (135–155) n=10	145mm (130–160) n=22	
HF female	128mm (115–145) n=16	135mm (115–170) n=16	
E male	86mm (80–90) n=10	74mm (61–90) n=24	
E female	84mm (80–90) n=16	73mm (62–83) n=18	
WT male	4.6kg n=116	5.9kg (4–8) n=24	5.9kg n=11
WT female	4.2kg n=163	4.7kg (3–5.7) n=20	4.6kg n=8

The ears are triangular, broad and relatively large; they are reddish on the outer surface and white on the inner surface. The rostrum is narrow, ventrally pale, black in the chin and reddish to black dorsally. The eyes, near frontally placed, take an oblique appearance. The body, back and sides are grey, like the outer surface of the hind limbs, which show on the lower rear side a characteristic black spot. A dark band, almost black, runs longitudinally along the trunk and tail dorsum. The tail is relatively long, bushy and grey, being black at the tip (Table 3.7.1). The belly and the inner surface of the limbs are pale grey to white. The outer surface of the front limbs and the distal surface of the hind limbs are reddish. Smaller size and lack of interparietal crest distinguish its skull from that of the culpeo (Zunino *et al.* 1995). Dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Three subspecies have been proposed (Massoia 1982). Their geographic limits are not precise and Massoia (1982) suggested that along their borders they could coexist and interbreed. This author did not clarify the subspecific status of the Pampas foxes from Entre Ríos Province in Argentina, and there is no data regarding the taxonomic position of Bolivian foxes.

— *P. g. gymnocercus* (subtropical grasslands of north-eastern Argentina – southern Misiones, northern Corrientes and eastern Formosa provinces – Uruguay, Paraguay and south-eastern Brazil, from Paraná to Rio Grande do Sul estates).

— *P. g. antiquus (*Pampas grasslands, Monte scrublands and Espinal open woodlands of central Argentina, from Córdoba and San Luis provinces to the Río Negro, and from the Atlantic coast to a poorly defined limit west of the Salado-Chadilevú River).

— *P. g. lordi* (restricted to the Chaco-Mountain Tropical Forest ecotone in Salta and Jujuy provinces of Argentina). The smallest subspecies, with pelage smoother and brighter, denser in the tail, and more contrasting in colour than in the other subspecies. There are characteristic dark (almost black) spots in the pectoral and axilar regions of the body. Its skull is smaller than in the other subspecies, average length and weight being 924mm and 4.3kg, respectively (Massoia 1982), compared with 960mm and 5.9kg in *P. g. gymoncercus* (Barlow, in Redford and Eisenberg 1992) and 967mm and 4.4kg in *P. g. antiquus* (Crespo 1971).

Similar species Chilla (*Pseudalopex griseus*): overlaps with the south-eastern portion of the range of the Pampas fox; similar in colour and body proportions, but usually smaller and with a more uniformly grey pelage and shorter

Figure 3.7.1. Current distribution of the Pampas fox.

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legs (Clutton-Brock *et al.* 1976; Novaro 1997a). Crab-eating fox (*Cerdocyon thous*): occurs in the northern part of the range; similar in size, but with shorter hair and rostrum, and dark-coloured, shorter, legs (Redford and Eisenberg 1992).

Current distribution

The Pampas fox inhabits the Southern Cone of South America (Figure 3.7.1), occupying chiefly the Chaco, Argentine Monte, and Pampas eco-regions. From eastern Bolivia, western Paraguay and east of Salta, Catamarca, San Juan, La Rioja and Mendoza provinces in Argentina, to the Atlantic coast; and from south-eastern Brazil to the Río Negro Province, Argentina, in the south. Information on the limits of its distribution and the extent to which it overlaps with congeneric species is uncertain.

Range countries Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Redford and Eisenberg 1992).

Relative abundance

Little quantitative data are available on the abundance of Pampas fox populations. However, it would be either abundant or common in most areas where the species has been studied.

In the coastal area of central Argentina, a study based on scent-stations found that Pampas fox signs were more frequent than the common hog-nosed skunk (*Conepatus chinga*) and grison (*Galictis cuja*) (García 2001). Similarly, the frequency of observation of Pampas fox was higher than that of skunk, grison, and the Geoffroy's cat (*Oncifelis geoffroyi*) in a Sierra grassland area of Buenos Aires Province (M. Lucherini *et al.* unpubl.). In areas where the Pampas fox is sympatric with the crab-eating fox, the former would be more abundant in open habitats, while the latter would more frequently inhabit woodland areas.

The Pampas fox seems to be tolerant of human disturbance, being common in rural areas, where introduced exotic mammals, such as the European hare (*Lepus europaeus*), could form the bulk of its food intake (Crespo 1971; Farias 2000a; D. Birochio and M. Lucherini unpubl.).

Estimated populations/relative abundance and population trends The highest density has been reported for the Bañados del Izozog in the Bolivian Chaco (1.8 individuals/km²; Ayala and Noss 2000). In an Argentine Pampas area, Crespo (1971) found a density of 1.04 foxes/km², while Brooks (1992) estimated a density of 0.64 fox groups/km² for the Paraguayan Chaco, where fox abundance appeared to be correlated with annual rodent abundance. In La Pampa Province, Argentina, data from scent stations showed a stable tendency in the abundance of this species between 1992 and 1998 (Table 3.7.2) (R. Dosio and M. Pessino unpubl.).

Habitat

The Pampas fox is a typical inhabitant of the Southern Cone Pampas grasslands. It prefers open habitats and tall grass plains and sub-humid to dry habitats, but is also common in ridges, dry scrub lands and open woodlands (Brooks 1992; Redford and Eisenberg 1992). In the driest habitats in the southerly and easterly parts of its range, the species is replaced by the chilla. Where its range overlaps with that of the crab-eating fox, the Pampas fox would select more open areas. Apparently, the Pampas fox has been able to adapt to the alterations caused by extensive cattle breeding and agricultural activities to its natural habitats.

Food and foraging behaviour

Food Like most other medium-sized foxes, the Pampas fox is a generalist and adaptable carnivore. Its diet shows great geographic variation and may include both wild and domestic vertebrates (particularly rodents and birds), fruit, insects, carrion and garbage. Based on stomach contents, wild mammals and sheep appeared to be the two most important food items in Uruguay (Cravino *et al.* 1997), while in La Pampa Province, Argentina, European hares and rodents were the most important food items, followed by birds and carrion (Crespo 1971). Recent studies in Buenos Aires Province, Argentina, using faecal analysis, report high frequencies of occurrence of rodents and birds, but also of insects and fruits (Farias 2000a; D. Birochio and M. Lucherini unpubl.) and crabs (in a coastal

Table 3.7.2. The status of Pampas foxes in various regions (Population: A=abundant, C=common, X=present but abundance unknown; Trend: I=increasing, S=stable). When shown, numeric abundance indicated as rough estimates based on the densities given above.

	Protected areas		Other areas		Total	
Region	Population size	Trend	Population size	Trend	Population size	Trend
La Pampa (Argentina)	150	S/I	150,000	S	>150,000	S/I
Buenos Aires (Argentina)	C	S/I	C	S/I	C	S/I
Uruguay	X	?	C	?	C	?
Rio Grande do Sul (Brazil)	X	?	C	?	C	?
Paraguayan Chaco	X	?	C	?	180,000	?
Bolivian Chaco	X	?	C	?	350,000	?

area; Vuillermoz and Sapoznikow 1998). However, in a study where ingested biomass was estimated, mammal carrion, rodents and hares were the main dietary components (Farias 2000a). Seasonal and local variations in diet are likely connected to variations in food availability (Vuillermoz and Sapoznikow 1998; Farias 2000a; García 2001; D. Birochio and M. Lucherini unpubl.). No sex/age differences in food habits have been reported, but occasional observations of food remains at den sites (M. Lucherini pers. obs.) suggest that cubs feed mostly on small- to medium-sized vertebrate prey.

Foraging behaviour The Pampas fox is a typical solitary and opportunistic carnivore, foraging both during the day and night (E. Luengos Vidal unpubl.), although feeding activity would become mainly nocturnal where heavily hunted. Large, highly concentrated food resources (i.e., large mammal carcasses) may cause several individuals to gather, possibly through movements exceeding the borders of normal home range size (E. Luengos Vidal and M. Lucherini unpubl.). Food caching behaviour has been observed, apparently related to an increase in the availability of a food resource, i.e., rodents (J. Pereira pers. comm.).

Damage to livestock or game Predation on domestic stock traditionally has been one of the main reasons to justify this fox's persecution by rural people. Nevertheless, it is likely that mainly adult sheep are scavenged, while some studies found evidence of predation on newborn lambs, but concluded that foxes were only a secondary factor of lamb mortality (2.9% of total lamb mortality in Uruguay, Cravino *et al.* 1997; 4.1% and 6.9% in Argentina, Bellati 1980 and Olachea *et al.* 1981, respectively), especially when compared to climate (Cravino *et al.* 1997). High levels of predation on poultry have never been supported by observations or dietary studies. Similarly, although Pampas foxes are commonly accused of causing important reductions in game populations, particularly by feeding on eggs and chicks of ground-nesting birds, there is little data to support this view (Vuillermoz and Sapoznikow 1998; Farias 2000a).

Adaptations

Very little is known about the behavioural, morphological and physiological adaptations of this species.

Social behaviour

Pampas foxes are thought to form monogamous pairs. However, they spend most of their time solitarily: in the Paraguayan Chaco (Brooks 1992) and La Pampa Province, Argentina (Branch 1994) 88–93% of observations, respectively, were of single individuals. Pairs are frequently observed from mating until cubs leave the natal den.

In a Sierra grassland area, the home ranges of two adult males have been estimated at 40 and 45ha (E. Luengos Vidal and M. Lucherini unpubl.). In the same area, foxes showed a relatively low frequency of re-use of scat marking sites, and a tendency to mark latrines used by Geoffroy's cats and common hog-nosed skunks (M. Lucherini and C. Manfredi unpubl.). Defecation site features suggest that scats are used in intraspecific communication (M. Lucherini and D. Birochio unpubl.; A.A. Farias pers. obs.).

The long-distance calls of Pampas foxes, which show a peak in frequency during the breeding period, may serve to maintain contact between pair members, as well as in territorial behaviour (Branch 1994). During the breeding season, both pair mates have been observed using a brief and repeated alarm call when detecting potential threats to the young (M. Lucherini pers. obs.).

Reproduction and denning behaviour

In central Argentina, cubs are born in spring, from October to December. Gestation lasts 55–60 days, and litter size ranges from 3–5 (Crespo 1971; M. Lucherini and E. Luengos Vidal unpubl.). Dens may be located in a variety of shelters, e.g., a hole at the base of a tree trunk, in armadillo dens, or among rocks. Cubs are frequently moved to a new location (M. Lucherini and E. Luengos Vidal pers. obs.). Young stay at the den for the first three months. Both pair mates have been observed to guard the den (M. Lucherini pers. obs.) and males provide food to cubs and females at the den. Females may breed at 8–12 months of age. In a Sierra Pampas area, reproductive dens did not appear to be re-used in following years (M. Lucherini pers. obs.).

Competition

In the Lihuel Calel National Park, Argentina, remains of armadillos (*Zaedyus pichy* and *Chaetophractus villosus*), plain viscachas (*Lagostomus maximus*), small rodents (*Ctenomys* spp., *Galea musteloides*) and European hares appeared in the droppings of both the puma (*Puma concolor*) and Pampas fox (M. Pessino unpubl.).

Partial dietary overlap has also been found with the Geoffroy's cat, a similar-sized carnivore whose range widely overlaps that of the Pampas fox. In Buenos Aires Province, most of the food items in the droppings of these two carnivores (e.g., *Cavia, Oligorizomys* and *Akodon* rodents), European hares, small passerines and doves were the same, although their frequency of occurrence was different (Vuillermoz and Sapoznikow 1998, M. Lucherini and C. Manfredi unpubl.). However, signs of presence, suggest that spatial segregation between the Pampas fox and Geoffroy's cat may occur in Mar Chiquita, Atlantic coast of Buenos Aires Province (A.A. Farias unpubl.).

In Uruguay, although temporal segregation has been suggested, a very large food niche overlap was reported between the Pampas fox and crab-eating fox (Cravino *et al.* 2000).

Very little information is available on two other species that share a large proportion of their ranges with the Pampas fox: the Pampas cat (*Oncifelis colocolo*) and the common grison. Some data from scat analysis suggest extensive food niche overlap between the Pampas fox and the grison in a Sierra Pampas area (M. Lucherini *et al.* unpubl.).

Mortality and pathogens

Natural sources of mortality Little is known about natural causes of mortality. Pampas fox remains have been found in puma scats collected in the Lihuel Calel National Park, Argentina (Wander *et al.* unpubl.). Kills by feral dogs have also been reported (A.A. Farías pers. obs., A. Canepuccia and D. Queirolo Morato pers. comm.).

Persecution In Argentina and southern Brazil (Rio Grande do Sul State, C. Indrusiak pers. comm.), the Pampas fox has been considered an important predator of sheep and goats, and consequently has been actively persecuted by livestock ranchers. In the provinces of La Pampa, Buenos Aires, and San Luis, control campaigns were carried out against this species between 1949 and the early 1970s, in order to reduce economic losses caused by predation. As a result, 361,560 individuals were killed using different methods, including leg-hold traps, selective traps with toxic cartridges, shooting, dogs and poisoned baits (Godoy 1963; M. Pessino and R. Sosa unpubl.). Pampas foxes were also hunted by the bounty system in the provinces of San Juan, Catamarca, and Río Negro during 1959 and Córdoba during 1960.

In 2001, the bounty system was used again for the control of this species in La Pampa Province, while fox hunting has been re-opened in Buenos Aires Province. In Brazil, although the fox is protected by law, control measures are regularly taken by sheep breeders with no legal permission (C. Indrusiak pers. comm.). In Uruguay, special hunting authorisation may be easily obtained by the government to control predation on sheep herds (Cravino *et al.* 2000).

Hunting and trapping for fur Rural residents have traditionally hunted the Pampas fox for its fur, and this activity has been an important source of income for them. From 1975 to 1985, *Pseudalopex* fox skins (mostly belonging to *P. gymnocercus*; García Fernández 1991) were among the most numerous to be exported legally from Argentina (Chebez 1994). However, exports have declined from the levels of the early and mid-1980s mainly due to a decline in demand (Novaro and Funes 1994). From 1997 to 1999, national fox pelt exports averaged a mere 8,000 specimens per annum (M. Elisetoh unpubl.). In Uruguay, because of their relatively high commercial value, illegal trade of *P. gymnocercus* fur is still widespread (D. Queirolo Morato pers. comm.), while in Paraguay no illegal fox pelts were confiscated during 1995 to 2000 (J. Cartes pers. comm.).

Road kills Pampas foxes are frequently struck by cars (N. Fracassi and D. Queirolo Morato pers. comm.). However, no data are available in order to establish the impact of road kills on fox populations.

Pathogens and parasites Animals kept in captivity are susceptible to parvovirus and distemper (F. Baschetto pers. comm.). Ectoparasites in the Pampas fox include ticks (*Amblyomma maculatum, A. auriculare*) and fleas (*Pulex irritans, Ctenocephalides felix, Hectopsylla broscus, Malacopsylla grossiventris, Tiamastus cavicola, Polygenis* spp.). In a sample of 132 foxes, the most common parasites were *A. maculatum*, *M. grossiventris* and *P. irritans* (A. Bischoff de Alzuet unpubl.). Recorded endoparasites include *Taenia pisiformis* (*Taenidae*), *Dipylidium caninum* (*Dilepididae*), *Joyeuxiella* spp. (*Dilepididae*), and many species from the *Cestoda* Class. Nematodes such as *Molineus felineus* (*Trichostrongylidae*), *Toxocara canis* (*Ascariidae*), *Ancylostoma caninum* (*Ancylostomidae*), *Rictularia* spp. (*Rictularidae*), and *Physaloptera* spp. (*Physalopteridae*) (Led *et al.* 1970), as well as *Echinococcus granulosus* and *E. cepanzoi*, have also been noted. Another internal parasite, *Athesmia foxi* (*Trematoda: Dicrocoeliidae*), was found in the small intestine. Cases of *Sarcoptes scabiei* infection have also been reported (S. Deem pers. comm.).

Longevity Few individuals are likely to live more than a few years in the wild, but a captive animal lived nearly 14 years (Jones 1982).

Historical perspective

Fox furs were used by native communities for making shawls. When white traders appeared, fox furs became valued merchandise. Rural people inhabiting La Pampa Province use Pampas fox fat for medicinal purposes (M. Pessino pers. obs.). Among natives and settlers, foxes in general, and particularly the Pampas fox, have been the main characters of numerous stories and proverbs, which have been passed down from generation to generation. Also, these communities have interpreted their presence and behaviour in certain circumstances as omens.

Conservation status

Threats The implementation of control measures (promoted by ranchers) by official organisations, coupled with the use of non-selective methods of capture, represent actual threats for the Pampas fox. Fox control by government agencies involves the use of bounty systems without any serious studies on population abundance or the real damage that this species may cause. In rural areas, direct persecution is also common, even where hunting is officially illegal.

Most of the species' range has suffered massive habitat alteration. For instance, the Pampas, which represents a large proportion of the species' distribution range, has been affected by extensive cattle breeding and agriculture. Approximately 0.1% of the original 500,000km² range remains unaffected. However, due to the species' adaptability, the Pampas fox seems able to withstand the loss and degradation of its natural habitat, as well as hunting pressure. Since no studies are available on its population dynamics in rural ecosystems, caution is required, since the sum of these threats may eventually promote the depletion of fox populations. Hunting pressure has resulted in diminished populations in the provinces of Tucumán (Barquez *et al.* 1991) and Salta (Cajal 1986) of north-western Argentina.

Commercial use Considering that the Pampas fox trade is banned, no statistical information on the fur harvest is available. Different authors have pointed out that Argentine exports corresponding to the chilla historically included other species, such as the crab-eating fox and the Pampas fox (Ojeda and Mares 1982; García Fernandez 1991).

Occurrence in protected areas

- In Uruguay, the Pampas fox has been reported in many protected areas which are included in a law passed in 2000 establishing the national protected areas system. However, this law has not been implemented yet (R. Rodríguez-Mazzini and D. Queirolo Morato pers. comm.).
- *Argentina:* National Parks Chaco (Chaco), Mburucuyá (Corrientes), Calilegua (Jujuy), El Palmar (Entre Ríos), Lihuel Calel (La Pampa) (Heinonen Fortabat and Chebez 1997), E. Tornquist and Bahía Samborombón Provincial Parks, and Campos del Tuyú Wildlife Reserve (Buenos Aires). The Pampas fox is the least well represented among the *Pseudalopex* species in the National Park system of Argentina (Heinonen Fortabat and Chebez 1997).

Protection status CITES – Appendix II.

The Argentina Red List of Mammals (Diaz and Ojeda 2000) assigned the Pampas fox to the "Least Concern" category.

Current legal protection In Argentina, it was declared not threatened in 1983, and its trade was prohibited in 1987. However, this species continues to be hunted and demand for its fur exists.

In Uruguay, all foxes are protected by law, and the only legal exception is the government's so-called "control hunting permission", which does not allow the taking of animals for the fur trade. The situation is very similar in Paraguay.

Conservation measures taken None.

Occurrence in captivity

In Argentina, the Pampas fox has been successfully bred in captivity and presently is the best represented carnivore species in captivity in the country (Aprile 1999).

Current or planned research projects

In the Argentina Pampas grassland, the GECM (Grupo de Ecología Comportamental de Mamíferos), Universidad Nacional del Sur, Argentina, is presently comparing the abundance, spatial behaviour and social organisation as well as food niche of the Pampas fox in a protected site versus a site affected by farming.

A. Farias and V.B. García (Pontificia Universidad Católica de Chile) have started studies on the trophic ecology of the Pampas fox in two coastal areas of Buenos Aires Province.

S.J. O'Brien and W.E. Johnson (National Cancer Institute, USA) have proposed a DNA-based study on the phylogeny of *Pseudalopex* foxes.

S. González *et al.* (División Citogenética-IIBCE, Unidad Asociada Facultad de Ciencias, Uruguay) initiated a study aimed at determining the genetic variability of *P. gymnocercus* and the crab-eating fox in wooded areas in northern and eastern Uruguay in order to test whether hybridisation occurs.

Gaps in knowledge

Most aspects of the species' ecology remain unknown. Studies on population dynamics in agricultural land, impact and sustainability of hunting, effect of predation on livestock and game species are needed, particularly for an appropriate management of wild populations. In addition, resolution of the species' taxonomic status is essential.

Core literature

Crespo 1971; Massoia 1982; Zunino *et al.* 1995.

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3.8 Sechuran fox
Pseudalopex sechurae (Thomas, 1900)
Data Deficient (2004)

C. Asa and E.D. Cossíos

Other names

English: Sechura desert fox, Peruvian desert fox; **French:** renard de Sechura; **German:** Sechurafuchs, perufuchs; **Spanish:** perro de monte de Sechura, zorra Pampera (Ecuador), zorro costeño, zorro de Sechura, Pacha zorro, Juancito (Peru); **Indigenous names:** Pacha zorro (Cajamarca Department); Moche and Olmo: Pacter, Pacterillo (Peru).

Taxonomy

Canis sechurae Thomas, 1900. Ann. Mag. Nat. Hist., ser. 7, 5:148. Type locality: "Desert of Sechura, N.W. Peru… Sullana".

Simpson (1945) included the Sechuran fox in the genus *Dusicyon*. Langguth (1969) also considered *Pseudalopex* a subgenus of *Dusicyon*, although he subsequently (1975) regarded it as a subgenus of *Canis* (as did Van Gelder 1978). Clutton-Brock *et al.* (1976) also included the species in the genus *Dusicyon*, but did not recognise subgenera. Berta (1987) recognised *Pseudalopex* as a distinct genus including the Sechuran fox. This treatment was followed by Wozencraft (1993) and Nowak (1999).

Chromosome number is not known.

Description

The Sechuran fox is the smallest species of the genus *Pseudalopex* (Huey 1969) (Table 3.8.1). The head is small, with relatively long ears (about 2/3 the length of the head) and a short muzzle. Face is grey, and there is a rufous-brown ring around the eyes (Thomas 1900). The ears may be reddish on the back; the dark muzzle may have paler hairs around the lips. The pelage consists of pale underfur with agouti guard hairs, while the underparts are fawn or cream-coloured. There is sometimes a dark stripe down the back. The frontal limbs (up to the elbows) and the back limbs (up to the heels) are usually reddish in colour. The tail is relatively long and densely furred, ending in a dark tip. The dental formula is 3/3-1/1-4/4-2/3=42. The carnassials are slightly smaller, and the grinding teeth larger, than in allied forms (Thomas 1900); the canines are "fox-like" (Clutton-Brock *et al.* 1976).

Table 3.8.1. Body measurements for male Sechuran foxes from Coto de Caza El Angolo, Piura (CDC Universidad Nacional Agraria Molina).

HB	670mm (500–780) n=4
T	292mm (270–340) n=4
SH	288mm (220–360) n=4
E	70mm (60–80) n=4
WT	3.6kg (2.6– 4.2) n=4

Subspecies Monotypic.

Similar species Chilla (*Pseudalopex griseus*): usually presents a rufous tinge on the face and muzzle and a black spot on the chin; muzzle slightly narrower. Hoary fox (*P. vetulus*): rufous face and muzzle; well-marked dark stripe along the dorsal line of the tail; general colour normally brighter.

Daniel Ascensios

Adult male Sechuran fox. Lambayeque, Peru, 2001.

Current distribution

The Sechuran fox can be found in the coastal zones of north-western Peru and south-western Ecuador, between 3 and 12°S (Figure 3.8.1). In Peru, it is distributed on the western slope of the Andes between the frontier with Ecuador and Lima. Specimens living further south may be the chilla or another species not yet described (E. Vivar pers. comm.).

Range countries Ecuador, Peru (Eisenberg and Redford 1999).

Relative abundance

Little known. This species was judged by Grimwood (1969) as abundant and not in need of protection. The species is easily observed in rural areas and disturbed environments from Piura department to La Libertad department in Peru. Surveys based on footprints in Coto de Caza El Angolo in Piura, Peru, show an average of 12.6 foxes per km (CDC 1989). The Sechuran fox is uncommon in Ecuador.

Estimated populations/relative abundance and population trends

Table 3.8.2. The status of Sechuran foxes in various regions (Population: A=abundant, C=common, U=uncommon; X=present but abundance unknown, ?=current presence not confirmed; Trend: S=stable, D=declining, ?=unknown).

Country	Population size	Trend
Ecuador	U	D
Peru	A	S
Tumbes Department	C	S
Piura Department	A	S
Lambayeque Department	A	S
La Libertad Department	A	S
Cajamarca Department	C	S
Ancash Department	X	?
Ica Department	?	?
Lima Department	U	?

Habitat

The Sechuran fox occupies habitats ranging from sandy deserts with low plant density to agricultural lands and dry forests (Cabrera 1931; Huey 1969; Langguth 1975).

Food and foraging behaviour

Food A generalist, omnivorous species, the Sechuran fox varies its diet opportunistically, preferentially consuming vertebrate prey or carrion when available, but often depending predominantly on seeds or seed pods. Studies during late winter and early spring in the inland Sechuran desert found droppings containing mainly the remnants of seeds or seed pods of *Prosopis juliflora* (algarrobo), *Capparis scabrida* (zapote) and *C. avicennifolia* (vichayo) (Huey 1969; Asa and Wallace 1990). Seeds in faeces were not digested, indicating that the syrupy matrix surrounding the seeds may be the actual source of nourishment. In a germination study (C. Asa unpubl.), seeds recovered from faeces sprouted earlier than those gathered from the ground, suggesting that the foxes not only act as seed dispersers, but affect the ability of the seeds to germinate rapidly when sporadic rains occur.

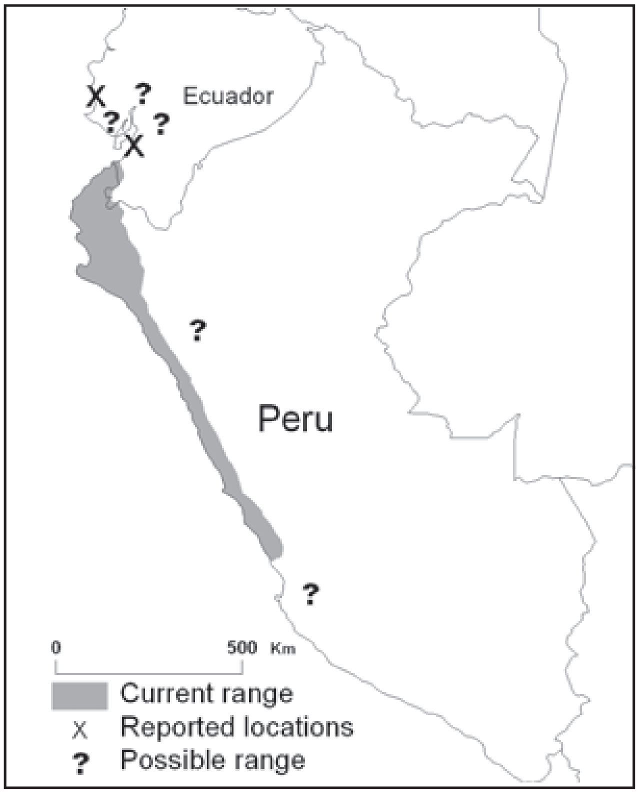

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Figure 3.8.1. Current distribution of the Sechuran fox.

Fox droppings along the coast contained crabs and several bird species, probably obtained as carrion that washed ashore (Huey 1969; Asa and Wallace 1990). However, following the El Niño rains of 1983/1984, fox droppings revealed a dramatic dietary shift to grasshoppers and mice (*Phyllotis gerbillus*) as these prey became more abundant (Asa and Wallace 1990). During summer in Reserva Nacional Lachay (coastal loma in central Peru), the main foods were insects, scorpions (*Carica candicans*), fruits and rodents (Asa and Wallace 1990). The lack of standing water in the inland desert habitat suggests that the foxes can survive without drinking. However, foxes may lick condensation from vegetation on foggy mornings.

Foraging behaviour The Sechuran fox is primarily nocturnal. Radio-telemetry data indicated that individuals emerged from daytime sleeping dens in rocky buttes before sunset and remained active through most of the night before re-entering dens at dawn (Asa and Wallace 1990).

The phases of the moon did not influence this activity pattern, perhaps because foxes were consuming seeds and seed pods rather than hunting. Occasionally, foxes can be seen during the day (Huey 1969; C. Asa and M.P. Wallace pers. obs.). No food caching has been recorded.

Damage to livestock or game Damage to poultry and guinea pigs has not been measured, but some rural habitants (principally of Lambayeque, La Libertad and Piura departments, Peru) often report such damage, principally from September to January (D. Cossíos unpubl.). There are no reports of damage to game.

Adaptations

In addition to the species' nocturnal activity, the small size and somewhat large ears of the Sechuran fox may also be adaptation to desert life. The species' ability to exist in areas with no standing water also attests to its adaptation to arid habitats.

Social behaviour

Little is known about the social behaviour of this species. Groups larger than three individuals are rare, and usually only observed in cases where food sources are concentrated. Of four radio-collared foxes, the home range of one adult male adjoined that of one adult female accompanied by two almost full-grown juveniles (one male and one female) (Asa and Wallace 1990). However, each individual foraged separately during the night and occupied separate, though nearby, dens during the day.

Reproduction and denning behaviour

Birdseye (1956) reported births occurring primarily in October and November. Abdominal distension suggested that one adult radio-collared female may have been pregnant when captured in August (Asa and Wallace 1990). If this female was indeed pregnant, it is significant that the adult male in the adjoining territory did not associate with her at that time, as might be expected if he was her mate. The male in her territory appeared to be juvenile, but could possibly have been her mate. However, the other juvenile within her territory was female, suggesting that both juveniles may have been her offspring from the previous breeding season.

Competition

Occasional competition with the culpeo (*P. culpaeus*) may arise when this species moves to the coast. There is probably competition with the chilla at the southern limit of its range.

Mortality and pathogens

Natural sources of mortality According to local reports boa constrictors prey on pups. Predation by other carnivores, like pumas (*Puma concolor*), other felids and culpeo foxes is possible in some areas, but pumas and jaguar (*Panthera onca*) are now uncommon in the Sechuran fox´s habitat. Large raptors in these areas normally prey on smaller animals (e.g., *Geranoetus melanoleucus*, *Sarcorhamphus papa*, *Buteo* spp., and others).

Persecution The Sechuran fox is persecuted in some zones where it is considered a predator of poultry, guinea pigs and other domestic animals.

Hunting and trapping for fur Although the use of this species for fur is not permitted, the illegal practice does exist though on a very small scale. Illegal hunting and trapping for making amulets and dissecting specimens is more extensive.

Road kills Road kills are common in northern Peru, but the number of the road kills is not estimated.

Pathogens and parasites Not known.

Longevity Not known.

Historical perspective

Shamans in northern Peru use dissected specimens or parts of the fox's body (e.g., paws, tails or heads), to perform traditional magic-religious rituals.

Conservation status

Threats The most important threats are from the market for handicrafts and amulets and from persecution because of damage to livestock. In Peru, the rural inhabitant's attitude towards the species is one of persecution (68.3% of correspondents) or indifference (31.7%). The stated reasons for persecution were due to damage on domestic fowl and guinea pigs (65% of correspondents), the consumption of vegetal or stored goods (13.3%), and the belief of goat predation (10%) (D. Cossíos unpubl.). The Sechuran fox also faces some pressure in agricultural zones and from urbanisation and habitat degradation; habitat reduction or loss is considered the principle threat to this species in Ecuador (Tirira 2001).

Commercial use Illegal sale of puppies, of amulets made from body parts, and of handicrafts made from fur occurs principally in the markets of Tumbes, Chiclayo, Piura and Lima city. The most common type of handicraft made with coastal fox parts consists of preserved adult animals in a "sitting" position. This activity is limited almost exclusively to the department of Piura, Peru.

The practice of magic-religious rituals by shamans involving preserved Sechuran fox specimens or parts is the principal human use of this species in Peru. The specimens are used to attract "good spirits" or "positive energies" during premonition rituals or to manufacture amulets, called seguros, with different purposes. Some shamans use also the Sechuran fox's fat for the treatment of bronchial illness and stomach disorders (D. Cossíos unpubl.).

Occurrence in protected areas

- *Ecuador*: Parque Nacional Machalilla, Manabí; Reserva Ecológica Manglares Churute, Guayas.
- *Perú*: Zona Reservada de Tumbes, Tumbes; Parque Nacional Cerros de Amotape, Tumbes; Coto de Caza el Angolo, Piura; Coto de Caza Sunchubamba, Cajamarca; Santuario Histórico Bosque de Pomac, Lambayeque; Zona Reservada Algarrobal el Moro, Lambayeque; Zona Reservada de Laquipampa, Lambayeque; Reserva Nacional de Calipuy, Ancash; Reserva Nacional de Lachay, Lima.

Protection status CITES – not listed.

Current legal protection Between 1975 and 2000, a governmental authorisation was required to hunt the species in Peru. Since 2000, hunting outside the established areas and trade of the species has been prohibited. The police and the Ministry of Agriculture are responsible for the control of illegal trade. However, it has proven especially difficult to control trade in rural areas and in some cities. Currently, there are no international treaties or conventions regarding this species.

Conservation measures taken The Sechuran fox was not traditionally protected, for cultural reasons, until recently. Now it is protected in Santa Catalina de Chongoyape, a rural community of Lambayeque department, because they are considered important for tourism and as seed dispersers (D. Cossíos unpubl.).

Occurrence in captivity

Some specimens are kept in the following authorised collections: Parque de las Leyendas Zoo, Lima (26 specimens) and Atocongo Zoo, Lima (3 specimens).

Current or planned research projects

E. Vivar (Museum of Natural History, U.N.M.S.M, Lima, Peru) is currently conducting research on the taxonomy and distribution of the Sechuran fox.

Investigations of its relationship with humans, its role in seed dispersal and its diet in Peru are being conducted by D. Cossíos (Instituto Nacional de Recursos Naturales – INRENA, Peru).

Core literature

Asa and Wallace 1990; Birdseye 1956; Cabrera 1931; Huey 1969; Langguth 1975.

Reviewers: Elena Vivar, Michael P. Wallace. **Editors:** Michael Hoffmann, Claudio Sillero-Zubiri.

3.9 Hoary fox
Pseudalopex vetulus (Lund, 1842)
Data Deficient (2004)

J. Dalponte and O. Courtenay

Other names

English: hoary zorro, small-toothed dog; **French:** renard du Brésil; **German:** Brasilianischer, kampfuchs; **Portuguese:** raposa-do-campo, raposinha (Brazil); **Spanish:** zorro de campo común; **Indigenous names:** Tupy: jaguarapitanga; Xavante: waptsã wa (Brazil).

Taxonomy

Canis vetulus Lund, 1842. K. Dansk. Vid. Selsk. Naturv. Math. Afhandl., 9:4. Type locality: Lagoa Santa, Minas Gerais [Brazil] (Cabrera 1958).

Burmeister (1854) created the genus *Lycalopex* for the hoary fox. Osgood (1934) reduced *Lycalopex* to a subgenus of *Dusicyon*, followed by Simpson (1945), Cabrera (1958) and Clutton-Brock *et al.* (1976). Langguth (1969, 1975) placed the species in *Lycalopex*, and Van Gelder (1978) included it in *Canis* (*Lycalopex*). Berta (1987) placed the species in *Pseudalopex* and was followed by Wozencraft (1993).

Chromosome number: 2n= 37 (Wurster-Hill and Benirschke 1968).

Description

The hoary fox is a slender animal with a relatively short, pointed muzzle, and large ears (Table 3.9.1). Pelage colour is variable: the upper body regions are pale grey, whereas the underparts are generally buff yellow to chestnut including the neck, chest and patch behind the ears. The anterior part of the neck is buff white, but the underside of

Table 3.9.1. Combined body measurements for the hoary fox from Pirapora (Minas Gerais), Franca (São Paulo) (Vieira 1946); Chapada dos Guimarães (Mato Grosso) (Thomas 1903); São Miguel (Minas Gerais) (Courtenay unpubl.); Nova Xavantina, Cuiabá, Chapada dos Guimarães (Mato Grosso), Arinos (Minas Gerais) (J. Dalponte unpubl.); Planaltina (Distrito Federal), São Miguel (Minas Gerais) (J. Marinho-Filho pers. comm.)

HB male	587mm (490–715) n=13
HB female	575mm (510–660) n=6
T male	338mm (270–380) n=13
T female	282mm (250–310) n=5
HF male	129mm (120–135) n=11
HF female	129mm (127–130) n=3
E male	69mm (60–76) n=10
E female	67mm (60–75) n=3
WT male	3.3kg (2.5–4) n=8
WT female	3.4kg (3.0–3.6) n=3

Hoary fox, age and sex unknown. São Paulo State, Brazil, 2003.

Adriano Gambarini

the lower jaw is dark, almost black, as is both the tail base and tail tip; a dark spot on dorsal surface of tail base variably present. Near melanic forms have been described (Cabrera 1931; Vieira 1946; Cabrera and Yepes 1960; J. Dalponte pers. obs.). Dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Monotypic (Stains 1975).

Similar species Crab-eating fox (*Cerdocyon thous*): sympatric throughout the geographical range of the hoary fox; more robust, larger (4.5–8.5kg), and has coarse bristly pelage; colour variation is substantial within and between populations, ranging from dark grey/black (e.g., Amazonia, central Brazil) to grey/yellow rufous (e.g., Ceará, north-east Brazil), with or without a dark dorsal line along the body to tail tip (specimens of the lighter colour type could be confused with the hoary fox); footpad (and footprint) differentiation of the two species is possible by the experienced field worker (Becker and Dalponte 1991). Pampas fox (*P. gymnocercus*): possibly sympatric with the hoary fox in southern São Paulo state; more robust and larger (4–6kg); pelage colour and body proportions are similar. Sechuran fox (*P. sechurae*): not sympatric, occurring in north-west Peru and south-west Ecuador; similar size (4–5kg), and pelage colour, but lacks the dark stripe along the dorsal line of the tail.

Current distribution

The hoary fox is confined to Brazil (Figure 3.9.1), associated with the cerrado habitats (mosaic of grasslands and xerophytic vegetation) of the central Brazilian plateau, and peripheral transitional zones including dry open habitats of the Pantanal (Mato Grosso state). Confirmed in the states of Minas Gerais, São Paulo, Mato Grosso do Sul, Mato Grosso, Tocantins and Goiás (J. Dalponte unpubl.), southern and western Bahia (Juarez and Marinho-Filho 2002; J. Dalponte pers. obs.), and western Piauí in Parque Nacional Serra da Capivara (F. Olmos pers. comm.). Capture records of an extant specimen held in Teresina Zoological Park indicate its northerly geographical limit is probably in north Piauí (Costa and Courtenay 2003). A previous report of its occurrence in Ceará (north-east Brazil) (Deane 1956) was contested by Courtenay *et al.* (1996). Records along the Brazil-Bolivian border in Mato Grosso (Anderson 1997) are unsubstantiated; the nearest record is 70km to the south in the Pantanal (Mato Grosso do Sul) (J. Dalponte unpubl.).

Figure 3.9.1. Current distribution of the hoary fox.

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Historical distribution A single fossil record exists from Vila de Lujan, Província de Buenos Aires, Argentina, dating back to the Lujanian period, late Pleistocene (Berta 1987). In Brazil, fossil records are those of Lund's expeditions in Lagoa Santa caves, Minas Gerais, southeast Brazil (Lund 1842).

Range countries Brazil (Cabrera 1958).

Relative abundance

There are no reliable data available. Locally abundant in the central highland cerrado biome, but populations appear smaller than those of the sympatric Crab-eating fox for which population estimates are similarly lacking.

Habitat

Occurs in open cerrado habitats, but readily adapts to insect-rich livestock pastures and areas of agriculture (soybean, rice, corn, eucalyptus plantation). Rarely observed in densely wooded cerrado, floodplains, dry or gallery forests.

Food and foraging behaviour

Food Omnivorous, though diet mainly of insects, particularly ground-dwelling harvester termites (*Synthermes* spp. and *Cornitermes* spp.), recorded in 87% of faeces collected in six localities across its geographical range (Dalponte 1997; Silveira 1999; Juarez and Marinho-Filho 2002; O. Courtenay unpubl.; J. Dalponte unpubl.). Dung beetles are consumed in great quantities when seasonally abundant. Other dietary items include small mammals, grasshoppers, birds and reptiles. Seasonal variation in most diet components has been noted (Dalponte 1997; Silveira 1999; Juarez and Marinho-Filho 2002; O. Courtenay unpubl.).

Foraging behaviour Hoary foxes are predominantly nocturnal and tend to hunt as individuals, or in loosely-knit pairs, with or without their juvenile offspring. Foraging group sizes of 3–5 were most common during periods of insect swarming (O. Courtenay unpubl.). They consume termites directly from the ground surface, or from the underside of dried disks of cattle dung which they flip over by pushing the dried disks along the ground at speed. Hoary fox cubs consume insects from the age of at least two months (O. Courtenay unpubl.). During the early rainy season, adult and young foxes catch swarming winged ant and termite elates, and dung beetles, on the wing by acoustic and visual location.

Damage to livestock or game There is no evidence that hoary foxes prey upon livestock or domestic fowl, despite their frequent close proximity to human dwellings (Dalponte 1997; Silveira 1999; Juarez and Marinho-Filho 2002; O. Courtenay unpubl.).

Adaptations

Small carnassials and wide crushing molars and the exceptionally large auditory bullae (Clutton-Brock *et al.* 1976) suggest adaptations to a predominantly insectivorous rather than larger prey-based diet. However, their cranio-dental morphology is not dissimilar to members of the *Dusicyon* [*Pseudalopex*] group (Clutton-Brock *et al.* 1976), which are not insectivorous. Whether their small size and slender build is an adaptation to, or consequence of, a small prey-base and/or hunting in grasslands is not known. Their preference for insects allows them to partition food resources and coexist with other sympatric canids such as the crab-eating fox and maned wolf (*Chrysocyon brachyurus*) (Juarez and Marinho-Filho 2002).

Social behaviour

Monogamous. One study group living in pasture comprised an adult breeding pair and five (3M:2F) juvenile offspring that shared largely overlapping home ranges of 4.6km² (range = 4.5–4.6km²) (O. Courtenay unpubl.). In Bahia, an adult female occupied a home range of 3.8km² (Juarez and Marinho-Filho 2002). Contact rates of a single breeding pair estimated by radio-telemetry indicated that they spend up to 35% of their activity period in close proximity, with substantial variation during offspring rearing (October to May) (O. Courtenay unpubl.). Spot sightings in different habitats and localities revealed that groups were composed of single animals on 75% of occasions, followed by pairs (30%), and groups larger than two (4%) (J. Dalponte and E. Lima unpubl.).

Vocalisations include a roar and threat bark; vocalisations are most common during the mating season (J. Dalponte unpubl.). Hoary foxes urinate using a raised leg urination position; frequent urination in small quantities is typical of territory marking behaviour (J. Dalponte unpubl.).

Reproduction and denning behaviour

In the wild, females produce litters of 4–5 offspring once a year during July and August, at observed male:female sex ratios of 4:2 (O. Courtenay unpubl.), and 2:2 (J. Dalponte and E. Lima unpubl.). A similar parturition season (September/mid-October) occurs in captive animals, with litter sizes of 3–4 (n=2) (Coimbra-Filho 1966, J. Dalponte pers. obs.). The precise length of the gestation period is not known, but mating occurs in late May/early June suggesting that it falls within the range of other members of the *Pseudalopex* group (53–60 days).

Pups are born in dens in disused armadillo holes, particularly that of the yellow armadillo (*Euphractus sexcinctus*) (n=5 social groups, J. Dalponte and E. Lima unpubl., O. Courtenay unpubl.). Offspring are cared for by the breeding male and female; there is currently no evidence of helpers. In one case, a lone breeding female was observed to successfully nurse and rear four cubs to six months of age (J. Dalponte and E. Lima unpubl.). During late lactation, the female visits the den perhaps a couple of times per night to nurse; in her absence, the male baby-sits, grooms and guards the cubs against potential predators (O. Courtenay unpubl.). Post-weaning, adult gender roles change: female contact declines substantially, whereas the male stays with the cubs as chaperone during hunting expeditions to insect patches close to the den (O. Courtenay unpubl.). The estimated lactation period in the wild is three months indicated by the cessation of nursing in mid-November (O. Courtenay unpubl.). Juveniles of both sexes disperse in May when 9–10 months old and may establish home-ranges adjacent to their natal territory (J. Dalponte and E. Lima unpubl., O. Courtenay unpubl.).

Competition

The main competitors are likely to be the similarly sized crab-eating fox (4.5–8.5kg) and the larger-sized maned wolf (23kg) which often occur in sympatry. Inter-specific divergence in diet composition appears to allow these three canid species to coexist (Juarez and Marinho-Filho 2002). Adult hoary foxes with their young have been observed to tolerate the presence of crab-eating foxes at insect foraging grounds (Courtenay *et al.* unpubl.). Due to its predominantly insectivorous diet, the hoary fox potentially competes also with the large guild of myrmecophagous predators of the cerrado biome. However, the latter group tend to forage termite species that are mound builders and produce chemical secretions, making them largely inaccessible to the hoary fox.

Mortality and pathogens

Natural sources of mortality Hoary fox remains (hairs, teeth and bone fragments) have been identified in 0.3–4% of maned wolf faeces from three different sites in Central Brazil: Parque Nacional de Chapada dos Guimarães (J. Dalponte and E. Gomes da Silva unpubl.), Parque Nacional de Emas (Silveira 1999; A.T. Jácomo pers. comm.), and Parque Nacional Grande Sertão Veredas (J. Dalponte unpubl.), suggesting that maned wolves are opportunist consumers of hoary foxes, presumably as scavengers. It is debatable that maned wolves actively hunt live adult foxes. Hoary foxes are not represented in stomach contents or faeces of large predatory birds or large felines, though Xavante hunters in the Rio das Mortes Indigenous Reserve, Mato Grosso state, reported at least one fox being killed and eaten by a puma (*Puma concolor*) (E. Lima pers. comm.).

Persecution Hoary foxes are killed indiscriminately as predators of domestic fowl, although they probably earn this reputation from crab-eating foxes which are formidable thieves (Courtenay and Maffei chapter 3.2 this volume). Young foxes are often taken as pets, and domestic dogs are responsible for cub deaths when dens are located in peri-urban areas.

Hunting and trapping for fur Occasional hunting occurs as a predator control measure, but populations are not trapped for fur.

Road kills In north-east São Paulo state, seven hoary fox deaths were recorded along 13,500km of road between January 1981 and December 1983, with a ratio of crab-eating to hoary foxes of about 10:1 (J. Dalponte and J.A. Tavares-Filho unpubl.). The proportion of male to female hoary foxes in an additional sample of 19 road-killed foxes in central Brazil was approximately 2:1 (J. Dalponte unpubl.).

Pathogens and parasites Population declines due to pathogen infection have not been documented; however, at least one death due to sarcoptic mange is thought to have occurred in the Serra da Canastra (J. Dietz pers. comm.). Two other individuals, a female and her infant, which had been radio-tracked in the Rio Pratudão ranch, Posse, W Bahia, seemingly died following a sarcoptic mange infection that was also seen to infect at least one maned wolf (J. Marinho-Filho pers. comm.). Reports of hoary fox infection with the rabies virus and the protozoan parasite *Leishmania infantum* in the state of Ceará (Deane 1956; Barros *et al.* 1989) almost certainly refer to crab-eating fox and not hoary fox (Courtenay *et al.* 1996). Disease outbreaks due to other common canid pathogens (e.g., canine distemper virus and canine parvovirus) have not been reported in the wild. Other documented parasites of hoary foxes include *Trypanosoma cruzi* (Albuquerque and Barretto 1970), and *Angiostrongylus vasorum* found in eight animals captured in Minas Gerais (Lima *et al*. 1994).

Longevity No information available, however an eight-year-old captive female (in August 2002) was observed in Teresina Zoological Park (Costa and Courtenay 2003).

Historical perspective

Unknown.

Conservation status

Threats The principal biome where hoary foxes occur is the cerrado which is being destroyed at a rate of 3% each year, largely in the interests of agriculture (livestock and soybean) (MMA-BRASIL 1998). It appears that hoary foxes adapt to livestock pasture rich in termites and dung beetles. Breeding hoary foxes are found in deforested wooded areas (J. Dalponte pers. obs.), thus it is possible that deforestation may not have a negative impact on the species. Areas of high human population density are unlikely to be suitable. There are no population estimates available.

Commercial use Not exploited for fur or any other products.

Occurrence in protected areas *Brazil:* Parque Nacional de Chapada dos Guimarães, Parque Nacional da Serra da Capivara, Parque Nacional da Serra da Canastra, Parque Nacional de Emas, Parque Nacional Grande Sertão Veredas, Estação Ecológica de Águas Emendadas, Parque Nacional de Brasília, Refúgio de Vida Silvestre da Fazenda Nhumirim e RPPN do Rio Negro, Parque Estadual da Serra do Lageado, Parque Estadual de Santa Bárbara, Santuário de Vida Silvestre do São Miguel, Fazenda São Miguel.

Protection status CITES – not listed.
Listed as "Vulnerable" by the Canid Conservation Assessment and Management Plan (CAMP) 1993 meeting in São Paulo; "Vulnerable" in individual state faunal status accounts, but not listed in the Brazilian official list of threatened mammals (Fonseca *et al*. 1994).

Current legal protection Hunting and trade in wildlife is generally forbidden in Brazil. There is no specific hunting legislation for hoary foxes.

Conservation measures taken Nothing proposed. No cultural protection reported.

Occurrence in captivity

Specimens in Brazilian zoos at the time of writing include: Brasilia (1); São Paulo (1); Ribeirão Preto (1); Belo Horizonte (5); Teresina (1). High mortality rates due to starvation amongst captive cubs are reported. There are no current plans to reintroduce hoary foxes into the wild.

Current or planned research projects

J. Dalponte (Universidade de Brasília, Brazil) is currently studying the ecology and behaviour of the hoary fox in Mato Grosso, Brazil.

Gaps in knowledge

Areas for further research include focusing on aspects of behavioural ecology, population status, geographical range, the potential role of disease in population regulation, and their status as potential reservoirs of veterinary (e.g., scabies, distemper) and public health (e.g., leishmaniasis, rabies) pathogens.

Core literature

Costa and Courtenay 2003; Dalponte 1997, 2003; Juarez and Marinho-Filho 2002; Silveira 1999.

Reviewers: Louise Emmons, Jader Soares Marinho-Filho.
Editors: Claudio Sillero-Zubiri, Michael Hoffmann.

3.10 Bush dog
Speothos venaticus (Lund, 1842)
Vulnerable – VU: C2a(i) (2004)

G.L. Zuercher, M. Swarner, L. Silveira
and O. Carrillo

Other names

English: vinegar dog, savannah dog; **Dutch:** boshond, busdagoe (Suriname); **French**: chiens des buissons, zorro; **German**: waldhund; **Italian:** speoto, itticione; **Portuguese:** cachorro-do-mata, cachorro-do-mato-vinagre, cachorro-do-mato-cotó, cachorro-pitoco (Brazil); **Spanish:** zorrito vinagre (Argentina); zorro/perro vinagre, perro/perrito de monte (Bolivia/Ecuador/Venezuela); perrito venadero, umba (Colombia); perro de la selva, pero selvático, perro de agua, Guanfando (Ecuador – origin undetermined); **Indigenous languages:** Cubeo: maca tawimi, Huitoto: itón+maido, Shuku: puinave, Yucuna: huerateyaniminami (Colombia); Achuar: tuwen'k, patukam yawa, Chachi: pikucha, Huaorani: babeguinta, Quichua: sacha alcu, Secoya: airo jo'ya, masioco yai (Ecuador); Aché: mbetapa, Guarani: jagua yvyguy (Paraguay); Amarakaeri: dumba cuhua, cuan cuan, Shibipo: hueshes (Peru).

Taxonomy

Cynogale venatica Lund, 1842. K. Dansk. Vid. Selsk. Naturv. Math. Afhandl. 9:67. Type locality: "Lagoa Santa" [Minas Gerais, Brazil, *c.* 19°39'S, 43°44'W].

The bush dog is accepted as the sole extant representative of the monotypic genus *Speothos*. *Speothos pacivorus* Lund, 1839, an extinct species, is known only from fossil deposits discovered at the Lagoa Santa caves in Minas Gerais, Brazil, and may not have existed past the Holocene (Berta 1984). This is the same site for the type locality specimen of *S. venaticus*. The two species are distinguished by several dental features, including the presence of a metaconule and hypocone on M_1, a large, double-rooted M_2, as well as the larger size of *S. pacivorus* (Berta 1987). A third species, *S. major* (Lund 1843), is now considered synonymous with *S. venaticus* (Berta 1984).

The taxonomic relationship of bush dogs to other canids remains debatable. The presence of a unicuspid M_1 talonid led to the inclusion of the bush dog in the subfamily Simocyoninae, along with two other species that share this characteristic, the African wild dog (*Lycaon pictus*), and dhole (*Cuon alpinus*). Berta (1984, 1987) suggested bush dogs are most closely related to small-eared dogs (*Atelocynus microtis*), and members of the *Cerdocyon* clade (one of four monophyletic groups of South American canids). This group includes the raccoon dog (*Nyctereutes procyonoides*). Berta (1987) suggests a single ancestor for this group, ranging over Eurasia and North America, with isolation of the raccoon dog occurring when the Bering Land Bridge disappeared. Recent molecular analyses,

Adult male (front) and female (behind) bush dog. Oklahoma City Zoo, USA.

Gerald L. Zuercher

based on mitochondrial DNA, suggest bush dogs and maned wolves (*Chrysocyon brachyurus*) constitute a monophyletic group distinct from other South American canids (Wayne *et al*. 1997).

Chromosome number: 2n=74 (Schreiber and Dmoch 1994).

Description

The bush dog is characterised by an elongate body, a short and sometimes stubby tail, broad face with short muzzle, small rounded ears, brown eyes, and short legs (Table 3.10.1). Head and neck are generally reddish/tan or tawny, gradually darkening to black or dark brown hindquarters and legs. The underside is also dark and some individuals may show a pale white throat (i.e., Bolivia) or chest patch. Coat patterns can, however, be highly variable, ranging from almost all black to very light blonde. Feet are partially webbed and tracks are nearly identical to those of the domestic dog. Bush dogs are one of three canid species with trenchant heel dentition, a unicuspid talonid on the lower carnassial molar that increases the cutting blade length. Dental formula is 3/3-1/1-4/4-2/2=40.

Table 3.10.1. Body measurements for the bush dog from Paraguay (Van Humbeck and Perez 1998; Nowak 1999).

HB	630mm (575–750)
T	140mm (125–150)
E	30mm
SH	200mm (200–300)
WT	5–8kg

Subspecies Three subspecies are recognised (Cabrera 1961).

- — *S. v. panamensis* (Panama)
- — *S. v. venaticus* (Argentina, Bolivia, northern and central Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Suriname, Venezuela).
- — *S. v. wingei* (south-eastern Brazil).

Similar species Short-eared fox (*Atelocynus microtis*): distinguished by a grizzled, blackish/grey coat, erect pointed ears, longer legs, and a bushy tail long enough to touch the ground. Tayra (*Eira barbara*): longer bushy tail and a yellow throat and head patch.

Current distribution

This species occurs from extreme eastern Central America and northern South America, south to Paraguay and north-eastern Argentina (Figure 3.10.1). Isolated populations may also still occur in Ecuador (Tirira 2001) and Colombia, west of the Andes. However, historical distribution may have extended as far north as Costa Rica (De la Rosa and Nocke 2000), where the species may still survive in suitable habitat.

Range countries Argentina, Bolivia, Brazil, Colombia, Costa Rica (?), Ecuador, French Guiana, Guyana, Panama, Paraguay, Peru, Suriname, Venezuela (Fonseca and Redford 1984; Defler 1986; Strahl *et al*. 1992; Aquino and Puertas 1997; Silveira *et al*. 1998; De la Rosa and Nocke 2000; Barnett *et al*. 2001; Tirira 2001; Zuercher and Villalba 2002).

Figure 3.10.1. Current distribution of the bush dog.

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Relative abundance

Although there is currently no information available regarding the species' density, it is important to note that, despite its large distributional range and occurrence in a variety of habitats (i.e., cerrado and rainforest), the species has never been reported as abundant. Thus, it seems to be naturally rare throughout its range, independent of human disturbance.

Habitat

Bush dogs are reported to be a habitat generalist by indigenous peoples, within the context of occurring generally near water sources, particularly small streams, and near available prey populations, especially *Agouti paca* (O. Carrillo and M. Swarner pers. obs.). Bush dogs have been observed in lowland (below 1,500m a.s.l.) forested habitats including primary and gallery forest (Defler 1986), semi-deciduous forest, and seasonally flooded forest (Aquino and Puertas 1997). Observations have also been recorded from cerrado habitat in Brazil (Silveira *et al*. 1998; C. Brady pers. comm.) and Paraguay (Zuercher and Villalba 2002) and pampas (wet savannah) edge/riparian areas (Strahl *et al*. 1992; Emmons 1998). In some cases, they have been observed as far as 5,700m from forest habitat (Silveira *et al*. 1998). The species is also occasionally reported from secondary forest, ranchland (M. Swarner pers. obs.) and fragmented cerrado ranchland (L. Silveira and A. Jácomo pers. comm.).

Food and foraging behaviour

Food Primarily carnivorous, bush dogs are most commonly observed hunting large rodents such as paca (*Agouti paca*) and agouti (*Dasyprocta* spp.) (53.1% and 28.1%, respectively, of reported sightings in central western Amazonia; Peres 1991). Their diet may also include small mammals (i.e., rats, *Oryzomys* spp. and *Proechimys* spp., rabbits, *Sylvilagus brasiliensis*, opossums, *Didelphis* spp. and nine-banded armadillo *Dasypus novemcinctus*; Van Humbeck and Perez 1998; Zuercher and Villalba 2002). Other prey items include teju lizards (M. Swarner pers. obs.), snakes, and possibly ground-nesting birds. Local people report that bush dogs can take prey considerably larger than themselves such as capybaras (*Hydrochaeris hydrochaeris*), and rheas (*Rhea americana*), as well as deer (*Mazama* spp.), and possibly even tapir (*Tapirus terrestris*) (R. Wallace pers. comm.) by hunting in packs (Deutsch 1983; Peres 1991; Strahl *et al*. 1992). Their diet is reported to vary seasonally.

Foraging behaviour Peres (1991) reported 92% of observed bush dog hunting parties consisted of at least two individuals (mean=4.5; range=2–8). Local people describe a variety of cooperative hunting strategies employed by bush dogs (M. Swarner unpubl.). For example, in Bolivia, they are commonly reported to hunt *Mazama* deer by attacking the legs until the animal tires and falls. Olfaction may play a large role when foraging. When hunting burrowing animals, some individuals reportedly enter the prey's burrow while other pack members wait at possible escape routes. Once flushed, prey is pursued with seemingly relentless endurance by the pack, even into deep water. Solitary hunting has been observed (Deutsch 1983).

Damage to livestock or game In Bolivia and Ecuador, bush dogs are considered predators of chickens (M. Swarner pers. obs.).

Adaptations

Modified carnassial teeth suggest an exclusively carnivorous diet. Webbed feet suggest swimming capability and imply that large rivers do not represent barriers to distribution (Strahl *et al*. 1992). Small compact body may be an adaptation to pursue burrowing prey and navigate through dense forest. Stocky, muscular neck may aid in prey capture or extraction from burrows. Dark coat colour is a reported general adaptation to humid, forest environments. Nomadic behaviour may reflect responses to changing densities of favoured prey species as well as avoidance of competitors and/or predators.

Social behaviour

Although solitary individuals have been observed, the bush dog is considered the most social of the small canids (Ginsberg and Macdonald 1990; Sheldon 1992), reportedly living in groups ranging from 2–12 individuals with most observed groups comprising 2–6 members (M. Swarner unpubl.; L. Silveira pers. obs.). Captive bush dogs, too, are compulsively social, rarely spending more than a few minutes from companions (Macdonald 1996). Strahl *et al*. (1992) state that the bush dog is probably a cooperative species, and report observations by indigenous hunters and colonists in Venezuela of bush dogs hunting in groups of up to six individuals. The ability of a pack to subdue larger prey appears to be a primary benefit of sociality for bush dogs (Kleiman 1972; Drüwa 1983).

Drüwa (1983) suggests a monogamous pair-bond is likely with multiple years' offspring living with the pair at any given time. A mostly diurnal species, the pair and any family members spend the night in a den (Kleiman 1972; I. Porton pers. comm.). Males exhibit a high degree of parental care that includes food supplementation to females prior to birth and throughout nursing (I. Porton pers. comm.). Silveira *et al*. (1998) estimate the home range as between 4.56 and 4.72km^2; this estimate is derived from a canid home range regression based on body mass by Gittleman and Harvey (1982).

Porton (1983) suggests urine marking is important in formation and maintenance of pair-bonds. Indigenous people report a strong smell associated with bush dogs (Swarner unpubl.), lending further evidence that urine is a particularly effective communication medium for this species. Sex-specific urine-marking behaviour characterises bush dogs. Males extrude the penis and move laterally, creating a spray rather than a stream (Kleiman 1972). Females drag the ano-genital region over a surface or display either a forelimb handstand or a squat. The raised posture of the female allows urine to be deposited approximately 150mm higher than the spray of the male (Kleiman 1972).

Adult bush dog vocalisations have been classified into six categories: (1) whines; (2) repetitive whines; (3) pulsed vocalisation; (4) screams; (5) barks; and (6) growls (Brady 1981). Infant vocalisations include whines, grunts, growls, and barks and are thought to either elicit care or reduce aggression. Habitat and social organisation are thought to influence the physical structure of bush dog vocalisations. The elaborate set of close-range vocalisations assists in communicating subtle changes in mood as well as changes in location (Kleiman 1972; Brady 1981). The use of this close-contact call has been noted in a bush dog group travelling through tall grass during the day in Colombia (Defler 1986). Bush dogs also have a vocalisation similar to the short-distance vocalisation (Brady 1981) but at a different frequency. This particular vocalisation has been reported from Paraguay during the early morning (K. DeMatteo pers. comm.) and night (Beccaceci 1994).

Reproduction and denning behaviour

Free-ranging bush dogs have an unknown mating season, although pups have been found in the wet season (M. Swarner pers. obs.). The majority of information regarding bush dog reproduction comes from captive studies. Captive females have two oestrous cycles per year (Kleiman 1972), demonstrating the species' physiological potential. Oestrus is aseasonal and likely influenced by social factors (Porton *et al.* 1987). Dominant females appear to suppress the oestrus of daughters (Porton *et al.* 1987; Macdonald 1996). Gestation is 67 days, and mean litter size is 3.8 (range=1–6). Lactation lasts approximately eight weeks. Bush dogs are believed to be sexually mature by one year.

Competition

No direct measures of competition are available. However, there is a high degree of overlap in the reported diets of bush dogs and many other Neotropical carnivore species and humans. This potential competition with humans for food resources may partially explain the absence of bush dogs near human settlements. Den-site competition is unlikely as the species is considered very nomadic and often reported to use pre-existing burrows of paca or armadillos. Direct interactions with sympatric carnivore species are unknown.

Mortality and pathogens

Natural sources of mortality Indigenous peoples in Paraguay, Bolivia, and Ecuador report finding bush dogs killed by jaguars and puma.

Persecution Bush dogs are occasionally killed in Bolivia and Ecuador for depredation of chickens (M. Swarner pers. obs.).

Road kills No substantial data exist to quantify bush dog susceptibility to automobile collisions. However, in Brazil, bush dogs have been found as road kills (L. Silveira, pers. obs.).

Hunting and trapping for fur The bush dog is not currently, nor was it historically, valued for its pelt. Local people report that they were an extremely rare by-catch during the pre-1978 spotted-cat skin trade.

Pathogens and parasites Known disease-causing organisms and parasites of bush dogs include bacteria (*Escherichia coli, Proteus vulgaris, Staphylococcus aureus, S. epidermis, Klebsiella* sp., *Shigella* sp.), protozoans (*Giardia* sp.), fungi (*Candida* sp.) (Van Humbeck and Perez 1998), nematodes (*Lagochilascaris* sp.) and cestodes (*Echinococcus* sp.) (Volcán and Medrano 1991). Captive individuals also have shown susceptibility to parvovirus (Janssen *et al.* 1982) and vaccine-induced canine distemper virus (McInnes *et al.* 1992).

Longevity A captive bush dog reportedly lived for more than 13 years (Jones, in Nowak 1999), but is likely to be around 10 years in the wild.

Historical perspective

Indigenous people have occasionally kept bush dogs as pets and hunting dogs, emphasising their superior hunting abilities when pursuing burrowing prey, especially paca and armadillos (M. Swarner unpubl.). However, other informants report that bush dogs are difficult or impossible to domesticate because of the fierceness, all-meat diet, or susceptibility to domestic dog diseases.

Some lowland Quichua of eastern Ecuador report that bush dogs have owners like any domestic dog (M. Swarner pers. obs.). The "owners" are referred to as *sacha runa* (forest people or spirits) and use them as hunting dogs. Due to this belief, some Quichua are reluctant to capture or kill bush dogs because it would be equivalent to stealing or killing a neighbour's hunting dog.

Many indigenous peoples consider the bush dog to be one of the best hunters in the forest, sometimes singing songs to their own dogs in hopes of passing on the bush dog's skills (Descola 1996). Human hunters often report killing prey pursued by bush dogs whenever encountered and taking it for themselves, even following the bush dog's high-pitched hunting barks in the hope of a stealing opportunity (M. Swarner unpubl.).

Conservation status

Threats Only serious perceived threat is from habitat conversion and human encroachment.

Commercial use None known.

Occurrence in protected areas

— *Argentina:* Iguazu National Park and Urugua-í Provincial Park;
— *Bolivia:* Carrasco National Park, Amboro National Park, Rios Blancos and Negros Reserve, Beni Biosphere Biological Station and Reserve and Madidi National Park, and Noel-Kempff Mercado National Park;
— *Brazil:* Emas National Park, Iguaçu National Park, Cantão State Park, Tocantins State and Serra das Araras State Park, Mato Grosso, IGBE's Ecological Reserve, Gurupi Biological Reserve, Amazonia National Park, Rio Trombetas Biological Reserve, Tapirapé Biological/Tapirapé-Aquiri National Forest, and Mirador State Park; *Colombia:* Tuparro National Park;
— *Ecuador:* Sumaco-Napo Galeras National Park (Centro de Datos para la Conservación del Ecuador), Yasuni National Park, Cotocachi-Cayapas Ecological Reserve, and Cuyabeno Faunistic Reserve;
— *Guyana:* Kaieteur National Park;
— *Paraguay:* Reserva Biosfera del Bosque Mbaracayú, San Rafael National Park, Reserva Privada Golondrina, Reserva Natural Privada Morombi, Reserva Natural Privada Ypeti, and Reserva Natural Privada Ka'I rague;
— *Peru:* Tamshiyacu-Tahuayo Communal Reserve, and National Reserve of Pacaya-Samiria, Biabo Cordillera Azul Reserve, Centro Río Amigos, and Bahauja-Sonene National Park and Tambopata Candamo Reserve;
— *Venezuela:* Canaima National Park.

Protection status CITES – Appendix I (2000).
Declared "Vulnerable" in Argentina (Beccaceci, in Ginsberg and Macdonald 1990).

Current legal protection Hunting is prohibited in Colombia (Law Number 848:1973), Ecuador (Law Number 74:1981), French Guiana (Law Number JO19860625:1986), Panama (Law Number 2-80:1980), Paraguay (Law Number 18796:1975) and Peru (Law Number 5056:1970). Hunting and trade is regulated in Argentina (Law Number 22.421:1981), Bolivia (Law Number 12301:1975), Brazil (Law Number 5197:191967), and Venezuela (Law Number 276:1970). There is no Information for Guyana and Suriname.

Conservation measures taken None known.

Occurrence in captivity

Bush dogs do occur in captivity and are breeding successfully. No known attempts at reintroduction.

Current or planned research projects

G. Zuercher (Kansas Cooperative Fish and Wildlife Research Unit, Kansas State University and Sunset Zoological Park, Manhattan, Kansas, USA), with additional support by Sedgwick County Zoo (Wichita, Kansas), and the American Zoo and Aquarium Association, is investigating the ecological role of the bush dog as part of a greater mammalian carnivore community within the Interior Atlantic Forest of eastern Paraguay.

L. Silveira (Pró Carnívoros, São Paulo, Brazil), A. Jácomo (Pró Carnívoros), and C. Brady (Memphis Zoo, Memphis, Tennessee, USA) are exploring the distribution and conservation of bush dogs within the Brazilian cerrado biome, where conservation units of confirmed bush dog presence are being examined, and potential corridor sites are being identified. The project is sponsored by Pró Carnívoros and Memphis Zoo (Memphis, Tennessee, USA).

M. Swarner (University of Maryland, College Park, Maryland, USA) undertook an inventory of indigenous knowledge of bush dogs throughout western Amazonia between July 2000 and August 2001 (a study supported by the Thomas J. Watson Foundation).

K. DeMatteo (St. Louis Zoo and St. Louis University, St. Louis, Missouri, USA) is continuing an ongoing captive study to investigate the reproductive physiology of female bush dogs and the role of social stimulation in ovulation.

Gaps in knowledge

The distribution of bush dogs should be re-evaluated. There are no population estimates or demographic data for bush dogs in any of their range countries. Our understanding of dietary habits is based mostly on anecdotal information and does not address seasonal or geographic variation. Habitat associations are not clearly understood – the species was once thought to be dependent on forests but is now regularly observed in open habitats. The impact of disease, both historically and currently, is unclear (this is especially true for diseases introduced by domestic animals). Accepted ideas of behaviour and social structure, obtained from captive animals, have not yet been verified in wild populations. Interspecific relationships with sympatric carnivores need to be further evaluated.

Core literature

Aquino and Puertas 1997; Brady 1981; Drüwa 1983; Kleiman 1972; Macdonald 1996; Porton 1983; Silveira *et al*. 1998; Strahl *et al*. 1992; Van Humbeck and Perez 1998.

Reviewers: Melissa Rodden; Karen DeMatteo. **Editors:** Michael Hoffmann, Claudio Sillero-Zubiri.

Chapter 4

Central and North America (Nearctic)

4.1 Coyote
Canis latrans Say, 1823
Least Concern (2004)

E.M. Gese and M. Bekoff

Other names

English: brush wolf, prairie wolf, American jackal; **Spanish:** coyote; **Indigenous names:** Aztec: coyotl; Maya: pek'i'cash (Central America); Cree and Saulteaux: mista-chagonis; Dakota: mica or micaksica; Omaha: mikasi; Mandan: scheke; Hidatsa: motsa; Arikarus: stshirits pukatsh; Klamath: ko-ha-a; Piute: eja-ah; Chinook: italipas; Yakima: telipa; Flathead: sinchlep (North America) (Young and Jackson 1951; Reid 1997).

Taxonomy

Canis latrans Say, 1823 (described by Thomas Say in Long and Long 1823:168). Type locality: "engineer cantonment"...reported in Young and Jackson (1951) as "about 12 miles south-east of the present town of Blair, Washington County, Nebraska..."

"By the late Pliocene, the ancestral coyote, *Canis lepophagus*, was widespread throughout North America" (Bekoff 1982). In the north-eastern United States, the eastern coyote may be a subspecies having coyote ancestry with some introgression of wolf and dog genes (Hilton 1978; Wayne and Lehman 1992; but see Thurber and Peterson 1991; Larivière and Crête 1993).

Chromosome number: 2n=78 (Wayne *et al*. 1987).

Description

Coyotes appear slender with "a long, narrow, pointed nose; small rounded nose pads; large pointed ears; slender legs; small feet; and a bushy tail..." (Young and Jackson 1951). Size varies geographically (Young and Jackson 1951) (Table 4.1.1), although adult males are heavier and larger than adult females. They range in colour from pure grey to rufous; melanistic coyotes are rare (Young and Jackson 1951). Fur texture and colour varies geographically: northern subspecies have long coarse hair, coyotes in the desert tend to be fulvous in colour, while coyotes at higher latitudes are darker and more grey (Young and Jackson 1951). The belly and throat are paler than the rest of the body with a saddle of darker hair over the shoulders. The tip of the tail is usually black. Hairs are about 50–90mm long; mane hairs tend to be 80–110mm long. Pelage during

Table 4.1.1 Body measurements for the coyote.

	Las Animas County, Colorado, USA (E.M. Gese unpubl.)	**Maine, USA** (Richens and Hugie 1974)
HB male	842mm (740–940) n=38	888 mm, n=26
HB female	824mm (730–940) n=36	836 mm, n=21
T male	323mm (290–350) n=10	363 mm, n=26
T female	296mm (260–340) n=10	343 mm, n=21
HF male	186mm (180–200) n=6	209 mm, n=23
HF female	180mm (170–190) n=6	197 mm, n=21
WT male	11.6kg (7.8–14.8) n=86	15.8kg, n=28
WT female	10.1kg (7.7–14.5) n=73	13.7kg, n=20

David Shackleton

Adult coyote, sex unknown, in full winter coat. Manning Provincial Park, British Columbia, Canada.

summer is shorter than in winter. The dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Young and Jackson (1951) recognised 19 subspecies. However, the taxonomic validity of individual subspecies is questionable (Nowak 1978).

— *C. l. latrans* (Great Plains region of the U.S. and southern Canada)
— *C. l. ochropus* (west coast of the U.S.)
— *C. l. cagottis* (south-eastern Mexico)
— *C. l. frustror* (parts of Oklahoma, Texas, Missouri, Kansas in the U.S.)
— *C. l. lestes* (intermountain and north-west U.S., south-west Canada)
— *C. l. mearnsi* (south-western U.S., north-western Mexico)
— *C. l. microdon* (north-eastern Mexico, southern Texas in the U.S.)
— *C. l. peninsulae* (Baja California of Mexico)
— *C. l. vigilis* (south-western Mexico)
— *C. l. clepticus* (Baja California of Mexico)
— *C. l. impavidus* (western Mexico)
— *C. l. goldmani* (southern Mexico, Belize, Guatemala)
— *C. l. texensis* (Texas and New Mexico in the U.S.)
— *C. l. jamesi* (Tiburon Island, Baja California of Mexico)
— *C. l. dickeyi* (El Salvador, Honduras, Nicaragua, Costa Rica)
— *C. l. incolatus* (Alaska in the U.S., north-western Canada)
— *C. l. hondurensis* (Honduras)
— *C. l. thamnos* (Great Lakes region of the U.S. and Canada, north central Canada)
— *C. l. umpquensis* (west coast of north-western U.S.)

Similar species Coyotes can be confused with grey wolves (*C. lupus*), red wolves (*C. rufus*), and domestic dogs. Coyotes usually can be differentiated from these congenerics using serologic parameters, dental characteristics, cranial measurements, neuroanatomical features, diameter of the nose pad, diameter of the hindfoot pad, ear length, track size, stride length, pelage, behaviour, and genetics (Bekoff 1982; Bekoff and Gese 2003; and references therein). Coyotes may be differentiated from domestic dogs using the ratio of palatal width (distance between the inner margins of the alveoli of the upper first molars) to the length of the upper molar tooth row (from the anterior margin of the alveolus of the first premolar to the posterior margin of the last molar alveolus) (Howard 1949; Bekoff 1982; and references therein). If the tooth row is 3.1 times the palatal width, then the specimen is a coyote; if the ratio is less than 2.7, the specimen is a dog (this method is about 95% reliable) (Bekoff 1982). Unfortunately, fertile hybrids are known between coyotes and dogs, red and grey wolves, and golden jackals (Young and Jackson 1951; Bekoff and Gese 2003; and references therein).

Grey wolf (*C. lupus*): larger than coyotes, though with a relatively smaller braincase; nose pad and hindfoot pads are larger (Bekoff 1982; and references therein). There is no overlap when comparing large coyotes to small wolves in zygomatic breadth, greatest length of the skull, or bite ratio (width across the outer edges of the alveoli of the anterior lobes of the upper carnassials divided by the length of the upper molar toothrow) (Paradiso and Nowak 1971; Bekoff 1982; and references therein).

Red wolf (*C. rufus*): usually larger than coyotes with almost no overlap in greatest length of skull; more pronounced sagittal crest (Bekoff 1982; and references therein).

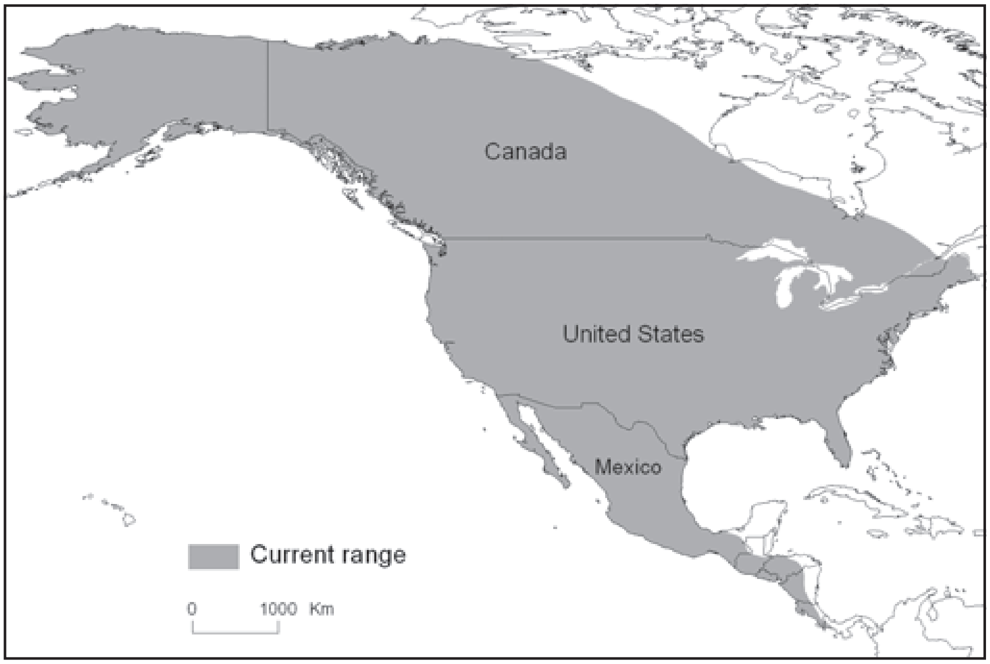

Figure 4.1.1. Current distribution of the coyote.

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Distribution

Historical distribution Coyotes were believed to have been restricted to the south-west and plains regions of the U.S. and Canada, and northern and central Mexico, prior to European settlement (Moore and Parker 1992). During the 19th century, coyotes are thought to have expanded north and west. With land conversion and removal of wolves after 1900, coyotes expanded into all of the U.S. and Mexico, southward into Central America, and northward into most of Canada and Alaska (Moore and Parker 1992).

Current distribution Coyotes continue to expand their distribution and occupy most areas between 8°N (Panama) and 70°N (northern Alaska) (Figure 4.1.1). They are found throughout the continental United States and Alaska, almost all of Canada (except the far north-eastern regions), south through Mexico and into Central America (Bekoff 1982; Reid 1997; Bekoff and Gese 2003).

Range countries Belize, Canada, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, United States of America (Moore and Parker 1992; Reid 1997; Bekoff and Gese 2003).

Relative abundance

Coyotes are abundant throughout their range (Table 4.1.3) and are increasing in distribution as humans continue to modify the landscape. Elimination of wolves may also have assisted coyote expansion. Coyote density varies geographically with food and climate, and seasonally due to mortality and changes in pack structure and food abundance. Local control temporarily reduces numbers on a short-term basis, but coyote populations generally are stable in most areas.

Coyote densities in different geographic areas and seasons (Table 4.1.2) vary from 0.01–0.09 coyotes/km² in the winter in the Yukon (O'Donoghue *et al*. 1997) to 0.9/km² in the fall and 2.3/km² during the summer (post-whelping) in Texas (Knowlton 1972; Andelt 1985).

Table 4.1.2. Coyote densities in different geographic areas and seasons.

Location	Density	Season	Source
Alberta	0.1–0.6	Winter	Nellis & Keith 1976
	0.08–0.44	Winter	Todd *et al*. 1981
Colorado	0.26–0.33	Pre-whelp	Gese *et al*. 1989
	0.7	Winter	Hein & Andelt 1995
Montana	0.15	Spring	Pyrah 1984
	0.39	Summer	Pyrah 1984
Tennessee	0.35	Pre-whelp	Babb & Kennedy 1989
Texas	0.9	Post-whelp	Knowlton 1972
	1.5–2.3	Autumn	Knowlton 1972
	0.9	Pre-whelp	Andelt 1985
	0.12–0.14	Pre-whelp	Henke & Bryant 1999
Yukon	0.01–0.09	Winter	O'Donoghue *et al*. 1997

Estimated populations/relative abundance and population trends

Table 4.1.3. The status of coyotes in various range countries (Population: A=abundant, C=common, U=uncommon; Trend: I=increasing, S=stable, D=declining).

Country	Population abundance	Trend
Belize	U	I
Canada	A	I
Costa Rica	U	I
El Salvador	C	I
Guatemala	C	I
Honduras	C	I
Mexico	A	I
Nicaragua	C	I
Panama	U	I
United States	A	I

Habitat

Coyotes utilise almost all available habitats including prairie, forest, desert, mountain, and tropical ecosystems. The ability of coyotes to exploit human resources allows them to occupy urban areas. Water availability may limit coyote distribution in some desert environments.

Food and foraging behaviour

Food Coyotes are opportunistic, generalist predators that eat a variety of food items, typically consuming items in relation to changes in availability. Coyotes eat foods ranging from fruit and insects to large ungulates and livestock. Livestock and wild ungulates may often be represented in coyote stomachs and scats as carrion, but predation on large ungulates (native and domestic) does occur (Andelt 1987). Predation by coyotes on neonates of native ungulates can be high during fawning (Andelt 1987). Coyotes in suburban areas are adept at exploiting human-made food resources and will readily consume dog food or other human-related items.

Foraging behaviour Studies on the predatory behaviour of coyotes show that age of the coyote, wind, habitat, and snow conditions all influence their ability to capture small mammals (Bekoff and Wells 1986; Gese *et al*. 1996a). Coyotes hunt small mammals alone, even when pack size is large (Gese *et al*. 1996a). When preying on native ungulates, cooperation among pack members may facilitate the capture of prey, but is not essential. Environmental factors are important to the success of an attack on adult ungulates. Presence of the alpha pair is important in determining the success of the attack, and younger animals generally do not participate. The number of coyotes is not as important as who is involved in the attack (Gese and Grothe 1995). Also, the ability of the ungulate to escape into water, defensive abilities of the individual and cohorts, and nutritional state of the individual under attack, contribute to the outcome (Gese and Grothe 1995). In areas with an ungulate prey base in winter, resource partitioning and competition for a carcass may be intense, even among members of the same pack (Gese *et al*. 1996b). When coyotes prey on sheep, they generally attack by biting the throat and suffocating the animal. Defensive behaviours by sheep sometimes can deter coyotes from continuing their attack.

Coyotes may be active throughout the day, but they tend to be more active during the early morning and around sunset (Andelt 1985). Activity patterns change seasonally, or in response to human disturbance and persecution (Kitchen *et al*. 2000a). Activity patterns change during winter, when there is a change in the food base (Bekoff and Wells 1986; Gese *et al*. 1996b).

Damage to livestock or game Coyotes are a major predator of domestic sheep and lambs. In areas with predator control, losses to coyotes were 1.0–6.0% for lambs and 0.1–2.0% for ewes (USFWS 1978). In areas with no predator control, losses to coyotes were 12–29% of lambs and 1–8% of ewes (McAdoo and Klebenow 1978; O'Gara *et al*. 1983). However, coyote predation is not always the major cause of losses. In 1999, the value of sheep reported lost to predators was estimated at US$16.5 million (USDA 2000). In 1999, predators killed an estimated 273,600 sheep and lambs, with coyotes causing 60.7% of those losses (USDA 2000). Of the 742,900 sheep and lambs reported lost in 1999, only 165,800 (22.3%) were killed by coyotes (USDA 2000). However, not all losses are necessarily reported.

Predation by coyotes on game species can be very high, particularly among fawns (Andelt 1987). Losses due to predation can be 40–90% of the ungulate fawn crop, with coyotes being one of the major predators (Andelt 1987). Predation by coyotes on adult ungulates is less pronounced compared to neonatal predation. The effect that coyote predation has on the adult segment of ungulate populations is poorly understood, but in some situations increased predation may be correlated with winter severity.

Adaptations

Coyotes are very versatile, especially in their ability to exploit human-modified environments. Their plasticity in behaviour, social ecology, and diet allows coyotes to not only exploit, but to thrive, in almost all environments modified by humans. Physiologically, the insulative properties of their fur allow coyotes to adapt to cold environments (Ogle and Farris 1973). In deserts, lack of free water may limit their distribution compared to smaller canids.

Social behaviour

Coyotes are considered less social than wolves (but see Gese *et al*. 1996b, c). The basic social unit is the adult, heterosexual pair, referred to as the alpha pair. Coyotes form heterosexual pair bonds that may persist for several years, but not necessarily for life. Coyotes may maintain pair bonds and whelp or sire pups up to 10–12 years of age. Associate animals may remain in the pack and possibly inherit or displace members of the breeding pair and become alphas themselves. Associates participate in territorial maintenance and pup rearing, but not to the extent of the alpha pair. Other coyotes exist outside of the resident packs as transient or nomadic individuals. Transients travel alone over larger areas and do not breed, but will move into territories when vacancies occur.

One factor that may affect coyote sociality is prey size or prey biomass. In populations where rodents are the major prey, coyotes tend to be in pairs or trios (Bekoff and Wells 1986). In populations where elk and deer are available, large packs of up to 10 individuals may form (Bekoff and Wells 1986; Gese *et al*. 1996b, c).

Coyotes are territorial with a dominance hierarchy within each resident pack (Bekoff 1982; Bekoff and Gese 2003, and references therein). In captivity, coyotes show early development of aggressive behaviour and engage in dominance fights when 19–24 days old (Bekoff *et al*. 1981). The early development of hierarchical ranks within litters appears to last up to 4.5 months (Bekoff 1977). Territoriality mediates the regulation of coyote numbers as packs space themselves across the landscape in relation to available food and habitat (Knowlton *et al*. 1999). The dominance hierarchy influences access to food resources within the pack (Gese *et al*. 1996b, c).

Home-range size varies geographically (Laundré and Keller 1984), and among residents, varies with energetic requirements, physiographic makeup, habitat, and food distribution (Laundré and Keller 1984). Home-range size is influenced by social organisation, with transients using larger areas, and residents occupying distinct territories (Andelt 1985; Bekoff and Wells 1986). Resident coyotes actively defend territories with direct confrontation, and indirectly with scent marking and howling (Camenzind 1978; Bekoff and Wells 1986). Only packs (2–10 animals) maintain and defend territories (Bekoff and Wells 1986). Fidelity to the home range area is high and may persist for many years (Kitchen *et al*. 2000b). Shifts in territorial boundaries may occur in response to loss of one or both of the alpha pair (Camenzind 1978).

Dispersal of coyotes from the natal site may be into a vacant or occupied territory in an adjacent area, or they may disperse long distances. Generally, pups, yearlings, and non-breeding adults of lower social rank disperse (Gese *et al*. 1996c). Dispersal seems to be voluntary as social and nutritional pressures intensify during winter when food becomes limited (Gese *et al*. 1996c). There seems to be no consistent pattern in dispersal distance or direction. Dispersal by juveniles usually occurs during autumn and early winter. Pre-dispersal forays may occur prior to dispersal.

Coyotes communicate using auditory, visual, olfactory, and tactile cues. Studies have identified different types of vocalisations, seasonal and diel patterns, and the influence of social status on vocalisation rates (Bekoff and Gese 2003; and references therein). Howling plays a role in territorial maintenance and pack spacing by advertising territorial boundaries and signalling the presence of alpha animals which will confront intruders and defend the territory. Studies on scent marking have shown that alpha coyotes perform most scent marking, scent marking varies seasonally, and scent marks contribute to territory maintenance (Bekoff and Gese 2003; and references therein). Scent marking may also be a mechanism for sex recognition and an indicator of sexual condition, maturity, or synchrony (Bekoff and Gese 2003; and references therein).

Reproduction and denning behaviour

Descriptions of spermatogenesis and the oestrous cycle show that both males and females show annual cyclic changes in reproductive anatomy and physiology (Kennelly 1978). Females are seasonally monoestrus, showing one period of heat per year between January and March, depending on geographic locale (Kennelly 1978). Pro-oestrus lasts 2–3 months and oestrus up to 10 days. Courtship behaviour begins 2–3 months before copulation (Bekoff and Diamond 1976). Copulation ends with a copulatory tie lasting up to 25 minutes. Juvenile males and females are able to breed.

The percentage of females breeding each year varies with local conditions and food supply (Knowlton *et al.* 1999). Usually, about 60–90% of adult females and 0–70% of female yearlings produce litters (Knowlton *et al.* 1999). Gestation lasts about 63 days. Litter size averages about six (range=1–9) and may be affected by population density and food availability during the previous winter (Knowlton *et al.* 1999). In northern latitudes, coyote litter size changes in response to cycles in snowshoe hares (*Lepus americanus*) (Todd and Keith 1983; O'Donoghue *et al.* 1997). Gese *et al.* (1996b) found an increase in litter size after cold, snowy winters had increased the number of ungulate carcasses available to ovulating females. Litter sex ratio is generally 1:1 (Knowlton 1972).

Coyotes may den in brush-covered slopes, steep banks, under rock ledges, thickets, and hollow logs. Dens of other animals may be used. Dens may have more than one entrance and interconnecting tunnels. Entrances may be oriented to the south to maximise solar radiation (Gier 1968). The same den may be used from year-to-year. Denning and pup rearing are the focal point for coyote families for several months until the pups are large and mobile (Bekoff and Wells 1986).

The pups are born blind and helpless in the den. Birth weight is 240–275g; length of the body from tip of head to base of tail is about 160mm (Gier 1968). Eyes open at about 14 days and pups emerge from the den at about three weeks. The young are cared for by the parents and other associates, usually siblings from a previous year (Bekoff and Wells 1986). Pups are weaned at about 5–7 weeks of age and reach adult weight by about nine months.

Competition

Direct and indirect competition between coyotes and wolves, and pumas (*Puma concolor*) has been documented. Coyotes have been killed by wolves and may avoid areas and habitats used by these larger carnivores. Direct predation and competition for food and space with wolves may limit coyote numbers in some areas under certain conditions (Peterson 1995).

In some areas, coyotes may not tolerate bobcats (*Lynx rufus*; but see Major and Sherburne 1987) and red foxes (*Vulpes vulpes*; e.g., Major and Sherburne 1987), but appear to be more tolerant when food is abundant (Gese *et al.* 1996d). Coyotes will also kill smaller canids, mainly swift fox (*V. velox*), kit fox (*V. macrotis*), and gray fox (*Urocyon cinereoargenteus*). Coexistence between these canids may be mediated by resource partitioning (e.g., White *et al.* 1995; Kitchen *et al.* 1999).

Mortality and pathogens

Natural sources of mortality Coyotes of various ages have different mortality rates depending on the level of persecution and food availability (Knowlton *et al.* 1999). Pups (<1 year old) and yearlings (1–2 years old) tend to have the highest mortality rates. For individuals >1 year of age, mortality rate varies geographically (Knowlton 1972). Knowlton (1972) reported high survival from 4–8 years of age. About 70–75% of coyote populations are 1–4 years of age (Knowlton *et al.* 1999).

Predation by large carnivores and starvation may be substantial mortality factors, but their effects on coyote populations are poorly understood. Increased mortality is often associated with dispersal as animals move into unfamiliar areas and low-security habitats (Knowlton *et al.* 1999).

Persecution Even in lightly exploited populations, most mortality is attributable to humans. Human exploitation can be substantial in some coyote populations (Knowlton *et al.* 1999). Human activity causes a high proportion of deaths of coyotes, with protection of livestock and big game species constituting one of the greatest motives for persecuting coyotes. Harvest of coyotes as a furbearer also continues throughout its range.

Hunting and trapping for fur Coyotes are harvested for their fur in many states in the U.S. and several provinces in Canada.

Road kills Coyotes are subject to vehicular collisions throughout their range.

Pathogens and parasites Disease can be a substantial mortality factor, especially among pups (e.g., Gese *et al.* 1997). Serological analyses for antibodies in coyotes show that they have been exposed to many diseases. Generally, the effects of these diseases on coyote populations are unknown. Prevalence of antibodies against canine parvovirus, canine distemper, and canine infectious hepatitis varies geographically (Bekoff and Gese 2003; and references therein). The prevalence of antibodies against plague (*Yersinia pestis*) ranges from <6% in California (Thomas and Hughes 1992) to levels >50% (Gese *et al.* 1997); prevalence of antibodies against tularemia (*Francisella tularensis*) ranges from 0% in coyotes in Texas (Trainer and Knowlton 1968) to 88% in Idaho (Gier *et al.* 1978). Serologic evidence of exposure to brucellosis and leptospirosis varies across locales (Bekoff and Gese 2003; and references therein). Coyotes in an urban area are equally exposed to pathogens (Grinder and Krausman 2001).

Coyotes are inflicted with a variety of parasites, including fleas, ticks, lice, cestodes, round-worms, nematodes, intestinal worms, hookworms, heartworms, whipworms, pinworms, thorny-headed worms, lungworms, and coccidia fungus (see Gier *et al.* 1978; Bekoff and Gese 2003; and references therein). Coyotes may carry rabies and suffer from mange, cancer, cardiovascular diseases, and aortic aneurysms (Bekoff and Gese 2003; and references therein).

Longevity Coyotes in captivity may live as long as 21 years (Linhart and Knowlton 1967), but in the wild, life expectancy is much shorter; maximum age reported for a wild coyote is 15.5 years (Gese 1990).

Historical perspective

Coyotes were an important element in Native American mythology. The term coyote is derived from the Aztec term "coyotl." In Crow mythology, Old Man Coyote played the role of trickster, transformer, and fool. In the south-west, the Navajo called the coyote "God's dog." Among the tribes of the Great Plains, the coyote was "God of the Plains." In the culture of the Flathead Indians, the coyote was regarded as "most powerful, and favourable to mankind" (Young and Jackson 1951). With European expansion into the western U.S., the coyote came into conflict with domestic livestock. Predator control programmes began in the 1800s with the intention of ridding the west of predators. While the wolf and grizzly bear were reduced or extirpated throughout most of their former ranges, the coyote thrived and expanded into these human-modified landscapes. Today, the coyote is distributed throughout the continental U.S. and Mexico, most of Canada and Alaska, and much of Central America. While local control continues, the coyote has firmly established itself as the "trickster" of native lore and is here to stay.

Conservation status

Threats There are no current threats to coyote populations throughout their range. Local reductions are temporary and their range has been expanding. Conservation measures have not been needed to maintain viable populations. Coyotes adapt to human environs and occupy most habitats, including urban areas. Hybridisation with dogs may be a threat near urban areas. Genetic contamination between dogs, coyotes, and wolves may be occurring in north-eastern U.S. Hybridisation between coyotes and red wolves is problematic for red wolf recovery programmes.

Commercial use Coyote fur is still sought by trappers throughout its range, with harvest levels depending upon fur prices, local and state regulations, and traditional uses and practices. Many states and provinces consider coyotes a furbearing species with varying regulations on method of take, bag limit, and seasons.

Occurrence in protected areas The coyote occurs in almost all protected areas across its range.

Protection status CITES – not listed.

Current legal protection No legal protection. Restrictions on harvest and method of harvest depend upon state or provincial regulations.

Conservation measures taken None at present.

Occurrence in captivity

Over 2,000 coyotes occur in captivity in zoos, wildlife centres, and so on throughout their range. They readily reproduce in captivity and survival is high.

Current or planned research projects

Due to the wide distribution of coyotes throughout North and Central America, coyote research continues across its range. Because the coyote is so numerous, much of the research does not focus on conservation measures, but usually on community dynamics, predator-prey relationships, disease transmission, and coyote-livestock conflicts. Over 20 studies are currently being conducted in the U.S., Canada, Mexico, and Central America.

Gaps in knowledge

Several gaps in knowledge still remain: coyote reproductive physiology and possible modes of fertility control; selective management of problem animals; effects of control; genetic differentiation from other canids (particularly the red wolf); development of non-lethal depredation techniques; interactions of coyotes and other predators; coyote-prey interactions; human-coyote interactions and conflicts at the urban interface; factors influencing prey selection; communication; adaptations in urban and rural environments; and interactions with threatened species.

Core literature

Andelt 1985, 1987; Bekoff and Gese 2003; Bekoff and Wells 1986; Gese *et al*. 1996a, b, c; Gier 1968; Knowlton *et al*. 1999; Young and Jackson 1951.

Reviewers: William Andelt, Lu Carbyn, Frederick Knowlton. **Editors:** Claudio Sillero-Zubiri, Deborah Randall, Michael Hoffmann.

4.2 Red wolf

Canis rufus Audubon and Bachman, 1851

Critically Endangered – CR: D (2004)

B.T. Kelly, A. Beyer and M.K. Phillips

Other names

None.

Taxonomy

Canis rufus Audubon and Bachman, 1851. Viviparous quadrupeds of North America, 2:240. Type locality: not given. Restricted by Goldman (1937) to "15 miles of Austin, Texas" [USA].

In recent history the taxonomic status of the red wolf has been widely debated. Mech (1970) suggested red wolves may be fertile hybrid offspring from grey wolf (*Canis lupus*) and coyote (*C. latrans*) interbreeding. Wayne and Jenks (1991) and Roy *et al*. (1994b, 1996) supported this suggestion with genetic analysis. Phillips and Henry (1992) present logic supporting the contention that the red wolf is a subspecies of grey wolf. However, recent genetic and morphological evidence suggests the red wolf is a unique taxon. Wilson *et al*. (2000) report that grey wolves (*Canis lupus lycaon*) in southern Ontario appear genetically very similar to the red wolf and that these two canids may be subspecies of one another and not a subspecies of grey wolf. Wilson *et al*. (2000) propose that red wolves and *C. lupus lycaon* should be a separate species, *C. lycaon*, and their minor differences acknowledged via subspecies designation. A recent meeting of North American wolf biologists and geneticists also concluded that *C. rufus* and *C. lupus lycaon* were genetically more similar to each other than either was to *C. lupus* or *C. latrans* (B.T. Kelly unpubl.). Recent morphometric analyses of skulls also indicate that the red wolf is likely not to be a grey wolf × coyote hybrid (Nowak 2002). Therefore, while the red wolf's taxonomic status remains unclear, there is mounting evidence to support *C. rufus* as a unique canid taxon.

Chromosome number: 2n=78 (Wayne 1993).

Description

The red wolf generally appears long-legged and rangy with proportionately large ears. The species is intermediate in size between the coyote and grey wolf. The red wolf's almond-shaped eyes, broad muzzle, and wide nose pad contribute to its wolf-like appearance. The muzzle tends to be very light with an area of white around the lips extending up the sides of the muzzle. Coloration is typically brownish or cinnamon with grey and black shading on the back and tail. A black phase occurred historically but is

Male red wolf, age unknown.

Art Beyer

Table 4.2.1 Body measurements for the red wolf from Alligator River National Wildlife Refuge, North Carolina, USA (USFWS unpubl.).

HB male	1,118mm (1,040–1,250) n = 58
HB female	1,073mm (990–1,201) n = 51
HF male	234mm (213–270) n = 55
HF female	222mm (205–250) n = 42
E male	116mm (107–129) n = 54
E female	109mm (99–125) n = 49
SH male	699mm (640–772) n = 60
SH female	662mm (590–729) n = 45
T male	388mm (330–460) n = 52
T female	363mm (295–440) n = 47
WT male	28.5kg (22.0–34.1) n = 70
WT female	24.3kg (20.1–29.7) n = 61

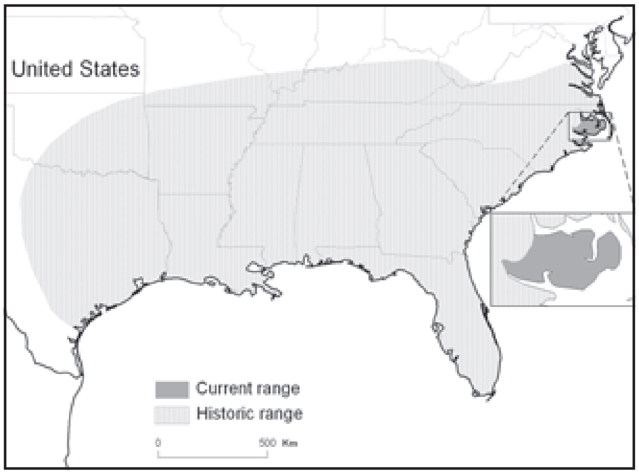

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Figure 4.2.1. Current distribution of the red wolf.

probably extinct. The dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies *C. rufus gregoryi, C. rufus floridanus, and C. rufus rufus* were initially recognised by Goldman (1937) and subsequently by Paradiso and Nowak (1972). *Canis rufus gregoryi* is thought to be the only surviving subspecies and is the subspecies believed to have been used for the current reintroduction and conservation effort of red wolves in the eastern United States. Genetic methodologies have not been applied to subspecific designation. Current disagreement about the relatedness of wolves in eastern North America (see Taxonomy section above), if resolved, may alter currently accepted subspecific classification of *C. rufus*.

Similar species The red wolf, as a canid intermediate in size between most grey wolves and coyotes, is often noted as being similar to both of these species in terms of general conformation. However, the coyote is smaller overall with a more shallow profile and narrower head. Grey wolves typically have a more prominent ruff than the red wolf and, depending on subspecies of grey wolf, typically are larger overall. Also, most grey wolf subspecies have white and/or black colour phases. Although red wolves historically had a black phase, no evidence of this melanism has expressed itself in the captive or reintroduced population.

Distribution

Historical distribution As recently as 1979, the red wolf was believed to have a historical distribution limited to the south-eastern United States (Nowak 1979). However, Nowak (1995) later described the red wolf's historic range as extending northward into central Pennsylvania and more recently has redefined the red wolf's range as extending even further north into the north-eastern USA and extreme eastern Canada (Nowak 2002). Recent genetic evidence (see Taxonomy section above) supports a similar but even greater extension of historic range into Algonquin Provincial Park in southern Ontario, Canada.

Current distribution Red wolves exist only in a reintroduced population in eastern North Carolina, USA (Figure 4.2.1). The current extant population of red wolves occupies the peninsula in eastern North Carolina between the Albermarle and Pamilico Sounds.

Range countries Historically, red wolves occurred in the United States of America and possibly Canada (Wilson *et al.* 2000; Nowak 2002). Currently, red wolves only reside in eastern North America as a reintroduced population (Phillips *et al.* 2003) and possibly Canada (Wilson *et al.* 2000).

Relative abundance

Extinct in the Wild by 1980, the red wolf was reintroduced by the United States Fish and Wildlife Service (USFWS) in 1987 into eastern North Carolina. The red wolf is now common within the reintroduction area of roughly 6,000km^2 (Table 4.2.2). However, the species' abundance outside the reintroduction area is unknown.

Estimated populations/relative abundance and population trends

Table 4.2.2 The status of red wolves in USA (Trend: S=stable, EX=extinct).

	Population size	Trend
Reintroduced population	<150	S
Former range (south-eastern USA)	–	EX

Habitat

Very little is known about red wolf habitat because the species' range was severely reduced by the time scientific investigations began. Given their wide historical distribution, red wolves probably utilised a large suite of habitat types at one time. The last naturally occurring population utilised the coastal prairie marshes of south-west Louisiana and south-east Texas (Carley 1975; Shaw 1975). However, many agree that this environment probably does not typify preferred red wolf habitat. There is evidence that the species was found in highest numbers in the once extensive bottomland river forests and swamps of the south-east (Paradiso and Nowak 1971, 1972; Riley and McBride 1972). Red wolves reintroduced into north-eastern North Carolina and their descendants have made extensive use of habitat types ranging from agricultural lands to pocosins. Pocosins are forest/wetland mosaics characterised by an overstory of loblolly and pond pine (*Pinus taeda* and *Pinus serotina*, respectively) and an understory of evergreen shrubs (Christensen *et al.* 1981). This suggests that red wolves are habitat generalists and can thrive in most settings where prey populations are adequate and persecution by humans is slight. The findings of Hahn (2002) seem to support this generalisation in that low human density, wetland soil type, and distance from roads were the most important predictor of potential wolf habitat in eastern North Carolina.

Food and foraging behaviour

Food Mammals such as nutria (*Myocastor coypus*), rabbits (*Sylvilagus* spp.), and rodents (*Sigmodon hispidus*, *Oryzomys palustris*, *Ondatra zibethicus*) are common in south-east Texas and appear to have been the primary prey of red wolves historically (Riley and McBride 1972; Shaw 1975). In north-eastern North Carolina, white-tailed deer (*Odocoileus virginianus*), raccoon (*Procyon lotor*), and rabbits are the primary prey species for the reintroduced population, comprising 86% (Phillips *et al.* 2003) of the red wolves' diets.

Foraging behaviour Red wolves are mostly nocturnal with crepuscular peaks of activity. Hunting usually occurs at night or at dawn and dusk (USFWS unpubl.). While it is not uncommon for red wolves to forage individually, there is also evidence of group hunting between pack members (USFWS unpubl.). Also, resource partitioning between members of a pack sometimes occurs. In one study, pack rodents were consumed more by juveniles than adults, although use of rodents diminished as the young wolves matured (Phillips *et al.* 2003).

Damage to livestock or game Historically, the red wolf was believed to be a killer of livestock and a threat to local game populations, despite lack of data to support such a belief. As of September 2002, the reintroduced population in north-eastern North Carolina has been responsible for only three depredations since 1987 (USFWS unpubl.).

Adaptations

Red wolves are well adapted to the hot, humid climate of the south-eastern United States. Their relatively large ears allow for efficient dissipation of body heat, and they moult once a year, which results in them replacing their relatively thick, heat-retaining, cold-season pelage with a thin and coarse warm-season pelage. Such a moult pattern ensures that red wolves are not only able to tolerate the warm humid conditions that predominate in the south-eastern United States, but also the wide range of annual climatic conditions that characterise the region in general. A potential specific adaptation appears to be the ability of the red wolf to survive heartworm infestation. All the adult wild red wolves tested for heartworm in the restored population in North Carolina test positive for heartworm; yet, unlike in domestic dogs and other canids, it is not known to be a significant cause of mortality. More general adaptations include the tolerance of the red wolf's metabolic system to the feast/famine lifestyle that results from the species' predatory habits.

Social behaviour

Like grey wolves, red wolves normally live in extended family units or packs (Phillips and Henry 1992; Phillips *et al.* 2003). Packs typically include a dominant, breeding pair and offspring from previous years. Dispersal of offspring typically occurs before individuals reach two years of age (Phillips *et al.* 2003). Group size in the reintroduced population typically ranges from a single breeding pair to 12 individuals (Phillips *et al.* 2003; USFWS unpubl.). Red wolves are territorial and, like other canids, appear to scent mark boundaries to exclude non-group members from a given territory (Phillips *et al.* 2003; USFWS unpubl.). Home range size varies from 46–226km^2, with variation due to habitat type (Phillips *et al.* 2003).

Reproduction and denning behaviour

Red wolves typically reach sexual maturity by 22 months of age, though breeding at 10 months of age may occur (Phillips *et al.* 2003). Mating usually occurs between February and March, with gestation lasting 61–63 days (Phillips *et al.* 2003). Peak whelping dates occur from mid-April to mid-May producing litters of 1–10 pups (USFWS unpubl.). In a given year, there is typically one litter per pack produced by the dominant pair. Two females breeding within a pack is suspected but has not yet been proven. During the denning season, pregnant females may establish several dens. Some dens are shallow surface depressions located in dense vegetation for shelter at locations where the water table is high, while other dens are deep burrows often in wind rows between agricultural fields or in canal banks; dens have also been found in the hollowed out bases of large trees (Phillips *et al.* 2003; USFWS unpubl.). Pups are often moved from one den to another before abandoning the den altogether, and den attendance by male and female yearlings and adult pack members is common (USFWS unpubl.).

Competition

The degree of competition for prey and habitat between red wolves, coyotes and red wolf × coyote hybrids, is uncertain. Studies to determine this are currently underway (see Current or planned research projects below). In contrast, competition for mates between red wolves and coyotes or red wolf x coyote hybrids appears to be significant (Kelly *et al.* 1999) (see Conservation status: Threats below). Red wolves may also compete, to a lesser degree, with black bears (*Ursus americanus*). The destruction of red wolf dens by black bears has been observed, although it is unknown if these dens had already been abandoned (USFWS unpubl.). Conversely, wolves have also been observed killing young bears (USFWS unpubl.).

Mortality and pathogens

Natural sources of mortality Natural mortality accounts for approximately 21% of known mortality. There are no known major predators of red wolves, although intraspecific aggression accounts for approximately 6% of known red wolf mortalities (USFWS unpubl.).

Persecution Human-induced mortality in red wolves is significant in the reintroduced population and more substantial than natural causes of mortality. It accounts for approximately 17% of known red wolf deaths (primarily from gunshot, traps, and poison) (USFWS unpubl.). Direct persecution by humans was a key factor in the eradication of red wolves from much of the south-eastern United States.

Hunting and trapping for fur There are currently no legal hunting or trapping for fur programmes for red wolves in the United States. Wolves purported to be red wolf-like wolves *Canis lupus lycaon* (see Taxonomy section above) are trapped for fur in Canada when they migrate out of Algonquin Provincial Park.

Road kills In the reintroduced population, road kills are the most common mortality factor accounting for 18% of known red wolf deaths (USFWS unpubl.). However, a proportionately higher number of deaths from vehicle strikes occurred earlier in the reintroduction efforts when captive wolves were released, suggesting that a tolerance in those wolves to human activities predisposed them to spend more time on or near roads (Phillips *et al.* 2003; USFWS unpubl.).

Pathogens and parasites Heartworms (*Dirofilaria immitis*), hookworms (*Ancylostoma caninum*), and sarcoptic mange (*Sarcoptes scabiei*) have been considered important sources of mortality in red wolves (USFWS 1990). In the reintroduced population in North Carolina, both heartworms and hookworms occur, but, neither appear to be a significant source of mortality (Phillips and Scheck 1991; USFWS unpubl.). Mortalities related to demodectic mange and moderate to heavy tick infestations from American dog ticks (*Dermacentor variabilis*), lone star ticks (*Amblyomma americanum*), and black-legged ticks (*Ixodes scapularis*) have also occurred in the reintroduced population but, likewise, do not appear to be significant mortality factors (USFWS unpubl.). Tick paralysis of a red wolf has been documented in North Carolina (Beyer and Grossman 1997).

Longevity Appears to be similar to other wild canids in North America. In the absence of human-induced mortality, red wolves have been documented to have lived in the wild as long as 13 years (USFWS unpubl.).

Historical perspective

Although red wolves ranged throughout the south-eastern United States before European settlement, by 1980 they were considered Extinct in the Wild (McCarley and Carley 1979; USFWS 1990). There are no known traditional uses of red wolves by Native Americans or early settlers. Rather, it is likely that red wolves were viewed by early settlers as an impediment to progress and as pests that were best destroyed. Demise of the species has largely been attributed to human persecution and destruction of habitat that led to reduced densities and increased interbreeding with coyotes (USFWS 1990). These factors were largely responsible for the eradication of the species, with the exception of those individuals found occupying marginal habitats in Louisiana and Texas in the 1970s. In these habitats, red wolves frequently suffered heavy parasite infestation (Goldman 1944; Nowak 1972, 1979; Carley 1975).

The plight of the species was recognised in the early 1960s (McCarley 1962), and the red wolf was listed as endangered in 1967 under United States legislation that preceded the Endangered Species Act (ESA) of 1973. A recovery programme was initiated after passage of the ESA in 1973. It was during the early 1970s that the USFWS determined recovery of the species could only be achieved through captive breeding and reintroductions (see Conservation measures taken below) (USFWS 1990).

Conservation status

Threats Hybridisation with coyotes or red wolf x coyote hybrids is the primary threat to the species' persistence in the wild (Kelly *et al.* 1999). While hybridisation with coyotes was a factor in the red wolf's initial demise in the wild, it was not detected as a problem in north-eastern North Carolina until approximately 1992 (Phillips *et al.* 1995). Indeed, north-eastern North Carolina was determined to be ideal for red wolf reintroductions because of a purported absence of coyotes (Parker 1986). However, during the 1990s, the coyote population apparently became well established in the area (P. Sumner pers. comm.; USFWS unpubl.).

It has been estimated that the red wolf population in North Carolina can sustain only one hybrid litter out of every 59 litters (1.7%) to maintain 90% of its genetic diversity for the next 100 years (Kelly *et al.* 1999). However, prior to learning of this acceptable introgression rate, the introgression rate noted in the reintroduced population was minimally 15% (Kelly *et al.* 1999) or approximately 900% more than the population can sustain to maintain 90% of its genetic diversity for 100 years. If such levels of hybridisation continued beyond 1999, non-hybridised red wolves could disappear within 12–24 years (3–6 generations). An adaptive management plan designed to test whether hybridisation can be reduced to acceptable levels was initiated in 1999 (Kelly 2000) (see Current or planned research projects below). Initial results from this plan suggest that the intensive management specified in the plan may be effective in reducing introgression rates to acceptable levels (B. Fazio pers. comm.).

In the absence of hybridisation, recovery of the red wolf and subsequent removal of the species from the U.S. Endangered Species List is deemed possible. It is noteworthy that similar hybridisation has been observed in the population of suspected red wolf-type wolves in Algonquin Provincial Park, Ontario, Canada (see Taxonomy above). If these wolves are ultimately shown to be red wolf-type wolves, this will enhance the conservation status of the species and nearly triple the known number of red wolf-type wolves surviving in the wild.

As noted above (see Mortality), human-induced mortality (vehicles and gunshot) can be significant. However, the threat this mortality represents to the population is unclear. Most vehicle deaths occurred early in the reintroduction and were likely due to naive animals. Nonetheless, the overall impact of these mortality factors will depend on the proportion of the losses attributable to the breeding segment of the population (effective population (N_e) and what proportion of the overall population is lost due to these human factors (both N and N_e).

Commercial use None.

Occurrence in protected areas The only free-ranging population of red wolves exists in north-eastern North Carolina in an area comprised of 60% private land and 40% public land. This area contains three national wildlife refuges (Alligator River NWR, Pocosin Lakes NWR, and Mattamuskeet NWR) which provide important protection to the wolves. Red wolves or a very closely related taxon may also occupy Algonquin Provincial Park, Ontario, Canada (see Taxonomy above).

Protection status CITES – not listed.

Current legal protection The red wolf is listed as 'endangered' under the U.S. Endangered Species Act (ESA) (United States Public Law No. 93-205; United States Code Title 16 Section 1531 *et seq.*). The reintroduced animals and their progeny in north-eastern North Carolina are considered members of an experimental non-essential population. This designation was promulgated under Section 10(j) of the ESA and permits the USFWS to manage the population and promote recovery in a manner that is respectful of the needs and concerns of local citizens (Parker and Phillips 1991). Hunting of red wolves is prohibited by the ESA. To date, federal protection of the red wolf has been adequate to successfully reintroduce and promote recovery of the species in North Carolina.

Conservation measures taken A very active recovery programme for the red wolf has been in existence since the mid-1970s (Phillips *et al.* 2003; USFWS 1990), with some measures from as early as the mid-1960s (USFWS unpubl.). By 1976, a captive breeding programme was established using 17 red wolves captured in Texas and Louisiana (Carley 1975; USFWS 1990). Of these, 14 became the founders of the current captive breeding programme. In 1977, the first pups were born in the captive programme, and by 1985, the captive population had grown to 65 individuals in six zoological facilities (Parker 1986).

With the species reasonably secure in captivity, the USFWS began reintroducing red wolves at the Alligator River National Wildlife Refuge in north-eastern North Carolina in 1987. As of September 2002, 102 red wolves have been released with a minimum of 281 descendants produced in the wild since 1987. As of September 2002, there is a minimum population of 66 wild red wolves in north-eastern North Carolina, with a total wild population believed to be at least 100 individuals. Likewise, at this same time, there is a minimum population of 17 hybrid canids present in north-eastern North Carolina. The 17 known hybrids are sterilised and radio-collared (USFWS unpubl.).

During 1991 a second reintroduction project was initiated at the Great Smoky Mountains National Park, Tennessee (Lucash *et al.* 1999). Thirty-seven red wolves were released from 1992 to 1998. Of these, 26 either died or were recaptured after straying onto private lands outside the Park (Henry 1998). Moreover, only five of the 32 pups known to have been born in the wild survived but were removed from the wild during their first year (USFWS unpubl.). Biologists suspect that disease, predation, malnutrition, and parasites contributed to the high rate of pup mortality (USFWS unpubl.). Primarily because of the poor survival of wild-born offspring, the USFWS terminated the Tennessee restoration effort in 1998 (Henry 1998).

Occurrence in captivity

As of September 2002, there are approximately 175 red wolves in captivity at 33 facilities throughout the United States and Canada (USFWS unpubl.). The purpose of the captive population is to safeguard the genetic integrity of the species and to provide animals for reintroduction. In addition, there are propagation projects on two small islands off the South Atlantic and Gulf Coasts of the U.S. which, through reintroduction of known breeding individuals and capture of their offspring, provide wild-born pups for release into mainland reintroduction projects (USFWS 1990).

Current or planned research projects

In an effort to understand and manage red wolf hybridisation with coyotes and red wolf x coyote hybrids, the USFWS is implementing a Red Wolf Adaptive Management Plan (RWAMP) (Kelly 2000). The plan, which employs an aggressive science-based approach to determine if hybridisation can be managed, was developed after consultation with numerous wolf biologists and geneticists and first implemented in 1999 (Kelly *et al.* 1999; Kelly 2000). The goal of the plan is to assess whether hybridisation can be managed such that it is reduced to an acceptably low level (see Conservation status: Threats above). As of September 2002, the initial results from the RWAMP indicate that this seems to be the case. If these initial results hold, the next questions that need to be addressed for the conservation of the red wolf in the wild will be: (1) what is the long-term feasibility of sustaining the intensive management of the RWAMP?; and (2) will introgression rates remain at an acceptable level in the absence of the current intensive management? As part of the RWAMP, several research projects are underway:

L. Waits and J. Adams (University of Idaho, USA) are using non-invasive genetic techniques to monitor presence and distribution of canids in the reintroduction area, and are working to improve genetic identification techniques.

The USFWS is examining whether red wolves and coyotes compete with each other for space or share space and partition resources, and is testing the use of captive-reared pups fostered into the wild red wolf population to enhance genetic diversity.

P. Hedrick and R. Frederickson (Arizona State University, USA) are conducting sensitivity analyses of a deterministic genetic introgression model.

D. Murray (Trent University, Canada) is developing a survival-based spatial model of wolf-coyote interactions.

M. Stoskopf and K. Beck (North Carolina State University, USA) are studying the use of GPS collars to monitor wolf movements, the social behaviour of red wolves and coyotes, and the epidemiology of coyote introgression into the wild red wolf population.

K. Goodrowe (Point Defiance Zoo and Aquarium, Washington, USA) is conducting extensive research regarding various aspects of the red wolf reproductive cycle.

D. Rabon (University of Guelph, Canada) is studying the roles of olfactory cues and behaviour in red wolf reproduction.

Core literature

Kelly 2000; Kelly *et al*. 1999; Nowak 1979, 2002; Paradiso and Nowak 1972; Phillips. *et al*. 1995, 2003; Riley and McBride 1972; USFWS 1990.

Reviewers: David Mech, Richard Reading, Buddy Fazio.
Editors: Claudio Sillero-Zubiri, Deborah Randall, Michael Hoffmann.

4.3 Gray fox
Urocyon cinereoargenteus
(Schreber, 1775)
Least Concern (2004)

T.K. Fuller and B.L. Cypher

Other names

English: tree fox; **Spanish:** zorro, zorro gris, zorra gris (Mexico), zorro plateado, gato de monte (southern Mexico), gato cervan (Honduras).

Taxonomy

Canis cinereoargenteus Schreber, 1775. Die Säugethiere, 2(13):pl. 92[1775]; text: 3(21):361[1776]. Type locality: "eastern North America" ("Sein Vaterland ist Carolina und die Wärmeren Gegenden von Nordamerica, vielleicht auch Surinam").

Gray foxes traditionally were considered to be distinct from other foxes. Clutton-Brock *et al*. (1976) and Van Gelder (1978) proposed reclassifying gray foxes as *Vulpes*. However, Geffen *et al*. (1992e) determined that gray foxes represent an evolutionary lineage that is sufficiently distinct from vulpine foxes to warrant recognition as a separate genus.

A molecular phylogenetic analysis of the Canidae showed that there are four monophyletic clades (*Canis* group, *Vulpes* group, South American foxes and the bush dog/maned wolf clade) and three distantly related basal taxa, one of which is the gray fox (*U. cinereoargenteus*; Wayne *et al*. 1997). The gray fox often clusters with two other ancient lineages, the raccoon dog (*Nyctereutes procyonoides*) and the bat-eared fox (*Otocyon megalotis*) but the exact relationship among these taxa is unclear. The early origination of these lineages has resulted in significant sequence divergence that may have masked unique sequence similarities (i.e., synapomorphies) that would have resulted from common ancestry (Wayne *et al*. 1997). Despite the unclear affinities, *Urocyon* is currently considered a basal genus within the Canidae and has only two surviving members, the gray and island fox (*Urocyon littoralis*).

Chromosome number is 2n=66 (Fritzell and Haroldson 1982).

Description

The gray fox is medium sized with a stocky body, moderately short legs and medium-sized ears (Table 4.3.1). The coat is grizzled grey on the back and sides with a dark longitudinal stripe on top of a black-tipped tail, dark and white markings on its face, and a conspicuous cinnamon-rusty colour on its neck, sides and limbs. There is also white on its ears, throat, chest, belly and hind limbs, while the undercoat is mostly buff and grey. The tail is thick and bushy, and the fur is coarse-appearing. The dental formula is 3/3-1/1-4/4-2/3=42. The posterior ventral border of the dentary has a prominent notch or "step", and on the cranium, the temporal ridges are separated anteriorly but connect posteriorly to form a distinctive "U" shape (Hall 1981).

Table 4.3.1 Body measurements for the gray fox from California, USA (Grinnell *et al*. 1937).

Total length male	981mm (900–1,100) n=24
Total length female	924mm (825–982) n=20
T male	385mm (333–443) n=24
T female	357mm (280–407) n=20
HF male	137mm (100–150) n=24
HF female	130mm (115–140) n=20
E male	79mm (60–89) n=24
E female	77mm (55–101) n=20
WT male	4.0kg (3.4–5.5) n=18
WT female	3.3kg (2.0–3.9) n=16

Adult gray fox, sex unknown. Fresno, California, USA, 2003.

Karen Brown

Subspecies Up to 16 subspecies are recognised (Fritzell and Haroldson 1982):

— *U. c. borealis* (New England)
— *U. c. californicus* (southern California)
— *U. c. cinereoargenteus* (eastern United States)
— *U. c. costaricensis* (Costa Rica)
— *U. c. floridanus* (Gulf states)
— *U. c. fraterculus* (Yucatan)
— *U. c. furvus* (Panama)
— *U. c. guatemalae* (southernmost Mexico south to Nicaragua)
— *U. c. madrensis* (southern Sonora, south-west Chihuahua, and north-west Durango)
— *U. c. nigrirostris* (south-west Mexico)
— *U. c. ocythous* (Central Plains states)
— *U. c. orinomus* (southern Mexico, Isthmus of Tehuantepec)
— *U. c. peninsularis* (Baja California)
— *U. c. scottii* (south-western United States and northern Mexico)
— *U. c. townsendi* (California and Oregon)
— *U. c. venezuelae* (Colombia and Venezuela)

Similar species Island fox (*Urocyon littoralis*): very similar in appearance to the gray fox, but tends to be somewhat darker and is 25–50% smaller (Crooks 1994; Moore and Collins 1995); confined to the Channel Islands off the southern coast of California, and considered to be descended from mainland gray foxes (Collins 1982; Wayne *et al*. 1991; Moore and Collins 1995).

Current distribution

The gray fox is widespread in forest, woodland, brushland, shrubland, and rocky habitats in temperate and tropical regions of North America, and in northernmost montane regions of South America.

Historical distribution In North America, the historical northernmost distribution of the gray fox probably was somewhat further south than its current northern limit (Fritzell and Haroldson 1982). Also, the range of the species probably did not extend significantly into the Great Plains because of the lack of brushy cover. Habitat modifications, such as fire suppression and tree planting, have facilitated occupation of this biome (Fritzell 1987). The species also was formerly found on Martha's Vineyard, a small offshore island in the state of Massachusetts (Waters 1964). In Central America, gray foxes were much more widespread before the conversion of forested land into pastures and urban areas (de la Rosa and Nocke 2000).

Current distribution The gray fox ranges from the southern edge of central and eastern Canada, and Oregon, Nevada, Utah, and Colorado in the United States south to

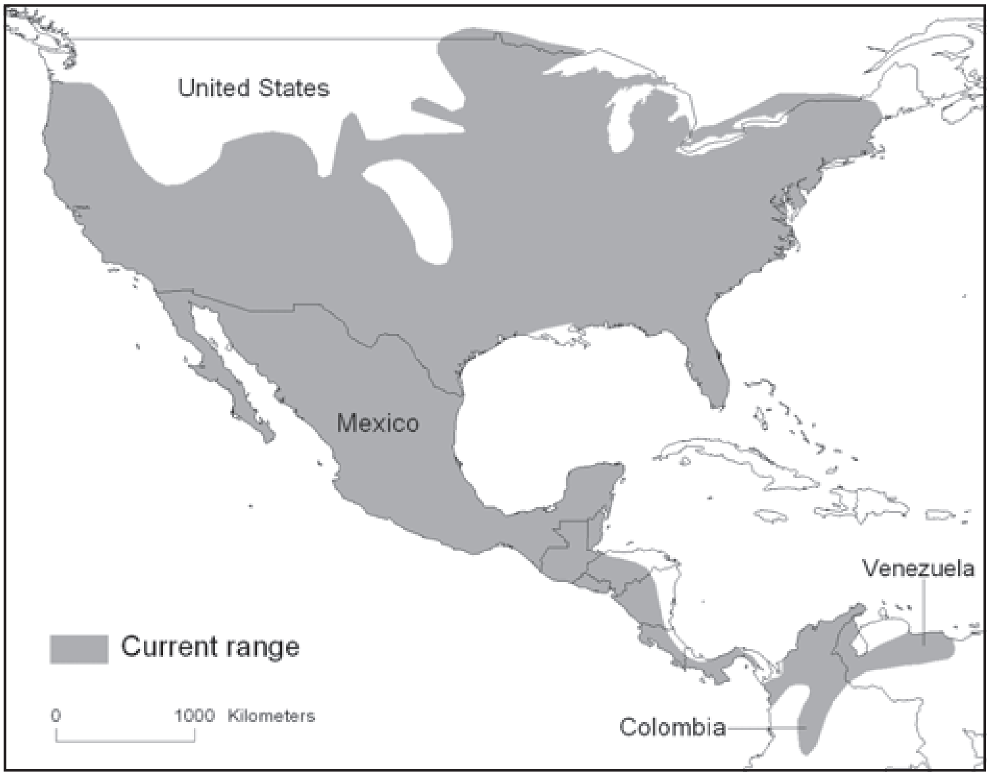

Figure 4.3.1. Current distribution of the gray fox.

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northern Venezuela and Colombia; and from the Pacific coast of the United States to the Atlantic and Caribbean oceans. The species is not found in the northern Rocky Mountains of the United States, or in the Caribbean watersheds of Honduras, Nicaragua, Costa Rica, and western Panama (Figure 4.3.1).

Range countries Belize, Canada, Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, United States of America, Venezuela (Hall 1981; Fritzell 1987; Eisenberg 1989; de la Rosa and Nocke 2000).

Relative abundance

The gray fox is common in occupied habitat, but appears to be restricted to locally dense habitats where it is not excluded by sympatric coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) (Farias 2000b).

Estimated populations/relative abundance and population trends No estimates of total gray fox abundance have been attempted. Reported densities range from 0.4/km² in California (Grinnell *et al.* 1937) to 1.5/km² in Florida (Lord 1961). There is no good evidence that gray fox numbers are increasing or decreasing in any part of their range.

Habitat

In eastern North America, the gray fox is most closely associated with deciduous/southern pine forests interspersed with some old fields and scrubby woodlands (Hall 1981). In western North America, it is commonly found in mixed agricultural/woodland/chaparral/riparian landscapes, and shrub habitats. The species occupies forested areas and thick brush habitats in Central America, and forested montane habitats in South America (Eisenberg 1989). Gray foxes occur in semi-arid areas of the south-western U.S. and northern Mexico where cover is sufficient. They appear to do well on the margins of some urban areas (Harrison 1997).

Food and foraging behaviour

Food Gray foxes have been identified as the most omnivorous of all North American fox species (Fritzell and Haroldson 1982). They consume primarily rabbits (*Sylvilagus* spp.) and rodents during cold winter months, then greatly diversify their diets in spring and summer to include insects, particularly Orthoptera (e.g., grasshoppers), birds, natural fruits and nuts, and sometimes carrion. Fruit and nut consumption often increases in the autumn as availability of these foods increases (Fritzell and Haroldson 1982).

Foraging behaviour Gray foxes are more active at night than during the day. They also increase their home ranges during late autumn and winter, possibly in response to changes in food resource availability and distribution. Male foxes also may increase their ranges during spring, probably in response to increased food requirements of more sedentary females and newborn pups (Follman 1973;

Nicholson *et al.* 1985). No information has been reported on specific hunting behaviour of gray foxes.

Damage to livestock or game Although historically considered a potentially significant predator of small game and poultry, gray foxes currently are not considered an important threat to game populations or livestock (Fritzell and Haroldson 1982).

Adaptations

With relatively short legs, a greater ability to rotate the radius on the ulna compared to other canids, and a relatively greater ability to abduct the hind limb, gray foxes are notable tree climbers (Feeney 1999). They can climb branchless, vertical trunks to heights of 18m, as well as jump vertically from branch to branch.

Social behaviour

Monogamy with occasional polygyny is probably most typical in gray foxes (Trapp and Hallberg 1975), but few quantitative data are available, and it is not known if breeding pairs remain together during consecutive years. The basic social unit is the mated pair and their offspring of the year (Trapp and Hallberg 1975; Greenberg and Pelton 1994). Offspring typically disperse at 9–10 months of age, and although long distance dispersal (over 80km) has been reported (Sheldon 1953; Sullivan 1956), young foxes may also return to and settle down near their natal ranges (Nicholson *et al.* 1985). Gray foxes exhibit some territoriality, as home ranges of adjacent family groups may overlap, but core areas appear to be used exclusively by a single family (Chamberlain and Leopold 2000). Home range size ranges from 0.8km^2 (Yearsley and Samuel 1982) to 27.6km^2 (Nicholson 1982), and size may vary with habitat quality and food availability.

Gray foxes scent mark by depositing urine and faeces in conspicuous locations (Fritzell and Haroldson 1982). They also communicate vocally via growls, alarm barks, screams, and "coos" and "mewing" sounds during greetings (Cohen and Fox 1976). Gray foxes engage in allogrooming with adults grooming juveniles and each other (Fox 1970).

Reproduction and denning behaviour

Gray foxes reach sexual maturity at 10 months of age, although not all females breed in their first year (Wood 1958; Follman 1978). Breeding generally occurs from January to April with gestation lasting about 60 days (Sullivan 1956). Litter size ranges from 1–10 and averages around four pups (Fritzell 1987). Eyes of pups open at about 10–12 days. Pups accompany adults on foraging expeditions at three months and forage independently at four months (Trapp and Hallberg 1975). Females appear to be responsible to provision pups (Nicholson *et al.* 1985), although there is some evidence that males may also contribute to care of pups (Chamberlain 2002). Juveniles reach adult size and weight at about 210 days (Wood 1958).

During parturition and pup rearing, gray foxes use earthen dens, either dug themselves or modified from burrows of other species. They will also den in wood and brush piles, rock crevices, hollow logs, hollows under shrubs, and under abandoned buildings (Trapp and Hallberg 1975). Gray foxes may even den in hollows of trees up to nine metres above the ground (Davis 1960). In eastern deciduous forests, dens are in brushy or wooded areas where they are less conspicuous than dens of co-occurring red foxes (*Vulpes vulpes*) (Nicholson and Hill 1981). Den use diminishes greatly during non-reproductive seasons when gray foxes typically use dense vegetation for diurnal resting locations.

Competition

Red foxes are sympatric with gray foxes over much of the gray fox range, but competitive interactions between the two species are not well understood. Historically, differences in food and habitat preferences may have reduced competition between the species, but recent deforestation and other anthropogenic disturbances appear to have resulted in increased habitat use overlap (Churcher 1959; Godin 1977). Competition between gray and kit (*Vulpes macrotis*) or swift (*Vulpes velox*) foxes has not been recorded, probably because of differences in habitat preference (wooded and brushy versus shrub-steppe, arid and semi-arid desert and open grasslands, respectively) that precludes interactions between the species. Coyotes, on the other hand, opportunistically kill gray foxes (Wooding 1984; Farias 2000b; B. Cypher unpubl.), and appear to limit gray fox abundance in some areas (but see Neale and Sacks 2001). Gray fox abundance is inversely related to coyote abundance in California (Crooks and Soulé 1999), and gray fox numbers increased following coyote removal in Texas (Henke and Bryant 1999). In southern California, coyotes may limit gray foxes to thicker chaparral cover (Farias 2000b; Fedriani *et al.* 2000). Bobcats also may kill gray foxes (Farias 2000b). Conversely, gray fox populations may limit the number of weasels (*Mustela* spp.) in some areas (Latham 1952; Hensley and Fisher 1975).

Mortality and pathogens

Natural sources of mortality In addition to coyotes and bobcats, golden eagles (*Aquila chrysaetos*) and mountain lions (*Felis concolor*) kill gray foxes (Grinnell *et al.* 1937; Mollhagen *et al.* 1972).

Persecution In the past, gray foxes may have been persecuted because they were deemed predators of domestic livestock or poultry, or hunted as a result of general bounties, but persecution currently is not a significant mortality factor for the species.

Hunting and trapping for fur Trapping of gray foxes is legal throughout much of their range, and is likely to be the most important source of mortality where it occurs and probably can limit their populations locally. Annual harvests of gray foxes were approximately 182,000 in the 1970s and increased to 301,000 in the 1980s (Obbard *et al.* 1987). During 1994 to 1995, more than 80,000 gray foxes were harvested in 40 states (International Association of Fish and Wildlife Agencies unpubl.). In the south-eastern United States, gray foxes are traditionally hunted with hound dogs (Fritzell 1987). There is little evidence that regulated trapping has adversely affected gray fox population numbers.

Road kills Occasionally, gray foxes are hit by vehicles, but this does not appear to be a significant source of mortality. In Alabama, 14% of gray fox deaths were attributed to vehicles (Nicholson and Hill 1984).

Pathogens and parasites Local populations have been reduced as a result of distemper (Nicholson and Hill 1984) and rabies (Steelman *et al.* 2000). In Alabama, 36% of gray fox deaths were attributed to distemper (Nicholson and Hill 1984). Of 157 gray fox carcasses examined in the south-eastern United States, 78% were diagnosed with distemper (Davidson *et al.* 1992). A variety of external and internal parasites have been found among gray foxes including fleas, ticks, lice, chiggers, mites, trematodes, cestodes, nematodes, and acanthocephalans (Fritzell and Haroldson 1982). Gray foxes appear to be highly resistant to infestation by sarcoptic mange mites (Stone *et al.* 1972).

Longevity It is rare for a gray fox to live longer than 4–5 years, although Seton (1929) reported that some individuals could live 14–15 years.

Historical perspective

Humans have probably harvested gray foxes for their fur for as long as the two have been in contact with one another. Gray foxes are trapped for utilitarian and economic reasons (including the perceived elimination of livestock depredation), and also for recreation. However, recent changes in social attitudes towards trapping have resulted in lower participation in the activity and its outright ban in some states (e.g., Arizona, California, Colorado, Florida, Massachusetts, New Jersey) (Armstrong and Rossi 2000).

Conservation status

Threats No major threats, but habitat loss, fragmentation, and degradation, may be particularly problematic in regions where human numbers are increasing rapidly and important habitat is converted for agricultural, industrial, and urban uses.

Commercial use Because of its relatively lower fur quality compared to other species, commercial use of the gray fox is somewhat limited. However, 90,604 skins were taken in the United States during the 1991 and 1992 season (Linscombe 1994). In Mexico, gray foxes are frequently sold illegally as pets (R. List pers. comm.).

Occurrence in protected areas Gray foxes occur in numerous protected areas throughout their range, such as Big Bend NP, San Joaquin National Wildlife Refuge, Rocky Mountain NP and Everglades and Dry Tortugas NP, and Adirondack NP.

Protection status CITES – not listed.

Current legal protection The gray fox is legally protected as a harvested species in Canada and the United States (Fritzell 1987).

Conservation measures taken No specific measures are currently being implemented, and none appear necessary at this time.

Occurrence in captivity

According to ISIS, there are 74 foxes in captivity, although there may be more in the hands of private collections/ individuals who do not report to ISIS. Gray foxes appear to fare well in captivity and commonly are on display at zoos and wildlife farms.

Current or planned research projects

R. Sauvajot (U.S. National Park Service, Thousand Oaks, California) and collaborators at the Santa Monica Mountains National Recreation Area in California recently investigated gray fox ecology, space use, interspecific interactions, and response to human development.

Researchers at the Savannah River Ecology Laboratory (Aiken, South Carolina) are investigating the demographic characteristics of a non-harvested population of gray foxes in South Carolina.

R. List (Instituto de Ecologia, National University of Mexico) and colleagues are studying the ecology and demography of a closed gray fox population, in a 1.6km^2 reserve within central Mexico City, to determine management needs.

M. Gompper (University of Missouri, Columbia) has proposed a genetic and ecological investigation of an island gray fox population on Cozumel, Mexico.

Gaps in knowledge

Because of the relatively high abundance and low economic value of gray foxes, surprisingly little research has been conducted on this species. Basic ecological and demographic information is needed for each of the major habitats occupied by gray foxes. Also, data on the response of gray foxes to human-altered landscapes (e.g., urban environments) are needed. No region-wide or range-wide population estimate has been produced. Furthermore, extremely little is known about the status and ecology of gray foxes outside of the USA and Canada. The effects of gray foxes on populations of smaller vertebrates, especially in urban and suburban settings without larger predators, may be important.

Core literature

Fritzell 1987; Fritzell and Haroldson 1982; Hall 1981; Harrison 1997; Lord 1961; Trapp and Hallberg 1975.

Reviewers: Gary Roemer, Rurik List. **Editors:** Deborah Randall, Claudio Sillero-Zubiri, Michael Hoffmann.

4.4 Island fox
Urocyon littoralis (Baird, 1858)
Critically Endangered – CR:A2be+3e (2004)

G.W. Roemer, T.J. Coonan, L. Munson and R.K. Wayne

Other names

English: island gray fox, Channel Islands fox, California Channel Island fox.

Taxonomy

Vulpes littoralis Baird, 1858:143. Type locality: San Miguel Island, Santa Barbara County, California, USA [34°02'N, 120°22'W].

Urocyon is currently considered a basal genus within the Canidae and has only two surviving members, the gray fox (*U. cinereoargenteus*) and the island fox (*U. littoralis*) (Wayne *et al*. 1997). The island fox is believed to be a direct descendant of the gray fox, having reached the Channel Islands either by chance over-water dispersal or human-assisted dispersal (Collins 1991a, b). Each island population differs in genetic structure and of the five mtDNA haplotypes found in island foxes, none are shared with a nearby mainland sample of gray foxes. However, all island fox populations share a unique restriction enzyme site, clustering the populations into a single monophyletic clade (Wayne *et al*. 1991b). Population specific restriction-fragment profiles have been identified from minisatellite DNA (Gilbert *et al*. 1990), and multilocus genotypes from hypervariable microsatellite DNA were used to correctly classify 99% of 183 island/gray fox samples to their population of origin (Goldstein *et al*. 1999). The two misclassifications occurred between nearby island populations. These data clearly justify the current classification of island foxes as a separate species (Wozencraft 1993) and the subspecific classifications of the six island populations (Hall 1981; Moore and Collins 1995).

Chromosome number is identical to *U. cinereoargenteus* with 2n=66; 62 acrocentric chromosomes, a submetacentric pair and two sex chromosomes (Wayne *et al*. 1991b).

Description

Island foxes are the smallest North American canid. Males are significantly heavier than females (Moore and Collins 1995) (Table 4.4.1). The head is grey with black patches on the lateral sides of the muzzle in the vicinity of the vibrissae, with black outlining the lips of both jaws. White patches

Table 4.4.1. Body measurements for the Island fox. Measures of adult foxes were taken in 1988 for all subspecies except for San Clemente (R. Wayne unpubl.). Weight for San Clemente foxes was measured in 1988 (D. Garcelon and G. Roemer unpubl.), other measures for San Clemente foxes are from Moore and Collins (1995).

	Northern Channel Islands	Southern Channel Islands
HB male	536mm	548mm
	(470–585) n=44	(513–590) n=28
HB female	528mm	538mm
	(456–578) n=50	(475–634) n=30
T male	213mm	272mm
	(145–255) n=44	(230–310) n=51
T female	202mm	248mm
	(115–265) n=50	(180–295) n=46
HF male	111mm	112mm
	(94–124) n=44	(104–120) n=51
HF female	107mm	107mm
	(95–122) n=50	(92–115) n=46
E male	60mm	63mm
	(53–68) n=44	(55–72) n=51
E female	60mm	62mm
	(54–67) n=50	(59–67) n=46
WT male	2.0kg	2.0kg
	(1.4–2.5) n=44	(1.4–2.5) n=51
WT female	1.8kg	1.8kg
	(1.5–2.3) n=50	(1.3–2.4) n=46

Adult female island fox, San Miguel Island, California, USA, 1994.

Timothy J. Coonan

on the muzzle extend behind the lateral black patches to the cheek and blend into the ventral surface of the neck which is mostly white and bordered by rufous dorsally. Small white patches are present lateral to the nose. Variable degrees of white and rufous colour the chest and extend throughout the belly. The body and tail are mostly grey, with the latter having a conspicuous black stripe on the dorsal surface ending in a black tip. The grey of the body extends partially down the legs giving way to mostly rufous, both in the middle and towards the rear. On both San Clemente and San Nicolas Islands, a brown phase coat colour occurs in which the grey and black of the body are largely replaced with a sandy brown and deeper brown, respectively. It is unclear if the brown phase is a true coat colour morph, a change that occurs with age or possibly a change that occurs because of an interaction with *Opuntia* spines that get imbedded within the pelt (Sheldon 1990). Pelage is relatively short (20–40mm deep) with a single moult resulting in a thin summer coat and a dense winter coat. Eight mammae are present. Dental formula is 3/3-1/1-4/4-2/3=42. Island foxes typically have fewer caudal vertebrae, 15–22 (n=47), than the gray fox, 21–22 (n=31) (Moore and Collins 1995).

Subspecies Six subspecies are currently recognised (Moore and Collins 1995):
Northern Channel Islands
— *U. l. littoralis* (San Miguel Island, 34°02'N, 120°22'W)
— *U. l. santarosae* (Santa Rosa Island, 33°57'N, 120°10'W)
— *U. l. santacruzae* (Santa Cruz Island, 33°57'N, 119°45'W)
Southern Channel Islands
— *U. l. dickeyi* (San Nicolas Island, 33°14'N, 119°30'W)
— *U. l. clementae* (San Clemente Island, 32°52'N, 118°27'W
— *U. l. catalinae* (Santa Catalina Island, 33°24'N, 118°24'W)

Similar species Gray fox (*Urocyon cinereoargenteus*): coloration very similar with a similar dark longitudinal stripe on top of a black-tipped tail. The gray fox also has dark and white markings on its face, and a conspicuous cinnamon-rusty colour on its neck, sides and limbs. There is also white on the gray fox's ears, throat, chest, belly and hind limbs, while the undercoat is mostly buff and grey. The gray fox is at least 30% larger than the island fox (Fritzell and Haroldson 1982).

Current distribution

The current distribution is thought to be a consequence of waif dispersal to the northern Channel Islands during the late Pleistocene, followed by Native American assisted dispersal to the southern Channel Islands (Collins 1982, 1991a, b, 1993; Wayne *et al.* 1991b; Goldstein *et al.* 1999; see also Historical perspective). The species is now geographically restricted to the six largest of the eight California Channel Islands located off the coast of southern California, USA (Figure 4.4.1).

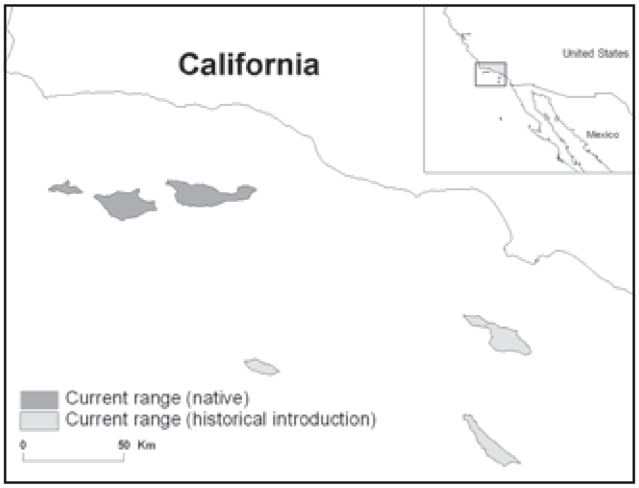

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Figure 4.4.1. Current distribution of the island fox.

Range countries United States (Moore and Collins 1995).

Relative abundance

Island foxes exhibit substantial variability in abundance, both spatially and temporally.

Estimated population size, relative abundance and population trends Total island fox numbers have fallen from approximately 6,000 individuals (Roemer *et al.* 1994)

Figure 4.4.2. Trend in fox population size on San Clemente (SCL), Santa Cruz (SCR) and San Miguel (SMI) Islands.

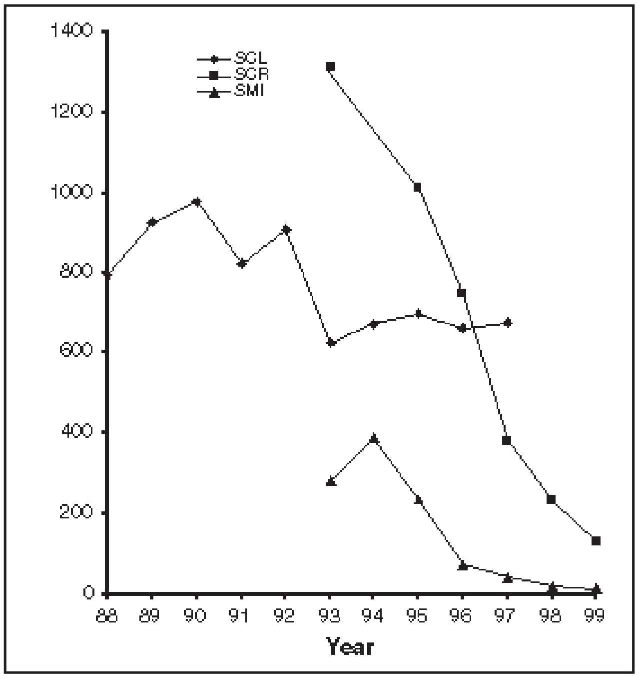

Table 4.4.2. Status of island foxes in the Channel Islands (Trend: S=stable, D=decreasing).

		Current population[1]					
	Initial	Protected areas		Other areas		Total	
Island	Population[1]	Population	Trend	Population	Trend	Population	Trend
San Miguel	450	28	D			28	D
Santa Rosa	?	45	D			45	D
Santa Cruz	1,312	17	D	60–80		77–97	D
San Nicolas	520			435–734	S	435–734	S
Santa Catalina	1,342	24		200	D	224	D
San Clemente	825			410	D	410	D

1 Initial population sizes (N_0) were estimated from date collected in the mid- to late 1980s or early 1990s using a capture-recapture approach (Kovach and Dow 1981; Roemer *et al*. 1994; Garcelon 1999; Roemer 1999; Coonan *et al*. 2000). Current population sizes (N) are the best estimates for 2002 (Garcelon 1999; Roemer 1999; Coonan 2002, 2003; Coonan *et al*. 2000; Timm *et al*. 2000; Roemer and Wayne 2003; G. Smith unpubl.).

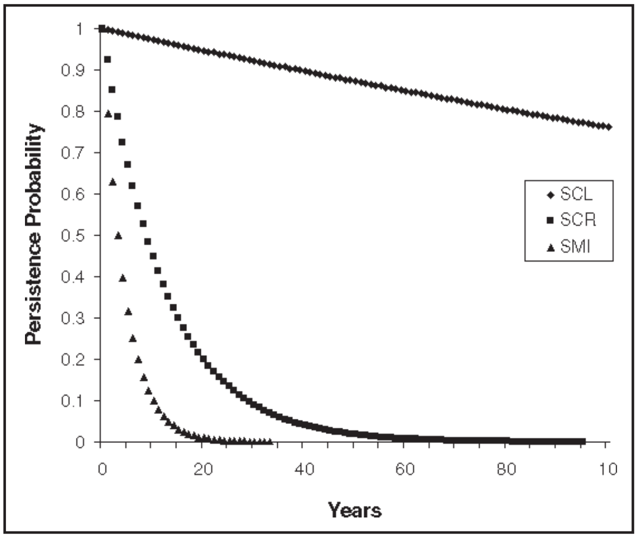

Figure 4.4.3. The probability of population persistence for each of three island fox populations: San Clemente (SCL), Santa Cruz (SCR) and San Miguel (SMI). The estimates of $T_e(n_0)$ used to generate the population persistence probabilities are 381, 5 and 13 years, respectively (G. Roemer *et al*. unpubl.).

to less than 1,500 in 2002 (Table 4.4.2). Four of the six island fox subspecies have experienced precipitous declines in the last four years. Fox populations on both San Miguel and Santa Cruz Islands declined by >90% between 1995 and 2000 (Figure 4.4.2). Similar declines also occurred on Santa Rosa and Santa Catalina Islands (Roemer 1999; Timm *et al.* 2000; Roemer *et al.* 2001a, 2002; Coonan 2003). Only 28 foxes are left on San Miguel and 45 foxes on Santa Rosa, and all are in captivity (Coonan 2002, 2003). The Santa Cruz population has dropped from an estimated 1,312 foxes in 1993 to 133 foxes in 1999 (Roemer 1999; Roemer *et al.* 2001a). Estimates for 2001 suggest that this population may have declined to as low as 60–80 individuals in the wild (Coonan 2002). A captive-breeding facility was initiated on Santa Cruz Island in 2002 when three adult pairs were brought into captivity; one pair had five pups in the spring (Coonan 2002). The subspecies on all three northern Channel Islands are in imminent danger of extinction (Figure 4.4.3). Fox populations on San Miguel and Santa Cruz Islands have an estimated 50% chance of persistence over the next decade, are in need of immediate conservation action (Roemer 1999; Roemer *et al.* 2001a, 2002; Coonan 2003). On Santa Catalina, island foxes are now rare on the larger eastern portion of the island as a result of a canine distemper outbreak that swept through the population in 1999 (Timm *et al.* 2000). The San Clemente population could be as low as 410 adult foxes, down from a high of 800–900 foxes. The causes of this decline are not yet clear (Garcelon 1999; Roemer 1999); however, it has been suggested that management actions aimed at protecting the threathened San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*) may be a major factor in this decline (Cooper *et al.* 2001; Schmidt *et al.* 2002; Roemer and Wayne 2003). The San Nicolas population appears to be at high density (5.6–16.4 foxes/km^2) and currently harbours one of the largest populations (estimate=734 foxes, Roemer *et al.* 2001b). However, this estimate may be positively biased and the actual population size may be closer to 435 foxes (G. Smith pers. comm.).

All of the current estimates of density and population size in island foxes have been conducted using modifications of a capture-recapture approach (Roemer *et al.* 1994). In its simplest application, population size is determined by multiplying average density among sampling sites times island area. Population estimates could be improved by first determining habitat-specific estimates of density and multiplying these densities times the area covered by the specific habitat (Roemer *et al.* 1994), an approach amenable to analysis with geographical information systems. However, density estimates made from aggregating home ranges suggest that the use of capture-recapture data may also overestimate density. For example, fox density estimated at Fraser Point, Santa Cruz Island using the capture-recapture approach was 7.0 foxes/km^2 (Roemer *et al.* 1994). A simultaneous estimate of density based on the distribution of home ranges for 14 radio-collared foxes with overlapping home ranges was approximately 31% lower (4.8 foxes/km^2) (Roemer 1999). Thus, the size of island fox populations may be lower than current capture-recapture analyses suggest.

Habitat

Island foxes occur in all habitats on the islands including native perennial and exotic European grassland, coastal sage scrub, maritime desert scrub, *Coreopsis* scrub, *Isocoma* scrub, chaparral, oak woodland, pine woodland, riparian, and inland and coastal dune.

Although fox density varies by habitat, there is no clear habitat-specific pattern. When fox populations were dense, foxes could be trapped or observed in almost any of the island habitats, except for those that were highly degraded owing to human disturbance or overgrazing by introduced herbivores. More recently, foxes have become scarce owing to precipitous population declines. On the northern Channel Islands where the declines are principally a consequence of hyperpredation by golden eagles (*Aquila chrysaetos*) (Roemer *et al*. 2001a, 2002), foxes are more numerous in habitats with dense cover, including chaparral and introduced stands of fennel (*Foeniculum vulgare*) (G. Roemer pers. obs.).

Food and foraging behaviour

Food Island foxes are omnivorous and feed on a wide variety of insects, vertebrates, fruits, terrestrial molluscs and even near-shore invertebrates (Laughrin 1973, 1977; Collins 1980; Kovach and Dow 1981; Crooks and van Vuren 1995; Moore and Collins 1995; Roemer *et al.* 2001b). The relative abundance of insects, mammals and plant material in the fox diet has been found to differ by habitat type (Laughrin 1977; Crooks and van Vuren 1995; Roemer *et al*. 2001b), and by island, depending upon availability of food items (Laughrin 1973; Collins and Laughrin 1979). For example, on San Miguel Island where deer mouse (*Peromyscus maniculatus*) densities are high, they form a large proportion of the diet of the island fox (Collins 1980). On Santa Cruz Island, Jerusalem crickets (*Stenopelmatus fuscus*) are a principal prey whereas on San Clemente Island, Jerusalem crickets are absent from the fauna and therefore unavailable. In contrast, the fruits of the coastal prickly pear cactus (*Opuntia littoralis*) are a principal food on San Clemente Island, especially during winter, but the cactus was nearly eradicated from Santa Cruz Island (Goeden *et al*. 1967) and thus comprises only a small portion of the fox diet there. The frequency of bird remains in the scat of island foxes is usually low (3–6%) but on San Miguel Island bird remains were found in 22% of scats (n=208) examined (Laughrin 1977; Collins and Laughrin 1979; Crooks and van Vuren 1995). For an exhaustive list of foods consumed by island foxes and the inter-habitat and inter-island variability see Laughrin (1973, 1977), Collins and Laughrin (1979) and Moore and Collins (1995).

Foraging behaviour Island foxes primarily forage alone, mostly at night, but they are also active during the day (Laughrin 1977; Fausett 1982; Crooks and van Vuren 1995). Dependent young accompany adults on forays and adult foxes may also forage together on occasion (G. Roemer pers. obs.). Foxes forage by coursing back and forth through suitable habitat patches and then moving, rather directly, through little-used habitats to other suitable habitat patches. Foxes are unable to extract prey as easily from the denser habitat and thus forage in more open habitats where prey availability, but perhaps not abundance, is greater (Roemer and Wayne 2003).

Damage to livestock or game Island foxes are not known to prey on livestock, but the introduced chukar (*Alectoris chukar*), occurs in the diet (Moore and Collins 1995), and it is probable that foxes feed on California quail (*Callipepla californica*), which are found on both Santa Catalina and Santa Cruz Islands.

Adaptations

Island foxes are a dwarf form of the mainland gray fox and this reduction in body size may be a consequence of an insular existence (Collins 1982). Reduced interspecific competition, reduced predation and lack of large prey may have contributed to their smaller body size.

Social behaviour

Island foxes typically exist as socially monogamous pairs that occupy discrete territories (Crooks and van Vuren 1996; Roemer *et al*. 2001b). It is not uncommon for full-grown young to remain within their natal range into their second year or for independent, territory-holding offspring to visit their parents in their former natal range (Roemer *et al*. 2001b).

The home range size of the island fox is one of the smallest recorded for any canid. On Santa Cruz Island, fox home ranges varied by season and habitat type, generally ranging between 0.15 and 0.87km^2 (Crooks and van Vuren 1996; Roemer *et al*. 2001b). Mean annual home range on Santa Cruz Island was 0.55km^2 (n=14, Roemer *et al*. 2001b). On San Clemente Island, mean home range size was larger (0.77km^2, n=11), perhaps due to the lower productivity of this more southerly island (Thompson *et al*. 1998). On Santa Cruz Island, fox home ranges expanded when territorial neighbours were killed by golden eagles, suggesting that density of foxes and the spatial distribution of neighbours may influence territory size (Roemer *et al*. 2001b).

Foxes communicate using visual, auditory and olfactory cues. Both submissive and aggressive behaviours have been observed and are similar to those described for the gray fox (Laughrin 1977; Fausett 1982; Moore and Collins 1995). Males have been observed chasing other male foxes and have also been observed fighting. Bite wounds were noted in 4 of 1,141 captures of foxes on Santa Cruz Island but were observed only in males and only during the breeding season (Roemer 1999). Foxes demarcate territory boundaries with latrine sites and have been observed urinating as frequently as every 6–9m (Laughrin 1977).

Reproduction and denning behaviour

Foxes breed once a year with parturition usually occurring in early April. Recent research suggests this canid may have induced ovulation (C. Asa pers. comm.), a physiological character that may allow for plasticity in the timing of reproduction. Pups have been born in early February on San Clemente Island and as late as 27 May on Santa Catalina Island (Schmidt *et al.* 2002; Timm *et al.* 2002). Of 35 foxes captured and killed in the month of February 1928 on Santa Cruz Island, 11 (46%) were pregnant (Sheldon 1990). An increase in territory vigilance by males occurs as early as January with actual copulations in captivity typically observed in early March (Coonan and Rutz 2000; Roemer *et al.* 2001b).

Length of gestation is unknown but has been estimated at 50–53 days (Moore and Collins 1995). Litter size varies from one to five but most litters are smaller, from one to three. Of 24 dens located on Santa Cruz Island, average litter size was 2.17 (Laughrin 1977). Average litter size for two captive breeding facilities on the northern islands was 2.6 (n=5, Coonan and Rutz 2000). In 2002, one captive pair on Santa Cruz Island produced a litter of five pups (Coonan 2002). Weaning is complete by mid- to late June and pups reach adult weight and become independent by September (Garcelon *et al.* 1999). Although most foxes are typically monogamous, extra-pair fertilisation has been recorded. Of 16 pups whose paternity was determined by genetic analysis, 25% were the result of extra-pair fertilisations (Roemer *et al.* 2001b). Dens used include rock piles, dense brush and naturally occurring cavities in the ground or under tree trunks.

Competition

The only known competitors of island foxes are island spotted skunks (*Spilogale gracilis amphiala*) on Santa Cruz and Santa Rosa Islands (von Bloeker 1967; Laughrin 1977; Crooks and van Vuren 1995; Roemer *et al.* 2002) and feral cats on all three southern Channel Islands (Laughrin 1977; Kovach and Dow 1981).

Mortality and pathogens

Natural sources of mortality Hyperpredation by golden eagles has been identified as a primary mortality factor for island foxes on the northern Channel Islands, and is likely responsible for the recent catastrophic population declines of those three subspecies (Roemer 1999; Roemer *et al.* 2001a, 2002.). The presence of an exotic omnivore, the feral pig (*Sus scrofa*), enabled eagles to colonise the islands, increase in population size, and overexploit the fox. Evidence from 28 fox carcasses from Santa Cruz and San Miguel Islands implicated eagles in nearly 90% of the mortalities, and a logistic model of hyperpredation showed that pigs would have been necessary to support a large, resident eagle population (Figure 4.4.4) (Roemer 1999; Roemer *et al.* 2001a, 2002). Further, the prevalence of other potential mortality factors, such as disease and parasites, were found to be incongruent with the pattern of fox population declines (Roemer *et al.* 2000a, 2001a). Red-tailed hawks (*Buteo jamaicensis*) may kill kits (Laughrin 1977). Interspecific aggression is another source of natural mortality.

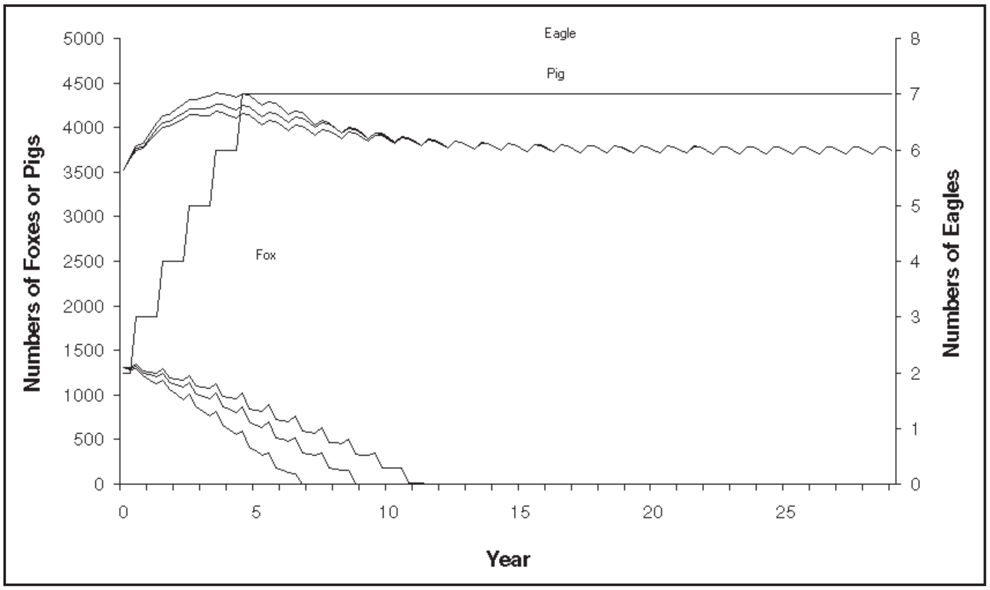

Figure 4.4.4. Trend in the fox, pig and eagle populations on Santa Cruz Island predicted from a logistic model of hyperpredation. Our time unit is a day and we plotted population size every 90 days. The regular peaks in fox population size are due to modelling growth as a single pulse each year. The three trajectories for each of the prey populations are due to differences in predator preference for the prey (pigs: foxes). The preference ratios modelled are 3, 1, and 0.33. Time to extinction for the fox populations given these preferences was 11.5 years, 8.7 years, and 6.7 years, respectively.

Persecution Island foxes are not persecuted except for the predator control programme currently being instituted by the U.S. Navy to protect the San Clemente loggerhead shrike.

Hunting and trapping for fur Island foxes are not currently hunted or trapped for their fur, but may have been historically. Sheldon (1990) took 155 foxes in the winter of 1927–1928 during 20 days of trapping with the intent of selling the pelts. It is not known if a market for fox pelts was established. Native Americans used fox pelts to create ceremonial headdresses, arrow-quivers, capes and blankets (Collins 1991b).

Road kills On San Clemente, Santa Catalina and San Nicolas Islands, trauma from automobiles is a significant source of mortality (Garcelon 1999; G. Smith pers. comm.).

Pathogens and parasites Canine diseases are considered important potential mortality sources for island foxes (Garcelon *et al.* 1992). This is underscored by the epidemic of canine distemper virus (CDV) that decimated the Santa Catalina Island fox population in 1998 to 2000 (Timm *et al.* 2000). CDV was apparently introduced sometime between late 1998 to mid-1999 and has caused an estimated 95% reduction in the fox population on the eastern 87% of Catalina Island. Human settlement on a narrow isthmus likely formed a barrier to fox dispersal and the spread of the disease to the western portion of the island. A total of 148 foxes have been captured in 2000 to 2001 on the western 13% of Santa Catalina Island supporting the contention that foxes there were not exposed to CDV (S. Timm pers. comm.). Antibodies to CDV were recently detected in foxes from San Nicolas Island but the titre levels observed may represent false positives (Coonan 2002; S. Timm pers. comm.).

Exposure to other various canine pathogens has been confirmed but morbidity or mortality has not been substantiated (Timm *et al.* 2000; L. Munson unpubl.). Positive antibody titres have been detected for canine parvovirus, canine adenovirus, canine herpesvirus, canine coronavirus, leptospirosis, toxoplasmosis and for heartworm (*Dirofilaria immitis*) (Garcelon *et al.* 1992; Roemer 1999; Roemer *et al.* 2000a, 2001a; Crooks *et al.* 2001). In addition a number of intestinal pathogens have been identified including *Ancylostoma*, *Toxascaris*, *Mesocestoides*, *Isospora*, *Sarcocytis*, and *Neospora* (Roemer *et al.* 2001a). Island foxes from San Miguel are infested with three pathogenic parasites, *Uncinaria*, *Angiocaulus* and an as yet unidentified spirurid that causes granulomas in the intestinal tract and mesentery (L. Munson unpubl.). These parasitic granulomas are likely the cause of the rectal prolapses that were observed in two wild foxes, one of which later died (G. Roemer pers. obs.) and in two captive foxes that recovered after reinsertion (K. Rutz pers. comm.). Other sources of mortality include trauma as a result of injury and aspiration pneumonia. A captive fox on Santa Rosa recently died from an aggressive oral cavity cancer (M. Willett and L. Munson unpubl.) and cancer of the ear canal (ceruminous gland carcinomas) has been observed in three foxes from Santa Catalina Island (L. Munson unpubl.).

Foxes on all islands also have thyroid atrophy, hepatic fibrosis and amyloidosis, and recently foxes from San Clemente Island have shown evidence of Quintox poisoning (L. Munson unpubl.), an anti-coagulant rodenticide used to control rodents as part of the San Clemente Loggerhead Shrike Recovery Program (Cooper *et al.* 2001).

Longevity Foxes as old as 10 years of age have been captured on San Miguel Island (Coonan *et al.* 1998).

Historical perspective

Island foxes played a spiritual role in earlier Native American societies on the Channel Islands (Collins 1991b). Native Americans of the Channel Islands harvested foxes to make arrow-quivers, capes and headdresses from their pelts, they ceremonially buried foxes, conducted an Island Fox Dance and most likely kept foxes as pets or semi-domesticates (Collins 1991b). Their current distribution is a direct consequence of historical interaction with humans (Collins 1991a, b; Wayne *et al.* 1991b; Goldstein *et al.* 1999). Fossil evidence dates the arrival of foxes to the northern Channel Islands (Santa Cruz, Santa Rosa and San Miguel) from 10,400–16,000 ybp (years before present) (Orr 1968). Their actual colonisation probably occurred between 18,000 and 40,000 years ago, when these northern islands were joined into one large island known as "Santarosae" (Collins 1982, 1993). At its closest, Santarosae was a mere 6km from the North American continent, having reached its maximum size 18,000–24,000 ybp. It is hypothesised that sometime during this period, mainland gray foxes, the progenitor of the island fox, colonised Santarosae by chance over-water dispersal, by either swimming or by rafting on floating debris (Collins 1982, 1993). As glaciers retreated and sea levels rose, Santarosae was subdivided into separate islands. Santa Cruz Island was formed first, some 11,500 ybp. Sea levels continued to rise separating the remaining land mass once again, approximately 9,500 ybp, to form Santa Rosa and San Miguel Islands. Native Americans then colonised the Channel Islands 9,000–10,000 ybp, and after establishment of an extensive trade route, transported foxes to the southern islands. The southern islands were thought to have been colonised by foxes between 2,200 and 5,200 ybp (Collins 1991a, b, 1993; Wayne *et al.* 1991b; Vellanoweth 1998).

Island foxes also represent a significant scientific resource. Their geographic distribution and resulting isolation has created a set of model populations that has extended our knowledge regarding the effects of insularity on mammalian social organisation (Roemer *et al.* 2001b), has contributed to an understanding of the molecular evolution of highly variable gene regions (Gilbert *et al.* 1990; Goldstein *et al.* 1999) and their recent decline is a clear example of the potential impact that invasive species can have on insular systems (Roemer *et al.* 2001a, 2002).

Conservation status

Threats The current primary threats to the species include golden eagle predation on the northern Channel Islands (Roemer 1999; Roemer *et al.* 2001a, 2002) and the possible introduction of canine diseases, especially CDV, to all populations (Garcelon *et al.* 1992; Roemer 1999; Timm *et al.* 2000). All populations are small, several critically so, and are threatened by demographic stochasticity and environmental variability. The small populations are especially vulnerable to any catastrophic mortality source, be it predation, canine disease, or environmental extremes (Roemer *et al.* 2000b).

Recently, there has also been a management conflict between island foxes and the San Clemente Island loggerhead shrike (Roemer and Wayne 2003). Island foxes were euthanised on San Clemente Island in 1998 as part of a programme to protect nesting shrikes (Elliot and Popper 1999; Cooper *et al.* 2001). Although euthanasia of foxes has stopped, a number of foxes are now retained in captivity each year, during the nesting and fledging stage of the shrike, and subsequently released back into the environment. The impact to fox reproduction and the potential disruption of the social system are unknown, but may be significant. These actions may have contributed to a 60% decline in the fox population on San Clemente Island (Cooper *et al.* 2001; Schmidt *et al.* 2002; Roemer and Wayne 2003). Considering the precipitous declines in foxes on four of six islands and the continued decline in the San Clemente population, this current management practice needs further scrutiny.

Commercial use There is no commercial use of island foxes.

Occurrence in protected areas The three subspecies on the northern Channel Islands occur within the Channel Islands National Park. Approximately two-thirds of Santa Cruz Island is owned by The Nature Conservancy (TNC), and managed as the Santa Cruz Island Preserve. The Preserve is within the boundaries of the Channel Islands National Park, and the TNC and NPS (National Parks Service), co-manage natural resources together under a cooperative agreement. Approximately 87% of Santa Catalina Island is owned by the Santa Catalina Island Conservancy, a non-profit conservation organisation, and both San Clemente and San Nicolas Islands are owned and managed by the U.S. Navy.

Protection status CITES – not listed.

Current legal protection The species was formerly a category II candidate for federal listing, but is not currently listed by the U.S. Fish and Wildlife Service (USFWS) as ‘threatened’ or ‘endangered’ under the Federal Endangered Species Act. The species is listed by the state of California as a ‘threatened’ species (California Department of Fish and Game 1987). The current legal status has not been sufficient to prevent recent catastrophic population declines. In June 2000, the USFWS was petitioned to list the populations on the three northern Channel Islands and Santa Catalina Island as ’endangered’ (Suckling and Garcelon 2000). The USFWS recently proposed to list these four subspecies as ‘endangered’ (USDI 2001).

Conservation measures taken Based upon recommendations from an *ad hoc* recovery team, the Island Fox Conservation Working Group, the National Park Service (NPS) began initiating emergency actions in 1999, with the objectives being to remove the primary mortality factor currently affecting island foxes (golden eagle predation), and to recover populations to viable levels via captive breeding. Between November 1999 and June 2002, 22 eagles were removed from Santa Cruz Island and relocated to north-eastern California. In 1999, the NPS established an island fox captive breeding facility on San Miguel Island, added a second facility on Santa Rosa in 2000 and a third on Santa Cruz Island in 2002 (Coonan 2002, 2003; Coonan and Rutz 2000, 2002). Fourteen foxes were originally brought into captivity on San Miguel; current captive population is now 28. There are currently 45 foxes in captivity on Santa Rosa, and 12 adult foxes in the Santa Cruz facility that produced a single litter of five pups (Coonan 2002, 2003).

The NPS has prepared an island fox recovery plan for the northern Channel Islands (Coonan 2001) and an island-wide restoration plan for Santa Cruz Island (USDI 2002). The measures taken thus far on the northern Channel Islands (golden eagle removal and captive breeding) will form the basis for long-term recovery for the subspecies on the northern Channel Islands. In addition, the reintroduction of bald eagles (*Haliaeetus leucocephalus*), the eradication of feral pigs, and the removal of exotic plants have been recommended and are being implemented (Roemer *et al.* 2001a; USDI 2002). Demographic modelling indicates that recovery to viable population levels could take up to a decade (Roemer *et al.* 2000b).

On Santa Catalina Island, The Santa Catalina Island Conservancy has taken a series of measures to mitigate the effects of canine distemper virus on that subspecies. Close to 150 foxes from the west end have been field-vaccinated for CDV, and both translocation and captive breeding programmes have been established to aid in recolonising the eastern portion of the island (Timm *et al*. 2000, 2002).

Although the Island Fox Conservation Working Group recognised the need for a species-wide recovery plan, there is currently no formal vehicle to accomplish such a planning effort, because the species is not listed under the Federal Endangered Species Act. Nonetheless, the Working Group recognised that the following actions need to be implemented in order to ensure recovery of island fox populations to viable levels (Coonan 2002, 2003):

- Complete removal of golden eagles from northern Channel Islands.
- Implement monitoring/response programme for future golden eagles.
- Remove feral pigs from Santa Cruz Island.
- Reintroduce bald eagles to the northern Channel Islands.
- Eliminate canine distemper as a mortality factor on Santa Catalina Island.
- Vaccinate wild foxes against canine distemper virus, as needed.
- Monitor populations for diseases causing morbidity and mortality through necropsy and faecal and blood testing.
- Enforce no-dog policy on islands, and vaccinate working dogs.
- Educate the public about potential disease transmission from domestic dogs.
- Establish and maintain captive breeding facilities on San Miguel, Santa Rosa, Santa Cruz and Santa Catalina Islands.
- Supplement wild populations with captive-reared foxes.
- Implement annual population monitoring of each subspecies/population.
- Halt management actions to protect the San Clemente loggerhead shrike that are adversely affecting the San Clemente island fox.
- Develop adaptive management programme.

Occurrence in captivity

Island foxes currently are kept in captivity on four islands. The National Park Service's captive breeding programme maintains facilities on San Miguel, Santa Rosa and Santa Cruz Islands, in which there are currently 28, 45 and 17 island foxes, respectively. The Santa Catalina Island Conservancy and the Institute for Wildlife Studies have established a captive breeding facility on that island, and there are currently 12 adult pairs of foxes there (Timm *et al*. 2002). Small numbers (1–4) of San Clemente Island foxes are kept in a total of four zoos on the mainland with a variable number of foxes held in captivity each year on that island (Cooper *et al*. 2001).

Current or planned research projects

M. Gray (UCLA, Los Angeles, California), G.W. Roemer (New Mexico State University, Las Cruces, New Mexico) and E. Torres (California State University, Los Angeles, California) are currently conducting a genetic analysis of captive island foxes, assessing genetic relatedness to formulate captive breeding strategy and maintain genetic diversity of founders.

A. Aguilar and R.K. Wayne (UCLA, Los Angeles, California) are assessing variation at the major histocompatiblity complex (Mhc) in the island fox.

C. Asa (St. Louis Zoo, Saint Louis, Missouri) is studying timing of the reproductive cycle via hormonal analysis of captive island foxes.

D.K. Garcelon (Institute for Wildlife Studies, Arcata, California) conducted transect trapping and radio-telemetry studies in 2001 which will be used to estimate basic population parameters for Santa Cruz Island foxes and determine mortality factors for this subspecies. Ongoing work will include annual population monitoring, and studies on spatial organisation and survival of island foxes on San Clemente Island using capture-recapture and radio-telemetry. This work will also include annual population monitoring on San Nicolas Island, using a grid-based, capture-recapture study for estimating density, survival and recruitment

S. Timm (Institute for Wildlife Studies, Arcata, California) is studying survival of translocated foxes on Santa Catalina Island.

L. Munson and D. Fritcher (University of California, Davis, California) are monitoring disease in the island fox. They aim to determine all diseases and parasites present in island foxes from all populations, both historically through archived frozen carcasses and presently through necropsy of dead foxes.

G.W. Roemer (New Mexico State University, Las Cruces, New Mexico) and P. Miller (IUCN Conservation Breeding Specialist Group) are undertaking a population viability analysis of the island fox with the aim to refine previous analyses of population viability and threat.

Gaps in knowledge

It is known that wild island fox pairs are unrelated and that extra-pair copulations occur (Roemer *et al*. 2001b), but little is known about how island foxes select mates and whether mate choice could play a role in improving the currently low reproduction characterising captive foxes (Coonan and Rutz 2002). Controlled mate-choice experiments are needed.

It has been suggested that intense predation by golden eagles could have altered island fox activity patterns and selected for greater nocturnal activity in those foxes that have survived predation (Roemer *et al*. 2002). The survival of the remaining wild island foxes on Santa Cruz Island is being monitored, but there has been no attempt to document daily activity levels (Dennis *et al*. 2001). The pattern of daily activity of wild Santa Cruz Island foxes needs to be assessed, and compared to the activity of captive and captive-reared foxes that are released into the wild. If captive-reared foxes are more active during diurnal and crepuscular periods than their wild counterparts, it is probable that captive-reared foxes reintroduced into the wild will suffer higher mortality owing to golden eagle predation.

There has been only a single study that has examined dispersal in island foxes (Roemer *et al.* 2001b) and the number of dispersal events recorded was small (n=8). Additional information on island fox dispersal patterns on different islands and during periods of high and low density are needed.

Core literature

Collins 1991a,b, 1993; Crooks and van Vuren 1996; Laughrin 1977; Moore and Collins 1995; Roemer 1999; Roemer *et al.* 2001a,b, 2002; Roemer and Wayne 2003; Wayne *et al.* 1991b.

Reviewers: Lyndal Laughrin, David K. Garcelon, Paul Collins. **Editors:** Claudio Sillero-Zubiri, Deborah Randall, Michael Hoffmann.

4.5 Kit fox
Vulpes macrotis Merriam, 1888
Least Concern (2004)

R. List and B.L. Cypher

Other names

English: desert fox; **German:** wüstenfuchs; **Spanish:** zorra del desierto, zorra norteña.

Taxonomy

Vulpes macrotis Merriam, 1888. Type locality: "Riverside, Riverside County, California" [United States, *c.* 34°00'N, 117°15'E].

The kit fox has been considered conspecific with the swift fox, *V. velox*, based on morphometric similarities and protein-electrophoresis (Clutton-Brock *et al.* 1976; Hall 1981; Dragoo *et al.* 1990). Others have treated *V. macrotis* as a distinct species based on multivariate morphometric data (Stromberg and Boyce 1986) and more recently based on mitochondrial DNA (Mercure *et al.* 1993).

Chromosome number not known.

Description

The kit fox is one of the smallest foxes in the Americas (Table 4.5.1). The most conspicuous characteristic is the large ears. The fur is short, with yellowish to greyish head, back and sides; the shoulders and the outside of the legs are brown-yellow; the belly and the inner side of legs are white-yellowish; the tip of the tail is black. The neck, legs and belly may have buffy highlights. The hair is dense

Table 4.5.1 Body measurements for the kit fox from Janos, Chihuahua, Mexico (List and Jimenez Guzmán in press).

HB male	537mm (485–520) n=7
HB female	501mm (455–535) n=5
T male	308mm (280–340) n=8
T female	289mm (250–305) n=5
E male	82mm (71–95) n=8
E female	80mm (74–95) n=6
WT male	2.29kg (1.7–2.7) n=8
WT female	1.9kg (1.6–2.2) n=6

Adult kit fox, sex unknown, standing at the entrance of its burrow. Janos, Chihuahua, Mexico, 2001.

Rurik List

between the foot-pads. Dental formula: 3/3-1/1-4/4-2/3=42. Mean cranial measurements from 35 specimens of *V. m. mutica* were: condylobasal length 114.4mm; zygomatic breadth 62.1mm; palatal length 57.8mm; interorbital breadth 23.1mm; postorbital breadth 21.4mm (Waithman and Roest 1977).

Subspecies Eight subspecies have been recognised (McGrew 1979). Fewer taxonomic studies have been conducted on kit foxes in Mexico, and therefore the taxonomy of kit foxes in Mexico is less certain.

- *V. m. arsipus* (south-eastern California, southern Arizona, and northern Sonora)
- *V. m. devia* (southern Baja California)
- *V. m. macrotis* (south-western California – extinct)
- *V. m. mutica* (San Joaquin Valley of California)
- *V. m. neomexicana* (New Mexico, western Texas, and north-west Chihuahua)
- *V. m. nevadensis* (Great Basin of the U.S.)
- *V. m. tenuirostris* (northern Baja California)
- *V. m. zinseri* (north central Mexico).

Similar species Swift fox, *Vulpes velox*: Sympatric with the kit fox only in a small contact zone (*c.* 100km wide); shorter, more rounded ears that are set farther apart on the head, and a shorter tail relative to body length.

Current distribution

The kit fox inhabits the deserts and arid lands of western North America (Figure 4.5.1). In the United States, it occurs from southern California to western Colorado and western Texas, north into southern Oregon and Idaho. In Mexico, it occurs across the Baja California Peninsula and across northern Sonora and Chihuahua to western Nuevo León, and south into northern Zacatecas (McGrew 1979; Hall 1981).

Range countries Mexico, USA (Hall 1981).

Relative abundance

The species is common to rare. Density fluctuates with annual environmental conditions, which are dependent upon precipitation (Cypher *et al.* 2000). In Utah, density ranged from 0.1–0.8/km^2 (Egoscue 1956, 1975). In California, density varied from 0.15–0.24/km^2 over a period of three years on one study site (White *et al.* 1996) and from 0.2–1.7/km^2 over 15 years on another study site (Cypher *et al.* 2000). Kit fox densities in prairie dog town complexes in Mexico were 0.32–0.8/km^2 in Chihuahua (List 1997) and 0.1/km^2 in Coahuila and Nuevo Leon (Cotera 1996).

Estimated populations/relative abundance and population trends In Mexico, data on which to base a population estimate for kit foxes are only available from two localities with very specific characteristics (presence of prairie dog towns). Therefore, the estimation of a population size for the country or even population trends is not possible with current information. However, because natural habitats occupied by the kit fox are being transformed, it is safe to assume that, overall, populations of the kit fox in Mexico are declining. In the past 10 years, about 40% of prairie dog towns in Coahuila and Nuevo Leon were converted to agriculture (L. Scott and E. Estrada unpubl.).

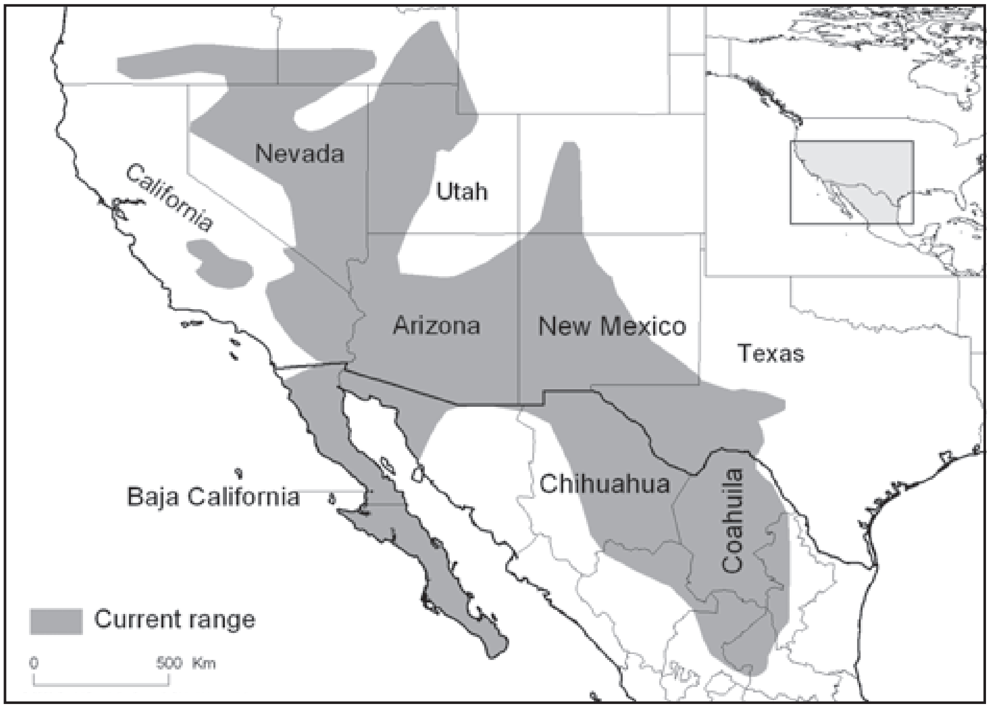

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Figure 4.5.1. Current distribution of the kit fox.

In the United States, kit fox abundance is unknown. Population trends are assumed to be relatively stable in Texas, New Mexico, Arizona, Utah, and Nevada where harvests for fur continue. Populations in Idaho, Oregon, and the Mojave Desert in California also may be relatively stable due to a lack of significant threats. Populations are potentially increasing in Colorado where foot-hold trapping was recently banned. Populations of the 'endangered' San Joaquin kit fox in the San Joaquin Valley of California are likely still declining due to continuing habitat loss, fragmentation, and degradation (USFWS 1998).

Habitat

The kit fox inhabits arid and semi-arid regions encompassing desert scrub, chaparral, halophytic, and grassland communities (McGrew 1979; O'Farrell 1987). It is found in elevations ranging from 400–1,900m a.s.l., although kit foxes generally avoid rugged terrain with slopes >5% (Warrick and Cypher 1998). Loose textured soils may be preferred for denning. Kit foxes will use agricultural lands, particularly orchards, on a limited basis, and kit foxes also can inhabit urban environments (Morrell 1972).

Food and foraging behaviour

Food Kit foxes primarily consume rodents, leporids, and insects. Primary prey includes kangaroo rats (*Dipodomys* spp.), prairie dogs (*Cynomys* spp.), black-tailed jackrabbits (*Lepus californicus*), and cottontails (*Sylvilagus* spp.). Other items consumed include birds, reptiles, and carrion (Egoscue 1962; Jiménez-Guzmán and López-Soto 1992; White *et al.* 1995; List 2003; Cypher *et al.* 2000). Plant material is rarely consumed, although cactus fruits are occasionally eaten (Egoscue 1956).

Foraging behaviour Kit foxes mostly forage solitarily. They are mainly active by night and occasionally exhibit crepuscular activity (List 1997).

Damage to livestock and game There is no evidence that kit foxes significantly impact game or livestock populations.

Adaptations

Kit foxes are well adapted to a life in warm, arid environments. To dissipate heat while conserving water, they have a large surface area to body mass ratio and large ears which favour non-evaporative heat dissipation and can vary panting rates (Klir and Heath 1992). Predominantly nocturnal activity and diurnal den use also reduce water loss. Kit foxes can obtain all necessary water from their food, but to do so must consume approximately 150% of daily energy requirements (Golightly and Ohmart 1984).

Social behaviour

Kit foxes are primarily monogamous with occasional polygyny (Egoscue 1962). Pairs usually mate for life (Egoscue 1956). Young from previous litters, usually females, may delay dispersal and remain in natal home ranges where they may assist with raising the current litter (List 1997; Koopman *et al.* 2000). Kit foxes are not strongly territorial and home ranges may overlap, although core areas generally are used exclusively by one family group (White and Ralls 1993; Spiegel 1996). Home range size is variable, even within similar vegetation types, and ranges from 2.5km² (Knapp 1978) to 11.6km² (White and Ralls 1993).

Kit foxes sometimes bark at approaching predators or to recall pups, and they sometimes emit a "hacking growl" during intraspecific encounters. Foxes in dens or captivity make a closed-mouth vocalisation during times of anxiety (Egoscue 1962). Scent-marking by kit foxes has not been investigated.

Reproduction and denning behaviour

Kit foxes mate from mid-December to January and give birth from mid-February to mid-March after a gestation of 49–55 days (Egoscue 1956; Zoellick *et al.* 1987). Litter size ranges from 1–7 (mean=4; Cypher *et al.* 2000). Reproductive success is considerably lower for yearling females and varies annually with food availability for all age classes (Spiegel 1996; Cypher *et al.* 2000). Pups emerge from dens at about four weeks, are weaned at about eight weeks, begin foraging with parents at about 3–4 months, and become independent at about 5–6 months (Morrell 1972; R. List unpubl.). Mean dispersal age in California was eight months (Koopman *et al.* 2000).

Kit foxes use dens year round and have multiple dens within their home ranges (White and Ralls 1993; Koopman *et al.* 1998). Although they can excavate their own dens, kit foxes frequently occupy and modify the burrows of other species, particularly prairie dog, kangaroo rats, squirrels (*Spermophilus* spp.) and badgers (*Taxidea taxus*) (Morrell 1972; Jiménez-Guzmán and López-Soto 1992; Cotera 1996; List 1997). Occasionally, they will den in man-made structures (e.g., culverts, pipes), but young are almost always born in earthen dens (Spiegel 1996; Zoellick *et al.* 1997).

Competition

Potential competitors for food and dens include coyotes (*Canis latrans*), bobcats (*Lynx rufus*), red foxes (*Vulpes vulpes*), badgers, skunks (*Mephitis* spp. and *Spilogale* spp.), and feral cats (White *et al.* 1995; Cypher and Spencer 1998; B. Cypher unpubl.). Strategies such as year-round den use, resource partitioning, and habitat partitioning allow kit foxes to mitigate competitive effects and coexist with most of these species. Non-native red foxes are increasing within the range of kit foxes (Lewis *et al.* 1993), and may present a more significant competitive threat due to greater overlap in resource exploitation patterns and potential for disease transmission. Although coyotes compete with and even kill kit foxes, they also may provide a benefit to kit foxes by limiting the abundance of red foxes (Cypher *et al*. 2001).

Mortality and pathogens

Natural sources of mortality Predation, mainly by coyotes, usually is the main source of mortality for kit foxes and commonly accounts for over 75% of deaths (Ralls and White 1995; Spiegel 1996; Cypher and Spencer 1998). Other predators include bobcats, red foxes, badgers, feral dogs, and large raptors (O'Farrell 1987).

Persecution In Mexico, kit foxes sometimes are shot opportunistically, but they are not actively persecuted. In the USA, large numbers of kit foxes were killed during predator control programmes that targeted other species, particularly coyotes and wolves (*Canis lupus*). However, such programmes have been discontinued or are more species-specific.

Hunting and trapping for fur Kit fox fur has relatively low value, and kit foxes are usually caught incidentally in traps set for other furbearers. About 1,200 were harvested in the United States between 1994 and 1995 (International Association of Fish and Wildlife Agencies unpubl.).

Road kills Vehicles are an important source of mortality and are the primary mortality factor in some areas (Cotera 1996; B. Cypher unpubl.).

Pathogens and parasites Kit foxes frequently carry antibodies to a variety of viral and bacterial diseases indicating exposure. However, disease does not appear to be a significant source of mortality, although rabies could have contributed to a decline in one population of the San Joaquin kit fox (White *et al*. 2000). A variety of ectoparasites (e.g., fleas, ticks, lice) and endoparasites (e.g., cestodes and nematodes) have also been found in kit foxes, but no morbidity or mortality associated with these parasites has been reported.

Longevity Kit foxes on two sites in California were known to reach at least seven years of age (B. Cypher unpubl.).

Historical perspective

Because of their small size and nocturnal habits, kit foxes are relatively inconspicuous. Thus, they are not particularly important for native or modern cultures, and are not well represented in arts and crafts or traditional uses.

Conservation status

Threats The main threat to the long-term survival of the kit fox is habitat conversion, mainly to agriculture but also to urban and industrial development. In both western and eastern Mexico, prairie dog towns which support important populations of kit foxes are being converted to agricultural fields, and in eastern Mexico the road network is expanding, producing a concomitant increase in the risk of vehicle mortality. In the San Joaquin Valley of California, habitat conversion for agriculture is slowing, but habitat loss, fragmentation, and degradation associated with industrial and urban development are still occurring at a rapid pace.

Commercial use In Mexico, kit foxes are occasionally sold illegally in the pet market. Kit foxes are harvested for fur in some states in the USA, but otherwise are not used commercially.

Occurrence in protected areas

- In Mexico, kit foxes are found in the Biosphere Reserves of El Vizcaino, Mapimi and El Pinacate, in the Area of Special Protection of Cuatro Ciénegas, and are probably found in another eight protected areas throughout their range.
- In the United States, they occur in numerous protected areas throughout their range. The 'endangered' subspecies *V. m. mutica* occurs in the Carrizo Plain National Monument and various other federal, state, and private conservation lands.

Protection status CITES – not listed (considered a subspecies of *V. velox*).

The kit fox is considered 'vulnerable' in Mexico (SEDESOL 1994). In the United States, the San Joaquin kit fox (*V. m. mutica*) is federally classified as 'endangered', and as 'threatened' by the state of California (USFWS 1998). In Oregon, kit foxes are classified as 'endangered'.

Current legal protection Harvests are not permitted in Idaho, Oregon, or California, and the kit fox is a protected furbearer species (i.e., regulated harvests) in Utah, Colorado, Arizona, New Mexico, and Texas.

Conservation measures taken In Mexico, the 'vulnerable' status of the kit fox grants conservation measures for the species, but these are not enforced. In the United States, state and federal protections for kit foxes are being enforced.

Efforts are underway to protect the prairie dog towns of both eastern (Pronatura Noreste) and western Mexico (Institute of Ecology from the National University of Mexico), which are known to be strongholds for the kit fox, but no specific actions focused on the kit fox are being undertaken in Mexico. In the United States, a recovery plan has been completed (USFWS 1998) and is being implemented for the San Joaquin kit fox. Recovery actions include protection of essential habitat, and demographic and ecological research in both natural and anthropogenically modified landscapes.

Occurrence in captivity

No captive breeding efforts are currently being conducted for kit foxes. Facilities such as the Arizona-Sonora Desert Museum in Tucson, Arizona, California Living Museum in Bakersfield, California, and several zoos keep live kit foxes for display and educational purposes. Also, Humboldt State University in Arcata, California maintains a small number of kit foxes for research and education.

Current or planned research projects

R. List (Institute of Ecology, National University of Mexico) is currently assessing the abundance of kit foxes in the prairie dog towns of north-western Chihuahua to compare the densities to those in 1994 to 1996. He is also planning to map the current distribution in Mexico using GIS.

B. Cypher, D. Williams, and P. Kelly (California State University-Stanislaus, Endangered Species Recovery Program – ESRP) are conducting a number of investigations on the San Joaquin kit fox, including ecology and demography in agricultural lands and urban environments, use of artificial dens, kit fox-red fox interactions, highway impacts, pesticide effects, and restoration of retired agricultural lands.

K. Ralls and colleagues (Smithsonian Institution, Washington D.C., USA), in collaboration with the ESRP, are conducting range-wide genetic analyses for the San Joaquin kit fox and investigating the use of tracker dogs (to find scats) in gathering information on kit fox presence and ecology.

Two working groups of the National Center for Ecological Analysis and Synthesis (University of California, Santa Barbara, USA) are conducting population modelling studies and investigating conservation strategies for the San Joaquin kit fox.

The California State University, San Luis Obispo and the California Army National Guard are investigating the effects of military activities on the San Joaquin kit fox and monitoring kit fox abundance on military lands in California.

R. Harrison (University of New Mexico, Albuquerque) is investigating kit fox ecology in New Mexico.

The U.S. Army is sponsoring an investigation of military effects and kit fox ecology on the Dugway Proving Grounds in Utah.

Gaps in knowledge

In general, demographic and ecological data are needed throughout the range of the kit fox so that population trends and demographic patterns can be assessed. In Mexico, information available on the kit fox is scarce. The most important gaps in our knowledge of the species are the present distribution of the species and population estimates throughout its range. General biological information is needed from more localities in the Mexican range of the kit fox. In the United States, information is required on the San Joaquin kit fox including assessing the effects of roads and pesticides on kit foxes, investigating dispersal patterns and corridors, determining metapopulation dynamics and conducting viability analyses, developing conservation strategies in anthropogenically altered landscapes, assessing threats from non-native red foxes, and range-wide population monitoring.

Core literature

Cypher *et al.* 2000; Egoscue 1962, 1975; McGrew 1979; O'Farrell 1987; Spiegel 1996.

Reviewers: Mauricio Cotera, Patrick Kelly, Ellen Bean. **Editors:** Claudio Sillero-Zubiri, Michael Hoffmann, Deborah Randall.

4.6 Swift fox
Vulpes velox (Say, 1823)
Least Concern (2004)

A. Moehrenschlager and M. Sovada

Other names

French: renard véloce; **German:** flinkfuchs; **Indigenous names:** senopah (Blackfeet Tribe, Canada and USA).

Taxonomy

Canis velox Say, 1823. James, Account of an Exped. from Pittsburgh to the Rocky Mtns, 1:487. Type locality: "camp on the river Platte, at the fording place of the Pawnee Indians, twenty-seven miles below the confluence of the North and South, or Paduca Forks."

The swift fox is phenotypically and ecologically similar to the kit fox (*Vulpes macrotis*) and interbreeding occurs between them in a small hybrid zone in west Texas and eastern New Mexico (Rohwer and Kilgore 1973; Mercure *et al*. 1993; Rodrick 1999). Some morphometric comparisons and protein-electrophoresis have suggested that these foxes constitute the same species (Ewer 1973; Clutton-Brock *et al.* 1976; Hall 1981; Dragoo *et al.* 1990; Wozencraft 1993). Conversely, other multivariate morphometric approaches (Stromberg and Boyce 1986), as well as mitochondrial DNA restriction-site and sequence analyses (Mercure *et al.* 1993; Rodrick 1999) have concluded that they are separate species. Swift and kit foxes are most closely related to Arctic foxes (*Alopex lagopus*), and this genetic association is the closest among the *Vulpes*-like canids (Wayne and O'Brien 1987), although Arctic foxes are classified in a different genus.

Description

The swift fox is one of the smallest canids, with an average weight of 2.4kg (Table 4.6.1). The winter pelage is dark greyish across the back and sides extending to yellow-tan across the lower sides, legs, and the ventral surface of the tail. The ventral fur is white with some buff on the chest. In summer, the fur is shorter and more rufous. Swift foxes can be distinguished from other North American canids, except the closely related kit fox, by black patches on each side of the muzzle, a black tail tip, and their small body size. Dental formula: 3/3-1/1-4/4-2/3=42.

Subspecies Stromberg and Boyce (1986) concluded that significant geographic variation exists among swift foxes, but Merriam's (1902) classification of swift foxes into northern (*V. velox hebes*) and southern (*V. v. velox*) subspecies is likely unjustified (Stromberg and Boyce 1986; Mercure *et al*. 1993).

Table 4.6.1 Body measurements for the swift fox from specimens at least nine months old in north-eastern New Mexico (Harrison 2003).

HB male	523mm (500–545) n=11
HB female	503mm (475–540) n=10
T male	286mm (250–340) n=11
T female	278mm (250–302) n=10
HF male	121mm (115–127) n=11
HF female	116mm (109–126) n=10
E male	64mm (59–68) n=10
E female	62mm (57–68) n=10
WT male	2.24kg (2.0–2.5) n=18
WT female	1.97kg (1.6–2.3) n=9

Similar species Kit foxes (*V. macrotis*) have longer, less rounded ears that are set closer to the midline of the skull, a narrower snout, and a proportionately longer tail to their body length than swift foxes.

Distribution

Historical distribution The swift fox is native to short-grass and mixed-grass prairies of the Great Plains in North America (Egoscue 1979). On the northern limit of its range, swift foxes were present in the Canadian provinces of Alberta, Saskatchewan, and Manitoba. The southern species boundary was New Mexico and Texas in the United States. Historical records also exist for areas in Montana, Wyoming, North Dakota, South Dakota, Nebraska, Kansas, Colorado, and Oklahoma. Some historical range descriptions mention swift foxes in Minnesota and Iowa; however, there are no verified records of occurrence in either state (Sovada and Scheick 1999). Iowa has one fossil record and several unconfirmed accounts. Minnesota has no records and no account of any merit.

Current distribution Following swift fox extirpation from Canada by 1938 (Soper 1964), reintroduction releases since 1983 have established a small swift fox population in Alberta, Saskatchewan, and Montana which now constitutes the northern extent of the species' range (Moehrenschlager and Moehrenschlager 2001) (Figure 4.6.1). The southern periphery of the range is still central New Mexico and north-western Texas, and, in terms of historic distribution, swift foxes are currently not found in Manitoba or North Dakota. Current estimates for the United States suggest that swift foxes are located in 39–

Juvenile swift fox, approximately 2.5 to 3 months old, sex unknown. Near Shirley Basin, Wyoming, USA, 1998.

Travis Olson

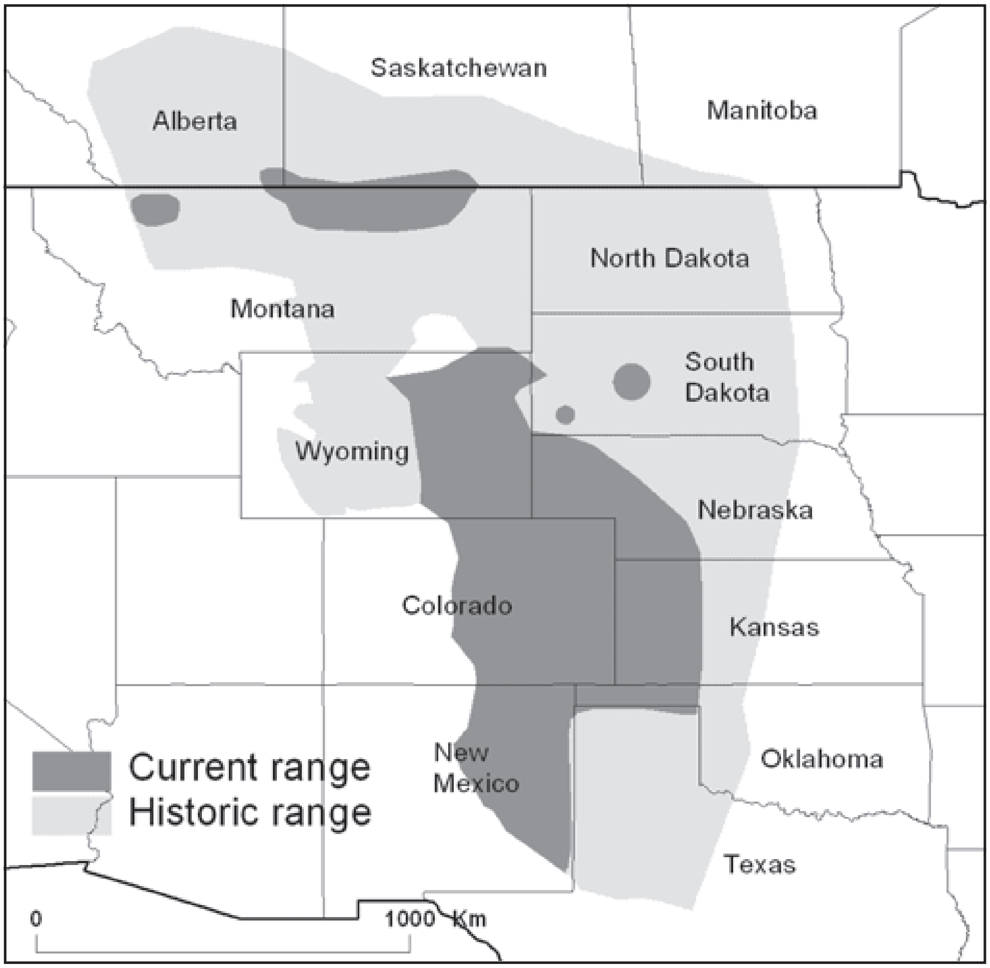

Figure 4.6.1. Current distribution of the swift fox.

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42% of their historic range depending on conservative versus liberal estimates of historic range and the time span of records that are considered (Sovada and Scheick 1999). As such, the conservative estimate, based on the relative presence or absence of swift foxes in counties throughout individual states, is that swift foxes are distributed across 505,149km^2 while the liberal estimate is 607,767km^2 (Sovada and Scheick 1999). But in much of the distribution populations are fragmented.

Range countries Canada, USA (Sovada and Scheick 1999).

Relative abundance

Historically, the swift fox was considered an abundant predator of the prairies, but their numbers were severely depleted by the late 1880s and early 1900s. In Canada, the last recorded specimen was collected in 1928 (Carbyn 1998) and a single sighting was made in 1938 (Soper 1964). Zumbaugh and Choate (1985) provided evidence that, in Kansas, swift foxes were extremely abundant in the mid-1800s, but became less abundant by the turn of the 20th century. The species was probably extirpated from Kansas by the 1940s (Black 1937; Cockrum 1952; Hall 1955; Sovada and Scheick 1999). There are similar reports of population declines from other states (see Sovada and Scheick 1999).

Swift fox populations began to recover over portions of their former range beginning in the 1950s (Martin and Sternberg 1955; Glass 1956; Anderson and Nelson 1958; Andersen and Fleharty 1964; Kilgore 1969; Sharps 1977; Egoscue 1979; Hines 1980). In the core of their distribution, in Kansas, Colorado, the Oklahoma panhandle, and New Mexico, populations are considered stable whereas populations in Texas and Wyoming are fragmented and more susceptible to decline. Swift foxes are rare in Nebraska, South Dakota, and Montana, and extirpated from North Dakota (Allardyce and Sovada 2003).

Estimated populations/relative abundance and population trends Following approximately 50 years of extirpation, a swift fox reintroduction programme was initiated in Canada in 1983. By 1997, 942 foxes had been released, primarily utilising captive breeding but also through the use of translocations (Moehrenschlager and Macdonald 2003). Using live trapping, a 1996/1997 census estimated the Canadian population to consist of 289 individuals in two isolated subpopulations. A second census that re-sampled these sites during the same season in 2000/2001 also expanded the survey area into Montana (Moehrenschlager and Moehrenschlager 2001; Moehrenschlager *et al.* 2004). The results showed that swift fox population size in Canada had increased three-fold since 1996/1997, the total known distribution including Montana spanned at least 17,500km^2, the combined population size was approximately 877 individuals, and that 98.6% of the population is now wild-born. This population is considerably isolated from the contiguous swift fox range in the United States and needs to be considered separately in terms of population viability.

In the United States, swift fox populations are believed to be stable in Texas, New Mexico, Oklahoma, Colorado, and Kansas. The population in Wyoming is relatively stable but fragmented. Less is known about the population in Nebraska, but there appear to be four disjunct populations of unknown status. In South Dakota, populations are small and fragmented; some are considered stable. Swift foxes are extinct in North Dakota. Reintroductions of swift foxes are being implemented at two sites in South Dakota. The Turner Endangered Species Fund began reintroducing foxes in 2002 in the Bad River Ranch south-west of Pierre. Reintroduction to the Badlands National Park began in 2003. The Defenders of Wildlife are currently supporting (1998–present) a swift fox reintroduction in northern Montana's Blackfeet Reservation.

Habitat

The swift fox is predominately found on short-grass and mixed-grass prairies in gently rolling or level terrain (Kilgore 1969; Hillman and Sharps 1978; Hines 1980). In Kansas, swift foxes have been found to den and forage in fallow cropland fields such as wheat (Jackson and Choate 2000; Sovada *et al.* 2003). Survival rates (and reproductive rates, although sample sizes were small; Sovada *et al.* 2003) between foxes in grassland and cropland sites were not significantly different suggesting that swift foxes may be able to adapt to such habitat in some cases (Sovada *et al.* 1998). Notably, the distribution and density of dens are considered important components of swift fox habitat requirements (Herrero *et al.* 1991), particularly in terms of evading coyote predation or red fox competition (Tannerfeldt *et al.* 2003).

Food and foraging behaviour

Food Swift foxes are opportunistic foragers which feed on a variety of mammals, but also birds, insects, plants, and carrion (Kilgore 1969; Hines 1980; Cameron 1984; Uresk and Sharps 1986; Hines and Case 1991; Zimmerman 1998; Kitchen *et al.* 1999; Moehrenschlager 2000; Sovada *et al.* 2001b). Leporids have been reported as a primary prey item in several studies (Kilgore 1969 [winter]; Cameron 1984; Zumbaugh *et al.* 1985). In South Dakota, mammals accounted for 49% of prey occurrences with prairie dogs (*Cynomys ludovicianus*) as the primary prey item (Uresk and Sharps 1986). Sovada *et al.* (2001b) in Kansas, and Hines and Case (1991) in Nebraska, found that murid rodents were the most frequently occurring prey in swift fox diets. Several studies have reported a high frequency of insects, but insects likely constituted a small portion of biomass (Kilgore 1969). Birds and bird eggs have been identified as a food of swift foxes (Kilgore 1969; Uresk and Sharps 1986; Sovada *et al.* 2001a). Swift fox studies typically have reported a relatively high frequency of plant materials found in samples, but most often in relatively small amounts per sample. However, several studies identified prickly pear cactus fruit, wild plums, and sunflower seeds as a food resource (Kilgore 1969; Hines and Case 1991; Sovada *et al.* 2001b).

Foraging behaviour Swift foxes are mostly solitary hunters, foraging throughout the night. They also exhibit some crepuscular activity and will hunt diurnal species such as birds and ground squirrels during the summer. Caching of food by swift foxes has been observed (Sovada *et al.* 2001b).

Damage to livestock and game There is no evidence that swift foxes significantly impact game or livestock populations.

Adaptations

Swift foxes can run at speeds of up to 60km/hr, which helps to elude predators, and facilitates the hunting of fast prey such as jackrabbits. Predominantly nocturnal activity and diurnal use of dens reduces water loss.

Social behaviour

The typical social group consists of a mated pair with pups. Occasionally, the social group is a trio or group of two males and two or three females, with one breeding female and non-breeding helpers (Kilgore 1969; Covell 1992; Sovada *et al.* 2003; Tannerfeldt *et al.* 2003). Pups remain with the parents until dispersal, which commences in August or September in Oklahoma (Kilgore 1969), September/October in Colorado and Kansas (Covell 1992; Sovada *et al.* 2003) and August in Canada (Pruss 1994). Moehrenschlager (2000) reported that only 33% (n=12) of juveniles had left natal home ranges at 9.5 months of age while all recaptured individuals aged 18 months or older had dispersed (n=7).

Published estimates of swift fox home ranges are quite variable and difficult to compare because different techniques and criteria have been used to estimate home-range size (Tannerfeldt *et al.* 2003). Hines and Case (1991) reported an average home range size of 32.3km^2 (range=

7.7–79.3km²) for seven swift foxes in Nebraska using the minimum convex polygon method, but four animals were followed for fewer than five nights in winter or very early spring. Andersen *et al.* (2003) reported a similar average MCP home-range size of 29.0km² (range=12.8–34.3km²) on the Pinon Canyon Maneuver Site in south-eastern Colorado (1986 to 1987) for five swift foxes with >34 locations over a minimum period of seven months. A slightly smaller estimate (MCP) of average home range, 25.1km² (SE=1.9, range=8.7–43.0km²), was determined for 22 swift foxes with >60 locations in western Kansas (Sovada *et al.* 2003). Zimmerman *et al.* (2003) estimated average MCP home-range size of 10.4km² (range=7.3–16.9km²) for five swift foxes in Montana. Using the 95% adaptive kernel method, Kitchen *et al.* (1999) reported average home-range size of 7.6km² for foxes (with >60 locations per season) on the Pinon Canyon Maneuver Site during 1997 to 1998. In western Kansas, Sovada *et al.* (2003) reported a mean ADK estimate of 19.5km² for 22 foxes (SE=1.4). Pechacek *et al.* (2000) estimated mean 95% ADK home range sizes of 11.7km² and 100% MCP estimates of 7.7km² for 10 swift foxes in south-eastern Wyoming.

Early studies suggested that swift foxes were not territorial (Hines 1980; Cameron 1984), although more recent data have provided evidence of territoriality. Andersen *et al.* (2003) reported nearly total exclusion of an individual swift fox's core activity area to other same-sex individuals. Pechacek *et al.* (2000) and Sovada *et al.* (2003) found areas used by mated pairs had minimal overlap with areas used by adjacent pairs, and core areas were exclusive. In Canada, Moehrenschlager (2000) reported swift fox home ranges overlapped by 77.1% among mates and 21.4% between neighbours.

Avery (1989) described the vocal repertoire of the swift fox from recordings made of captive foxes. He identified eight different vocalisations: courting/territorial call, agonistic chatter, submissive whine, submissive chatter, precopulatory call, growls, excited yip/bark, and social yips.

Reproduction and denning behaviour

Swift foxes are primarily monogamous (Kilgore 1969) although additional females that act as helpers in raising pups are occasionally observed at den sites (Kilgore 1969; Covell 1992; Olson *et al.* 1997; Sovada *et al.* 2003; Tannerfeldt *et al.* 2003). Also, a male has been seen with litters of two different adult females on the same day (Moehrenschlager 2000). Swift foxes are monoestrus and the timing of breeding is dependent upon latitude (Asa and Valdespino 2003). Breeding occurs from December to January in Oklahoma (Kilgore 1969), from January to February in Colorado (Scott-Brown *et al.* 1987; Covell 1992), from February to early March in Nebraska (Hines 1980) and in March among wild and captive Canadian foxes (Pruss 1994; Moehrenschlager 2000). The mean gestation period is 51 days (Schroeder 1985). Average litter sizes of 2.4–5.7 have been reported based on counts of pups at natal dens (Kilgore 1969; Hillman and Sharps 1978; Covell 1992; Carbyn *et al.* 1994; Schauster *et al.* 2002b; Andersen *et al.* 2003). In Colorado, litter sizes were greater for mated pairs with helpers than for those without (Covell 1992). Pups open their eyes at 10–15 days, emerge from the natal den after approximately one month, and are weaned at 6–7 weeks of age (Kilgore 1969; Hines 1980). Both members of the pair provide for the young and young foxes remain with the adults for 4–6 months (Covell 1992), which is longer than other North American canids.

Swift foxes are among the most burrow-dependent canids and, unlike most others, depend on dens throughout the year (Kilgore 1969; Egoscue 1979; Hines 1980; Tannerfeldt *et al.* 2003). Swift foxes will excavate their own dens and modify the burrows of other species. Dens serve several functions, such as providing escape cover from predators, protection from extreme climate conditions in both summer and winter, and shelter for raising young.

Competition

Predation by and interspecific competition with coyotes (*Canis latrans*) and expansion of red fox (*Vulpes vulpes*) populations may be the two most serious limiting factors to swift fox recolonisation of suitable habitat identified within the species' historic range (Moehrenschlager *et al.* 2004). Coyote killing of swift foxes significantly affected the reintroduction efforts of swift foxes in Canada (Scott-Brown *et al.* 1987; Carbyn *et al.* 1994). Since coyotes frequently do not consume swift foxes, their killing may primarily be a form of interference competition (Sovada *et al.* 1998). Since red foxes and swift foxes have greater dietary overlap than swift foxes and coyotes in sympatric areas of Canada (A. Moehrenschlager unpubl.), the potential for exploitative competition is highest between the two fox species. Moreover, contrasted to coyotes, red foxes tend to be found in higher densities, with smaller home ranges, and they move as individuals rather than as pairs or groups. Therefore, in sympatric populations there is greater chance of red fox-swift fox encounters than coyote-swift fox encounters. Preliminary results from an experimental study examining the swift fox-red fox relationship suggest that red foxes can be a barrier preventing swift fox populations from expanding into unoccupied, but suitable areas (M. A. Sovada unpubl.). In Canada, red fox dens were significantly closer to human habitation than coyote dens while swift fox dens were found at all distances (Moehrenschlager 2000). As coyotes avoid high human activity areas, red foxes may utilise these sites to begin their invasion of swift fox home ranges. While coyotes reduce swift fox numbers through direct, density-dependent killing within the swift fox range, red foxes could potentially exclude swift foxes through a combination of interference and exploitative competition.

Mortality and pathogens

Reported annual mortality rates range from 0.47 to 0.63 (Covell 1992; Sovada *et al*. 1998; Moehrenschlager 2000; Schauster *et al*. 2002b; Andersen *et al*. 2003), and those of translocated foxes have been similar to those of wild residents in Canada (Moehrenschlager and Macdonald 2003).

Natural sources of mortality Coyotes have been identified as the principal cause of swift fox mortality (Covell 1992; Carbyn *et al*. 1994; Sovada *et al*. 1998; Kitchen *et al*. 1999; Moehrenschlager 2000; Andersen *et al*. 2003). Other predators of swift foxes that have been identified include golden eagles (*Aquila chrysaetos*) and American badgers (*Taxidea taxus*) (Carbyn *et al*. 1994; Moehrenschlager 2000; Andersen *et al*. 2003).

Persecution Mortality factors associated with human activities include poisoning, shooting, and trapping (Kilgore 1969; Carbyn *et al*. 1994; Sovada *et al*. 1998).

Hunting and trapping for fur Swift foxes formed an important part of the North American fur trade. Records of the American Fur Company's Upper Missouri Outfit (near the confluence of the Big Sioux and Missouri Rivers) from 1835 to 1838 included 10,427 swift fox pelts compared to 1,051 red fox pelts and 13 gray fox (*Urocyon cinereoargenteus*) pelts received during the same period (Johnson 1969). Alexander Henry's journals noted the take of 117 "kit" foxes from 1800 to 1806 in north-eastern North Dakota with an additional 120 "kit" foxes received from the Hudson's Bay Company at Pembina in 1905–1906 (Reid and Gannon 1928).

Currently, swift foxes are legally protected under State laws in all 10 states and are protected from harvest through laws or regulations in seven of these. Colorado, Montana, North Dakota, and Oklahoma list swift fox as furbearers but the harvest season is closed all year. Nebraska lists swift fox as "endangered," and in South Dakota they are "threatened." Wyoming lists swift fox in their non-game regulations, and only incidental harvest is allowed to provide additional distribution data. States that do provide harvest opportunities, Kansas, New Mexico, and Texas, regulate harvest by season length and monitor harvest numbers annually. Harvest is minimal (e.g., 181 foxes harvested in Kansas in 1994–2001), and largely incidental captures by coyote trappers. In Canada, where swift foxes are federally listed as 'endangered', swift foxes cannot be legally harvested; however, incidental injuries or mortalities occur in traps or snares set for other species (Moehrenschlager 2000).

Road kills Collisions with automobiles are a significant mortality factor for young animals in some landscapes (Sovada *et al*. 1998).

Pathogens and parasites No significant disease outbreaks have been documented in swift fox populations to date; however, Olson (2000) reported deaths of two swift foxes to canine distemper. Swift foxes host a variety of internal and external parasites (Kilgore 1969; Pybus and Williams 2003). Fleas (*Opisocrostos hirsutus* and *Pulex* spp.) are the most common and abundant ectoparasite. Kilgore (1969) suggested that the large numbers of fleas found in swift fox dens might be a reason for the frequent changes in dens used by foxes. Other parasites include hookworms (*Ancylostoma caninum, Uncinaria* sp.) and whipworms (*Trichuris vulpis*), as well as miscellaneous protozoans and ectoparasites (Pybus and Williams 2003).

Longevity Captive-born and translocated swift foxes in Canada that were marked at the time of release have been recaptured as late as eight years old, with extremely worn teeth (A. Moehrenschlager unpubl.).

Historical perspective

Swift foxes were of cultural importance to many Plains Indian Nations. The Kit (Swift) Fox Society of the Blackfeet Tribe of south-western Alberta and northern Montana ranked high in status and performed sacred functions. Remains of swift foxes have been found in archaeological sites dating back several thousand years.

Conservation status

Threats Since swift foxes are primarily prairie specialists, ongoing conversion of grassland to cropland threatens to reduce population sizes and further fragment populations. The conversion of native grassland prairies has been implicated as one of the most important factors for the contraction of the swift fox range (Hillman and Sharps 1978). We believe that alteration of the landscape likely influences local and seasonal prey availability, increases risk of predation for swift foxes, and leads to interspecific competition with other predators such as the coyote and red fox. Moreover, an increasing trend towards irrigation of crops from the dry-land farming practices of fallow cropland every other year could exclude swift foxes that have adapted to den and forage successfully under the dryland farming rotational practices. The planting of tall, dense vegetation as a part of the United States Conservation Reserve Program, may also negatively impact swift foxes because they avoid these densely vegetated habitats. In Canada, the oil and gas industry is expanding dramatically and previously isolated prairie areas are now targeted for exploration. Associated road developments will potentially decrease the habitat carrying capacity and increase vehicle-caused swift fox mortalities. Greater urbanisation coupled with coyote control may facilitate red fox expansion, which could lead to the competitive exclusion of swift foxes in established prairie areas. In the United States, the 1972 presidential ban on predator toxicant use (e.g., strychnine, compound 1080) on Federal lands may have contributed to swift fox recovery. However, 1080 is currently being legalised in prairie areas of Saskatchewan, Canada, which will likely limit reintroduced swift fox populations. Moreover, landowners that are attempting to protect their livestock from coyote depredation use poisons illegally and swift foxes readily consume such baits (Moehrenschlager 2000).

Commercial use None.

Occurrence in protected areas In Canada, swift foxes are found mainly on unprotected lands, but approximately one-sixth of the population falls within the boundaries of Grasslands National Park. In the United States, there are 24 National Park Service Units (Parks, Monuments, Historic Sites) located in the historic range of swift foxes. Although there are no records of swift foxes in any of these units, 14 have potential for swift fox presence. One unit, Badlands National Park in South Dakota, began a reintroduction in 2003.

Protection status CITES – not listed.
The swift fox has been down-listed from 'extirpated' to 'endangered' in Canada as a result of the swift fox reintroduction programme.

Current legal protection In the United States, the swift fox was petitioned for listing under the Endangered Species Act. In 2001 the U.S. Fish and Wildlife Service determined listing to be unwarranted.

Conservation measures taken

- In Canada, the National Swift Fox Recovery Team is currently revising its national swift fox recovery strategy, which will be implemented through national and provincial action plans as of 2003. The Canadian federal government has just passed the country's first 'Species at Risk Act', which will provide greater legal protection of swift foxes and promote landowner stewardship programmes facilitating local conservation efforts.
- In the United States, the Swift Fox Conservation Team operates under a Swift Fox Conservation Strategy Plan with identified goals up to the year 2005. The team continues to monitor populations, assess critical habitat conditions, review the potential for reintroductions, and provide research support for ongoing projects.

Occurrence in captivity

In Canada, swift foxes are present in the Calgary Zoo, Cochrane Ecological Institute, Kamloops Wildlife Park, and Saskatoon Zoo. In the United States, swift foxes are represented in the Bismarck Zoo, Bramble Park Zoo, Houston Zoo, Lee Richardson Zoo, Living Desert, Minnesota Zoo, Philadelphia Zoo, Pueblo Zoo, Sunset Zoo, Tulsa Zoo, and Wild Canid Center. The Fort Worth Zoo has put forward a petition to manage a swift fox Species Survival Plan on behalf of the American Zoo Association. On behalf of the Canid Taxon Advisory Group, the St. Louis Zoo is currently devising recommendations for swift fox space allocations in the North American programme.

Current or planned research projects

M. Sovada (Northern Prairie Wildlife Research Centre, U.S. Geological Survey, Jamestown, North Dakota, USA) is working in the state of Kansas, where she is developing methodology for long-term monitoring of swift foxes on a landscape scale with spatial smoothing. Preliminary assessments have been conducted for western Kansas and the final model will provide the basis for determining future expansion or retraction of swift fox range.

The Swift Fox Conservation Team, M. Sovada (Northern Prairie Wildlife Research Centre, U.S. Geological Survey, Jamestown, North Dakota, USA) and others are examining swift fox habitat requisites at a range-wide scale. They intend to use location and remote-sensing habitat data, multivariate statistical techniques, and GIS to model swift fox habitat range wide.

R. Harrison and Jerry Dragoo (University of New Mexico, Albuquerque, New Mexico, USA) in conjunction with the New Mexico Department of Game and Fish, are developing a monitoring plan for tracking swift fox relative to population density, range-wide in New Mexico. They are testing scat collection followed by species verification with mitochondrial DNA analysis.

R. Harrison, M.J. Patrick (Pennsylvania State University, Altoona, Pennsylvania, USA) and C. G. Schmitt (New Mexico Department of Game and Fish, Santa Fe, New Mexico, USA) are also identifying and creating voucher specimens of fleas from four fox species in New Mexico (swift, kit, grey, and red foxes).

E. Gese (National Wildlife Research Center, Utah State University, Utah, USA) is continuing a long-term study on swift foxes on the U.S. Army Pinon Canyon Maneuver Site in south-eastern Colorado. Entering the sixth year of this study, over 200 swift foxes have been radio-collared and tracked. Currently, a Ph.D. student is examining the influence of land-use patterns on plant composition and productivity, the small mammal community, and swift fox demographics. An M.Sc. student will be investigating helper behaviour and swift fox pup survival from den emergence to independence.

A. Moehrenschlager (Calgary Zoo and University of Calgary, Calgary, Alberta, Canada), P. Fargey (Grasslands National Park, Parks Canada, Saskatchewan, Canada), and S. Alexander (University of Calgary, Calgary, Alberta, Canada) are developing a predictive GIS habitat suitability model for the reintroduced Canadian/Montana swift fox population.

A. Moehrenschlager (Calgary Zoo and University of Calgary, Calgary, Alberta, Canada) and C. Strobeck (University of Alberta, Edmonton, Alberta, Canada) are testing gene flow and connectivity in the reintroduced Canada/Montana swift fox population using hair samples collected from 1995 to 2001.

A. Moehrenschlager (Calgary Zoo and University of Calgary, Calgary, Alberta, Canada) and A. Aguirre (Wildlife Trust, Palisades, New York, USA) have tested swift fox serology in Canada and will create a serological profile for all sympatric prairie canids (swift fox, red fox, coyote and domestic dog).

Gaps in knowledge

In Canada and the United States assessments of historical distribution and the identification of critical swift fox habitats for legal protection are hampered by the fact that swift fox habitat use is not well understood. Future studies should assess to what degree swift foxes can utilise differing types of habitats, including habitats considered atypical, such as those dominated by cropland. Information is needed to identify why swift foxes are unable to move into areas of apparently suitable habitat. Identification of barriers, both physical and ecological (e.g., competitive exclusion with other canids), to dispersal would improve the ability to manage and ultimately conserve this species. Future investigations should focus on parameters that might affect the range-wide, long-term viability of the populations.

The primary stochastic factor influencing small canid populations around the world is disease (Woodroffe *et al*. 1997; Laurenson *et al*. 1998; Woodroffe and Ginsberg 1999a), and such risks are enhanced when animals are transferred between populations (Woodford and Rossiter 1994). Although the Canadian population was partly established through translocation, swift fox exposure to canid diseases has not been assessed in Canada. The prevalence of disease exposure in different age classes and regions should be assessed in both countries and the likelihood of disease transfer between swift foxes and sympatric coyotes, red foxes, and domestic dogs should be evaluated. In addition, genetic analyses should be conducted to examine bottlenecks, genetic variability, connectivity, and dispersal distances in Canada and within isolated population fragments of the United States. Finally, data on swift fox demography, disease prevalence, genetics, habitat use, and population trends should be incorporated into population viability models to guide conservation planning on a provincial/state or federal basis.

Core literature

Egoscue 1979; Hines and Case 1991; Jackson and Choate 2000; Kilgore 1969; Kitchen *et al*. 1999; Moehrenschlager 2000; Moehrenschlager and Macdonald 2003; Schauster *et al.* 2002a,b; Sovada and Carbyn 2003; Sovada *et al*. 1998, 2001b, 2003.

Reviewers: Eric Gese, Devra Kleiman. **Editors:** Claudio Sillero-Zubiri, Deborah Randall, Michael Hoffmann.

Chapter 5

Europe and North and Central Asia (Palearctic)

5.1 Arctic fox
Alopex lagopus (Linnaeus, 1758)
Least Concern (2004)

A. Angerbjörn, P. Hersteinsson and M. Tannerfeldt

Other names

English: polar fox; **Finnish:** naali; **French:** renard polaire, isatis; **German:** polarfuchs; **Icelandic:** tófa; **Russian:** Песец; **Swedish:** fjällräv; **Indigenous names:** Saami: njálla, svála (Norway, Sweden, Finland, Russia).

Taxonomy

Canis lagopus Linnaeus, 1758. Syst. Nat., 10th ed., 1: 40. Type locality: "alpibus Lapponicis, Sibiria," restricted to "Sweden (Lapland)".

The Arctic fox is sometimes placed in a subgenus of *Vulpes* and sometimes in *Canis*. However, the species is still most often placed in *Alopex* (e.g., Corbet and Hill 1991). The most closely related species are swift fox (*Vulpes velox*) and kit fox (*V. macrotis*), neither of which occurs in the tundra. Viable hybrids between Arctic fox and red fox (*Vulpes vulpes*) are routinely produced by artificial insemination in fur farms, but both sexes appear to be infertile (Nes *et al.* 1988). Only one case of such hybridisation has been recorded in the wild, the progeny of a silver fox vixen that had escaped from captivity in Iceland and a native Arctic fox male (Gudmundsson 1945).

Variable chromosome numbers of 2n=48–50, due to Robertsonian translocation (Mäkinen 1985), and 2n=52 (Wipf and Shackelford 1949) have been recorded. Relative frequencies of karyotypes in nature are not known but in Finnish fur farms, foxes with the 2n=49 chromosome constitution are less fertile than females with 2n=48 or 2n=50. Furthermore, in these foxes the segregation of the karyotypes within litters of biparental 2n=49 matings is in favour of the 2n=48 karyotype such that its frequency may be increasing in captivity (Mäkinen 1985).

Description

The Arctic fox is a small fox with rather short legs and a long fluffy tail (Table 5.1.1). Males are slightly larger than females. The Arctic fox has very thick and soft winter fur with dense underfur and long guard hairs. The species occurs in two distinct colour morphs, "blue" and "white". Each morph also changes seasonally: "blue" moults from chocolate brown in summer to lighter brown tinged with blue sheen in winter. In winter, the "white" morph is almost pure white with a few dark hairs at the tip of the tail and along the spine, while in summer, it is brown dorsally and light grey to white on its underside. Colour morphs are determined genetically at a single locus, "white" being recessive (Adalsteinsson *et al.* 1987). The "blue" morph comprises less than 1% of the population throughout most of its continental range, but comprises 25–30% in Fennoscandia (Norway, Sweden and Finland) and 65–70% in Iceland (Adalsteinsson *et al.* 1987). The proportion of blue morphs also increases in coastal areas and on islands, where it can reach up to 100% (e.g., Mednyi Island, Russia; St. Paul Island, Alaska). Within each morph, there is considerable variation in appearance, which seems to be independent of the locus for colour morph (Hersteinsson 1984). In Sweden, there occasionally are sand-coloured foxes in summer, but they appear to be of the white morph without brown pigment, while in

Table 5.1.1 Body measurements for the Arctic fox in Iceland (P. Hersteinsson unpubl.).

HB male	578mm ± 31 n=89
HB female	548mm ± 33 n=85
T male	271mm ± 20 n=65
T female	262mm ± 23 n=55
WT male	June–July: 3.58kg ± 0.45 n=478 November–February: 4.23kg ± 0.60 n=338
WT female	June–July: 3.14kg ± 0.38 n=514 November–February: 3.69kg ± 0.55 n=245

Adult male Arctic fox. Härjedalen, Sweden, 2000.

Magnus Tannerfeldt

Iceland, cinnamon coloured foxes of both the white and blue colour morph occur (Adalsteinsson *et al.* 1987, unpubl.). The dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Audet *et al.* (2002) recognise eight subspecies, but we list only four:

- — *A. l. lagopus* (most of the range).
- — *A. l. semenovi* (Mednyi Island, Commander Islands, Russia).
- — *A. l. beringensis* (Bering Island, Commander Islands, Russia).
- — *A.l. pribilofensis* (Pribilof Islands, Alaska).

Similar species The Arctic fox cannot be mistaken for any other tundra-living animal. The red fox (*Vulpes vulpes*), which is the only other small canid in tundra areas, is larger, with relatively longer tail and ears, as well as a slightly longer and narrower muzzle and distinctly red fur, although the black (silver) and cross phenotypes are common in the far north.

Distribution

Current distribution The Arctic fox has a circumpolar distribution in all Arctic tundra habitats. It breeds north of and above the tree line on the Arctic tundra in North America and Eurasia and on the alpine tundra in Fennoscandia, ranging from northern Greenland at 88°N to the southern tip of Hudson Bay, Canada, 53°N. The southern edge of the species' distribution range may have moved somewhat north during the 20th century resulting in a smaller total range (Hersteinsson and Macdonald 1992). The species inhabits most Arctic islands but only some islands in the Bering Strait.

The Arctic fox was also introduced to previously isolated islands in the Aleutian chain at the end of the 19th century by fur industry (Bailey 1992). It has also been observed on the sea ice up to the North Pole.

Historical distribution During the last glaciation, the Arctic fox had a distribution along the ice edge, and Arctic fox remains have been found in a number of Pleistocene deposits over most of Europe and large parts of Siberia (Chesemore 1975).

Range countries Canada, Denmark (Greenland), Finland, Iceland, Norway, Russia, Sweden, USA (Alaska) (Hall and Kelson 1959; Vibe 1967; Nasimovic and Isakov 1985; Mitchell-Jones *et al.* 1999).

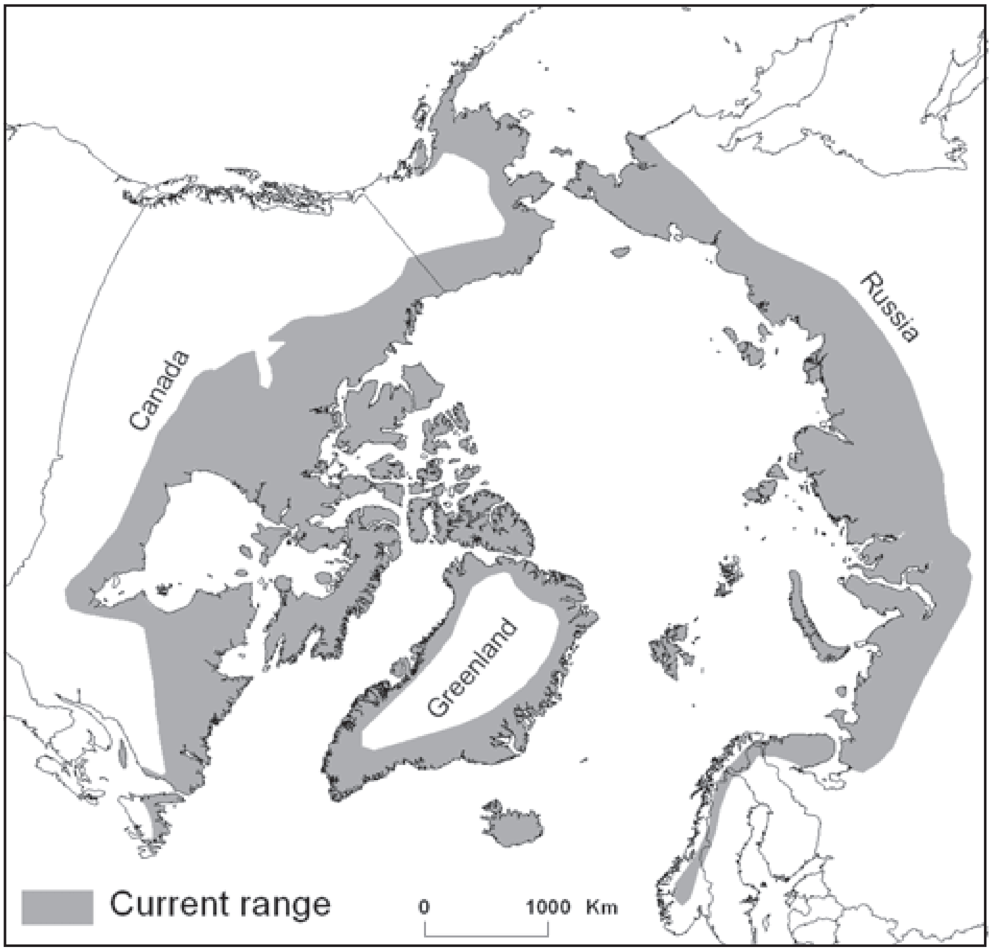

Figure 5.1.1. Current distribution of the Arctic fox.

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Relative abundance

The world population of Arctic foxes is in the order of several hundred thousand animals (Table 5.1.2). Most populations fluctuate widely in numbers between years in response to varying lemming numbers. Only a few populations have been studied directly, so the following population figures must be treated with caution. In most areas, however, population status is believed to be good. The species is common in the tundra areas of Russia, Canada, coastal Alaska, Greenland and Iceland. Exceptions are Fennoscandia, Mednyi Island (Russia) and Pribilof Islands, where populations are at critically low levels. On the Pribilof Islands, fox populations are now low and appear to be declining further. Vagrant Arctic foxes are common over the northern sea-ice where they follow polar bears as scavengers.

Table 5.1.2. The status of Arctic fox in various range countries (Population: C=common, R=rare; Trend: S=stable, I= increasing, D= declining).

Country (area)	Population/ abundance	Approx number	Trend
Canada	C	100,000 ?	S ?
USA (coastal Alaska)	C	10,000 ?	S ?
Greenland	C	> 10,000 ?	S ?
Russia (mainland)	C	2–800,000 ?	S/I ?
Russia (Mednyi Island)	R	100	?
Russia (Bering Island)	C	800–1,000	S
Iceland	C	> 6,000	I
Finland	R	20	D
Norway (mainland)	R	50	D
Norway (Svalbard)	C	2–3000	S
Sweden	R	50	D

Estimated populations/relative abundance and population trends The density of occupied natal Arctic fox dens varies from 1–3/100km^2 in the whole tundra zone of Siberia and North America (Boitzov 1937; Macpherson 1969), to about 4/100km^2 in coastal Alaska, Svalbard and Fennoscandia (Eberhardt *et al.* 1982; Prestrud 1992c; Dalerum *et al.* 2002), 7/100km^2 on Herschel Island, Yukon (Smits and Slough 1993) and up to 8/100km^2 in protected areas in Iceland (Hersteinsson *et al.* 2000).

In North America, there are no published population estimates for Canada or the USA. If North America's fur harvest until the 1980s is compared with production figures from Russia, the total Canadian Arctic fox population should be in the order of 100,000 animals and the Alaskan population around 10,000 individuals. Historically numbering thousands of individuals, Pribilof fox populations have declined to only a few hundred (White 1992).

The total Russian population size is unknown but could be in the order of 200,000–800,000 animals; Nasimovic and Isakov (1985) reported the number of live animals on the Taymyr Peninsula alone to be 52,000 during a low period and up to 433,000 animals in a peak year (1970 to 1971). A decline during the 1960s to 1980s was reported from many Siberian areas (Nasimovic and Isakov 1985), but lower fur prices and a breakdown of the Soviet trading system have probably relieved the pressure on the species. The endangered population of the subspecies *A. l. semenovi* on Mednyi Island comprises around 100 animals (Goltsman *et al.* 1996). The population on the neighbouring Bering Island (*A. l. beringensis*) is reported as stable at around 800–1,000 animals; the same review reports the Kola Peninsula population to number 1,000–2,000 animals (Potansky 1993). However, adjacent areas in Finland harbour less than 20 Arctic foxes, so this figure appears to be an overestimate.

In Fennoscandia, the population decreased dramatically due to over-harvest at the beginning of the 20th century. Local populations have been driven to near extinction by hunting; for example, on mainland Fennoscandia. Furthermore, the situation deteriorated during the 1980s and 1990s because of an absence of lemming peaks. Recent population estimates total 120 adults, around 50 of which are found in Sweden (Angerbjörn *et al.* 1995; Löfgren and Angerbjörn 1998), 50 in Norway (Frafjord and Rofstad 1998), and less than 20 in Finland (Kaikusalo *et al.* 2000). On the island Svalbard (Norway), the Arctic fox is common, with a population density of 1–1.5 animals per 10km^2 and an approximate total autumn population of 2,000–3,000 individuals (P. Prestrud pers. comm.). In Iceland, the population has gone through long-term population fluctuations with a low in the 1970s of around 1,300 individuals in autumn to a high of over 6,000 individuals in 1999 and apparently still increasing (Hersteinsson 2001). Little information is available on fox population density in Greenland, but it is common in coastal areas.

Habitat

Arctic and alpine tundra on the continents of Eurasia, North America and the Canadian archipelago, Siberian islands, Greenland, inland Iceland and Svalbard. Subarctic maritime habitat in the Aleutian island chain, Bering Sea Islands, Commander Islands and coastal Iceland.

Food and foraging behaviour

Food The Arctic fox is an opportunistic predator and scavenger but in most inland areas, the species is heavily dependent on fluctuating rodent populations. The species' main prey items include lemmings, both *Lemmus* spp. and *Dicrostonyx* spp. (Macpherson 1969; Angerbjörn *et al.* 1999). In Fennoscandia, *Lemmus lemmus* was the main prey in summer (85% frequency of occurrence in faeces) followed by birds (Passeriformes, Galliformes and Caridriiformes, 34%) and reindeer (*Rangifer tarandus*) (21%; Elmhagen *et al.* 2000). In winter, ptarmigan and grouse (*Lagopus* spp.) are common prey in addition to rodents and reindeer (Kaikusalo and Angerbjörn 1995). Changes in fox populations have been observed to follow those of their main prey in three- to five-year cycles (Macpherson 1969; Angerbjörn *et al*. 1999).

Foxes living near ice-free coasts have access to both inland prey and sea birds, seal carcasses, fish and invertebrates connected to the marine environment, leading to relatively stable food availability and a more generalist strategy (Hersteinsson and Macdonald 1996). In late winter and summer, foxes found in coastal Iceland feed on seabirds (*Uria aalge, U. lomvia*), seal carcasses and marine invertebrates. Inland foxes rely more on ptarmigan in winter, and migrant birds, such as geese and waders, in summer (Hersteinsson and Macdonald 1996). In certain areas, foxes rely on colonies of Arctic geese, which can dominate their diet locally (Samelius and Lee 1998).

Foraging behaviour Arctic foxes forage singly, presumably the most efficient foraging technique in view of the species' main prey base of rodents and birds. When food is abundant, Arctic fox cache food for later use. Caches can be either of single prey items or large items, with varying contents that may include lemmings or goose eggs (Chesemore 1975).

Damage to livestock and game In Iceland, lamb carcasses frequently are found among prey remains at dens resulting in the species being considered a pest. Although individual foxes may indeed prey on lambs, it is more likely that a large proportion of the lambs have been scavenged (Hersteinsson 1996). Arctic foxes are known to prey on wildfowl (Sovada *et al*. 2001a) and occasionally kill reindeer calves (Prestrud 1992a).

Adaptations

The Arctic fox has many physical adaptations to the Arctic environment. Arctic fox fur has the best insulative properties among all mammals, and individuals do not, under any naturally occurring temperatures, need to increase metabolic rate to maintain homoeothermy (Prestrud 1991). Arctic foxes change between summer and winter pelage, thereby adjusting their insulating capabilities and enhancing their camouflaging potential. Arctic foxes further conserve body heat by having fur on the soles of their feet (Linnaeus thus named it *lagopus*, literally hare-foot), small ears, short noses, and the ability to reduce blood flow to peripheral regions of their bodies. In autumn, their weight may increase by more than 50% as fat is deposited for insulation and reserved energy (Prestrud 1991).

The species demonstrates a number of other physiological adaptations for energy conservation in winter. Resting metabolic rate, body-core temperature and food intake is lower in winter (Fuglei 2000). When travelling long distances, the Arctic fox falls into an energy-effective short gallop, similar to that of wolverines. Surprisingly, for Arctic foxes, the energetic cost of running is lower in winter than in summer, and is also lower during starvation than when feeding *ad lib* (Fuglei 2000).

Social behaviour

The basic social unit of the Arctic fox is the breeding pair. Both parents take an active part in rearing the cubs. For the first three weeks after birth, while the cubs are mostly dependent on milk, the female rarely leaves the den for any length of time and the male brings most of the food on which the female feeds during this energetically demanding period. As meat increasingly forms a larger constituent of the cubs' diet, the roles of the parents become more similar and the female takes an active part in hunting and provisioning the cubs. Non-breeding helpers, usually yearlings from the previous litter, may occur. Supernumerary females generally emigrate before pups attain independence of the den at 8–10 weeks (Hersteinsson and Macdonald 1982). However, on Mednyi Island, there are permanent Arctic fox groups comprising up to six adults (Frafjord and Kruchenkova 1995). Complicated social systems have also been observed on other islands (e.g., Iceland: Hersteinsson 1984; St Paul Island, Alaska: White 1992; Wrangel Island, Russia: Ovsyanikov 1993). Temporary groups of non-breeding individuals are also sometimes formed (Ovsyanikov 1993).

Arctic foxes normally are strongly territorial when breeding, with natal dens generally used by only one family group. Pairs may remain together in the same territory and use the same den for up to five years (Ovsyanikov 1993; A. Angerbjörn unpubl.). In some cases, individuals may maintain territories that include more than a single breeding pair. Furthermore, there are cases when breeding pairs have shared a den. However, this phenomenon seems to be restricted to close relatives (A. Angerbjörn and M. Tannerfeldt unpubl.).

Home ranges in inland areas vary with lemming abundance (15–36km^2; Angerbjörn *et al*. 1997), but generally are smaller in coastal habitats (Iceland, 9–19km^2: Hersteinsson and Macdonald 1982; Greenland, 10–14km^2: Birks and Penford 1990; Alaska 5–21km^2: Eberhardt *et al*. 1982) and vary widely on Svalbard (10–125km^2; Frafjord and Prestrud 1992). Home ranges of group members generally overlap widely with each other, and very little with those of neighbouring groups. Combined group ranges contribute to territories from which occupants rarely stray (Hersteinsson and Macdonald 1982). Scent marking of territories with urine is common, while faeces appear to have little or no significance with regard to territory marking (Hersteinsson 1984). Vocalisations and postures aimed to attract the attention of conspecifics, such as an erect tail, are common during territory disputes (Hersteinsson 1984).

In Alaska, seasonal migrations are reported when individuals leave breeding grounds in autumn, travel to the coast, and return in late winter or early spring (Eberhardt *et al*. 1983). Large-scale emigrations have been recorded in Canada, Fennoscandia and Russia. These may result from drastic reductions in food supplies, such as a population crash in lemmings. The longest recorded movement was by a male who was recovered 2,300km from the point of tagging (Garrott and Eberhardt 1987).

Reproduction and denning behaviour

Mating occurs between February and May and births take place from April to July. Gestation lasts 51–54 days. Pup weight at birth is 80–85g in Iceland (P. Hersteinsson unpubl.) but may be less in areas with larger litter sizes. Captive foxes in Sweden had a birth weight of 73g for females and 77g for males (E. Derefeldt and A. Angerbjörn unpubl.). Litter size varies with food availability, being smaller in areas without rodents and larger in areas with rodents (Tannerfeldt and Angerbjörn 1998). Mean litter sizes at weaning were 2.4 on St. Paul Island (White 1992), 4.2 in Iceland (Hersteinsson 1993), 5.3 in Svalbard (Prestrud and Nilssen 1995), 6.7 in Canada (Macpherson 1969), 7.1 in Russia (Chirkova *et al.* 1959), and 6.3 in Fennoscandia (Tannerfeldt and Angerbjörn 1998). On Wrangel Island, in years with high lemming abundance, up to 19 pups per litter have been observed (Ovsyanikov 1993).

The ability of Arctic foxes to produce large litters is facilitated by their access to large and relatively safe dens. The primary function of breeding dens seems to be to provide shelter and protection against predators. Den sites are large with complex burrow systems, and the largest dens are preferred for breeding (Dalerum *et al*. 2002). These may have up to 150 entrances and are usually situated on elevated mounds, pingoes, tops of eskers, river banks or ridges, although dens located in bedrock and screes are more common in Svalbard (Prestrud 1992b) and Iceland (A. Angerbjörn pers. obs.). Good denning sites lie above the permafrost layer, accumulate comparatively little winter snow and are sun-exposed, often facing south. The average lifespan of dens in the Canadian tundra has been estimated at 330 years (Macpherson 1969). Some are used repeatedly, year after year, others infrequently.

Pup rearing is confined to the snow-free period from June to September, after which the young gradually become independent. Lactation generally lasts 8–10 weeks. In Sweden, growth rate from weaning in early July to late August was about 30g/day (C. Bergman and A. Angerbjörn unpubl.), and in Svalbard growth rate was 34g/day (Frafjord 1994). Foxes reach sexual maturity at 10 months.

Competition

The red fox is an especially dominant competitor and severe predator on juvenile Arctic foxes (Frafjord *et al.* 1989). The red fox is also known to have a similar diet and to take over Arctic fox breeding dens (Tannerfeldt *et al.* 2002). A northward spread of the red fox has been recorded in Canada (Hersteinsson and Macdonald 1992) and an increasing range above the tree-line in Scandinavia, where the red fox has the potential to restrict the range of the Arctic fox (Tannerfeldt *et al.* 2002). Other species feeding in the same small rodent guild are rough-legged buzzard (*Buteo lagopus*), snowy owl (*Nyctea scandiaca*) and skuas (*Stercorarius longicaudus*, *S. pomarinus*, *S. parasiticus*), but the degree of competition between these species is not known.

Mortality and pathogens

Natural sources of mortality The Arctic fox is a victim of predation, mainly from the red fox, wolverine (*Gulo gulo*) and golden eagle (*Aquila chrysaëtos*), while the brown bear (*Ursus arctos*) and wolf (*Canis lupus*) are also known to dig out dens. For Arctic foxes dependent on cyclic lemmings, starvation is an important cause of mortality during some years, particularly for juveniles (Garrott and Eberhardt 1982, Tannerfeldt *et al.* 1994). Cubs are known to eat their siblings, but there is no evidence of siblicide (ArvidSon and Angerbjörn 1996).

Persecution In Norway (Svalbard), Greenland, Canada, Russia, and Alaska, trapping is limited to licensed trappers operating in a specified trapping season. The enforcement of these laws appears to be uniformly good. In Iceland, a law was passed in 1957 stipulating that the state would pay two-thirds of all costs of an extermination campaign on the Arctic fox. The law was changed in 1994, but restricted government-sponsored hunting still continues over most of the country as the Arctic fox is considered a pest to sheep farmers and eider down collectors (Hersteinsson *et al*. 1989). On St Paul Island persecution has caused a dramatic decrease in population size in recent years (White pers. comm.).

Hunting and trapping for fur Hunting for fur has long been a major mortality factor for the Arctic fox. The total harvest for North America between 1919 and 1984 was approximately 40,000–85,000 annually (Garrott and Eberhardt 1987). Macpherson (1969) stated that the Canadian production was 10,000–68,000 pelts per year, and by the 1980s around 20,000 (Garrott and Eberhardt 1987). The yield from Alaska for the period 1925 to 1962 was from 3,900–17,000 pelts per year (Chesemore 1972). The Alaska harvest later decreased to 1,000–2,000 per year (Garrott and Eberhardt 1987).

The total fur returns from Siberia reached more than 100,000 animals in some years in the 1970s and 39–59% of the population could be killed each year (Nasimovic and Isakov 1985). These populations fluctuate widely and a large proportion of killed animals are young-of-the-year. A decline during the last few decades is apparent in many

Siberian areas (Nasimovic and Isakov 1985), but lower fur prices and a breakdown of the Soviet trading system have probably relieved the pressure on the species.

In Greenland, in the year 1800, the number of exported pelts per year was around 2,000. In 1939, the catch had increased to over 7,000 animals per year (Braestrup 1941). It later decreased to 2,000–5,000 pelts annually (Vibe 1967), and subsequently has decreased even further. See also Commercial use.

Road kills No assessment has been made, but it is probably very infrequent in tundra areas due to low traffic intensity. However, it is increasing in St. Paul Island due to increased vehicular traffic and in Iceland over the last two decades due to an increasing Arctic fox population and improved road system, leading to more traffic and higher motoring speeds (P. White unpubl., P. Hersteinsson unpubl.).

Pathogens and parasites The Arctic fox is a major victim and vector during outbreaks of Arctic rabies (Prestrud 1992c). In Iceland, encephalitozoonosis is suspected of playing a part in population dynamics (Hersteinsson *et al.* 1993). As a result of mange caused by the ear canker mite (*Otodectes cynotis*) introduced by dogs, the subspecies *A. l. semenovi* on Mednyi Island was reduced by some 85–90% in the 1970s to around 90 animals (Goltsman *et al.* 1996). The same parasite can be found in Icelandic Arctic foxes but apparently does not result in increased mortality there (Gunnarsson *et al.* 1991). In Iceland, the diversity and magnitude of intestinal parasite infestation was much higher among Arctic foxes in coastal than in inland habitats (Skírnisson *et al.* 1993). Kapel (1995) has reviewed the occurrence and prevalence of helminths in Arctic foxes in Greenland, North America and Siberia. In a study conducted in Sweden, Arctic fox cubs were found to have no serious parasitic infestations (Aguirre *et al.* 2000). *Trichinella* infestations of Arctic foxes seem to be largely associated with feeding from polar bear (*Ursus maritimus*) carcasses (Prestrud *et al.* 1993; Kapel 1995). There is a risk that domestic dogs transfer diseases to Pribilof Arctic foxes (White unpubl.).

Longevity The average lifespan for animals that reach adulthood is approximately three years. The oldest recorded individuals were 11 years of age (P. Hersteinsson unpubl.).

Historical perspective

The importance of the Arctic fox fur trade has a very long history. In Jordanes 'Getica' (Jordanes 551), Romans are described wearing dark-blue furs bought from the Suehans (Swedes), presumably traded from the "Screrefennae" (=Sami). The economy of the Inuits is closely tied to Arctic fox abundance (Chesemore 1972). Arctic fox skins were legal tender along with lamb skins and some other products in Iceland during the Middle Ages (Hersteinsson 1980). This may also have been so in other Nordic countries.

Conservation status

Threats Hunting for fur has long been a major mortality factor for the Arctic fox. With the decline of the fur hunting industry, the threat of over-exploitation is lowered for most Arctic fox populations (see Commercial use). In some areas gene swamping by farm-bred blue foxes may threaten native populations (see Occurrence in captivity). There can also be indirect threats such as diseases and organochlorine contaminants, or direct persecution (as on St. Paul Island for example). Misinformation as to the origin of Arctic foxes on the Pribilofs continues to foster negative attitudes and the long-term persistence of this endemic subspecies is in jeopardy.

Commercial use The Arctic fox remains the single most important terrestrial game species in the Arctic. Indigenous peoples have always utilised its exceptional fur; and with the advent of the fur industry, the Arctic fox quickly became an important source of income. Today, leg-hold traps and shooting are the main hunting methods. Because of their large reproductive capacity, Arctic foxes can maintain population levels under high hunting pressure. In some areas, up to 50% of the total population has been harvested on a sustainable basis (Nasimovic and Isakov 1985). However, this does not allow for hunting during population lows, as shown by the situation in Fennoscandia. The Arctic fox has nevertheless survived high fur prices better than most other Arctic mammals. Hunting has declined considerably in the last decades, as a result of low fur prices and alternative sources of income. In the Yukon, for example, the total value of all fur production decreased from $1.3 million in 1988 to less than $300,000 in 1994.

Occurrence in protected areas Good information is available only for Sweden and Finland. For Iceland, Arctic foxes could potentially appear in most protected areas.

— *Finland*: Malla, Käsivarren erämaa, Iiton palsasuot, Saanan luonnonsuojelualue, Muotkatunturin erämaa, Hanhijänkä Pierkivaaran jänka, Pieran Marin jänkä, Kevo, Kaldoaivin erämaa, Paistunturin erämaa, Pulmankijärvi;

— *Sweden*: The National Parks Sarek, Padjelanta, and Stora Sjöfallet, in the county of Norrbotten; the Nature Reserves Vindelfjällen, Marsfjället, and Gitsfjället, in the county of Västerbotten; the Nature Reserves Hamrafjället, Henvålen–Aloppan, Vålådalen, Gråberget–Hotagsfjällen, Frostvikenfjällen, Sösjöfjällen and Skäckerfjällen, in the county of Jämtland.

Protection status CITES – not listed.

The Arctic fox is threatened with extinction in Sweden

(EN), Finland (CR) and mainland Norway (E). In 1983, following the introduction of mange due to ear canker mites (*Otodectes cynotis*) via dogs, the Mednyi Island foxes were listed in the Russian Red Data Book.

Current legal protection In most of its range, the Arctic fox is not protected. However, the species and its dens have had total legal protection in Sweden since 1928, in Norway since 1930, and in Finland since 1940. In Europe, the Arctic fox is a priority species under the Actions by the Community relating to the Environment (ACE). It is therefore to be given full protection. On St. Paul Island the declining Arctic fox population has currently no legal protection.

In Norway (Svalbard), Greenland, Canada, Russia, and Alaska, trapping is limited to licensed trappers operating in a defined trapping season. The enforcement of these laws appears to be uniformly good. In Iceland, bounty hunting takes place over most of the country outside nature reserves.

Conservation measures taken An action plan has been developed for Arctic foxes in Sweden (Löfgren and Angerbjörn 1998) and status reports have been published for Norway (Frafjord and Rofstad 1998) and Finland (Kaikusalo *et al*. 2000). In Sweden and Finland, a conservation project is under way (SEFALO). In 1993, Mednyi Island gained protected status as a Nature Reserve.

Occurrence in captivity

The Arctic fox occurs widely in captivity on fur farms and has been bred for fur production for over 70 years. The present captive population originates from a number of wild populations and has been bred for characteristics different from those found in the wild, including large size. Escaped "blue" foxes may already be a problem in Fennoscandia (and to a lesser extent in Iceland) due to gene swamping (Hersteinsson *et al.* 1989).

Current or planned research projects

There are a large number of projects currently underway (or planned initiatives) across the distribution range.

A. Angerbjörn, M. Tannerfeldt, B. Elmhagen, and L. Dalén (Stockholm University, Sweden) are studying conservation genetics, predation patterns, and relationships between red and Arctic foxes in Fennoscandia.

N. Eide (Norwegian Polar Institute Tromsø, Norway) is exploring habitat use and population ecology of Arctic foxes in Svalbard.

E. Fuglei (Norwegian Polar Institute, Tromsø, Norway) is investigating the ecophysiology and genetics of Arctic foxes at Svalbard, as well as the effects of persistent organic pollutants in the Arctic fox.

P. Prestrud (Norwegian Polar Institute, Tromsø) continues long-term population monitoring of Arctic foxes in Svalbard.

K. Frafjord (Tromsø University, Norway) is looking at the ecology of Arctic fox dens and patterns of den use by Arctic and red foxes in northern Norway.

J. Linnell (Strand Olav, NINA, Norway) is studying captive breeding and behavioural ecology of Arctic foxes in Norway.

P. Hersteinsson (University of Iceland) is researching juvenile dispersal, including timing and mode of dispersal and dispersal distance in western Iceland.

Multiple researchers, including E. Fuglei (Norwegian Polar Institute Tromsø, Norway), E. Geffen and M. Kam (University of Tel Aviv, Israel), A. Angerbjörn (Stockholm University, Sweden) and P. Hersteinsson (University of Iceland) are investigating the energy costs of parental care in free-ranging Arctic foxes across the species' range.

G. Samelius (University of Saskatchewan, Canada) is studying population ecology, and the relationship of Arctic foxes to Arctic geese in the Queen Maud Gulf Bird Sanctuary in Nunavut, Canada.

P. White (Museum of Vertebrate Zoology, University of California, Berkeley, California, USA) is studying behavioural ecology, disease, and organochlorine contaminants of Arctic foxes on St. Paul Island.

R.K. Wayne and C. Vila (University of California, Los Angeles, California, USA) are undertaking an investigation into the population genetics of the species.

M. Zakrzewski and B. Sittler (University of Freiburg, Germany) study population dynamics in North-east Greenland.

Gaps in knowledge

1. Little is known concerning the impact of diseases introduced by humans on fox populations. Allied to this is our lack of knowledge of the epidemiology of Arctic rabies.
2. Considering the northward spread of the red fox in certain areas, studies are necessary to determine the effects of competition between red foxes and Arctic foxes on various population parameters and Arctic fox life-history patterns.
3. The non-recovery of the Fennoscandian population is a cause for concern, and requires specific attention, especially in terms of disease and genetics.

Core literature

Angerbjörn *et al.* 1995; Audet *et al.* 2002; Eberhardt *et al.*1982, 1983; Frafjord and Prestrud 1992; Garrott and Eberhardt 1982, 1987; Hersteinsson *et al.* 1989; Hersteinsson and Macdonald 1982, 1992; Macpherson 1969; Nasimovic and Isakov (eds). 1985; Tannerfeldt and Angerbjörn 1998.

Reviewers: Karl Frafjord, Gustaf Samelius, Pål Prestrud, Paula White. **Editors:** Deborah Randall, Michael Hoffmann, Claudio Sillero-Zubiri.

5.2 Grey wolf
Canis lupus Linnaeus, 1758
Least Concern (2004)

L.D. Mech and L. Boitani

Other names

English: timber wolf, tundra wolf, plains wolf, Mexican wolf, Arctic wolf; **Albanian:** ujku; **Croatian:** vuk; **Czech:** vlk; **Danish and Norwegian:** ulv; **Dutch:** wolf; **Estonian:** hunt, susi; **Faeroese:** ulvur, fjallaúvur; **Finnish:** susi; **French:** loup; **German:** wolf; **Hungarian:** farkas; **Icelandic:** úlfur; **Italian:** lupo; **Latvian:** vilks; **Lithuanian:** vilkas; **Maltese:** lupu; **Polish:** wilk; **Portuguese:** lobo; **Romanian:** lup; **Russian:** wilk; **Slovakian:** vlk dravý; **Slovenian:** volk; **Spanish:** lobo; **Swedish:** varg; **Turkish:** kurt; **Indigenous names:** Arapaho: haqihana; Caddo: tasha; Navaho: mai-coh; Nunamiut: amaguk (USA).

Taxonomy

Canis lupus Linnaeus, 1758. Syst. Nat., 10th ed., 1:39. Type locality: “Europæ sylvis, etjam frigidioribus”; restricted by Thomas (1911) to “Sweden”.

Two recent proposals have been made for major taxonomic changes in the grey wolf in North America: Nowak (1995) presented data reducing the 24 North American subspecies to five; and Wilson *et al.* (2000), using molecular genetics data, proposed that wolves in eastern North America had evolved in North America contrary to wolves elsewhere that evolved in Eurasia and spread to North America. The authors proposed the name *Canis lycaon* for the wolf that they believe evolved in North America.

Chromosome number: 2n=78 (Wayne 1993).

Note: The Wolf Specialist Group has not taken a position on whether *Canis aureus lupaster* is a grey wolf (see Ferguson 1981), or whether *Canis lycaon* (Wilson *et al.* 2000) is valid.

Description

The grey wolf is the largest wild canid weighing up to 62kg (Table 5.2.1). General appearance and proportions are not unlike a large German shepherd dog except legs longer, feet larger, ears shorter, eyes slanted, tail curled, and winter fur longer and bushier, and with chin tufts in winter. Fur is thick and usually mottled grey, but can vary from nearly pure white, red, or brown to black. Dental formula 3/3-1/1-4/4-2/3=42.

Table 5.2.1 Body measurements for the grey wolf. Wolf body measurements vary greatly. Examples from Wrangel, Alaska, USA (Young and Goldman 1944:454).

HB+T male	1,650mm
HB+T female	1,585mm
T male	453mm
T female	435mm
HF male	298mm
HF female	279mm


Rurik List

Adult female Mexican wolf. San Cayetano breeding facility, Mexico State, Mexico, 1992.

Subspecies See Nowak (1995) for maps and measurements of seven Eurasian and five North American subspecies:
— *C. l. albus* (northern Russia)
— *C. l. arctos* (Canadian High Arctic)
— *C. l. baileyi* (Mexico, south-western USA)
— *C. l. communis* (central Russia)
— *C. l. cubanensis* (east central Asia)
— *C. l. hattai* (Hokkaido, Japan)
— *C. l. hodophilax* (Honshu, Japan)
— *C. l. lupus* (Europe, Asia)
— *C. l. lycaon* (south-eastern Canada, north-eastern USA)
— *C. l. nubilis* (central USA, east-central Canada)
— *C. l. occidentalis* (Alaska, north-western Canada)
— *C. l. pallipes* (Middle East, south-western Asia)

Similar species Red wolf (*C. rufus*): slightly smaller than *C. lupus*. Coyote (*C. latrans*): about one-third to one-half size of *C. lupus*. Golden jackal (*C. aureus*): about one-third size of *C. lupus*.

Distribution

Historical distribution Originally, the wolf was the world's most widely distributed mammal, living throughout the northern hemisphere north of 15°N latitude in North America and 12°N in India. It has become extinct in much of Western Europe (Boitani 1995), in Mexico and much of the USA (Mech 1970).

Current distribution Present distribution is more restricted; wolves occur primarily in wilderness and remote areas, especially in Canada, Alaska and northern USA, Europe, and Asia from about 75°N to 12°N (Figure 5.2.1).

Range countries Afghanistan, Albania, Armenia, Azerbaijan, Belarus, Bhutan, Bosnia Herzegovina, Bulgaria, Canada, China, Croatia, Czech Republic, Denmark (Greenland), Estonia, Finland, France, Germany, Georgia, Greece, Hungary, India, Iran, Iraq, Israel, Italy, Jordan, Kazakhstan, Korea, Kyrgyztan, Latvia, Lebanon, Lithuania, Macedonia, Mexico, Moldova, Mongolia, Montenegro, Myanmar, Nepal, Norway, Oman, Pakistan, Poland, Portugal, Romania, Russia, Saudi Arabia, Slovakia, Slovenia, Spain, Sweden, Syria, Tajikistan, Turkey, Turkmenistan, Uzbekistan, Ukraine, United Arab Emirates, United States of America, Yemen, Yugoslavia (Montenegro, Kosovo and Serbia) (Mivart 1890; Ognev 1931; Pocock 1935; Young and Goldman 1944; Mech 1970, 1974; Mech and Boitani 2003).

Relative abundance

Because of the diversity in climate, topography, vegetation, human settlement and development of wolf range, wolf populations in various parts of the original range vary from extinct to relatively pristine. Wolf densities vary from about 1/12km^2 to 1/120km^2.

Estimated populations/relative abundance and population trends Details are provided below on subspecies present, population status, approximate numbers, the percentage of former range occupied at present, main prey (where known), legal status, and cause of decline. Countries (provinces, states or regions whenever appropriate) are listed by geographical region and roughly follow a west to east and north to south order.

North America (Nearctic)

— *Alaska (USA)*: Subspecies: *C. l. occidentalis*. Status: Fully viable, about 6,000. Former range occupied: 100%. Main prey: Moose, caribou, sheep, deer, beaver, goat. Legal status: Animals are hunted and trapped in limited seasons with bag limits. Some control work, enforcement active.

— *British Columbia (Canada)*: Subspecies: *C. l. occidentalis*, *C. l. nubilus*. Status: Fully viable, about 8,000. Range occupied: 80%. Main prey: Moose, caribou, sheep, deer, beaver, goat, elk. Legal status: Game species, furbearer, no closed season.

— *Yukon Territory (Canada)*: Subspecies: *C. l. occidentalis*. Status: Fully viable, about 4,500. Range

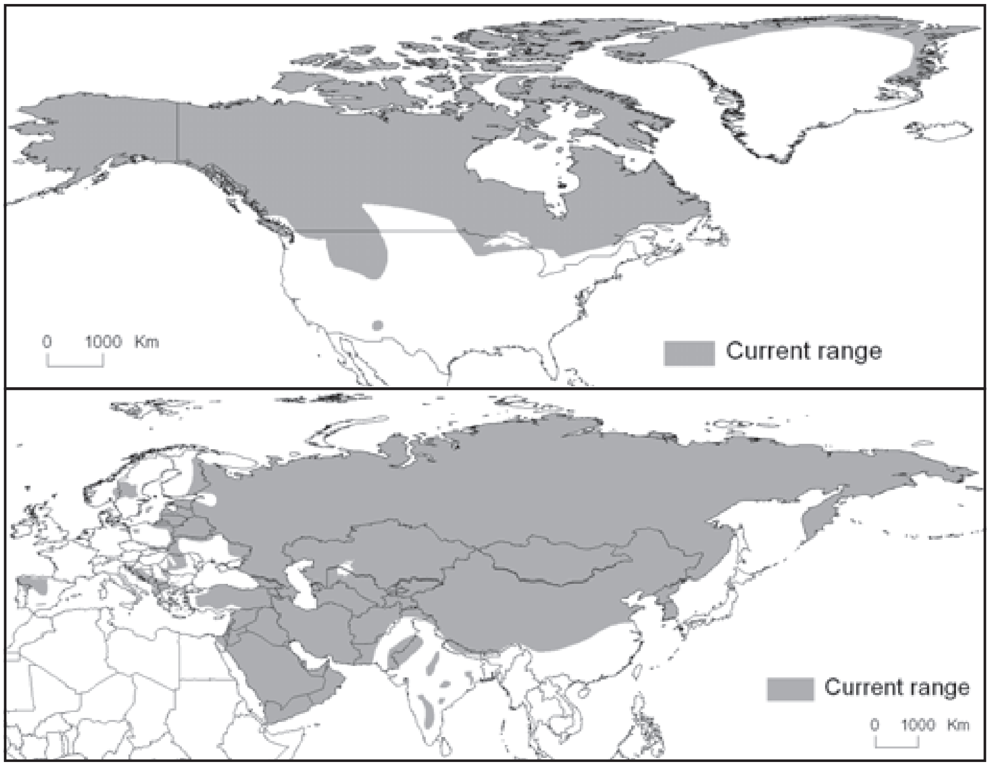

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Figure 5.2.1. Current distribution of the grey wolf.

occupied: 100%. Main prey: Moose, caribou, sheep, deer, beaver, goat, elk. Legal status: Game species, furbearer, no closed season.

- *North-west Territories and Nunavut (Canada)*: Subspecies: *C. l. arctos*, *C. l. nubilus*, *C. l. occidentalis*. Status: Fully viable, about 10,000. Range occupied: 100%. Main prey: Moose, caribou, musk oxen, sheep, beaver, goat. Legal status: Furbearer.
- *Greenland (Denmark)*: Subspecies: *C. l. arctos*. Status: Threatened, lingering at 50? Range occupied: Unknown. Main prey: Musk oxen, lemmings, arctic hares. Legal status: Unknown. Cause of decline: Persecution.
- *Alberta (Canada)*: Subspecies: *C. l. occidentalis.* Status: Fully viable, about 4,000. Range occupied: 80%. Main prey: Moose, caribou, sheep, deer, beaver, goat, elk, bison. Legal status: Furbearer.
- *Saskatchewan (Canada)*: Subspecies: *C. l. occidentalis*, *C. l. nubilis*. Status: Fully viable, about 4,300. Range occupied: 70%. Main prey: Moose, elk, deer, beaver, bison, caribou. Legal status: Furbearer.
- *Manitoba (Canada)*: Subspecies: *C. l. occidentalis*, *C. l. nubilis*. Status: Fully viable, about 5,000. Range occupied: 50%. Main prey: Moose, elk, deer, beaver, caribou. Legal status: Furbearer.
- *Ontario (Canada)*: Subspecies: *C. l. lycaon*, *C. l. nubilis* (but see Taxonomy). Status: Fully viable, <8,500. Range occupied: 80%. Main prey: Moose, deer, caribou, beaver. Legal status: Furbearer.
- *Quebec (Canada)*: Subspecies: *C. l. lycaon*, *C. l. nubilis* (but see Taxonomy). Status: Fully viable, number unknown but probably thousands. Range occupied: 80%. Main prey: Moose, deer, caribou, beaver. Legal status: Furbearer.
- *Labrador (Canada)*: Subspecies: *C. l. nubilis*. Status: Fully viable, 1,000–5,000. Range occupied: 95%. Main prey: Moose, caribou, beaver, musk oxen, hares. Legal status: Furbearer.
- *Newfoundland (Canada)*: Subspecies: *C. l. nubilis*, extinct since 1911.
- *North-western USA*: Subspecies: *C. l. occidentalis* (reintroduced in Wyoming and Idaho). Status: Increasing, about 400, Endangered. Range occupied: 20%. Main prey: Elk, moose, sheep, goats, deer, beaver. Legal status: Full protection, except for government reactive depredation control.
- *Minnesota (USA)*: Subspecies: *C. l. nubilis* (but see Taxonomy). Status: Viable, about 2,600. Range occupied: 40%. Main prey: Deer, moose, beaver. Legal status: Full protection, except for reactive government depredation control.
- *Michigan and Wisconsin (USA)*: Subspecies: *C. l. nubilis* (but see Taxonomy). Status: Increasing, about 400. Range occupied: 25%. Main prey: Deer, beaver, moose. Legal status: Full protection.
- *South-western USA*: Subspecies: *C. l. baileyi*. Status: Reintroduced (about 25 in 2000). Range occupied: <5%. Main prey: Deer, elk, livestock. Legal status: Full protection. Cause of decline: Persecution, habitat destruction.
- *Mexico*: Subspecies: *C. l. baileyi*. Status: Highly endangered. Possibly lone wolves or pairs, <10. Range occupied: <10%. Main prey: Livestock. Legal status: Full protection, but not enforced. Cause of decline: Persecution, habitat destruction.

Europe (Palaearctic)

- *Norway*: Subspecies: *C. l. lupus*. Status: About 20. Range occupied: 5%. Main prey: Ungulates and livestock. Legal status: Protected. Threat: Culling.
- *Sweden*: Subspecies: *C. l. lupus*. Status: Increasing, about 100. Range occupied: 20%. Main prey: Ungulates. Legal status: Protected.
- *Finland*: Subspecies: *C. l. lupus*. Status: About 100. Range occupied: 20%. Main prey: Ungulates and livestock. Legal status: Partial protection.
- *Estonia, Latvia, Lithuania*: Subspecies: *C. l. lupus*. Status: Viable, about 2,000, stable. Range occupied: 75%. Main prey: Ungulates and livestock. Legal status: Hunted as game species. Threat: Overhunting, habitat destruction.
- *Russia (Europe), Belarus, Ukraine*: Subspecies: *C. l. lupus, C. l. albus*. Status: Fully viable, about 20,000. Range occupied: 60%. Main prey: Ungulates, livestock. Legal status: Reduction and control even in nature reserves. Cause of decline: Persecution, habitat destruction.
- *Poland*: Subspecies: *C. l. lupus*. Status: Viable, about 600. Range occupied: 50%. Main prey: Moose, roe deer, red deer, wild boar, mufflon. Legal status: Protected. Threat: Persecution, habitat destruction.
- *Czech Republic*: Subspecies: *C. l. lupus*. Status: Increasing, 20. Range occupied: 5%. Main prey: Ungulates and livestock. Legal status: Protected. Threat: Persecution.
- *Slovakia*: Subspecies: *C. l. lupus*. Status: Stable, 350–400. Range occupied: 50%. Main prey: Roe deer, red deer, wild boar. Legal status: Protected. Cause of decline: Persecution, habitat destruction.
- *Hungary*: Subspecies: *C. l. lupus*. Status: Stable, <50. Range occupied: 5%. Main prey: Unknown. Legal status: Protected. Threat: Habitat suitability.
- *Romania*: Subspecies: *C. l. lupus*. Status: Increasing, 2,500. Range occupied: 80%. Main prey: Roe deer, red deer, wild boar, livestock. Legal status: Protected.
- *Bulgaria*: Subspecies: *C. l. lupus*. Status: Increasing, 800–1,000. Range occupied: 40%. Legal status: Game species. Main prey: Roe deer, red deer, wild boar.
- *Greece*: Subspecies: *C. l. lupus*. Status: In decline, >500. Range occupied: 50%. Main prey: Deer, wild boar,

chamois, livestock. Legal status: Partial protection. Cause of decline: Persecution, habitat destruction.

- *Former Yugoslav Federation*: Subspecies: *C. l. lupus*. Status: Stable, about 500. Range occupied: 55%. Main prey: Deer, wild boar, livestock. Legal status: Partial protection. Threat: Persecution, habitat destruction.
- *Croatia and Slovenia*: Subspecies: *C. l. lupus*. Status: 150–200. Range occupied: 30%. Main prey: Ungulates and livestock. Legal status: Fully protected. Threat: Illegal persecution.
- *Albania*: Subspecies: *C. l. lupus*. Status: 250. Range occupied: 50%. Main prey: Deer and wild boar, livestock. Legal status: Hunted as game species. Cause of decline: Overhunting.
- *Former Yugoslav Republic of Macedonia*: Subspecies: *C. l. lupus*. Status: Viable, about 1,000. Range occupied: 75%. Main prey: Ungulates and livestock. Legal status: Hunted. Cause of decline: Persecution, habitat destruction.
- *Bosnia Herzegovina*: Subspecies: *C. l. lupus*. Status: Stable?, about 500. Range occupied: 50%. Main prey: Ungulates and livestock. Legal status: Hunted as game species. Threat: Persecution, habitat destruction.
- *Spain*: Subspecies: *C. l. lupus*. Status: Increasing, 2,000. Range occupied: 30%. Main prey: Livestock, roe deer, wild boar. Legal status: Partial protection. Threat: Persecution, habitat destruction.
- *Portugal*: Subspecies: *C. l. lupus*. Status: Stable, lingering, low population density, 200–300. Range occupied: 20%. Main prey: Livestock, roe deer, wild boar. Legal status: Protected. Threat: Persecution, habitat destruction.
- *France*: Subspecies: *C. l. lupus*. Status: Increasing, about 30. Range occupied: 5%. Main prey: Ungulates and livestock. Legal status: Protected. Threat: Persecution.
- *Italy*: Subspecies: *C. l. lupus*. Status: Increasing, 500 individuals. Threatened. Range occupied: 25%. Main prey: Wild boar, deer, livestock, garbage. Legal status: Full protection, not enforced. Threat: Persecution.

North and Central Asia (Palaearctic)

- *Former USSR*: Subspecies: *C. l. lupus, C. l. albus*. Status: Fully viable, about 50,000. Range occupied: 75%. Main prey: Ungulates and livestock. Legal status: Reduction and control even in nature reserves. Threat: Persecution, habitat destruction.
- *Turkmenistan*: Subspecies: *C. l. lupus*. Status: Viable, >1,000. Range occupied: 85%. Main prey: Ungulates and livestock. Legal status: Reduction and control even in nature reserves. Threat: Active persecution, habitat destruction.
- *Mongolia*: Subspecies: *C. l. lupus*. Status: Viable, possible decline, >10,000. Range occupied: 100%. Main prey: Livestock, saiga. Legal status: Extermination efforts active.
- *China*: Subspecies: *C. l. lupus*. Status: Stable, about 6,000. Range occupied: 20%. Main prey: Saiga, other ungulates, livestock. Legal status: Protected but no enforcement. Threat: Persecution, habitat destruction, extermination efforts active.

Middle East (Palaearctic)

- *Egypt (Sinai)*: Subspecies: *C. l. pallipes*. Status: Highly endangered, 30?. Range occupied: 90%. Main prey: Hares, livestock. Legal status: No protection. Cause of decline: Persecution.
- *Turkey*: Subspecies: *C. l. lupus, C. l. pallipes*. Status: Viable, but in decline. 5,000–10,000. Range occupied: 75% of former range. Main prey: Livestock, wild boar, brown hare. Legal status: No protection. Cause of decline: Persecution, poisoning.
- *Lebanon*: Subspecies: Unknown. Status: Highly endangered. Lone wolves or pairs, >10.. Range occupied: Unknown. Main prey: Garbage, carrion. Legal status: No protection. Cause of decline: Persecution.
- *Syria*: Subspecies: *C. l. lupus, C. l. pallipes*. Status: Highly threatened. Lingering, low population density, 200–300? Range occupied: 10%. Main prey: Livestock, carrion, small wildlife. Legal status: No protection. Threat: Persecution.
- *Jordan*: Subspecies: Unknown. Status: Highly threatened. Lingering, low population density, 200? Range occupied: 90%. Legal status: No protection. Main prey: Unknown. Threat: Persecution.
- *Israel*: Subspecies: *C. l. pallipes, C. l. arabs*. Status: Highly threatened. Lingering, low population density, 150–200. Range occupied: 60%. Main prey: Hares, livestock, carrion. Legal status: Full protection. Cause of decline: Habitat destruction.
- *Saudi Arabia, United Arab Emirates, Oman, Yemen*: Subspecies: *C. l. pallipes*. Status: In decline, 500–600. Range occupied: 75%. Main prey: Garbage, carrion, livestock. Legal status: No protection. Threat: Persecution.
- *Iraq*: Subspecies: Unknown. Status: Unknown. Range occupied: Unknown. Main prey: Unknown. Legal status: Unknown. Cause of decline: Unknown.
- *Iran*: Subspecies: *C. l. pallipes*. Status: Viable >1,000. Range occupied: 80%. Main prey: Gazelle, mountain sheep, livestock, wild boar, deer, *Capra* sp. Legal status: Game species. Threat: Persecution.
- *Afghanistan*: Subspecies: *C. l. pallipes*. Status: Viable, suspected decline, 1,000? Range occupied: 90%. Main prey: Unknown. Legal status: Unknown.

South Asia – south of the Himalaya (Oriental)

- *Pakistan*: Subspecies: *C. l. pallipes*. Status: Declining, 200. Range occupied: 10%. Main prey: Livestock, gazelle. Legal status: Protected, no enforcement. Cause of decline: Active persecution.

- *India*: Subspecies: *C. l. pallipes*. Status: Endangered. 1,000–2,000 in small fragmented populations. Range occupied: 20%. Main prey: Livestock, hare, deer, antelope. Legal status: Full protection, but not enforced. Cause of decline: Decreasing prey, habitat loss, persecution.
- *Nepal*: Subspecies: *C. l. lupus.* Status: Unknown. Range occupied: Unknown. Main prey: Unknown. Legal status: Unknown.
- *Bhutan*: Subspecies: *C. l. lupus*. Status: Unknown. Range occupied: Unknown. Main prey: Unknown. Legal status: Protected.

Habitat

All northern habitats where there is suitable food (Mech 1970), densities being highest where prey biomass is highest (Fuller 1989).

Food and foraging behaviour

Food Extremely variable, but the majority is large ungulates (moose, caribou, deer, elk, wild boar, etc.). Wolves will also eat smaller prey items, livestock, carrion, and garbage.

Foraging behaviour In winter, wolves hunt in packs, which are usually families, but in summer, they hunt singly, in pairs, or in small groups. Chases ranging from 100m to more than 5km are the rule, and generally wolves end up with, or tend to select, older individuals, young-of-the-year, debilitated animals, or those in otherwise poor condition (Mech and Boitani 2003). Average daily food consumption varies from 2.5–6.3kg or more per day, and kill rates vary accordingly. Wolves first attack the rump of larger prey, but the head, shoulders, flanks, or rump of smaller prey. Usually they eat most of the carcass, leaving only the larger bones and chunks of hide. When there is surplus food, wolves will cache either regurgitated chunks or large pieces (Mech and Boitani 2003).

Damage to livestock and game Wolves sometimes come into conflict with ranchers (Young and Goldman 1944; Mech 1970) and can reduce wild prey (Mech and Karns 1977).

Adaptations

The grey wolf is well adapted for cursorial predation, having long legs and thick and blocky, but flexible, feet. Year-round pair bond insures that more hunting units include at least two adults.

Social behaviour

Wolves are pack-living animals, with most packs comprising family groups. The dominant pair breeds, with any maturing females reproductively suppressed unless food is abundant. Packs include up to 36 individuals, but smaller sizes (5–12) are more common. They occupy territories of 75–2,500km^2 depending on prey density, and these are maintained through howling, scent-marking, and direct killing (Mech 1970, 1974; Mech *et al.* 1998).

Reproduction and denning behaviour

Time of mating is from January to April, depending on latitude (Mech 2002). Gestation is nine weeks. Dens are in holes, caves, pits, hollow logs, etc. Litter size is 1–11 (mean=6). Duration of lactation is 8–10 weeks. Age at sexual maturity is 22–46 months, occasionally 10 months (Mech 1970, 1974).

Competition

Bears, cougars, tigers, dogs (Mech 1970; Mech and Boitani 2003).

Mortality and pathogens

Natural sources of mortality Primarily intraspecific strife and starvation.

Persecution Primarily in agricultural areas where competing with humans for domestic animals.

Hunting and trapping for fur Primarily Alaska, Canada, Russia, Kazakhstan, Mongolia.

Road kills Not significant to populations.

Pathogens and parasites Susceptible to mange, canine parvovirus, distemper, rabies.

Longevity Up to 13 years in the wild, and 16 years in captivity (Mech 1988).

Historical perspective

The primary cultural importance of the wolf has been as an enemy seen by most agricultural people as a creature to be feared, persecuted and extirpated. Some indigenous people in North America, however, respected the wolf, although they still killed it. Most cultures used its fur as parkas and clothing. Conservation measures were not taken in most areas until after about 1970 and are still lacking in most of Asia, where they mostly are unnecessary, except in parts of China and India.

Conservation status

Threats Their original worldwide range has been reduced by about one-third, primarily in developed areas of Europe, Asia, Mexico, and the United States by poisoning and deliberate persecution due to depredation on livestock. Since about 1970, legal protection, land-use changes, and rural human population shifts to cities have arrested wolf population declines and fostered natural recolonisation in parts of Western Europe and the United States, and reintroduction in the western United States. Continued threats include competition with humans for livestock, especially in developing countries, exaggerated concern by the public concerning the threat and danger of wolves, and fragmentation of habitat, with resulting areas becoming too small for populations with long-term viability.

Commercial use Sustainable utilisation of fur in Canada, Alaska, and the former Soviet Union and Mongolia.

Occurrence in protected areas Occurs in many protected areas across its range.

Protection status CITES – Appendix II, except populations from Bhutan, India, Nepal and Pakistan, which are listed on Appendix I. See individual countries listed above.

Current legal protection Variable, from complete protection, well enforced, to concerted efforts to control some populations. See individual areas above.

Conservation measures taken Protected in various national parks and reserves in Canada and the United States. Extensive legal protection in many European countries; however, enforcement is variable and often non-existent. See individual areas above. Recently reintroduced to Yellowstone National Park, Idaho, and Arizona.

Occurrence in captivity

Lives and breeds well in captivity and is common in many zoological gardens.

Current or planned research projects

Several projects underway in Europe, India, Canada and the United States. See http://www.wolf.org

Gaps in knowledge

One of the most important questions still remaining about wolves involves the nature of their interaction with prey populations. The conditions under which wolves limit, regulate, or control their population is still open and important (Mech and Boitani 2003). Of more academic interest are questions involving wolf genetics, scent-marking behaviour, pseudopregnancy, and diseases (Mech 1995a).

Core literature

Boitani 1995; Carbyn *et al.* 1995; Harrington and Paquet 1982; Mech 1970, 1974; Mech *et al.* 1998; Mech and Boitani 2003; Nowak 1995. A list of about 2,000 references is available at http://www.wolf.org

Reviewers: Lu Carbyn, Christoph Promberger, Devra Kleiman. **Editors:** Claudio Sillero-Zubiri, Michael Hoffmann.

5.3 Red fox
Vulpes vulpes Linnaeus, 1758
Least Concern (2004)

D.W. Macdonald and J.C. Reynolds

Other names

English: silver fox, cross fox; **Albanian:** dhelpra; **Croatian:** lisica; **Czech:** liška obecná; **Danish:** ræv; **Dutch:** vos; **Estonian:** rebane; **Faeroese:** revur; **Finnish:** kettu; **French:** renard roux; **German:** rotfuchs; **Hungarian:** vörös róka; **Irish:** sionnach, madra rua; **Italian:** volpe rossa, volpe comune; **Latvian:** lapsa; **Lithuanian:** rudoji lapë; **Luxembourgish:** fuuss; **Maltese:** volpi; **Norwegian:** rev, rødrev; **Polish:** lis; **Portuguese:** raposa; **Romanian:** vulpe; **Russian:** Красная дисица; **Slovakian:** líška hrdzavá; **Slovenian:** lisica; **Spanish:** zorro rojo; **Swedish:** räv; **Turkish:** tilki.

Taxonomy

Vulpes vulpes Linnaeus, 1758. Syst. Nat., 10th ed., 1:40. Type locality: "Europa, Asia, Africa, antrafodiens" restricted by Thomas (1911), to "Sweden (Uppsala)".

The North American red fox, *Vulpes fulva*, previously has been considered a separate species (as have some other putative subspecies), but is now considered conspecific with the Palaearctic *V. vulpes* (Nowak 1991). Many subspecies were described (see below) on the basis of regional variation, but these have doubtful ecological significance as evidenced by successful introductions and re-introductions around the world.

Chromosome number: The red fox has a diploid number of 34 chromosomes and 3–5 microsomes (Rausch and Rausch 1979).

Description

A medium-sized canid, and the largest fox in the genus *Vulpes* (Table 5.3.1). Muzzle slender and pointed with white on upper lip. Ears large, pointed, erect and black-backed. Pelage is reddish-brown but may vary from brown to russet red to yellowish grey. Three main colour morphs: red, silver (black with variable amount of frosting due to silver tips on guard hairs) and cross (greyish brown with long black guard hairs down back and across shoulders) (Banfield 1987; Johnson and Hersteinsson 1993). Some individuals have dark grey-black under throat and belly and the underfur of females during the breeding season may appear pink-tinged. Throat and/or chest may have white markings. Legs long and slender. Lower legs black, may be splashed with white. Tail long, thick and bushy, sometimes with white tip. Enormous geographical variation in size. Adult head and body length may range from 455–900mm, tail length from 300–555mm and body weight from 3–14kg with males generally being larger than females (Nowak 1991). The species is substantially smaller in the

Table 5.3.1. Body measurements for the red fox.

	Several studies from Cavallini (1995)	**Ontario, Canada** (Voigt 1987)	**Canberra, Australia** (McIntosh 1963)	**Kent, UK** (Hatting 1956)	**Hokkaido, Japan** (Zhan *et al.* 1991)
Total length male		1,026mm n=37	1,048mm n=84	1,064mm n=9	
Total length female		973mm n=34	1,002mm n=60	1,022mm n=10	
HB male	660mm (590–720) n=11 (studies)				
HB female	630mm (550–680) n=11				
T male	400mm (360–440) n=11				
T female	370mm (280–490) n=11				
WT male	6.3kg (4.4–7.6) n=20	4.1kg (n=37)	6.3kg (n=84)	6.7kg (n=33)	8.7kg (n=20)
WT female	5.3kg (3.6–6.5) n=20	3.4kg (n=37)	5.5kg (n=60)	5.5kg (n=29)	6.1kg (n=25)

Adult male red fox. United Kingdom.

David Macdonald

Middle East deserts (Macdonald *et al.* 1999) than in Europe. Smaller also in North America (Voigt 1987). Skull measurements of specimens from northern Algeria are also much smaller than central European populations (Kowalski and Rzebik-Kowalska 1991). Dental formula 3/3-1/1-3/4-3/3=42.

Red foxes from North America are comparatively light, rather long for their mass, and with a high sexual dimorphism. British foxes are heavier but relatively short. European foxes are closer to the general average among populations. Additionally, body mass and length are positively related to latitude (i.e., follow Bergmann's Rule), but this is a smaller effect than that related to geographical origin.

Subspecies Larivière and Pasitschniak-Arts (1996) recognised 44 subspecies, although many are doubtful:

— *V. v. abietorum* (Stuart Lake, British Columbia, Canada)
— *V. v. aegyptiaca* (Egypt)
— *V. v. alascensis* (Andreafski, Alaska, USA)
— *V. v. alpherakyi* (Geok Tepe, Araisk, Kazakhstan)
— *V. v. anatolica* (Smyrna, western Asia Minor, Turkey)
— *V. v. arabica* (Muscat, Oman)
— *V. v. atlantica* (Atlas Mountains, Mitiya, Algeria)
— *V. v. bangsi* (L'Anse au Loup, Strait of Belle Isle, Labrador, Canada)
— *V. v. barbara* (Barbary Coast, north-western Africa)
— *V. v. beringiana* (shore of Bering Strait, north-eastern Siberia)
— *V. v. cascadensis* (Cascade Mountains, Skamania County, Washington, USA)
— *V. v. caucasica* (near Vladikawkaz, Caucasus, Russia)
— *V. v. crucigera* (Thuringia, Germany)
— *V. v. daurica* (Kharangoi, 45km west of Troizkosavsk, Siberia)
— *V. v. deletrix* (Bay St-George, Newfoundland, Canada)
— *V. v. dolichocrania* (Sidemi, southern Ussuri, SE Siberia)
— *V. v. flavescens* (northern Iran)
— *V. v. fulva* (Virginia, USA)
— *V. v. griffithii* (Kandahar, Afghanistan)

— *V. v. harrimani* (Kodiak Island, Alaska, USA)
— *V. v. hole* (near Amoy, Fukien, S. China)
— *V. v. ichnusae* (Sarrabus, Sardinia, Italy)
— *V. v. induta* (Cape Pyla, Cyprus)
— *V. v. jakutensis* (Taiga, south of Yakutsk, E. Siberia)
— *V. v. japonica* (Japan)
— *V. v. karagan* (Kirghiz Steppes, Khirghizia, Russia)
— *V. v. kenaiensis* (Kenai Peninsula, Alaska, USA)
— *V. v. kurdistanica* (Gelsk Valley, NE Turkey)
— *V. v. macroura* (Wasatch Mountains, near Great Salt Lake, Utah, USA)
— *V. v. montana* (Himalaya)
— *V. v. necator* (Whitney Meadow, near Mt Whitney, Tulare County, California, USA)
— *V. v. ochroxantha* (Aksai, Semirechyia, E Russian Turkestan, Kirgizia)
— *V. v. palaestina* (Ramleh, near Jaffa, Occupied Palestinian Territory)
— *V. v. peculiosa* (Korea)
— *V. v. pusilla* (Salt Range, Punjab, Pakistan)
— *V. v. regalis* (Elk River, Sherburne County, Minnesota, USA)
— *V. v. rubricosa* (Digby, Nova Scotia, Canada)
— *V. v. schrencki* (Sakhalin, Russia)
— *V. v. silacea* (near Silos, Burgos, Spain)
— *V. v. splendidissima* (north and central Kurile Islands, Russia)
— *V. v. strepensis* (steppes near Kherson, Russia)
— *V. v. tobolica* (Obdorsk, Tobolsk, Siberia)
— *V. v. tschiliensis* (Peiping, Chihli, NE China)
— *V. v. vulpes* (Sweden)

Similar species Arctic fox (*Alopex lagopus*): A white morph superficially resembles white red foxes (some of which are albino) but they are up to 25% smaller, with muzzle shorter and ears shorter and rounder. Similarly, "silver" (actually black) or "cross" red foxes might be confused with blue morph of Arctic foxes.

Grey wolf (*Canis lupus*), and golden jackal (*Canis aureus*), are larger, have longer legs and relatively shorter tail. Confusion of pelts with those of smaller species more likely, due to clinal variation in body size and coloration between the largest red foxes (probably those in Scotland), and the smallest (perhaps in remote Saudi Arabia).

Great potential for confusion between red fox pelts and all the small Old World foxes (e.g., Tibetan fox, *V. ferrilata*, and corsac, *V. corsac*), the prairie foxes of North America (*V. macrotis* and *V. velox*), and some South American foxes.

A mutant of the red fox found in the wild, the so-called "Samson fox", lacks guard hairs.

Current distribution

Distributed across the entire northern hemisphere from the Arctic Circle to North Africa, Central America, and the Asiatic steppes, the red fox has the widest geographical range of any member of the order Carnivora (covering nearly 70 million km^2) (Figure 5.3.1). Not found in Iceland, the Arctic islands, some parts of Siberia, or in extreme deserts. European subspecies introduced into eastern United States and Canada in 17th century, subsequently mixed with local subspecies. The species was also introduced to Australia in 1800s. Elsewhere introduced to the Falkland Islands (Malvinas) and to the Isle of Man (UK), although it may subsequently have disappeared there.

Range countries Afghanistan, Albania, Algeria, Andorra, Armenia, Australia, Austria, Azerbaijan, Bahrain, Bangladesh, Belarus, Belgium, Bolivia, Bosnia and Herzegovina, Bulgaria, Cambodia (?), Canada, Channel Islands, China, Croatia, Cyprus, Czech Republic, Denmark, Egypt, Estonia, Faeroe Islands, Falkland

Figure 5.3.1. Current distribution of the red fox.

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Islands (Malvinas), Finland, France, Georgia, Germany, Gibraltar (?), Greece, French Guiana, Guyana, Hungary, India, Iran, Iraq, Ireland, Israel, Italy, Japan, Jordan, Kazakhstan, Kyrgyzstan, Korea (North and South), Kuwait, Laos PDR (?), Latvia, Lebanon, Libya, Liechtenstein, Lithuania, Luxembourg, Macedonia, Malta (?), Moldova, Monaco (?), Mongolia, Morocco, Myanmar, Nepal (?), Netherlands, Norway, Oman, Pakistan, Occupied Palestinian Territory, Poland, Portugal, Qatar, Romania, Russian Federation, San Marino, Saudi Arabia, Slovakia, Slovenia, Spain, Sudan, Suriname, Sweden, Switzerland, Syria, Tajikistan, Tunisia, Turkey, Turkmenistan, Ukraine, United Arab Emirates, United Kingdom, United States of America, Uzbekistan, Vietnam (?), Yemen, Yugoslavia (Lloyd 1980, Macdonald and Barrett 1993, Larivière and Pasitschniak-Arts 1996).

Relative abundance

Red fox density is highly variable. In the UK, density varies between one fox per 40km² in Scotland and 1.17/km² in Wales, but can be as high as 30 foxes per km² in some urban areas where food is superabundant (Harris 1977, Macdonald and Newdick 1982, Harris and Rayner 1986). Social group density is one family per km² in farmland, but may vary between 0.2–5 families per km² in the suburbs and as few as a single family per 10km² in barren uplands (Macdonald 1981, Lindsay and Macdonald 1986).

Fox density in mountainous rural areas of Switzerland is 3 foxes per km² (Meia 1994). In northern boreal forests and Arctic tundra, they occur at densities of 0.1/km², and in southern Ontario, Canada at 1/km² (Voigt 1987). The average social group density in the Swiss mountains is 0.37 family per km² (Weber *et al*. 1999).

Estimated populations/relative abundance and population trends The pre-breeding British fox population totals an estimated 240,000 (195,000 in England, 22,000 in Wales; Harris *et al*. 1995). Mean number of foxes killed per unit area by gamekeepers has increased steadily since the early 1960s in 10/10 regional subdivisions of Britain, but it is not clear to what extent this reflects an increase in fox abundance. Although an increase in fox numbers following successful rabies control by vaccination was widely reported in Europe (e.g., fox bag in Germany has risen from 250,000 in 1982–1983 to 600,000 in 2000–2001), no direct measures of population density have been taken.

Habitat

Red foxes have been recorded in habitats as diverse as tundra, desert and forest, as well as in city centres (including London, Paris, Stockholm, etc.). Natural habitat is dry, mixed landscape, with abundant "edge" of scrub and woodland. They are also abundant on moorlands, mountains (even above the treeline, known to cross alpine passes), deserts, sand dunes and farmland from sea level to 4,500m a.s.l. In the UK, they generally prefer mosaic patchworks of scrub, woodland and farmland. Red foxes flourish particularly well in urban areas. They are most common in residential suburbs consisting of privately owned, low-density housing and are less common where industry, commerce or council rented housing predominates (Harris and Smith 1987). In many habitats, foxes appear to be closely associated with man, even thriving in intensive agricultural areas.

Food and foraging behaviour

Food Red foxes are adaptable and opportunistic omnivores, with a diet ranging from invertebrates (e.g., earthworms and beetles) to mammals and birds (including game birds), and fruit. They also scavenge in rural areas (e.g., in Europe and Canada on deer and sheep carcasses which may be the major food source in upland areas in winter), and in urban areas (on bird tables, compost heaps and refuse). As predators, foxes typically kill birds and mammals up to about 3.5kg (equivalent to an adult brown hare). They require about 500g food per day, caching food that is in excess to their requirements and having a highly developed memory for location of hoards (Macdonald 1976, 1977a).

Foraging behaviour Foraging is mainly nocturnal and crepuscular, although more diurnal where they are undisturbed. They are independent and thus generally solitary foragers, although individuals may forage in close proximity where resources are clumped. Accounts of cooperative hunting, for example of young ungulates have not been studied systematically (Macdonald 1980a).

Damage to livestock or game Foxes are considered a major predator of ground-nesting colonial birds such as terns (many species of which are of conservation concern), and their effect on harvestable game-bird populations can be significant. They also predate hand-reared and released game-birds. Lambs may be taken locally but losses caused by foxes are typically only a small percentage (<2%) of all lambs born (Macdonald *et al*. 2000).

Adaptations

Paradoxically, it is probably the red fox's generalist conformation and lack of specialist adaptations that makes it the widely successful species that it is. The weakest element in this general formula, exploited by man and other predators, is the period of vulnerability of the young at the breeding den.

The red fox has great endurance and can gallop for several kilometres if pursued, they are able to run at speeds of up to 48km/h, jump fences two metres high and swim well (Haltenorth and Roth 1968). Red foxes can locate sounds to within one degree at 700–3,000Hz, though less accurately at higher frequencies. They are adapted to pounce on their prey with great precision, manipulating take-off angle to adjust length of jump and force of landing. They have relatively longer hind legs than other members of the dog family thereby increasing their propulsive force.

Dense, but short, fur covers approximately one-third of the body's surface area, particularly the face, dorsal part of head, nose, ears, lower legs and paws, and likely functions as a major heat exchange surface for thermoregulation (Klir and Heath 1992). The nose is used for evaporative cooling and probably forms part of a brain cooling mechanism as described in domestic dogs (Klir and Heath 1992). The physiology of their senses and their physical size and agility mean foxes are particularly well suited to preying on small rodents.

Red foxes can dig their own dens or may enlarge the burrows of other species, such as rabbits (*Oryctolagus cuniculus*), marmots (*Marmota* spp.), European badgers (*Meles meles*), or even other foxes. Dens normally are dug into banks, tree root systems, rocky crevices and even under buildings.

Social behaviour

The basic social unit is a pair, but groups with up to six members (usually one adult male and 2–5, probably related, vixens) may share a territory, depending on habitat. Range size is habitat dependent and can cover from less than 0.40km² (e.g., urban foxes in Oxford, UK), to as much as >40km² (>30km² in Arctic), depending on habitat (reviewed by Voigt and Macdonald 1984). One fox in the deserts of Oman had a range spanning 50km² (Lindsay and Macdonald 1986). There are reports of overlapping home ranges in some (but not all) urban (e.g., Harris 1979) and rural environments (Meia and Weber 1996) and drifting territories in other urban settings (Doncaster and Macdonald 1991).

Red foxes communicate with facial expressions, vocalisations and scent marking. Scent marking involves urine and faeces (urine marking is sometimes confined to dominant females within a group), anal sac secretions, violet or supracaudal gland (more active in males during breeding season) as well as glands around lips, in the angle of the jaw and between pads of the feet. Some 28 different categories of vocalisation have been described, and are used to communicate over long distances and at close quarters. Individuals have characteristically different voices.

Mating behaviour is highly variable, and may include monogamous pairs, a single male with two breeding vixens that may or may not share a communal den, to a single breeding female with several non-breeding female helpers. There is always only one breeding male in the group although additional matings do occur outside the group. Territorial male red foxes make frequent excursions beyond their territories during the mating season, during which itinerant males also make incursions into territories (Macdonald 1987).

Juveniles may disperse between six and 12 months of age, mostly between October and January. All or most males disperse but the proportion of each sex dispersing varies between habitats and may depend on extent of mortality (e.g., due to rabies or control). Males typically disperse further than females (e.g., males 13.7km, females 2.3km in Welsh hills; Lloyd 1980; Trewhella *et al*. 1988). Dispersal distance correlates positively with home range size (Macdonald and Bacon 1982). In the UK, distances are generally less than 5km to more than 50km, but distances up to 394km have been recorded in the USA (Ables 1975) to 250km in Sweden (Englund 1970).

Reproduction and denning behaviour

Males are seasonally fecund. Mating occurs between December and February (June to October in Australia); the onset of breeding is correlated with day length and so starts earlier at more southerly latitudes. Females are receptive over a period of three days. Following a gestation period of 49–55 days, births occur from March to May. Birth weight is around 100g. Underground dens are needed to shelter cubs while they are very young. Lactation lasts for four weeks, and the cubs are fully weaned at 6–8 weeks. Sexual maturity is reached at 9–10 months. The proportion of breeding females in the group, and litter size (3–12 young per litter, usually 4–5 in Europe, 6–8 in Ontario; Voigt and Macdonald 1984), varies with food availability. Fox populations that are dense relative to food resources are generally less productive than those that are less dense. A single litter per year is the norm.

In high-density red fox populations where interactions with the dominant vixen are high, subordinate females do not usually breed, although they may breed successfully in low-density populations (in the UK, usually only one or two females in a group breed) (Macdonald 1980b, 1987). Both parents, and sometimes other females in the group, care for the young (Macdonald 1979b). The male provides food to the lactating female which is generally confined to the den prior to weaning. Weaned food is provided for the cubs by both parents. Non-breeding females may also feed, groom and tend the cubs and have been known to adopt them if orphaned (Macdonald 1979b). If two females breed within a group, they may share a den and litters may be communally suckled.

There is socially-mediated suppression of reproduction amongst females, with lowest productivity tending to occur where fox density is high or food supply poor. Where food is not limited, social status itself can suppress reproduction, with only the dominant female breeding. Behavioural mechanisms by which this occurs include harassment of subordinates, infanticide and cannibalism of subordinate vixens' cubs, and possibly the dominant male courting only the dominant females (Macdonald

1977b, 1980). A hormonal mechanism whereby stress leads to lowered productivity through foetal reabsorption has also been identified (Hartley *et al.* 1994). Consistent with this mechanism, Heydon and Reynolds (2000) found that in populations where productivity was low, reproductive performance was suppressed consistently at all stages of pregnancy, from conception to birth.

Competition

Red foxes compete with Arctic foxes where the two species occur sympatrically in the Eurasian tundra. Red foxes are larger and generally out-compete Arctic foxes (and has been known to kill both adults and young), but are limited to the north of their range, partly by the cold and partly by limited resources. Although both species are well adapted to cold conditions, adaptations of Arctic foxes are superior: 70% Arctic fox pelage is underfur, *cf.* 20% in red foxes; the lower critical temperature for Arctic fox *c.* -40°C, *cf. c.* -13°C for red fox). Larger red foxes also have greater energy requirements and reach a point (as productivity decreases in the north) where they cannot maintain a large enough home range to provide sufficient prey (Hersteinsson and Macdonald 1982). See also *Alopex lagopus* account.

Grey wolves and red foxes were originally sympatric throughout their shared range, but there is little dietary overlap between the two, and they may or may not use different habitats. Similar diets between coyotes (*Canis latrans*) and red foxes lead to interference competition. In this case, the larger coyote tends to be distributed wherever there are sufficient food resources and no other limiting factors, while red foxes occupy adjacent areas with lower amounts of food resources. Red fox numbers tend to be greater where coyotes are absent and foxes do not rear cubs where coyotes are active (Voigt and Earle 1983). Ratio of coyotes to foxes is lower where wolves are present than where wolves are absent in the USA (Peterson 1995). Diets are also similar between red and gray foxes (*Urocyon cinereoargenteus*), which are similar in size. In this case, exploitative competition for food is likely and habitat partitioning common. There is some evidence that gray foxes, despite being smaller, dominate red foxes in parts of eastern North America (Follmann 1973, Tuller and Berchielle 1982). Red foxes also kill kit foxes (*Vulpes macrotis*) (Ralls and White 1995). Red foxes kill stone martens (*Martes foina*) in areas where they feed on similar resources (Weber *et al.* 2002). European badgers will charge and displace foxes at feeding sites (D. Macdonald pers. obs.).

Mortality and pathogens

Natural sources of mortality Red fox life-history patterns are typified by high juvenile and subordinate adult mortality and lower adult mortality. Although demography can differ markedly between populations, roughly 75% of foxes die in their first year, and thereafter mortality is approximately 50% in each adult year.

Red foxes have few natural predators, although golden eagles (*Aquila chrysaetos*) may kill both cubs and adults, and badgers and domestic dogs may kill cubs. Red foxes are a regular prey of the Eurasian lynx (*Lynx lynx*) in the Swiss Jura Mountains (Jobin *et al.* 2000). In addition, coyotes and wolves have both been recorded killing adults and cubs (Voigt and Earle 1983; Pacquet 1992).

Persecution In the UK, people (through secondary poisoning, shooting and other methods of attempted control) are typically the major cause of fox mortality, which is especially high amongst dispersers. Foxes are widely culled as pests. In the UK, for instance, culling is widespread, though highly variable among regions in methods, intensity and impact (Heydon and Reynolds 2000). Shooting is the principal method. Controversially, foxes are also hunted with dogs in the UK, France, Belgium, Portugal, Italy, Germany, Switzerland, Australia, the USA and Canada. Mounted fox hunts, together with upland foot and gun packs, probably are responsible for the deaths of about 21,500–25,000 foxes annually in the UK, which at this national level is about 4% of total mortality (Macdonald *et al.* 2000). Reliable estimates of numbers dying through other individual causes not available (for example, the extent of both deliberate and secondary poisoning is largely unknown).

Hunter bags in other countries are: Germany 600,000 (2000–2001); Austria 58,000 (2000–2001); Sweden 58,000 (1999–2000); Finland 56,000 (2000–2001); Denmark 50,000 (1976–1977); Switzerland 34,832 (2001); Norway 17,000 (2000–2001); Saskatchewan (Canada) 2,000 (2000–2001); Nova Scotia (Canada) 491 (2000–2001); New Mexico (USA) 69 (1999–2000).

Hunting and trapping for fur Worldwide trade of wild-caught foxes in 1985–1986 was 1,543,995 pelts. In the USA, red fox made up 45% of trade in wild-caught pelts worth $50 million in 1983. Most red foxes are killed for a variety of reasons, of which their value as fur is only one.

Road kills Where road-traffic is a dominant feature in modern landscapes, many red foxes are killed by vehicles. Juvenile and dispersing (mostly juvenile male) foxes are thought to be particularly susceptible. The impact of this mortality on population dynamics is not clear, and in both urban and rural environments, red fox populations exist alongside heavy road traffic. Fox density among three regions of England and Wales matched variation in culling pressure but did not match variation in road traffic density (Heydon *et al.* 2000).

Pathogens and parasites Populations are locally and periodically reduced by rabies epizootics (mortality rates estimated at 60–80% by simulation models; Voigt *et al.* 1985), although recovery appears to be swift (e.g., Western Europe, USA; Wandeler *et al.* 1974). Red foxes are a widespread reservoir of rabies, especially in central Europe, south-eastern Canada and north-eastern USA (Chomel 1993). Oral vaccines have been successfully used in some European countries (Kappeler *et al.* 1988) but there are still areas where rabies control has failed (Funk *et al.* 2001). Oral vaccination is regarded by the World Health Organization and European Union as an ongoing experiment. The red fox is host to a wide range of parasites including at least 58 species of helminths in Europe alone (Wolfe *et al.* 2001; Simpson 2002). One of the most serious of the parasites infecting foxes is the skin-dwelling mite (*Sarcoptes scabei* var. *vulpes*) which causes sarcoptic mange. This disease is locally and temporally prevalent. It appeared in Finland in 1967 and spread to Norway and Sweden in the 1970s and 1980s, where it reduced the red fox population by over 70% (Holt and Berg 1990; Lindström 1992). Since then it has spread across most of Europe including England, where it wiped out over 90% of the fox population in Bristol, UK in the early 1990s (Macdonald *et al.* 1997) and south-west to Spain (Gortazar *et al.* 1998) and New York (Tullar *et al.* 1974). Several other diseases are also recorded, including canine distemper, parvovirus, toxoplasmosis, bovine tuberculosis, and paratuberculosis but these do not appear to be major determinants of fox density (Little *et al.* 1982; Voigt 1987; Beard *et al.* 1999).

Longevity Foxes can live up to nine years in the wild, although only an estimated one in 10,000 will do so. Foxes in agricultural Europe generally live less than three years.

Historical perspective

Red foxes are widely represented in folklore. They have been hunted since the 4th century B.C. Fox hunting with dogs has been a notable part of European culture since at least the 11th century and was spread world-wide by British colonists. Red foxes are an increasingly important component of fur harvest taken from North America. As with most other furbearers, 20th century sales numerically far exceeded those in any previous century (Obbard *et al.* 1987). In 1992–1993, red fox fur was the third most important wild-caught furbearer in North America, in terms of commercial value (Sheiff and Baker 1987). Numbers sold, and therefore presumably harvests, fluctuate heavily with demand, although in settled regions culls are also related to pest status.

Conservation status

Threats Habitat degradation, loss, fragmentation; exploitation, direct and indirect persecution; government policies. Other threats: Local, national, or international socio-economic and political factors. Increasing human population and thus increasing development.

Red foxes' versatility and eclectic diet are likely to ensure their persistence despite changes in landscape and prey base. Culling may be able to reduce numbers well below carrying capacity in large regions (Heydon and Reynolds 2000), but no known situations exist where this currently threatens species persistence on any geographical scale. There are currently bounties on subspecies *V. v. pusilla* (desert foxes) in Pakistan to protect game birds such as Houbara bustards (*Chlamydotis undulata macqueenii*), with a high hunting value.

Commercial use The number of foxes raised for fur (although much reduced since the 1900s) exceeds that of any other species, except possibly mink (*Mustela vison*) (Obbard 1987). Types farmed are particularly colour variants ("white", "silver" and "cross") that are rare in the wild.

Worldwide trade in ranched red fox pelts (mainly "silver" pelts from Finland) was 700,000 in 1988–1989 (excluding internal consumption in the USSR). Active fur trade in Britain in 1970s was negligible.

Occurrence in protected areas Present in most temperate-subarctic conservation areas with the exception of some inaccessible islands in the Old World and South America.

Protection status Widely regarded as a pest and unprotected. CITES – not listed.
V. v. necator in the Sierra Nevada, California, USA, is rare, possibly declining (Nowak 1991). The subspecies *griffithi*, *montana* and *pusilla* (=*leucopus*) are listed as CITES – Appendix III (India).

Current legal protection Most countries and/or states where trapping or hunting occurs have regulated closed versus open seasons and restrictions on methods of capture. In the European Union, Canada, and the Russian Federation, trapping methods are regulated under an agreement on international trapping standards between these countries which was signed in 1997. Other countries are signatories to ISO/DIS 10990-5.2 animal (mammal) traps which specifies standards for trap testing.

Conservation measures taken In Europe and North America, hunting traditions and/or legislation impose closed seasons on fox hunting. In the UK and a few other European countries, derogation from these provisions allows breeding season culling for pest-control purposes. Here, traditional hunting ethics encouraging restrained "use" may be at odds with harder hitting pest-control ambitions. This apparent conflict between different interest groups is particularly evident in the UK, where fox control patterns are highly regionally variable (Macdonald *et al.* 2003). In some regions, principal lowland areas where classical mounted hunting operates, limited economic analyses suggest that the principal motive for these communal fox hunts is as a sport – the number killed is small compared with the cost of the hunting. In these regions, most anthropogenic mortality is by individual farmers shooting foxes. The mounted communal hunts do exhibit restraint – hunting takes place for a limited season, and for a prescribed number of days per week. Elsewhere, in upland regions, communal hunting by foot with guns and dogs may make economic sense, depending on the number of lambs lost to foxes (data on this is poor), and also on the current value of lost lambs. This type of fox hunting may also be perceived as a sport by its participants.

An individual deciding whether or not to control foxes, and by what means, has a complex set of factors to consider, including other interest groups, practicality and economics. For some farmers, there is evidence that a decision to control foxes may be economically perverse. Macdonald *et al.* (2003) modelled the interactions between foxes, rabbits, and rabbit-induced crop damage. For some farmers at least, a decision to kill a fox may, in some circumstances, cost that farmer a significant amount of crop loss to the rabbits that the fox and its descendants would have killed.

Occurrence in captivity

In addition to fur farms, red foxes are widely kept in small wildlife parks and zoos, but there appears to be no systematic data on their breeding success. Being extremely shy they are often poor exhibits.

Current or planned research projects

Controlling red foxes may be necessary where rare species, or threatened populations, are under threat, e.g., nest predation by foxes, has completely prevented recruitment to an internationally important sandwich tern colony in a number of consecutive years (Musgrave 1993). Attempting to control predation by lethal means can be problematic, i.e., intensive fox removal has been shown to have only local and short-term effects on predation because of swift replacement by conspecifics (Chesness *et al.*1968; Reynolds *et al.* 1993). Non-lethal methods might prove useful in managing undesirable behaviour, with some potential shown for learned food aversions for manipulating fox feeding behaviour (Macdonald and Baker 2003).

Core literature

Baker and Harris 2004; Doncaster and Macdonald 1991; Harris and Rayner 1986; Larivière and Pasitschniak-Arts 1996; Lloyd 1980; Macdonald 1977a, 1979b, 1987; Meia 1994.

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5.4 Raccoon dog *Nyctereutes procyonoides* (Gray, 1834)

Least Concern (2004)

K. Kauhala and M. Saeki

Other names

Chinese: háo/háo-zi; **Croatian:** kunopas; **Czech:** psíik mývalovitý; **Danish and Norwegian:** mårhund; **Dutch:** wasbeerhond; **Estonian:** kährikkoer; **Finnish:** supikoira; **French:** chien viverrin; **Georgian:** entiseburi dzagli; **German:** marderhund; **Hungarian:** nyestkutya; **Indonesian:** tjerpelai; **Italian:** cane procione; **Japanese:** tanuki; **Korean:** nurgoori; **Latvian:** jenotsuns; **Lithuanian:** usûrinis ðuo; **Polish:** jenot; **Portuguese:** câo-mapache; **Romanian:** câinele enot; **Russian:** enotovidnaya sobaka; **Slovakian:** psík medviedikovitý; **Slovenian:** rakunasti pes; **Spanish:** perro mapache; **Swedish:** mårdhund.

Taxonomy

Canis procyonoides Gray, 1834. Illustr. Indian Zool., 2: pl. 1. Type locality: Unknown; restricted to "vicinity of Canton, China" by Allen (1938).

The raccoon dog lineage diverged from other canids probably as early as 7–10 million years ago (Wayne 1993). Some features of the skull resemble those of South American canids, especially that of the crab-eating fox (*Cerdocyon thous*), but genetic studies have revealed that they are not close relatives (Wayne *et al.* 1997).

It has been suggested that *N. p. viverrinus* and *N. p. albus* (collectively called 'tanuki') can be separated as a different species from the other subspecies. Tanuki has fewer chromosomes than other continental subspecies with 2n=38 (Wada *et al.* 1998), while others have 2n=54 (Mäkinen 1974; Mäkinen *et al.* 1986; Ward *et al.* 1987; Wada *et al.* 1991). The chromosome number of tanuki has decreased as a result of Robertsonian translocations, which usually happens during speciation. In addition to a number of phenotypic and behavioural differences, preliminary DNA-analyses also suggest that there are considerable differences in gene frequencies between tanuki and *N. p. ussuriensis* from Finland (K. Kauhala unpubl.), and skull and tooth morphometrics also differ (Kauhala *et al.* 1998a). In addition, there are differences in the quality of fur and physiology; since the Japanese raccoon dog is adapted to mild marine climate, it has a stomach of small volume, thin fur with poor insulation properties and a poor ability to alter its body energy reserves seasonally (Korhonen *et al.* 1991).

Description

For *N. p. ussuriensis*: In autumn and winter, the raccoon dog is very fat and has thick fur, giving an expression of a round animal with short and thin legs. The black facial

Table 5.4.1. Body measurements for the raccoon dog.

	N. p. ussuriensis **Finland** (Kauhala 1993, unpubl.).	***N. p. viverrinus*** **Honshu, Japan** (Fukue 1993; Y. Fukue pers. comm.; Saeki 2001, unpubl.; S. Yachimori pers. comm.).
HB male	601mm (490–705) n=348	556mm (292–669) n=37
HB female	599mm (515–690) n=821	567mm (505–654) n=24
T male		173mm (50–230) n=37
T female		178mm (150–205) n=26
HF male		109mm (60–124) n=38
HF female		109mm (98–119) n=26
E male		44mm (20–56) n=36
E female		46mm (30–58) n=26
WT male	6.2kg (2.9–12.4) n=662	4.5kg (3.04–6.25) n=43
WT female	6.1kg (3.1–12.5) n=843	4.5kg (3.05–5.85) n=29

mask, small rounded ears and pointed muzzle are typical for the species. Hair is long on cheeks. The body colour varies from yellow to grey or reddish. There are black hairs on the back and shoulders and also dorsally on the tail. Legs, feet and chest are dark. Underhair is grey or reddish. 'Samson' raccoon dogs have no guard-hairs and underhair is reddish. The tail is rather short and covered with thick hair (Table 5.4.1). In summer when the fur is thin and fat reserves small, the animal looks much slimmer than in autumn. Dental formula is 3/3-1/1-4/4-2/3=42; m3 sometimes missing.

Subspecies There are six recognised subspecies of the raccoon dog (Ellerman and Morrison-Scott 1951; Ward and Wurster-Hill 1990):

— *N. p. albus* (Hokkaido, Japan: north of Blakiston's line at the Tsugaru straight). Body size is smaller than that of *N. p. ussuriensis*.

— *N. p. koreensis* (Korean Peninsula)

— *N. p. orestes* (south-western China)

— *N. p. procyonoides* (China and northern Indochina)

— *N. p. ussuriensis* (original range: south-eastern Russia and eastern China; introduced range: north-western parts of Russia, Finland, Sweden, the Baltic states, Belarus, Ukraine, Moldova, Poland, Germany, Hungary, Slovakia, Czech Republic, Romania, Bulgaria and Serbia, occasionally seen in Norway, Denmark, the Netherlands, France, Switzerland, Austria, Slovenia and Bosnia)

— *N. p. viverrinus* (Honshu, Shikoku and Kyushu, Japan: between Blakiston's and Miyake lines). Similar to *N. p. albus* but with somewhat shorter fur, shorter hind legs, and generally darker colour. Skull and teeth are smaller than those of *N. p. ussuriensis* (Kauhala *et al*. 1998a). Mandible width and jaw height for the skull and the lower and upper molars clearly distinguish the two subspecies.

Similar species Raccoon dogs can be confused with the raccoon (*Procyon lotor*) in Japan, Germany, France and Hungary, or the Eurasian badger (*Meles meles*), although neither are canid species. The badger has black stripes on the white head, is more strongly built and has shorter legs and tail than the raccoon dog. The tail of the raccoon is

Raccoon dog, age and sex unknown. Fukui Prefecture, Japan, 1993.

Great Tanuki Club

furry with dark bands. The badger and raccoon have five toes in each foot.

Distribution

Historical distribution In the Far East from northern Indochina to the south-east corner of Russia, also in Mongolia. In the Japanese Archipelago, the species was confined to Hokkaido, Honshu, Shikoku, Kyushu, Awaji island, Sado island and other islets of Japan except those south of Kyushu (e.g., Okinawa islands, Nansei islands, Miyako islands and Ogasawara islands). There has been a recent introduction in Yakushima island (S. Azuma pers. comm.).

Current distribution The species has been widely introduced. It is now widespread in northern and eastern Europe (Figure 5.4.1), thriving in moist forests with abundant undergrowth. The northern limit of distribution lies in areas where the mean temperature of the year is just above 0°C, the snow cover about 800mm, the duration of the snow cover 175 days and the length of the growing season 135 days (for example, in Finland the northern limit of permanent distribution is between 65°N and the Arctic Circle). If winters become milder, the raccoon dog may expand its range northwards.

Range countries (including introductions): Belarus, Bulgaria, China, Estonia, Finland, Germany, Hungary, Japan, Korea, Latvia, Lithuania, Moldova, Poland, Romania, Russia, Serbia, Sweden (only in the county of Norrbotten), Ukraine, Vietnam. Occasionally seen in Austria, Bosnia, Denmark, France, the Netherlands, Norway, Slovenia and Switzerland (Ellerman and Morrison-Scott 1951; Mitchell-Jones *et al.* 1999).

Relative abundance

Abundance is unknown in the Far East outside of Japan where it is common. Population estimates have never been conducted in the latter country, but indirect indices (e.g., road-kills per km of the National Expressways and harvest density per prefecture), suggest that relative abundance is high in south-western parts of Japan (i.e., Kyushu, Shikoku, and Chugoku) and low in Hokkaido, Chubu, and extremely urban areas (M. Saeki and D.W. Macdonald unpubl.). See Table 5.4.2 for the status of the raccoon dog in different countries.

Estimated populations/relative abundance and population trends

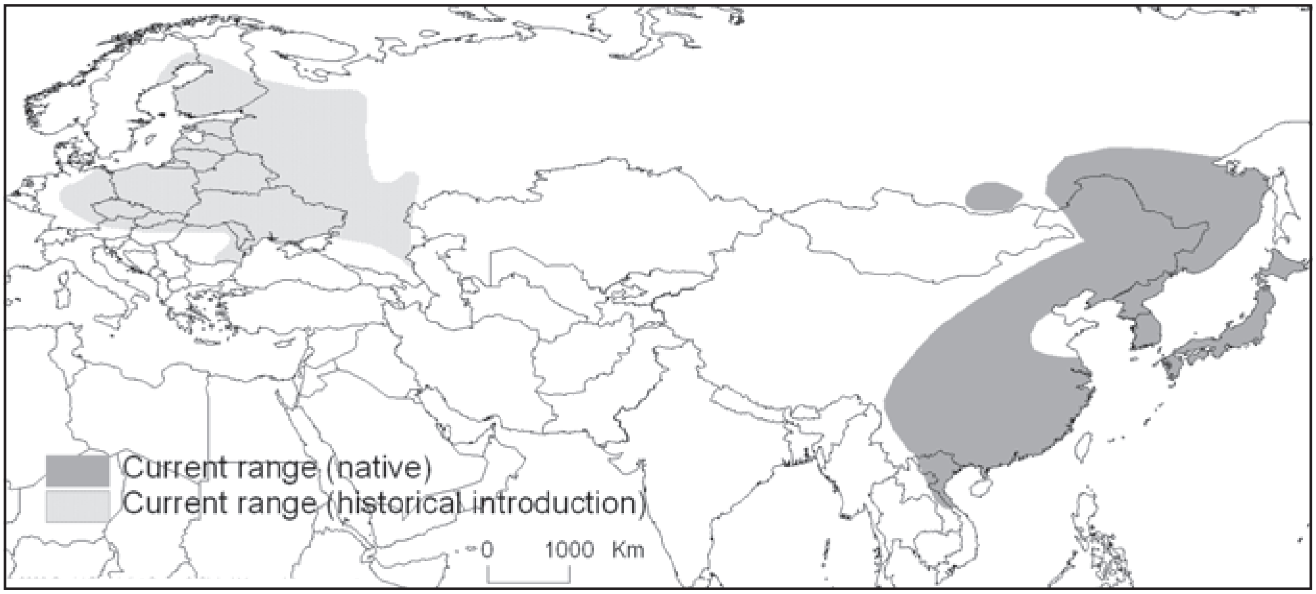
Table 5.4.2. The status of raccoon dogs in various range countries (A=abundant; C=common; R=rare; X: present, but abundance unknown; I=increasing; S=stable).

Country	Population/abundance	Trend
Belarus	A	
Denmark	R	
Estonia	A	
Finland	45,000	S
Germany	C	
Hungary	X	I
Latvia	C	S
Lithuania	C	
Poland	C	
Russia	C	
Sweden	R	
Ukraine	X	

Habitat

Two features are typical of the habitat of raccoon dogs: 1) they are often found near water, and 2) during autumn

Figure 5.4.1. Current distribution of the raccoon dog.



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they are more or less dependent on fruits and berries, which affects their habitat selection.

In Japan, raccoon dog habitat includes deciduous forests, broad-leaved evergreen forests, mixed forests, farmlands, and urban areas from coastal to subalpine zones. In the countryside, the species prefers herbaceous habitat and uses less *Cryptomeria* plantation throughout year, while riparian areas are often used (M. Saeki and D.W. Macdonald unpubl.). In urban areas, raccoon dogs inhabit areas with as little as 5% forest cover. In the Russian Far East, the raccoon dog favours open landscape, especially damp meadows and agricultural land and avoids dark forests (Judin 1977).

In the introduced range, raccoon dogs favour moist forests and shores of rivers and lakes, especially in early summer (Korneev 1954; Nasimovic and Isakov 1985; Kauhala 1996). In late summer and autumn raccoon dogs favour moist heaths with abundant berries (Morozov 1947; Kauhala 1996). In the Finnish archipelago, however, they favour barren pine forests where they feed on crowberries (*Empetrum nigrum*) (Kauhala and Auniola 2000).

Food and foraging behaviour

Food Raccoon dogs are true omnivores and seasonal food habits shift as food availability changes (Ivanova 1962; Kauhala *et al.* 1993a). In most areas small rodents form the bulk of their diet in all seasons (Bannikov 1964; Nasimovic and Isakov 1985). Frogs, lizards, invertebrates, insects (including adults and larvae of *Orthoptera, Coleoptera, Hemiptera, Diptera, Lepidoptera, Odonata*), birds and their eggs are also consumed, especially in early summer (Barbu 1972; Kauhala *et al.* 1993a, 1998b). Plants are frequently eaten; berries and fruits are favoured in late summer and autumn when they serve as an important food source before raccoon dogs enter winter dormancy. Oats and other agricultural products (e.g., maize/sweet corn, watermelon, loquat, tangerine, pear) are often found in raccoon dog stomachs. Carrion (e.g. ungulate carcasses), fish and crustaceans (e.g., crabs, crayfish) are consumed when available.

Foraging behaviour As opportunistic generalists, raccoon dogs forage by searching close to the ground and, in Japan, may also climb trees for fruits. They are mainly nocturnal and forage in pairs, leaving their dens 1–2 hours after sunset (Kauhala *et al.* 1993b). When they have pups, females also forage during the daytime while the male is babysitting (Kauhala *et al.* 1998c). Usually the foraging pair wanders some distance apart from each other. Raccoon dogs decrease their food intake before entering winter dormancy (Korhonen 1988).

Damage to livestock or game Waterfowl and their eggs are consumed at the seashore and the archipelago in early summer (Ivanova 1962; Naaber 1971, 1984). Fish from fish ponds may also be consumed (Saeki 2001). In the inland habitats of Finland, birds occur in the diet less often, and most of them are passerines (Kauhala *et al.* 1998b). Remains of grouse are found only occasionally in the faeces of raccoon dogs (Judin 1977). When the diets of raccoon dogs, red foxes (*Vulpes vulpes*) and badgers in early summer were compared in southern Finland, the diet of raccoon dogs was the most diverse, and raccoon dogs consumed game animals less frequently than foxes (Kauhala *et al.* 1998b).

Adaptations

Among canids, winter lethargy is a unique feature of raccoon dogs. In areas where winters are harsh, raccoon dogs spend the winter asleep; for example, in southern Finland, they start hibernation in November and become active again in March (K. Kauhala pers. obs.). Adults usually settle in the dens first (the pair together) and young later. Adult raccoon dogs almost double their weight between June and October; in June they weigh 4.5kg on average, in October 8.5kg, and sometimes 12kg (Kauhala 1993). Adults start to fatten themselves first and young when they have finished growing in late September. Autumn fattening is a consequence of decreased activity rather than increased food intake. The rate of metabolism (which is measured by thyroid activity) decreases during winter lethargy and increases again in spring. This results in weight loss which is a precisely controlled process (Korhonen 1987, 1988).

Raccoon dogs can be seen during daytime in spring, when they are sunbathing on the southern slopes of hills; they sit with their dark chest towards the sun to warm their body and save energy (Harri and Korhonen 1988).

Social behaviour

The raccoon dog is strictly monogamous, the male and female forming a permanent pair (Judin 1977; Kauhala *et al.* 1993b). Pair formation may take place before the breeding season (e.g., in September; M. Saeki pers. obs.). Pairs share their home range and also forage together. Only if one of the pair dies, will the remaining member form a new pair bond with a new mate. Some non-paired adults may stay within the same area and/or share the resting or feeding sites or dens, but, unlike pairs, non-paired adults usually do not move together. Sometimes two males move together as a pair, while in Finland, two females have not been observed together after the young have dispersed in autumn (S. Puonti pers. comm.).

Both male and female defend the home range against individuals of the same sex. The home range size varies according to the abundance of food. The core areas of different pairs are totally exclusive, especially during the breeding season. The peripheral areas of home ranges may overlap to some extent. In autumn there is more overlap than in spring and summer. Different pairs seem to avoid each other even when their home ranges overlap to some extent (Kauhala *et al.* 1993b). Resting sites may be shared with related family members (Yachimori 1997), and latrine sites may be shared by several individuals (Ikeda 1982).

The following home range sizes have been calculated from various reported population densities: 10–20km² in the introduced range in European Russia; 7–10km² in the regions of Volga and Tatar, 4–10km² in Ukraine; 1.5km² in the Novgorod area, and 0.4–1.3km² in the Gorki area (Kozlov 1952, Morozov 1953, Popov 1956, Bannikov 1964). In Bialowieza Forest and in Suwalki Landscape Park, Poland, home ranges are 4–10km² (Jedrzejewski and Jedrzejewska 1993; Goszczynski 1999; Kowalczyk *et al.* 2000). In eastern Germany, mean home range was 3.97km² (Drygala *et al.* 2000). In Japan, home range size varies greatly, from as little as 0.07km² in an urban setting to 6.1km² in a subalpine setting (Fukue 1991, Yamamoto *et al.* 1994, respectively). According to radio-tracking studies in southern Finland, the home range size varies between 2.8 and 7.0km² (Kauhala *et al.* 1993a; K. Kauhala and K. Kiviaho unpubl.).

Raccoon dogs do not bark, but growl when menaced. In Japan, their vocalisations are higher in tone than those of a domestic dog and more or less resemble the sounds of a domestic cat. Dominant raccoon dogs can raise their tails in an inverted U-shape.

Reproduction and denning behaviour

The basic reproductive physiology of the raccoon dog is similar to that of other canids. Testosterone levels in males peak in February/March, and progesterone levels in females coincide even with absence of males, suggesting that the species is “a monoestrous, seasonal and spontaneous ovulator” (Yoshioka *et al.* 1990). Raccoon dogs achieve sexual maturity at 9–11 months and can breed in the first year, but a first-year female will enter oestrus later (>1 month) than older females (M. Saeki pers. obs.). Females can reproduce every year. Mating usually occurs in March (Helle and Kauhala 1995). This indicates the impact of climate on reproduction; the onset of spring and the length of winter lethargy determine the time of ovulation. Mating occurs in the back-to-back copulatory posture typical of other canids (Ikeda 1982).

The gestation period is nine weeks, with most parturition occurring in May (varies from April to June). The parents settle in a den about a week before the pups are born. Raccoon dogs will den in old badger sets or fox dens or they will dig dens in soft sandy soil. They will also use active badger setts, usually together with badgers (Kowalczyk *et al.* 1999). Winter dens are usually located within their home range but if suitable dens are not available, the winter den may be several kilometres outside the summer home range.

In Japan, the mean litter size (only four to five) is smaller than in other parts of the distribution area and birth weight is around 100g. However, in Finland and Poland, the mean litter size is nine and birth weight about 120g; (Helle and Kauhala 1995; Kowalczyk *et al.* 2000). Similarly, in the original distribution area in south-east Russia, the mean litter size is nine (Judin 1977). On the other hand, in north-west Russia, litter size is smaller (six to seven) because of the continental climate with harsh winters. The abundance of wild berries also affects litter size; when berries are abundant, females are in good condition the following spring, and foetal mortality rate is low and litter size is large. Furthermore, in areas where spring comes late, the young are born late and remain small and slim in late autumn, and may not reproduce the following spring. Therefore, the productivity of the population is lower in areas with long winters compared to areas with milder climates (Kauhala and Helle 1995).

Pups start emerging from the den at three to four weeks of age and are weaned at approximately four to five weeks. Both sexes exhibit parental care, taking turns to attend the den during the early nursing period (Ikeda 1983). Because the food items of raccoon dogs are small, food is not carried to the den, and the pups are fed with milk until they start to forage for themselves (Yamamoto 1984; Kauhala *et al.* 1998c). The young usually reach adult body size by the first autumn.

Competition

Potential competitors include red fox and Eurasian badger. Direct and indirect competition may take place as their diets are similar and raccoon dogs often use burrows that were dug by foxes or badgers (Yamamoto 1994). However, the degree of competition is unclear since some differences in diet do exist: the badger consumes more invertebrates and the fox consumes more mammals and birds than the raccoon dog. Furthermore, food is abundant in summer and competition between these carnivores is not likely to be severe. In winter, food is scarce but raccoon dogs and badgers hibernate and, hence, no food competition exists in winter in northern areas. In Finland, a rapid raccoon dog population increase during the 1970s and 1980s coincided with a badger population increase, suggesting that competition is not severe between these species.

In addition to these, direct and indirect competition may take place with the Japanese marten (*Martes melampus*) and with the introduced masked palm civet (*Paguma larvate*) in Japan. In Belarus, the native generalist predator populations began to decline after the raccoon dog reached a high population density; competition on carcasses in winter was proposed as a factor in the observed decline (Sidorovich 2000). Conversely, a population increase in the common raccoon in Hokkaido, Japan, may have caused a decrease in the raccoon dog population (Ikeda 1999).

Mortality and pathogens

Natural sources of mortality In Japan, stray dogs often kill raccoon dogs. Raccoon dogs, especially puppies, also fall victims to other predators such as foxes, wolves, lynxes and large predatory birds. In Japan, a masked palm civet was observed entering a raccoon dog den and possibly predated on the pups (Y. Fukue pers. obs.). Puppies may also die because of malnutrition and parasites.

Persecution They seldom are hunted for their fur (because the fur of wild raccoon dogs currently has little value), but rather because they are considered pests. In Finland, the yearly hunting bag for 2000 was 60,000–70,000 (Finnish Game and Fisheries Research Institute 2001). In Hungary, raccoon dogs have been hunted since 1997, with the yearly bag being only one to nine animals (Heltai *et al.* 2000). In Poland, raccoon dogs are hunted from August to March and the annual bag was 450–600 in the early 1990s (Biuletyn Stacji Badawczej Czempiniu 1994), but 6,200 were shot in 2002/2003 (M. Panek pers. comm.). In Sweden, the annual catch is two to seven individuals.

In Japan, legal culling has increased since the 1970s, with 4,529 annual kills on average during 1990 and 1998 (Environment Agency 1972 to 1999). However, the numbers harvested have declined. Between 18,000 and 76,000 raccoon dogs were harvested each year in Japan after World War II, declining since 1982 (although still the largest among five fur-bearer species in Japan). The scale of poaching is not known but can be substantial because people are generally unaware of the law prohibiting the capture/killing of wildlife. Furthermore, poaching is routinely overlooked in Japan. In continental Asia, little is known about the persecution level. In Finland, some raccoon dogs are killed in summer when females with puppies are protected; hunters first kill the female and then the entire litter.

Hunting and trapping for fur See Persecution and Commercial use.

Road kills Many raccoon dogs, especially young dispersing in August and September, fall victims of traffic. In Japan, conservative estimates of road kills were 110,000–370,000 per year (M. Saeki and D.W. Macdonald unpubl.).

Pathogens and parasites Raccoon dogs face a serious problem with infestation of scabies or sarcoptic mange (*Sarcoptes scabies*), which seems to be widespread in many parts of Japan and northern Europe (Wildlife Management Office, Inc. 1998; Shibata and Kawamichi 1999). Mass deaths of the infested animals can occur in winter but raccoon dogs may also recover from the disease (M. Saeki pers. obs.). Raccoon dogs are potential vectors of *Echinococcus multilocularis*, a dangerous parasite that also infects humans. Raccoon dogs can also spread trichinosis. In Belarus, raccoon dog numbers fluctuate because of helminth infections (V. Sidorovich pers. comm.).

The raccoon dog is an important vector of rabies in Europe, with increasing significance towards the east and north. In Poland, 7% of rabies cases between 1990 and 1998 have been found in raccoon dogs, 9% in Lithuania, 12% in Latvia, and 16% in Estonia (Müller 2000). During a rabies epidemic in Finland in 1988 and 1989, 77% of the cases identified were in raccoon dogs (Westerling 1991). An outbreak of canine distemper in 1991 was reported to have eliminated about 70% of the local population in western Tokyo (Machida *et al.* 1993).

Longevity Maximum life span is seven to eight years (exceptionally 10 years), with a record in captivity of 13 years. Only about 1% of raccoon dogs live to five years, and 88% of the young (in Finland) die before their first year.

Historical perspective

The raccoon dog or tanuki has often appeared in Japanese folklore (Nakamura 1990; Matsutani 1995). Tanuki used to be raised for fur and was exported mostly to the USA before World War II (Kitamura 1934).

Conservation status

Threats Road kills, persecution, government attitudes, epidemics (scabies, distemper and rabies), and pollution (organtins, lead, PCDDs, PCDFs and PCBs) remain the major threats to the species across its range.

Commercial use The Russians introduced raccoon dogs into the wild in the European part of the former Soviet Union because they wanted to establish a valuable new fur animal in the wild. Raccoon dog furs continue to be commercially sold, although today they are produced in fur farms. While the species is still commonly farmed for fur in Finland, raccoon dogs are no longer farmed in Sweden (J.-O. Helldin pers. comm.) or Hungary, where the last fur farm was closed in 1995 (M. Heltai pers. comm.). In Japan, raccoon dog fur is also used in the production of calligraphic brushes, stuffed animals, and other products.

Occurrence in protected areas Raccoon dogs occur in national parks and other wildlife protection areas in Japan, where hunting and some other activities are prohibited. Raccoon dogs occur in national parks also in Finland (although they are hunted in some parks). Elsewhere across their range, they occur in numerous protected areas and wildlife sanctuaries.

Protection status CITES – Not listed.

Current legal protection In many countries where the raccoon dog is legally hunted, hunting is permitted year round (e.g., Sweden, Hungary and Poland). However, in Finland, females with pups are protected in May, June and July, and in Belarus hunting is allowed from 1 October to the end of February. In Japan, hunting/trapping of the species requires a licence or other form of permission and can only occur within the designated hunting season (November 15 to February 15). The raccoon dog on Mukojima island (18.4km^2), Hiroshima prefecture, is designated as a natural monument under the Law for the Protection of Cultural Properties, and permission from the Director-General of the Agency of Cultural Affairs is required for capturing the animals on the island.

Conservation measures taken There have been no conservation measures developed for the raccoon dog to date.

Occurrence in captivity

In Japan, around 40 zoos hold captive animals and successful breeding has been reported (e.g., Kobe Municipal Zoo). Captive raccoon dogs still exist on fur farms in Finland.

Current or planned research projects

In south-east Finland, K. Kauhala (Finnish Game and Fisheries Research Institute) is heading up a radio-tracking study. The aim of the study is to examine the home range size, use and overlap of raccoon dogs, red foxes and badgers, and interactions between individuals of different species in order to build a model of how rabies might be spread in the Finnish environment. Domestic cats are also included in the study.

In Japan, M. Saeki (Wildlife Conservation Research Unit, University of Oxford, UK) recently completed a study on the ecological and conservation issues of the raccoon dog, including habitat ecology, home range, movements, road kills, and agricultural damage in Japan (fieldwork in Chiba Prefecture). Ecological studies on the species and other medium-sized carnivores are continuing in the countryside.

Y. Sonoda (Meiji University, Japan) has undertaken investigations into suburban raccoon dogs in the Kanagawa Prefecture, concerning placement of protected areas for the species, habitat use, and road kills.

M. Kishimoto (Wildlife Management Office, Inc, Japan) has surveyed the distribution of latrines in order to analyse environmental factors used by the raccoon dog and to establish a large-scale survey method (in Hyogo, Tokushima and Kyoto Prefectures).

Gaps in knowledge

Although basic ecological studies on the raccoon dog have been conducted in Japan and in Finland, they were sporadic in several small study areas. There are no data available on the structure or demographic trends of the total population in Japan. Also, little is known about geographical genetic variation. In order to establish long-term conservation plans, extensive and intensive research is crucial. In addition, DNA studies to clarify the taxonomic status of the subspecies *N. p. viverrinus* and *N. p. albus* are needed.

Core literature

Ikeda 1982, 1983; Judin 1977; Kauhala 1992; Kauhala *et al*. 1998a,b,c; Saeki 2001.

Reviewers: Yuko Fukue, Hiroshi Ikeda, Bogumila Jedrzejewska, Rafal Kowalczyk. **Editors:** Claudio Sillero-Zubiri, Deborah Randall, Michael Hoffmann.

5.5 Corsac
Vulpes corsac (Linnaeus, 1768)
Least Concern (2004)

A. Poyarkov and N. Ovsyanikov

Other names

English: corsac fox; **French:** renard corsac, corsac; **German:** steppenfuchs, koraskfuchs; **Russian:** corsac; **Indigenous names:** Gobi Mongols: kirassu (Mongolia); Mongolian: kirsa, kiresa (Mongolia); Kalmic: bagata (Russian Federation); Tatarian: khorsic, corsac (Russian Federation); Kazach: karsac (Kazakhstan); Turkmenian: gorsac (Turkmenistan).

Taxonomy

Canis corsac Linnaeus, 1768:223. Type locality: "in campis magi deserti ab Jaco fluvio verus Irtim"; restricted by Ognev (1935) as " USSR, N. Kazakhstan, steppes between Ural and Irtysh rivers, near Petropavlovsk" (in Honacki *et al*. 1982).

It has been suggested that *Canis eckloni* described by Przhevalski (1883) from Northern Tibet is a subspecies of the corsac (Ellerman and Morrison-Scott 1951). However, *Canis eckloni* is in fact a junior synonym for *Vulpes ferrilata* (Geptner *et al.* 1967). This confusion probably originated from earlier work by Przhevalski referring to the latter as "corsac".

Chromosome number: 2n=36, FN=72 (Aristov and Baryshnikov 2001).

Description

The corsac is typically vulpine in appearance. Males slightly bigger than females (Table 5.5.1), but sexual dimorphism not pronounced. Head greyish-ochre or brown, ears banded brown on front side, back of ears ochre-grey or reddish-brown. Breast, belly, and groin white or slightly yellowish. Front of fore legs light yellow, rusty-yellow on sides; hind legs similarly coloured, but paler. Summer fur short and scarce; winter fur dense, soft and silky, straw-

Table 5.5.1. Body measurements for the corsac.

	Northern Kazakhstan (Kadyrbaev and Sludskii 1981)	**Turkmenistan** (Scherbina 1995)
SK male	113mm (105–119) n=22	106mm (99–115) n=6
SK female	106mm (101–109) n=10	105mm (102–112) n=3
BL male	500mm (450–560) n=22	562mm (499–595) n=9
BL female	490mm (450–500) n=10	
T male	270mm (250–300) n=22	224mm (190–245) n=9
T female	265mm (250–300) n=10	
E male	68mm (60–75) n=22	(50–65)mm n=9
E female	68mm (60–75) n=10	
WT male	2.75kg (2.5–3.2) n=22	1.92kg (1.6–2.8) n=9
WT female	2.1kg (1.9–2.4) n=10	

greyish with ochre, brownish along the backbone line. Awn hairs tipped silver-white. Tail about half body length or slightly more, greyish-brown, covered with dense bushy hair, tipped in dark often even black. Skull similar to that of red fox (*Vulpes vulpes*), but smaller, shorter and wider, and with canine teeth more robust. The dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies There is marked geographical variation. The following subspecies are defined within the former USSR (Geptner *et al.* 1967):

— *V. c. corsac* (northern part of range to PredAltai steppe, not expanding further southward than the latitude of the northern end of Aral Sea)

— *V. c. turcmenica* (plains of Middle Asia and Kazakhstan, northern Afghanistan and north-eastern Iran). There is supposedly a wide area of overlap with *V. c. kalmykorum.*

— *V. c. scorodumovi* (Russia's Transbaikalye, Mongolia and China)

— *V. c. kalmykorum* (Volgo-Ural steppes and right side of Volga basin).

Similar species Red fox (*Vulpes vulpes*): almost twice as large; lips and front of lower jaw white, back of ears darkly brown or even black; legs with dark brown or black markings; tail-tip white.

Tibetan fox (*V. ferrilata*): slightly larger; usually with two dark stripes on both sides of neck; flanks greyish, contrasting with belly; tail-tip white.

Indian fox (*V. bengalensis*): back of ears light sandy-greyish; legs uniform colour, lacking any black markings; black tail-tip.

This species may also possibly be confused with Blanford's fox (*V. cana*) and Rüeppell's fox (*V. rueppellii*), although the latter two species share little of their range. The former is noticeably smaller, with a conspicuous dark marking under the eye, and tail exceeds body length by more than half (and has dark tip); the latter is rather similar to *V. bengalensis*, but with longer tail with white tip, back of broad ears and back of head light grey, and legs without black markings.

Distribution

Historical distribution The species range was much vaster during the Quaternary. During the early Pleistocene an ancestor species *V. praecorsac* inhabited the territory of Austria and Hungary. At the end of the Pleistocene the corsac spread from Switzerland to northern China. From the end of the Pleistocene–early Holocene, the range was reduced from the west due to climate change.

Current distribution Narrower than the historical range and includes two parts. The first covers the Middle Asian republics of Turkmenistan, Uzbekistan, Tajikistan and

Corsac, age and sex not noted. Duisburg Zoo, Germany, 1995.

Chris and Tilde Stuart

Figure 5.5.1. Current distribution of the corsac.

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Kazakhstan, as well as steppe and forest-steppe areas of Russia, including the southern region of Western Siberia. In Europe its range reaches the Samara Region, Tatarstan to the North and northern Caucasia to the South (Figure 5.5.1). The second, much smaller area lies in southern Transbaikalye representing the northern periphery of the Mongolian and Manchurian section of the species area. Outside Russia the species area includes the steppe part of north-eastern China, including Manchuria, Inner Mongolia, and the region between Argun and Big Khingan, the entire Mongolian republic except for its forested and mountain regions, Dgungaria, Kashgaria, Afghanistan (probably only northern) and north-eastern Iran. Southern limit of distribution is unknown, but possibly it reaches to the mountain ridges separating the Tibet Highland from the North. Thus, the two ranges (western and eastern) are connected by a relatively narrow neck in the Dgungar Gate and Zaisan Basin region. In recent years a westward area expansion has been recorded, particularly into the Voronezh region following active recovery of baibak (*Marmota bobac*) populations. Occasionally, the species is recorded from the Ukrainian steppe (as far as Pavlodar to the West), eastern Transcaucasia (Azerbaijan) and, probably, western Kyrgyzstan.

Range countries Afghanistan, Azerbaijan?, China, Iran, Kazakhstan, Kyrgyzstan?, Mongolia, Russia, Tajikistan, Turkmenistan, Ukraine?, Uzbekistan (Ognev 1931, Geptner *et al.* 1967, Scherbina 1995).

Relative abundance

In Russia the corsac is rare in most regions, but common in West Siberia and Transbaikalie. It sometimes occurs in northern parts of West Siberia's forested steppes, but in low numbers. The species is common everywhere between the Volga and Ural rivers. In Turkmenistan, Kazakhstan, Mongolia and northern China, the corsac is common or abundant, although in Tajikistan and Uzbekistan the species is usually rare. Population status in Afghanistan and Iran is unknown.

Corsac populations fluctuate significantly. Population decreases are dramatic, caused by catastrophic climatic events, and numbers can drop tenfold within the space of a single year. On the other hand, in favourable years numbers can increase by the same margin and more within a three to four year period. Dramatic population changes were reported during the last century in PredKavkazie, between Kuma and Terek rivers and in Kuma-Manich Channel region. A drastic population decline was reported at the beginning of the last century (Dinnik 1914). Numbers had recovered by 1924 to 1925; one hunter during that time could take up to 15–30 corsacs in one season (Ognev 1931). By 1931 numbers decreased again with a subsequent increase in 1951 (Verezhagin 1959). In the Ural region during particular years up to 5,500 animals were taken by trappers, and up to 1,700 in the Gurievskaya region. To the south, in Mangishlak and Ustyurt, the corsac is widespread and in some years abundant.

Estimated populations/relative abundance and population trends: The following population densities have been recorded: in Kalmykia (Russian Federation), 16–29 per 10km^2 (Blyznuk 1979); in Omsk region, 0.8–6.8 per 10km^2 during the summer period (Sidorov and Poleschuk 2002); in Kazakhstan, during population peaks, four to six animals per 10km^2 during the autumn-winter season (Chirkova 1952); in Eastern Transbaikalia, 1.0–6.8 per 10km^2, in Tuva, 3.5 per 10km^2, and in south-east Altai, 2.7 per 10km^2 (Sidorov and Botvinkin 1987).

In Turkmenistan the average population density varies in different parts of the country. In north-western and western Turkmenistan average population density is 0.4 per 10km^2. In the south-west corsac density is higher, and during years with high numbers of prey, such as Libyan jird (*Meriones libycus*) and great gerbil (*Rhombomys opimus*), can reach 23 per 10km^2. In the south-west (Karabil region) density is 8.4 per 10km^2 on average. In Badkhiz Nature Reserve, corsac population density during favourable years can reach very high levels, and as many as nine breeding dens per 15km^2 have been recorded (Sludskyi and Lazarev 1966).

Corsac population trends were studied in south-eastern Transbaikalia from 1952 to 1983 (Sidorov and Botvinkin 1987), showing populations peaking in eight general and two local populations. Peaks were repeated within a period of three to six years. Corsac fluctuations are correlated with population trends of the main prey species (Daurian pikas (*Ochotona daurica*), narrow-headed vole (*Microtus gregalis*), and Brandt's vole (*M. branti*)). Current information on population trends in different countries is not available due to lack of centralised information on pelt harvest and research projects. However, in Orenburg (Russia) it has been estimated that there are approximately 1,500 foxes, with numbers declining (Rudi 1996). Similarly, populations are thought to be declining in Turkmenistan (Scherbina 1995) and Uzbekistan (Ishunin 1987).

During years with low prey abundance, wide migrations and animal dispersion occur. Migrations are typical for corsac populations in Western Siberia, Kazakhstan, Transbaikalia and, probably, Mongolia and China, but are not reported in Middle-Asian countries (Turkmenistan, Uzbekistan, Tajikistan, Afghanistan and Iran).

Habitat

The corsac typically inhabits steppes, semi-deserts and deserts, avoiding mountains, forested areas and dense bush. In the western part of the range they occur in low-grass steppe, avoiding dense and tall grass steppes. In Kaspyi Sea region the steppes and tarragon-cereal semi-deserts are favoured. It also occurs in fixed-sand habitats (Nogaiskaya Steppe). In Volgo-Ural watershed the corsac inhabits most usual habitats, but prefers semi-deserts. To the east of the Ural Mountains, the species inhabits steppes and in favourable years occurs even in forested steppes. In Kazakhstan typical habitats are low grass steppes and semi-deserts, often inhabiting low hills, but avoiding low mountains. In Middle-Asia it inhabits semi-deserts and ephemeral-deserts, avoiding drifting sands. One limiting factor is snow height in winter, and this species avoids areas where the depth of snow exceeds 150mm, preferring areas where the snow is either shallower or highly compressed.

Corsacs appear to depend on distribution of ground squirrels and marmots for food and shelter (the burrows being enlarged and used for refuge).

Food and foraging behaviour

Food In general, the corsac is opportunistic in its foraging habits. Prey species vary widely over the species' range, with the bulk of its diet comprising the most common small- and medium-sized rodent species in the area. Rodents and lagomorphs make up the bulk of the diet, although birds, reptiles (lizards, snakes and young tortoises) and insects are also commonly preyed upon, especially in summer. Occasionally, corsacs eat small amounts of vegetation. When the main prey species becomes uncommon, such as during winters and periods of low prey abundance, the remains of wolf kills and carcasses of wild and domestic ungulates become a major source of food for corsacs. They will also make use of human garbage.

Typical prey in Western Siberia includes narrow-headed vole (*Microtus gregalis*) and steppe lemming (*Lagurus lagurus*), and, more rarely, red-cheeked souslik (*Cittellus erythrogenys*), water vole (*Arvicola terrestris*), great jerboa (*Allactaga major*) and skylarks (Alaudidae). During winter, small rodents, Arctic hare (*Lepus timidus*), ptarmigans (*Perdix perdix*) and snow buntings (*Pleptrophenax nivalis*) are common prey (Geptner *et al*. 1967; Sidorov and Botvinkin 1987). Some vegetable food was also found in stomachs of animals, which were captured during the winter season with abnormally high snow level (Sidorov and Polyschuk 2002).

In the forest-steppe part of Kazakhstan, the diet consists primarily of steppe lemmings and large-toothed souslik (*Ñittelus fulvus*) (Geptner *et al*. 1967). In deserts of northern Kazakhstan the proportion of prey species in corsac's diet varies, with jerboas (Dipodidae), sousliks (*Cittelus pygmaeus, C. maximus*) and rock conies (*Ochotona* spp.) dominating (Sidorov and Botvinkin 1987). On the Ustyurt Plateau and in Turkmenistan the main prey are gerbils (*Meriones* spp., *Rhombomys opimus*), while in TransBaikalie and Mongolia main species are Brandt's vole, tarbagan marmot (*Marmota sibirica*) and Daurian pika. Birds, Tolai hare (*Lepus tolai*) and long-tailed souslik (*Citellus undulatus*) are uncommon prey (Geptner *et al*. 1967).

Foraging behaviour Corsacs are active during twilight and at night. Hunting starts in the evening and continues through the first part of the night, with a second peak of activity before dawn. Sometimes they are also active during daytime, especially the young. They are solitary foragers, although near carrion or remains of wolf kills up to several corsacs may gather together (and sometimes with red foxes). Corsacs hunt by stalking prey and employing sudden short-distance attacks. Lunges on prey are very quick, faster than red fox. Corsacs find ground-nesting birds and other small prey by sound and smell. Despite their small size they can kill prey up to the size of young marmots, hares, ducks, pheasant and geese.

Damage to livestock or game Corsacs do not cause any significant damage to livestock or game.

Adaptations

Corsacs have the ability to forego water and food for extended periods of time. Although in desert regions they are often seen near springs, water pools and wells, they seem to be attracted there not by thirst, but by the abundance of rodents. In captivity corsacs do not drink water when on a protein diet, and corsacs reportedly can live without food for 7–15 days (Kadyrbaev and Sludskii 1981).

Corsacs are well adapted to a hot and dry climate. However, according to Kalabukhov (1950), corsacs have imperfect thermoregulation, due to some of their breathing features, whereas the insulating quality of their fur is close to that of the Arctic fox. Corsacs are not resistant to strong cold, and during periods of strong frost and blizzards they do not come out from the den at all for 2–3 days. One behavioural adaptation against cold is the gathering of several animals (up to seven) in one wintering den (Sludskyi and Lazarev 1966).

Corsacs are not well adapted for walking on snow. Despite their small body-weight, their specific weight-pressure is relatively high – 68–80g/cm² in corsacs from Betpak-Dala – and their legs relatively short. By comparison, in red foxes from snowy regions this parameter is 27–30g/cm² (Geptner *et al.* 1967).

Social behaviour

The species' social organisation has not been studied in detail, but some general characteristics are known from studies of the species biology in the wild. The basic social unit is the breeding pair. Monogamous pairs may persist during the entire life of the partners. Even in captivity, a male corsac that was held in a cage with two females in the Moscow Zoo, copulated with only one of them, even though the second female also entered into oestrus.

Pups disperse by the end of summer. However, dispersing young do not go far from their natal range (Scherbina 1995), and some are likely to return to stay over the autumn-winter season. During winters several corsacs often are found in one den, indicating a relatively high degree of sociality. Polygynic families are probable under favourable feeding conditions; Sidorov and Botvinkin (1987) noted finding two litters and two females in one den, thus confirming occurrence of polygyny.

Home range sizes vary widely depending on region and density of foxes. In optimal habitats during favourable years of high prey abundance the home range of a family pair can be as small as 1km² (Scherbina 1995). In the Celenograd area the size of breeding territories varies from1.9–3.7km² (Tchirkova 1952). In contrast, in low quality habitats with low food abundance, home ranges are significantly larger – in PriKaspyi Lowland, for instance, some 35–40km² (Geptner *et al.* 1967). There is no evidence of territoriality during winter.

Scent marking is most important for maintaining territories, and marking with urine and faeces is most frequent near maternity dens (Geptner *et al.* 1967). Barking is the corsacs most common vocalisation and has many different tonal variations (as detected by the human ear) and is produced in a variety of situations, such as courtship, territorial demonstrations and alarm. Barking sounds are higher than the red fox's and have a certain similarity to a cat's mew. An alarm call sounds like "Vyak". Close distance vocalisations are characterised by high-tone rhythmic sounds, peeping, chirping, and yelping.

Reproduction and denning behaviour

Across the range of the species, mating takes place from January until the beginning of March, although the actual period in any particular region is shorter. For example, in Kazakhstan and Turkmenistan, mating takes place between January and February. Gestation has been reported as 52–56 days (Geptner *et al.* 1967) and 60 days (Kadyrbaev and Sludskii 1981). The earliest birth time is mid-March, with most births occurring in April. Average litter size in Kalmikiya, Kazakhstan was 5.5 (range=2–10), similar to that recorded in Turkmenistan. Pups emerge from the dens from mid-May, earlier in southern parts of the species range. There is only one litter per year (Ognev 1931).

Newborn pups weigh 60–65g and measure 130–140mm in length (data from Moscow Zoo; A. Petrova pers. comm.). Pups are born blind with the auditory meatus closed. Eyes open on day 14–16. At the age of 28 days pups start eating meat. The male takes active part in parental care by feeding the young, and in favourable years helpers may join the parental pair to assist with feeding and guarding the young. Often pups play at the den during the morning. They grow rapidly, reaching the size of adults at four to five months. In captivity pups become sexually mature in nine months (Kadyrbaev and Sludskii 1981).

Corsacs develop shelters by modifying those of rodents that construct big, well-developed dens such as marmots, sousliks and great gerbils. Dens are constructed on gentle slopes or on plains. Maternity dens usually have two entrances. Near the maternity den there is a temporary shelter – dens with one entrance and a shallow corridor beneath the surface. The opening of the corridor is about 200mm in diameter. The length of the maternity den corridor varies from 1,400–4,500mm, whereas for temporary dens the corridor is from 500–1,200mm in length. The main chamber is 300 x 400mm in size, 550–1,150mm deep under ground, used for nesting but without any nesting material (Kadyrbaev and Sludskii 1981). In some areas the structure of maternity dens is more complicated. For instance, in Turkmenistan corsac dens with as many as 23 entrances have been found. Such big dens are always constructed on a great gerbil colony (Scherbina 1995). In Turkmenistan, where the climate is warmer, corsacs do not use dens during winter, whereas in colder Kazakhstan, TransBaikalie and Western Siberia, the use of dens during winter is common.

Competition

The main competitors for food within the former Soviet Union and Mongolia include red fox, steppe polecat (*Mustella eversmanii*) and grey wolf (*Canis lupus*), and, in desert regions, also steppe cat (*Felis libyca*), manul cat

(*Otocolobus manul*) and marbled polecat (*Vormella peregusna*) (Geptner *et al*. 1967). The chief competitors are red fox, which generally are better adapted and more successful hunters. In addition, red foxes compete with corsacs for dens – the stronger red fox can displace corsacs from their maternity dens and even kill them; red foxes may dig out the maternity dens of the corsac and kill litters (Geptner *et al*. 1967). When food is plentiful, corsacs and red foxes live next to each other in the same habitats and sometimes are seen feeding together on carrion. Several raptors also compete with corsacs, such as several buzzard species (*Buteo lagopus, B. rufinus, B. hemilasius*), pallid and hen harriers (*Circus macrourus, C. cyaneus*), tawny and golden eagles (*Aquilla rapax, A. chrisaetus*) and Saker falcon (*Falco cherrug*).

Mortality and pathogens

Natural sources of mortality The major mortality factor for the corsac probably is death from starvation during winter, caused by lack of availability of rodents due to deep snow-cover or decline of rodent populations. Strong frost and long periods of winter blizzards can cause significant losses in corsac populations. Predation from grey wolves during winter is also important, and wolves sometimes kill corsacs during the summer and dig out corsac dens. However, wolves play an important role for corsacs, as remains of wolf kills are an important food source for corsacs during winter. This role of wolves as food provider is more pronounced in areas of Kalmikiya, Kazakhstan, inhabited by saiga (*Saiga tatarica*). Stray and feral dogs also kill corsacs. Corsac remains were found among prey remains of tawny and golden eagles (Sidorov and Botvinkin 1987). In Semipalatinsk remains of three corsacs eaten by eagle owl (*Bubo bubo*) were reported (Geptner *et al*. 1967).

Persecution Corsacs do not fear humans, and often allow humans to approach within about 10m, before running away. They do not escape in dens from humans, unlike their reaction to wolves, dogs or eagles. When dug out of a den, corsacs sham death by lying motionless with closed eyes (Geptner *et al*. 1967).

Hunting and trapping for fur The corsac is a valuable fur-bearer species and has been trapped for a long time. For example, the following number of pelts were brought to a fur fair in Irkutsk: 1881 – 5,000; 1884 – 30,000; 1885 – 25,000; 1886 – 15,000; 1887 – 5,000; 1888 – 15,000; 1889 – 45,000; 1890 – 6,000 (Sludskyi and Lazarev 1966). In Turkmenistan, from 1924 to 1989, 103,500 corsac pelts were taken, which caused a significant decrease in corsac numbers during the same period. From 1924 to 1929, more than 4,000 animals were taken every year; from 1930 to 1939, the harvest was close to 3,000; from 1940 to 1949, the take was close to 1,000; from 1950 to 1959, approximately 1,500; from 1960 to 1969, slightly more than 1,000; from 1970 to 1979, less than 500; and from 1980 to 1989 close to 500 (Scherbina 1995). In Uzbekistan, 1,905 pelts were taken in 1923. From 1935 to 1937, the take was 732 to 1,511 pelts every year; from 1946 to 1949 between 535 and 1,359 pelts; and from 1959 to 1967, between 1,508 and 2,739 pelts. In 1980 the harvest had fallen to only 65–100 pelts per year (Ischunin 1987). In Mongolia at the beginning of the 20th century about 15,000 corsac pelts were taken to Kalgan. In this country about 20% of pelts are used in local markets. This trend is also common for regions of Russia and countries of the former Soviet Union – a certain proportion of the total take is left for local sales. This trend became more pronounced after the break-up of the Soviet Union. Current take is unknown, although Sidorov and Poleschuk (2002) indicated that at the end of 1980s and early 1990s more than 98% of corsac skins were traded in local markets and unregistered by government officers.

Road kills Road kills are not a significant mortality factor for corsacs.

Pathogens and parasites Corsacs are susceptible to rabies (Geptner *et al*. 1967). The following helminths have been found in corsacs: *Mesocestoides lineatus, Macracanthorhynnchus catulinus* (Agapova and Sapozhenkov 1961) and *Isopoda buriatica*. In Turkmenistan several flea species were found on corsacs, among them *Pulex irritans* and *Chaetopsylla korobkovi* (Scherbina 1995). In south-eastern TransBaikalie, during a period of several years, more than 6,400 fleas were found on 195 corsacs, and representing the following species: *Pulex irritans* 70%, *Oropsylla silantiewi* 4%, *Chaetopsylla homoeus* 5%, *Ctenophyllus hirticus* 12%, and *Amphalius runatus* 3% (Geptner *et al*. 1967). The number of fleas on a fox varies over months, increasing in summer and peaking in early autumn (Brom *et al*. 1948, in Geptner *et al*. 1967)

Longevity Maximum recorded longevity is nine years (Sidorov and Botvinkin 1987).

Historical perspective

The corsac harvest is known in Kazakhstan since the Bronze Age. Kazakh and Kirgiz people in the 13th century used corsac pelts almost as a means of purchasing goods. Corsacs are traditional game for hunting with aboriginal greyhounds (tazi), and with Saker falcons and golden eagle.

Conservation status

Threats Development in Kazakhstan in the mid-1850s caused a significant reduction of corsac numbers in previously undisturbed habitats. In the 20th century several catastrophic population declines were recorded. During such crashes hunting on corsacs in the former Soviet Union was banned. For example, hunting of corsacs was stopped within the entire Kazakhstan territory from 1928 to 1938. Current population status, and the nature of major threats, is unknown in most regions. The western part of the range populations are recovering and their range expanding. In Kalmikiya large desert areas are changing into grass steppes, less suitable for corsacs. In Middle Asia and Kazakhstan a dramatic decrease of livestock during the last decade influenced many ecosystems and wildlife populations. However, the exact influence of this process on corsac populations remains unknown.

Commercial use Corsac pelts have been intensively traded. In general, over much of Russia during the 19th century, as many as 40,000–50,000 corsac pelts were traded in some years. For the time being, corsac pelts are not as highly appreciated as red fox pelts, and corsacs are usually trapped only incidentally.

Occurrence in protected areas Corsacs are protected in the following strict nature reserves (the highest protection status for the territory) (Z) and in national parks (NP):

— *China*: Chernyi Irtish (Z), Ksilingolskyi (Z), Bogdedskyi (Z), Dalainurskyi (Z);
— *Russia*: Chernie Zemli Kalmikyi (Black Soils of Kalmik) (Z), Rostovskyi (Z), Orenburgskyi (Z), Altaiskyi (Z), Ubsunurskaya Kotlovina (Z), Daurskyi (Z);
— *Kazakhstan*: Alma-Atinskyi (Z), Kurgaldzhyiskyi (Z), Naurzumskyi (Z), Barsa-Kelmes (Z), Bayanoulskyi (NP);
— *Turkmenistan*: Krasnovodskyi (Z), Repetekskyi (Z), Syunt-Khasardagskyi (Z), Kaplankirskyi (Z), Badkhiz (Z);
— *Uzbekistan*: Arnasaiskyi (Z), Karakulskyi (Z), Kizilkumskyi (Z), Nuratinskyi (Z), Chatkalskyi (Z), Uzbekskyi (NP);
— *Tadzhikistan*: Tigrovaya Balka (Z), Dashti-Djumskyi (Z);
— *Mongolia*: Oton-Tengerekskyi (Z), Nemgerekskyi (Z), Great Goby Biosphere Reserve (Z), Malyi Gobyiskyi (Z), Malyi Gobyiskyi (Z), Eastern Mongolian Mongol-Daurskyi (Z), Ubsu-Nur (Z), Khorgo (NP), Gurvan-Saikhanskyi (NP).

Protection status CITES – not listed.
Listed in some regional Red books in Russia: Bashkir (Volga tribute) and Buryat (Transbaikalia region) with category III status (species with declining populations).

Current legal protection Hunting of corsacs is regulated by special national legislation, in which the species is considered a fur-bearer species (Russia, Kazakhstan, Turkmenistan, Uzbekistan, Mongolia). Trapping/hunting is allowed only from November through March in Russia, Kazakhstan, and Turkmenistan. Certain methods of hunting are prohibited, such as digging or smoking animals out of dens, den flooding, and poisoning.

Conservation measures taken No special conservation programmes have been carried out. Outside of protected areas, the corsac has the status of game species.

Occurrence in captivity

Corsacs breed well in captivity, and there are some 29 animals currently listed in ISIS. In Moscow Zoo during 1960s one pair of corsacs produced six litters during the time that they remained together. Corsacs are easily habituated to humans.

Current or planned research projects

None known.

Gaps in knowledge

There are several aspects of this species' biology that require investigation, including social organisation and behaviour, population structure, current distribution and population status in different regions, current levels of trapping/hunting impact, and other threats to the species.

Core literature

Chirkova 1952; Sludskyi and Lazarev 1966; Geptner *et al.* 1967; Kadyrbaev and Sludskii 1981; Ognev 1931, 1935; Scherbina 1995; Sidorov and Botvinkin 1987; Sidorov and Poleschuk 2002.

Reviewer: Nikolay A. Poyarkov. **Editors:** Claudio Sillero-Zubiri, Deborah Randall, Michael Hoffmann.

5.6 Tibetan fox
Vulpes ferrilata (Hodgson, 1842)
Least Concern (2004)

G.B. Schaller and J.R Ginsberg

Other names

English: Tibetan sand fox, sand fox; **Chinese:** shahuli(li), caohu(li); **French:** renard sable du Thibet; **German:** Tibetfuchs; **Tibetan:** wa, wamo.

Taxonomy

Vulpes ferrilatus Hodgson, 1842. J. Asiatiac Soc. Bengal 11:278. Type locality: near Lhasa, Tibet.

Chromosome number 2n = 36 (Xu and Gao 1986).

Description

The Tibetan fox is small and seemingly compact with a soft, dense coat, a conspicuously narrow muzzle and a bushy tail (Table 5.6.1). It is tan to rufous-coloured on the

Table 5.6.1. Body measurements for the Tibetan fox.

	China (Feng *et al*. 1986; Gao *et al*. 1987).	**South-central Tibet** (G. Schaller, unpubl.).
HB male	587mm (560–650) n=7	515mm n=1
HB female	554mm (490–610) n=8	
T male	279mm (260–290) n=7	270mm n=1
T female	239mm (220–260) n=8	
HF male	131mm (125–140) n=7	140mm n=1
HF female	120mm (110–124) n=8	
E male	57mm (52–61) n=7	60mm n=7
E female	60mm (55–63) n=8	
WT male	4.1kg (3.8–4.6) n=7	3.25kg n=1
WT female	3.5kg (3.0–4.1) n=5	

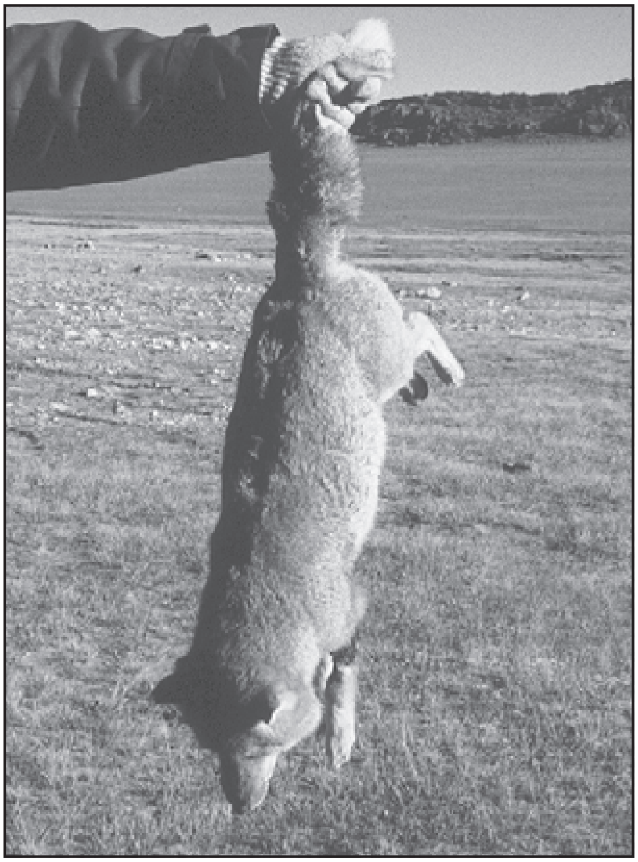
muzzle, crown, neck, back, and lower legs. The cheeks, sides, upper legs and rump are grey; the tail is also grey except for a white tip. The back of the relatively short ears is tan to greyish-tan and the inside is white. The undersides are whitish to light grey.

Subspecies No subspecies have been described.

Similar species The corsac (*Vulpes corsac*) is similar in size, but has relatively longer legs and conspicuously large ears. Its pelage is reddish grey with white underparts.

Current distribution

Widespread in the steppes and semi-deserts of the Tibetan Plateau from the Ladakh area of India, east across China including parts of the Xinjiang, Gansu, Qinghai, and Sichuan provinces and all of the Tibet Autonomous Region. Also present in Nepal north of the Himalaya, known specifically from the Mustang area (Figure 5.6.1).



George Schaller

Dead Tibetan fox, age and sex unknown, held by hunter.

Range countries China, India, Nepal (Schaller 1998; Nowak 1999).

Relative abundance

In general, fox density appears to be low. Its abundance depends partly on prey availability and partly on human

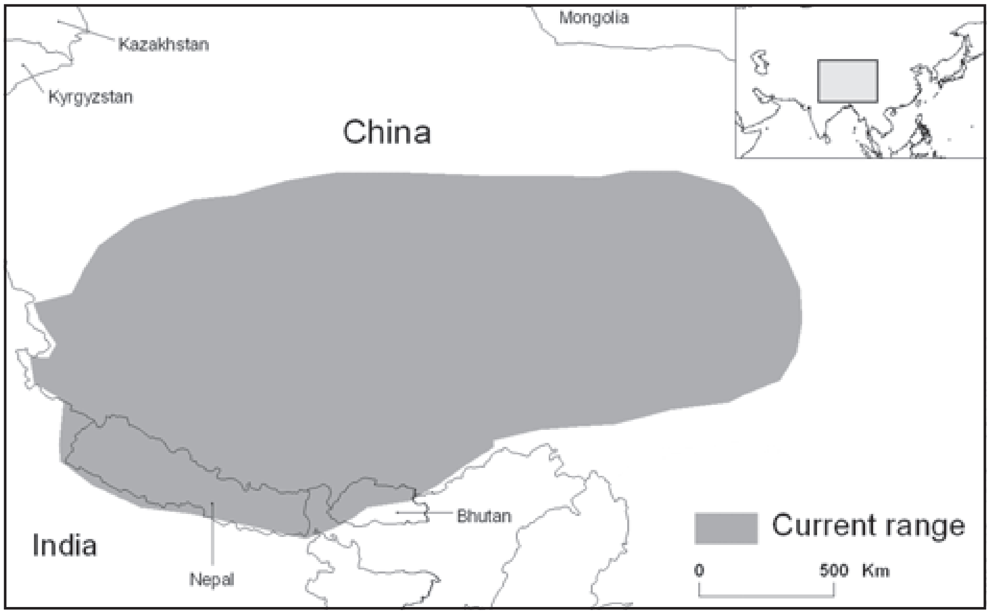


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Figure 5.6.1. Current distribution of the Tibetan fox.

hunting pressure. In north-west Tibet, in a remote region of desert steppe with little prey, only five foxes were seen in 1,848km of driving. In south-west Qinghai in a benign environment with much prey, 15 foxes were tallied in 367km (Schaller 1998). In Serxu county, north-west Sichuan Province, an area with abundant with black lipped pika (*Ochotona curzoniae*) eight Tibetan foxes were sighted along 11km country road during a night count in 2001 (Anon., 2000b), and 27 sightings (at least 12 individuals) were recorded along line transects in the same area in August 2003 (Wang Xiaoming and Wang Zhenghuan, pers. obs.).

Estimated populations/relative abundance and population trends A survey of 43 counties of Tibet's autonomous region estimated around 37,000 Tibetan foxes (Piao 1989).

Habitat

The species is found in upland plains and hills from about 2,500–5,200m a.s.l. Much of its habitat consists of alpine meadow, alpine steppe, and desert steppe, all treeless vegetation types. The climate is harsh with temperatures reaching 30°C in summer and dropping to -40°C in winter. Most of the fox's range lies in semi-arid to arid environments with average annual precipitation of 100–500mm, most of it falling in summer.

Food and foraging behaviour

Food The principal diet of the Tibetan fox consists of pikas (*Ochotona* spp.) and rodents. An analysis of 113 droppings from north-west Tibet revealed a content of 95% pika (*O. curzoniae*) and small rodents (*Pitymus*, *Alticola*, *Cricetelus*). Another 2.7% was Tibetan antelope (*Pantholops hodgsoni*) probably scavenged, and the remainder insects, feathers, and vegetation, including *Ephedra* berries (Schaller 1998). Feng *et al.* (1986) also list Tibetan woolly hare (*Lepus oiostolus*) and a lizard species (*Phrynocephalus* sp.) as prey items, and Zheng (1985) further noted the remains of marmot (*Marmota himalayana*), musk deer (*Moschus* sp.), blue sheep (*Pseudois nayaur*) and livestock in 58 droppings collected in eastern Qinghai Province.

Foraging behaviour Since pikas are diurnal, foxes often hunt in daytime, trotting through or stalking in pika colonies. Of 90 foxes observed, all but six pairs were solitary, suggesting that they mainly hunt alone (G. Schaller pers. obs.).

Damage to livestock or game No quantitative data are available other than occurrence of livestock in diet.

Adaptations

Little is known about this generic small fox.

Social behaviour

Tibetan foxes have never been studied and all aspects of their reproductive and social behaviour remain unknown. As noted, they are usually seen alone or in pairs consisting of a male and female, although one family was observed in 2001, comprised by three adults and two juveniles (Wu Wei *et al.* 2002). Burrows are found at the base of boulders, along old beach lines, low on slopes, and other such sites. There may be one to four entrances to a den, the entrance about 25–35cm in diameter (Schaller 1998).

Reproduction and denning behaviour

Nowak (1999) suggests mating occurs in February with 2–5 young born in May, but the source of these data is not given. Wang Zhenghuan *et al.* (2003a) studied the main habitat factors associated to the location of summer dens in 2001 (n=54 den holes); these were, in order of importance: water distance, slope degree, position along the slope, small mammal den numbers, and vegetation type. Most dens were located in grasslands (96.3%) with moderate slope (68.52% between 5–25°).

Competition

The geographic ranges of red fox (*Vulpes vulpes*) and Tibetan fox overlap, though the former favours mountains, including forested ones, and the latter open steppes. The two species have a similar diet. Indeed, pikas, the principal prey in their region of overlap, are also a staple of brown bear (*Ursus arctos*), polecat (*Mustela eversmannii*), manul (*Felis manul*) and various raptors, as well as on occasion the grey wolf (*Canis lupus*).

Mortality and pathogens

Natural sources of mortality Unknown.

Pathogens The infection rate of *Echinococcus* spp. in Tibetan foxes in Serxu county Sichuan province is high, estimated by Qiu *et al.* (1995) at 59.1%. Recent evidence from western Sichuan, China, indicates that Tibetan foxes are definitive hosts of Alveolar Hydatid Disease (AHD), a rare but serious zoonosis caused by *Echinococcus* spp. (Wang *et al.* 2003b).

Hunting and trapping for fur The Tibetan sand fox is hunted for its pelt, which is made into hats, but red fox is preferred as such adornment. Feng *et al.* (1986) reported of high hunting pressures in the whole Tibetan plateau since the 1960s and the Tibetan fox population in Serxu is under heavy human hunting pressure (Wang Zhenghuan *et al.,* 2003a). Over 300 foxes have been killed per year since the 1990s in Shiqu County, Sichuan Province, China (Wang Xiaoming, unpubl.). Hunting methods include shooting and traps laid at the entrance of den holes, the latter been the main method as guns in the area have been restricted in the recent years.

Road kills No data available.

Longevity Unknown.

Historical perspective

The fox is used to make hats by local people. No explicit conservation measures undertaken to date.

Conservation status

Threats Unknown, but the species is not under threat.

Commercial use No data available.

Occurrence in protected areas Present in the Arjin Shan (45,000km²), Xianza (40,000km²), Chang Tang (*c.*334,000km²), and Hoh Xil (*c.*45,000km²). Likely to occur in other protected areas throughout the species' range, but no reliable information available.

Protection status CITES – not listed.

Current legal protection Species legally protected in several large Chinese reserves (see above), but actual protection remains minimal. The species lacks special protection outside reserves.

Conservation measures taken No information available, although it is unlikely that any proactive measures have been taken by any of the range countries.

Specific actions being undertaken or completed None.

Occurrence in captivity

No records in Western zoos; occurrence in Chinese and Russian zoos unknown.

Current or planned research projects

Recently Wang Xiaoming (East China Normal University, Shanghai, China) began a study of the species in Sichuan.

Gaps of knowledge All aspects of the fox's natural history need study.

Core literature

Piao 1989; Schaller 1998; Wang Zhenghuan *et al*. 2003a; Zheng 1985.

Reviewers: Andrew T. Smith, Wang Xiaoming. **Editor:** Claudio Sillero-Zubiri.

Chapter 6

Sub-Saharan Africa (Ethiopian)

6.1 Side-striped jackal
Canis adustus Sundevall, 1847
Least Concern (2004)

R.P.D. Atkinson and A.J. Loveridge

Other names

Afrikaans: witwasjakkals; **French:** le chacal à flancs rayés; **German:** streifenschakal; **Indigenous names:** Amharic: Balegone Mesmer Kebero (Ethiopia); Karamojong: Oloo (Uganda); Kikinga: Ngwe (Tanzania); Kinyakyusa: Akambwe, Imbira (Tanzania); Kinyiha: Habila (Tanzania); Kiswahili: Bweha, Bweha Miraba (East Africa); Luganda: Akabowa, Ekihe (Uganda); Lugbara: Bowa (Uganda); Lwo: Too (Sudan); Madi: Uba (Uganda); Ndebele: kanka (South Africa, Zimbabwe); Runyankole: Emuha (Uganda); Runyoro: Eboa (Uganda); Sebei: Bleyit (Uganda); Shona: Gava (Zimbabwe, South Africa).

Taxonomy

Canis adustus Sundevall, 1847. Ofv. K. Svenska Vet.-Akad. Forhandl. Stockholm 1846, 3:121 [1847]. Type locality: "Caffraria Interiore"; fixed by Sclater (1900) as "Magaliesberg" [South Africa].

Description

Medium-sized canid (Table 6.1.1), overall grey to buff-grey in colour, with a white side stripe blazed on the flanks, and a diagnostic white tip to the tail. Head is grey-buffy, ears dark buffy. The back is grey, darker than the underside, and the flanks are marked by the indistinct white stripes running from elbow to hip with black lower margins. The boldness of markings, in particular the side

Table 6.1.1. Body measurements for the side-striped jackal from Zimbabwe (Smithers 1983)

TL male	1,082mm (960–1,165) n=50
TL female	1,075mm (1,000–1,170) n=50
T male	361mm (305–390) n=50
T female	354mm (310–410) n=50
HF male	172mm (160–192) n =50
HF female	168mm (153–178) n=50
E male	88mm (80–97) n=50
E female	86mm (80–95) n=50
SH male	448mm (420–490) n=9
SH female	437mm (420–460) n=6
WT male	9.4kg (7.3–12.0) n=50
WT female	8.3kg (7.3–10.0) n=50


Chris and Tilde Stuart

Side-striped jackal, age and sex unknown. Nairobi National Park, Kenya, 1993.

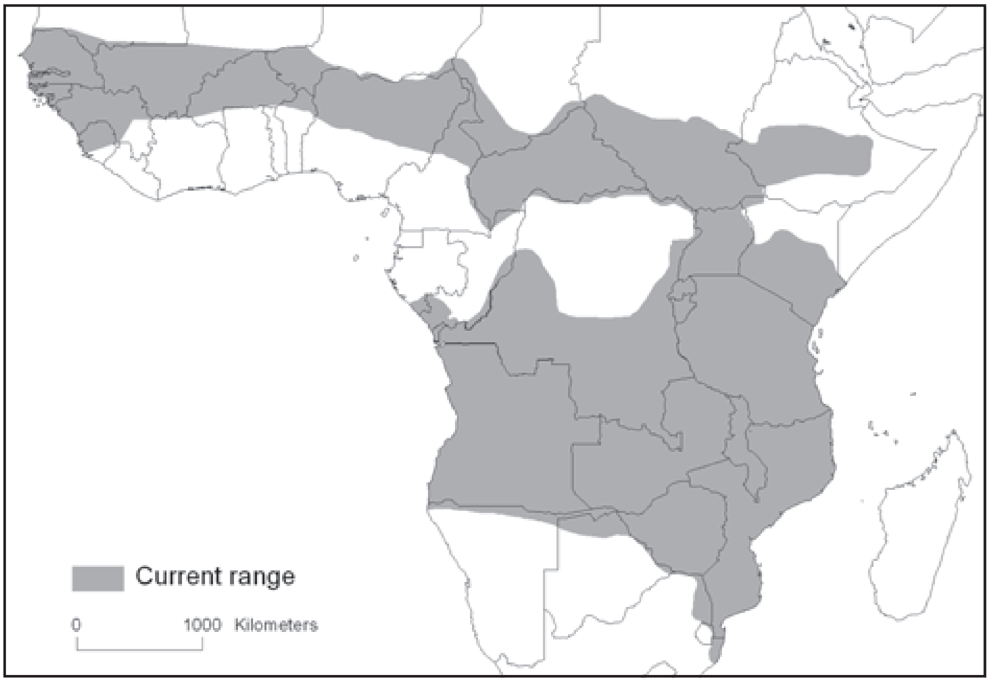

Figure 6.1.1. Current distribution of the side-striped jackal.

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stripes, varies greatly between individuals; those of juveniles are less well defined than those of adults. The legs are often tinged rufous, and the predominantly black tail nearly always bears the distinctive white tip, which Kingdon (1977) suggests may be a "badge" of the species' nocturnal status. The female has two pairs of inguinal teats.

Skull similar to that of the black-backed jackal (*Canis mesomelas*), but flatter, with a longer and narrower rostrum and having a distinct sagittal crest and zygomatic arches of lighter build. As a result of the elongation of the rostrum, the third upper premolar lies almost in line with the others and not at an angle as in the black-backed jackal (Skinner and Smithers 1990). The dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Allen (1939) listed seven subspecies from the continent, Coetzee (1977) five, and Kingdon (1997) recognises only three. Many authorities have pointed out that, as with the black-backed jackal, subspecies are hard to distinguish, and the differences may be a consequence of individual variation (Kingdon 1997).

Similar species Black-backed jackal (*C. mesomelas*): usually smaller size, characterised by a prominent dark saddle and black-tipped tail, as well as reddish flanks and limbs (see skull differences noted above); lacks white-tipped tail characteristic of the side-striped jackal.

Golden jackal (*C. aureus*): golden coat colour, and cream-coloured underparts; lacks white-tipped tail.

Current distribution

The side-striped jackal occurs in West, Central and southern Africa (excluding the southernmost part) (Figure 6.1.1), being replaced in the arid south-west and north-west of the continent by the black-backed jackal and in North Africa by the golden jackal. This species probably occurs extensively in the areas shown.

Range countries Angola, Botswana, Burkina Faso, Burundi, Cameroon, Central African Republic, Democratic Republic of Congo, Ethiopia, Gabon, Gambia, Ghana, Kenya, Malawi, Mali, Mozambique, Namibia, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, Somalia, South Africa, Sudan, Swaziland, Tanzania, Togo (probably in north), Uganda, Zambia, Zimbabwe (Ansell 1960; Rosevear 1974; Coetzee 1977; Kingdon 1977; Skinner and Smithers 1990; Grubb *et al.* 1998).

Relative abundance

Regional estimates of abundance are not available, but from work undertaken in two diverse habitats in Zimbabwe, it seems reasonable to assume the species is common and to estimate a total population in excess of three million. It is likely that the population is at least stable. This species' dietary flexibility and ability to co-exist with humans on the periphery of settlements and towns suggests that populations are only vulnerable in cases of extreme habitat modification or intense disease epidemics.

Estimated populations/relative abundance and population trends Jackal densities are estimated at around 1/km^2 in highveld commercial farmland in Zimbabwe (Rhodes *et al.* 1998), where rural density is probably highest. Density estimates from western Zimbabwe were between 0.5–0.8 individuals per km^2. In Senegal's Sahel jackal density was estimated at 0.07 per km^2 (Sillero-Zubiri *et al*. 1997).

Habitat

Side-striped jackals occupy a range of habitats, from game areas through farmland to towns within the broad-leaved savannah zones, including wooded habitats, bush, grassland, abandoned cultivation, marshes and montane habitats up to 2,700m (Kingdon 1977, 1997; Estes 1991). The species tends to avoid very open savannah (although Rowe-Rowe (1992) mentions they occur in open grassland in north-eastern KwaZulu-Natal), thickly wooded areas and arid zones (Stuart and Stuart 1988; Skinner and Smithers 1990; Kingdon 1997), but Kingdon (1997) states that it enters the equatorial forest belt in the wake of human settlement. Side-striped jackals frequently occur near rural dwellings and farm buildings (Skinner and Smithers 1990; Kingdon 1997), and penetrate peri-urban and urban areas (Liebenburg 1990; Skinner and Smithers 1990). In Botswana, Smithers (1971) recorded them where mean annual rainfall was 400–700mm, and many authors note that the species occurs in well-watered areas (e.g., Kingdon 1977; Skinner and Smithers 1990). Where side-striped jackals occur sympatrically with golden and black-backed jackals, they may avoid competition by ecological segregation (Fuller *et al.* 1989). In such areas of sympatry, side-striped jackals usually occupy areas of denser vegetation, while black-backed and golden jackals dominate in the more open areas (Loveridge 1999; Loveridge and Macdonald 2003).

Food and foraging behaviour

Food: The side-striped jackal is omnivorous, and their diet is very responsive to both seasonal and local variation in food availability. On commercial farmland in the Zimbabwe highveld, they eat mainly wild fruit (30%) and small- (<1kg) to medium-sized (>1kg) mammals (27% and 23%, respectively), with the remainder of their diet comprising birds, invertebrates, cattle cake, grass and carrion (Atkinson *et al.* 2002a). In wildlife areas of western Zimbabwe, side-striped jackals feed largely on invertebrates during the wet season and small mammals up to the size of a springhare (*Pedetes capensis*) during the dry months of the year. This species scavenges extensively from safari camp rubbish dumps and occasionally from large carnivore kills (although they are out-competed for this resource by black-backed jackals) (Loveridge and Macdonald 2002, 2003). In the Ngorongoro Crater, Estes (1991) recorded the species competing with black-backed jackals to catch Grant's gazelle (*Gazella granti*) fawns. Certain fruits may be taken almost exclusively when in season (Smithers and Wilson 1979; Atkinson *et al*. 2002a). The species appears less predatory than other jackals, although Estes (1991) states that they may be just as predatory as other jackals when prey is highly available.

Foraging behaviour The species forages solitarily, although in western Zimbabwe family groups have been observed feeding together on abundant resources, and Estes (1991) mentions that as many as 12 have been counted at kills or scavenging offal outside towns. Atkinson *et al*. (2002b) described jackals foraging opportunistically, exploiting food-rich habitats by random walks with fractal characteristics. They are primarily nocturnal, and, where persecuted, retain extreme flexibility in their foraging strategies (Atkinson 1997a). The species has an amazing ability to find food where none seems obvious to the human observer. A pair studied in the Zimbabwe highveld remained permanently in their territory after a bush fire had apparently destroyed all available food and somehow survived (Atkinson 1997b).

Damage to livestock or game There is very little evidence for extensive predation on domestic stock (Shortridge 1934; Roberts 1951; Smithers 1971; Coetzee 1977; Smithers and Wilson 1979; Rowe-Rowe 1992), or game larger than a baby antelope (Kingdon 1977, 1997; Estes 1991). They have never been recorded running anything down, and it may be pertinent that one was seen to enter a pen to eat ducks' mash, without attempting to harm the birds themselves (Kingdon 1977).

Adaptations

The species is unspecialised and well adapted anatomically and behaviourally for opportunism. The dentition appears well suited to an omnivorous diet (Skinner and Smithers 1990). The canines are long, curved and sharp-pointed, with a sharp ridge on their posterior surfaces. The upper outer incisors are canine-like, the carnassial shear well adapted for slicing, while the first and second upper molars are broad and developed for crushing. The side-striped jackal has relatively smaller carnassials than the more carnivorous black-backed jackal (Skinner and Smithers 1990), and is certainly less adapted for total carnivory than, for example, the African wild dog (*Lycaon pictus*), which has carnassials wholly adapted for shearing.

Social behaviour

Side-striped jackals occur solitarily, in pairs and in family groups of up to seven individuals (although see Foraging behaviour above). The basis of the family unit is the mated pair, which has been known to be stable over several years. In game areas of western Zimbabwe, home ranges varied seasonally from 0.2km^2 (hot dry season) to 1.2km^2 (cold dry season), whereas in highveld farmland, they were seasonally stable and in excess of 4.0km^2 (a third of the yearly total range). Sub-adults disperse from the natal territory, up to 12km in highveld farmland and 20km in game areas of western Zimbabwe. In highveld farmland, territories are configured to encompass sufficient patches of grassland, where resources are most available, and the structure of the habitat mosaic appears an important factor. Home ranges overlap by about 20% in highveld farmland and 33% in game areas. The residents use the core territory almost exclusively (Atkinson 1997a).

The species has a wide repertoire of sounds, including an explosive bark ("bwaa!"), growls, yaps, cackles, whines, screams, a croaking distress call, and a hooting howl (Estes 1991; Kingdon 1997). Calling occurs all year round, but is especially common between pair members during the mating period. Jackals from neighbouring territories sometimes answer each other. Captive pups have been heard calling at eight weeks, but may start earlier (Atkinson 1997a).

Reproduction and denning behaviour

Mating is most common during June and July in Zimbabwe, and the gestation period is about 60 days. Litters of 4–6 pups (Skinner and Smithers 1990) are born from August to November, coinciding with the onset of the rainy season. Pup mortality is thought to be high, and, since up to 12 foetuses have been found in pregnant females (Wolhuter, quoted in Shortridge 1934), some reabsorption may occur (Kingdon 1977).

Abandoned aardvark holes or excavated termitaria are common den sites (Skinner and Smithers 1990), with the den chamber occurring 0.75–1.0m below the surface and 2–3m from the entrance. The same pair may use such dens in consecutive years (Kingdon 1977). After weaning, both parents assist in rearing the young, returning at 2–3-hour intervals through the night to feed the pups on food that probably is regurgitated (Moehlman 1979). The pups are aggressive towards each other, as evidenced by the degree of wounding seen.

Year-old offspring remain in (or occasionally return to) the parental territory while additional offspring are raised. It appears likely that alloparental care of young occurs in this species, as has been observed in other jackal species (Moehlman 1989), and that side-striped jackals may be more social than has been previously suspected (Loveridge and Macdonald 2001).

Competition

Side-striped jackals compete for food with a wide variety of other animals, including other canids, mustelids, viverrids, felids, primates and humans. Many of these competitors are more specialised, and the side-striped jackal's survival is due to its own flexibility. An interesting case of inter-specific, intra-generic and intra-guild competition has been documented in wildlife areas of western Zimbabwe. Here black-backed and side-striped jackals occur in sympatry. Diet does not differ significantly between the species, but there are marked differences in habitat use. Black-backed jackals use open grassland, while side-stripes use woodland and scrub areas. Interestingly, and in an unusual and perhaps unique circumstance where a larger mammalian carnivore is displaced by a smaller one, black-backed jackals (7–9kg) aggressively displace the larger side-striped jackal (10–12kg) (Loveridge and Macdonald 2003).

Mortality and pathogens

Natural sources of mortality Leopards (*Panthera pardus*) are the only regular predator of the side-striped jackal, although they may fall prey to other large carnivores. As noted above, pup mortality is thought to be high.

Persecution In areas of high human population density, snaring may be the commonest cause of death in adult side-striped jackals, and may account for as much as a third of adult deaths in such areas (Atkinson 1997a).

Hunting and trapping for fur None known.

Road kills In towns and suburbs, they may be run over by vehicles (Kingdon 1977).

Pathogens and parasites They are vulnerable to rabies (Bingham and Foggin 1993), distemper, tick fever (Kingdon 1977) and mange, for all of which they are known or suspected reservoirs and vectors for domestic dog infection. Computer simulations (Rhodes *et al*. 1998) suggest rabies can only persist in side-striped jackal populations where the density is very high (such as around towns), and that most rabies occurrence in side-striped jackals is a result of spill-over from domestic dogs living on communally owned land. Side-striped jackals can contract the disease from domestic dogs, other jackal species and conspecifics and may spread it to domestic stock. Intra-specific infection is more likely during periods of the year when aggressive encounters are more common such as during the mating season, and after weaning when young disperse and may interact with other jackals (Loveridge and Macdonald 2001). The spread of rabies may be more restricted in stable populations than in those disturbed by culling regimes. Rabies in jackals is probably best controlled by oral vaccination (Rhodes *et al*. 1998).

Longevity As with the black-backed jackal, longevity has been given as 10–12 years (Haltenorth and Diller 1980), but is likely to be much shorter in the wild.

Historical perspective

Jackals of unspecified species play an important role in African folklore (for example, see Elliott 1939, 1947, 1957).

Conservation status

Threats Side-striped jackals are persecuted for their role in rabies transmission and their putative role as stock killers. It is unlikely that this persecution has an effect on the overall population, but indiscriminate culling through poisoning could affect local abundance. Side-striped jackals appear well capable of exploiting urban and suburban habitats, a factor which may help to ensure their persistent occurrence.

Commercial use There appears to be little or no trade in jackal products.

Occurrence in protected areas The side-striped jackal occurs in many protected areas across its range, including Niokola-Koba National Park (NP) in Senegal, Comoe NP in Ivory Coast, Queen Elizabeth NP in Uganda, Serengeti NP in Tanzania, Hwange NP in Zimbabwe, and Kruger NP in South Africa.

Protection status CITES – not listed.

Current legal protection Jackals have no legal protection outside protected areas.

Conservation measures taken None.

Occurrence in captivity

The species has been kept and bred in zoos, but it is not a common zoo exhibit and there are none currently listed on ISIS. Captive animals have been used in experiments testing rabies vaccine efficacy (Bingham *et al*. 1995).

Current or planned research projects

Although there are no current projects specifically focusing on this species, the side-striped jackal will likely become part of larger carnivore guild studies that are increasingly being conducted around the continent.

Gaps in knowledge

For many years the only major studies on the species' ecology remained those of Kingdon (1977) and Smithers and Wilson (1979), with additional observations by other authors. In the last five years, studies conducted in Zimbabwe by the authors have gone some way to increasing our understanding of this jackal species, particularly as concerns their role in rabies transmission. However, in comparison with the better-known black-backed jackal, the side-striped jackal has a much wider distribution, such that there are large parts of their range for which no information on populations or status is available.

Core literature

Atkinson 1997a,b ; Atkinson *et al*. 2002a,b; Kingdon 1977; Loveridge 1999; Loveridge. and Macdonald 2001, 2002, 2003; Moehlman 1979, 1989; Skinner and Smithers 1990.

Reviewers: Todd Fuller, Chris Stuart, Tilde Stuart. **Editors:** Michael Hoffmann, Claudio Sillero-Zubiri.

6.2 Golden jackal
Canis aureus Linnaeus, 1758
Least Concern (2004)

Y.V. Jhala and P.D. Moehlman

Other names

English: Asiatic Jackal, Common Jackal; **Albanian:** Cakalli; **Arabic:** Ibn Awee; **Croatian:** Èagalj; **Czech:** Šakal Obecný; **Danish and Swedish:** Sjakal; **Dutch:** Jakhals; **Estonian:** Šaakal; **Finnish:** Sakaali; **Faeroese:** Sjakalur; **French:** Chacal Doré, Chacal Commun; **German:** Goldschakal; **Greek:** Tóáêáë; **Hungarian:** Aranysakál; **Italian:** Sciacallo Dorato; **Latvian:** Zeltainais Ðakâlis; **Maltese:** Xakall; **Norwegian:** Gullsjakal; **Polish:** Szakal Zlocisty; **Portuguese:** Chacal-dourado; **Romanian:** Şakal; **Slovakian:** Šakal Obyèajný; **Slovenian:** Šakal; **Spanish:** Chacal; **Turkish:** Çakal; **Indigenous names:** Amharic: Tera Kebero (Ethiopia); Fulani: Sundu; Hausa: Dila; Hindi: Giddhad; Kanada: Nuree; Kiswahili: Bweha wa Mbugani, Bweha Dhahabu (Tanzania); Marathi (India): Kolha; Nepali (Nepal), Bengali, Gujarati and Kutchi (India): Shiyal; Singhelese: Nariya; Songhai: Nzongo; Tamil (India): Peria Naree; Wolof: Tili.

Taxonomy

Canis aureus Linnaeus, 1758. Syst. Nat., 10th edn. 1: 40 Type locality: "oriente"; restricted by Thomas (1911) to "Benna Mountains, Laristan, Southern Persia" [Iran, *c*. 27°30'N, 55°15'E].

Chromosome number: 2n=78 (Wurster-Hill and Benirschke 1968).

Description

Medium-sized canid, considered the most typical representative of the genus *Canis* (Clutton-Brock *et al*. 1976). There is approximately 12% difference in body weight between sexes (Moehlman and Hofer 1997) (Table 6.2.1). Basic coat colour is golden but varies from pale creamy yellow to a dark tawny hue on a seasonal basis. The pelage on the back is often a mixture of black, brown, and white hairs, such that they can appear to have a dark saddle similar to the black-backed jackal (*Canis*

Table 6.2.1. Body measurements for the golden jackal from Gujarat, India (Y. Jhala unpubl.).

HB male	793mm (760–840) n=6
HB female	760mm (740–800) n=3
T male	220mm (200–240) n=6
T female	205mm (200–210) n=3
E male	76mm (68–90) n=6
E female	80mm (75–85) n=3
WT male	8.8kg (7.6–9.8) n=6
WT female	7.3kg (6.5–7.8) n=4

Golden jackal, age and sex unknown. Bandipur National Park, Karnataka State, India, 1997.

Krupakar Senani

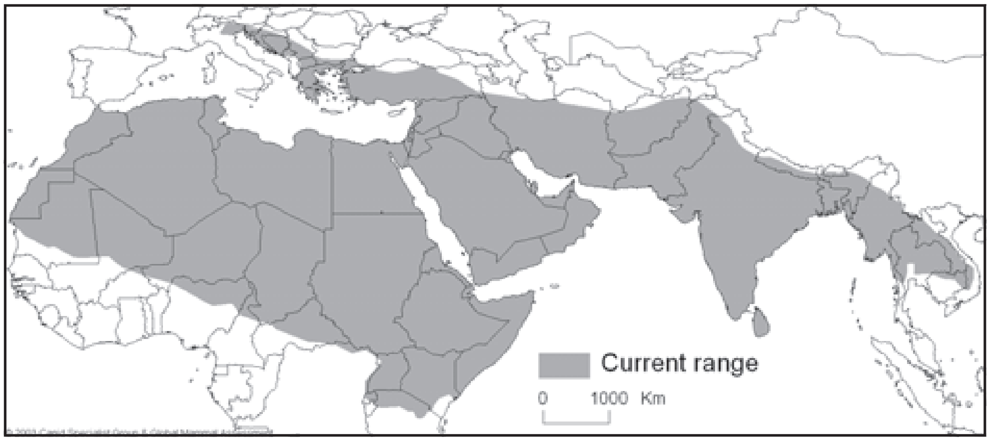

Figure 6.2.1. Current distribution of the golden jackal.

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mesomelas). Jackals inhabiting rocky, mountainous terrain may have a greyer coat shade (Sheldon 1992). The belly and underparts are a lighter pale ginger to cream. Unique lighter markings on the throat and chest make it possible to differentiate individuals in a population (Macdonald 1979a; Moehlman 1983). Melanistic and piebald forms are sometimes reported (Jerdon 1874; Muller-Using 1975). The tail is bushy with a tan to black tip. Legs relatively long, and feet slender with small pads. Females have four pairs of mammae (Sheldon 1992).

The skull of the golden jackal is more similar to that of the coyote (*C. latrans*) and the grey wolf (*C. lupus*), than that of the black-backed jackal, side-striped jackal (*C. adustus*), and Ethiopian wolf (*C. simensis*) (Clutton-Brock *et al*. 1976). The dental formula is 3/3-1/1-4/4-2/3=42.

Moehlman and Hofer (1997) give mean body mass for females as 5.8kg, and for males 6.6kg.

Subspecies As many as 12 subspecies are distinguished across the range (Ellerman and Morisson-Scott 1951; Coetzee 1977). However, there is much variation and populations need to be re-evaluated using modern molecular techniques.

Similar species Black-backed jackal (*C. mesomelas*): Distinguished by the reddish flanks and limbs, the shape of its skull, the position and angle of its ears, and usually the prominent dark saddle (the dark saddle is sometimes apparent in the golden jackal though usually not as prominent).

Side-striped jackal (*C. adustus*): Typically with relatively longer legs, a pale side stripe and a white-tipped tail.

Distribution

The golden jackal is widespread in North Africa and north-east Africa, occurring from Senegal on the west coast of Africa to Egypt in the east, in a range that includes Morocco, Algeria, and Libya in the north to Nigeria, Chad and Tanzania in the south. They have expanded their range from the Arabian Peninsula into western Europe to Austria and Bulgaria (Genov and Wassiley 1989; Sheldon 1992), and eastwards into Turkey, Syria, Iraq, Iran, Central Asia, the entire Indian subcontinent, then east and south to Sri Lanka, Myanmar, Thailand and parts of Indo-China.

Range countries Afghanistan, Albania, Algeria, Austria, Bahrain, Bhutan, Bosnia, Bulgaria, Central African Republic, Chad, Croatia, Djibouti, Egypt, Eritrea, Ethiopia, Greece, India, Iran, Iraq, Israel, Italy, Jordan, Kenya, Kuwait, Lebanon, Libya, Mali, Mauritania, Morocco (including Western Sahara), Myanmar, Nepal, Niger, Nigeria, Oman, Pakistan, Qatar, Saudi Arabia, Senegal, Sri Lanka, Somalia, Sudan, Syria, Tanzania, Thailand, Tunisia, Turkey, Turkmenistan, United Arab Emirates, Vietnam, Yemen, and Yugoslavia (Rosevear 1974; Kingdon 1977; Roberts 1977; Prater 1980).

Relative abundance

The golden jackal is fairly common throughout its range. High densities are observed in areas with abundant food and cover. In several parts of India, high densities of low-quality cattle are maintained. Due to religious beliefs, most people do not consume beef, and cattle carcasses are freely available for scavenging.

Estimated populations/relative abundance and population trends In India, jackal populations achieve high densities in pastoral areas such as Kutch, Maharashtra, Rajasthan, and Haryana. Based on intensive observations on breeding pack units and radio-collared individuals, jackal densities in the semi-arid Velavadar National Park were estimated between one and two jackals per km^2 (Y. Jhala *et al.* unpubl.); see Sharma (1998) for densities quoted for the Thar Desert in India. On the African continent, in the Serengeti National Park, densities can range as high as four adults per km^2 (Moehlman 1983, 1986, 1989).

Based on known density estimates for parts of India and considering that about 19% (i.e., about 637,000km^2) of the geographical area of India has forest cover with jackal populations (and that jackals are also found outside forested habitats), a minimum population estimate of over 80,000 golden jackals would not be unreasonable for the Indian sub-continent. Population estimates for Africa are not available.

Habitat

Due to their tolerance of dry habitats and their omnivorous diet, the golden jackal can live in a wide variety of habitats. These range from the Sahel Desert to the evergreen forests of Myanmar and Thailand. They occupy semi-desert, short to medium grasslands and savannahs in Africa; and forested, mangrove, agricultural, rural and semi-urban habitats in India and Bangladesh (Clutton-Brock *et al.* 1976; Poche *et al.* 1987; Y. Jhala pers. obs.). Golden jackals are opportunistic and will venture into human habitation at night to feed on garbage. Jackals have been recorded at elevations of 3,800m in the Bale Mountains of Ethiopia (Sillero-Zubiri 1996) and are well established around hill stations at 2,000m in India (Prater 1980).

Food and foraging behaviour

Food Golden jackals are omnivorous and opportunistic foragers, and their diet varies according to season and habitat. In East Africa, although they consume invertebrates and fruit, over 60% of their diet comprises rodents, lizards, snakes, birds (from quail to flamingos), hares, and Thomson's gazelle (*Gazella thomsoni*) (Wyman 1967; Moehlman 1983, 1986, 1989). In Bharatpur, India, over 60% of the diet comprised rodents, birds and fruit (Sankar 1988), while in Kanha, Schaller (1967) found that over 80% of the diet consisted of rodents, reptiles and fruit. In Sariska Tiger Reserve, India, scat analysis (n=136) revealed that their diet comprised mainly mammals (45% occurrence, of which 36% was rodents), vegetable matter (20%), birds (19%), and reptiles and invertebrates (8% each) (Mukherjee 1998). Great quantities of vegetable matter occur in the diet of jackals and, during the fruiting season in India, they feed intensively on the fruits of *Ziziphus* sp., *Carissa carvanda*, *Syzigium cuminii,* and pods of *Prosopis juliflora* and *Cassia fistula* (Kotwal *et al.* 1991; Y. Jhala pers. obs.).

Foraging behaviour Single jackals typically hunt smaller prey like rodents, hares and birds. They use their hearing to locate rodents in the grass and then pounce on them by leaping in the air; they also dig out gerbils (*Tatera indica*) from their burrows. They have been observed to hunt young, old, and infirm ungulates that are sometimes 4–5 times their body weight (Van Lawick and Van Lawick-Goodall 1970; Eisenberg and Lockhart 1972; Kotwal *et al.* 1991; Y. Jhala pers. obs.). During calving peaks of blackbuck (*Antelope cervicapra*), in Velavadar National Park, India, jackals were observed searching for hiding calves throughout the day with searches intensifying during the early morning and late evening (Y. Jhala pers. obs.). Although single jackals were observed hunting (n=4) and killing blackbuck calves (n=1), jackal packs (2–4 jackals) were more successful (n=4), as has been observed for predation on African antelope fawns (Wyman 1967; Kruuk 1972; Rosevear 1974). Indeed, cooperative hunting permits them to harvest much larger prey in areas where it is available, and cooperative hunting of langurs (*Presbytis pileata* and *P. entellus*) has been reported (Newton 1985; Stanford 1989). Aggregations of between five and 18 jackals have been sighted scavenging on carcasses of large ungulates (Y. Jhala pers. obs.), and Macdonald (1979a) reports similar aggregations on clumped food resources in Israel.

In Velavadar National Park, India, hundreds of harriers (*Circus macrourus* and *C. pygargus*) roost communally in the grasslands during the course of winter migration.

Jackals were observed to stalk close to roosting harriers and then rush at them attempting to catch one before the harriers could take off and gain height. In several areas of India and Bangladesh, jackals subsist primarily by scavenging on carrion and garbage (Poche *et al.* 1987; Y. Jhala pers. obs.). They have the habit of caching extra food by burying it (Kingdon 1977).

Damage to livestock or game Golden jackals cause damage to melon, peanut, grape, coffee, maize and sugarcane crops; they sometimes take to killing lambs, kids, weak sheep, goats and poultry (Jerdon 1874; Kingdon 1977; Prater 1980; Poche *et al.* 1987).

Adaptations

Jackals are generalists, adapting to local abundance of food resources. This adaptability permits them to occupy a wide variety of habitats and utilise a variety of food resources. A lithe body with long legs allows jackals to trot for large distances in search of food. They are reported to have the ability to forego water (Kingdon 1977), and jackals have been observed on Pirotan Island in the Gulf of Kutch, India, where there is no fresh water (Y. Jhala pers. obs.). Jackals can commute between this island and the mainland by traversing through mangroves and small islands that are exposed during extreme low tides.

Social behaviour

The social organisation of golden jackals is extremely flexible depending on the availability and distribution of food resources (Macdonald 1979a; Moehlman 1983, 1986, 1989; Fuller *et al.* 1989; Moehlman and Hofer 1997; and see Food and foraging behaviour). The basic social unit is the breeding pair, which is sometimes accompanied by its current litter of pups and/or by offspring from former litters (Moehlman 1983, 1986, 1989). In Tanzania, golden jackals usually form long-term pair bonds, and both members mark and defend their territories, hunt together, share food, and cooperatively rear the young (Moehlman 1983, 1986, 1989). Of a total of 270 recorded jackal sightings in the Bhal and Kutch areas of Gujarat, India, 35% consisted of two individuals, 14% of three, 20% of more than three, and the rest of single individuals (Y. Jhala unpubl.). Moehlman and Hofer (1997) give average group size as 2.5 in the Serengeti, Tanzania, while average pack size in Velavadar National Park, India, was 3.0 (n=7) (Y. Jhala unpubl.).

Scent marking by urination and defecation is common around denning areas and on intensively used trails. Such scent flag posts are considered to play an important role in territorial defence (Rosevear 1974). Although Moehlman (1983) reports maintenance of year-round exclusive territories in Tanzania, aggregations in Israel (Macdonald 1979a) and India (Y. Jhala pers. obs.) point towards the flexibility of social organisation depending on available food resources. Recent data obtained by telemetry from the Bhal area of India suggest that most breeding pairs are spaced well apart and likely maintain a core territory around their dens (Y. Jhala unpubl.). Feeding ranges of several jackals in the Bhal overlapped, as also reported by Van Lawick and Van Lawick-Goodall (1970). Jackals were observed to range over large distances in search of food and suitable habitat, and linear forays of 12–15km in a single night were not uncommon (A. Aiyadurai and Y. Jhala unpubl.). Non-breeding members of a pack may stay near a distant food source like a carcass for several days prior to returning to their original range. Recorded home range sizes vary from 1.1–20km^2 (Van Lawick and Van Lawick-Goodall 1970; Kingdon 1977; Poche *et al.* 1987; Y. Jhala unpubl.), depending on the distribution and abundance of food resources.

Affiliative behaviours like greeting ceremonies, grooming, and group vocalisations are common in jackal social interactions (Van Lawick and Van Lawick-Goodall 1970; Golani and Keller 1975). Vocalisation consists of a complex howl repertoire beginning with 2–3 simple, low-pitch howls and culminating in a high-pitched staccato of calls. Jackals are easily induced to howl and a single howl evokes responses from several jackals in the vicinity. Golden jackals often emit a warning call that is very different from that of their normal howling repertoire in the presence of large carnivores like tigers, hyaenas and wolves (Jerdon 1874; Y. Jhala pers. obs.). In India, howling is more frequent between December and April, a time when pair bonds are being established and breeding occurs, perhaps suggesting a role in territory delineation and defence (Jaeger *et al.* 1996).

Reproduction and denning behaviour

Reproductive activity commences from February to March in India and Turkmenistan, and from October to March in Israel (Golani and Keller 1975; Ginsberg and Macdonald 1990). In Tanzania, mating typically occurs from October to December with pups being born from December to March (Moehlman 1983, 1986, 1989). As with other canids, mating results in a copulatory tie that lasts for several minutes (Golani and Mendelssohn 1971; Golani and Keller 1975). Timing of births coincides with abundance of food supply; for example, the beginning of the monsoon season in northern and central India, and the calving of Thomson's gazelle in the Serengeti (Moehlman 1983; Ginsberg and Macdonald 1990). Females are typically monoestrus, but there is evidence in Tanzania of multiple litters (P. Moehlman pers. obs.). Gestation lasts about 63 days (Sheldon 1992). Moehlman and Hofer (1997) give mean litter size as 5.7 (range=1–8) in Tanzania, while in the Bhal area in India, average litter size was 3.6 (range=2–5; n=11) (Y. Jhala unpubl.). In Tanzania, Wyman (1967) reported an average of two pups emerging from the den at three weeks of age. Pups are born blind and their eyes open at approximately nine days and their teeth erupt at 11 days after birth (Moehlman and Hofer 1997). Lactation usually lasts for 8–10 weeks.

In India, den excavations begin in late April to May, with dens primarily located in natural and man-made embankments, usually in scrub habitat. Rivulets, gullies, road, and check-dam embankments are prime denning habitats (Soni *et al*. 1995; Y. Jhala pers. obs.), although drainage pipes and culverts have served as dens on several occasions in the Bhal. Dens may have 1–3 openings and typically are about 2–3m long and 0.5–1.0m deep. Young pups could be moved between 2–4 dens prior to joining their parents. In Tanzania, both parents and 'helpers' (offspring from previous litters) provision and guard the new pups. The male also feeds his mate during her pregnancy, and both the male and the 'helpers' provision the female during the period of lactation (Moehlman 1983, 1986, 1989; Moehlman and Hofer 1997). The 'helpers' are full siblings to the young pups that they are provisioning and guarding, and the presence of 'helpers' results in a higher pup survival (Moehlman 1986).

Competition

The existence of three sympatric species of jackals (golden, black-backed and side-striped) in East Africa is explained in part by resource partitioning and the high relative diversity of prey and predators in Africa (Fuller *et al*. 1989; Wayne *et al*. 1989).

Golden jackals have been observed to appropriate the dens of Bengal foxes (*Vulpus bengalensis*) and porcupines (*Hystrix indica*), and also to use abandoned grey wolf (*Canis lupus*) dens (Y. Jhala pers. obs.). Jackals often scavenge off the kills of larger predators like lion (*Panthera leo*), tiger (*P. tigris*), leopard (*P. pardus*), spotted hyaena (*Crocuta crocuta*), dhole (*Cuon alpinus*) and grey wolf (Jerdon 1874; Schaller 1967; Van Lawick and Van Lawick-Goodall 1970; Kruuk 1972; Moehlman 1986; Jhala 1994). Jackals have been observed following grey wolves on a hunt and scavenging off wolf kills without evoking any hostile reactions from wolves (Jhala 1991, 1994).

Mortality and pathogens

Natural sources of mortality In Kutch, India, jackals are predated by striped hyaenas (*Hyaena hyaena*), and one hyaena maternity den had three jackal carcasses (Y. Jhala unpubl.). Spotted hyenas also have been observed to kill and feed on golden jackals (Kruuk 1972; Kingdon 1977), and the same probably holds true of other large carnivores. Singh (1983) reports that pythons (*Python morulus*) were a major predator of jackals in Corbett National Park, India. Jackals are often chased and sometimes killed by feral dogs when they approach human habitation.

Persecution In India, pastoralists occasionally use poison to kill predators like wolves and leopards that predate on livestock, and jackals are killed by scavenging such poisoned kills (Y. Jhala unpubl.).

Hunting and trapping for fur Some tribal communities like the *kolis*, *vaghris* in Gujarat and *Rajasthan* and *nari kuravas* in Tamil Nadu do kill and eat jackals. This occasional hunting currently does not pose a threat to jackal populations in these states of India. However, there is a threat from organised poaching for skins and tails which are sometimes marketed.

Road kills Besides dogs, jackals are the most common road kills on rural roads in India. The incidence of road kills increases during the breeding season from February to March (Y. Jhala pers. obs.).

Pathogens and parasites Since golden jackals live in close proximity to human habitation, they often come into contact with feral dog populations. Jackals in India are often infected with diseases like rabies and distemper, and rabid jackals frequently attack domestic livestock, dogs and humans (Y. Jhala unpubl.). Skin diseases like mange and ectoparasites like ticks and fleas are common in jackals in areas where they occur at high densities. In Tanzania, golden jackals had positive seriological test results to canine parvovirus, canine herpesvirus, canine coronavirus and canine adenovirus (W.B. Karesh pers. comm.).

Longevity The maximum life span recorded in the Serengeti was 14 years (Moehlman and Hofer 1997).

Historical perspective

The jackal features in mythological and cultural accounts of several civilisations spanning Africa, India and Europe. The ancient Egyptians worshipped the jackal-headed god Anubis, and the Greek gods Hermes and Cerberus probably derived their origins from the golden jackal. In India, jackals feature in ancient texts like the *Jatakas* and *Panchtatra* that abound with animal stories. The jackal normally is portrayed as an intelligent or wily creature in these stories. Some tribes in India believe that a horn-like growth appears on the heads of some jackals called *shiyal shingi*; the possession of this organ is believed to bring good fortune. Coffee beans that have passed through the gut of a jackal are believed to have an added flavour, and these are collected and marketed in certain parts of southern India (Jerdon 1874; A.J.T. Johnsingh pers. comm.)

Conservation status

Threats Over its entire range except in protected areas like National Parks and Sanctuaries, the jackal population may be declining. Traditional land use practices, like livestock rearing and dry farming that were conducive to the survival of jackals and other wildlife, are being steadily replaced by industrialisation and intensive agriculture;

wilderness areas and rural landscapes are being rapidly urbanised. Jackal populations adapt to some extent to this change and may persist for a while, but eventually disappear from such areas like other wildlife. There are no other known threats, except for local policies of extirpation and poisoning (for example, Israel).

Commercial use There is no significant trade in jackal products, although skins and tails are occasionally sold.

Occurrence in protected areas Golden jackals are present in all protected areas of India except for those in the high elevation regions of the Himalaya. In East Africa, they occur in the Serengeti-Masai Mara-Ngorongoro complex, as well as numerous other conservation units. Thus they have a wide coverage in terms of protected populations.

Protection status CITES – Appendix II (in India).

Current legal protection Jackals feature on Schedule III of the Wildlife Protection Act (1972) of India and are afforded the least legal protection (mainly to control trade of pelts and tails). However, no hunting of any wildlife is permitted under the current legal system in India. The golden jackal could be considered as a "species requiring no immediate protection" with caution and knowledge that populations throughout its range are likely declining.

Conservation measures taken Besides being represented in a wide array of protected areas covering several landscapes, no species-specific conservation efforts have been undertaken.

Occurrence in captivity

Almost all zoos in India have golden jackals. In March 2000, there were 67 males, 72 females, and 54 unsexed individuals in Indian zoos (Central Zoo Authority India pers. comm.).

Current or planned research projects

P. Moehlman (Tanzania Wildlife Research Institute) is conducting ongoing, long-term studies in the Serengeti, Tanzania.

Y. Jhala (Wildlife Institute of India) is continuing with ongoing studies on wolves, jackals, and striped hyaenas in Bhal and Kutch areas of Gujarat, India.

M. Jaeger (Department of ESPM, University of California at Berkley, USA) is investigating crop damage, densities and ranging patterns of golden jackals in Bangladesh.

Gaps in knowledge

Little quantitative information is available on jackal densities, habitat use, and ranging patterns in relation to food availability. Information on dispersal, survival and mortality factors of adults, pups and dispersing individuals is needed. Jackal ecology needs to be studied in forested ecosystems of Southeast Asia where a different set of factors are likely to operate affecting food availability, ranging patterns and survival. Aspects of canid diseases in relation to population dynamics of jackals and transmission need to be better understood.

Core literature

Fuller *et al*. 1989; Macdonald 1979a; Moehlman 1983, 1986, 1989; Moehlman and Hofer 1997.

Reviewers: Asir J.T. Johnsingh. **Editors:** Michael Hoffmann, Claudio Sillero-Zubiri.

6.3 Black-backed jackal
Canis mesomelas Schreber, 1775
Least Concern (2004)

A.J. Loveridge and J.A.J. Nel

Other names

English: silver-backed jackal; **Afrikaans:** rooijakkals; **French:** chacal à chabraque; **German:** schabrakenschakal; **Indigenous names:** Amharic: tikur-jerba kebero (Ethiopia, Eritrea); Shona: hungubwe, gava (Zimbabwe); Ndebele: ikhanka (Zimbabwe); Zulu: mpungutshe, kanka (South Africa); Siswati: mpungutje; Shangaan: impungutshe (South Africa); Tswana: phokojwe (Botswana, South Africa); Venda: phungubwe (South Africa); Sotho: phokobje, phokojoe (South Africa); Herero/Ovambo: ombánji (Namibia); Nama/Damara: Girib, Gireb (Namibia); Kiswaheli: bweha nyekunda (East Africa).

Taxonomy

Canis mesomelas von Schreber, 1775. Die Säugethiere 2(14): pl. 95; text 1776, 3(21): 370. Type locality: "Vorgebirge der guten Hofnung" ["Cape of Good Hope", South Africa].

Chromosome number: 2n=78 (Wayne 1993).

Description

The black-backed jackal is somewhat fox-like in appearance, with a long, pointed muzzle. Diagnostic features include the dark saddle, black, bushy tail and reddish flanks and limbs; males are slightly larger and heavier than females (Table 6.3.1). The ears are large, erect, pointed and constantly mobile. The overall body colour is rufous brown, the colour gaining its greatest intensity on the ears, rump and flanks. A black stripe midway up each flank slopes obliquely from behind the shoulder to the top of the rump; the dark saddle is broadest at the shoulders and tapers to a narrow point at the base

Black-backed jackal, age and sex unknown. Etosha National Park, Namibia.

Chris and Tilde Stuart

Table 6.3.1. Body measurements for the black-backed jackal from the former Cape Province, South Africa (Stuart 1981).

HB male	785mm (690–900) n=65
HB female	745mm (650–850) n=42
T male	326mm (270–395) n=70
T female	316mm (260–381) n=45
HF male	160mm (130–185) n =66
HF female	156mm (140–180) n=43
E male	109mm (90–132) n=68
E female	104mm (80–120) n=41
WT male	8.1kg (5.9–12.0) n=59
WT female	7.4kg (6.2–9.9) n=42

of the tail. Anterior to this stripe, just behind the shoulder is a small vertical stripe, diffuse in some individuals. Above the side markings, the back is marbled black and white giving an overall silver appearance in mature animals (hence their alternative name of silver-backed jackal). Juveniles and subadults have similar markings but these are drabber and only gain their full intensity at around two years of age. In the drier west and Namib coast in southern Africa the winter coat is a deep reddish brown (especially in males). The bushy tail is dark brown to black with a distinctive black subcaudal marking. The markings, especially the side and shoulder stripes, are unique to each individual and can be used for identification purposes. Hair on the face is 10–15mm, lengthening to 30–40mm on the rump. Guard hairs on the saddle in the shoulder region are *c*. 60mm decreasing to 40mm at the base of the tail; on the tail they reach 70mm.

Skull elongated, braincase pear-shaped, rostrum narrow, supra-occipital crest well developed, bullae rounded, zygomatic arches broad and well developed, and post-orbital bars incomplete. Dental formula is 3/3-1/1-4/4-2/3=42. Outer upper incisors larger, more pointed and caniniform than others. Upper canines long, curved and pointed, with a sharp ridge on their posterior faces (Skinner and Smithers 1990).

In southern Africa black-backed jackals differ in size in different areas. Recorded mean mass of males from different regions include: 8.4kg (n=123) for KwaZulu-Natal (Rowe-Rowe 1978), 8.2kg (n=12) in the former Transvaal (Rautenbach 1982), and 9.7kg (n=7) for the Skeleton Coast of Namibia (Stutterheim *in litt*.). Average weight in East Africa is 8.5kg (Kingdon 1977).

Subspecies As many as six (Allen 1939) subspecies have been recognised. Coetzee (1977) listed five, while Meester *et al.* (1986) assigned all southern African material to the nominate subspecies, mentioning the two remaining subspecies from East Africa. However, considering the regional variation in the species, Kingdon's (1997) recognition of only two, geographically isolated subspecies is followed here.

— *C. m. mesomelas* (southern Africa)
— *C. m. schmidti* (East Africa).

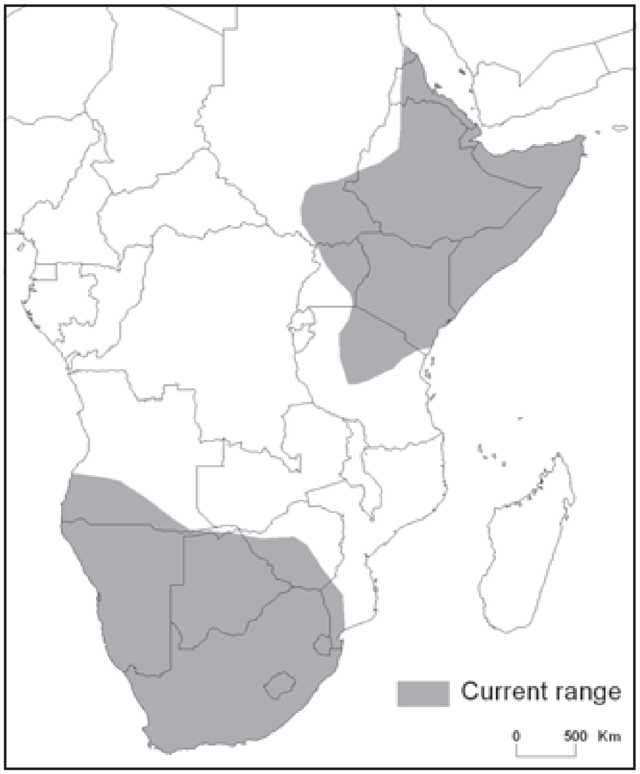
Similar species Both side-striped jackals (*Canis adustus*) and golden jackals (*Canis aureus*) occur in sympatry with the black-backed jackal in parts of East Africa, and the side-striped jackal occurs in sympatry with this species in parts of Zimbabwe, Botswana and South Africa. Both the side-striped jackal and golden jackal typically lack the prominent dark saddle, although this is sometimes apparent in the golden jackal. They also lack the reddish flanks and limbs. The side-striped jackal has a whitish stripe along the flanks and a characteristic white-tipped tail, while the golden jackal is sand-coloured and has cream-coloured underparts.

Distribution

Current distribution The black-backed jackal has a disjunct distribution range, and is found in two separate populations, one in East Africa, and the other in southern Africa (Figure 6.3.1). Ansell (1960) notes that this species is entirely absent from Zambia and it is absent through much of central and equatorial Africa. The disjunct distribution of this species is similar to that of other endemic African species adapted to dry conditions (e.g., aardwolf *Proteles cristatus*, bat-eared fox *Otocyon megalotis*, dik-dik *Madoqua kirkii*). The two black-backed jackal ranges are separated by as much as 1,000km and their discontinuous distribution suggests that regions of dry *Acacia* bush and savannah, the preferred habitat of this species, once connected south-west Africa and the Horn of Africa.

Historical distribution Fossils of black-backed jackals have been found in deposits in South Africa dating to at least two million years ago (Hendey 1974), but fossil remains have never been found north of Ethiopia suggesting that they have always been restricted to sub-Saharan Africa.

Figure 6.3.1. Current distribution of the black-backed jackal.



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Range countries Angola, Botswana, Djibouti, Eritrea, Ethiopia, Kenya, Lesotho, Mozambique, Namibia, Somalia, South Africa, Sudan, Swaziland, Tanzania, Uganda, Zimbabwe (Coetzee 1977; Kingdon 1977; Skinner and Smithers 1990).

Relative abundance

Regional estimates of abundance are not available. However, black-backed jackals are generally widespread, and, in Namibia and South Africa, they are common in protected areas where suitable habitat occurs. They occur in many livestock producing areas, where they are considered vermin, but despite strenuous control measures in many farming areas of southern Africa this species is still relatively abundant.

Estimated populations/relative abundance and population trends In the Drakensberg Mountains of South Africa, Rowe-Rowe (1982) found densities of 1 jackal/2.5–2.9km^2, while J.A.J. Nel *et al.* (unpubl.) recorded linear densities along the Namib Desert Coast of Namibia that varied from 0.1–0.53 jackal/km^2 along food-scarce beaches along the Skeleton Coast, to 7.0–9.0/km^2 at the food-rich seal rookery at Cape Cross, reaching a maximum of 16.0–32.0/km^2 along the centre of the seal rookery.

Habitat

Black-backed jackals are found in a wide variety of habitats including arid coastal desert (Dreyer and Nel 1990), montane grassland (Rowe-Rowe 1982), arid savannah and scrubland (Skinner and Smithers 1990), open savannah (Wyman 1967; Kingdon 1977; Lamprecht 1978; Moehlman 1983; Fuller *et al.* 1989; Estes 1991), woodland savannah mosaics (Smithers 1971; Loveridge and Macdonald 2002) and farmland. In general, black-backed jackals show a preference for open habitats tending to avoid dense vegetation (Pienaar 1969). In KwaZulu-Natal, they are recorded from sea level to more than 3,000m a.s.l. in the Drakensberg, and in localities receiving more than 2,000mm of rainfall (Rowe-Rowe 1982, 1992). Where more than one jackal species occur in sympatry the habitat is partitioned. The trend is for black-backed jackals to use either the open grassland (when sympatric with side-striped jackal; Loveridge and Macdonald 2000) or wooded savannah (when sympatric with golden and side-striped jackals; Fuller *et al.* 1989). In western Zimbabwe habitat partitioning was mediated by aggressive encounters in which black-backed jackals displaced side-striped jackals from grassland habitats (Loveridge and Macdonald 2002).

Food and foraging behaviour

Food Black-backed jackals are generalist feeders. Diet varies according to food availability (Skinner and Smithers 1990; Loveridge and Macdonald 2003), and, when occurring in sympatry with other carnivores sharing the same prey base, food resources are partitioned (Bothma *et al.* 1984). Dietary items typically include small- to medium-sized mammals (e.g., murids, springhares, young ungulates), reptiles, birds and birds' eggs, carrion and human refuse (Roberts 1922; Stuart 1976, 1981; Kingdon 1977, 1997; Ferguson 1980; Rowe-Rowe 1983; Dreyer and Nel 1990; Skinner and Smithers 1990; Kok 1996), as well as invertebrates and plants (Bothma 1971b), beached marine mammals, seals, fish and mussels on coasts (Nel and Loutit 1986; Avery *et al.* 1987; Oosthuizen *et al.* 1997). Invertebrates, such as termites and insects, are commonly eaten (Kingdon 1997; Loveridge 1999).

Foraging behaviour Pairs and small foraging groups are often seen foraging together. Groups of between 8 and 10 aggregate at large carcasses of herbivores, and more than 80 have been recorded at seal colonies on the Namib Desert coast (Oosthuizen *et al.* 1997). Such aggregations are accompanied by aggressive behaviour between territorial individuals. However, in the south-western Kalahari, where antelope carcasses are uncommon, groups of up to 15 pairs feed in succession without much overt aggression (J.A.J. Nel unpubl.). Mated black-backed jackal pairs will often cooperate in the capture of prey resulting in a higher success rate (Lamprecht 1978; Loveridge 1999). In Botswana, McKenzie (1990) found that, on occasion, they form 'packs' in order to hunt adult impala (*Aepyceros melampus*), and other authors have recorded them taking adult antelope (Van Lawick and van Lawick-Goodall 1970; Sleicher 1973; Lamprecht 1978). On the Namib Desert coast they patrol beaches for beached marine refuse and move along sheltered paths in-between food-rich patches; the top of coastal hummocks are used as feeding sites (Dreyer and Nel 1990). In this environment, they frequently occur in association with brown hyaenas (*Parahyaena brunnea*), following from a distance in the hope of securing the odd food item. The large, mobile ears are used to locate invertebrate and small mammalian prey. A leap, followed by an accurate pounce is employed to capture prey located in this fashion, after the manner of a red fox (*Vulpes vulpes*). They are largely nocturnal, but activity periods may extend well into daylight hours in areas where they are free from persecution.

Damage to livestock or game This species will prey on livestock (especially juvenile goats and sheep) and is thus considered vermin in many livestock producing regions (Van der Merwe 1953). However, such predation is usually localised and not extensive (Shortridge 1934; Roberts 1951; Smithers 1971; Rowe-Rowe 1975; Lawson 1989). In certain areas losses of up to 3.9% can result, or up to 18% on specific farms, which entail a high economic loss to farmers (Brand 1993). Where controlled herding is practiced, e.g., southern Namibia, losses amount to only 0.3–0.5% (Brown 1988).

Adaptations

Black-backed jackals are relatively unspecialised canids and well suited for an opportunistic lifestyle in a wide variety of habitats. They have a well-developed carnassial shear with a longer premolar cutting blade than other jackal species, an indication of a greater tendency towards carnivory (Van Valkenburgh 1991; Van Valkenburgh and Koepfli 1993). Examination of kidney structure suggests that this species is well adapted to water deprivation (Loveridge 1999) which may explain its presence in the drier parts of the African continent. Black-backed jackals are wary of unfamiliar objects and young follow the example of adults by avoiding poisoned baits (coyote getters) in control operations (Brand 1993; Brand and Nel 1996); here, as well as during foraging and selecting prey, social learning seems to play a role (Nel 1999).

Social behaviour

The monogamous mated pair is the basis of social structure in this species. The pair bond appears to be life-long in most cases, and if one member of a pair dies the other often will lose its territory (Moehlman 1978, 1979; Estes 1991). Black-backed jackals are territorial using faeces and urine to demarcate their territorial boundaries (Kingdon 1977; Ferguson *et al.* 1983; Skinner and Smithers 1990). Territories are spatially and temporally relatively stable, and intruders are aggressively expelled by territory holders. In Hwange National Park, Zimbabwe, a mated pair of black-backed jackals held the same territory for at least four years (Loveridge 1999). Water sources are shared with intruders but these perform submissive behaviour to territory holders, and even their pups (J.A.J. Nel unpubl.). Density and group size is dependent on food biomass and dispersion (J.A.J. Nel *et al.* unpubl.).

Recorded home range sizes vary across the range of the species. In South Africa, home range size averaged 18.2km^2, (n=14) in the Giants Castle Game Reserve in the KwaZulu-Natal Drakensberg (Rowe-Rowe 1982). In the more arid south-western Kalahari, ranges were smaller, with adult ranges varying from 2.6–5.2km^2, (mean 4.3km^2, n=7) and subadult ranges from 4.0–8.8km^2, (mean 6.3km^2, n=4) (Ferguson *et al.* 1983). In Zimbabwe, home ranges were largest in the cold, dry season (ca 1.0km^2 and 1.3km^2, n=3 and 6 respectively) and smaller in the hot dry season (ca 0.3km^2 and 0.6km^2, n=4) (Loveridge and Macdonald 2001), while in the Rift Valley in Kenya, home ranges varied between 0.7–3.5km^2, with a mean of 1.8km^2 (Fuller *et al.* 1989). Interestingly, at Cape Cross Seal Reserve on the Namibian coast, average home range size varied from 7.1–24.9km^2 (n=4). Here jackals did not defend their ranges and were not territorial (Hiscocks and Perrin 1988), whereas in all other cases ranges were defended and mutually exclusive for pairs.

The black-backed jackal is a very vocal species. A high-pitched, whining howl is used to communicate with group members and is often used to call the group together in the early evening; this may also function in territorial advertisement (Moehlman 1983; Estes 1991). Howling often stimulates the same behaviour in adjacent territories or in nearby individuals. A three- to five-syllable alarm call, consisting of an explosive yelp followed by a series of shorter high-pitched yelps, is used when disturbed and may be frantic and prolonged when mobbing leopard (*Panthera pardus*). A low-pitched, gruff bark is used to warn pups of intruders near the den, and whines are used to call to pups. Kingdon (1997) notes the use of a 'clattering distress call' and a loud yelp when alarmed. Interestingly, black-backed jackals are much less vocal where they occur alongside the golden jackal, which is the only jackal species heard to howl in East Africa (Kingdon 1977, 1997).

Reproduction and denning behaviour

Mating in this species is accompanied by increased vocalisation and territoriality in both sexes (Bernard and Stuart 1992; Loveridge and Macdonald 2001). The dominant individuals within the territory prevent same sex subordinates from mating by constant harassment. As with other canids, there is a copulatory tie after mating. In southern Africa mating generally occurs from late May to August and, following a gestation period of about 60 days, births occur from around July to October (Stuart 1981; Bernard and Stuart 1992). However, in the KwaZulu-Natal Drakensberg, Rowe-Rowe (1978) recorded a peak in births in July. Bernard and Stuart (1992) suggested that summer births are timed to coincide with the reproductive season of important prey like vlei rat (*Otomys irroratus*) and four-striped grass mouse (*Rhabdomys pumilio*), and winter births with an increase in the availability of ungulate carcasses at the end of winter.

Litter size is typically between one and six, and pups are born in modified termitaria or other convenient burrows, often with multiple entrances. The same den sites may be used from year to year. Pups first emerge from the den at three weeks, are weaned at 8–9 weeks, and are completely independent of the den at 14 weeks (Moehlman 1978).

Alloparental care, where young from previous years may remain within the territory to act as 'helpers', is well documented for this species (Moehlman 1978). Alloparents feed pups by regurgitation and guard them when the parents are foraging. One 'helper' may increase the average number of pups surviving per mated pair from one to three, and two 'helpers' further increases survival to four pups (Moehlman 1979, 1983).

Pups reach sexual maturity at about 11 months (Ferguson *et al.* 1983), and even at this early age they can disperse distances of more than 100km (Bothma 1971c).

Competition

Black-backed jackals compete to a small degree with many small carnivores, but this species' generalist habits ensure that such competition is rarely intense and food resources are partitioned (Bothma *et al.* 1984). They also compete for carrion with other scavengers, particularly hyaenas, lion and vultures. Wyman (1967) found that this species was much more common than golden jackals at large carnivore kills in the Ngorongoro crater, Tanzania, despite being less numerous in the area, while Estes (1991) notes that black-backed jackals are more likely to attempt to feed on lion and hyaena kills than other jackal species. Competition for resources with side-striped jackals has been recorded in western Zimbabwe. In this case black-backed jackals aggressively displaced side-striped jackals from prime grassland habitat, despite being around 3kg smaller. Indeed, black-backed jackals are reputed to be more aggressive than other species of jackal (Kingdon 1977; Skinner and Smithers 1990; Estes 1991) and Estes (1991) mentions that pups of this species become 'quarrelsome and unsociable' and are more likely to emigrate than golden jackal pups.

Mortality and pathogens

Natural sources of mortality Natural predators include leopard (Turnbull-Kemp 1967; A. Loveridge pers. obs) and spotted hyaena (*Crocuta crocuta*) which may prey on unprotected pups (Van Lawick and van Lawick-Goodall 1970). Estes (1967) observed 11 jackals taken by a leopard over the course of three weeks, and they may be a favourite prey item of leopard in some areas (Kingdon 1977). Interestingly, a golden jackal was seen killing a litter of four black-backed jackal pups (about 5–6 weeks old) while the adults were away hunting (O. Newman and A. Barrett pers. comm.). Other predators include birds of prey; Van Lawick and van Lawick-Goodall (1970) observed a martial eagle (*Polemaetus bellicosus*) fly away carrying a subadult black-backed jackal.

Persecution Snaring and road accidents may be the commonest cause of jackal mortality in areas of high human density.

Hunting and trapping for fur Hunting and trapping for skins occurs in some areas of southern Africa but is not a widespread industry.

Road kills see Persecution.

Pathogens and parasites Black-backed jackals succumb to diseases of domestic dogs, such as babesiosis and distemper (Kingdon 1977; Van Heerden 1980). Jackals are significant vectors of rabies in central southern Africa (Foggin 1988; Bingham and Foggin 1993). In some areas rabies control is undertaken by culling of wildlife, especially jackals, and is thus a major cause of mortality. Recent work suggests that culling is ineffective and rabies is less prevalent in areas where jackal populations are stable, such as national parks. Oral vaccination is the most effective method of rabies control.

Longevity Haltenorth and Diller (1980) give longevity as 10–12 years in the wild, although Rowe-Rowe (1992) states that few appear to live beyond seven years.

Historical perspective

Black-backed jackal livestock predation resulted in the formation of 'hunting clubs' in many farming districts of South Africa in the early to middle part of the last century (Van der Merwe 1954). Despite strenuous control measures (use of dogs, poison, shooting and gassing) this species was never eradicated and continues to occur in these areas today. Jackals appear regularly in African folklore, especially as an allegorical vehicle for greed or cunning.

Conservation status

Threats No major threats, but black-backed jackals are persecuted for their role as livestock killers and as rabies vectors. Population control efforts appear largely ineffective and probably only succeed in producing a temporary reduction in local numbers.

Commercial use There is no significant trade in jackal products, although body parts are used in traditional African medicine.

Occurrence in protected areas

- *Angola*: Iona National park;
- *Botswana*: Kgalagadi Transfrontier Park, Central Kalahari Game Reserve, Moremi Game Reserve, Chobe National Park;
- *Ethiopia*: Awash National Park, Mago National Park, Nechisar National Park, Omo National Park;
- *Kenya*: Masai Mara;
- *Lesotho*: Sehlabathebe National Park;
- *Mozambique*: Gorongoza National Park;
- *Namibia*: Skeleton Coast National Park, Namib-Naukluft National Park, Etosha National Park, Waterberg National Park;
- *Somalia*: unknown;
- *South Africa*: Augrabies Falls National Park; Kgalagadi Transfrontier Park, Karoo National Park, Kruger National Park, Ukahlamba-Drakensberg Park, Hluhluwe-Umfolozi Game Reserve, Suikerbosrand Nature Reserve, Tankwa Karoo National Park, Mountain Zebra National Park, Namaqua National Park;
- *Tanzania*: Serengeti National Park, Selous Nature Reserve;
- *Uganda*: Kidepo National Park, Queen Elizabeth National Park;
- *Zimbabwe*: Hwange National Park.

Protection status CITES – not listed.

Current legal protection Black-backed jackals have no legal protection outside protected areas

Conservation measures taken None.

Occurrence in captivity

Black-backed jackals have been maintained in captivity for use in experiments testing rabies vaccine (Bingham *et al*. 1995).

Current or planned research projects

S. Kaunda (Wildlife Conservation Research Unit, University of Oxford, United Kingdom) is currently undertaking ecological work on this species in Botswana.

S. Gowtage-Sequeira (Zoological Society London, United Kingdom) is studying the transmission of canid pathogens such as rabies and canine distemper between carnivores (black-backed jackals and brown hyaenas) on the Namibian coast.

M.J. Somers (Department of Zoology, University of Transkei, South Africa) is studying the ecology and intraguild relations among small carnivores along the Transkei Wild coast.

Other projects include ongoing monitoring by P. Moehlman in the Serengeti, an ecological study by L. Frank as part of the Laikipia Predator Project in Kenya, investigations into problem-animal control by R. Harrison-White in South Africa, and veterinary-related work by J. Bingham and C. Foggin.

Gaps in knowledge

A large amount of research focusing on the behaviour and ecology of this species has been undertaken, particularly in the last 25 years. In the last decade, however, the emphasis has generally shifted to the role that the animal plays as a vector of rabies, and as a problem animal. The study of Loveridge (1999) may provide a model for future research, whereby funds and efforts are directed towards better understanding their role, for example, in disease transmission and livestock predation, and ecological, behavioural and other data are gathered concurrently. In many settled areas this species, together with the caracal (*Caracal caracal*), represent the top predators in many ecosystems, yet their roles are poorly understood.

Core literature

Ferguson 1980; Lamprecht 1978; Loveridge and Macdonald 2001, 2002; Moehlman 1983, 1987; Rowe-Rowe 1982; Skinner and Smithers 1990.

Reviewers: Patricia D. Moehlman, J. du P. Bothma.
Editors: Michael Hoffmann, Claudio Sillero-Zubiri.

6.4 Ethiopian wolf
Canis simensis Rüppell, 1835
Endangered – EN: C2a(i), D (2004)

C. Sillero-Zubiri and J. Marino

Other names

English: Simien fox, Simien jackal; **French:** loup d'Abyssinie; **German:** Aethiopienfuchs; **Italian:** volpe rossa; **Spanish:** lobo Etiope; **Indigenous names:** Amharic: ky kebero; Oromo: jedalla farda (Ethiopia).

Taxonomy

Canis simensis Rüppell, 1835. Neue Wirbelt. Fauna Abyssin. Gehörig. Saugeth., 1:39, pl. 14. Type locality: "…in den Bergen von Simen…" [Ethiopia, mountains of Simen, *c.*13°15'N, 38°00'E].

Gray (1868) placed this species in a separate genus *Simenia*. Clutton-Brock *et al.* (1976) noted that *C. simensis* is the most distinct species in the genus *Canis*, and suggested close affinity with the side-striped jackal (*C. adustus*) and *Dusicyon* spp. The Ethiopian wolf has also been called the Simien or Simenian fox, but is not closely linked to the *Vulpes* group (Clutton-Brock *et al.* 1976), and Simien or Ethiopian jackal, suggesting a close relationship with jackals (Rook and Azzaroli-Puccetti 1997). Other vernacular names used include Abyssinian wolf and red fox, denoting the difficulty faced by naturalists in cataloguing this species correctly.

Phylogenetic analysis using mitochondrial DNA sequencing suggested that *C. simensis* is more closely related to the grey wolf (*C. lupus*) and the coyote (*C. latrans*) than to any African canid (Gottelli *et al.* 1994), and that the species may have evolved from a grey wolf-like ancestor crossing to northern Africa from Eurasia as recently as 100,000 years ago (Gottelli *et al.* 2004). There are fossils of wolf-like canids from the late Pleistocene in Eurasia (Kurtén 1968), but unfortunately no fossil record of *C. simensis*.

Microsatellite and mitochondrial DNA variability in *C. simensis* was small relative to other canid species (Gottelli *et al.* 1994, 2004), suggesting small population sizes may have characterised its recent evolution.

Chromosome number not known.

Description

A medium-sized canid with a reddish coat, distinctive white markings, long legs and an elongated muzzle, resembling a coyote in conformation and size. Males are significantly larger (20%) than females in terms of body mass (Table 6.4.1). The face, ears and upper parts of the muzzle are red. Ears broad, pointed, and directed forward; the pinnae are thickly fringed with long white hairs growing inward from the edge. Palate, gums, and naked borders of the lips entirely black. Characteristic facial markings include a white ascending crescent below the eyes, and a small white spot on the cheeks. The throat, chest, and

Table 6.4.1. Body measurements of the Ethiopian wolf from Bale Mountains (Sillero-Zubiri and Gottelli 1994).

HB male	963mm (928–1012) n=18
HB female	919mm (841–960) n=8
T male	311mm (290–396) n=18
T female	287mm (270–297) n=8
HF male	199mm (193–209) n=18
HF female	187mm (178–198) n=8
E male	108mm (100–119) n=18
E female	104mm (95–110) n=8
WT male	16.2kg (14.2–19.3) n=18
WT female	12.8kg (11.2–14.2) n=8

Claudio Sillero-Zubiri

Ethiopian wolf, Bale Mountains National Park, Ethiopia, 1999.

underparts are white, the ventral part of the neck with a distinctive white band. Pelage is soft and short, ochre to rusty red, with a dense whitish to pale ginger underfur. Boundary between the red coat and the white markings is sharp and well defined. The contrast of white markings against the red coat increases with age and social rank in both sexes; the female's coat is generally paler than the male's. The long, slender legs are reddish outside, with inner aspect white. Front feet have five toes, hind feet with four. The area around the anus is white. There is a short rufus-coloured stripe down the back of the tail, becoming a black stripe leading to a thick brush of black-tipped guard hairs.

The skull is very flat in profile, with only a shallow angle between frontals and nasals. The neuro-cranium is low and narrow, thick, and almost cylindrical. Its width is 30% of the total skull length. Facial length is 58% of the total skull length. The inter-parietal crest is slightly developed, and the coronal ridge is linear. Teeth small and widely spaced, especially the premolars. The dental formula is 3/3-1/1-4/4-2/3=42; m3 occasionally absent. Sharply pointed canines average 19mm in length (14–22mm); carnassials (P4 and m1) are relatively small (Sillero-Zubiri and Gottelli 1994).

Subspecies Coetzee (1977) recognised two subspecies:
- *C. s. simensis* (north-west of the Rift Valley). Nasal bones consistently shorter than those from the southern race (Yalden *et al.* 1980).
- *C. s. citernii* (south-east of the Rift Valley). Redder coat.

A recent study identified differences in the cranio-morphology of wolves on both sides of the Rift Valley (Dalton 2001), but mtDNA analysis from a larger sample of individuals do not support the subspecies criteria of reciprocal monophyly of the northern and southern clades (Gottelli *et al.* 2004).

Similar species Golden jackal (*Canis aureus*): smaller in size, relatively shorter legs, and lack the distinctive reddish coat, white underparts, and throat, chest, and tail markings.

Distribution

Endemic to the Ethiopian highlands, above the tree line at about 3,200m (Figure 6.4.1).

Historical distribution There are no recent records of the species at altitudes below 3,000m, although specimens were collected at 2,500m from Gojjam and north-western Shoa at the beginning of the century (references in Yalden *et al.* 1980). Reported in the Simien Mountains since the species was first described in 1835, but scattered and irregular sightings suggest numbers have been declining. Reported on the Gojjam plateau until early this century (Powell-Cotton 1902; Maydon 1932). South of the Rift Valley, wolves have been reported in the Arsi Mountains since the turn of the century, and, more recently (1959), in the Bale Mountains. Reports of small populations in North Sidamo (Haltenorth and Diller 1980) may be in error. There is no evidence that the Ethiopian wolf ever occurred in Eritrea (Coetzee 1977).

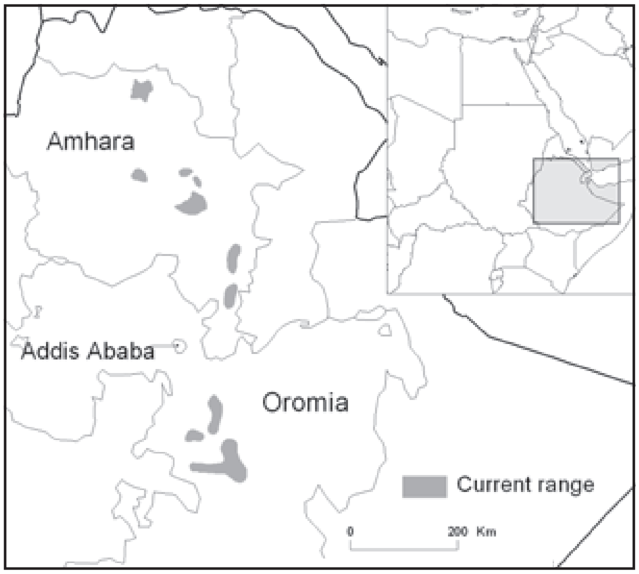

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Figure 6.4.1. Current distribution of the Ethiopian wolf.

Current distribution Confined to seven isolated mountain ranges of the Ethiopian highlands, at altitudes of 3,000–4,500m (Gottelli and Sillero-Zubiri 1992; Marino 2003). In the northern highlands wolves are restricted to land above 3,500–3,800m by increasing agricultural pressure (Yalden *et al.* 1980; Marino 2003). Wolf populations occur north of the Rift Valley in the Simien Mountains, Mount Guna, North Wollo and South Wollo highlands, and Menz. Recently extinct in Gosh Meda (North Shoa), and absent from Mt Choke, Gojjam, for a few decades. South-east of the Rift Valley there are populations in the Arsi Mountains (Mt Kaka, Mt Chilalo and Galama range) and in the Bale Mountains, including the Somkaru-Korduro range (Marino 2003).

Range countries: Ethiopia (Marino 2003).

Relative abundance

More than half of the species' population live in the Bale Mountains, where wolf density is high for a social carnivore of its size, and is positively correlated with density of rodent prey and negatively with vegetation height (Sillero-Zubiri and Gottelli 1995a). Highest wolf densities are found in short Afroalpine herbaceous communities (1.0–1.2 adults/km^2); lower densities are found in *Helichrysum* dwarf-scrub (0.2/km^2), and in ericaceous heathlands and barren peaks (0.1/km^2). Wolves are also present at low density (0.1–0.2/km²) in montane grasslands at lower altitudes.

Elsewhere, overall density is relatively lower. In Menz, wolf density was estimated at 0.2 animals per km² using transect data (Ashenafi 2001). Comparison of census transect data from recent comprehensive surveys (Marino 2003) indicates comparatively higher abundance in North Wollo (0.20 ± 0.20 sightings per km), intermediate in Arsi and Guna (0.10 ± 0.11 and 0.10 ± 0.14, respectively), and lower in South Wollo and Simien (0.08 ± 0.13 and 0.06 ± 0.11, respectively). These results were supported by counts of wolf signs (diggings and droppings) and interview results.

Estimated populations/relative abundance and population trends The most reliable population estimates are those from Bale and Menz where research has been more intense (Table 6.4.2.). The size of the populations in other mountain ranges was derived from field maps of current habitat distribution and extrapolations of wolf densities to the areas of 'optimal' and 'good' habitat in each isolated range (Marino 2003).

Table 6.4.2. The status of Ethiopian wolves in various montane regions of Ethiopia (Trend: I=increasing, S=stable, D=declining, Ex=extinct, ?=unknown).

Region	Population/Abundance	Trend
Simien	40–54	D
Guna	7–10	?
North Wollo	19–23	I
South Wollo	16–19	D
Gojjam	–	Ex
Menz	17–23	S
Gosh Meda	–	Ex
Arsi	93–108	S-D
Bale	250	I

Time series of count data from the Bale Mountains, spanning over 17 years, evidenced marked variation in wolf abundance in association with disease epizootics that affected high-density populations in the early 1990s (Marino 2004). Population numbers returned to previous levels revealing resilience to catastrophes, but at the lower extreme of densities the population rate of increase was inversely density-dependent; delays in the formation of new breeding units appeared to limit the capacity for immediate recovery (Marino 2004).

Habitat

A very localised endemic species, confined to isolated pockets of Afroalpine grasslands and heathlands where they prey on Afroalpine rodents. Suitable habitats extend from above the tree-line at about 3,200m up to 4,500m, with some wolves present in montane grasslands at 3,000m. However, subsistence agriculture extends up to 3,500–3,800m in many areas, restricting wolves to higher ranges (Marino 2003). Rainfall at high altitude varies between 1,000 and 2,000mm/year, with one pronounced dry period from December to February/March.

Wolves utilise all Afroalpine habitats, but prefer open areas with short herbaceous and grassland communities where rodents are most abundant, along flat or gently sloping areas with deep soils and poor drainage in parts. Prime habitats in the Bale Mountains are characterised by short herbs (*Alchemilla* spp.) and grasses and low vegetation cover, a community maintained in continuous succession as a result of molerat (*Tachyoryctes macrocephalus*) burrowing activity. Other good habitats include tussock grasslands (*Festuca* spp., *Agrostis* spp.), high-altitude scrubs dominated by *Helichrysum* spp. and short grasslands in shallow soils. In northern parts of the range, plant communities characterised by a matrix of '*guassa*' tussock grasses (*Festuca* spp.), '*cherenfi*' bushes (*Euryops pinifolius*) and giant lobelias (*Lobelia rhynchopetalum*) sustain high rodent abundance and are preferred by wolves. Ericaceous moorlands (*Erica* and *Phillipia* spp.) at 3,200–3,600m are of marginal value, with open moorlands having patches of herbs and grasses which are relatively good habitat.

Food and foraging behaviour

Food Ethiopian wolves feed almost exclusively upon diurnal rodents of the high-altitude Afroalpine grassland community. In the Bale Mountains, diurnal rodents accounted for 96% of all prey occurrences in faeces, with 87% belonging to three Bale endemic species, the giant molerat (300–930g), Blick's grass rat (*Arvicanthis blicki*), and the black-clawed brush-furred rat (*Lophuromys melanonyx*) (Sillero-Zubiri and Gottelli 1995b). Other prey species include typical vlei rat (*Otomys typus*), yellow-spotted brush-furred rat (*Lophuromys flavopunctatus*), Starck's hare (*Lepus starcki*), and goslings and eggs. Occasionally, wolves were observed feeding on rock hyrax (*Procavia capensis*), and young of common duiker (*Sylvicapra grimmia*), reedbuck (*Redunca redunca*) and mountain nyala (*Tragelaphus buxtoni*) (Sillero-Zubiri and Gottelli 1995b; Malcolm 1997; C. Sillero-Zubiri pers. obs.). Leaves of sedge (*Carex monostachya*) are occasionally ingested, probably to assist digestion or control parasites.

Where the giant molerat is absent, it is replaced in the wolf diet by the smaller East African molerat, *Tachyoryctes splendens* (i.e., *Gaysay* montane grassland in Bale – Malcolm 1997, and Menz – Ashenfi 2001). Similarly, in northern Ethiopia *Arvicanthis abyssinicus* and *Lophurmys flavopunctatus* replace their respective endemic relatives from Bale *A. blicki* and *L. melanonyx*. Elsewhere, *O. typus*, a rare prey item in Bale and Menz, was identified as the commonest prey in droppings collected in other five populations (Marino 2004). This study confirmed that wolves are specialised hunters of diurnal rodents all throughout their distribution, with some degree of dietary variation along climatic-induced gradients.

Foraging behaviour Although the Ethiopian wolf is a pre-eminent, solitary rodent hunter it is also a facultative, cooperative hunter. Occasionally, small packs have been seen chasing young antelopes, lambs, and hares and making a kill. Ethiopian wolves will take carrion or feed on carcasses; in fact, a sheep carcass is the most successful bait for attracting wolves (C. Sillero-Zubiri pers. obs.). The local name '*jedalla farda*' – the horse's jackal – refers to the wolves' habit of following mares and cows about to give birth so they can eat the afterbirth. In areas of grazing in Bale, wolves were often seen foraging among herds of cattle, a tactic that may aid in ambushing rodents out of their holes, by using the herd as a mobile hide.

In Bale, wolves are mostly diurnal. Peaks of foraging activity suggest that they synchronise their activity with that of rodents above the ground (Sillero-Zubiri *et al.* 1995). There is little nocturnal activity, with wolves seldom moving far from their evening resting site. They may become more crepuscular and nocturnal where human interference is severe (e.g., Simien: Brown 1964; Somkaro and Kaka Mountains: C. Sillero-Zubiri pers. obs.).

Rich food patches are carefully explored by wolves, which walk slowly, pausing frequently to investigate holes or to localise the rodents by means of their excellent hearing. Once the prey is located, the wolf moves stealthily towards it, taking short steps, and freezing, sometimes with its belly pressed flat to the ground. The quarry is grabbed with the mouth after a short dash. A stalk can last from seconds to up to one hour, especially in the case of a giant molerat. Occasionally, wolves run in zig-zags across rat colonies picking up the rodents in passing. Digging prey out is common and is the most favoured technique to catch giant molerats, with the effort expended varying from a few scratches at a rat hole to the total destruction of a set of burrows leaving mounds of earth one metre high. Sometimes, digging serves to reach a nest of grass rats. Kills are often cached and later retrieved.

Damage to livestock or game Until recently, wolves in Bale were unmolested by humans and did not appear to be regarded as a threat to sheep and goats, which are sometimes left unattended during the day (Gottelli and Sillero-Zubiri 1992). Only two instances of predation upon lambs were recorded during 1,800 hours of observation (Sillero-Zubiri and Gottelli 1994). Losses to wolves in the southern highlands were dismissed by herders as unimportant when compared to damage by spotted hyaenas (*Crocuta crocuta*) or jackals. Elsewhere, wolves have been persecuted in the past due to their reputation as predators of sheep and goats. Livestock predation is reported as important in some heavily populated areas of Wollo and Simien (Marino 2003) but livestock remains were uncommon in droppings collected from across the highlands (Marino 2004).

Adaptations

The legs are strikingly long and slender, seemingly suitable for coursing in open country. The muzzle is long, and the small, well-spaced teeth suggest morphological adaptation to feeding on rodents. They have an unusually good sense of smell, and bolt more readily at the scent rather than the sight of man.

The guard hairs are short and the underfur is thick, providing protection at temperatures as low as -15°C. Ethiopian wolves do not use dens to rest at night, and during the breeding season only pups and nursing females use the den. Wolves sleep in the open, alone or in groups, curled up, with nose beneath the tail. Several animals may sleep close together. During the cold nights in the dry season, a 'bed' is carefully prepared from a pile of vegetation debris, the product of giant molerat activity. During the day they take frequent naps, usually resting on their sides. Occasionally, they seek shelter from the rain under overhanging rocks and behind boulders.

Social behaviour

Ethiopian wolves live in packs, discrete and cohesive social units that share and defend an exclusive territory. Packs of 3–13 adults (mean=6) congregate for social greetings and border patrols at dawn, noon and evenings, and rest together at night, but break up to forage individually in the morning and early afternoon (Sillero-Zubiri and Gottelli 1995a).

Annual home ranges of eight packs monitored for four years averaged 6.0km², with some overlap in home ranges. Home ranges in an area of lower prey biomass averaged 13.4km² (n=4) (Sillero-Zubiri and Gottelli 1995a). Overlap and aggressive encounters between packs were highest during the mating season. Dispersal movements are tightly constrained by the scarcity of suitable habitat. Males do not disperse and are recruited into multi-male philopatric packs; some females disperse at two years of age and become 'floaters', occupying narrow ranges between pack territories until a breeding vacancy becomes available (Sillero-Zubiri *et al.* 1996a). Breeding females are typically replaced after death by a resident daughter. Pack adult sex ratio is biased toward males 1.8:1 (n=59), with small family groups closer to 1:1 (Sillero-Zubiri and Gottelli 1995a).

Scent marking of territory boundaries, via urine posts, scratching, and faeces (deposited on conspicuous sites like mounds, rocks and bushes), and vocalisations, are common and function in advertising and maintaining territories (Sillero-Zubiri and Macdonald 1998). All pack members, independent of social rank, regularly scent-mark objects along territory boundaries with raised-leg urinations and scratches. Aggressive interactions with neighbouring packs are common, highly vocal and always end with the smaller group fleeing from the larger (Sillero-Zubiri and Macdonald 1998).

Calls can be grouped into two categories: alarm calls, given at the scent or sight of man, dogs, or unfamiliar wolves; and greeting calls, given at the reunion of pack members and to advertise pack size, composition and position (Sillero-Zubiri and Gottelli 1994). Alarm calls start with a 'huff' (rapid expulsion of air through mouth and nose), followed by a quick succession of high-pitched 'yelps' (a series of 4–5 'yeahp-yeahp-yeahp-yeahp') and 'barks'. 'Yelps' and 'barks' can also be given as contact calls, and often attract nearby pack mates. Greeting calls include a 'growl' of threat, a high-frequency 'whine' of submission, and intense 'group yip-howls'. A lone howl and a group howl are long-distance calls used to contact separate pack members and can be heard up to 5km away. Howling by one pack of wolves may stimulate howling in adjacent packs. Communal calls muster pack members before a border patrol.

Reproduction and denning behaviour

The only detailed information available on the reproductive habits of these animals comes from four years of observations of nine wild packs in the Bale Mountains (Sillero-Zubiri 1994; Sillero-Zubiri *et al.* 2004).

Pre-copulatory behaviour by the dominant female includes an increase in the scent-marking rate, play soliciting, food-begging towards the dominant male, and agonistic behaviour towards subordinate females. The receptive period is synchronised in sympatric females to less than two weeks (Sillero-Zubiri *et al.* 1998). Courtship may take place between adult members of a pack or with members of neighbouring packs. After a brief courtship, which primarily involves the dominant male permanently accompanying the female, wolves copulate over a period of three to five days. Copulation involves a copulatory tie lasting up to 15 minutes. Other males may stand by a tied pair with no signs of aggression. Mate preference is shown, with the female discouraging attempts from all but the pack's dominant male, by either defensive snarls or moving away; the female is receptive to any visiting male from neighbouring packs. Sillero-Zubiri *et al.* (1996a) found that up to 70% of matings (n=30) involved males from outside the pack.

The dominant female of each pack gives birth once a year between October and January (Sillero-Zubiri *et al.* 1998). Only about 60% of females breed successfully each year. During breeding and pregnancy, the female coat turns pale yellow and becomes woolly, and the tail turns brownish, and loses much of its hair. Gestation lasts 60–62 days (based on the time from last day of mating to parturition). Pups are born in a den dug by the female in open ground, under a boulder or inside a rocky crevice. Neonates are born with their eyes closed and the natal coat is charcoal grey with a buff patch in chest and inguinal regions. Two to seven pups emerge from the den after three weeks. At this time, the dark natal coat begins to be replaced by the pelage typical of the species. Pups are regularly moved between dens, up to 1,300m apart. In eight out of 18 natal dens watched, a subordinate female assisted the mother in suckling the pups. At least 50% of extra nursing females showed signs of pregnancy and may have lost or deserted their own offspring before joining the dominant female's den (Sillero-Zubiri 1994; Sillero-Zubiri *et al.* 2004). Five and six placental scars were counted in the uteri of two females.

Development of the young comprises three stages: (1) early nesting (week 1 to week 4), when the young are entirely dependent on milk; (2) mixed nutritional dependency (week 5 to week 10), when milk is supplemented by solid foods regurgitated by all pack members until pups are completely weaned; and (3) post-weaning dependency (week 10 to six months), when the pups subsist almost entirely on solid foods supplied by helpers. Adults have been observed providing food to juveniles up to one year old. Juveniles will join adults in patrols as early as six months of age, but will not urinate with a raised leg posture until 11 months, if male, or 18 months, if female. Yearlings attain 80–90% of adult body mass, and full adult appearance is reached at two years. Both sexes become sexually mature during their second year.

Competition

The high densities and diversity of raptors (12 recorded species in Bale), many of which have been observed to feed on small mammals, are likely to pose the greatest competitive threat to the wolves (although they tend to clepto-parasitise eagles's kills – Sillero-Zubiri and Gottelli 1995a). In addition, free-ranging domestic dogs, golden jackals and servals (*Leptailurus serval*) may also feed upon the same prey species. There is interference competition with domestic dogs and spotted hyaenas (*Crocuta crocuta*) that will actively chase away wolves from large carcasses. Honey badgers (*Mellivora capensis*) are also possible competitors for food and burrows (Sillero-Zubiri 1996).

Mortality and pathogens

Natural sources of mortality There are no known predators, but unattended young might be taken by spotted hyaenas or the Verreaux eagle (*Aquilla verreauxi*). Attacks of the tawny eagle (*Aquilla rapax*) directed at small pups result in swift defence by guarding adults. Other causes of mortality include starvation of juveniles between weaning and one year of age. The sex ratio (see above) indicates that female mortality is higher than that of males. This is most likely associated with their dispersal as subadults.

Persecution During periods of political instability in the recent past, guns were more available and killings more frequent. In many regions, people living close to wolves believe numbers are recovering through successive years of good breeding and less persecution. The degree of conflict due to predation determines the negative attitude to wolves in some regions where persecution may persist (Marino 2003).

Hunting and trapping for fur There are no reports of exploitation for furs, although some opportunistic use may occur. For instance, in parts of Wollo wolf skins were seen used as saddle pads (C. Sillero-Zubiri pers. obs.). In the past, sport hunters occasionally killed wolves, but no hunting is currently permitted.

Road kills On the Sanetti Plateau in Bale, an all-weather road runs across 40km of prime wolf habitat and is used on average by 26 vehicles (mostly trucks) every day. At least four wolves have been killed by vehicles since 1988 (C. Sillero-Zubiri pers. obs.). Two other animals have been shot from the road and another two were left with permanent limps from collisions with vehicles. Similar accidents may occur on other roads across wolf habitat such as the Mehal Meda road in Menz, and the road to Ticho in Arsi.

Pathogens and parasites Rabies is the most dangerous and widespread disease to affect Ethiopian wolves, and is the main cause of mortality in Bale (Sillero-Zubiri *et al.* 1996b). The disease killed whole wolf packs in 1990 and 1991 and accounted for a major population decline with losses of up to 75% (Sillero-Zubiri *et al.* 1996b; Laurenson *et al.* 1998). A rabies epizootic was reported in late 2003 and has accounted for similar mortality levels, although the full impact of it has yet to be assessed fully (S. Williams pers. comm.). In other regions, rabies cases have been reported in domestic dogs, livestock, people and one Ethiopian wolf (Sillero-Zubiri *et al.* 2000; Marino 2003). The level of rabies awareness amongst people, and the frequency of the reports, suggests high incidence across the highlands.

In Bale dogs travel regularly with their owners in and out of wolf range, and are in contact with many other dogs which are attracted to garbage and carrion in villages, and they may provide the vehicle for pathogens such as rabies or distemper to reach their wild relatives (Laurenson *et al.* 1998). The risk of transmission, however, will depend on the probability of contact between wolves and dogs, which varies with grazing regimes in high-altitude pastures, dog husbandry and the spatial distribution of wolf habitat in relationship to settlements. Long-term population monitoring data from Bale, indicated that high wolf densities may be the most important factor in determining the vulnerability of a local population to epizootics, independently of the abundances of sympatric dogs, people and livestock within the wolf range (Marino 2004). A population viability model indicates that disease-induced population fluctuations and extinction risks can be markedly reduced with the vaccination against rabies of a relatively small proportion of wolves (Haydon *et al.* 2002).

Ethiopian wolves are exceptionally free of ectoparasites, perhaps because of the cold mountain climate; none were found on any of 67 animals handled. Nematodes and trematodes were present in faeces and in the gut of several carcasses, one of which was identified as *Taenia pisiformis* (M. Anwar pers. comm.).

Longevity In the wild 8–10 years; one known male in Bale lived 12 years (C. Sillero-Zubiri pers. obs.).

Historical perspective

There is little evidence of wolves playing a significant role in Ethiopian culture, and they seldom feature in folklore. Nonetheless, the wolf has been recognised by Ethiopian people, with the earliest mention in literature dating back to the 13th century (Sillero-Zubiri and Macdonald 1997). More recently, the government has used the wolf as a national symbol, and it has featured in two stamp series. No known traditional uses, although wolf livers may be used as a medicament in north Ethiopia (Staheli 1975, in Sillero-Zubiri and Macdonald 1997).

The Bale Mountains National Park was established in 1970 partly on the recommendation of British naturalist Leslie Brown to protect Ethiopian wolves (Brown 1964).

Conservation status

The species is more restricted now than in the past (Yalden *et al.* 1980). With probably only 500 individuals surviving, this distinctive carnivore is considered the rarest canid in the world and one of the rarest African carnivores. Recent exhaustive surveys, however, have confirmed the persistence of seven isolated populations, two previously undescribed (Marino 2003).

Threats Continuous loss of habitat due to high-altitude subsistence agriculture represents the major threat. Sixty percent of all land above 3,200m has been converted into farmland, and all populations below 3,700m are particularly vulnerable to further habitat loss, especially if the areas are small and of relatively flat relief (Marino 2003). Habitat loss is exacerbated by overgrazing of highland pastures by domestic livestock, and in some areas habitat is threatened by proposed development of commercial sheep farms and roads. Human persecution triggered by political instability in the past is currently less severe and is associated with conflicts over livestock losses (Marino 2003). Recent population decline in Bale is mostly due to disease epizootics, with road kills and shooting as secondary threats. Rabies is a potential threat to all populations. Most of these threats are exacerbated by the wolves' specialisation to life in the Afroalpine ecosystem.

In Bale the Ethiopian wolf hybridises with domestic dogs. Gottelli *et al.* (1994) used mitochondrial DNA restriction fragments and micro-satellite alleles to conclude that hybridisation was relatively common in western Bale as a result of crosses between female wolves and male domestic dogs. Hybrids have shorter muzzles, heavier-built bodies and different coat patterns. Although hybrids are confined to the Web Valley in western Bale they may threaten the genetic integrity of the wolf population. Following hybridisation, a population may be affected by outbreeding depression or reduction in fitness, although to date this does not seem to have taken place in Bale. To date there is no indication of hybridisation taking place outside western Bale.

Commercial use There is no exploitation for furs or other purposes.

Occurrence in protected areas Simien Mountains National Park; Bale Mountains National Park; Hunting blocks in Arsi; Denkoro State Forest in South Wollo; Guassa Community Management in North Shoa.

Protection status CITES – not listed.

Current legal protection Full official protection under Ethiopia's Wildlife Conservation Regulations of 1974, Schedule VI. Killing a wolf carries a sentence of up to two years.

Conservation measures taken A number of important steps have been taken in the interests of conserving this endemic species, including: 1) a dog vaccination campaign in Bale, currently extended to Wollo; 2) sterilisation programme for domestic dogs and hybrids in Bale; 3) vaccination of wolves in parts of Bale affected by rabies; 4) community and school education programme in Bale and Wollo; 5) strengthening the capacity of the Bale Mountains National Park – funding patrolling, maintenance of infrastructure, etc.; 6) surveys to determine the persistence and status of all populations of wolves; 7) monitoring of all wolf populations; 8) Ethiopian Wolf Conservation Strategy Workshop, Bale Mountains, November 1999, with representatives of national, regional and local governments and international scientists (Sillero-Zubiri *et al.* 2000); and 9) establishment of the Ethiopian Wolf Conservation Committee within Ethiopia as a national steering committee for dealing with conservation issues.

In 1983, the Wildlife Conservation Society set up the Bale Mountains Research Project, which publicised the wolf's plight and started a regular monitoring programme for the species. A detailed four-year field study followed (Sillero-Zubiri 1994). Based on its findings, the IUCN Canid Specialist Group produced an action plan for the Ethiopian wolf (Sillero-Zubiri and Macdonald 1997), providing a detailed strategy for the conservation and management of remaining wolf populations. This plan advocated immediate action on three fronts – education, wolf population monitoring, and rabies control in domestic dogs – to conserve the Afroalpine ecosystem and its top predator. As a result, the Ethiopian Wolf Conservation Programme (EWCP) was established in 1995 by Oxford University with support from the Born Free Foundation, UK. Its overall aim is to protect the Afroalpine ecosystem and many of its rare highland endemic plants and animals through better management in Bale and the establishment of other conservation areas in Menz and Wollo. The EWCP currently monitors the demography of Bale and selected populations in South and North Wollo, supports park patrols within the wolf range, undertakes domestic dog control and the removal of dog-wolf hybrids. Additionally, the EWCP carries out a community conservation education campaign that targets people living inside the wolf's range and is aimed at improving dog husbandry and combating disease in the park and surroundings. A large-scale dog vaccination programme (targeting up to 3,000 dogs a year) seeks to reduce the occurrence of rabies and distemper within the Ethiopian wolf range and is backed up by further epidemiological and demographic studies. The EWCP is also active elsewhere in Ethiopia, with representatives surveying and monitoring all wolf ranges and implementing education campaigns about the plight of the species. Zelealem Tefera Ashenafi set up the Guassa Biodiversity Project in 1996, looking at the relationships between pastoralists and wildlife in the highlands of Menz.

Occurrence in captivity

There are no animals in captivity. Recent attempts to establish captive populations were abandoned due to lack of permission from the Ethiopian government.

Current or planned research projects

S. Williams (Wildlife Conservation Research Unit, University of Oxford, UK) and Ethiopian Wolf Conservation Programme staff currently monitor the demography of the Bale and Wollo populations. Data collected include pack demographic structures, home ranges and pup survival.

J. Marino (Wildlife Conservation Research Unit, University of Oxford, UK) is studying the effect of habitat heterogeneity and fragmentation on the ecology of Ethiopian wolves at various spatial scales and levels of organisation.

L. Tallents and D. Randall (Wildlife Conservation Research Unit, University of Oxford, UK) have begun graduate studies on foraging ecology and reproductive strategies.

K. Laurenson and D. Knobel (Centre for Tropical Veterinary Medicine, University of Edinburgh, UK) are testing a combination of vaccination trial and field techniques to investigate the dynamics of canid pathogens, particularly rabies, in domestic and wild carnivore species.

Anteneh Shimelis and Ermias A. Beyene (Addis Ababa University), S. Williams (Wildlife Conservation Research Unit, University of Oxford), S. Thirgood (Frankfurt Zoological Society, Tanzania) are studying predator-prey interactions in Bale, assessing whether rodent populations are regulated by competition (with domestic livestock) or by predation (by wolves and raptors).

Gaps in knowledge

Although the behavioural ecology of the species is well known, this has been focused in the optimal habitats in the Bale Mountains. Additional information on dispersal distance and survival would be useful. Investigation into the role of the species in the epidemiology of canid-related diseases is necessary. Studies on wolf-prey relationships and prey availability in the high risk populations of northern Ethiopia are also urgently needed.

Core literature

Gottelli and Sillero-Zubiri 1992; Gottelli *et al.* 1994, 2004; Haydon *et* al. 2002; Laurenson *et al.* 1998; Marino 2003, 2004; Sillero-Zubiri 1994; Sillero-Zubiri and Gottelli 1994, 1995a,b; Sillero-Zubiri *et al.* 1996a,b, 2000, 2004a; Sillero-Zubiri and Macdonald 1997.

Reviewers: Neville Ash, M. Karen Laurenson, James R. Malcolm, Zelealam Tefera Ashenafi, Stuart Williams. **Editor:** Michael Hoffmann.

6.5 African wild dog
Lycaon pictus (Temminck, 1820)
Endangered – EN: C2a(i) (2004)

R. Woodroffe, J.W. McNutt and M.G.L. Mills

Other names

English: Cape hunting dog, painted hunting dog; **French:** lycaon, cynhyène, loup-peint; **Italian:** licaone; **German:** hyänenhund; **Spanish:** licaon; **Indigenous names:** Afrikaans: wildehond (Namibia, South Africa); Amharic: takula (Ethiopia); Ateso: apeete; isiNdebele: iganyana iketsi leKapa (South Africa); isiXhosa: ixhwili (South Africa); isiZulu: inkentshane (South Africa); Kalenjin: suyo (Kenya); Kibena: liduma; Kibungu: eminze; Kichagga: kite kya nigereni; Kihehe: ligwami; Kijita: omusege; Kikamba: nzui; Kikukuyu: muthige; Kikuyu: muthige (Kenya); Limeru: mbawa; Kiliangulu: eeyeyi; Kimarangoli: imbwa; Kinyaturu: mbughi; Kinyiha: inpumpi; Kinyiramba: mulula; Kisukuma: mhuge; Kiswahili: mbwa mwitu; Kitaita: Kikwau; Kizigua: mauzi; Lozi: liakanyani; Luo: sudhe, prude; Maasai: osuyiani (Kenya, Tanzania); Mandingue: juruto (Mali, Senegal); Nama and Damara:!Gaub (Namibia); Samburu: Suyian (Kenya); Sebei: kulwe, suyondet; Sepedi: lehlalerwa, letaya (South Africa); Sesotho: lekanyane, mokoto, tlalerwa (Lesotho, South Africa); Setswana: leteane, letlhalerwa, lekanyana (Botswana, South Africa); Shona: mhumhi (Zimbabwe); siSwati: budzatja, inkentjane (Swaziland, South Africa); Tshivenda: dalerwa; Woloof and Pulaar: saafandu (Senegal); Xitsonga: hlolwa (Mozambique, South Africa); Yei: umenzi (Botswana).

Taxonomy

Hyaena picta Temminck, 1820. Ann. Gen. Sci. Phys. 3: 54. Type locality: "à la côte de Mosambique" [coastal Mozambique].

The genus *Lycaon* is monotypic and was formerly placed in its own subfamily, the Simoncyoninae. While this subfamily division is no longer recognised (Wozencraft 1989), recent molecular studies have supported the separation of this species in its own genus (Girman *et al.* 1993). Wild dogs have been grouped with dhole (*Cuon alpinus*) and bush dogs (*Speothos venaticus*), but morphological similarities among these species are no longer considered to indicate common ancestry, and they are now considered close to the base of the wolf-like canids (Girman *et al.* 1993).

Genetic and morphological studies carried out by Girman *et al.* (1993) initially suggested the existence of separate subspecies in eastern and southern Africa. However, no geographical boundaries separated these proposed subspecies, and dogs sampled from the intermediate area showed a mixture of southern and eastern haplotypes, indication of a cline rather than distinct subspecies (Girman and Wayne 1997).

Chromosome number: 2n = 78 (Chiarelli 1975).

Description

A large, but lightly built canid, with long, slim legs and large, rounded ears (Table 6.5.1). The coloration of the pelage is distinctive but highly variable, with a combination of irregular black, yellow-brown and white blotches on the back, sides, and legs. Wild dogs in north-east Africa tend to be predominantly black with small white and yellow patches, while dogs in southern Africa are more brightly coloured with a mix of brown, black and white. Each animal's pelage coloration is unique, and this can be used to identify individual animals. Coloration of the head and tail is more consistent: almost all dogs have a yellow-brown head with a black 'mask', black ears, and a black line following the sagittal crest, and a white tip to

Table 6.5.1. Body measurements for the African wild dog.

	Kruger National Park, South Africa (M.G.L. Mills unpubl.).	**Laikipia and Samburu Districts**, Kenya (R. Woodroffe unpubl.).
HB male	1,229mm (1,060–1,385) n=16	962mm (845–1,068) n=5
HB female	1,265mm (1,090–1,410) n=15	990mm (930–1,045) n=4
T male	354mm (320–420) n=15	345mm (328–380) n=5
T female	326mm (310–370) n=13	328mm (320–333) n=4
HF male	250mm (230–260) n=13	245mm (225–318) n=5
HF female	241mm (230–250) n=14	224mm (215–229) n=3
E male	135mm (125–148) n=15	128mm (110–145) n=5
E female	130mm (125–135) n=15	129mm (120–136) n=4
WT male	28.0kg (25.5–34.5) n=12	21.0kg, n=1
WT female	24.0kg (19.0–26.5) n=12	18.0kg, n=1

the tail. The length of the pelage varies regionally, but hair is generally very short on the limbs and body but longer on the neck, sometimes giving a shaggy appearance at the throat. There are four digits on each foot, all with claws; and in most individuals, the pads of the second and third toes are partially fused. Females have six to eight pairs of mammae. Males are slightly heavier than females, and are easily recognised by the conspicuous penis sheath.

The dental formula is 3/3-1/1-4/4-2/3=42. In common with *Cuon* and *Speothos*, departure from the typical form of dentition within the Canidae is found in the lower carnassial where the inner cusp of the talonid is missing so that instead of forming a basin, this part of the tooth forms a subsidiary blade. This suggests a highly predacious diet, with corresponding diminished importance of vegetable matter (Ewer 1973).

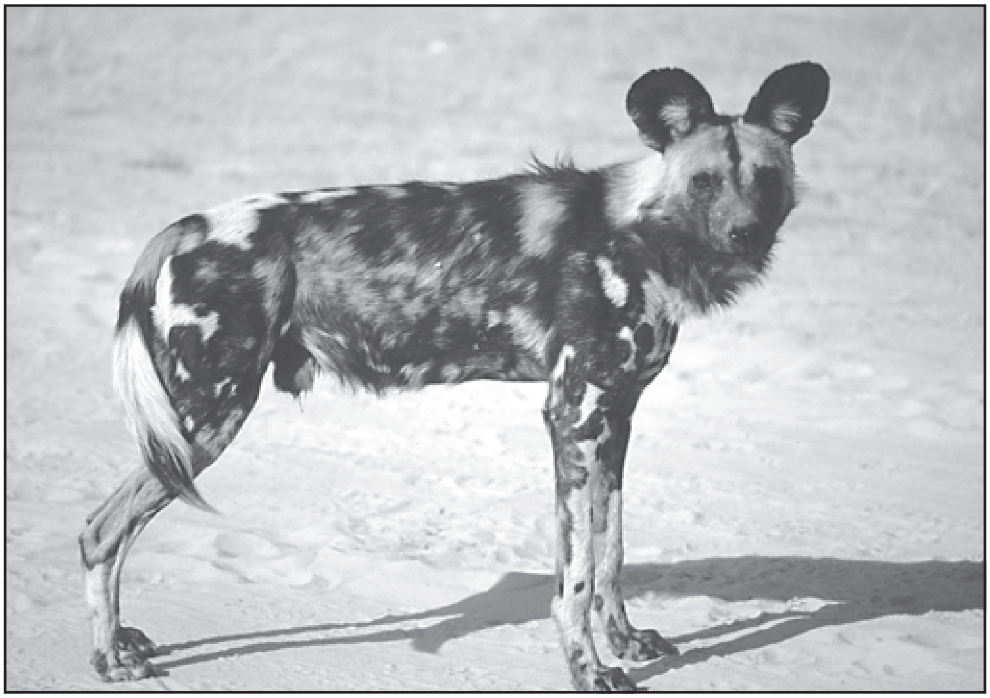
Subspecies No subspecies are currently recognised (Girman and Wayne 1997; Girman *et al*. 2001).

Similar species Wild dogs are occasionally confused with feral dogs and striped hyaenas (*Hyaena hyaena*), and even side-striped jackals (*Canis adustus*) and bat-eared foxes (*Otocyon megalotis*), but are morphologically distinct from all.

Distribution

Historical distribution Historical data indicate that wild dogs were formerly distributed throughout sub-Saharan Africa, from desert (Lhotse 1946) to mountain summits (Thesiger 1970), and probably were absent only from lowland rainforest and the driest desert (Schaller 1972).

Current distribution Wild dogs have disappeared from much of their former range – 25 of 39 former range states no longer support populations (Fanshawe *et al*. 1997). The species is virtually eradicated from West Africa, and greatly reduced in central Africa and north-east Africa.



Male African wild dog, age unknown. Moremi Wildlife Reserve, Okavango Delta, Botswana, 1990.

Chris and Tilde Stuart

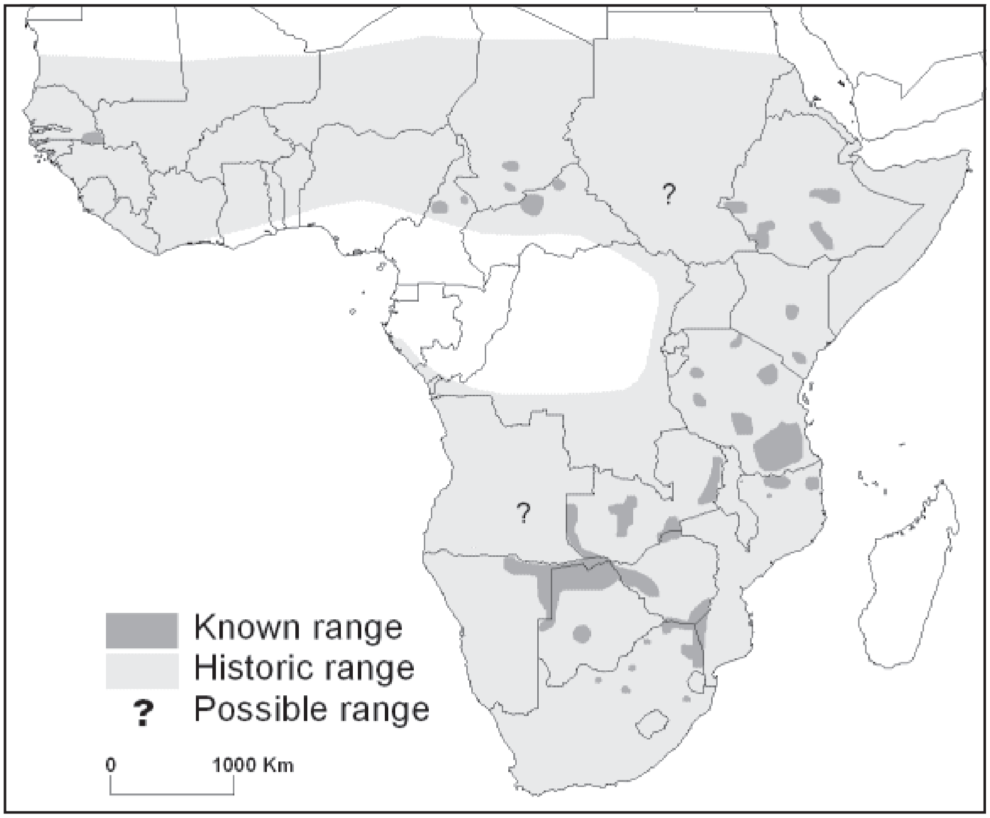


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Figure 6.5.1. Current distribution of the African wild dog.

The largest populations remain in southern Africa (especially northern Botswana, western Zimbabwe, eastern Namibia, and Kruger National Park, South Africa) and the southern part of East Africa (especially Tanzania and northern Mozambique). Details of current distribution and status are in Woodroffe *et al.* (1997).

Range countries Angola (?), Botswana, Cameroon, Central African Republic, Chad, Ethiopia, Kenya, Mozambique, Namibia, Senegal, South Africa, Sudan, Swaziland (vagrant), Tanzania, Zambia, Zimbabwe. (Fanshawe *et al.* 1997). Wild dogs are known to be, or presumed to be, extinct or near-extinct in Benin, Burkina Faso, Burundi, Democratic Republic of Congo, Eritrea, Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, Ivory Coast, Malawi, Mali, Niger, Nigeria, Rwanda, Sierra Leone, Togo and Uganda (Woodroffe *et al.* 1997). The situation in Angola is unknown, but it is possible that packs still occur there.

Relative abundance

Wild dogs are rarely seen, even where they are relatively common, and it appears that populations have always existed at very low densities. Population densities in well-studied areas are given below (Table 6.5.2), which Ginsberg and Woodroffe (1997a) used to estimate the size of remaining populations at between 3,000–5,500 free-ranging wild dogs in Africa.

Table 6.5.2. Population densities of wild dogs in various study areas across Africa (updated from Woodroffe *et al*. 1997).

Study site	**Population density (adults/100km^2)**
Aitong, near Maasai Mara, Kenya	2.6–4.6
Okavango Delta, Botswana	3.5
North-central Botswana	0.5
Hluhluwe-Umfolozi Park, South Africa	3.3
Hwange National Park, Zimbabwe	1.5
Zambezi Valley Complex	2.0
Kruger National Park, South Africa	0.8–2.0
Selous Game Reserve, Tanzania	4
Serengeti National Park, Tanzania 1967–1979	1.5
Serengeti National Park, Tanzania 1985–1991	0.67

Estimated populations/relative abundance and population trends The following estimated sizes and trends of national wild dog populations in Africa are updated from Woodroffe *et al.* (1997) (Table 6.5.3). Figures for protected and unprotected areas are approximate, since few wild dog populations are confined entirely to protected areas. For this reason, populations given for protected areas are almost universally over-estimated, with concomitant under-estimates for numbers outside protected areas.

Table 6.5.3. The status of wild dogs in range states across Africa (I=increasing, S=stable, D=declining).

Country	In and around protected areas		Outside protected areas		Total
	Population	Trend	Population	Trend	
Botswana	500	S	300		800
Cameroon	50	D?			50
Central African Republic	150	?			150
Chad	70	?			70
Ethiopia	200	?	200	?	400
Kenya	100	S?	250	I	350
Mozambique	200	?			200
Namibia	100	S	300	S?	400
Senegal	20	?			20
Somalia	0	?	20	?	20
South Africa	300	S	110	I?	410
Sudan			50	?	50
Tanzania	1,300	S?	500	S?	1,800
Zambia	430	?	?	–	430
Zimbabwe	400	SD?	200	I	600
Grand total					**5,750**

Habitat

Wild dogs are generalist predators, occupying a range of habitats including short-grass plains, semi-desert, bushy savannahs and upland forest. While early studies in the Serengeti National Park, Tanzania, led to a belief that wild dogs were primarily an open plains species, more recent data indicate that they reach their highest densities in thicker bush (e.g., Selous Game Reserve, Tanzania; Mana Pools National Park, Zimbabwe; and northern Botswana). Several relict populations occupy dense upland forest (e.g., Harenna Forest, Ethiopia: Malcolm and Sillero-Zubiri 2001; Ngare Ndare Forest, Kenya). Wild dogs have been recorded in desert (Lhotse 1946), although they appear unable to establish themselves in the southern Kalahari (M.G.L. Mills unpubl.), and montane habitats (Thesiger 1970; Malcolm and Sillero-Zubiri 2001), although not in lowland forest. It appears that their current distribution is limited primarily by human activities and the availability of prey, rather than by the loss of a specific habitat type.

Food and foraging behaviour

Food Wild dogs mostly hunt medium-sized antelope. Whereas they weigh 20–30kg, their prey average around 50kg, and may be as large as 200kg. In most areas their principal prey are impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), Thomson's gazelle (*Gazella thomsonii*) and wildebeest (*Connochaetes taurinus*) (Table 6.5.4). They will give chase of larger species, such as eland (*Tragelaphus oryx*) and buffalo (*Syncerus caffer*), but rarely kill such prey. Small antelope, such as dik-dik (*Madoqua* spp.), steenbok (*Raphicerus campestris*) and duiker (tribe *Cephalophini*) are important in some areas, and warthogs (*Phacochoerus* spp.) are also taken in some populations. Wild dogs also take very small prey such as hares, lizards and even eggs, but these make a very small contribution to their diet.

Foraging behaviour Wild dogs hunt in packs. Hunts are almost always preceded by a "social rally" which is believed to coordinate the pack in preparation for hunting. Once prey sight the dogs, they may flee, or stand and defend themselves alone or as a herd. During chases, wild dogs can run at speeds of up to 60km/h, and are specially adapted to deal with the heat stress that this involves (Taylor *et al*. 1971). After one dog has made the first grab, other pack members may help to drag the quarry to the ground. Once the quarry has been captured, the animal is killed by disembowelling. In some hunts, one pack member may restrain the head of the prey by biting its nose and holding on while others make the kill. Hunts can appear to be highly coordinated events, but in many areas packs tend to split during hunts with individual dogs often chasing and bringing down the prey alone, then leaving it to find and bring the rest of the pack to the kill.

Hunting success is high in comparison with other large carnivore species (e.g., in Serengeti, 70% of 133 wild dog hunts ended in a kill, compared with 23% of 523 lion hunts; Schaller 1972). As a result of social hunting, each pack member has a higher foraging success (measured as kg killed per km chased) than it would if it hunted alone (Creel and Creel 1995). Members of larger packs are also able to specialise on more profitable prey species (e.g., wildebeest; Creel and Creel 2002), and are better able to defend their kills against scavenging hyaenas (Fanshawe and FitzGibbon 1993). Wild dogs themselves very rarely scavenge (Mills and Biggs 1993).

Damage to livestock or game Wild dogs do take livestock in some areas, but this is a fairly rare occurrence. In and around the Maasai Mara National Reserve, Kenya, wild dogs ignored livestock, and Samburu and Maasai herders

Table 6.5.4. Diet of wild dogs in three selected study areas. 'n' indicates the number of kills recorded in each area.

Study area	n	impala	kudu	reedbuck	Thomson's gazelle	wildebeest	warthog	Reference
Kruger NP South Africa	78	69%	15%	15%	–	–	–	Mills and Biggs (1993)
Aitong, Kenya	60	17%	–	–	67%	8%	2%	Fuller and Kat (1990)
Selous GR, Tanzania	347	54%	–	–		29%	9%	Creel and Creel (2002)

interviewed in northern Kenya indicated that wild dogs rarely caused problems (R. Woodroffe unpubl.). A study of wild dog depredation on commercially raised livestock in Zimbabwe found that the dogs took fewer cattle than the farmers believed (26 cattle from a herd of >3,000, over a two year period, cf. 52 losses attributed to wild dogs; Rasmussen 1999). Wild dogs hunting in livestock areas outside Selous Game Reserve, Tanzania, were never observed to kill livestock in six years of observation (Creel and Creel 2002). Nevertheless wild dogs can become a severe problem for sheep and goats, with multiple animals being killed in a single attack (R Woodroffe unpubl.).

The impact of wild dogs on wild ungulates is likely to be small in intact ecosystems, where dogs are uncommon in comparison with other predators (e.g., lions *Panthera leo*, spotted hyaenas *Crocuta crocuta*) taking essentially the same prey (Mills and Biggs 1993; Creel and Creel 1996). However, historically, wild dogs have been perceived to have a serious impact on game species (e.g., Bere 1955) and are still reviled by game farmers who consider them a major competitor, taking prey that could have been sold to commercial hunters or purchasers of live game (P. Lindsey unpubl.).

Social behaviour

Wild dogs are intensely social animals, spending almost all of their time in close association with each other (e.g., McCreery 2000). Packs are dynamic and may fluctuate rapidly in numbers. They may be as small as a pair, or number as many as 30 adults and yearlings – average pack compositions for various study sites are summarised in Table 6.5.5. Packs are usually formed when small same-sex subgroups (usually litter-mates) leave their natal groups and join sub-groups of the opposite sex (McNutt 1996a; McCreery and Robbins 2001). Occasionally, new packs form by fission from larger groups, with males and females emigrating together. In newly formed packs, the females are typically closely related to one another, but not to the males, and the males are closely related to one another, but not to the females. Young born into such packs may remain there, or disperse as yearlings or young adults to form new packs. Because wild dogs are obligate social breeders, the pack, rather than the individual, should be considered the basic unit within the population.

Wild dogs have large home ranges (Table 6.5.6), which they defend infrequently but aggressively against neighbouring packs. Ranges are much larger than would be expected on the basis of their body size. Packs are confined to relatively small areas (50–200km^2) when they are feeding young pups at a den, but outside the denning period they range widely. As a result, wild dogs' large home ranges translate into very low population densities (Table 6.5.2). The home ranges of neighbouring wild dog packs overlap considerably, but wild dogs can, nevertheless, be considered territorial: packs rarely enter other packs' core areas and these areas are defended aggressively as well as by scent-marking. Even wild dog packs that inhabit protected areas may travel extensively outside the reserve borders where they encounter human activity and threats such as roads, snares and livestock and game farmers likely to persecute them. Wild dogs dispersing away from their natal packs may range even more widely. Dispersing wild dogs have been tracked over hundreds of kilometres (Fuller *et al*. 1992a), a characteristic that could account for the occasional reports of single wild dogs, or single-sex groups from countries such as Uganda, Democratic Republic of Congo and Swaziland, where there have been no resident wild dog populations for several decades.

Wild dogs have a complex communication system, including a number of unique vocalisations (Robbins

Table 6.5.5. Pack compositions of wild dogs in various study sites across Africa. Data updated from Woodroffe *et al*. (1997), with unpublished data from Botswana and Kruger.

Study site		Sample (pack-years)	Adults	Yearlings	Pups
Hwange National Park, Zimbabwe	1989–1990	5	7.8	3.2	5.4
	1992–2000	13	3.9	2.0	6.7
Kruger National Park, South Africa		76	4.0	2.2	4.5
Masai Mara National Reserve, Kenya		6	4.2	4.0	8.8
Northern Botswana		75	6.6	4.4	9.9
Selous Game Reserve, Tanzania		39	8.9	4.3	7.9
Serengeti National Park, Tanzania		7	6.6	6.0	11.2

Table 6.5.6. Home ranges of wild dogs in various study sites across Africa (updated from Woodroffe *et al*. 1997).

Study site	No. packs	Home-range size in km^2 (range)
Aitong, near Masai Mara, Kenya	1	659
Hwange National Park, Zimbabwe	4	423 (260–633)
Kruger National Park, South Africa	20	553 (150–1,110)
Moremi Game Reserve, Botswana	9	617 (375–1,050)
Selous Game Reserve, Tanzania	11	433 (SE±66)
Serengeti National Park, Tanzania	5	1318 (620–2,460)

2000), as well as olfactory communication both within and between packs (van Heerden 1981; M. Parker unpubl.).

Reproduction and denning behaviour

A pack consists of any group of wild dogs with a potentially reproductive pair. In a pack larger than two adults, the reproductive pair consists of the dominant male and the dominant female (Frame *et al.* 1979; Malcolm and Marten 1982). In most wild dog packs, the dominant female is the mother of all the pups, although two or even three females may breed on some occasions. Similarly, the dominant male fathers most (but not necessarily all) of the pups (Girman *et al.* 1997). Dominant males are usually no more assiduous in caring for pups than are other males in the pack (Malcolm and Marten 1982). In fact, all pack members are involved in caring for the pups. Such additional care is vital if pups are to survive; because very small packs (<4 members) rarely manage to raise any pups (J.W.McNutt unpubl.). Cooperative care may even extend to caring for adopted pups (McNutt 1996b).

Births are seasonal, and gestation lasts 71–73 days (J.W.McNutt unpubl.). Wild dogs have very large litters for their body size, averaging 10–11 and occasionally as many as 21 (Fuller *et al.* 1992b). Pup sex ratios are male-biased in some populations (Fuller *et al.* 1992b; J.W. McNutt unpubl.). The pups, each weighing approximately 300–350g, are born in an underground den which they use for the first three months of life. Such dens are often those of aardvark (*Orycteropus afer*), sometimes modified by warthog or spotted hyaenas. The mother is confined to the den during early lactation, and is reliant on other pack members to provision her during this time. Wild dogs feed the mother and pups (from four weeks of age) by regurgitating solid pieces of meat. Some pack members also "baby-sit" the pups and chase predators off while the remainder of the pack is away hunting. Pups are generally fully weaned by eight weeks but continue to use a den for refuge until 12–16 weeks of age. Wild dogs reach sexual maturity in their second year of life, but social suppression of reproduction in subordinates of both sexes means that few animals breed at this age (Creel *et al.* 1997). Few animals breed at any age due to reproductive suppression. However, it is common for two-year old females and less frequent for two-year old males to reproduce.

Competition

Competition with larger predators has a major impact on wild dogs' behaviour and population biology (Creel and Creel 1996; Mills and Gorman 1997). Lions, in particular, are a major cause of natural mortality (Table 6.5.7, 6.5.8), and wild dogs tend to move away if they detect the presence of lions (Creel and Creel 1996). Spotted hyaenas also occasionally kill dogs of all ages (J.W. McNutt pers. obs.). They also steal kills from wild dogs, particularly in open areas where such kills are easily located (Fanshawe and FitzGibbon 1993). While the loss of kills to hyaenas is much less common in more closed bush, wild dogs' high metabolic rate means that prey loss to competitors has the potential to seriously impact their energy balance (Gorman *et al.* 1998). Leopards (*Panthera pardus*) have also been recorded to kill pups (M.G.L. Mills unpubl.).

Competition with larger carnivores might help to explain wild dogs' wide-ranging behaviour. While larger predators tend to occur at higher densities where prey are more abundant, wild dogs (like cheetahs, *Acinonyx jubatus*) tend to avoid these areas. Because they range in areas of comparatively low prey densities requiring greater travel times during hunting, they are effectively forced to occupy larger home ranges. This wide-ranging behaviour, coupled perhaps with their preference for areas of reduced predator density, explains why wild dogs inhabiting isolated reserves are so exposed to human activity on and around reserve borders.

Mortality and pathogens

Wild dogs experience high mortality in comparison with other large carnivore species. Annual adult mortality varies between populations, with averages ranging from 20–57% (summarised in Creel and Creel 2002). Similarly, pup mortality during the first year of life is relatively high, and averages around 50% in most populations. There is some evidence to suggest that pup survival is higher in large packs where there are more helpers to assist with their care.

Natural sources of mortality The principal cause of natural mortality is predation by lions (Tables 6.5.7, 6.5.8), although hyaenas, crocodiles and leopards also kill wild dogs in some areas.

Persecution While pups die almost exclusively from "natural" causes (Table 6.5.8), more than half of the mortality recorded among adults is caused directly by human activity, even in some of the largest and best-protected areas (Table 6.5.7). Wild dogs using protected areas often range outside the borders and into areas used by people. Here they encounter high-speed vehicles, guns, snares and poisons, as well as domestic dogs, which represent reservoirs of potentially lethal diseases.

Hunting and trapping for fur There is no known trade in the fur of wild dogs and virtually no commercial hunting or trapping. Quotas for commercial hunting have been issued in the past in Cameroon, but the full quota has not been taken (Breuer 2003).

Road kills Road kills are an important cause of mortality for both adults and pups (Tables 6.5.7, 6.5.8), partly because wild dogs use roads to travel and may also rest on them.

Table 6.5.7. Causes of adult mortality in free-ranging populations of African wild dogs. Figures show the percentages of deaths attributed to each cause. Numbers in brackets give the total number of known deaths recorded in that study site. Updated from Woodroffe *et al*. (1997), using unpublished data provided by G. Rasmussen, S. Creel and K. McCreery and R. Robbins.

	Kruger NP, South Africa	**Northern Botswana**	**South-western Zimbabwe**	**Selous GR, Tanzania**	**Zambia**	**Total**
Natural causes						
Predators						
Lions	26% (19)	47% (15)	4% (85)	20% (10)	0% (36)	**10% (165)**
Spotted hyaenas	0% (19)	7% (15)	2% (85)	0% (10)	0% (36)	**2% (165)**
Unknown/others	11% (19)	7% (15)	1% (85)	0% (10)	3% (36)	**3% (165)**
Other wild dogs	16% (19)	0% (15)	0% (85)	40% (10)	0% (36)	**4% (165)**
Disease	0% (19)	0% (15)	0% (85)	0% (10)	22% (36)	**5% (165)**
Accident	0% (19)	33% (15)	2% (85)	0% (10)	0% (36)	**4% (165)**
Subtotal natural	**53% (19)**	**94% (15)**	**12% (116)**	**60% (10)**	**25% (36)**	**27% (196)**
Human causes						
Road kill	5% (19)	0% (15)	19% (116)	0% (10)	22% (36)	**16% (196)**
Snared	21% (19)	0% (15)	42% (116)	40% (10)	6% (36)	**30% (196)**
Shot	21% (19)	0% (15)	27% (116)	0% (10)	14% (36)	**20% (196)**
Poisoned	0% (19)	0% (15)	0% (116)	0% (10)	33% (36)	**6% (196)**
Unknown	0% (19)	7% (15)	0% (116)	0% (10)	0% (36)	**0.5% (196)**
Subtotal human	**47% (19)**	**7% (15)**	**88% (116)**	**40% (10)**	**75% (36)**	**73% (196)**

Table 6.5.8. Causes of pup mortality in free-ranging populations of African wild dogs. Figures show the percentages of deaths attributed to each cause. Numbers in brackets give the total number of known deaths recorded in that study site. Updated from Woodroffe *et al*. (1997), with unpublished data from S. Creel and G. Rasmussen.

	Kruger NP, South Africa	**Selous GR, Tanzania**	**South-western Zimbabwe**	**Total**
Natural causes				
Predators				
Lions	37% (38)	6% (36)	14% (22)	**20% (96)**
Spotted hyaenas	0% (38)	6% (36)	18% (22)	**6% (96)**
Monitor lizard	0% (38)	6%(36)	0% (22)	**2% (96)**
Other wild dogs	50% (38)	77% (36)	5% (22)	**50% (96)**
Disease	8% (38)	6% (36)	0%(22)	**5% (96)**
Subtotal natural	**95% (38)**	**100% (36)**	**37% (22)**	**83% (96)**
Human causes				
Road kill	0% (38)	0% (36)	27% (22)	**6% (96)**
Snared	5% (38)	0% 36)	9% (22)	**3% (96)**
Shot	0% (38)	0% (36)	27% (22)	**6% (96)**
Unknown	0% (38)	0% (36)	0% (22)	**0% (96)**
Subtotal human	**5% (38)**	**0% (36)**	**63% (22)**	**16% (96)**

Pathogens and parasites The impact of disease is almost certainly under-estimated in Tables 6.5.6 and 6.5.7 (disease outbreaks tend to be episodic, while these data come from stable populations unaffected by epizootics at the time of study), and is likely to be particularly severe in small populations. Rabies is known to have contributed to the extinction of the wild dog population in the Serengeti ecosystem on the Kenya-Tanzania border in 1990 to 1991, and is suspected to have caused the deaths of several packs in northern Botswana in 1995 and 1996. Canine distemper has also caused at least one whole-pack death in Botswana, although the impact of distemper appears smaller than that of rabies, with several populations showing evidence of non-fatal exposure. An unidentified *Toxoplasma* sp. was implicated in the deaths of 23 out of 24 pups from two litters at a den in the Kruger National Park (M.G.L. Mills pers. obs).

Longevity: In Hwange National Park, Zimbabwe, a male dog lived up to 11 years (G. Rasmussen pers. comm.). In Kruger National Park and northern Botswana, no wild dog has survived more than 10 years, and most dogs studied in Selous Game Reserve, Tanzania, lived six years or less (Creel and Creel 2002).

Historical perspective

Wild dogs play only a small role in traditional cultures, in comparison with other predators such as lions and hyaenas. They are valued in some areas as their kills are a source of meat; various body parts may also be considered to have medicinal and magical powers. In colonial times, wild dogs were almost universally reviled, with a reputation as ugly, cruel and bloodthirsty killers. Game managers' attitudes to them are exemplified by Bere's (1955) observation that they "*...hunt in packs, killing wantonly far more than they need for food, and by methods of the utmost cruelty... When the Uganda national parks were established it was considered necessary, as it had often been elsewhere, to shoot wild dogs in order to give the antelope opportunity to develop their optimum numbers...*". Such persecution in the name of "game" management and conservation continued as national parks' policy in some areas well into the 1970s, and unofficially this attitude still persists in a few areas.

Conservation status

Threats As described above, the principal threats to wild dogs are conflict with human activities and infectious disease. Both of these are mediated by habitat fragmentation, which increases contact between wild dogs, people and domestic dogs. The important role played by human-induced mortality has two long-term implications. First, it makes it likely that, outside protected areas, wild dogs may well be unable to co-exist with the increasing human population unless better protection and local education programmes are implemented. This will be a serious problem for wild dog populations outside protected areas. Second, wild dog ranging behaviour leads to a very substantial "edge effect", even in large reserves. Simple geometry dictates that a reserve of 5,000km^2 contains no point more than 40km from its borders – a distance well within the range of distances travelled by a pack of wild dogs in their usual ranging behaviour. Thus, from a wild dog's perspective, a reserve of this size (fairly large by most standards) would be all edge. As human populations rise around reserve borders, the risks to wild dogs venturing outside are also likely to increase. Under these conditions, only the very largest unfenced reserves will be able to provide any level of protection for wild dogs. In South Africa, proper fencing around quite small reserves has proved effective in keeping dogs confined to the reserve (although fencing has costs, as well as benefits, in conservation terms).

Even in large, well-protected reserves, or in stable populations remaining largely independent of protected areas (as in northern Botswana), wild dogs live at low population densities. Predation by lions, and perhaps competition with hyaenas, contribute to keeping wild dog numbers below the level that their prey base could support. Such low population density brings its own problems. The largest areas contain only relatively small wild dog populations; for example, the Selous Game Reserve, with an area of 43,000km^2 (about the size of Switzerland), contains about 800 wild dogs. Most reserves, and probably most wild dog populations, are smaller. For example, the wild dog population in Niokolo-Koba National Park and buffer zones (about 25,000km^2, larger than the state of Israel) is likely to be not more than 50–100 dogs. Such small populations are vulnerable to extinction. "Catastrophic" events such as outbreaks of epidemic disease may drive them to extinction when larger populations have a greater probability of recovery – such an event seems to have led to the extinction of the small wild dog population in the Serengeti ecosystem on the Kenya-Tanzania border. Problems of small population size will be exacerbated if, as seems likely, small populations occur in small reserves or habitat patches. As discussed above, animals inhabiting such areas suffer a strong "edge effect". Thus, small populations might be expected to suffer disproportionately high mortality as a result of their contact with humans and human activity.

Commercial use There are no commercial uses for wild dogs, other than non-consumptive ecotourism.

Occurrence in protected areas The occurrence of wild dogs in protected areas is described in detail in Fanshawe *et al.* (1997). The largest populations inside protected areas occur in:

— *Tanzania*: Selous Game Reserve and Ruaha National Park;
— *South Africa*: Kruger National Park;
— *Botswana*: Chobe National Park and Moremi Wildlife Reserve;
— *Zimbabwe*: Hwange National Park.

Protection status CITES – not listed.

Current legal protection Wild dogs are legally protected across much of their range. However, this protection is rarely enforced and wild dogs are extinct in several countries despite stringent legal protection (Table 6.5.9). Outside reserves, legal protection may have questionable value when it concerns a species that comes into conflict with people, often in remote areas with poor infrastructure. Under such circumstances, legal protection may serve only to alienate people from conservation activities.

Conservation measures taken The establishment of very large protected areas (e.g., Selous Game Reserve, Kruger National Park), as well as conservancies on private and communal land, has ensured wild dogs' persistence in parts of eastern and southern Africa, and maintenance of such areas remains the highest priority for wild dog conservation. Attempts are underway to re-establish wild

Table 6.5.9. The status of wild dog populations and their degree of protection across range states. The columns marked "Date" give, respectively, the date of the most recent information on which the population estimate is based, and the date of the protective legislation. Most of the information about the protected status of wild dogs was provided by the Environmental Law Centre, Bonn, Germany.

Country	Status of wild dogs	Date	Degree of protection	Date
Algeria	rare?	1989	?	–
Angola	rare?	1987	total?	1957
Benin	extinct?	1987	?	–
Botswana	present	1996	partial	1979
Burkina Faso	extinct?	1987	partial	1989
Cameroon	present	1992	partial?	?
Central African Republic	present	1987	total	1984
Chad	rare	1987	?	–
Congo	extinct	1992	total	1984
Côte d'Ivoire	rare?	1987	noxious	1965
Dem. Rep. Congo	extinct?	1987	partial	1982
Eritrea	extinct?	1992	?	–
Ethiopia	present	1995	total	1972
Gabon	extinct	1987	?	–
Ghana	extinct?	1987	partial	1971
Guinea	rare	1996	total	1990
Kenya	present	1996	partial	1976
Malawi	rare	1991	partial	?
Mali	extinct?	1989	?	–
Mozambique	rare	1996	total	1978
Namibia	present	1996	total	?
Niger	extinct?	1987	total?	?
Nigeria	extinct?	1991	total	1985
Rwanda	extinct	1987	total	1974
Senegal	present	1996	partial	1986
Sierra Leone	rare?	1996	?	–
Somalia	rare?	1994	total	1969
South Africa	present	1996	specially protected	?
Sudan	rare	1995	total?	?
Swaziland	extinct?	1992	?	–
Tanzania	present	1996	total	1974
Togo	rare?	1987	partial	1968
Uganda	rare?	1996	?	–
Zambia	present	1994	total	1970
Zimbabwe	present	1992	partial	1990

dogs in a network of very small reserves in South Africa, but this approach will demand intensive management in perpetuity and need not, at present, be used as a model for wild dog conservation elsewhere.

Conservation priorities include: (i) to maintain and expand connectivity of habitat available to wild dogs, particularly in northern Botswana/eastern Namibia/western Zimbabwe, South Africa/western Mozambique/south-east Zimbabwe, northern South Africa/south-east Botswana/south-west Zimbabwe and southern Tanzania/northern Mozambique; (ii) to work with local people to reduce deliberate killing of wild dogs in and around these areas, and also in smaller populations in Senegal, Cameroon and Kenya; (iii) to establish effective techniques for protecting small wild dog populations from serious infections such as rabies and distemper; (iv) to carry out surveys to establish the status of other potentially important populations, particularly in Algeria, Angola, Central African Republic, Ethiopia, Mozambique and Sudan, and (v) to continue long-term monitoring of 'sentinel' populations to identify emerging threats. Re-establishment of extinct populations through reintroduction currently has a low priority in most areas, although natural recolonisations should be encouraged.

Occurrence in captivity

There are more than 300 wild dogs in captivity in 55 zoos, as listed on ISIS and as many as 200 additional animals occur in zoos and private collections, particularly in South Africa. With the exception of a small number of animals held in the Mkomazi Game Reserve, Tanzania, all of the dogs held in captivity are of southern African origin. Successful breeding is patchy; some institutions have been extremely successful at breeding wild dogs in captivity, while others have failed. Juvenile mortality is high in most collections.

Early attempts to reintroduce captive-bred animals to the wild were hampered by the dogs' poor hunting skills and naive attitudes to larger predators. However, recent reintroductions have overcome this problem by mixing captive-bred dogs with wild-caught animals and releasing them together. This approach has been very valuable in re-establishing packs in several fenced reserves in South Africa, but is not considered a priority in other parts of Africa at present. Nevertheless, captive populations have important roles to play in developing conservation strategies for wild populations, through research (e.g., testing of vaccination protocols), outreach and education.

Current or planned research projects

J.W. McNutt (University of Montana, USA) runs the Botswana Wild Dog Research Project, a long-term monitoring study of wild dog ecology and behaviour in the Okavango Delta.

R. Woodroffe (University of California, Davis, USA), principal investigator of the Samburu-Laikipia Wild Dog Project, is studying the conflicts between people and wild dogs outside protected areas in northern Kenya.

M. Rainey (African Wildlife Foundation, Nairobi, Kenya) is currently monitoring wild dogs in the Kajiado District, Kenya.

M.G.L. Mills (South Africa National Parks and Endangered Wildlife Trust, South Africa) is continuing with long-term ecological monitoring of wild dogs in the Kruger National Park.

P. Lindsey (Mammal Research Institute, University of Pretoria, South Africa) has recently concluded a bio-economic analysis of wild dog conservation in South Africa.

D. Knobel (Mammal Research Institute, University of Pretoria, South Africa and Centre for Tropical Veterinary Medicine, University of Edinburgh, UK) is investigating the development of a bait and baiting system for the delivery of oral rabies vaccine to free-ranging wild dogs.

H. Davies (Wildlife Conservation Research Unit, University of Oxford, UK and Endangered Wildlife Trust, South Africa) is the principal investigator of the De Beers Venetia Reserve Wild Dog Project, which involves the study of the biology of a reintroduced wild dog pack and the value of the species to ecotourism in a small reserve.

A. Visee (George Adamson Wildlife Preservation Trust, Tanzania) is studying infectious disease and safety/effectiveness of vaccination, as well as husbandry, of captive wild dogs in Mkomazi, Tanzania.

K. Leigh (University of Sydney, Australia) is the principal investigator of the Lower Zambezi African Wild Dog Conservation Project, a study of the threats to wild dogs in Lower Zambezi National Park aimed at generating conservation recommendations for the Zambia Wildlife Authority.

G. Rasmussen (Wildlife Conservation Research Unit, University of Oxford, UK) runs Painted Dog Conservation, a long-running project aimed at monitoring and protecting wild dogs outside protected areas in Hwange and elsewhere in Zimbabwe.

J. Chambers (Lowveld Wild Dog Project, Save Valley, Zimbabwe) is involved in the ecological monitoring of wild dogs in south-eastern Zimbabwe.

K. McCreery and R. Robbins (African Wild Dog Conservancy, Olympia, Washington, USA) have recently surveyed wild dog populations in East Kenya.

R. Lines (Namibia Nature Foundation, Windhoek, Namibia) is studying wild dog livestock conflict in Namibia.

C. Sillero-Zubiri and J.-M. Andre (Wildlife Conservation Research Unit, University of Oxford, UK) are surveying wild dogs in and around protected areas of central and northern Mozambique.

The Wild Dog Advisory Group of South Africa is overseeing the strategic reintroduction of wild dogs in a network of fenced reserves across South Africa and conducting detailed monitoring of dogs in Hluhluwe-Umfolozi Park, Pilansberg National Park, Marekele National Park and Madikwe Game Reserve.

Other long- and short-term projects have been carried out in Tanzania (Selous Game Reserve, S. and N. Creel; Serengeti National Park, L. and H. Frame, J. Malcolm, H. van Lawick, J. Fanshawe, R. Burrrows), Kenya (P. Kat, T. Fuller), Zimbabwe (Hwange National Park, J. Ginsberg) and Senegal (Niokola-Koba National Park, C. Sillero-Zubiri). Restricted surveys have recently been carried out in Cameroon (T. Breuer), Mozambique (C. Sillero-Zubiri), Tanzania (Ruaha Game Reserve, Mikumi National Park, S. and N. Creel) and Nigeria (S. Baggett).

Gaps in knowledge

Several pieces of information are needed to enable more effective conservation of African wild dogs. These include: (1) establishing which techniques will be most effective and sustainable for protecting wild dogs from disease, including whether vaccinating wild dogs against rabies and distemper can ever be safe and effective, and whether other methods (including control or vaccination of domestic dogs) can reduce the risks to wild dogs; (2) determining the true impact of wild dogs on livestock under different conditions of husbandry, and the effectiveness of techniques to reduce this; (3) establishing the true impact of wild dogs on managed wild game and the effectiveness of techniques to resolve conflicts with game ranchers; (4) surveys of wild dog distribution and status are also required, particularly in Algeria, Angola, Cameroon, Central African Republic, Ethiopia, Mozambique and Sudan; (5) genetic research would be valuable to establish the distinctiveness of wild dog populations remaining in west, central and north-east Africa; and (6) the reasons for and degree of fluctuation in packs and populations need to be better understood. In addition, several aspects of wild dogs' basic biology require further study, particularly: (1) mechanisms of ranging and dispersal; (2) causes of increased mortality among dispersers; (3) reasons for large home range; (4) mechanisms of sex-ratio biasing; (5) paternity; and (6) communication.

Core literature

Creel and Creel 1995, 1996, 2002; Frame *et al.* 1979; Fuller and Kat 1990; Fuller *et al.* 1992a,b; Girman *et al.* 1997, 2001; Malcolm and Marten 1982; McNutt 1996a,b; Mills and Gorman 1997; Woodroffe and Ginsberg 1999a; Woodroffe *et al.* 1997.

Reviewers: Scott Creel, Joshua Ginsberg, Kim McCreery, Gregory Rasmussen, Robert Robbins. **Editors:** Claudio Sillero-Zubiri, Michael Hoffmann.

6.6 Bat-eared fox
Otocyon megalotis (Desmarest, 1822)
Least Concern (2004)

J.A.J. Nel and B. Maas

Other names

Afrikaans: bakoorvos, bakoorjakkals, draaijakkals; **French:** l'otocyon; **German:** löffelhund; **Indigenous names:** ǁK´auǁen and !Kung San (Bushmen): !u (Botswana and Namibia); Amharic: joro-kib kebero (Ethiopia); Swahili: bwega masigio; Karamojong: ameguru; Kichagga: kipara; Kigogo: nchenjeji; Kikomo: mchutu; Kinyaturu: bii; Kiramba: bili (Kenya, Tanzania); Herero: okata-ká-ha; Nama: bergdamara; Heiǁkum San (Bushmen): ǁab;

Ovambo: ombúü (Namibia); Northern Sotho: mo-tlhose; Tswana: motlósi; Zulu: udlamhloshwana (South Africa).

Taxonomy

Canis megalotis Desmarest, 1822. Mammalogie, in Encyclop. Meth., 2 (suppl): 538. Type locality: "le Cap de Bonne-Espérance" [South Africa, western Cape Province, Cape of Good Hope].

Included by some authors, e.g., Simpson (1945) and Ellerman *et al*. (1953), in a separate subfamily, the *Otocyoninae*, on account of its aberrant dentition; more recently (Clutton-Brock *et al.* 1976 and subsequent authors) this species is regarded as having affinities with the vulpine line.

Chromosome number: 2n=72 (Wayne *et al.* 1987).

Description

A small, slight canid with slim legs, a long bushy tail and conspicuously large ears. Males (4.1kg) are heavier than females (3.9kg) (average for both sexes 3.9kg) (see Gittleman 1989), although, in Botswana, females weigh marginally more than males (Table 6.6.1). The back of the ears, front part of the snout, face mask, front and lower part of the back legs, and the mid-dorsal part of the tail are black. A whitish band extends from across the forehead to below and up the first three-quarters of the frontal rim of the ears. Some animals have a broad, dark mid-dorsal band. Beige- to honey-coloured fur covers the lower jaw from behind the muzzle and extends across the throat, chest and under parts. Fur coloration is paler in older individuals. Body and tail fur are thick and soft on upper parts with a black base and white tip, giving a grizzled or grey appearance; sides appear more buff. Underfur on the upper body is about 30mm long, while the dense overcoat of guard hairs measures about 55mm. A sprinkling of tactile hairs (up to 65mm) occurs amongst the guard hairs (Skinner and Smithers 1990). Bat-eared foxes are unique amongst living eutherians (odontocetes excepted) in having four to five functional lower molars, and unique amongst modern canids in having three to four upper molars (Guilday 1962). The milk dentition is typically canid, with unreduced carnassials. In adults, the carnassial shear is lost and molars become the most bunodont, verging on zalambdodont, of any canid (see Kieser 1995). Supernumerary molars yield a dentition of 3/3-1/1-4/4-3-4/4-5=46-50, the largest number for any non-marsupial land mammal.

Table 6.6.1. Body measurements for the bat-eared fox from Botswana (Smithers 1971).

HB male	529mm (462–607) n=25
HB female	536mm (467–607) n=29
T male	298mm (230–340) n=25
T female	303mm (278–340) n=29
HF male	149mm (140–161) n=25
HF female	150mm (139–165) n=29
E male	124mm (119–137) n=25
E female	124mm (114–134) n=29
WT male	4.0kg (3.4–4.9) n=22
WT female	4.1kg (3.2–5.4) n=29

Subspecies Two subspecies are recognised (Coetzee 1977):
— *O. m. megalotis* (southern Africa)
— *O. m. virgatus* (East Africa)

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Bat-eared fox. Robertson Karoo, Western Cape Province, South Africa.

Similar species Cape fox (*Vulpes chama*): somewhat smaller; silver-grey upper parts, under parts off-white to pale fawn; head and back of ears reddish fawn; no black on back; tail more bushy, only tip black.

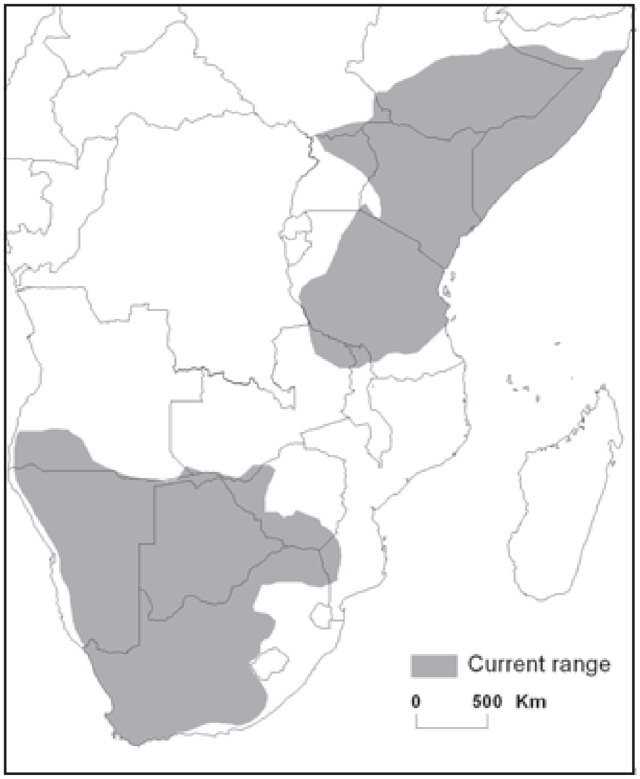
Current distribution

The bat-eared fox has a disjunct distribution range, occurring across the arid and semi-arid regions of eastern and southern Africa in two discrete populations (representing each of the known subspecies) separated by about 1,000km (Figure 6.6.1). *Otocyon m. virgatus* ranges from southern Sudan, Ethiopia and Somalia down through Uganda and Kenya to south-western Tanzania; *O. m. megalotis* occurs from Angola through Namibia and Botswana to Mozambique and South Africa (Coetzee 1977; Kingdon 1977; Skinner and Smithers 1990). The two ranges were probably connected during the Pleistocene (Coe and Skinner 1993). This disjunct distribution is similar to that of the aardwolf (*Proteles cristatus*) and black-backed jackal (*Canis mesomelas*).

Range extensions in southern Africa in recent years (e.g., Stuart 1981; Marais and Griffin 1993) have been linked to changing rainfall patterns (MacDonald 1982).

Range countries Angola, Botswana, Ethiopia, Kenya, Mozambique, Namibia, Somalia, South Africa, Sudan, Tanzania, Uganda, Zimbabwe (Smithers 1971; Smithers and Lobão-Tello 1976; Coetzee 1977; Kingdon 1977; Smithers and Wilson 1979; Skinner and Smithers 1990).

Figure 6.6.1. Current distribution of the bat-eared fox.



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Relative abundance

The species is common in conservation areas in southern and eastern Africa, becoming uncommon in arid areas and on farms in South Africa where they are occasionally persecuted. Within a circumscribed habitat, numbers can fluctuate from abundant to rare depending on rainfall, food availability (Waser 1980; Nel *et al.* 1984), breeding stage and disease (Maas 1993a, b; Nel 1993).

Estimated populations/relative abundance and population trends In the south-western Kalahari, bat-eared fox numbers can vary over time: regular counts along a 21km stretch of dry riverbed, with an area of *c.*10km^2, were of 7–140 individuals, i.e., 0.7–14/km^2 (Nel *et al.* 1984; Nel 1996). In the Limpopo province, South Africa, Berry (1978) found densities of 5.7 foxes/km^2, and in the nearby Mashatu Game Reserve, Botswana, densities of 9.2 foxes/km^2 in the breeding season, and 2.3 foxes/km^2 at other times. At the Tussen-die-Riviere Game Reserve, Free State province, South Africa, Mackie (1988) recorded densities that varied from 0.3–0.5 foxes/km^2 over a three-year period, while Kuntzsch (1992) found densities that ranged from 1.1–2.0 foxes/km^2 on two farms in the central Karoo of the Northern Cape province. Hendrichs (1972) recorded a density of 0.3–1.0 foxes/km^2 in the Serengeti.

Habitat

In southern Africa, the prime habitat is mainly short-grass plains and areas with bare ground (Mackie and Nel 1989), but they are also found in open scrub vegetation and arid, semi-arid or winter rainfall (fynbos or Cape macchia) shrub lands, and open arid savannah. The range of both subspecies overlaps almost completely with that of *Hodotermes* and *Microhodotermes*, termite genera prevailing in the diet (Mackie and Nel 1989; Maas 1993a). In the Serengeti, they are common in open grassland and woodland boundaries but not short-grass plains (Lamprecht 1979; Malcolm 1986); harvester termite (*H. mossambicus*) foraging holes and dung from migratory ungulates are more abundant in areas occupied by bat-eared foxes, while grass is shorter and individual plants are more widely spaced (Maas 1993a).

Food and foraging behaviour

Food In the Seregenti's woodland boundary, and the open grasslands of southern and East Africa, insects are the primary food sources, with harvester termite and beetles predominating, and supplemented by smaller numbers of orthopterans, beetle larvae and ants (Shortridge 1934; Berry 1978; Nel 1978; Lamprecht 1979; Waser 1980; Stuart 1981; Malcolm 1986; Mackie 1988;

Skinner and Smithers 1990; Maas 1993a). In open shrub savannah in Botswana other taxa such as arachnids can be more common, while fruit is taken seasonally (Nel 1978; Skinner and Smithers 1990) but can be important in open shrub vegetation with scattered trees (Skinner and Smithers 1990; Kuntzsch and Nel 1992). Small mammals, birds, eggs and reptiles are eaten sporadically in southern Africa (Nel 1978; Skinner and Smithers 1990) but rarely in eastern Africa (Lamprecht 1979; Maas 1993a).

Seasonal changes in the proportion of particular taxa occur (Nel 1978; Nel and Mackie 1990; Maas 1993a). In the Serengeti dung beetles are the main source of food during the rainy season when termite activity is reduced (Waser 1980; Maas 1993a). When both are scarce, beetle larvae are often dug up from the ground (Maas 1993a). *Hodotermes mossambicus* is patchily distributed throughout the Serengeti and may constitute a limiting resource in this part of the species' range (Maas 1993a). Harvester termites and dung beetles are more abundant in areas inhabited by clusters of bat-eared fox families, and local differences in *H. mossambicus* density are inversely related to territory size (Maas 1993a). *Hodotermes* foraging-hole density is positively related to a variety of demographic and reproductive variables, such as litter size and female recruitment rate (Maas 1993a). Although the animals' water requirements may be met by the high water content of their insect prey or, in southern Africa, berries during the summer (Nel 1978; Kuntzsch and Nel 1992), water constitutes a critical resource during lactation (Maas 1993a).

Foraging Foraging techniques depend on prey type (Maas 1993a), but food is often located by walking slowly, nose close to the ground and ears cocked forward. Prey is detected mostly by sound; sight and olfaction play a lesser role (Nel 1978). Changes in daily and seasonal *H. mossambicus* availability directly affect bat-eared fox activity patterns. In eastern Africa nocturnal foraging is the rule (Lamprecht 1979; Malcolm 1986; Maas 1993a). In southern Africa nocturnal foraging during summer gradually changes to an almost exclusively diurnal pattern in winter, mirroring activity changes of *H. mossambicus* (Nel 1990). By day, foraging peaks at the height of insect activity (Koop and Velimirov 1982; Nel 1990). Foraging and feeding rate is higher when feeding on termite patches, than on more dispersed insects (e.g., beetle larvae or grasshoppers) (Nel 1990).

In the Serengeti groups frequently patrol known *Hodotermes* patches in their territory after leaving the den in the evening (Maas 1993a). When feeding on termite patches, group members feed closely together, but when feeding on beetles, beetle larvae or grasshoppers group members can forage up to 200m apart (Nel 1978; Maas 1993a). Group members call each other to rich food patches with a low whistle. In the hard-capped soils of the Karoo shrubland and inter-dune, excavations made during foraging by bat-eared foxes, aardvark (*Orycteropus afer*), porcupines (*Hystrix africaeaustralis*) and Cape foxes (*Vulpes chama*) act as microsites, which foster germination of plant seedlings (Dean and Milton 1991). See also Reproductive and denning behaviour.

Damage to livestock or game There is no evidence for predation on livestock or game (e.g., Kok 1996). However, in South Africa bat-eared foxes are sometimes mistaken for livestock predators when seen feeding on fly larvae in lamb carcasses.

Adaptations

Bat-eared foxes are adapted to their predominantly insectivorous diet with a variety of morphological, demographic and behavioural characteristics. Morphologically, the animals' huge ears, used to detect insect prey, are the most conspicuous morphological adaptation and may also serve a thermoregulatory function (Maas 1993b). Insectivory has also affected the number and shape of the animals' teeth (see above). A modification in the insertion point of the digastric muscle facilitates very rapid chewing (Gaspard 1964; cited in Malcolm 1986).

In southern Africa nocturnal foraging during the hot summer changes to a diurnal pattern in winter, when subzero night temperatures are common (Nel 1990). Group members can huddle in dens by night or in the early morning to escape the cold, or seek shade to escape the worst heat, or in the open, facing multiple directions, to ease predator detection. In southern Africa, an eight-week moult takes place between August and September and again between January and February (Smithers 1971).

Male parental care, allo-suckling and, in some areas, communal breeding occurs because insect prey has a high renewal rate, the cost of food sharing is low and dispersal risk high amidst limited breeding territories (Maas 1993a; see also Reynolds 1977; and see Reproductive and denning behaviour).

Social behaviour

Bat-eared foxes in southern Africa live in monogamous pairs with cubs (Nel *et al.* 1984), while those in eastern Africa live in stable family groups consisting of a male and up to three closely related females with cubs (Maas 1993a). Group size varies with time of year, with a mean of 2.72 (range=1–10; n=623) for *O. m. megalotis* (Nel *et al.* 1984); in the Serengeti, average adult group size is 2.44 (±0.1; n=18), and group size prior to dispersal of pups is 6.0 (±0.4; n=18) (Maas 1993a). Additional females in extended family groups are philopatric daughters, sometimes from several generations, which form a hierarchy based on age. All females in such 'super families' breed (Maas 1993a, see also Reproductive and denning behaviour).

Groups forage as a unit, and have home ranges from less than 1km² to more than 3km². In southern Africa home ranges overlap widely (Nel 1978; Mackie and Nel 1989). However, in East Africa they can either overlap (Malcolm 1986) or, as in the Serengeti, where they cluster around harvester termite colonies, be defended as territories that are patrolled and urine-marked during part of the year (Lamprecht 1979; Maas 1993a). Group size determines the outcome during territorial conflict (Maas 1993a, 1993b). Territory inheritance is not uncommon in the Serengeti and neighbouring groups can be closely related, with animals visiting each other from time to time (Maas 1993a).

Bat-eared foxes engage in frequent and extended allo-grooming sessions, which serve to strengthen group cohesion (Maas 1993a). In the south-western Kalahari, it increases markedly (as does urine-marking) during courtship, when huddling, playing and mutual chasing. Vigorous and extended social play is very common in this species, not only in cubs but also adults even after the young have left (B. Maas unpubl.).

Communication is primarily visual, with a variety of ear and tail positions, emphasised by dark markings, used for displays (Nel and Bester 1983; B. Maas pers. obs.). The unique inverted U position of the tail is indicative of a range of states of arousal including fear, play and alarm (Nel and Bester 1983). Vocalisations are mostly soft and sparingly used (Lamprecht 1979; Nel and Bester 1983), except when the animals are highly alarmed or excited during play (Maas 1993a).

Reproductive and denning behaviour

Bat-eared foxes become sexually mature at 8–9 months of age. Pair-bonding and mating takes place from July to September with up to 10 copulations per day for several days (Rosenberg 1971), and with a copulatory tie lasting *c.* 4 minutes, followed by peculiar post-copulatory play (Le Clus 1971). Bat-eared foxes have one litter per year, with births occurring from October to December (Nel *et al.* 1984; Maas 1993a), following a gestation period of 60–75 days. Litter size ranges from 1–6, and in the Serengeti averages 2.56 (n=90). Neonates weigh from 99–142g.

Dens are excavated by breeding adults or adapted from disused dens of other mammals (e.g., springhare *Pedetes* spp., aardvark, and even termite mounds and warthog holes *Phacochoerus* spp.; Lamprecht 1979; Maas 1993a). Dens may have several entrances and chambers and tunnels up to 3m long (Smithers 1971; Berry 1978), and are used for protection against predators and the elements (e.g., flooding, temperature extremes), particularly by the newborn cubs. Small cubs nurse inside the den, later outside and first emerge for brief periods when they are 8–12 days old. Cubs are sometimes moved between dens (Maas 1993a; Pauw 2000, see above), and in the Serengeti, bat-eared foxes utilise 'foraging dens' for the protection of cubs in different parts of the territory (Maas 1993a). Dens are carefully maintained throughout the year, often for generations (Maas 1993a). Breeding dens can be clustered: in the south-western Kalahari six dens were found in a 0.5km² section of the riverbed in 1976 (J.A.J. Nel unpubl.), and each was occupied by an adult pair and 2–3 cubs (16 in total). Two further dens were nearby.

The male spends more time close to the cubs than females, grooming, guarding and playing with them and defending them against predators. Maternal investment during lactation is high in bat-eared foxes compared with other canids, but due to an insectivorous diet mothers and/or cubs cannot be provisioned directly in the conventional sense (Maas 1993a; but see Pauw 2000). The high level of male parental care, however, enables females to maximise their foraging time, which limits nutritional intake in small, dispersed food items. The disparity in care between the sexes becomes less prominent after weaning (10–15 weeks; Berry 1978; Maas 1993a), which in the south-western Kalahari occurs after the first rains and subsequent flush of insects.

Young cubs are initiated into foraging by the male (Nel 1978), and in the Serengeti parents facilitate better access to different *H. mossambicus* patches for small and vulnerable cubs by regularly guiding the cubs from the breeding den to 'nocturnal feeding dens' (Maas 1993a). Social learning by cubs seems to be involved (Nel 1999). The nuclear family group persists until the following June when cubs disperse and the pair – which mates for life (Maas 1993a) – reaffirm their pair bond (Nel 1984).

In East Africa (Serengeti), polygyny, communal breeding and indiscriminate allo-suckling is common. In extended family groups ('super families'; see Social behaviour), where there is more than one breeding female, nursing effort per cub is higher in daughters than in alpha females (Maas 1993a). The number of cubs to emerge from the den in 'super families' is inversely related to the number of breeding females. Cubs raised per 'super family' average 3.6 in the Serengeti (n=48), in contrast to the normal 2.56 (see above), but is subject to annual variation potentially linked to food availability (Maas 1993a). Because of the benefits, particularly amongst related females, of sharing both males and insect prey, additional breeding females spread the energetic costs associated with reproduction (Maas 1993a).

Although communal breeding is rare in southern Africa (Nel *et al.* 1984; Pauw 2000), family groups can also coalesce, with up to 10 non-suckling juveniles and three adults (J.A.J. Nel unpubl.).

Competition

In southern Africa bat-eared foxes are sympatric with other carnivores (e.g., suricates *Suricata suricatta*, yellow mongoose *Cynictis penicillata*, black-backed jackal *Canis* *mesomelas* and Cape fox *Vulpes chama*) that also feed on insects and therefore scramble (and even interference) competition cannot be ruled out. However, in most cases, although there is dietary overlap, rank order of particular prey in the diet of these sympatric carnivores differs (Bothma *et al*. 1984; MacDonald and Nel 1986; Kok and Nel 1992; Kok 1996; Nel and Kok 1999). Bat-eared foxes attack and mob and can displace Cape foxes, aardvarks, aardwolves, and black-backed jackals and even hyenas, especially if the latter approach a den with cubs.

Mortality and pathogens

Natural sources of mortality During droughts, or in the absence of suitable breeding territories (Maas 1993a), lack of food can cause starvation, or decrease ability to avoid predators. Predators include spotted hyaena (*Crocuta crocuta*), martial eagle (*Polemaetus bellicosus*), spotted eagle owl (*Bubo africanus*), Verreaux's eagle owl (*Bubo lacteus*), rock pythons (*Python sebae*) (Maas 1993a), cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*) (Rasmussen 1996), and leopard (*Panthera pardus*) (Bothma and Le Riche 1982; J.A.J. Nel pers. obs.). Pups also fall prey to black-backed jackal (*Canis mesomelas*) (Pauw 2000; J.A.J. Nel and B. Maas pers. obs.).

Persecution In southern Africa persecution is limited to farms where these foxes are sometimes erroneously regarded as predators of young lambs (see Kok 1996).

Hunting and trapping for fur Limited to indigenous peoples in southern Africa, especially Botswana, where hunting and trapping for fur in the colder months can be severe. Treated skins (often as blankets) are known as "macloutsi". Individuals and sometimes families are also captured for food in Botswana (see Sheldon 1992; B. Maas pers. obs.). Surprisingly, bat-eared foxes are sold as trophy animals in South Africa, but the extent of this trade is unknown.

Road kills In South Africa, Namibia and Tanzania, road kills can be numerous; often pairs and some young are run over together.

Pathogens and parasites Rabies (Maas 1993b; Nel 1993; Thomson and Meredith 1993) and canine distemper (Roelke-Parker *et al*. 1996; E.A.N. Le Riche pers. comm.) can cause drastic declines in populations. In East Africa, both diseases have been linked to reservoirs in domestic dogs (Cleaveland and Dye 1995; Carpenter *et al.* 1998). In the Serengeti, 90.4% of mortality was caused by disease (3.2% each by predation and road accidents (n=94)). Trichinellosis has been found in one Serengeti bat-eared fox, but any effect on mortality is unknown (Pozio *et al.* 1997). Canine parvovirus (CPV-2b) has also been isolated from a bat-eared fox (Steinel *et al.* 2001).

Longevity Recorded up to 13 years in captivity, but probably shorter in the wild.

Historical perspective

In southern Africa, especially Botswana, treated skins (macloutsi) are commonly used for making karosses (skin blankets).

Conservation status

Threats: In southern Africa the primary threats are hunting for skins or, because they are perceived as being predators of small livestock. Populations fluctuate due to disease or drought.

Commercial use Very limited, but winter pelts are valued and sold as blankets. They are also sold as hunting trophies in South Africa.

Occurrence in protected areas

— *Botswana*: Kgalagadi Transfrontier Park, Central Kalahari Game Reserve, Chobe National Park;
— *Ethiopia*: Abiata-Shalla Lakes National Park, Awash National Park, Mago National Park, Nachisar National Park, Omo National Park;
— *Kenya*: Maasai Mara;
— *Namibia*: Etosha National Park, Namib-Naukluft National Park, Fish River Canyon National Park;
— *South Africa*: Augrabies Falls National Park, Kgalagadi Transfrontier Park, Karoo National Park, Richtersveld National Park, Namaqua National Park, West Coast National Park, Mountain Zebra National Park, Goegap Nature Reserve, Bloemhof Nature Reserve, Soetdoring Nature Reserve, Willem Pretorius Nature Reserve, Tussen-die-Riviere Nature Reserve;
— *Tanzania*: Serengeti National Park;
— *Uganda*: Kidepo National Park;
— *Zimbabwe*: Hwange National Park.

Protection status CITES – not listed.

Current legal protection None known.

Conservation measures taken None known. Species widespread and mostly common.

Occurrence in captivity

Records from the International Species Information System (ISIS) indicate bat-eared foxes are kept in captivity in North America, Europe, South Africa and Asia, although never in large numbers. There are no management programmes or studbooks for the species in any of these regions. Importations have occurred throughout the history of the captive population despite successful captive breeding since 1970. Bat-eared foxes can coexist well with other species and are frequently seen in African plains exhibits at zoos.

In South Africa an unknown number are being kept as pets, while they are also kept at a small number of international zoos. South African zoos keeping bat-eared foxes include Cango, Bester Birds, Hartebeespoort Dam, World of Birds, Bloemfontein Zoological Gardens, Johannesburg Zoological Gardens, Emerald, and Monkey Den.

Current or planned research projects

H. Wright (Warwick University, UK) is studying the behavioural ecology of monogamy in the bat-eared fox in Kenya.

N. Jordan (Department of Zoology, Cambridge University, UK) is planning a research project in the south-western Kalahari.

Gaps in knowledge

There is a conspicuous lack of information about both abundance and population trends in this species across its range. In southern Africa, little is known about dispersal of young and the formation of new breeding pairs. The causal factors for differences in home range size in different localities, group size and changes in density as a function of food availability are poorly known. In the Serengeti, behavioural evidence on group and pair formation and the existence of 'super families', consisting of one male and up to three closely-related breeding females, raises interesting questions about regular inbreeding between males and their daughters from several generations (see Maas 1993a).

Core literature

Lamprecht 1979; Maas 1993a,b; Maas and Macdonald 2004; Mackie 1988; Mackie and Nel 1989; Malcolm 1986; Nel 1978, 1990, 1993; Nel *et al*. 1984.

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Editors: Michael Hoffmann, Claudio Sillero-Zubiri.

6.7 Cape fox
Vulpes chama (A. Smith, 1833)
Least Concern (2004)

C. Stuart and T. Stuart

Other names

Afrikaans: silwervos, silwerjakkals, draaijakkals; **English:** silver fox, silver jackal; **French:** le renard du Cap; **German:** Kapfuchs; **Spanish:** zorro chama, zorro del Cabo; **Indigenous languages**: Xhosa: uGqeleba (South Africa); Heikum San: !khama|girib; Herero: ombánji-ururápa (Namibia); Ovambo: ombánji-kalulúng, karurúnga (Namibia); Tswana: leSie, thósê, thlósê, khanína (Botswana, South Africa).

Taxonomy

Canis chama A. Smith, 1833. S. Afr. Quart. J. 2: 89. Type locality: "Namaqualand and the country on both sides of the Orange river", determined by Shortridge (1942: 41) as "Port Nolloth, Little Namaqualand" [South Africa, *c.* 29°15'N, 16°52'E].

Chromosome number not known.

Description

The smallest canid and only true fox occurring in southern Africa, the Cape fox has a slender build and a black-tipped bushy tail. Males are approximately 5% larger than females (Table 6.7.1). The overall coloration of the upperparts is grizzled silver-grey, with the lower limbs, head and back of the long ears reddish-brown to pale tawny-brown. There is some freckling of white hairs on the face with the greatest concentration being on the cheeks; the fronts of the ears are also fringed with white hairs. A narrow dark patch above and between the eyes and at the tip of the muzzle may be present. The upper chest is fawny-red, with the underparts coloured off-white to pale fawn, often with a reddish-brown tinge. The upper region of the front legs is reddish-yellow, paler as one descends to the paws, with a dark brown patch on the backs of the thighs of the hind legs. Overall, the body pelage is soft, with a dense underfur of wavy hairs (averaging about 25mm in length) overlaid by a thick guard coat, with individual hairs averaging 45mm in length; the latter are predominantly black in colour but with light-coloured bases and banded silver. Slightly longer black tactile hairs are scattered through the body coat. During the moulting period, from October to December, much of the guard coat is lost, giving the foxes a rather dull and 'naked' appearance. The upper surfaces of the paws are pale fawn to reddish, with the claws of the front feet being sharp, curved and averaging 15mm around the curve. There is pronounced hair growth between the foot-pads. The tail is very bushy with individual

Table 6.7.1. Body measurements for the Cape fox from the former Cape Province, South Africa (Stuart 1981).

HB male	554mm (450–610) n=21
HB female	553mm (510–620) n=15
T male	348mm (300–406) n=25
T female	338mm (250–390) n=17
HF male	131mm (123–140) n=20
HF female	126mm (115–140) n=17
E male	98mm (90–110) n=22
E female	97mm (87–105) n=17
WT male	2.8kg (2.0–4.2) n=17
WT female	2.5kg (2.0–4.0) n=11

Cape fox, age and sex unknown. Anakanirab, Central Namib-Naukluft Park, Namibia, 1993.

Chris and Tilde Stuart

hairs reaching 55mm in length. The tail hairs have buffy-white bases and are broadly black or dark brown towards the tips. From a distance, the overall impression is of a black to very dark-brown tail, although close at hand the tail has a paler appearance. Females have one pair of inguinal and two pairs of abdominal mammae. The skull is narrow and elongated (average total length is 115mm), with a narrow rostrum and a rather weak zygomatic arch. The bullae are large in relation to the size of the skull. The canines are long, slender and strongly curved and the two upper molars are broad as an adaptation to crushing. The dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Monotypic (Meester *et al.* 1986).

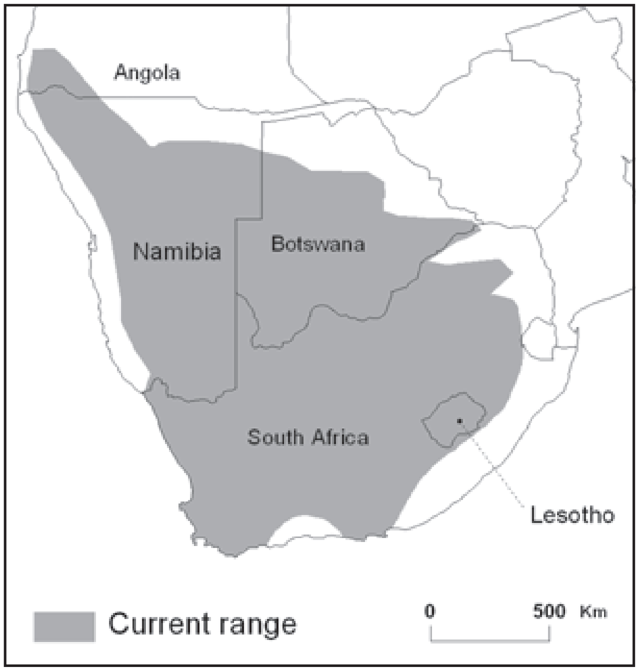
Similar species Bat-eared fox (*Otocyon megalotis*): distinguishable on grounds of coloration and the conspicuously large ears.

Current distribution

The species is widespread in the central and western regions of Southern Africa (Figure 6.7.1), reaching to about 15°N in south-western Angola (Crawford-Cabral 1989). It occupies mainly arid and semi-arid areas, but in parts, such as the fynbos biome of South Africa's Western Cape province, the species enters areas receiving higher precipitation and denser vegetation. The species has expanded its range over recent decades to the south-west where it reaches the Atlantic and Indian Ocean coastlines (Stuart 1981). Expansion through South Africa's Eastern Cape province has been documented (Coetzee 1979). Status in Swaziland is uncertain, but they may occur in the south-west (Monadjem 1998), as the species occurs in adjacent regions of north-western KwaZulu-Natal (Rowe-Rowe 1992); possible occurrence in Lesotho (Lynch 1994). Previous records of its occurrence in western Zimbabwe (Roberts 1951; Coetzee 1977) and Mozambique (Travassos Dias 1968) have not been substantiated, and it is considered unlikely that these records are valid.

Range countries Angola, Botswana, Lesotho (?), Namibia, South Africa, Swaziland (?) (Shortridge 1934; Smithers 1971; Crawford-Cabral 1989; Skinner and Smithers 1990; Lynch 1994; Monadjem 1998).

Figure 6.7.1. Current distribution of the Cape fox.



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Relative abundance

Generally common to fairly abundant across much of its range, although problem animal control activities have resulted in population reductions in some areas. Estimates are only available for South Africa's Free State province where an average density of 0.3 foxes per km² was estimated with a total population of 31,000 individuals (Bester 1982). Annual offtake resulting from problem animal control programmes averaged roughly 16% up to 1985, with no obvious declines in overall populations (Bester 1982). Range and numbers have increased in the south-west and east of South Africa (Coetzee 1979; Stuart 1981). Estimated population sizes or numbers are not available, but it is thought that populations are currently stable across their entire range.

Habitat

They mainly associate with open country, including grassland, grassland with scattered thickets, and lightly wooded areas, particularly in the dry Karoo regions, the Kalahari and the fringes of the Namib Desert. They also penetrate moderately dense vegetation in lowland fynbos in the Western Cape, as well as extensive agricultural lands where they lie up in surviving pockets of natural vegetation during the day and forage on arable and cultivated fields at night (Stuart 1981). Along the eastern flank of the Namib Desert, Namibia, they occupy rock outcroppings and inselbergs, ranging out onto bare gravel plains at night (Stuart 1975). In Botswana, they have been recorded from *Acacia*-scrubland, short grassland and especially on the fringes of shallow seasonal pans, as well as cleared and overgrazed areas (Smithers 1971; Skinner and Smithers 1990). In the central Karoo of South Africa, they occupy the plains as well as the low rocky ridges and isolated rock outcroppings. In the Free State, Lynch (1975) found that they were most abundant in areas receiving less than 500mm of rainfall, although in KwaZulu-Natal they have been recorded between 1,000 and 1,500m above sea level, where rainfall is roughly 720–760mm (Rowe-Rowe 1992).

Food and foraging behaviour

Food The Cape fox takes a wide range of food items, including small rodents (murids), hares, reptiles, birds, invertebrates and some wild fruits (Bothma 1966a, 1971d; Smithers 1971; Lynch 1975; Stuart 1981; Bester 1982; Kok 1996). A sample of the contents of 57 stomachs collected across much of western and central South Africa (former Cape Province) showed that rodents were by far the most important mammal prey items; beetles (larvae and adults) and grasshoppers comprised the majority of invertebrate intake (Stuart 1981). Other dietary studies, involving stomach analysis of specimens obtained from Botswana (n=23, Smithers 1971), Free State (n=58, Lynch 1975; n=192, Bester 1982), the former Transvaal province (n=66, Bothma 1971d) and South Africa in general (n=37, Bothma 1966a) have revealed similar trends. Birds and reptiles are occasionally included in the diet but these do not appear to be important. The largest wild prey species recorded include hares (*Lepus* spp.) and springhares (*Pedetes capensis*) (Lynch 1975). Prey utilisation seems to reflect prey availability and seasonal variation in prey use occurs (Bester 1982). They will also scavenge and occasionally include young lambs and goats in their diet (Stuart 1981; Bester 1982).

Foraging behaviour Although the Cape fox lives in monogamous pairs, foraging is a solitary activity (Bester 1982). However, occasionally they may gather in loose groupings to forage at an abundant food source (Stuart 1981). Foraging is an almost exclusively nocturnal activity, with peaks shortly after sundown and just before dawn. Much prey is obtained by rapid digging with the front paws, often preceded by intensive listening bouts. Caching of prey is common (Le Clus 1971; Bester 1982; C. Stuart and T. Stuart pers. obs.).

Damage to livestock or game Predation on domestic livestock, especially lambs up to the age of three weeks, has been well documented (Stuart 1981; Bester 1982). However, it is not always clear to what extent scavenging is involved, and at least in some areas damage levels are exaggerated. In our experience, lambs killed by the Cape fox are seldom older than four days. Although some authors (Roberts 1951; Bothma 1966) found no evidence of stock killing by Cape foxes, this may have been influenced by their particular study areas. The seasons when samples were taken could also have influenced their conclusions, as the majority of sheep farmers follow fixed lambing times. The highest incidence of lamb losses to the Cape fox has been documented from the Free State, where Bester (1982) recorded that they may take 4.5% of the lamb crop.

Adaptations

Large pinnae and enlarged bullae and auditory meatus suggest enhanced detection of prey as well as predators. Nocturnal activity could serve to reduce predation, especially by the larger diurnal raptors (as has been hypothesised for Blanford's fox, *Vulpes cana*; Geffen and Macdonald 1993).

Social behaviour

The ecology of the Cape fox is poorly known and much of what is known comes from the study undertaken by Bester (1982) in the Free State. Cape foxes live in monogamous pairs. They appear to have overlapping home ranges, especially in areas where food is abundant, although the defended territory is believed to be a limited area around the den in which the female has her litter (Skinner and Smithers 1990). Home ranges ranged in size from 1.0–4.6km² (Bester 1982) and are likely to vary according to rainfall and food abundance.

The main vocal communication consists of a high-pitched howl, ending with a sharp bark. The vixen may bark when a potential predator approaches a den occupied by pups (Smithers 1983). Facial expressions and tail positions play an important role in visual communication (Le Clus 1971; Bester 1982).

Reproduction and denning behaviour

Breeding appears to be non-seasonal in some areas, and strongly seasonal in others (Stuart and Stuart 2001). The majority of births take place in spring and summer, with births recorded in August and September in South Africa's west (Stuart 1981), and August to October, with a peak in September, in the Free State (Bester 1982). In captivity, at the National Zoological Gardens in Pretoria, births were recorded from mid-September to mid-October (Brand 1963). In the Kalahari, breeding apparently extends throughout the spring and summer months. In the Western and Northern Cape provinces, juveniles and subadults have been collected during November and December (Stuart 1981).

Gestation lasts about 52 days (Brand 1963) and litter size in the Free State (2.9; range=1–6; n=16) and Kalahari (2.8; range=2–4; n=5) is similar. Young are born in burrows which are dug in sandy soil, or otherwise the adults enlarge those dug by species such as the springhare or aardvark (*Orycteropus afer*). They have also been known to use crevices, cavities amongst boulder tumbles and, occasionally, dense vegetation (Stuart 1981; Bester 1982). Although both parents feed the pups, the vixen is the main provider; no helpers are found at dens. Both parents will defend the pups against potential predators (Bester 1982). Their habit of abandoning one den for another could avoid accumulation of parasites and confuse potential predators (Bester 1982). Bester (1982) established that pups first begin to hunt at about 16 weeks and are independent of the mother and disperse at the age of about five months.

Communal denning has been recorded in the southern Kalahari (M.G.L. Mills pers. comm.), and Bester (1982) found one litter consisting of eight pups in the Free State, perhaps evidence of a similar situation.

Competition

Although poorly known, it is likely that the black-backed jackal (*Canis mesomelas*) is a competitor, and an occasional predator. It is likely that other predators, such as the caracal (*Caracal caracal*), are also competitors. Where Cape foxes coexist with possible competitors, such as black-backed jackal, some separation in prey use is evident (Bothma *et al*. 1984; Kok 1996). Over much of its range, large predators have been eradicated or greatly reduced in numbers.

Mortality and pathogens

Natural sources of mortality C. Stuart and T. Stuart (pers. obs.) recorded two instances of predation by black-backed jackal, and Mills (1984) observed a single case of predation by a leopard (*Panthera pardus*) in the Kalahari.

Persecution This fox suffers direct and indirect mortality from problem animal control activities, particularly in South Africa and southern Namibia. In the past fairly accurate figures were kept by hunting clubs and associations of most problem animals killed during control operations. However, in recent years, most of these hunting clubs have been disbanded and control measures, by and large, have been left to individual farmers. This has resulted in a paucity of records and data that can only be quoted from the 1960s and 1970s. In the former Cape Province of South Africa, from 1966 to 1970 and 1974 to 1976, more than 6,000 Cape foxes were killed by registered hunters/hunting clubs in the districts to the south of the Orange River. During this same period, in six hunting districts in the Eastern Cape province, records show that more than 20% of all animals killed were Cape foxes (Stuart 1981). In the Free State in 1974, 4,000 Cape foxes were killed during organised control operations and an average of 2,000–3,000 animals were taken in each subsequent year (Bester 1978). The Cape fox is often indirectly killed as a 'by-catch' of efforts aimed at the black-backed jackal and the caracal. The main control methods employed are leg-hold traps, dog packs and poison.

Hunting and trapping for fur Although the occasional pelt may be seen for sale in South African and Namibian curio shops, numbers entering the trade are very small. In Botswana, the pelts of this fox and other species are used in the making of traditional blankets (kaross) but no figures are available. The availability of mass-manufactured blankets has probably greatly reduced demand for animal pelts. Fur trapping poses no threat to this fox anywhere within its range.

Road kills Although occasionally seen as a road kill, the incidence of road traffic death is very low, particularly when compared with that for the bat-eared fox. Bat-eared foxes tend to stand more easily for oncoming lights, whereas Cape foxes usually turn and move.

Pathogens and parasites They are susceptible to rabies but not to the same extent as some other mammalian carnivores. The following parasites have been collected from this fox in the former Cape province: Order Siphonaptera, *Ctenocephalides connatus* and *Echidnophaga gallinacea*; Order Acarina, *Haemaphysalis leachi* and *Rhipicephalus capensis*; Order Eucestoda, *Taenia endothoracicus*, *Joyeuxiella* sp. and *Mesocestoides* sp. (Stuart 1981). In general, the role of disease and parasites as mortality factors in the Cape fox is largely unknown.

Longevity Unknown, but unlikely to be more than about seven years in the wild.

Historical perspective

Pelts were used for the production of traditional blankets, especially by the Tswana people, along with those of species such as the bat-eared fox. However, their usage has greatly diminished.

Conservation status

Threats Habitat loss/changes are not a major factor influencing the conservation status of the Cape fox. In fact, in Western Cape province and elsewhere, changing agricultural practices have resulted in range extensions for this species, as well as for the bat-eared fox (Stuart 1981). Expansion of semi-arid karroid vegetation during the process of desertification, especially eastwards, has also resulted in range extensions of this canid. Heavy direct and indirect problem animal control measures do not seem to have had a major impact on populations of the Cape fox, even though they have resulted in declines in some areas. The illegal but widespread and indiscriminate use of agricultural poisons on commercial farms poses the greatest threat (C. Stuart and T. Stuart pers. obs.).

Commercial use The trade in Cape fox pelts is negligible and this situation is unlikely to change.

Occurrence in protected areas

— *Botswana*: Central Kalahari Game Reserve, Kgaligadi Transfrontier Park (shared with South Africa);
— *Namibia*: Etosha National Park, Damaraland Wilderness Reserve, Namib-Naukluft Park, Fish River Canyon Park, Skeleton Coast National Park;
— *South Africa*: Addo National Park, Augrabies Falls National Park, Bontebok National Park, Cape Peninsula National Park, Golden Gate Highlands National Park, Karoo National Park, Kgaligadi Transfrontier Park, Mountain Zebra National Park, Richtersveld National Park, West Coast National Park.

The Cape fox occurs in many provincial and private nature reserves, as well as on game ranches in all South African provinces, although the species has a much more restricted range in Limpopo Province and KwaZulu-Natal (Stuart 1981; Rautenbach 1982; Lynch 1975; Rowe-Rowe 1992). In Swaziland, the species may occur in Nhlangano Nature Reserve in the south-west, and pups have been successfully reared in Milwane Game Reserve (Monadjem 1998).

Protection status CITES – not listed.

Current legal protection Although treated as a problem animal across most of its range, it is partially protected in several South African provinces, as it does not appear on the official lists of problem species. However, no permit is required from any authority to kill this fox in problem animal control operations. No protection measures are currently enforced and at the present time, this is not necessary.

Conservation measures taken None.

Occurrence in captivity

None known.

Current or planned research projects

There are no formal research projects being undertaken or planned on the Cape fox anywhere within its range.

Gaps in knowledge

Although the Cape fox has been extensively studied in South Africa's Free State province (Lynch 1975; Bester 1982; Kok 1996), there is little information for elsewhere within its range. Aspects such as diet and reproduction are quite well known but little information is available on aspects of social ecology and behaviour in the wild. Some investigation into the role, if any, this species plays in disease transmission is necessary.

Core literature

Bester 1982; Lynch 1975; Stuart 1981.

Reviewers: M.G.L. Mills, Jan A.J. Nel, Gustav Peters.
Editors: Michael Hoffmann, Claudio Sillero-Zubiri.

Chapter 7

North Africa and the Middle East (Ethiopian)

7.1 Blanford's fox
Vulpes cana Blanford, 1877
Vulnerable – VU: C1 (2004)

E. Geffen, R. Hefner and P. Wright

Other names

Arabic: tha'leb sakhari; **English:** royal fox, hoary fox, king fox, Afghan fox; **French:** renard royale; **German:** Afghanfuchs; **Hebrew:** shual tzukim.

Taxonomy

Vulpes canus Blanford, 1877. J. Asiat. Soc. Bengal, 2: 315. Type locality: "Gwadar, Baluchistan" [Pakistan].

A cladistic analysis of mtDNA restriction-fragment and restriction-site data, and 402 base pairs of cytochrome b sequence in fox-like canids, revealed that Blanford's fox and the co-existing desert species, the fennec fox (*Vulpes zerda*), were consistently associated as sister taxa (Geffen *et al*. 1992e). Furthermore, these two taxa formed a monophyletic clade distinct from the other fox-like canids, and thereby defined a taxonomic grouping that previously has not been recognised. However, based on restriction-site data, the sequence divergence between the fennec fox and Blanford's fox is 8.7%, indicating an ancient divergence as much as 3–4 million years ago. This divergence is coincident with the appearance of desert regions in the Middle East and northern Africa (Wickens 1984).

Chromosome number not known.

Description

Blanford's fox is a small fox (*c.*1kg) with a long and very bushy tail (Table 7.1.1.). Sexual dimorphism is minimal, males having significantly longer bodies and front legs, but these differences are on a scale of 3–6%. The head is orange buff in colour, especially in the winter coat. The face is slender with a distinctive dark band extending from the upper part of the sharply pointed muzzle to the internal angle of the eyes. The iris is almost as dark as the pupil (Geffen 1994). The ears are pale brown on both sides with long white hairs along the antero-medial border (Harrison and Bates 1991; Geffen *et al*. 1992d; Geffen 1994). The body is brownish-grey, fading to pale yellow on the belly. The winter coat is soft and woolly with a dense, black under wool. Its dorsal region is sprinkled with white-tipped hair. The summer coat is less dense, the fur is paler, and the white-tipped hairs are less apparent. Specimens from the eastern part of the distribution may be predominantly grey. A distinctive mid-dorsal black band extends from the nape of the neck caudally, becoming a mid-dorsal crest throughout the length of the tail. The tail is similar in colour to the body. A distinctive dorsal black spot (violet gland) is present at the base of the tail, which usually has a black tip, although in some individuals the tip is white (4% in Israel and 26% in U.A.E.). The dark mid-dorsal band, which is a distinctive feature of the Israeli specimens, is less evident in specimens from Oman, although the black tail markings are equally developed (Harrison and Bates 1989). Also, specimens collected in Israel were lighter and had shorter bodies and ears than those collected in the United Arab Emirates (Smith *et al*. 2003). The fore feet and hind feet are dorsally pale yellowish-white, while posteriorly they are dark grey. Unlike the other fox species in the Arabian deserts, the blackish pads of the feet and digits are hairless and the claws are cat-like, curved, sharp, and semi-retractile (Geffen *et al*. 1992d; Geffen 1994). The baculum of Blanford's fox is similar in size to that of Rüppell's fox (*V. rueppellii*) (41mm), but it is broader and has an expanded bulbous tip (Harrison and Bates 1991).

The skull of Blanford's fox is intermediate in size (mean of greatest length is 94mm) between fennec fox and Rüppell's fox. The rostrum is slender, and the nasal bones are long and thin. The postorbital processes are well developed and are not deeply concave dorsally. The braincase is relatively narrow and weakly ridged. The

Table 7.1.1. Body measurements for Blanford's fox.

	Ein Gedi and Eilat, Israel (Geffen *et al*. 1992d).	**United Arab Emirates** (Smith *et al*. 2003).
HB male	427mm (385–470) n=19	744mm (700–800) n=8
HB female	411mm (385–450) n=17	711mm (657–762) n=11
T male	324mm (260–355) n=19	328mm (307–350) n=8
T female	317mm (290–340) n=17	322mm (300–350) n=11
HF male	92mm (80–100) n=19	98mm (91–105) n=8
HF female	93mm (82–110) n=17	93mm (85–100) n=11
E male	80mm (72–85) n=19	86mm (80–95) n=8
E female	78mm (74–87) n=17	86mm (82–91) n=11
WT male	1.0kg (0.8–1.3) n=19	1.2kg (0.9–1.4) n=9
WT female	1.0kg (0.8–1.5) n=17	1.3kg (1.0–1.5) n=6

Blanford's fox, Israel.

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palatines are narrow, and the mesopterygoid space also is long and thin. The tympanic bullae are relatively smaller than those of Rüppell's fox, and the coronoid process of the mandible is relatively more convex (Harrison and Bates 1991). The dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Monotypic (Mendelssohn *et al.* 1987).

Similar species Red fox (*Vulpes vulpes*), fennec fox (*V. zerda*) and Rüppell's fox (*V. rueppellii*). The tail of the Blanford's fox is bushy and longer (mean=323mm), relative to length of body (mean=426mm), than in the other Arabian desert foxes (6.8%, 9.8%, and 22.5% longer than that of Ruppell's fox, red fox, and fennec fox, respectively (Mendelssohn *et al.* 1987; Geffen *et al.* 1992d). The length of the hind foot, relative to body length, is significantly shorter in Blanford's fox (1.8%, 0.8%, and 3.2% shorter than that of Rüppell's, red, and fennec fox, respectively). The relative ear length is intermediate (2.0% longer than in red fox and 2.6% and 5.4% shorter than in Rüppell's and fennec fox, respectively; Harrison and Bates 1991; Geffen *et al.* 1992d).

Current distribution

Present in arid mountainous regions of the Middle East eastwards to Afghanistan (Figure 7.1.1). The Blanford's fox was first described from south-western Asia in 1877, and specimens were collected from Afghanistan, Pakistan, Iran and Turkistan (=Kazakhstan) (Novikov 1962; Bobrinskii *et al.* 1965; Lay 1967; Hassinger 1973; Roberts

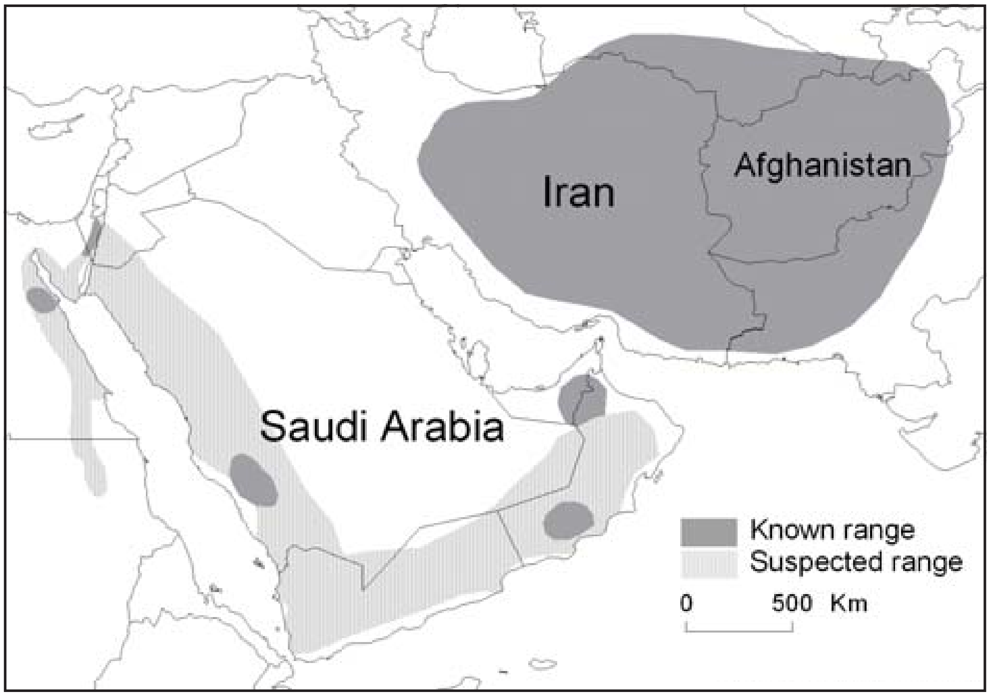

Figure 7.1.1. Current distribution of Blanford's fox.

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1977). In 1981, the species was discovered in Israel (Ilany 1983), and since then throughout the Middle East (Harrison and Bates 1989; Al Khalil 1993; Stuart and Stuart 1995; Amr *et al*. 1996; Amr 2000) and recently in Egypt (Peters and Rödel 1994).

Range countries Afghanistan, Egypt, Eritrea (?), Iran, Israel, Jordan, Kazakhstan, Oman, Pakistan, Saudi Arabia, Sudan (?), United Arab Emirates, Yemen (?) (Al Khalil 1993; Geffen *et al*. 1993; Peters and Rödel 1994).

Relative abundance

Fairly common in south-eastern Israel; in Israel, density estimates of 2.0/km² in Ein Gedi and 0.5/km² in Eilat have been recorded. Abundance in other countries is unknown.

Estimated populations/relative abundance and population trends

Table 7.1.1. Status of Blanford's foxes in Israel (C=common, S=stable).

Region	Population/abundance	Trend
Israel, Ein Gedi	C	S
Israel, Eilat	C	S

Habitat

Blanford's fox is confined to mountainous regions (Lay 1967; Roberts 1977). Hassinger (1973) concluded that Blanford's foxes are generally found below an altitude of 2,000m in dry montane biotopes. All the records collected on the Persian Plateau are from foothills and mountains in the vicinity of lower plains and basins (Hassinger 1973; Roberts 1977). In that region, the habitat of Blanford's fox comprises the slopes of rocky mountains with stony plains and patches of cultivation (Lay 1967; Roberts 1977). This species appears to avoid higher mountain ranges as well as lower, warmer valleys (Roberts 1977).

In the Middle East, Blanford's foxes are confined to mountainous desert ranges and inhabit steep, rocky slopes, canyons, and cliffs (Mendelssohn *et al*. 1987; Harrison and Bates 1989). In Israel, Blanford's fox is distributed along the western side of the Rift Valley, and, in the central Negev, specimens were collected in creeks that drain into the Rift Valley (Geffen *et al*. 1993). Apparently, Blanford's fox can occur on various rock formations as long as its other requirements are met. The distribution of Blanford's fox in the Arabian Desert is not limited by access to water (Geffen *et al*. 1992a). In Israel, Blanford's foxes inhabit the driest and hottest regions. The densest population is found in the Judaean Desert at elevations of 100–350m below sea level. This is in contrast to Roberts' (1977) remark that the species avoids low, warm valleys in Pakistan.

Geffen *et al*. (1992c) found that dry creek bed was the most frequently visited habitat in all home ranges in Israel. Home ranges at Ein Gedi (in km²), comprised an average (± SD) of 63.4 ± 3.2% gravel scree, 3.6 ± 2.6% boulder scree, 28.4 ± 4.0% dry creek bed, and 4.5 ± 3.5% stream and spring. Average time (± SD) spent by foxes at Ein Gedi in gravel scree was 148.8 ± 109.8 min/night, 46.0 ± 63.8 min/night in boulder scree, 359.9 ± 141.9 min/night in dry creek bed, and 13.0 ± 27.9 min/night near a water source (Geffen *et al*. 1992c). Dry creek bed provided abundant prey for the foxes and only sparse cover for their terrestrial predators. Creek bed patches were used in proportion to their size. Both the available area of creek bed in each range and the area of creek bed patches that was used by the foxes were independent of home range size. However, variance in home range size was explained by the mean distance between the main denning area and the most frequently used patches of creek bed (Geffen *et al*. 1992c; and see Social and reproductive behaviour).

Food and foraging behaviour

Food In Israel, Blanford's foxes are primarily insectivorous and frugivorous (Ilany 1983; Geffen *et al*. 1992b). Invertebrates are the major food with beetles, grasshoppers, ants, and termites eaten most often (Geffen *et al*. 1992b). Plant foods consisted mainly of the fruits of two caperbush species, *Capparis cartilaginea* and *C. spinosa*. Fruits and plant material of *Phoenix dactylifera*, *Ochradenus baccatus*, *Fagonia mollis*, and various species of Gramineae were also eaten. Remains of vertebrates were present in *c.*10% of faecal samples analysed (Geffen *et al*. 1992b). The diet differed significantly between two sites examined in Israel, but seasonal and individual differences in diet were not detected (Geffen *et al*. 1992b). Blanford's foxes in Pakistan are largely frugivorous feeding on Russian olives (*Elaeagnus hortensis*), melons, and grapes (Roberts 1977).

Foraging Blanford's foxes are almost always solitary foragers (92% of 463 observations; Geffen *et al*. 1992b), only occasionally foraging in pairs. Mated pairs, which shared home ranges, differed significantly in the time of arrival at fruitful food patches and in the pattern of use of their home range (Geffen and Macdonald 1993). Three types of foraging behaviour were observed: 1) unhurried movements back and forth between rocky patches in a small area (0.01–0.03km²), accompanied by sniffing and looking under large stones and occasionally digging a shallow scrape; 2) standing near a bush for a few seconds, alert with ears erect, prior to circling the bush or pouncing upon prey within, and then walking to another bush to repeat the sequence (on four occasions members of a pair were observed using this type of foraging behaviour simultaneously around the same bushes); and 3) short, fast sprint after small terrestrial or low-flying prey (Geffen *et al*. 1992b). Food caching is rare or absent in the Blanford's fox, contrary to other fox species. Food offered to foxes was either consumed on the spot or carried away and eaten (Geffen *et al*. 1992b).

Blanford's foxes are strictly nocturnal, likely an anti-predator response to diurnal raptors (Geffen and Macdonald 1993). The onset of activity is governed largely by light conditions, and closely follows sunset. Foxes were active *c.* 8–9 h/night, independent of duration of darkness. Average distance (± SD) travelled per night was 9.3 ± 2.7km, and size of nightly home range averaged 1.1 ± 0.7km² (Geffen and Macdonald 1992). Significant seasonal or sexual differences in duration of activity, nightly distance travelled, or nightly home range, were not detected (Geffen *et al.* 1992c). Climatic conditions at night in the desert appeared to have little direct effect on the activity of Blanford's foxes, except when conditions were extreme (Geffen and Macdonald 1993).

Damage to livestock or game Not known. May prey on free-ranging chickens.

Adaptations

Most canids are cursorial terrestrial carnivores adapted for long-distance travel over horizontal ground. Blanford's fox and the Arctic fox (*Alopex lagopus*) are the only canids known regularly to climb cliffs, and the gray fox (*Urocyon cinereoargenteus*) is the only species that routinely climbs trees. Compared with other small canids, the Blanford's fox has a relatively long, bushy tail. Large tails are typical of tree-dwelling carnivores such as stone martens (*Martens foina*) and ringtails (*Bassariscus astutus*). Jumping is usually an integral part of the locomotor pattern in fast-moving arboreal mammals and the large tail is probably an important counter-balance during jumps and may function like a parachute. Mendelssohn *et al.* (1987) described the jumping ability of Blanford's fox as astonishing; captive individuals bounced from one wall to another or jumped to the highest ledges (2–3m) in their cage with remarkable ease and as part of their normal movements. Their small feet and naked pads provide sure footing even on the narrow ledges of a vertical wall. In the field, these foxes were observed climbing vertical, crumbling cliffs by a series of jumps up the vertical sections. Their sharp, curved claws doubtless enhance traction on the more difficult vertical ascents.

Daily energy expenditure of free-ranging Blanford's foxes near the Dead Sea was 0.63–0.65kJ/g/day, with no significant seasonal difference (Geffen *et al.* 1992a). Mean rate of water intake was significantly higher in summer (0.11ml/g/day) than in winter (0.08ml/g/day). They concluded that foxes maintained water and energy balances on a diet of invertebrates and fruits without drinking. Furthermore, this study suggested that Blanford's foxes foraged more for water than for energy, because metabolic needs are met before water requirements when feeding on invertebrates. Blanford's foxes in Israel consume more fruit during the hot summer, which compensates for deficiencies in body water (Geffen *et al.* 1992a, b).

Social behaviour

Data from 11 radio-tracked Blanford's foxes studied over two years in Israel indicated that they were organised as strictly monogamous pairs in territories of *c.* 1.6km² that overlapped minimally (Geffen and Macdonald 1992; Geffen *et al.* 1992c). Locations and configurations of home ranges were stable during that study. A shift in location of home range was observed only once following the death of a pair member. Three of five territories contained one, non-breeding, yearling female during the mating season, but there was no evidence of polygyny (Geffen and Macdonald 1992).

Reproduction and denning behaviour

Blanford's foxes live in monogamous pairs (Geffen and Macdonald 1992). Females are monoestrus and come into heat during January and February (in Israel). Gestation period is *c.* 50–60 days, and litter size is 1–3 pups. Females have 2–6 active teats, and the lactation period is 30–45 days. Neonates are born with soft, black fur. Based on repeated measures of body mass of three young born in captivity, a neonate body mass of 29g has been estimated (Mendelssohn *et al.* 1987; Geffen 1994). The body mass of a subadult is reached in *c.* 3–4 months (700–900g). At about two months of age, the young start to forage, accompanied by one of the parents, and at three months of age they start to forage alone. Juveniles have similar markings as the adult, but their coat is darker and more greyish. Sexual maturity is reached at 10–12 months of age (Geffen 1994).

Young are entirely dependent upon their mother's milk for food and water until they begin to forage for themselves. Adult Blanford's foxes have never been observed to carry food to the young and only one den was found with remains of prey at the entrance (Geffen and Macdonald 1992). Observations of Blanford's foxes suggest that food is not regurgitated to the young, as in other small canids. Geffen and Macdonald (1992) have no indication that the male provides food either to the female or to the cubs, although they observed males grooming and accompanying 2–4-month-old juveniles. Therefore, it appears that the direct contribution to survival of the young by any individual other than the mother is probably minimal. Offspring often remain within their natal home range until autumn (October–November).

Dens used by Blanford's foxes in Israel were usually on a mountain slope and consisted of large rock and boulder piles or scree. Blanford's foxes appeared to use only available natural cavities and never dug burrows. Dens were used both for rearing young during spring and for daytime resting throughout the year. During winter and spring, both members of a pair frequently occupied the same den, or adjacent dens at the same site, while during summer and autumn they often denned in separate locations. Frequent changes in location of den from day to day were more common in summer and autumn (Geffen and Macdonald 1992).

Competition

Blanford's foxes have been observed to flee from a red fox. However, occasionally, individuals will stand at a safe distance and bark at larger potential predators (e.g., leopards and humans).

Mortality and pathogens

Natural sources of mortality In Israel, old age or rabies were the primary causes of death (Geffen 1994). Only a single known case of predation was recorded, where the suspect was thought to be a red fox.

Persecution Not known. There is a single poisoning record of three Blanford's foxes and two red foxes from U.A.E. However, we anticipate that poisoning is a rare cause of mortality in this species.

Hunting and trapping for fur Records by CITES showed that no furs were exported during 1983 and 1985 to 1986. In 1980 and 1982, seven were exported, and in 1981 *c.* 30 skins were exported from Afghanistan. In 1984, 519 Blanford's fox skins were reportedly exported, mostly from Canada, which is well beyond the distribution of this species (Ginsberg and Macdonald 1990). There is no hunting of this species in Israel.

Road kills A single record from Saudi Arabia. None reported elsewhere.

Pathogens and parasites Blanford's foxes appear to be susceptible to rabies. During 1988 to 1989, 11 dead Blanford's foxes were found in two populations in Israel, and two fresh carcasses tested positive for rabies. Individuals that are in poor body condition often have many ticks.

Longevity The lifespan of Blanford's foxes in the wild was estimated at 4–5 years. In captivity, individuals reached six years of age. Old individuals showed severe tooth wear, absence of some incisors and canines, and poor body condition.

Historical perspective

None.

Conservation status

Threats The threat from habitat loss in Israel is limited as most of the area where this species occurs is designated as protected. Political developments may change the status of the northern Judaean Desert. Human development along the Dead Sea coasts may also pose a considerable threat to existing habitat. Similar concerns exist for the populations in the U.A.E.

Commercial use At present, the trade in Blanford's fox fur is negligible and confined to Afghanistan. See Mortality and pathogens.

Occurrence in protected areas

— *Israel*: Ein Gedi Nature Reserve, Judaean Desert Nature Reserve, Maktesh Ramon Nature Reserve, Eilat Mountain Nature Reserve;
— *Jordan*: Dana Nature Reserve;
— *Oman*: Jebel Samhan Sanctuary, Dhofar.

Protection status CITES – Appendix II (2000)

Current legal protection Fully protected in Israel, with no hunting, trapping or trading permitted. Holding in captivity requires a special permit from the Nature Reserves Authority of Israel. There is a ban on hunting in Jordan and Oman. However, there is no legal protection in Egypt, Saudi Arabia, U.A.E., Iran, Afghanistan or Pakistan.

Conservation measures taken None.

Occurrence in captivity

In Israel, the species is kept in captivity at the Hai Bar Breeding Centre (near Eilat). In previous years, there was a pair at the Tel Aviv University Zoo. Captive individuals are also kept at the Breeding Centre for Endangered Arabian Wildlife, Sharjah, U.A.E. Foxes have been successfully bred at all the above facilities.

Current or planned research projects

Research on the life history and diseases in Blanford's foxes is currently being conducted in U.A.E., and extensive surveys are being carried out in Saudi Arabia, Oman and U.A.E. (M. Smith, K.J. Budd and C. Gross, Breeding Centre for Endangered Arabian Wildlife, Sharjah, United Arab Emirates).

Gaps in knowledge

The information on the biology of Blanford's foxes is mostly from the southern part of Israel. Nothing is known on the behaviour and ecology of the species in the eastern part of its distribution. Interactions with other predators and the susceptibility to diseases are poorly understood.

Core literature

Geffen 1994; Geffen *et al.* 1992a,b,c,d,e, 1993; Geffen and Macdonald 1992, 1993; Harrison and Bates 1989, 1991; Mendelssohn *et al.* 1987.

Reviewers: Yoram Yom-Tov, Gustav Peters, Chris Stuart and Tilde Stuart. **Editors:** Michael Hoffmann, Claudio Sillero-Zubiri.

7.2 Pale fox
Vulpes pallida (Cretzschmar, 1827)
Data Deficient (2004).

C. Sillero-Zubiri

Other names

Arabic: tsaaleb; **English:** pallid fox, African sand fox; **French:** renard pâlé; **German:** blassfuchs; **Spanish:** zorro pálido.

Taxonomy

Canis pallidus Cretzschmar, 1827. In Rüppell, Atlas Reise Nordl. Afr., Zool., Säugeth. (dated 1826), pp. 33, pl. 11. Type locality: "Kordofan" [Sudan].

Thomas (1918) associated *Vulpes pallida* with Rüppell's fox (*V. rueppellii*) and the fennec fox (*V. zerda*). Clutton-Brock *et al.* (1976) support this grouping and suggest that these desert foxes are also closely related to the Indian fox (*V. bengalensis*) and the Cape fox (*V. chama*).

Chromosome number not known.

Description

A small, very pale fox with longish legs and large ears (Table 7.2.1). Pale face, elongated muzzle with relatively long whiskers, and a black eye-ring. Large ears, white inside and rufous-brown on the outer surface. Body creamy-white to sandy fawn, relatively thin coat, back sometimes flecked with black or rufous, with darker mid-dorsal line. Flanks paler than dorsal pelage, merging into white or buffy-white undersides, and legs rufous. Long, bushy tail, reddish brown with conspicuous black tip and a dark patch above tail gland. Females have three pairs of mammae. The skull is small with a relatively short maxillary region, and well-developed upper molars in relation to relatively weak carnassial teeth (Clutton-Brock *et al.* 1976). Bullae of the pale fox are slightly larger and the nasals appreciably longer than in Rüppell's fox (Rosevear 1974). Dental formula is 3/3-1/1-4/4-2/3=42.

Table 7.2.1. Combined body measurements for the pale fox from across the range (Dorst and Dandelot 1970; Rosevear 1974; Happold 1987).

HB	380–550mm
T	230–290mm
HF	100mm
E	65–72mm
WT	2.0–3.6kg

Subspecies Five races have been described, four of which are listed here (following Coetzee 1977). According to Rosevear (1974), variation may be clinal.

— *V. p. pallida* (Sudan, from Kordofan to Dongola)
— *V. p. edwarsi* (Mali, Senegal)
— *V. p. harterti* (northern Nigeria northwards to Air in Niger, and westwards to Burkina Faso)
— *V. p. oertzeni* (Nigeria, northern Cameroon and Chad to Libya in the north and Darfur province of Sudan in the south).

Similar species Red fox (*Vulpes vulpes*): larger, with shorter legs and ears. Rüppell's fox (*V. rueppellii*): ears larger; longer tail without black tip (usually white); carnassials 1–3mm longer. Fennec fox (*V. zerda*): ears much larger and thicker, longer coat.

Current distribution

The pale fox is distributed in the semi-arid Sahelian region of Africa bordering the Sahara, from Mauritania and Senegal through Nigeria, Cameroon and Chad to the Red Sea (Figure 7.2.1). Southern limit of geographical range extends into northern Guinean savannah zones.

Range countries Algeria(?), Burkina Faso, Cameroon, Central African Republic (?), Chad, Eritrea, Ethiopia, Gambia, Libya, Mali, Mauritania, Niger, Nigeria, Senegal, Somalia (?), Sudan (Lavauden 1926; Rosevear 1974;

Figure 7.2.1. Current distribution of the pale fox.

Pale fox, age and sex unknown.

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Happold 1987; Yalden *et al.* 1980, 1996; Granjon *et al.* 1995; Grubb *et al.* 1998).

Relative abundance

Widespread and present throughout range but in most parts locally rare. It is one of the least known canid species.

Estimated populations/relative abundance and population trends There is no detailed information on its abundance or status.

Habitat

Typically inhabiting very dry sandy and stony sub-Saharan desert and semi-desert areas, but extending to some extent southwards into moister Guinean savannahs. Therefore, they have a very extensive distribution within an unstable and fluctuating ecological band lying between true desert and the Guinean savannahs. May occur near human habitation and cultivated fields where food is more readily available than in natural habitats (Rosevear 1974).

Food and foraging behaviour

Food Well-developed molars suggest pale foxes are essentially herbivorous, eating mainly berries, wild fruit such as melons, and vegetable matter. They also feed on small rodents, ground-nesting birds, small reptiles and invertebrates (Dorst and Dandelot 1970; Kingdon 1997).

Foraging behaviour Unknown.

Damage to livestock or game: Unlikely, although they are known to kill domestic birds (Rosevear 1974).

Adaptations

Pale foxes tolerate heat well. They can survive lengthy hot, dry seasons, presumably on fruits and the residual moisture of their prey, although they are unable to bear completely waterless conditions (Kingdon 1997).

Social behaviour

Little is known of their habits, but they are gregarious and have been observed in pairs and small family parties (Dorst and Dandelot 1970; Rosevear 1974; Coetzee 1977). In captivity, a group of one female and two males got along amicably (Bueler 1973). They are active from dusk till dawn, resting during the day in extensive burrows, occupied by several individuals (Coetzee 1977).

Reproduction and denning behaviour

Pale foxes dig extensive burrows, 2–3m deep and up to 15m in length, with inner chambers lined with dry vegetation, often under sandy tracks or in the neighbourhood of villages (Haltenorth and Diller 1980). Gestation is likely to be in the region of 7–8 weeks. A captive female gave birth to a litter of four in June (Bueler 1973). Gestation period in captivity is 51–53 days. Three to six young are born; weaning takes six to eight weeks.

Competition

Unknown.

Mortality and pathogens

Unknown, but probably susceptible to predation by other desert carnivores and aerial predators and pathogens like rabies and canine distemper. Anderson (1902) mentioned skulls of the species found in the nest of a kite near Khartoum.

Longevity A captive animal lived to three years (Rosevear 1974), but it is likely that they live to at least twice this age.

Historical perspective

No information available.

Conservation status

Threats Unknown, although occasional persecution by chicken raiders may take place.

Commercial use None.

Occurrence in protected areas Likely to occur in a number of protected areas throughout the species' range, but no reliable information available.

Protection status CITES – not listed.

Current legal protection No information available.

Conservation measures taken No information available, although it is unlikely that any proactive measures have been taken by any of the range countries.

Occurrence in captivity

There are no pale foxes in captivity in collections reporting to ISIS or the International Zoo Year Book. There have been no breeding records for the last decade.

Current or planned research projects

None known.

Gaps in knowledge

This is one of the least known canid species, and studies on distribution, status, basic biology and ecological requirements are needed.

Core literature

Coetzee 1977; Dorst and Dandelot 1970; Happold 1987; Kingdon 1997; Rosevear 1974.

Reviewers: Joshua R. Ginsberg, Chris Stuart and Tilde Stuart. **Editor:** Michael Hoffmann.

7.3 Rüppell's fox
Vulpes rueppellii (Schinz, 1825)
Data Deficient (2004)

F. Cuzin and D.M. Lenain

Other names

Arabic: tsaaleb (name in use for all foxes), tsaaleb Sahir (Saudi Arabia), taaleb (Maghreb); **English:** Rüeppell's fox, sand fox, Rüppell's sand fox; **French:** renard famélique, renard de Rüppell; **Hebrew:** shual holot, shual Negev; **Indigenous names:** Berber: abarhourh (Tachelhaït), akanouch (Zenet), aalboun (Tamazight) (name in use for all foxes); Tuareg: tazbat mallet, achorri, ehadjeh, avarran; Tubu: tourkou fidji tchou ouma (means literally jackal with white tail tip).

Taxonomy

Canis rüppelii Schinz, 1825. In G. Cuvier, Das Thierreich, 4: 508. Type locality: "Vatherland Dongola" [Sudan].

Originally included in *Canis*, but subsequently included in the genus *Vulpes*. The specific name has been misspelt in various ways (e.g*., V. rüppelli*: Ellerman and Morrison-Scott 1951). It is most commonly cited *as V. rueppelli* (Coetzee 1977; Corbet and Hill 1980), but the correct spelling of the name is *V. rueppellii*, as used by Wozencraft (1993). The specific name *rueppellii* is the genitive form of "rueppellius", the Latinisation of Rueppell's name (P. Grubb pers. comm.).

Chromosome number: 2n=40 (Ewer 1973).

Description

One of the smaller *Vulpes* species, Rüppell's fox is slighter in build than the red fox (*V. vulpes*), and has smaller limbs (Table 7.3.1). The ears are long and large in relation to the head, rather similar to the fennec fox (*V. zerda*), but this species lacks darker markings on the back of the ears. Coat colour is variable. The head is beige to a pale sand colour. The ears and face are usually pale, with most animals having black whisker patches running up to the eye, although this too is variable. The colour on the back varies from pale sandy to greyish and even sometimes reddish, with a more or less silvery sheen due to black speckling being present. Flanks and the underbody are usually paler. The legs are beige to a fawn colour, and plantar and digital pads are almost completely covered by hairs. The black speckling from the back culminates in a dense black patch at the base of the tail, which is full and bushy and usually tipped white (a useful diagnostic feature). The fur is very fine and soft with two coats, a thicker darker coat for winter and a lighter colour coat for summer. Females have three pairs of mammae.

Rosevear (1974) remarked that the skull is like a smaller version of the side-striped jackal (*Canis adustus*), but without such well-developed occipital crests. The braincase is rounded, the postorbital processes are blunt and narrow, the zygomatic arches are strong, and the bullae are relatively large (though not so expanded as in fennec fox). The dental formula is 3/3-1/1-4/4-2/3=42.

Rüppell's fox captured from Rhub Al Khali, age and sex not noted. Dubai, United Arab Emirates, 1998.

Chris and Tilde Stuart

Table 7.3.1. Body measurements for the Rüppell's fox.

	Mahazat as-Sayd Protected Area, Saudi Arabia (Lenain 2000)	**Israel** (H. Hefner and E. Geffen unpubl.)	**Egypt** (Osborn and Helmy 1980)
HB male	462.3mm (400–520) n=35	474mm (430–550) n=9	466.0mm (419–519) n=28
HB female	434.7mm (345–487) n=15	450mm (420–480) n=1	419.4mm (411–559) n=16
T male	307.0mm (251–361) n=35	295mm (260–330) n=9	340.9mm (290–387) n=28
T female	275.0mm (230–332) n=15	268mm (220–300) n=5	320.7mm (273–363) n=16
HF male	111.8mm (100–127) n=35		126.8mm (115–138) n=29
HF female	104.7mm (96–115) n=15		121.5mm (110–131) n=16
E male	92.8mm (80–106) n=35	98mm (80–110) n=9	98.4mm (89–110) n=27
E female	86.4mm (75–93) n=15	90mm (80–100) n=5	96.4mm (88–110) n=16
WT male	1.62kg (1.10–2.30) n=179	1.638kg (1000–1800) n=9	1.79kg (1.4–2.3) n=13
WT female	1.48kg (1.10–1.80) n=93	1.470kg (1250–1700) n=5	1.67kg (1.4–1.8) n=6

Subspecies Many subspecies have been described (e.g., Allen 1939; Coetzee 1977), but the variability of specimens seems high (Hüfnagl 1972; Rosevear 1974). The following races seem to be the most valid:

— *V. r. rueppellii* (Egypt and Sudan)
— *V. r. caesia* (north-west Africa and Western Sahara)
— *V. r. cyrenaica* (including *V. r. cufrana*?) (Libya, south-western Egypt, extreme north-western Sudan)
— *V. r. somaliae* (Eritrea and Somalia)
— *V. r. sabaea* (Middle East and Arabic Peninsula)
— *V. r. zarudnyi* (Baluchistan)

Similar species The species may be confused with the red fox (*Vulpes vulpes*), which has darker markings to the back of the ears, especially by European observers who may be unfamiliar with the sleekness, pallor and long ears of local red foxes (Osborne 1992). Their small size may lead to confusion with the fennec fox (*V. zerda*), but the latter has a darker tail tip. The pale fox (*V. pallida*) has a relatively shorter, black-tipped tail, smaller ears, and smaller carnassials (Rosevear 1974).

Current distribution

Widespread in arid biotopes of desert and semi-desert regions of North Africa (north of 17°N) from Morocco and Mauritania to Egypt and Somalia, the northern limit of which is the northern fringes of the Sahara Desert (Figure 7.3.1). Also present in arid regions across the Arabian Peninsula eastwards to Pakistan (68°E) and north-west to Israel and Jordan. Suspected historical expansion of distribution area is likely due to desertification, compensated by competition with the red fox due to new human settlements. It seems to avoid the extreme arid regions in the middle of the Sahara, and the Arabian Empty Quarter, being more abundant on the fringes, in mountain massifs and near oases.

Range countries Afghanistan, Algeria, Chad, Djibouti, Egypt, Eritrea, Ethiopia, Iran, Iraq, Israel, Jordan, Libya, Mali (?), Mauritania, Morocco (including Western Sahara), Niger, Oman, Pakistan, Palestine (?), Qatar (?), Saudi Arabia, Somalia, Sudan, Syria, Tunisia, United Arab Emirates, Yemen. (Valverde 1957; Ingersoll 1968; Hüfnagl 1972; Rosevear 1974; Osborn and Helmy 1980; Gasperetti *et al.* 1985; Aulagnier and Thévenot 1986; De Smet 1988; Le Berre 1990; Harrison and Bates 1991; Kowalski and Rzebik-Kowalska 1991; Dragesco-Joffé 1993; Cuzin 1996; Lenain 2000).

Relative abundance

Although widespread throughout the Arabian Peninsula, the species is limited by the large desert areas (Harrison and Bates 1991) and is mainly confined to the arid and steppe regions. In southern Morocco, Rüppell's foxes seem to be rare and the population trend is unknown.

The density of Rüppell's fox is usually low, but seems higher in areas where food is more freely available, such as near human settlements (Valverde 1957; K. De Smet pers. comm). In a large, fenced, protected area of 2,244km² in Saudi Arabia, densities are 0.68/km² (Lenain 2000). Lower population estimates outside the fenced reserve indicate that the species may be very vulnerable in the over-grazed, human-influenced landscape of central Arabia. In the reserve, the population is stable, but there is a need to document long-term population dynamics (Lenain 2000).

Estimated populations/relative abundance and population trends There is no detailed information on its abundance or status.

Habitat

Their typical habitat includes sand and stone deserts. In Saudi Arabia, they have been found in open and stony habitat often with sparse vegetation cover, including a few herb and grass species (*Fagonia indica*, *Indigofera spinosa*, *Tribulus* spp., *Stipagrostis* spp. and *Panicum turgidum*). Taller vegetation, such as grasses and trees, was usually

Figure 7.3.1. Current distribution of Rüppell's fox.

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sparse. Annual rainfall averaged 100mm per year with a maximum of 240mm per year (Lenain 2000).

On the northern fringe of the Sahara, Rüppell's fox may be found in areas with up to 150mm annual rainfall. In Morocco (including Western Sahara), the general habitat presents sparse to very sparse vegetation cover, dominated by small brushes (*Hammada scoparia, Panicum turgidum, Fagonia* spp.) mostly concentrated in wadis (with *Acacia* spp., *Argania spinosa, Balanites aegyptiaca, Maerua crassifolia* and *Capparis decidua* trees). In Niger (Dragesco-Joffé 1993) and Morocco (F. Cuzin pers. obs.), this species avoids large sand dune areas, where the fennec fox is the only other reported canid species; however, in Algeria, they also occur in large ergs (De Smet 1988).

The Rüppell's fox also lives in coastal areas, with extremely sparse vegetation and without any trees. They are able to survive in areas without any available water, as in central Saudi Arabia (Mahazat as-Sayd protected area) on the fringes of the Arabian Empty Quarter, in Algeria (De Smet 1988) and in Western Sahara, where observations do not show any relationship with distance to the nearest available water (F. Cuzin unpubl.).

Food and foraging behaviour

Food Rüppell's foxes are generalist predators. Their diet includes a high invertebrate content, as well as rodents, lizards, snakes, birds, and wild fruits (Valverde 1957; Osborn and Helmy 1980; Lindsay and Macdonald 1986; Kowalski 1988; Kingdon 1997). Lenain (2000) found that small mammals are an important component of their diet and that in the absence of small mammals, they will turn to beetles (Coleoptera). Scats also contained the remains of desert locusts (*Schistocera gregaria*), which were found in large numbers during some study periods (Olfermann 1996; Lenain 2000), suggesting that they may be very opportunistic.

Foraging behaviour Little is known except that they are solitary foragers (Olfermann 1996) and usually scavenge at camps and permanent human settlements (Valverde 1957; Harrison and Bates 1991; K. De Smet pers. comm; F. Cuzin pers. obs.). The species is mainly crepuscular/nocturnal, but active animals have been seen during the daytime in winter in the Western Sahara (F. Cuzin pers. obs.) and in Tunisia (K. De Smet pers. comm). Lenain (2000) recorded that departure from the den site usually took place in the hour following sunset. This was followed by alternating periods of activity and inactivity throughout the night, the latter usually taking place in the early hours of the morning. Foxes usually re-entered the den site before sunrise, remaining in the den throughout the day.

Damage to livestock or game Local breeders have reported that Rüppell's foxes prey on chickens, lambs and young goats in Saudi Arabia (Lenain 2000), Egypt (Osborn and Helmy 1980), Niger (Dragesco-Joffé 1993) and in Algeria Hoggar (K. De Smet pers. comm).

Adaptations

Their ability to survive in a hyper-arid environment, where the opportunity to drink would be extremely rare, appears to be facilitated by various ecological, behavioural and physiological adaptations (though not to the extent seen in the fennec fox); even a captive specimen never drank (Petter 1952). The diet, which includes plant material, fruits and roots (Rosevear 1974; Lenain 2000), likely provides much of their moisture requirements, and behavioural (e.g., nocturnal activity patterns) and morphological adaptations (e.g., coat colour, hair on feet, large ears) help in thermoregulation. The role of physiological mechanisms (e.g., urinary concentrating ability) has yet to be established. They are reportedly able to squirt the noxious contents of their anal glands at potential aggressors (Kingdon 1997).

Social behaviour

Little is known, but reports indicate that the species may be gregarious, having been sighted in groups of 3–15 (I. Linn pers. comm.). These may represent extended family groups. Grouping may be incidental, a result of close aggregation of dens in the few areas where denning sites are available.

In Oman, Lindsay and Macdonald (1986) found that home ranges were very expansive covering some 69km², and social units were spatially separate. In Mahazat as-Sayd, Olfermann (1996) found a mean annual home range of 16.3km², while Lenain (2000) gives a figure of 10.2km². Olfermann (1996) found that males had significantly larger seasonal home ranges than females. Adults were usually organised as monogamous pairs.

Reproduction and denning behaviour

In Saudi Arabia, studies show that mating takes place from December to February (Olfermann 1996; Lenain 2000), which usually coincides with the first rains after the harsh summer period. Tracks of two adult animals obviously engaged in a courtship display were found in southern Morocco in November, a few days after heavy rainfall (F. Cuzin pers. obs.). Captures of young cubs have been made in early March in Saudi Arabia (Lenain 2000) and in March in Western Sahara (Valverde 1957). Petter (1952) recorded very young animals in the area of Beni Abbès (Algeria) in May, and peaks of captures of young cubs in Saudi Arabia were made from July to August following the dependency period (Lenain 2000). Gestation lasts 7–8 weeks (Olfermann 1996) and litter size is 2–3 in the Mahazat as-Sayd protected area in Saudi Arabia (Olfermann 1996). Young cubs remain dependent on their parents for an undefined period, after which they venture out from the den site area. Both sexes reach sexual maturity at around 9–10 months (Olfermann 1996).

Dens are commonly located under slabs of rock or dug at the base of trees or bushes (Lindsay and Macdonald 1986; Harrison and Bates 1991; Kingdon 1997). In areas with few shelters (like in southern Western Sahara), the species may use very exposed dens, often in the middle of plains (some of these burrows are dug by honey badgers, *Mellivora capensis*). In such areas, any disturbance induces the flight of the animal (F. Cuzin pers. obs.), and, in Niger, Dragesco-Joffé (1993) states that they often prefer to flee from their den in case of danger. This behaviour is very common for the Arabian red fox too.

In Oman, Lindsay and Macdonald (1986) found that study animals changed den sites frequently, likely as an anti-predator strategy or perhaps due to resource availability in other areas of a home range. Lenain (2000) recorded an instance where a shift occurred due to cooling: a male Rüppell's fox used a shallow scrape in a sabkha-type substrate (packed silt), with a maximum depth of 700mm. This type of substrate offers effective cooling, and midday temperatures may be 12–15°C lower inside the den than outside. This type of shallow scrape was recorded throughout the study area, although its cooling facility varied depending on the substrate.

Competition

In Saudi Arabia, Israel and Morocco, the red fox is present in the fringes of the desert, particularly those colonised by man. Rüppell's foxes may only be able to compete in the harshest desert areas, where the red fox is not able to survive, or in protected areas where red fox control is taking place (Yom-Tov and Mendelssohn 1988). The settlement of new areas represents an opportunity for the red fox to increase its range, at the expense of Rüppell's fox. In the Aïr, Niger, Dragesco-Joffé (1993) suggests that the density of Rüppell's fox is higher in areas where other carnivores, such as golden jackal (*Canis aureus*), caracal (*Caracal caracal*), sand cat (*Felis margarita*), striped hyaena (*Hyaena hyaena*) and fennec fox are absent.

Mortality and pathogens

Natural sources of mortality The fragments of the jaws of a young fox were found in pellets of an owl (*Bubo ascalaphus*) near Idjil (Mauritania) by Heim de Balsac and Heim de Balsac (1954), while Olfermann (1996) recorded predation by steppe eagles (*Aquila nipalensis*) and owls (*Bubo ascalpahus*) in Arabia. Lenain and Ostrowski (1998) recorded the death of a Rüppell's fox in a cage trap as a result of a honey badger attack. However, the honey badger is unlikely to be a predator of Rüppell's foxes and this was probably an opportunistic attack.

Persecution Poisoned baits are used indiscriminately to control predators in Saudi Arabia (Gasperetti *et al.* 1985), Niger (Dragesco-Joffé 1993) and Morocco (Cuzin 1996). Individuals are accidentally killed by jaw-traps used against jackals (Dragesco-Joffé 1993). They are occasionally killed for food by nomads (Ginsberg and Macdonald 1990; F. Cuzin pers. obs.).

Hunting and trapping for fur Rüppell's fox furs have been found on sale (D. Lenain pers. obs.).

Road kills No road kills were recorded in Morocco (F. Cuzin pers. comm) or in Algeria and Tunisia (K. De Smet pers. comm) or Saudi Arabia (D. Lenain pers. obs.).

Pathogens and parasites Susceptibility to disease is poorly known. However, Lenain (2000) reported seroprevalence to canine distemper virus, canine parvovirus and canine rotavirus. Rabies does affect this species (S. Ostrowski pers. comm.), and they may be infested by ticks (e.g., *Rhipicephalus sanguineus*) and by various species of fleas (Olferman 1996; Lenain 2000).

Longevity Ostrowski (1999) estimated an age of 87.5–88.5 months for a male tagged in 1992 in the wild in Saudi Arabia; the maximum confirmed age in the wild is seven years, but it could be higher (Olfermann 1996). Haltenorth and Diller (1980) give longevity as 6.5 years in captivity.

Historical perspective

None.

Conservation status

Threats Habitat loss, fragmentation and degradation, direct and indirect persecution by hunting, and indiscriminate use of poisons, appear to represent the main threats in Morocco. In Israel, the species is on the verge of extinction due to competitive exclusion by red foxes that are expanding their range following human settlements in the Negev Desert (Yom-Tov and Mendelssohn 1988).

Commercial use Rarely hunted for food or for sale of furs.

Occurrence in protected areas
— *Algeria*: Ahaggar and Tasili n'Ajjer National Parks;
— *Egypt*: Gebel Elba Conservation Area;
— *Israel*: Maktesh Ramon National Park, Tznifim Nature Reserve;
— *Jordan*: Al-Shaumari Wildlife Reserve;
— *Libya*: Nefhusa National Park, Zellaf Nature Reserve;
— *Mauritania*: Banc d'Arguin National Park;
— *Niger*: Aïr and Tenere National Reserve;
— *Oman*: Jiddat al Harasis;
— *Saudi Arabia*: Mahazat as-Sayd, Harrat al' Harrah, Hawat bani Tamim, Uruq Bani Ma'arid, Majami Al Hadb, Saja / Umm ar Rimth;
— *Tunisia*: Sidi Toui National Park.

Protection status CITES – not listed.
The species is classed as Lower Risk: Near Threatened in Morocco (including Western Sahara) (Cuzin 1996).

Current legal protection In Saudi Arabia, there is currently no effective legislation for the protection of native carnivores (P. Seddon pers. comm.). It is not illegal to shoot, poison or trap mammalian carnivores. Hunting laws (Decree No. 457 and Decrees M/22, No.128) restrict such activities within the National Commission for Wildlife and Conservation Development protected areas network. Some of the areas encompass and protect carnivore populations, although none to date have been established with the protection of Rüppell's foxes listed as the main objective.

In Israel, the species is fully protected by law, and no hunting, trapping or trading is allowed. In Morocco, according to the annual hunting decree, Rüppell's foxes and red foxes may be hunted during the whole year, as they are considered as pests. There is no information for other countries.

Conservation measures taken None known.

Occurrence in captivity

Rüppell's foxes are held in captivity. According to the International Zoo Yearbook (1992), only two cases of successful breeding occurred in zoos (Nikolaev, Ukraine and Tel Aviv, Israel). Attempts to breed Rüppell's foxes have not been very successful (Ginsberg and Macdonald 1990), although they have been successfully bred in the Hai Bar Breeding Centre, Eilat, Israel (E. Geffen pers. comm.). According to ISIS data, 2 males, 4 females and 1 unsexed animal are kept in zoos, without any recent reproduction noted. One female is kept in Rabat Zoo, Morocco.

Current or planned research projects

J.B. Williams (Ohio State University, Columbus, USA) and D.M. Lenain and S. Ostrowski (National Wildlife Research Center, Taif, Saudi Arabia) are investigating metabolic response and water turnover of Rüppell's foxes in an arid environment in Saudi Arabia.

S. Ostrowski and D.M. Lenain (National Wildlife Research Centre, Taif, Saudi Arabia) and M. van Vuren (University of Pretoria, South Africa) are undertaking research into seroprevalence of canine diseases in the Rüppell's fox population at Mahazat as-Sayd, Saudi Arabia.

R. Hefner and E. Geffen (Tel Aviv University, Israel) are studying habitat use of Rüppell's foxes in Israel.

Gaps in knowledge

The status and ecology of North African populations remains largely unknown. Monitoring of populations in well-established protected areas throughout the species' range is encouraged. There is scope for detailed study of competition between Rüppell's and red foxes.

Core literature

Lenain 2000; Lindsay and Macdonald 1986; Kowalski 1988; Olfermann 1996.

Reviewers: Eli Geffen, Stephane Ostrowski, Koenraad J.M. De Smet. **Editors:** Michael Hoffmann, Claudio Sillero-Zubiri.

7.4 Fennec fox
Vulpes zerda (Zimmermann, 1780)
Data Deficient (2004)

C.S. Asa, C. Valdespino and F. Cuzin

Other names

Arabic: Fenek: rhorchi, gorchi, arhorchi, aqorchi (Maghreb); **English:** fennec; **French:** fennec; **German:** fenek, wüstenfuchs; **Spanish:** fenec; **Indigenous names:** Tuareg: akori, akorhal, eresker, ahuneski.

Taxonomy

Canis zerda Zimmermann, 1780. Geogr. Gesch. Mensch. Vierf. Thiere 2: 247. Type locality: "Es bewohnt die Soara und andere Theile von Nordafrika hinter des Atlas, der Ritter Bruce behautet, man Fände es auch in tripolitanischen." [Sahara].

Placed in the genus *Fennecus* by Stains (1975), Coetzee (1977) and Nowak (1999) . Wozencraft (1993) included *Fennecus* in the genus *Vulpes*, an arrangement in agreement with many other authorities (e.g., Clutton-Brock *et al.* 1976; Geffen *et al.* 1992e) and followed here. Note that two previously described races, *saarensis* Skjöledbrand, 1777 and *zaarensis* Gray, 1843 are synonyms.

Chromosome number: 2n=64 (Ewer 1973).

Description

The fennec fox is the smallest canid, with extremely large ears that give it the greatest ear to body ratio in the family (Table 7.4.1). The muzzle and legs are slender and delicate. Pelage is typically sandy or cream-coloured, although it may have a light fawn, red or grey cast; underparts are paler. The large ears are darker on the back and white or nearly so inside; ear edges are white. Eyes are large and dark, with dark streaks extending from the inner eye down and outward to either side of the muzzle. Upper parts of limbs reportedly coloured reddish-sand in individuals from North Africa, whereas those from further south are nearly white in these areas. The coat is very thick and long; dense fur on the feet extends to cover the pads. The tail is also well furred with a darker tip and a slightly darker spot

Table 7.4.1. Body measurements for the fennec fox.

	Saint Louis Zoo, St. Louis, MO, USA	**West Africa, Sudan, and northern Africa** (Rosevear 1974) (gender not reported)	**Egypt** (Osborn and Helmy 1980) (gender not reported)
HB male	392mm (390–395) n=2	362mm (333–395) n=9	368mm (337–387) n=46
HB female	382mm (345–395) n=5		
T male	232mm (225–240) n=2	169mm (125–187) n=9	206mm (186–230) n=46
T female	241mm (230–250) n=5		
HF male	105mm (100–110) n=2	93mm (90–98) n=9	103mm (93–111) n=46
HF female	98mm (92–100) n=5		
E male	100mm (100) n=1	91mm (86–97) n=9	96mm (88–104) n=46
E female	93mm (90–95) n=5		
WT male	1.5kg (1.3–1.7) n=2		1.1kg (0.8–1.15) n=9
WT female	1.4kg (1.0–1.9) n=5		

Six year-old female fennec fox. St Louis Zoo, Missouri, USA, 2001.

Chuck Dresner

covering the caudal gland. Females have three pairs of mammae. It has a vulpine skull, but with very large tympanic bullae (Clutton-Brock *et al*. 1976). The canines are small and narrow. The dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Monotypic (Coetzee 1977).

Similar species Rüppell's fox (*Vulpes rueppellii*): larger; upper parts silvery grey. Pale fox (*V. pallida*): larger; upper parts pale sandy fawn suffused with black hairs (Dorst and Dandelot 1970).

Current distribution

Widespread in the sandy deserts and semi-deserts of northern Africa to northern Sinai (Figure 7.4.1) (Saleh and Basuony 1998).

Historical distribution Morocco, Algeria, Tunisia, Libya, and Egypt south to the Sudan.

Current distribution They are common throughout the Sahara (Harrison and Bates 1991) and may occur to north Sahelian areas in the south to 14°N (Dragesco-Joffé 1993; Granjon *et al*. 1995). References to fennec fox sightings in the United Arab Emirates were based on an animal in the Al Ain zoo (Al-Robbae 1982), which was, in fact, a Rüppell's fox (Gasperetti *et al*.1985). Thesiger (1949) reported fennec fox tracks in the region of Abu Dhabi but whether the tracks were accurately identified is uncertain. The only documented regression concerns northern Moroccan Sahara, where the fennec foxes disappeared during the 1960s from four localities, which were restricted sandy areas close to permanent human settlements (F. Cuzin pers. obs.).

Range countries Algeria, Chad, Egypt, Libya, Mali, Mauritania, Morocco (including Western Sahara), Niger, Sudan, and Tunisia (Hufnagl 1972; De Smet 1988; Bel Hadj Kacem *et al*. 1994; Granjon *et al*. 1995; Poilecot 1996; Saleh and Basuony 1998).

Relative abundance

Current statistics are not available, but the population is assumed to be adequate based on the observations that the fennec fox is still commonly trapped and sold commercially in northern Africa. In southern Morocco, fennec foxes were commonly seen in all sandy areas away from permanent human settlements (F. Cuzin pers. obs.).

Estimated populations/relative abundance and population trends There is no detailed information on its abundance or status.

Habitat

Fennec foxes subsist in arid desert environments, preferring this substrate for burrowing. Stable sand dunes are believed to be ideal habitat (Dorst and Dandelot 1970; Coetzee 1977), although they also live in very sparsely vegetated sand dunes near the Atlantic coast (F. Cuzin pers. obs.). Annual rainfall is less than 100mm per year on the northern fringe of the fennec fox's distribution. On the southern fringe, it may be found up to the Sahelian areas that receive as much as 300mm rainfall per year. In the Sahara, sparse vegetation is usually dominated by *Aristida* spp., and *Ephedra alata* in large sand dunes. In small sand dunes, it is dominated by *Panicum turgidum*, *Zygophyllum* spp., and sometimes by trees like *Acacia* spp. and *Capparis decidua* (F. Cuzin pers. obs.). The fennec fox is claimed to be the only carnivore of the Sahara living completely away from water sources (Dekeyser and Derivot 1959, in Noll-Banholzer 1979).

Food and foraging behaviour

Food Fennec foxes are omnivorous and are reported to consume insects, small rodents (e.g., *Jaculus jaculus, Gerbillus* spp. and *Meriones* spp.), lizards (e.g., *Acanthodactylus* spp.), geckos (e.g., *Stenodactylus* spp.), skinks (e.g., *Scincus albifasciatus*), eggs, small birds (e.g., larks and sandgrouse), various fruits and some tubers (Dragesco-Joffé 1993; F. Cuzin pers. obs.). Captive fennec foxes have also been reported to capture and kill an adult rabbit (Gauthier-Pilters 1962).

Foraging behaviour Fennec foxes hunt alone (Coetzee 1977), probably because solitary hunting of small prey is more efficient. They have not been seen using the "mouse jump" hunting strategy typical of most fox species (Ewer 1973), but reportedly dig to find insects and small vertebrates. However, like other foxes, they do cache food by burying. Fennec foxes are very opportunistic and commonly visit temporary human settlements during the night in search of food (Dragesco-Joffé 1993; F. Cuzin pers. obs.)

Damage to livestock or game In Niger, some individuals have been reported raiding poultry coops (Dragesco-Joffé 1993).

Adaptations

The fennec fox is well adapted to desert living. They are primarily nocturnal, although crepuscular activity is also reported (Gauthier-Pilters 1967). In southern Morocco, animals were commonly active in winter until around mid-morning (F. Cuzin pers. obs.). The pale, dense fur presumably serves to protect against cold nights, whereas the well-furred feet facilitate walking on hot, sandy substrates. The exceptionally large ears likely help in heat dissipation, but may also aid in locating insects and small

Figure 6.3.1. Current distribution of the fennec fox.

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vertebrates (Ewer 1973). Nocturnal activity patterns, the use of burrows during the day, and the moisture content of their prey probably contribute to their ability to go without drinking water (Schmidt-Nielsen 1964; Dragesco-Joffé 1993; F. Cuzin pers. obs.). In addition, their kidneys filter extremely high concentrations of urea with little water loss (Gasperetti *et al.* 1985).

Social behaviour

Fennec foxes are thought to be moderately social, but this evidence is based mainly on captive animals. The basic social unit is believed to be a mated pair and their offspring, and, like some other canids, the young of the previous year may remain in the family even when a new litter is born (Gauthier-Pilters 1967). Play behaviour is common, even among adults, although males show more aggression and urine-marking around the time of oestrus. Captive fennec foxes engage in high levels of affiliative behaviour, and typically rest in contact with each other. In captivity, fennec foxes often bury faeces by pushing loose substrate with their noses or hind feet (Gauthier-Pilters 1962).

Reproduction and denning behaviour

First mating is reported at nine months (Bekoff *et al.* 1981) to one year (Gauthier-Pilters 1967). In the wild, fennec foxes mate in January and February and give birth in March and April (Gauthier-Pilters 1967). In captivity, births can occur year round, but most litters are born between March and July (Bauman 2002). Data from captivity are more extensive than those from the wild, but, because captive animals are maintained in a broad range of environmental conditions, inter-oestrous intervals vary considerably. Individual differences are also likely to contribute to this variability. Fennec foxes most commonly give birth once annually, but more than one litter per year is possible under some conditions (Koenig 1970; Valdespino *et al.* 2002).

The fennec fox monoestrous cycle is characterised by a pro-oestrous phase of about six days and a one- to two-day oestrus (Gauthier-Pilters 1967; Koenig 1970; Valdespino *et al.* 2002). There is no sanguineous discharge in association with oestrus or pro-oestrus. In non-fertile cycles, ovulation is followed by an approximately 50-day di-oestrous period, also called pseudopregnancy because it is equivalent in hormonal pattern and duration to gestation (Asa and Valdespino 1998; Valdespino 2000). Most remarkable is the exceptionally long copulatory tie of as long as 2 hrs 45 min (Valdespino 2000; Valdespino *et al.* 2002). The male becomes very aggressive and protective of the female after mating, and he provisions her during pregnancy and lactation (Sowards 1981).

Gestation is 50–52 days (Petter 1957; Volf 1957; Saint Giron 1962; Koenig 1970); however, Gangloff (1972) reported 62- and 63-day gestations for two fennec foxes at the Strasbourg Zoo. Litter size ranges from 1–4 (Petter 1957; Gauthier-Pilters 1967; Koenig 1970; Gangloff 1972; Bauman 2002), and weaning takes place at 61–70 days (Koenig 1970).

Dens are always dug in sand, in open areas or places sheltered by plants such as *Aristida pungens,* and *Calligonum comosum* (Dragesco-Joffé 1993; F. Cuzin pers. obs.). Dens may be huge and labyrinthine, especially in the most compacted soils, covering up to 120m², with as many as 15 different entrances (Dragesco-Joffé 1993). Bueler (1973) reports that dens may be close together or even interconnected. In soft sand, dens are usually small and simple, with just one entrance and one tunnel leading to a chamber (Dragesco-Joffé 1993; Cuzin 1996).

Competition

The fennec fox is partly sympatric with, and thus may face competition from, Rüppell's fox (Lindsay and Macdonald 1986), although direct observations have not been made. In southern Morocco, encounters between these species are rare, as Rüppell's fox rarely goes into large sandy areas (F. Cuzin pers. obs.). At its southern limit, the fennec fox is sympatric with the pale fox (Dragesco-Joffé 1993).

Mortality and pathogens

Natural sources of mortality In the wild, jackals, striped hyaenas (*Hyaena hyaena*) and domestic dogs are reported to prey on fennec foxes (Gauthier-Pilters 1967), though this is anecdotal and possibly questionable. The capture of fennec foxes is likely very difficult, as they are fast and able to change direction very quickly. Nomads consider them very difficult to capture, even for the saluki, a local greyhound-like dog (Monteil 1951; Dragesco-Joffé 1993). However, the eagle owl may prey on young fennec foxes (Dragesco-Joffé 1993). There is significant mortality of neonates in captivity, generally attributed to the sensitivity of the parents to disturbance (Petter 1957; Volf 1957; Gangloff 1972).

Persecution Young foxes are captured in their burrow by humans for photographic exhibition, to be sold to tourists (F. Cuzin pers. obs.), or to locals to be raised for meat (Schmidt-Nielsen 1964). In southern Morocco, however, fennec fox meat is not eaten because it is considered foul smelling (F. Cuzin pers. obs.).

Hunting and trapping for fur Fennec foxes are commonly trapped for sale to the pet trade and for fur by the indigenous people of northern Africa.

Road kills Because roads are rare in large sandy areas, only one mortality has been recorded in southern Morocco (F. Cuzin pers. obs.).

Pathogens and parasite Fennec foxes are presumed to be susceptible to pathogens and parasites that affect domestic dogs. There is some evidence that modified-live canine distemper vaccine may induce canine distemper in fennec foxes (Montali *et al.* 1994), but the newer sub-unit vaccines should not (R. Junge pers. comm.).

Longevity Lifespan in the wild is unknown. In captivity, the recorded maximum longevity is 14 years for males and 13 years for females (Bauman 2002).

Historical perspective

None.

Conservation status

Threats The primary threat appears to be trapping for commercial use. In sandy areas commonly visited by tourists, the fennec fox is well known, but because it is otherwise difficult to see, it is trapped for exhibition or sale to tourists (F. Cuzin pers. obs.). Though restricted to marginal areas, new permanent human settlements such as those in southern Morocco have resulted in the disappearance of fennec foxes in these areas (F. Cuzin pers. obs.).

Commercial use See Mortality and pathogens.

Occurrence in protected areas

— *Algeria*: Ahaggar and Tasili n"Ajjer National Parks;
— *Egypt*: Bir El Abd Conservation Area;
— *Libya*: Nefhusa National Park, Zellaf Nature Reserve;
— *Mauritania*: Banc d'Arguin and Diawling National Parks;
— *Niger*: Aïr and Tenere National Reserve;
— *Tunisia*: Sidi Toui National Park.

Protection status CITES – Appendix II (2000)
Listed as Lower Risk: Least Concern (Cuzin 1996) in Morocco, which probably reflects their threat status across their range.

Current legal protection Legally protected in Morocco (including Western Sahara).

Conservation measures taken No specific measures taken.

Occurrence in captivity

Historically, the North American Regional Studbook (Bauman 2002) lists some 839 individuals that have been held in the North American region between 1900 and 2001. At the end of 2001, there were 131 individuals in 51 institutions. The Australian Regional Studbook lists 81 historically, with only 12 in the captive population at present. Although fennec foxes occur in European zoos, there is no studbook or management plan. Fennec foxes are also kept as pets and bred privately, but these records are not available.

Current or planned research projects

None known.

Gaps in knowledge

While studies of captive animals have gone some way towards improving our knowledge of this enigmatic species (particularly as regards reproduction), much remains unknown of their basic ecology and behaviour in the wild. Work on captive populations is encouraged, but an in-depth study of the species, with particular emphasis on habitat use and population dynamics in the wild, is overdue.

Core literature

Bauman 2002; Gangloff 1972; Gautier-Pilters 1962, 1967; Petter 1957; Valdespino 2000; Valdespino *et al.* 2002.

Reviewer: Karen L. Bauman. **Editors:** Michael Hoffmann, Claudio Sillero-Zubiri.

Chapter 8

South Asia – South of the Himalaya (Oriental)

8.1 Dhole
Cuon alpinus (Pallas, 1811)
Endangered – EN: C2a(i) (2004)

L.S. Durbin, A.Venkataraman, S. Hedges
and W. Duckworth

Other names

English: Asiatic wild dog, Indian wild dog, red dog; **French:** chien sauvage d'Asie, cuon d'Asie; **German:** der alpenwolf, rotwolf; **Spanish:** perro salvaje Asiatico; **Indigenous names:** Assamese: kuang-kukur, rang kukur; Bahasa Indonesia: adjag or ajag, anjing hutan; Bahasa Malaysia: srigala, Bengali: ban-kutta, ban-kukur; Bhutanese: phara, phou; Burmese: tan-kwe; Buryat: zurbi; Chinese: tsai-lang; Gujarati: kutra; Gurkhali: ban-kukur; Hindi: adivi-kuta, son-kuta, sona-kuta, rasa-kuta, jungli kuta; Javanese: asu alas; Kachin: kyi-kwa-lam; Kashmiri: jungli-kuta, ram-hun, ban-kuta, bhansa; Kazakh: chue; Kirgizian: chue, nyar; Kannada: kadu nai, korku, bun-seeta; Khmer: chkai prey [wild dog]; Ladakh: farra; Lao: ma nai [big dog]; Tibetan: farra; Manipuri: huithou; Lepcha: sa-tun; Malayalam/Tamil: chen nai; Marathi: kolsun; Mongolian: dshergul; Nepali: bwaso; Oriya: balia kukura; Russian: krasnyi volk [red wolf], dikaya sobaka [wild dog],chikalka; Telegu: resu kukka; Thai: maa nay; Telegu: resu kukka; Tungus: dzergil; Vietnamese: cho soi lua.

Taxonomy

Canis alpinus Pallas, 1811:34. Type locality: near Udskoi Ostrog, Uda R., Amur region, former USSR.

The genus *Cuon* is post-Pleistocene in origin, and related more closely to the extant jackals than to wolves (Thenius 1954). Simpson (1945) placed the dhole in the subfamily Simocyoninae of the family Canidae, together with the African wild dog (*Lycaon pictus*) and the bush dog (*Speothos venaticus*) of South America on the basis of shared anatomical features, most notably the reduction of the role of the crushing post-carnassial molars. Many have questioned Simpson's classification arguing that similarities in dentition are due to convergent evolution because of a highly predatory diet (Thenius 1954).

Clutton-Brock *et al.* (1976) provided further support for Thenius's view by analysing morphological, ecological and behavioural characteristics across 39 canid species. Their study found that *Cuon* was more similar to *Canis, Dusicyon* and even *Alopex*, than to *Speothos* or *Lycaon.* However, *Cuon* resembled *Speothos* and *Lycaon* only when skull and dental characters were considered. According to Kleiman (1972) and Lorenz (1975), *Cuon, Lycaon* and *Speothos* appear more closely related to other canid genera than to each other. Further evidence of the taxonomic distinctiveness between *Speothos, Cuon* and *Lycaon* comes from analysis of sequences from mitochondrial genes (Wayne *et al.* 1997); both *Lycaon* and *Cuon* were classified as *Canis*-like canids and *Speothos* within a clade with another South American canid, the maned wolf (*Chrysocyon brachyrus*).

Chromosome number: 2n=78 (Aristov and Baryshnikov 2001).

Description

Dholes are large canids (typically 12–20kg) (Table 8.1.1), usually having a reddish or brown coat and a darker, bushy tail (sometimes with a white tip). Sexual dimorphism is not very distinct with no quantitative anatomical differences known. The ears are triangular with rounded tips (about half the length of the face). The pinnae are usually whitish-fawn on the inside and reddish-brown on the outside. The muzzle is brown, relatively short, and slightly convex in profile. The nose is black and the eyes slightly hooded with amber irises. The dorsal and lateral pelage is red to brown and the foreneck, chest and undersides are often whitish or light ginger coloured. In the south and south-west of the dhole's range, the fur is shorter and rusty-red coloured. In the north and north-

Table 8.1.1. Body measurements for the dhole.

	Cohen (1978)	**Phu Khieo Wildlife Sanctuary**, Thailand (L. Grassman unpubl.).	**Kanha**, India (L. Durbin unpubl.).
HB	880–1,130mm	male: 970mm (880–1,050) n=3	1,355mm n=1
T	410–500mm	male: 340mm (320–360) n=3	421mm n=1
WT male	15–20kg	16.0kg (15.0–17.0) n=3	15.5kg, n=1
WT female	10–13kg		

Two-year-old male dhole. Bandipur National Park, Karnataka State, India, 1996.

Krupakar Senani

east, the fur is longer, brownish-red or yellowish-brown. The legs are notably shorter in some alpine regions and the coat is a yellowish-grey colour in Himalayan regions. In Thailand, the coat is more uniform brown lacking the lighter throat and chest. The coat is occasionally grizzled (Duckworth *et al*. 1998). The toes are red, brown and/or white; the hairless fore-toe pads (on all feet) are joined at the base (near the main pad) unlike most domestic dogs. Dentition is unique within the Canidae having one fewer lower molar tooth (3/3-1/1-4/4-2/2), with the heal of the lower carnassial M_1 crested and with a single cusp (all other canids within the range of *Cuon* have two cusps). There are usually six or seven pairs of mammae, rather than the five pairs typical for *Canis* (Burton 1940).

Subspecies Mivart (1890) distinguished two species of *Cuon*, the southern dhole (*C. javanicus*) and the northern dhole (*C. alpinus*), on the bases of body size and the second upper and lower molars. Ellerman and Morrison-Scott (1951), however, recognised 10 subspecies, later revised to nine (Ellerman and Morrison-Scott 1966) or 11, according to Ginsberg and Macdonald (1990), which are given below. The validity of many of these forms is doubtful.

— *C. a. alpinus* (east of eastern Sayans, East Russia). Thick tawny red coat greyish neck and ochre muzzle.
— *C. a. lepturus* (south of Yangze River, China). Uniform red coat with thick underfur.
— *C. a. dukhunensis* (south of the Ganges, India). Reddish coat, short hair on the paws and black whiskers.
— *C. a. adjustus* (North Myanmar and north-east India). Reddish brown coat.
— *C. a. primaevus* (Himalayan Nepal, Sikkim and Bhutan). Longer redder coat than *C. a. dukhunensis*, long hair on paws.
— *C. a. laniger* (Kashmir and southern Tibet). Full, yellowish-grey coat, tail not black but same colour as body.
— *C. a. hesperius* (East Russia and China). Long yellow-tinted coat, white underside and pale whiskers.
— *C. a. fumosus* (West Szechuan, China and Mongolia). Luxuriant yellowish-red coat, dark back and grey neck.
— *C. a. infuscus* (South Myanmar, Malaysia, Thailand, Laos, Cambodia and Vietnam). Relatively uniform brown coat.
— *C. a. sumatrensis* (Sumatra, Indonesia). Short red coat and dark whiskers.
— *C. a. javanicus* (Java, Indonesia). Short, bright red coat.

Similar species Dingo (*Canis lupus dingo*): Tail less bushy and when held upright often bends forward towards the head; penis more visible from side and ears pointed; proportionally longer jaw relative to head length.

Golden jackal (*Canis aureus*): Notably smaller (*c.* 2/3 size of dhole), with proportionally shorter tail to body; coat yellowish-brown and always grizzled; face thin and ears pointed; distinctive fast trotting gait.

Grey wolf (*Canis lupus*): Notably larger; distinctive greyish coat; ears pointed; penis more visible from side; proportionally longer jaw relative to head length.

Distribution

Historical distribution Most of South, East, and South-east Asia. Extending from the Tian-Shan and Altai mountains and the Maritime Province of the former USSR southwards through Mongolia, Korea, China, Tibet, Nepal, India, and south-eastwards into Myanmar and Indochina (Cambodia, Vietnam, and Laos), Thailand, the Malaysian peninsula, and the Indonesian islands of Sumatra and Java.

Current distribution

Central and eastern Asia: There have been no confirmed, recent reports of dholes from Russia, Mongolia, Kazakhstan, Kyrgyzstan (where they were found formerly in the Tian-Shan area), or Tajikistan (where they were found formerly in the eastern Pamir area) (A. Poyarkov and N. Ovsyanikov *in litt*. D. Miquelle pers. comm.). There is a recent report of a dhole that was captured in Jiangxi district, south China (C. Bellamy pers. comm.). Dholes were once present in parts of western China in the Tian-Shan Range, but the species' current status in this area is unclear. The species is still found in Tibet today, particularly in areas bordering the Ladakh region of India (R. Wangchuk pers. comm.), and the Tibet Forestry Bureau has reported that dholes are still "common" in parts of south-east Tibet (S. Chan, *in litt*.). Dholes occurred in northern Korea (Won Chang Man and Smith 1999) and a few small populations may still exist. There have been no records from Pakistan, but the species occurred on the alpine steppes of Ladakh, Kashmir, and India (Johnsingh 1985) that extend into the region termed Pakistan-occupied Kashmir by India.

India: Dholes are still found throughout much of India south of the river Ganges, and especially in the Central Indian Highlands and the Western and Eastern Ghats of the southern states. They are also found throughout north-east India, in the states of Arunachal Pradesh, Assam, Meghalaya, and West Bengal (A. Venkataraman, A.J.T. Johnsingh and L. Durbin pers. comm.). In the Himalaya and north-western India, the status of dholes seems more precarious with a much more fragmented distribution. Dholes reportedly still occur in the Ladakh area of Kashmir, which is contiguous with the Tibetan highlands in China (R. Wangchuk pers. comm.).

Nepal Formerly recorded in the Terai region of the Indo-gangetic plain, including the Royal Chitawan National Park in Nepal, but there have been few recent reports. There is an unconfirmed report of dholes in Dhorpatan Hunting Reserve in the late 1990s (R.C. Kandel pers. comm.).

Bhutan: There have been recent press reports that dholes have recovered from a government-initiated mass poisoning campaign in the 1970s, and there have apparently been numerous recent incidents of dholes killing livestock in the lower Kheng region. Two recent, independent, eye-witness reports identify dholes in six protected areas in Bhutan (S. Wangchuk pers. comm.; T. Wangchuk pers. comm.). In some regions, dhole predation on wild boar (*Sus scrofa*) may be viewed in a positive light by local people (T. Wangchuk pers. comm.).

Bangladesh: Dholes were thought to occur in the forested tracts of the Chittagong and Sylhet Districts (Johnsingh 1985). It is not certain whether any remain in Bangladesh.

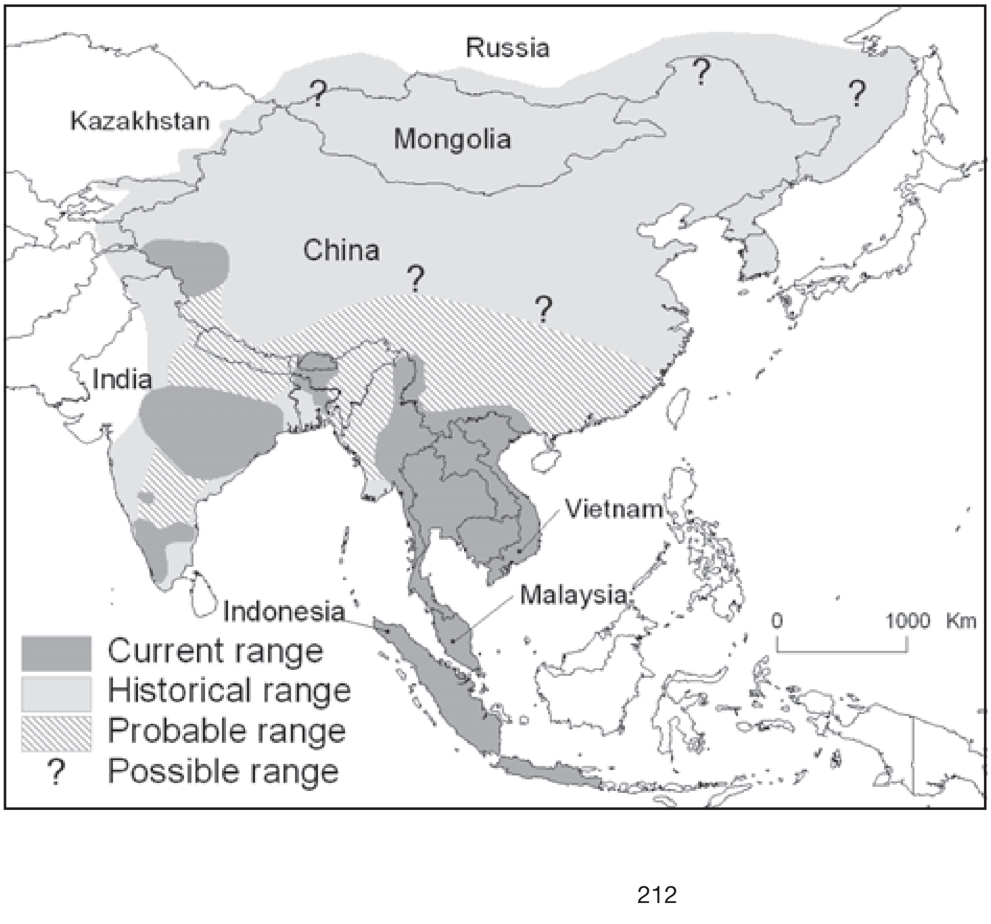

Figure 8.1.1. Current distribution of the dhole.

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Myanmar: In Myanmar, dholes were recorded by camera trapping at 11 of 15 survey areas scattered across the country, only four of which were protected. Dholes and/or leopards have apparently replaced tigers as the top predator in these areas (Myanmar Forest Department 2003).

Indochina (Laos, Cambodia, Vietnam) and Thailand: Dholes probably ranged over all or almost all of Laos, Cambodia, Vietnam, and Thailand, although reliable site-specific information is scarce. Present distribution is highly fragmented, and large parts, particularly of Vietnam and Thailand are without any regular occurrence of dholes, although they persist in a number of protected areas (Duckworth *et al*. 1999; Waltson 2001; M. Baltzer and R. Shore *in litt*.; A. Lynam pers. comm.).

Indonesia and Malaysia: Their historical range probably included all or most of the Malaysian peninsula and the Indonesian islands of Sumatra and Java, but reliable information is scarce. Current distribution is poorly known but is thought to be highly fragmented. On the Malaysian peninsula, dholes are known to occur in four sites in northern and central areas of the peninsula (from recent camera-trap surveys; J.B. Abdul pers. comm.). On Java, dholes appear to be most common in the protected areas at the eastern and western ends of the island. On Sumatra, very little is known, but dholes are known to occur in major protected areas in the southern, central, and northern parts of the island (e.g., from camera trapping; D. Martyr pers. comm.).

Range countries Bangladesh (?), Bhutan, Cambodia, China (including Tibet), India, Indonesia (Sumatra and Java), Kazakhstan (Ex?), Kyrgyzstan (Ex?), North Korea (?), South Korea (?), Laos, Malaysian peninsula, Mongolia (?), Myanmar, Nepal (?), Pakistan (?), Russia (?), Tajikistan (Ex?), Thailand, and Vietnam (Johnsingh 1985; Sosnovskii 1967; A. Poyarkov and N. Ovsyanikov *in litt*.; D. Miquelle pers. comm.).

Relative abundance

The only information on dhole abundance comes from a few protected areas in southern and central India. These estimates have not been obtained through systematic sample-based survey methods, but are based on estimates of the number of packs within the protected areas (derived using known home range areas and knowledge of mean pack sizes).

Estimated populations/relative abundance and population trends Reported densities of dholes in protected areas include: Bandipur Project Tiger Reserve (Karnataka, southern India), 0.13 dholes/km^2 (A. Venkataraman and V. Narendra Babu unpubl.); Mudumalai Sanctuary (Tamil Nadu, southern India), 0.095 dholes/km^2 (A. Venkataraman and V. Narendra Babu unpubl.); Pench National Park (Madhya Pradesh, central India), 0.3 dholes/km^2 (B.B. Acharya and A.J.T. Johnsingh unpubl.).

In the Mudumalai Sanctuary, dhole numbers have been monitored for the last 13 years, and there are indications that overall numbers are stable though substantial annual variations do occur. However, in parts of the adjoining Bandipur National Park, a significant decline in numbers has been observed in the years 2002 to 2003 (A. Venkataraman, pers. obs.). The reason for this decline is unknown. A.J.T. Johnsingh (pers. comm.) noted a decline of dholes during the 1970s in the Mundanthurai Plateau area of the Kalakad-Mundanthurai Project Tiger Reserve in southern India. There has been a recent increase in the number of dhole packs seen.

In general dholes are thought to be abundant in protected areas in southern and central India, including Bandipur and Nagarahole National Parks (Karnataka), Periyar Project Tiger Reserve (Kerala), Kanha National Park (Madhya Pradesh), and Melghat and Tadoba Project Tiger Reserves (Maharashtra). Abundance is relatively lower in West Bengal, Assam and Arunachal Pradesh. In the rest of north-east India (Nagaland, Mizoram), dholes are currently extinct or close to extinction.

No remotely comparable information on density is available for any part of Southeast Asia, and there are no empirical data on trends in this region.

Habitat

The dhole is found in a wide variety of vegetation types, including: primary, secondary and degraded forms of tropical dry and moist deciduous forest; evergreen and semi-evergreen forests; dry thorn forests; grassland–scrub–forest mosaics; and alpine steppe (above 3,000m a.s.l.). They are not recorded from desert regions.

In India, tropical dry and moist deciduous forest may represent optimal habitats, based on the regions thought to hold the largest dhole populations. Ungulate biomass, particularly that of cervid species, is highest in these vegetation types when compared to others in the same region (A. Venkataraman and V. Narendra Babu unpubl.). In India, tropical dry and moist deciduous forests are subject to seasonal monsoon climates.

Important factors that may influence habitat selection include the availability of medium to large ungulate prey species, water, the presence of other large carnivore species, human population levels, and suitability of breeding sites (proximity to water, presence of suitable boulder structures, and sufficient prey).

Food and foraging behaviour

Food The main prey of dholes varies throughout their range. Beetles, rodents, and birds have all been recorded among dhole prey items (e.g., Adams 1949; Davidar 1975); and dholes also occasionally consume grass and other plants like most other carnivores (A.J.T. Johnsingh pers. comm.). However, dholes hunt mainly vertebrate prey, with a preference for medium to large ungulates. Studies of prey selection by sympatric carnivores in Nagarahole, in southern India, showed that dholes prefer medium-sized prey between 31kg and 175kg in weight (Karanth and Sunquist 1995, 2000). The average weight of prey killed by dholes was 43kg in Nagarahole. In Bandipur, prey weighing less than 50kg were most preferred (Johnsingh 1992). In Mudumalai Sanctuary, India, Venkataraman *et al.* (1995) reported the occurrence of prey remains in scats for two packs: chital remains comprised 70% and 41%, sambar (*Cervus unicolor*) 22% and 23%, cattle 4% and 15%, and lagomorphs 3% and 20%, for the two packs, respectively. In parts of Russia, the main prey species were reported to be reindeer (*Rangifer rangifer*), wild sheep (*Ovis* spp.), and wild goats (*Capra* spp.) (Sosnovski 1967). In Alas Purwo National Park in East Java, Indonesia, banteng (*Bos javanicus*) were frequently eaten by dholes during a study in the mid- to late-1990s (Hedges and Tyson 1996). Elsewhere on Java, dholes seem to take Javan rusa (*Cervus timorensis*) and red muntjac (*Muntiacus muntjac*) in preference to banteng (Hedges and Tyson 1996). In Khao Yai, Thailand, prey occurrence in scats comprised: sambar, 63%; red muntjac, 18%; East Asian porcupine (*Hystrix brachyura*), 5%; insects, 3%; birds, 3%; reptiles, 3% and vegetation, 5% (S. Austin unpubl.).

In Kanha National Park, India, dholes have been seen to return to scavenge on prey remains several days after the prey was killed (L. Durbin pers. obs.). Dholes were also occasionally observed to eat carrion (elephant (*Elephas maximus*) and gaur (*Bos gaurus*) carcasses), in Mudumalai Sanctuary (A. Venkataraman and R. Arumugam unpubl.) and have been seen feeding on a red muntjac carcass originally killed by a python in Thailand (Nettelbeck 1995). It has, however, been suggested that such scavenging only occurs during periods of prey scarcity, particularly during the dry season.

Dholes will occasionally eat vegetation and invertebrate prey. Grass is ingested, but may serve an anti-helminthic function rather than a nutritional one (L. Durbin unpubl.). Prater (1971) also writes "*In the South Indian hill ranges dholes are said to feed greedily on the fallen fruits of bael and black wood trees*". Cohen (1977) found vegetable matter in only 25% of scats; Johnsingh (1983) found grass to be a major component in only 7% of scats.

Foraging behaviour Dholes are communal hunters, occasionally forming packs of over 30 animals (Fox 1984), but are more often found in hunting groups of fewer than 10 animals. Depending on prey availability, dholes may also hunt alone or in pairs, taking smaller prey such as infant deer or hares (Cohen 1977; Venkataraman *et al.* 1995). The dhole is primarily a crepuscular forager but can hunt at any time of the day or night (Johnsingh 1982; L. Durbin, S. Hedges, and M. Tyson pers. obs.). In central India, dholes rarely run their prey to exhaustion and most chases extend for less than a few hundred metres (L. Durbin pers. obs.). This is generally the case when dholes hunt deer and banteng in East Java, but occasionally dholes chase banteng until the latter appear exhausted (S. Hedges and M. Tyson pers. obs.). During hunts, some dholes may lie in ambush while others drive prey towards them. Dholes often drive deer into water, where they surround them and swim out to capture them. It is common for certain individuals to take particular roles in the hunt, such as leading the chase or taking the first grab at the prey. Pack members communicate their whereabouts with whistles and yelps, and cooperate in bringing down and killing the prey. They eat quickly (e.g., up to 1kg per dog in 4 minutes; Johnsingh 1983), with relatively little aggression, except when dealing with small prey. Usually one or more dholes take turns as sentinel (who possibly look out for leopards and tigers that could prey on dholes or appropriate their kills or humans who scavenge kills in some areas) when feeding on large prey (L. Durbin, pers. obs.). Dholes hunt successfully both in open meadows and in denser forest. They prefer to kill their own prey, but sometimes steal the kills of other species, or scavenge from old kills.

Damage to livestock or game Dholes generally prefer to kill wild prey species and ignore domestic livestock (Venkataraman *et al.* 1995; L. Durbin pers. obs.). Sometimes they resort to stock predation (e.g., domestic cattle or goats) when their natural prey is diminished (Venkataraman *et al.* 1995; L. Durbin, S. Hedges and M. Tyson pers. obs.). Dholes sometimes prey on threatened species; for example, it was feared that the banteng population of Alas Purwo National Park in Java was being driven to local extinction by dhole predation (Hedges and Tyson 1996). It was the dholes that finally "disappeared" when banteng numbers reached a level that, apparently, could no longer sustain them. Possibly, these dholes turned to cattle predation and suffered retributive human persecution (S. Hedges and M. Tyson unpubl.). In Kanha, central India, dholes prey on a rare, endemic subspecies of swamp deer (*Cervus duvauceli branderi*). The two species seem to coexist, as chital, which constitute the dholes' principal prey, are numerous in Kanha (L. Durbin pers. obs.).

Adaptations

The presence of only a single crested cusp (two in other canids) on the lower carnassial M_1 may enhance the sheering capacity of the teeth and hence the speed at which prey can be consumed. This may improve the dholes' ability to compete with kleptoparasites.

Dholes have the capacity to hold large quantities of meat in their stomachs (*c.* 3kg). Like African wild dogs, they can also regurgitate small quantities at will, thus allowing the transportation of food to pack-mates and neonates. This is an adaptation to communal breeding, providing food for the pups, the mother, and other adult helpers that remain at the den.

Social behaviour

Dholes usually live in packs of 5–10 individuals, but groups of as many as 18 (Alas Purwo, Java, Indonesia; Hedges and Tyson 1996), 24 (Kanha, India; L. Durbin unpubl.), and 25 (Mudumalai Sanctuary, India; Venkataraman *et al*. 1995) have been recorded on a regular basis. These group sizes included juvenile animals. Group size and composition may vary under different environmental conditions, but most of the current data are from India. Packs studied by Johnsingh (1983), Venkataraman *et al.* (1995), and L. Durbin (unpubl.), contained significantly more males than females, perhaps a reflection of female-biased dispersal (Venkataraman 1998).

Pack members regularly play together, engaging in mock-fights, rolling, and allo-grooming. Social rank is established by pushing and holding, but rarely by aggressive biting (M. Boeer pers. comm., L. Durbin unpubl.). Groups have a strong hierarchical structure, with a dominant male and female who are the main, or sole, breeders.

Pack members over-mark each other's faeces and urine, producing latrines throughout the group's range. Latrines may serve intra-group communicative functions (e.g., relaying information about hierarchical or sexual status) as well as territorial ones. The ranges (or at least core areas) of neighbouring packs are often quite separate (Johnsingh 1982; Venkataraman *et al.* 1995; L. Durbin unpubl.), though interactions between groups can be either friendly or hostile.

In Bandipur, India, Johnsingh (1983) reports a home range size of 40km^2 and Venkataraman *et al.* (1995) found ranges of 54 and 83km^2 in Mudumalai. Durbin *et al.* (pers. comm.) radio-tracked an adult male within a breeding pack (12 adults; 12 pups) in Kanha, India, and during the three month tracking period, when adults were tending pups at den sites, the pack used a range of 55km^2. In a more recent study in Thailand, three adult male dholes were captured, radio-collared, and tracked for one to ten months in Phu Khieo Wildlife Sanctuary, Thailand, between March 2000 and June 2002. A total of 101 radio-locations were recorded for two animals and used to calculate home range sizes. The overall home range sizes of two of the males were 12.0km^2 and 49.5km^2 respectively, while the third male could not be tracked after radio-collaring. The dholes did not utilise the habitat within their ranges in a uniform manner; instead, open forest/grassland was used proportionately more than closed forest (L. Grassman *in litt*.).

Dholes have a broad and unusual vocal repertoire that includes whines, mews, and squeaks (Fox 1984). Growls, growl-barks, chattering calls, and screams are used as alarms to alert other pack-mates to danger (Johnsingh 1982). This large range of alarm calls may have evolved to alert pack-mates to danger from humans or other predators (e.g. leopard, tiger). Such calls could also act as a threat to intimidate adversaries. A repetitive whistle-like contact call may allow dispersed pack members to identify one another and to re-group (Durbin 1998). Maintaining group cohesion in this way is likely to be highly adaptive in areas with other large predators. Whistle calls travel well at ground level due to their frequency and structure and allow easy location of the source (L. Durbin unpubl.).

Reproduction and denning behaviour

Dholes give birth once a year and have a gestation period of about nine weeks (Sosnovskii1967). Mating occurs between November and April (dry season) in India, with a peak during December and January (Davidar 1973; L. Durbin pers. obs; but see Venkataraman 1998; Johnsingh 1982). In East Java, dholes are thought to mate mainly during January and May (i.e., end of the wet season) (S. Hedges and M. Tyson pers. obs.). Females exhibit seasonal polyoestrus with a cycle of 4–6 weeks (M. Boeer pers. comm.). The dominant pair engages in vigorous play and marking, culminating in a copulatory tie (Davidar 1973; Paulraj *et al.* 1992). It is usually only the dominant female that breeds, but exceptions have been noted. Johnsingh (1979) has observed lone females breeding outside the group, with limited or no success in rearing their litters. By contrast, three females have been seen suckling within a single group (Davidar 1974). Whether this represents plural breeding or "wet nursing" is uncertain. Subordinate males sometimes show sexual interest in the alpha female and may contribute to the paternity of the litter (Venkataraman 1998; M. Boeer pers. comm.).

Litter sizes vary dramatically, even within the same pack in different years (e.g., up to 8, and 5–10, for two packs in Mudumalai; Venkataraman *et al* 1995). The largest litter size recorded is 12, with only one lactating female in the group (Kanha, India; L. Durbin *et al.* unpubl.).

In captivity, newborn pups can weigh 200–350g, although by the age of 10 days their body weight can double, and they have a total body length of about 340mm (Sosnovskii 1967). Pups suckle from the mother until they are about three weeks old, when they start to receive regurgitated meat from other pack members. Pups are weaned by about 6–7 weeks (L. Durbin *et al.* unpubl.), although, in captivity, weaning has been recorded at 8–9 weeks (M. Boeer pers. comm.). In their early weeks, the pups are quarrelsome, but with age they become more vigilant and less aggressive, noticeably so by around eight weeks (L. Durbin *et al.* unpubl.). All adults take part in guarding, feeding, grooming, and playing with the pups. By about three months, the pups accompany the adults during hunts (Johnsingh 1982); however, the pack may not be fully mobile until about eight months (Venkataraman 1998). Dholes reach adult size by about 15 months. Venkataraman (1998) states that female dholes breed for the first time at three years. This is probably due to behavioural, as well as physiological, constraints. In captivity, dholes of both sexes can reproduce at two years of age (M. Boeer pers. comm.).

Den types range from earthen burrows to rocky caverns. Johnsingh (1982) and Fox (1984) provide more information on dhole den sites.

Competition

A number of instances have been recorded where dholes were killed and eaten by tigers and leopards (Venkataraman 1995). However, Venkataraman (1995) reported that injuries or deaths as a result of interactions between dholes and leopards or tigers were rare. Interactions are usually limited to intimidation and harassment, presumably to reduce competition resulting from use of common hunting grounds. In Nagarahole National Park, southern India, Karanth and Sunquist (1992) found dhole hairs in leopard scats, evidence that dholes are occasionally eaten by leopards. However, the effect of intra-guild competition on dhole densities is unknown.

In some areas humans scavenge dhole kill; for example, Kurumba tribes of the Niligiris in southern India (Venkataraman 1999), and among at least one Mon Khmer speaking tribal group in Laos (Chamberlain 2003).

Mortality and pathogens

Natural sources of mortality Most observed injuries to dholes are probably inflicted by prey animals, but dholes have been wounded and killed by leopards and tigers (e.g., Connell 1944; Venkataraman 1998).

Persecution Dholes are persecuted throughout their range. In India, bounties were paid for carcasses until the Wildlife Act of 1972, when dholes were given legal protection. Perhaps the most common reason for persecution is the fear of stock predation. Methods of persecution include poisoning of carcasses, snaring, shooting, and clubbing of animals at den sites. In India, farmers can be compensated if there is proof that their stock has been killed by wild animals outside core protected areas. Despite this, stock predation is a common reason for dhole persecution by local people in India, e.g., Arunachal Pradesh (N. Babu pers. comm.). In India, British colonial hunters also shot and poisoned dholes because they saw them as a threat to the wild ungulate populations. Today, human persecution still occurs, but levels vary regionally depending on the enforcement of wildlife laws, levels of stock predation, and cultural beliefs. Across Laos, Cambodia, and Vietnam, levels of hunting are very high, sufficient to reduce almost all species of mammal larger than a hare to very low densities, except in the largest wildernesses, and to cause widespread local extinction of most species of large carnivores and ungulates. There is little if any evidence of dholes being specifically hunted anywhere in these three countries, but because many hunting techniques are essentially non-selective (e.g., snaring), dholes are affected. Any dholes moving out of wilderness areas into human-settled areas are at risk of being killed, either as a result of indiscriminate snaring or as presumed stock predators.

Hunting and trapping for fur Not thought to be a significant mortality factor at present. Skins have been reported as curios (Duckworth *et al.* 1999). In the countries of the former USSR, dholes were not hunted for fur to any great extent because they occurred at too low densities (A. Poyarkov and N. Ovsyanikov *in litt.*). However, in the mid-19th century, dhole pelts were valuable in Ussuryisk Krai, and at the beginning of the 20th century, in Manchzhuriya, prices for dhole pelts were high (Geptner *et al.* 1967).

Road kills In India, many roads cut through dhole habitat and injuries and death by traffic are possibly significant causes of dhole mortality.

Pathogens and parasites When dholes are in contact with other species, especially other canids, they are at risk of contracting and transmitting infectious diseases. Dholes may occasionally present human health risks. Their faeces contain infectious pathogens such as *Toxocara canis.* Dholes have also been known to suffer from rabies (Morris 1942), canine distemper (Davidar 1975; M. Boeer pers. comm.), mange (Morris 1937; L. Durbin pers. obs.), trypanosomiasis (S.K. Ray pers. comm.), canine parvovirus (seroprevalences found in Chennai and Hodenhagen zoos, M. Boeer pers. comm.), and endoparasites such as cestodes and roundworms. In the 1940s, a rabies epidemic in the Billigirirangan Hills, India, resulted in villagers being bitten by rabid dholes and subsequently dying (Morris 1942).

Longevity Dholes can live to at least 16 years in captivity (Sosnovskii 1967), but this is uncommon in the wild. Venkataraman (1998) found that older dholes often "disappeared" from packs when 7–8 years old.

Historical perspective

No information.

Conservation Status

Threats

Depletion of the dhole's prey base. Across almost all of Cambodia, Laos, and Vietnam, as well as within protected areas, ungulates occur at levels well below natural. All species of ungulate except muntjacs (*Muntiacus* spp.), pigs (*Sus* spp.) and in some areas southern serow (*Naemorhedus sumatraensis*) are ecologically or fully extinct across extensive parts of the region. Only a few of the largest wildernesses support nearly intact species assemblages and even in these, the larger species (*Bos* spp., *Cervus* spp., hog deer *Axis porcinus*) are very rare. This situation will likely hinder any possibility of recovery by the region's dhole populations, even if the other issues could be addressed. While not as depressed as in Indochina, prey levels in Indonesia also exist at levels much below carrying capacity (because of illegal hunting and habitat degradation). In protected areas in southern and central India, where dhole numbers are stable, prey densities are high. In north-east India, prey densities are very low in protected areas with dholes.

Habitat loss and transformation. Currently, extensive areas of natural or semi-natural vegetation remain in Laos and Cambodia, some areas encompassing many hundreds of square kilometres of potential dhole habitat. However, habitat conversion and fragmentation are proceeding apace. In Vietnam, very few natural areas of over 50km^2 remain. Habitat loss and fragmentation is a major threat to protected areas in Indonesia, particularly those on Sumatra. Habitat loss and degradation are also serious threats to dholes in South Asia, and the disappearance of dholes from many of the forested tracts in India has been attributed in large part to loss of habitat.

Persecution by cattle graziers through poisoning, shooting, trapping, and killing of pups at dens. This certainly occurs in Indochina, although it is unclear how often. In Indonesia, too, it is a threat but again its significance is unknown. In India, such persecution can play a serious role in limiting local populations. Dholes living outside or on the edge of core protected areas are particularly vulnerable to human kleptoparasitism, snaring (non-selective) and direct persecution. For example, during a radio-tracking study in 2000, in the buffer zone of Kanha Tiger Reserve, central India, at least 16 out of 24 dholes in one pack died from a sudden strychnine poisoning (L. Durbin pers obs). In southern India, such persecution is moderate to low, and often occurs indirectly when cattle graziers and others inadvertently go close to dhole dens and disturb adults and pups, disrupting breeding and rearing (A. Venkataraman pers. obs.). "By-catch" in snares and other traps is probably a significant threat to dholes across Indochina at least.

Competition with other species including feral domestic dogs for prey species. Apparently, free-living dogs have been seen and/or camera trapped in many parts of Indochina, but there is no evidence for existence of large populations. Undoubtedly, the main competitor for prey species in Indochina is people. There is no evidence that feral dogs are significant competitors with dholes in Indonesia. In many parts of their range, dholes are sympatric with tigers and leopards and so the potential for significant interspecific competition for prey exists, especially if the prey populations are reduced as a result of hunting by people.

Disease and pathogens. Particularly those transmitted by feral and/or domestic dogs, e.g., mange, canine distemper, parvovirus and rabies. The significance of disease is unclear in Indochina, but diseases are a significant threat in South Asia, and probably in parts of Indonesia.

Commercial use There is no widespread exploitation for fur or other purposes, though medicinal use should be investigated in China.

Occurrence in protected areas

— *Bhutan*: Reliable reports of dholes in Thrumshingla National Park, Royal Manas National Park, Jigme Dorji National Park, Jigme Singye Wangchuck National Park, Bumdeling Wildlife Sanctuary, Toorsa Strict Nature Reserve, and Phiposs Wildlife Sanctuary (CSG Dhole Database 2003: Sanjay pers. comm., T. Wangchuk pers. comm.).

— *Cambodia*: Reliable reports of dholes in The Trapeang Thom and Russei Thom areas of Preah Vihear Province; Virachey NP in Ratanakiri Province; the Koh Nhek area of Mondulkiri Province; Lomphat WS in Ratanakiri Province; Kulen Promtep WS in Preah Vihear Province; the Chhep area in Preah Vihear Province; Phnom Samkos WS in Pursat Province; and in the Central Cardamoms (Prek Tatai area) in Koh Kong Province. The last two listed are unconfirmed, since they are based on footprints only (Long *et al.* 2000). The other reports are primarily from the camera-trap surveys conducted by the Wildlife Conservation Society's Cambodia Program and WWF Cambodia.

— *China*: Reliable reports of dholes from two protected areas in the 1990s (Taohongling NR and Li Shan NR) and unconfirmed reports from at least five other sites (CSG Dhole Database 2003). There is also a report of a dhole trapped near Poyang Lake Nature Reserve in Jiangxi province, South China, and currently being held in captivity (C. Bellamy pers. comm.).

— *India*: Reliable reports of dholes from at least 38 protected areas in India (15 in southern India, 11 in central India, 6 in western India, and 6 in northern India; CSG Dhole Database 2003).

— *Indonesia*: Dholes are known to occur, or to have occurred recently (in the 1990s) on Java: Alas Purwo National Park, Baluran National Park, and Ujung Kulon National Park. There are unconfirmed reports from at least six other protected areas on the island. Sumatra: dholes are known to have occurred recently (in the 1990s), in Bukit Barisan Selatan National Park, Kerinci-Seblat National Park, and Gunung Leuser National Park. Outside of these areas information is sparse (CSG Dhole Database 2003). In Way Kambas National Park, Sumatra, dholes were previously listed; however, a three-year camera trapping study failed to record any dholes (R. Tilson pers. comm.).

— *Laos*: Dholes have been recorded from eight declared or proposed national protected areas and there are unconfirmed reports from another 11 areas. Four of the five existing or proposed protected areas without records or reports are those least well surveyed. The fifth, Xe Bang-Nouan, was surveyed with a very rigorous approach to village-interview derived data and species were only listed as reported where a dated, site-located, claim was discussed in detail with the original observer. The species may well have occurred into the 1990s in all declared or proposed national protected areas in Laos. There is no more recent information from most areas (CSG Dhole Database 2003).

— *Malaysian peninsula*: Dholes were photographed recently (using camera traps; e.g., J.B. Abdul, pers. comm.) in the following protected areas, Taman Negara (national park), Cameron Highlands Wildlife Sanctuary, Ulu Lepar Forest Reserve, and Krau Wildlife Reserve (CSG Dhole Database 2003).

— *Myanmar*: There are recent reliable records from eight areas in Myanmar, including the Alaungdaw Kathapa National Park, Mamamyaing Reserve Forest, and the Southern Rakhine Yoma Elephant Range.

— *Thailand*: There are confirmed reports of dholes in three protected areas from 1999 or 2000 (Khao Yai NP, Phu Khieo WS, Thapraya NP) and unconfirmed reports from seven other sites (CSG Dhole Database 2003).

— *Vietnam*: Dholes were thought to occur in Vu Quang NR, Pu Mat NR, Ngoc Linh (Quang Nam) NR, and Phong Nha NR in the 1990s, there were unconfirmed reports from 18 other sites (CSG Dhole Database 2003).

Protection status CITES – Appendix II (2003)

Current legal protection In Cambodia, the current wildlife decrees give the dhole protection from all hunting. A new forestry law is under preparation, and a proposal to list the species as a fully protected species is under discussion. In India, the dhole is protected under Schedule 2 of the Wildlife Act of 1972 (permission is required to kill any individual unless in self defence or if an individual is a man killer). The creation of Project Tiger Reserves in India has provided some protection for populations of the *C. a. dukhunensis* subspecies (A.J.T. Johnsingh pers. comm., L. Durbin pers. obs.). In the Russian Federation, dholes received the status of "protected animal" in 1974 (A. Poyarkov and N. Ovsyanikov *in litt*.); however, the poisoning of grey wolves may inadvertently affect any remnant dhole populations (V. Puzanskii pers. comm.). In Vietnam, the dhole is protected by Decree 18/HDBT (17/01/1992) and the amendment Decree 48/2002/ND-DP (22/04/2002) under category IIB, which limits extraction and utilisation. However, the levels of extraction or utilisation are not quantified (B. Long *in litt*. 2003).

Conservation measures taken None specifically focused on dholes have been reported for most range states. In India, Project Tiger could potentially maintain dhole prey bases in areas where tigers and dholes coexist. There do not appear to be any specific measures for dhole conservation in Indochina, although the declaration of relatively large protected area networks in Cambodia, Laos, and Vietnam will, when these areas become functional realities on the ground, form a suitable conservation system for the species in at least Cambodia and Laos.

Occurrence in captivity

There are at least 110 dholes in captivity, and the sex ratio is approximately even. Except for some captive populations in India heterozygosity appears to be good, but there is little chance of breeding the putative subspecies as animals from diverse geographical origins have been widely interbred (M. Boeer pers. comm.). Dholes are known to breed in Beijing, Winnipeg, Dresden, Novosibirsk, Chennai (Madras), Hodenhagen, Safari Park Beekse Bergen, Magdeburg, and Howletts (M. Boeer pers. comm.). To our knowledge there have been no attempts to reintroduce the species, and at present there is no evidence that this would be justified.

Current or planned research projects

L. Durbin, B.B. Acharya, A.J. Durbin, and A.J.T. Johnsingh (Centre for Ecology and Hydrology, UK and Wildlife Institute of India) undertook an ecological study of dholes in Kanha Tiger Reserve, central India, between May 1998 and March 2000. Radio-telemetry data were restricted to a three-month period for a male in a large breeding pack.

L.I. Grassman (Texas A and M University, USA) carried out a ten-month radio-telemetry study of a pack-living male dhole in Phu Khieo Wildlife Sanctuary, Thailand, between March 2000 and June 2002.

S. Hedges and M.J. Tyson (Wildlife Conservation Society, Indonesia) studied the impact of predation by dholes, leopards, and human poachers on the ungulate prey base in Baluran and Alas Purwo National Parks in East Java, Indonesia, from September 1991 to January 1999. There are plans to begin a radio-telemetry study of dholes in East Java.

M. Boeer (Hodenhagen Safari Park, Germany) is involved in studies of reproductive biology and behaviour of a pack of dholes in a large enclosure at Hodenhagen Safari Park, from 1995 to present.

C. Sommer (Philipps-University of Marburg, Germany) is carrying out a comparative study of dhole, African wild dog, and grey wolf in captivity, with special emphasis on dominance hierarchy, communication, individual distances, and mating behaviour.

A. Iyengar, S. Hedges, A. Venkataraman, V. Narendra Babu, and P.A. Morin (Laboratory of Conservation Genetics, Max Planck Institute for Evolutionary

Anthropology, Germany, the Indian Institute of Science, and the Wildlife Conservation Society) are studying the conservation genetics of dholes.

A. Venkataraman and V. Narendra Babu (Asian Nature Conservation Foundation, Bangalore, India) are currently undertaking a conservation assessment of dholes in southern and central India.

A.J.T. Johnsingh, K. Sankar, and B. B. Acharya (Wildlife Institute of India) are conducting a radio-telemetry study of dholes in Pench, central India.

Gaps in knowledge

Data on distribution, status, relative abundance and population trends in Southeast Asia, and data on relative abundance and population trends in India, are essential. Furthermore, the possible existence of remnant populations of dholes in central and north-east Asia (i.e., Korea, China, Mongolia, Russia, Kazakhstan, Kyrgyzstan and Tajikistan) needs to be investigated. Additional research on threats emerges as an immediate area requiring additional research, particularly regarding the role of disease in dhole population dynamics, the significance of road kills and the ability of dhole to persist on small prey items (e.g., lagomorphs, rats and mice) in areas where populations of large (or indeed of all) ungulates have been reduced to negligible levels.

Core literature

Burton 1940; Cohen 1978; Davidar 1975; Durbin 1998; Fox 1984; Johnsingh 1982, 1985; Venkataraman 1995, 1998; Venkataraman and Johnsingh 2004; Venkataraman *et al.* 1995.

Reviewers: Arati Iyengar, A.J.T. Johnsingh. **Editors**: Claudio Sillero-Zubiri, Michael Hoffmann.

8.2 Indian fox
Vulpes bengalensis (Shaw, 1800)
Least Concern (2004)

A.J.T. Johnsingh and Y.V. Jhala

Other names

English: Bengal fox; **Indigenous names:** Hindi: lomri (India); Tamil: kulla naree (India); Telugu: gunta nakka (India); Kanada: kanka nari, sanna nari (India); Marathi: kokri(India); Nepali: phiamro (Nepal); Gujarati and Kutchi: lokdi (India).

Taxonomy

Canis bengalensis Shaw, 1800. Gen. Zool. Syst. Nat. Hist., 1(2), Mammalia, p. 330. Type locality: “Bengal” [India, *c.* 22°00'N, 86°00'E].

Chromosome number not known.

Description

Medium-sized fox with typical vulpine appearance, though smaller than any of the subspecies of the red fox *V. vulpes* (Table 8.2.1). The species’ ears are proportional, with darker brown hair on the back. The nose and lips are black, and the eyes have dark tear marks. The muzzle is pointed with tan to black hair around the upper part and near the eyes. The pelage is grey, varying between yellowish grey to silver grey, and lacking the rusty red hair that is typical of the red fox. The dorsal region is darker, while the underside is a paler cream to dirty white. The winter coat can be quite luxuriant. The limbs are slender with some rufous on them, and the tail is more than half the body length. The tip of the tail is black. The tail is carried trailing during normal travel, it is kept horizontal when the fox is running, and it is raised to almost vertical when the fox makes sudden turns. Females have three pairs of mammae. The dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies Monotypic.

Table 8.2.1. Body measurements for the Indian fox from Bombay Natural History Society museum specimens (Y. Jhala unpubl.).

HB male	500mm (390–575) n=6
HB female	472mm (460–480) n=3
T male	289mm (247–320) n=5
T female	276mm (245–312) n=3
HF male	118mm (110–125) n=5
HF female	114mm (112–116) n=3
E male	71mm (68–73) n=4
E female	75mm(72–79) n=3
WT male	2.7–3.2kg
WT female	>1.8kg

Adult Indian fox, sex unknown. Ahmednagar, Maharashtra, India, 2002.

Hira Punjabi

Similar species Desert fox (*Vulpes vulpes pusilla*) sympatric in western Indian and Pakistan, larger and taller at the shoulders, and with white-tipped tail.

Current distribution

The Indian fox is endemic to the Indian subcontinent (Figure 8.2.1). It ranges from the foothills of the Himalaya in Nepal to the southern tip of the Indian peninsula. In the northern part of the Indian subcontinent, the species' range extends from Sindh province of Pakistan to north Bengal in India.

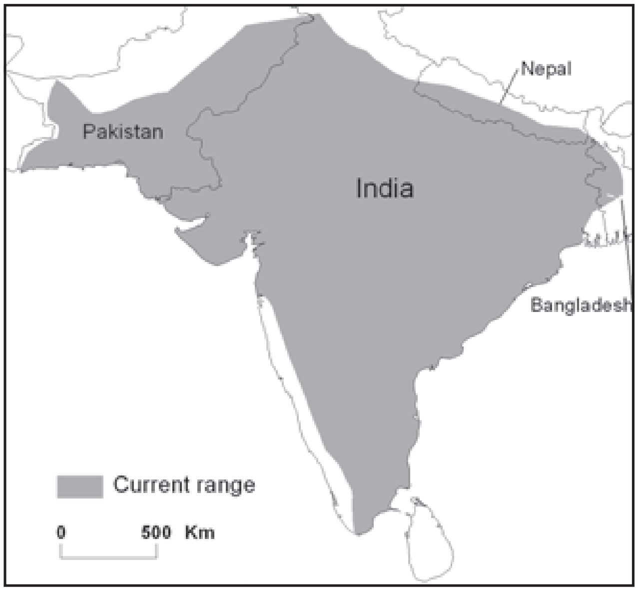
Range countries India, Nepal, and Pakistan (Prater 1971; Roberts 1977; Shrestha 1997).

Relative abundance

Nowhere in its range is the Indian fox abundant. Densities seem to track rodent abundance in the Bhal area of Gujarat (Y.V. Jhala unpubl.), which fluctuates widely between years in the species' prime habitat (arid and semi-arid zones of India) (Prakash 1975; Tripathi *et al.* 1992). Occurrence of the Indian fox in Langtan National Park and Shey Wildlife Reserve in Nepal was reported by Shresta (1997); however, this has not been confirmed and is considered unlikely.

Estimated populations/relative abundance and population trends Densities of breeding pairs range from 0.15–0.1/km^2 during periods of peak rodent abundance (1995 to 1996) to 0.01/km^2 during periods of low rodent abundance (1999 to 2000) (Y.V. Jhala unpubl.). In more diverse and stable prey systems (e.g., the Kutch), fox densities are more constant (0.04–0.06/km^2 over the past five years) (Y.V. Jhala unpubl.). Fox densities also range from 1.62/km^2 in protected grassland plots (Rollapadu Wildlife Sanctuary, Andhra Pradesh) to 0.37/km^2 in unprotected areas; in this area populations declined five-fold due to an epidemic in 1995 (Manakadan and Rahmani 2000). Due to loss of short grassland-scrub habitat to intensive agriculture, industry and development projects the Indian fox population is on the decline. However, there is no available estimate on the rate of these declines.

Figure 8.2.1. Current distribution of the Indian fox.



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Habitat

The Indian fox prefers semi-arid, flat to undulating terrain, scrub and grassland habitats where it is easy to hunt and dig dens. It avoids dense forests, steep terrain, tall grasslands, and true deserts. The species is relatively abundant in the biogeographic zones 3, 4, and 6 of India, in which rainfall is low, and the vegetation is typically scrub, thorn or dry deciduous forests, or short grasslands (Rodgers *et al.* 2000). In the Indian peninsula, the species is restricted to the plains and open scrub forest.

Food and foraging behaviour

Food Indian foxes are omnivorous, opportunistic feeders and generally consume any food that they can handle. Their diet consists mainly of insects (e.g., crickets, winged termites, grasshoppers, ants, beetle grubs, spiders), small rodents, including soft-furred field rats (*Millardia meltada*), field mice (*Mus booduga*), and Indian gerbils (*Tatera indica*), and birds and their eggs, including Indian mynah (*Acridotheres tristis*), ashy-crowned finch lark (*Eremopterix grisea*) and grey partridge (*Francolinus ponticerianus*). Other prey species include ground lizards, rat snakes (*Ptyas mucuosus*), hedgehogs (*Paraechinus nudiventris*), and hares (*Lepus nigricollis*) (Johnsingh 1978; Rahmani 1989; Manakadan and Rahmani 2000). Shepherds have also seen Indian foxes eating the freshly voided pellets of sheep (Johnsingh 1978). Amongst vegetable matter, the Indian fox has been reported to feed on fruits of ber (*Ziziphus* spp.), neem (*Azadirachta indica*), mango (*Mangifera indica*), jambu (*Syizigium cumini*), banyan (*Ficus bengalensis*), melons, fruits and the shoots and pods of *Cicer arietum* (Mivart 1890; Prater 1971; Mitchell 1977; Roberts 1977; Johnsingh 1978; Manakadan and Rahmani 2000). The scats of pups are almost exclusively composed of rodent hair (Johnsingh 1978; Manakadan and Rahmani 2000).

Foraging behaviour In most parts of its range Indian foxes are crepuscular and nocturnal. Therefore, individuals usually wait for darkness before starting their evening hunt. However, if the temperature is mild, as on rainy days, they may also hunt at mid-day. While the basic social unit consists of a breeding pair, foraging is normally done singly (Johnsingh 1978).

Damage to livestock and game There have been no reports of the Indian fox raiding poultry or attacking sheep.

Adaptations

The Indian fox, being a specialist of hot, arid, short grass-scrub habitats, has large external ears for an animal of its size (probably an adaptation for thermoregulation).

Social behaviour

The basic social unit of the Indian fox is the breeding pair, formed through pair bonds that may last for several years. Larger aggregations may exist when grown pups remain in the natal group for longer than normal (Johnsingh 1978). Other observations suggest that the Indian fox may be more social at times. Johnsingh (1978) reported observing two lactating females suckling pups in a single den during one year. Four adult-sized foxes were also observed resting together on two occasions and once emerging from a single den in Rollapadu (Manakadan and Rahmani 2000).

The common vocalisation of the Indian fox is a chattering cry that seems to have a major role in maintaining territoriality and may also be used as an alarm call. Besides this, foxes also growl, whimper, whine and make a sound which could be called a growl-bark (Johnsingh 1978). Scent marking by scats and urine may serve as a "book keeper" (Henry 1977) to indicate if an area has been hunted recently.

Reproduction and denning behaviour

The Indian fox breeds from December to January in Bhal and Kutch (Y.V. Jhala unpubl.). During the breeding season, the male vocalises intensively, sometimes through the night but mostly during the early part of the night and morning. The gestation period of Indian foxes is 50–53 days (Jerdon 1984; Sheldon 1992), with parturition occurring between January and March (Acharjyo and Misra 1976; Johnsingh 1978). Litter size is 2–4 (Roberts 1977; Sheldon 1992), and averaged 2.7 in the Bhal area (Y.V. Jhala unpubl.). Responsibility for post-natal care of the pups is shared by both sexes. Both parents bring food to the pups and guard the den. The presence of helpers has not been observed in the species (Y.V. Jhala unpubl.). Rarely is the den left unguarded in the first two months after the pups are born since the parents take turns foraging. Post-natal care lasts approximately 4–5 months, after which young disperse, usually at the onset of the monsoon in north-western India, when food is plentiful (June/July) (Y.V. Jhala unpubl.).

Den use by the Indian fox is primarily restricted to the pup-rearing period (Johnsingh 1978; Manakadan and Rahmani 2000). Dens are excavated in open habitat, never in dense vegetation (Manakadan and Rahmani 2000). Indian foxes will usually excavate their own dens but occasionally they will appropriate and enlarge gerbil holes (Manakadan and Rahmani 2000). The species exhibits great site fidelity with sites being reused by breeding pairs year after year (Johnsingh 1978; Y.V. Jhala pers. obs.). Dens consist of a mosaic of tunnels in various stages of excavation leading to a small chamber about 0.5–1.0m below the surface where the pups are born. The number of holes in a den complex is usually between two and seven (although as many as 43 have been recorded) (Manakadan and Rahmani 2000). The holes and tunnels of a well-used den site in the Bhal area of Gujarat covered an area 10 x 8m (Y.V. Jhala unpubl.). Pups are rarely moved between dens during the denning period (Manakadan and Rahmani 2000; Y.V. Jhala pers. obs.), although, once pups become more mobile, Indian foxes may use any of the numerous dens excavated within the territory of the parents (Manakadan and Rahmani 2000).

Competition

Grey wolves (*Canis lupus pallipes*) have been observed to appropriate fox holes and enlarge them to make their dens in the Bhal and Kutch areas (Jhala 1991). Wolves and jackals (*C. aureus*) were both recorded to appropriate fox holes in Rollapadu (Manakadan and Rahmani 2000). On one occasion wolf pups and fox pups shared the same den site in Velavadar National Park (Y.V. Jhala unpubl.).

Mortality and pathogens

Natural sources of mortality Wolves and feral dogs do predate on the Indian fox, but such events are not a threat to the population.

Persecution In the study area of Tamil Nadu, humans are a major mortality factor for the fox, especially nomadic tribals, *Nari kuravas*, and their dogs. Occasionally, the tribals visit the area where they use their ability to mimic fox calls to easily net and kill foxes for flesh, teeth, claws and skin. They also use handmade, animal fat-covered, country bombs to kill foxes (Johnsingh 1978). In Rollapadu, the fox is hunted by certain castes of people using smoke, nets and dogs at dens (Manakadan and Rahmani 2000). Further mortality is caused by the local 'hunters' who do not hesitate to shoot or attempt to kill foxes with their dogs. In Tamil Nadu people often block fox dens with stones (Johnsingh 1978). In Gujarat and Rajasthan, a major stronghold for the species, humans rarely persecute foxes, though the *waghri* and *koli* tribes kill and eat foxes occasionally.

Hunting and trapping for fur There is no organised fur trade, since the pelt is of poor quality. Illegal hunting of hare (*Lepus nigricollis*) by the use of dogs sometimes results in the killing of the Indian fox. In such cases the pelt is taken and kept due to local beliefs that the pelt brings good luck (A.J.T. Johnsingh pers. comm.).

Road kills Indian foxes are often killed by fast moving traffic and the development of major highways, in the semi-arid tracts, are likely to become barriers to dispersal.

Pathogens and parasites The Indian fox is susceptible to infectious diseases. There has been no local authenticated report of the Indian fox suffering from or transmitting rabies. In Rollapadu Wildlife Sanctuary, a disease epidemic which could have been caused by either rabies or distemper resulted in a five-fold variation in population density within a period of three years (Manakadan and Rahmani 2000). Mass mortality in certain years has also been observed in the Bhal and Kutch areas of Gujarat and in Rollapadu (Y.V. Jhala pers. obs., Manakadan and Rahmani 2000). The cause of this mortality was not ascertained, but it may have been caused by distemper that was prevalent amongst dogs, wolves and jackals in the Bhal area during that time (Y.V. Jhala unpubl.).

Longevity In captivity, the Indian fox lives 6–8 years (Y.V. Jhala pers. obs.).

Historical perspective

The Indian fox features in several animal short stories of the ancient Jataka texts and the Panchatantra. The fox is depicted as a clever and sometimes cunning creature in these tales.

Conservation status

Threats Although the Indian fox is widespread, it occurs at low densities throughout its range, and populations can undergo major fluctuations due to prey availability. It is also quite sensitive to human modifications of its habitat. With expanding human populations and continued development of grasslands and "wastelands" for agricultural and industrial uses, the habitat of the Indian fox is continuously being depleted. The combination of above factors along with disease and/or natural mortality could potentially cause local extinctions. In certain states like Gujarat, Maharashtra, and Rajasthan the Indian fox habitat is widespread with minimal threats while in other states like Karnataka and Tamil Nadu the specialised habitats of the Indian fox are limited and on the decrease. In such areas the survival of the Indian fox is under serious threat.

Commercial use There are no known commercial uses for the Indian fox, although there is limited localised trade for skin, tail, teeth and claws (for medicinal and charm purposes). There is no trade or potential for trade of the Indian fox.

Occurrence in protected areas

— *India*: the Indian fox occurs in a number of protected areas in Rajasthan (16), Gujarat (9), Maharashtra (5), Madhya Pradesh (17), Andhra Pradesh (10) and over 25 protected areas in other states;

— *Nepal*: it is reported to occur in Royal Bardia National Park, Royal Chitwan National Park, Royal Shukla Phanta Wildlife Reserve and in Kosi Tappu Wildlife Reserve (Majupuri and Kumar 1998).

Protection status CITES – not listed.

Current legal protection The Indian Wildlife Protection Act (1972 as amended up to 1991) prohibits hunting of all wildlife and lists the Indian fox in Schedule II. It is not on any special category for protection in the wildlife legislation of Nepal.

Conservation measures taken There have been no conservation efforts targeted specifically for the species.

Occurrence in captivity

The Indian fox is held in captivity in several zoos in India, where the species breeds well. In 2001, there were 15 males, 14 females, and 11 unsexed individuals in several zoos (Central Zoo Authority pers. comm.).

Current or planned research projects

Y.V. Jhala (Wildlife Institute of India) is studying the food habits distribution and densities of the Indian fox in the Bhal and Kutch areas of Gujarat, India.

Gaps in knowledge

A status survey is needed to identify areas throughout the species' range that have large, relatively secure fox populations. In some of these areas, an in-depth, long-term study is needed on population dynamics of the Indian fox. This would help elucidate the fox's relationship with prey population cycles and disease outbreaks. Research is also needed on ranging patterns, territoriality, and behaviour of this poorly studied species.

Core literature

Johnsingh 1978; Manakadan and Rahmani 2000.

Reviewers: Asad Rahmani, Ullas Karanth. **Editors:** Deborah Randall, Michael Hoffmann, Claudio Sillero-Zubiri.

Chapter 9

Australia and Oceania (Australasian)

9.1 Dingo
Canis lupus dingo (Meyer, 1793)
Vulnerable – VU: A2e (2004)

L.K. Corbett

Other names

French: dingo; **German:** dingo; **Indonesian:** tengger dog; **Japanese:** akita, hokkaido, shikoku, kai, shiba, kishu; **Korean**: jindo, jingo; **Thai**: maa; **Indigenous names:** Australian Aborgine: warrigal, tingo, joogoong, mirigung, noggum, boolomo, papa-inura, wantibirri, maliki, kal, dwer-da, kurpany; Melanesia: koli, kuli; Micronesia: kiti, kiri, komoa; New Guinea: New Guinea singing dog, singer, waia, sfa, katatope, kurr ona, agl koglma, yan-kararop; New Zealand: kirri, kuri, pero, ghooree; Philippines: aso; Polynesian: kuri, ilio, kurio, maile, uli, ooree.

Taxonomy

Canis antarticus Kerr, 1792. Animal Kingdom, vol.i, p.136. Type locality: Port Jackson, New South Wales [Australia].

The nomenclature is based on Honacki *et al.* (1982) as well as usage in recent dingo publications and major Australian institutions, including the Australian Museum and CSIRO. Furthermore, recent research clearly indicates the long antiquity of the dingo and the evolutionary line of the wolf-dingo-domestic dog (Corbett 2004).

Europeans did not discover the dingo in Australia until the 17th century and taxonomists originally thought the dingo was a feral domestic dog (hence one of the earlier names *Canis familiaris dingo*). Many early zoologists and anatomists assumed that Aborigines introduced the dingo into Australia in Pleistocene times, and this led to much confusion about the dingo's nomenclature and relationships for about 200 years. It is only since recent investigations have shown that the dingo is a primitive dog transported to Australia by Asian seafarers about 4,000 years ago (Corbett 1985) that the taxonomy is better understood.

Today, the wild population comprises dingoes, feral dogs and hybrids of the two. The names *C. f. dingo* for the dingo proportion of the wild dog population and *C. f. familiaris* for both wild-living and commensal domestic dogs have had the greatest use in scientific literature over the past 50 years. Corbett (1995) concludes that wild-living dogs in Australia are subspecies of the grey wolf (*C. lupus*), that is *C. l. dingo* and *C. l. familiaris*, and these designations are currently being investigated (W.D.C. Ride pers. comm.).

Chromosome number: 2n=78 (Hsu and Benirschke 1967–1976).

The relatively extended isolation of a dingo-like dog population in Papua New Guinea – initially described as the New Guinea singing dog (*Canis hallstromi*) (Troughton 1957; Schultz 1969) – and subsequent adaptations to the mountainous habitat it occupies (Ortolani 1990; Brisbin *et al*. 1994; Bino 1996; Koler-Matznick *et al*. 2000), strongly suggests that it could be designated an "evolutionarily significant unit" (Crandall *et al*. 2000) within dingoes (Bininda-Emonds 2002).

Further research based on valid morphological and molecular comparisons is required to elucidate the taxonomic status of dingo-like dog populations in Papua New Guinea, Asia, Africa and North America. There is, however, mounting evidence that recent and extant populations are now hybrid. For example, the morphology of all New Guinea singing dog skulls examined to date, including the holotype and paratype, matches that of hybrid dingoes (L. Corbett unpubl.). Further research is also required to confirm whether or not the 'Carolina dog' (Brisbin and Risch 1997) and 'basenji' (Coe 1997), in North America and Africa, respectively, have descended from pure dingoes.

The following definitions of dingoes and other wild, dingo-like dogs are based on Fleming *et al.* (2001):

— *Dingoes*: Native dogs originating in Asia. Dingoes were present in Australasia and Oceania before European settlement. Pure dingoes are populations or individuals that have not hybridised with domestic dogs or hybrids.

— *Domestic dogs*: Dog breeds (other than dingoes) selectively bred by humans, initially from wolves and/or dingoes that usually live in association with humans. Introduced to Australia and other range countries by Europeans.

— *Hybrids*: Dogs resulting from crossbreeding of a dingo and a domestic dog and the descendants of crossbred progeny. Some hybrids are phenotypically indistinguishable from pure dingoes (e.g., hybrid populations in south-eastern Australia – see Daniels and Corbett 2003).

— *Wild dogs*: All wild-living dogs (including dingoes and hybrids).

— *Feral dogs*: Wild-living domestic dogs.

— *Free-roaming dogs*: Dogs that are 'owned' by humans but not restrained so they are free to travel away from their owner's residence and breed.

— *Commensal dogs*: Wild dogs (including dingoes and free-roaming domestic dogs) living in close association with, but independent of humans.

Description

Dingoes are dog-like with a fairly broad head and tapered muzzle, erect ears about half the head length, legs about half the head-body length and without dewclaws, hind feet about a third of the leg length, short body hair and a fairly bushy tail that does not extend beyond the hocks. In order of frequency of occurrence, the adult pelage colours are ginger (red to sandy), black with tan areas (cheeks, muzzle, ears, legs), all white, and all black. Most individuals have small white markings on the chest, feet/legs and tail tip, and some have white belly markings and/or a black muzzle. In ginger animals, there is a faint but distinctive shoulder stripe. All other colorations indicate hybridisation with domestic dogs (Daniels and Corbett 2003). Males are universally larger and heavier than females of the same age (Table 9.1.1). Dingoes from northern and north-western Australia are larger than dingoes in central and southern regions; all Australian dingoes are larger and heavier than those in Asia (Corbett 1985, 1995; see body measurements). Relative to similar-sized domestic dogs, dingoes have longer muzzles, larger bullae, larger carnassial teeth, longer canine teeth, and flatter crania with larger nuchal crests (Newsome *et al.* 1980). Dental formula is 3/3-1/1-4/4-2/3=42.

Table 9.1.1. Body measurements for the wild and commensal dingo and the New Guinea singing dog. All Australian and Thailand measurements were of adults with ginger pelts and females that were not obviously pregnant (Corbett 1985, 1995). Australian measurements are means of samples from northern (Kakadu National Park) and central (Alice Springs) regions, and Thai measurements are from north-eastern (Tharee) and North Thailand (Chieng Mai) (Corbett 1985, 1988a). All New Guinea measurements were of captive specimens one year of age or older (J. Koler-Matznick unpubl.). Wild specimens may weigh less.

	Australia (wild dingoes)	**Thailand** (wild and commensal dingoes)	**New Guinea** (New Guinea singing dogs)
HB male	914mm (835–1,110) n=50	824mm (750–917) n=20	849mm (780–910) n=10
HB female	883mm (813–1,010) n=38	755mm (703–810) n=16	802mm (710–889) n=9
T male	324mm (280–370) n=50	264mm (210–301) n=20	252mm (220–280) n=10
T female	311mm (247–350) n=38	239mm (200–270) n=16	235mm (230–250) n =9
HF male	190mm (176–220) n=51	166mm (149–190) n=21	156mm (140–168) n=10
HF female	180mm (165–195) n=38	152mm (143–165) n=16	148mm (140–168) n=9
E male	103mm (95–110) n=50	85mm (76–99) n=21	95mm (70–110) n=10
E female	98mm (87–107) n=38	79mm (71–87) n=16	90mm (65–105) n=9
WT male	15kg (12–22) n=51	12kg (7–17) n=21	12.2kg (9.3–14.4) n=9
WT female	13kg (11–17) n=38	10kg (8–14) n=16	11.2kg (8.6–13.2) n=7

Yearling male dingo. Strathmore Station, Gulf of Carpentaria, Australia, 1997.

Lee Allen

Subspecies Based on skull morphology, size, coat colour and reproduction, regionally distinct populations of dingoes appear to exist between Australia and Thailand (Corbett 1985, 1995) but not within Australia (Corbett 2001). There may, therefore, be a case for subspecific names for dingo populations in Thailand and Australia.

Similar species Grey wolves (*Canis lupus*), are generally larger, more slender and with relatively longer legs than dingoes. Dingo-like dogs and hybrids are usually distinguished from pure dingoes by coat colours other than ginger, black-and-tan, all black and all white.

Distribution

Historical distribution Based on fossil (Olsen and Olsen 1977), molecular (Vilà *et al*. 1997; Corbett 2004) and anthropological evidence (Corbett 1995), the early primitive dingoes formerly had a cosmopolitan distribution (Corbett 1995). The primitive dingoes were associated with nomadic, human hunter-gatherer societies and later with sedentary agricultural population centres where the primitive dingoes were tamed and subsequently transported around the world. Austronesian-speaking people transported the dingo from mainland Asia to Australia and other islands in Southeast Asia and the Pacific between 1,000 and 5,000 years ago (Corbett 1985).

Current distribution Pure dingoes have been demonstrated to occur only as remnant populations in central and northern Australia and throughout Thailand. However, based on external phenotypic characters, they may also occur in Burma, Cambodia, China, India, Indonesia, Laos, Malaysia, Papua New Guinea, Philippines and Vietnam.

Range countries Australia, Burma, Cambodia, China, India, Indonesia, Laos, Malaysia, Papua New Guinea, Philippines, Thailand, Vietnam (De Vis 1911; Troughton 1957; Menzel and Menzel 1960; Schultz 1969; Fernando 1977; Medway 1977; Corbett 1985, 1988a, 1995; Koler-Matznick *et al.* 2000).

Relative abundance

Estimating dingo abundance is difficult because the external phenotypic characters of many hybrids are indistinguishable from pure dingoes. For example, populations of 'wild dogs' in the south-eastern highlands of Australia have been fairly abundant over the past 50 years. However, the proportion of pure dingoes, as based on skull morphometrics, has declined from about 49% in

Figure 9.1.1. Current distribution of the dingo.

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the 1960s (Newsome and Corbett 1985) to about 17% in the 1980s (Jones 1990) and the pure form may now be locally extinct (Corbett 2001). Such quantitative data is not available for countries other than Australia, Thailand and Papua New Guinea so that the following qualitative estimates of abundance refer to pure dingo and/or hybrid populations as based on general body form, pelage colour and breeding pattern.

In Australia, pure dingoes are common in northern, north-western and central regions, rare in southern and north-eastern regions, and probably extinct in the south-eastern and south-western regions. The density of wild dogs (dingoes and hybrids) varies between 0.03 and 0.3 per km^2 according to habitat and prey availability (Fleming *et al*. 2001). Dingoes are rare in New Guinea and possibly extinct as there have been no confirmed sightings for about 30 years (Newsome 1971; Brisbin *et al*. 1994; Bino 1996; Koler-Matznick *et al*. 2000). Dingoes are common in Sulawesi but their abundance elsewhere in Indonesia is unknown. They are common throughout the northern and central regions of Thailand, but less so in the southern regions; considered rare in the Philippines and probably extinct on many islands. Present in Malaysia, Vietnam, Cambodia, Laos, China, Burma and India, but abundance unknown. Dingoes are probably extinct in the wild in Korea, Japan and Oceania, although several local dog breeds share dingo-like characteristics.

Estimated populations/relative abundance and population trends Dingoes were formerly widespread throughout the world (Corbett 1995) and although populations of wild dogs remain abundant in Australia and other countries, the proportion of pure dingoes is declining through hybridisation with domestic dogs (Table 9.1.2). The data in the following table refers to estimated populations of pure dingoes and/or hybrid populations as based on general body form, pelage colour and breeding pattern.

Table 9.1.2. The status of dingoes in various range countries (Population: A=abundant, C=common, U=unknown, Ex=extinct, ?=current presence not confirmed; Trend: D=decreasing).

Country	Population/abundance	Trend
Australia	C	D
north/north-west	A	D
central	A	D
south-west	U	D
north-east	C	D
south-east	Ex?	D
Burma	U	D
Cambodia	U	D
China	U	D
India	?	D
Indonesia	U	D
Laos	U	D
Malaysia	U	D
New Guinea	Ex?	D
Philippines	Ex?	D
Thailand	C	D
Vietnam	U	D

The ecological and behavioural information in the following sections is largely based on wild-living dingoes in Australia and Thailand.

Habitat

Dingoes occupy all habitats, including tropical alpine moorlands above 3,800m a.s.l. in Papua New Guinea (Troughton 1957; Newsome 1971), forested snow-clad peaks in temperate eastern Australia, arid hot deserts in central Australia, and tropical wetlands and forests of northern Australia (Corbett 1995). The absence of dingoes in many grassland habitats of Australia is due to persecution by humans (Fleming *et al.* 2001).

Food and foraging behaviour

Food Most of the dietary information comes from studies conducted in Australia, where dingoes eat a diverse range of prey types and over 170 species have been identified ranging from insects to buffalo (Corbett 1995). However, in a particular region they usually specialise on the most available (common) vertebrate prey. The main prey in Australia are magpie geese (*Anseranas semipalmata*), rodents (*Rattus colletti*) and agile wallabies (*Macropus agilis*) in the northern tropical wetlands (Corbett 1989); rabbits (*Oryctolagus cuniculus*), rodents (*Rattus villosisimus, Mus musculus*), lizards (*Ctenophorus nuchalis*) and red kangaroos (*Macropus rufus*) in arid central Australia (Corbett and Newsome 1987; Corbett 1995); euros (*Macropus robustus*) and red kangaroos in arid north-western habitats (Thomson 1992); rabbits in the south-western deserts (Marsack and Campbell 1990); and wallabies (*Wallabia bicolor*, *Macropus rufogriseus*), possums (*Trichosurus vulpecula, Pseudocheirus peregrinus*) and wombats (*Vombatus ursinus*) in the east and south-eastern highlands (Newsome *et al*. 1983; Robertshaw and Harden 1985; Corbett 1995). In recent years, rabbit populations throughout Australia have greatly declined due to rabbit calicivirus disease, and dingo diet in former rabbit-infested regions is likely to change (Fleming *et al.* 2001).

In Asia, dingoes live commensally with humans in most regions and their main food items are rice, fruit and other table scraps provided by people or scavenged (Corbett 1995). In rural areas of Thailand and Sulawesi, dingoes have been observed hunting insects, rats and lizards along roadsides, rice paddies and in forests (Corbett 1985, 1988a). In the Papua New Guinea highlands, Newsome (1971) reported rodents in canid scats. Bino (1996) noted that wild dogs commonly eat cuscus (*Phalanger* spp.) and scavenge harpy eagle kills and human-trapped animals.

Foraging behaviour Dingoes change their group size and hunting strategy in order to maximise hunting success. For example, packs have greater success than solitary dingoes in hunting kangaroos (Thomson 1992) and vice versa when hunting rabbits. Dingoes also scavenge and steal prey from other predators (Corbett 1995).

Damage to livestock or game In Australia, dingoes (and hybrids) kill livestock, particularly sheep, cattle and goats, and can threaten the economic viability of properties in some areas (Fleming *et al.* 2001). Many attacks occur when native prey is scarce (e.g., during droughts or as a result of human disturbance to habitats). However, there is evidence of seasonal peaks in predation on livestock, possibly related to the seasonal breeding activity of dingoes, as well as the timing of lambing, calving and control activity (Fleming *et al.* 2001).

Adaptations

During droughts in Australia, dingo packs fragment and the likelihood of death is high for all pack members, irrespective of social status. During good seasons, population recruitment is also low due to infanticide where the alpha female kills the pups of subordinate females (Corbett 1988b). This behaviour is believed to be an adaptation to the capricious Australian environment that has demanded a common reproductive selection strategy: the more pups born, the greater the chance that some will survive adverse periods. Since most breeding dingoes are closely related, at least some of the alpha's genes will survive to the next generation if all pregnancies go to term and if some of the smaller pack units survive the drought (Corbett 1995).

Other adaptations to drought are the dingoes' ability to survive on free and metabolic water from prey in waterless regions in winter (Green 1973), and female's regurgitating water to weaned pups confined to den sites in summer (Corbett 1995).

Social behaviour

Throughout most of their range in Australia and Asia, dingoes are usually seen alone but most individuals belong to socially integrated groups whose members meet every few days or coalesce during the breeding season to mate and rear pups. At such times, scent marking and howling is most pronounced and there are frequent skirmishes with adjacent groups (Corbett 1995).

In remote areas of Australia, where dingoes and their prey are least disturbed by humans, discrete and stable packs of 3–12 dingoes occupy territories throughout the year. The home ranges of individual pack members overlap considerably but neighbouring pack territories do not (Thomson 1992; Corbett 1995). Packs have distinct male and female hierarchies where rank order is largely determined and maintained by aggression, especially in male ranks. The dominant pair may be the only successful breeders but other pack members assist in rearing the pups including coaching the pups in hunting (Corbett 1988b, 1995).

Territory size varies with prey resources and terrain but is not correlated with pack size. For individuals, home range size also varies with age (Thomson 1992). The largest recorded home ranges (90–300km²) occur in the deserts of south-western Australia (Thomson and Marsack 1992). Home ranges recorded elsewhere are 45–113km² in north-western Australia (Thomson and Marsack 1992), 25–67km² for arid central Australia (Corbett 1995; L. Best pers. comm.), mean 39km² for tropical northern Australia (Corbett 1995) and 10–27km² for forested mountains in eastern Australia (Harden 1985; McIlroy *et al.* 1986). Most dingoes remain in their natal area and mean distances travelled per day average less than 20km. Some dingoes disperse, especially young males, and the longest recorded distance for a tagged dingo is about 250km (Thomson and Marsack 1992; Corbett 1995).

Dingoes frequently howl but rarely bark as domestic dogs do. There are three basic howls (moans, bark-howls and snuffs) with at least 10 variations (Corbett 1995). Dingoes howl over large distances to locate other dingoes for the purposes of attracting pack members and repelling intruders. Dingoes howl with distinct pitches in a chorus howl and as the number of animals howling in a group increases, so do the variation in pitches (Ortolani 1990); this suggests that dingoes can estimate the size of an unseen pack. The frequency of howling varies and is influenced by breeding, dispersal and social stability of packs (Thomson 1992; Corbett 1995). The New Guinea singing dog has a distinctive shriek-like howl that is characterised by a very sharp rise in pitch at the start and ends at a very high frequency (Ortolani 1990).

Dingoes also communicate with pack members and rival packs by defecating and urinating on grass tussocks and other conspicuous objects at shared sites such as waters, trails and hunting grounds. Males scent-mark more than females and both sexes perform more in the breeding season (Corbett 1995). Dingoes also scent-rub whereby an animal rolls on its neck, shoulders or back on a 'smell' that is usually associated with food or the scent markings of conspecifics (Thomson 1992; Corbett 1995).

Reproduction and denning behaviour

Dingoes breed once each year. Litters are usually whelped in winter (May to July) although in tropical habitats breeding can occur in any month. This breeding pattern is determined by the female's annual oestrous cycle, as males are fertile most of the year in most regions (Catling *et al.* 1992). Most wild females commence breeding at two years (Catling *et al.* 1992) and, in packs, the alpha female (usually the oldest) tends to come into oestrus before the subordinate females. Pro-oestrus and oestrous periods for captive dingoes last about 10–12 days (Corbett 1995). However, in the wild, behavioural data suggest that pro-oestrus may last up to 60 days (Thomson 1992). Males reach full sexual maturity at 1–3 years. Gestation lasts 61–69 days in captive dingoes and is similar for wild dingoes. The average litter size for dingoes is five (range=1–10) throughout Australia and Thailand, and usually more males are born than females. Pups usually become independent at 3–6 months or if in a pack, at 12 months when the next breeding season begins (Corbett 1995).

In contrast to dingoes, female feral dogs and hybrids of similar size to dingoes may have two oestrous cycles each year, although it is unlikely that they successfully breed twice every year in the wild. Gestation is 58–65 days for hybrids and the average litter size is similar to dingoes.

In contrast to wolves in the northern hemisphere, where alpha wolves prevent subordinates from breeding, the Australian dingo's main method of suppressing reproduction is infanticide: all the pups of subordinate females are killed by the alpha female (Corbett 1988b).

In Australia most dens are 'underground' and have been recorded in enlarged rabbit holes, caves in rocky hills, under debris in dry creek beds, under large tussocks of spinifex, among protruding tree roots, hollow logs, fallen trees, enlarged goanna (*Varanus* spp.) holes and old wombat burrows (Thomson 1992; Corbett 1995).

Competition

The demise of two endemic marsupial carnivores, the thylacine (*Thylacinus cynocephalus*) and the Tasmanian devil (*Sarcophilus harrisii*), on the Australian mainland soon after the dingo's arrival about 4,000 years ago is attributed to competition. It is assumed that the dingoes' superior social organisation enabled them to better exploit scarce resources during droughts or after extensive wildfire (Corbett 1995).

Dingoes may now present red foxes (*Vulpes vulpes*) and feral cats, both exotic species to Australia, with a similar kind of competition. There is some evidence that dingoes limit fox and feral cat access to resources and there is evidence of an inverse density relationship between dingoes and foxes (Fleming *et al.* 2001). One implication of these findings is that reducing dingo density (via human control) might result in an increase in other predators with overlapping diets ('mesopredator release'). It is therefore possible that removing dingoes from a system where foxes and cats also occur will result in an increase in their numbers with consequent increased predation on small native mammals.

Mortality and pathogens

Natural sources of mortality Starvation and/or dehydration during drought or after extensive wildfire; infanticide; drowning by kangaroos (Corbett 1995); snakebite; predation on pups by wedge-tailed eagles (Fleming *et al.* 2001); buffalo and cattle goring and kicking (Fleming *et al.* 2001).

Persecution A major cause of dingo mortality in Australia is a cycle involving dingo population density, food supply and human control. When food becomes scarce for a large population of dingoes in a 'safe' area (source), they disperse to pastoral and agricultural areas where there are fewer dingoes. At those sites, intense human control measures (poisoning, trapping or shooting) create vacant areas (sinks) and perpetuate the dispersal-mortality cycle (Thomson 1992). Dingoes have been eliminated in most of south-eastern Australia through such human control and loss of habitat, and this situation is maintained with a 5,614-km-long barrier fence (Breckwoldt 1988). In Australia dingoes are also chased and killed by people on horseback.

In Asia and Oceania, dogs (dingoes, hybrids and domestic dogs) are considered a delicacy (Titcomb 1969) and are regularly killed for human consumption. For example, in north-east Thailand, at least 200 dingoes are butchered each week and sold in markets for human consumption (Corbett 1985). Prior to the mid-20th century, dingoes were regularly eaten by Australian Aborigines (Breckwoldt 1988).

Persecution due to predation on stock has decreased over the past 30 years following the results of scientific research and better understanding of dingo movements, sociality and predation. It is recognised that in particular seasons, dingo predation may limit increases in competing feral and native herbivores.

A bounty system operated throughout mainland Australia from 1836 until recently, but despite the billions of dollars paid out, there is little evidence that bounty systems are (or were) an effective management tool for dingoes (Fleming *et al.* 2001).

Hunting and trapping for fur Not practiced.

Road kills Animals are occasionally run over by vehicles.

Pathogens and parasites Thirty-eight species of parasites and pathogens have so far been recorded in dingoes in Australia (Corbett 1995; Fleming *et al.* 2001), but in most cases diseases have little effect on the survival of adult wild dogs. Exceptions include: canine distemper, hookworms (*Unicinaria stenocephala* and *Ancylostoma caninum*) and heartworm (*Dirofilaria immitis*) in northern Australia and south-eastern Queensland. Pups are also killed by lungworm (*Oslerus osleri*), whipworm (*Trichurus vulpis*), hepatitis (Adenovirus), coccidiosis (*Isospora rivolta*, *Eimeria canis*), lice (*Trichodectes canis* and unidentified species) and ticks (*Ixodes holocyclus*, *Rhipicephalus sanguineus* and *Amblyomma triguttatum*). Sarcoptic mange (causal agent *Sarcoptes scabiei*) is a widespread parasitic disease in dingo populations throughout Australia but it is seldom debilitating. Hydatidosis (caused by the cestode *Echinococcus granulosus* and part of a dingo-wallaby sylvatic cycle) results in serious illness in infected humans and in the devaluation of infected livestock carcases at slaughter. However, this parasite does not cause mortality in dingoes (Fleming *et al.* 2001).

Longevity Dingoes live up to 7–8 years in the wild and up to 13 years in captivity (Corbett 1995).

Historical perspective

Dingoes often accompanied Asian seafarers when they migrated to Australia and other regions of the world several millennia ago (Corbett 1985). Those journeys and other associations continue to be an integral part of oral and written culture of native people in those areas including the traditional use of dingoes as food, of canine teeth in necklaces and hair for ceremonial costumes (Titcomb 1969; Medway 1977; Breckwoldt 1988; Corbett 1995). The dingo is also an important animal in Australian Aboriginal mythology; dingoes are associated with sacred sites, totems and Dreamtime characters (Breckwoldt 1988). Aborigines also used dingoes as hunting aids (for macropods and small game), camp dogs and their scalps as a form of currency (Corbett 1995).

Conservation status

Threats Cross-breeding with domestic dogs represents a significant threat to the long-term persistence of dingoes. Hybrids exist in all populations worldwide (including Fraser Island, Australia; Woodall *et al.* 1996) and the proportion of hybrids is increasing (see Relative abundance). A related threat to dingoes in Australia concerns the actions and consequences of 'so-called' dingo preservation societies, dingo 'farms' and legislation allowing legal ownership of dingoes by members of the public because most are based on known hybrids or untested dingo stock and thus effectively increase the hybridisation process (Corbett 2001). The increasing interest of private individuals and groups in keeping 'dingoes' as pets in Australia and other countries including Switzerland and USA, also poses a threat via human selection of form and behaviour.

Commercial use Bounties for dingo skin and scalps exist in some regions of Australia. Dingoes are also sold in human food markets in several Asian countries. They are also bred by private individuals and companies in Australia and USA and sold as pets.

Occurrence in protected areas Protected areas for dingoes only occur in Australia. Within Australia, dingoes are 'legally protected' in national parks, nature reserves and the Arnhemland Aboriginal Reserve in the Northern Territory (NT), National Parks and Nature Reserves in New South Wales (NSW), National Parks in Victoria, and throughout the Australian Capital Territory (ACT). Dingoes occur in all of the NT's 17 national parks including Kakadu, Litchfield, Gregory, Davenport Range, Nitmiluk and Uluru-Kata Tjuta. Dingo occurrence and abundance is unknown for most of the 117 national parks in NSW and the 20 national parks in Victoria. Known sites include Kosciusko, Barrington Tops and Kinchega National Parks and Nadgee Nature Reserve in NSW; Alpine, Mt Buffalo, Baw baw and Croajingolong National Parks in Victoria; and forested highland areas of the ACT.

Protection status CITES – not listed.

Current legal protection Although protected in Federal National Parks, World Heritage areas, Aboriginal reserves, and the Australian Capital Territory, the dingo is a 'declared' pest throughout much of its remaining range, and landholders are obliged to manage populations; the dingo is 'undeclared', but not protected, in the Northern Territory (Fleming *et al.* 2001). The dingo is not protected in any other countries of its range.

Conservation measures taken No conservation measures have been taken other than that the dingo has been nominated as a threatened species in the State of NSW and the Australian Federal Government has recently published 'best practice' guidelines to manage and conserve dingoes (Fleming *et al.* 2001). The efforts of dingo 'preservation' societies in Australia are currently ineffective because most of their stock is untested or known to be hybrid (Corbett 2001). There are no conservation measures for wild dingoes in Asia. However, in New Guinea, the Department of Environment and Conservation has indicated that measures will be initiated to protect New Guinea singing dogs (I.L. Brisbin pers. comm.).

Occurrence in captivity

Dingoes and/or dingo-like hybrids occur in many zoos and private facilities worldwide. Tests using skull measurements of deceased animals or valid DNA tests (see below) are required to assess the purity of captive populations.

Current or planned research projects

A. Wilton (University of New South Wales, Australia) is investigating methods to identify genetically pure dingoes (and hybrids, domestic dogs and New Guinea singing dogs). This research aims to provide a method to test the purity of live dingoes; however, it is essential that control samples in Australia should be taken from pre-European material, so that samples are unequivocally dingo. Unfortunately, this is not the case to date (Wilton 2001).

L. Corbett (EWL Sciences, Darwin, Australia) is involved in a comparative morphometric study of skulls of dingoes and hybrids from Australia, Thailand, New Guinea and Japan.

L. Allen (Queensland Department of Natural Resources, Australia) is examining relationships between dingo abundance, dingo predation on cattle and control methods in Queensland, Australia.

A dingo and wild dog management programme is underway in south-east New South Wales and ACT (Australia Capital Territory), which aims to integrate control of dingoes and other wild dogs to prevent predation of livestock with conservation of dingoes in national parks (D. Jenkins, Australian Hydatids Control and Epidemiology Program; P. Fleming, New South Wales Agriculture; H. Cathles, Yass Rural Lands Protection Board). The Program includes DNA studies (A. Wilton), movement and behaviour studies, and assessment of control strategies for dingoes and other wild dogs.

M. Feinstein (Hampshire College, Amherst, MA, USA) and A. Ortolani (Disney's Animal Kingdom, Orlando, FL, USA) are undertaking a comparative study of the larynx and throat anatomy of captive New Guinea singing dogs and domestic dogs.

J. Koler-Matznick is involved in ongoing behavioural studies of captive New Guinea singing dogs (New Guinea Singing Dog Conservation Society, Central Point, OR, USA).

Gaps in knowledge

1. Morphological and genetic assessment of the taxonomic status of dingo-like dogs in Papua New Guinea, Indonesia, Malaysia, Vietnam, Cambodia, Laos, China, Burma, India, Philippines, and where present, their distribution, abundance, ecology and behaviour.
2. The ecological role of hybrids in Australia. If pure dingoes become extinct, will hybrids alter predation rates on native fauna and livestock?
3. Rabbits are a major prey in Australia but their populations have recently been decimated by rabbit calicivirus disease. What will be the effect on dingo ecology including predation on livestock?
4. What are the ecological effects of dingo control on feral cat and fox populations in Australia (mesopredator release)?

Core literature

Corbett 1985, 1995, 2001, 2004; Fleming *et al*. 2001; Newsome and Corbett 1985; Thomson 1992.

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PART 3

Major issues in Canid Conservation

Chapter 10

Canid Sociology – a Brief Overview

D.W. Macdonald

10.1 Introduction

Canids demonstrate enormous diversity in appearance and lifestyle. This variation, and particularly the salient themes in canid behavioural ecology, is the topic of six substantial reviews and 14 detailed case studies in *The Biology and Conservation of Wild Canids* (Macdonald and Sillero-Zubiri 2004a). In particular, Macdonald *et al.* (2004) summarise the nature of canid societies, and discuss the selective pressures that have fashioned them. Here, we provide a brief synopsis of this aspect of canid biology, with the purpose of ensuring that those planning their conservation are alert to the relevant features of their societies.

10.2 Canid diversity

Canid species vary in size, distribution, diet, habitat and home range, all of which are reflections of diverse adaptations. The impressiveness of their interspecific diversity in behaviour (previous reviews include Macdonald and Moehlman 1982; Creel and Macdonald 1995) is almost matched by the extent of intraspecific variation in their biology (e.g., Englund 1970; Macdonald 1981). However, for all the diversity that exists amongst canids, differences are merely variations upon the strikingly consistent themes of canid biology, notably their opportunism and versatility, their territoriality, and their societies built from a foundation of behavioural monogamy with its attendant intrasexual dominance hierarchies, social suppression of reproduction and helpers (Macdonald and Sillero-Zubiri 2004b).

Formerly, wild canids were thought of as approximating one of two models. Either they were small, ate small prey and lived essentially solitary lives, as was supposed to be the model of the red fox (*Vulpes vulpes*). Alternatively, they were large, ate large prey and used the collective power of a pack to hunt, catch and defend it. The idea that canid society was a reflection of their food (and other resources) was well founded, but the simplicity of this early distinction was not. This is clearly illustrated by the mixture of attributes of the Ethiopian wolf (*Canis simensis*). As summarised by Sillero-Zubiri *et al.* (2004a), this canid is relatively large, eats almost exclusively small prey, lives in packs but mostly hunts alone. Furthermore, it became clear that while red foxes did live in territorial pairs in some circumstances, elsewhere they formed groups (Macdonald 1987) and, conversely, although wolves do often live in packs and kill large prey, some individuals and some populations do not, at least in some seasons (e.g., Mech and Boitani 2003). In short, the adaptive significance of canid society required more explanation than initially supposed.

Canids are highly communicative. Studies of their postures (e.g., Golani and Keller 1975), vocalisations (e.g., Tembrock 1962; Harrington 1987; Frommolt *et al*. 2003) and scent marking (e.g., Peters and Mech 1975; Bekoff 1978; Macdonald 1980c; Sillero-Zubiri and Macdonald 1998), all reveal subtleties of communication that make it clear that their societies must be complex. An overview allows their societies to be classified, very broadly, into three categories, which differ in terms of body weight, group size, group composition and dispersal behaviour. Amongst mammals in general, dispersal distances tend to be greater in males than females and, where there is a skew, males tend to be the dispersing sex (Greenwood and Harvey 1982). Macdonald and Moehlman (1982) and Moehlman (1986, 1989) noticed that this generalisation did not apply uniformly throughout the canids. In brief, small canids (<6kg) tend to live in pairs or, when they form groups these tend to female-biased sex ratios, young males tend to emigrate, and females stay in their natal range as helpers (most species of small vulpine canids are examples). Medium-sized canids (6–13kg) have an equal adult sex ratio and emigration rate, and both sexes may be helpers – examples include three species of jackal and coyotes (*Canis latrans*), and some of the South American canids such as the crab-eating fox (*Cerdocyon thous*) (Macdonald and Courtenay 1996). Large-sized canids (>13kg) exhibit an adult sex ratio skewed towards males, female emigration and male helpers. Notwithstanding variation between populations (see McNutt 1996a), examples would be African wild dogs (*Lycaon pictus*), dholes (*Cuon alpinus*) and Ethiopian wolves. However, this simple classification is no more than a guide – for example, the bush dog (*Speothos venaticus*) is rather small, but fits the third behavioural model (Macdonald 1996), whereas the maned wolf (*Chrysocyon brachyurus*) is large and does not (Dietz 1984).

10.3 Selection for sociality

With this variation in canid societies, what might determine the way a particular species, or population of a species, behaves? Creel and Macdonald (1995) summarised five general families of selective pressure, or conditions, which may select for sociality in carnivores generally. Two of these selective pressures reduce the costs of tolerating conspecifics:

1. *Resource dispersion*: most obviously, abundant prey, rich or variable prey patches, or rapid prey renewal, may all lead to low costs of tolerating conspecifics;
2. *Dispersal costs*: constraints on dispersal opportunities such as lack of suitable habitat, low mate availability, or intraspecific competition may favour the retention of young within their natal group past the age of maturity. In short, the balance of these two essentially ecological factors may facilitate group formation, respectively by making the costs of doing so minimal and the costs of not doing so high. In contrast, the balance of three essentially behavioural selective pressures may increase the benefits of tolerating conspecifics (up to some optimum group size);
3. *Resource acquisition*: groups may use strength of numbers in the acquisition and retention of resources, e.g., hunting in groups may increase foraging success, where prey are large or difficult to kill, groups may also fare better in territorial defence and intra- and inter-specific competition for food, especially at large kills;
4. *Defence against predation*: groups may be less vulnerable to predation or attack; and
5. *Reproductive advantages*: group membership offers the opportunity for shared feeding and protection of young.

It is clear that various different types of society would result depending on the balance of these five categories of selective pressure (as explored by Macdonald and Carr 1989). For example, all else being equal, group size is likely to be less where dispersal opportunities are greater, whereas cub survival to weaning might be expected to increase in the presence of allo-parents.

These outcomes are relevant to conservation planners insofar as the prey base, opportunities for dispersal or recruitment, and patterns of grouping will affect the viability of a population and the options for its conservation.

What evidence exists that these five categories of selective pressure do affect canid societies? Consider first the three behavioural selective pressures for group living.

10.3.1 Behavioural selective pressures for sociality

Strength in numbers

The notion that canids hunt together in order to more effectively overwhelm prey too challenging to be hunted alone is intuitively plausible. However, it has proved extremely difficult to support empirically. Early data on black-backed jackals (*Canis mesomelas*) (e.g., Wyman 1967; Lamprecht 1978) proved inconclusive. Even with the most conspicuous pack-hunters, African wild dogs, evidence that individual pack members did better when hunting in larger groups proved equivocal when the measure of success was the quantity of prey eaten (Fanshawe and Fitzgibbon 1993). Indeed, a review of wolf hunting success by Schmidt and Mech (1997) revealed a general decline in food intake per wolf per day with larger pack sizes, and Vucetich *et al*. (2004) illustrate that in the absence of scavengers, wolves would do better hunting in pairs not packs. However, when Creel and Creel (1995) shifted the focus from the bulk of prey eaten to the profit and loss account of catching them, it became more convincing that wild dogs hunting in large groups may provide a net benefit to participating individuals (Creel 1997; Creel and Creel 2002).

Intraspecific interference competition at kills can be considerable and the outcome of such competition generally appears to be affected by group size. Irrespective of the contribution of collaboration to making a kill, larger groups of coyotes emerged as more successful at defending kills (Bekoff and Wells 1982). Interspecific interference competition is similarly a major component of canid ecology, with a sequence of species competing to retain kills (Mills 1989a, 1989b). It is not clear what function of aggregate body weight and numbers of sets of teeth determines the algebra of victory when a larger number of smaller carnivores battles with a smaller number of larger ones, but it is clear that strength of numbers is important when, for example, wild dogs strive to repel hyaenas from a kill (McNutt 1996a), or grey wolves (*Canis lupus*) seek to keep scavenging corvids at bay (Vucetich *et al*. 2004). Strength of numbers may also be important in territorial defence, and evidence accumulates that larger groups are more successful at defending territories (e.g., Bekoff and Wells 1982; Creel and Creel 1998). A large pack of golden jackals (*Canis aureus*) habitually stole food from a smaller pack (Macdonald 1979a), and amongst Ethiopian wolves, larger packs invariably prevail in territorial clashes (Sillero-Zubiri and Macdonald 1998). Territorial clashes may account for a substantial proportion of adult mortality (e.g., Mech 1977; Creel and Creel 1998).

Predation

There are few data from canids to support the intuition that larger groups are more vigilant, having more pairs of eyes, ears and nostrils with which to detect predatory danger more rapidly. Wild dogs will aggressively mob potential predators if pups are threatened (e.g., Kühme 1965; Estes and Goddard 1967) and this becomes more effective for larger packs. Larger groups of bat-eared foxes (*Otocyon megalotis*) appear better able to repel predators approaching their dens (Maas and Macdonald 2004). The magnitude of predation as a force in canid lives is illustrated by the fact that lions are responsible for 43% of the natural mortality of wild dogs in Kruger National Park (Mills and Gorman 1997; see also Carbone *et al.* 1997).

Reproductive advantages

Canid pups have a prolonged period of dependency on adults and are commonly tended by both parents (Kleiman and Eisenberg 1973). Lupine canids are the only Carnivore group to regurgitate, and males also provision pregnant and lactating mates allowing them to better direct energy into gestation and lactation, and also to guard young uninterruptedly (Oftedal and Gittleman 1989). The original list of species for which non-breeding 'helpers' fed and tended the young (e.g., red foxes, black-backed jackals, grey wolves – Macdonald 1979b; Moehlman 1979; Fentress and Ryan 1982) has expanded with the number of species studied, revealing allo-parental care as a widespread trait of the canids (e.g., Bekoff and Wells 1982). While allo-parental care appears self-evidently helpful (Moehlman 1979), demonstration that helping translates into improved reproductive success has also proven difficult. Perhaps the most extreme form of allo-parental behaviour is allo-suckling, observed in, for example, red and Arctic foxes (*Alopex lagopus*), grey and Ethiopian wolves, coyotes and bat-eared foxes. Various mechanisms may lead to allo-suckling: a subordinate female may lose her pups through the dominant's infanticide (van Lawick 1974; Malcolm and Marten 1982; Corbett 1988b), reproductive suppression may fail leading to mixed litters, and some females appear to lactate spontaneously (Sillero-Zubiri *et al.* 2004a). Evidence that allo-suckling benefits the pups has proved elusive (Malcolm and Marten 1982; Zabel and Taggart 1989; Roulin and Heeb 1999), perhaps because they materialise only in the long term (Emlen 1991) making pup survival to weaning or dispersal an inappropriate measure. Similarly, when it comes to measuring the consequences of any form of allo-parental behaviour, a plausible measure might be the life-time reproductive success of the mother rather than the survival of a particular litter of offspring – the underlying mechanism being that the helpers' contribution reduced the energetic burden on the mother, thereby extending her subsequent performance. However, long-term life-history studies with the capacity to test for such effects are few.

Canid society is typified by reproductive suppression exerted by dominant females on their subordinates (see Moehlman 1986, 1989) and has been recorded in at least 44% of 25 species for which there is information (Moehlman and Hofer 1997). The degree of suppression, however, varies both intra- and interspecifically (Creel and Waser 1991, 1994) and subordinates do reproduce, albeit at lower rates than dominants (Packard *et al.* 1983; Macdonald 1987; Fuller and Kat 1990). Although behavioural suppression appears to be common in males (e.g., Packard *et al.* 1983), multiple paternity has been reported (Gottelli *et al.* 1994), and the likelihood is that a combination of behavioural and genetic techniques will increasingly reveal that complications in mating systems are widespread. Various mechanisms may be involved in social suppression of reproduction (Packard *et al.* 1985), but whatever the mechanism, the outcome is that amongst

Hólmfríður Sigþórsdóttir

Páll Hersteinsson weighs an Arctic fox cub in Hlöðuvík Bay after luring it out of the den by imitating the parents' call and ear-tagging it. Hornstrandir Nature Reserve, Iceland.

grey wolves, subordinates rarely have offspring and generally lose those they do have (Peterson *et al*. 1984). Nonetheless, in Kruger National Park, 40% of 25 dens contained pups of more than one female wild dog (although only 9% of pups were the offspring of subordinates) (Girman *et al*. 1997).

The benefits provided by helpers may vary according to the sex of the helper; clearly, only females have the potential to allo-suckle, but less obviously, data on grey wolves and wild dogs indicate that males provide more solid food to pups per capita than do females (Fentress and Ryon 1982; Malcolm and Marten 1982).

In short, membership of larger groups may bring canids advantages due to combinations of improved foraging efficiency, breeding success, and survivorship. In some cases, and it has been argued for wild dogs, the advantages of sociality may be reflected as an Allee effect: a positive feedback loop of poor reproduction and low survival culminating in failure of the whole pack (Courchamp and Macdonald 2001; Courchamp *et al*. 2001). In so far as pack sizes reflect some optimum of different selective pressures, one would expect a dome-shaped distribution of pack sizes, with populations subject to inverse density dependence at low density and direct density dependence at high density, exactly as observed by Creel (1997) for wild dogs.

10.3.2 Ecological selective pressures for sociality

While behavioural benefits may be amongst the selective pressures favouring sociality in wild canids, ecological factors create the framework within which these pressures operate, and dictate the balance of costs and benefits between group membership and dispersal. Alexander (1974) was the first to suggest that group formation (and cooperative behaviour between their members) is a secondary consequence of group living that is initially favoured by some other ecological reason. One crucial ecological factor is resource dispersion.

Resource dispersion

Irrespective of the advantages of group living, resource dispersion may significantly affect the costs of grouping. The idea that certain patterns of resource availability might facilitate group formation by making coexistence feasible, grew especially out of observations on badgers (*Meles meles*) (Kruuk 1978), and was formalised as the Resource Dispersion Hypothesis (RHD) by Macdonald (1983) and Carr and Macdonald (1986). The hypothesis is that groups may develop where resources are dispersed such that the smallest economically defensible territory for a pair can also sustain additional animals. The RDH offers an explanation of group size variance, regardless of whether individuals gain from each other's presence or not. Not only may it apply to current societies, but it may describe the conditions that favoured the evolution of sociality. While RDH can only be tested by manipulative experiments (Johnson *et al*. 2002), several field studies of canids are broadly in line with its predictions (Hersteinsson and Macdonald 1982; Macdonald 1983; Geffen *et al*. 1992c; but see Baker and Harris 2004).

Dispersal

Dispersal is crucial both to understanding life-history processes (Waser 1996) and to conservation (Macdonald and Johnson 2000). However, it is poorly understood, and philopatry brings with it the risk of inbreeding. Examples of neighbourhood relatedness and return from dispersal are mounting amongst canids and may be widespread (Lehman *et al*. 1992; Macdonald and Courtenay 1996). Inbreeding may also occur locally between related pack founders derived from neighbouring packs (Mech 1987). Messier and Barrette (1982) conclude that the most influential factor leading to group formation in coyotes is the absence of dispersal opportunities. The ethology of dispersal is correspondingly poorly understood and is often reported as a summary bee-line distance. However, such distances often disguise a more complicated reality (Macdonald 1980d). The time between emigrating and settling can be highly variable (Gese and Mech 1991). Some animals mate while on forays but never actually settle in that group, and coalitions of females may also leave their natal range as a group to settle in previously unoccupied territory, where they are joined by an emigrating male (Gese and Mech 1991). Although Mech's (1987) study of wolves illustrates almost every variant imaginable, some generalisations may emerge – for example, Macdonald and Bacon (1982) noted that the mean bee-line distance of red fox dispersal correlated with territory sizes, with the result that foxes travelling very different distances were crossing rather similar numbers of territories.

10.4 Trends in canid sociality

Extending the broad association between body size and social system, Moehlman (1986, 1989) reported that female body mass was positively correlated with gestation length, neonate mass, litter size and litter mass, and that from these corollaries of size she deduced generalisations about interspecific differences in adult sex ratio, dispersal, mating, and neonate rearing systems. Female body weight was argued to be the ultimate driver of a cascade effect such that relative to smaller species, larger canids invest more in prepartum reproduction (having larger neonates and a large number of offspring), live, and hunt, in larger groups, generally prey on larger, vertebrate prey, and have a greater incidence of reproductive suppression and allo-parental behaviour (Moehlman and Hofer 1997). Diet breadth, maximum prey size and incidence of cooperative hunting all scale allometrically with body size in canids. Amongst carnivores as a whole, litter mass, litter growth rate and total investment are higher in communally breeding species with reproductive suppression (Gittleman 1986; Creel and Creel 1991).

In a similar comparative analysis, Geffen *et al.* (1996) found a high correlation and isometric relationship between neonatal weight and female body weight and interpreted this as evidence that the size of newborn canids is constrained either by female body size directly or by some allometric correlate of female body size e.g., pelvic width (Leutenegger and Cheverud 1982). Their analysis, unlike Moehlman's (1986), took account of phylogeny, and found litter size to be only weakly and non-isometrically correlated with female body weight, suggesting that litter size may be adjusted in response to the availability of resources. They suggested also that female pre-birth investment can only be adjusted by varying litter size – red and Arctic foxes, and wolves are amongst canid species exhibiting decreases in litter size with decreases in prey abundance (Macpherson 1969; Harrington *et al.* 1983; Lindström 1989; Angerbjörn *et al.* 1991; Hersteinsson and Macdonald 1992). On this view, changes in body size, litter size and social organisation within the Canidae may be attributed primarily to differences in food availability. Thus, small canids (e.g., fennec fox *Vulpes zerda*) are usually associated with arid and poor habitats in which only a small body mass can be supported year round, whereas large canids are often associated with habitats in which prey are at least very abundant (e.g., Ethiopian wolves) and more generally, abundant and large (e.g., African wild dogs, grey wolves).

The relationship between group size and territory size is intriguing. As Kruuk and Macdonald (1985) noted, starting from a minimum defensible territory there are two possibilities for group formation. First, contractionism or building up a group by bringing extra members into the minimum territory that will support a pair. Second, expansionism is the alternative, where the benefits of sociality may be so great, that it pays the group to expand to a bigger territory. Insofar as group size and territory size may be uncorrelated in red foxes, but strongly correlated in Ethiopian wolves, there is evidence for both scenarios. Furthermore, an analysis of group metabolic requirements plotted against home range sizes reveals that some group-living canids have smaller home ranges than predicted by their collective body weight, whereas for others the group home ranges are larger than predicted (Johnson *et al.* in press). Macdonald *et al.* (2004) argue that RDH may explain both negative and positive deviations by social canids from the home range size predicted by their metabolic needs. In both cases ecological circumstances create conditions that diminish or obliterate the costs of group formation: a patch of invertebrates may allow several canids to feed together, as may the body of a single large ungulate; groups of canids feeding on the former tend to be associated with smaller than expected territories, groups of canids feeding on the latter tend to be associated with larger ranges than expected. In both cases, it will be a matter of local, autecological circumstances whether a particular species or population opts to form groups up to the size potentially accommodated in such sharable enclaves, or even to form larger groups requiring expansionist territories, or not to share at all.

Chapter 11

Conservation Genetics of Canids[1]

R.K. Wayne, E. Geffen and C. Vilà

11.1 Introduction

In this chapter, population genetic data for canid species that have recently been studied with molecular genetic techniques, and that warrant conservation concern, will be reviewed. A brief summary of the pertinent findings for each studied species is followed by specific conservation implications. For a full discussion of findings on these canid species and others, please see Wayne *et al.* (2004) and Wayne (1996).

In general, because canids are highly mobile carnivores, levels of genetic differentiation are low; however, habitat fragmentation and loss has caused some populations to become isolated and genetic drift in these small populations has accelerated differentiation and loss of genetic variation. Moreover, genetic loss has occurred in some endangered species because of persistent small population sizes. Also, in many species, a history of dynamic changes in abundance and distribution are superimposed on current demographic conditions. For example, genetic analysis of grey wolves (*Canis lupus*) and coyotes (*C. latrans*) has suggested range contractions during glacial maxima followed by reinvasion across several continents (Frati *et al.* 1998; Vilà *et al.* 1999).

High mobility also influences the degree to which interspecific hybridisation affects the genetic composition of hybridising species (Lehman *et al.* 1991; Jenks and Wayne 1992; Wayne 1992; Mercure *et al.* 1993; Wilson *et al.* 2000; Wayne and Brown 2001). The width of a hybrid zone is a function of the distance travelled from birth to the place of first reproduction and the degree of natural selection against hybrids (Barton and Hewitt 1989). If selection is weak, hybrid zones may span a considerable distance in highly mobile species and interspecific gene flow may strongly affect the genetic heritage of hybridising forms (Jenks and Wayne 1992; Wilson *et al.* 2000; Wayne and Brown 2001). Interspecific hybridisation contributed to the genetic extinction of red wolves (*C. rufus*) in the wild, has greatly compromised the genetic composition of the Great Lakes wolf (*C. lupus lycaon*) and has flooded New England with wolf-coyote hybrids (Nowak 1979; Lehman *et al.* 1991; Jenks and Wayne 1992; Roy *et al.* 1994b, 1996; Wilson *et al.* 2000; P. J. Wilson *et al.* unpubl.). Further, hybridisation between domestic dogs and Ethiopian wolves (*C. simensis*) (Gottelli *et al.* 1994) and perhaps between grey wolves and domestic dogs in certain areas may be consequential (Vila and Wayne 1999; Andersone *et al.* 2002; Randi and Lucchini 2002; Vilà *et al.* 2003a).

11.2 Review of studies on rare and endangered canids

11.2.1 Ethiopian wolf

The Ethiopian wolf is one of the most endangered living canids (Gottelli and Sillero-Zubiri 1992; Sillero-Zubiri and Macdonald 1997; Marino 2003). The total population in 2000 was less than 500 individuals. The species is dispersed across the Ethiopian highlands above 3,000m a.s.l. in small, highly isolated populations (Gottelli and Sillero-Zubiri 1992; Marino 2003). Phylogenetic analysis of mtDNA sequences showed that the closest living relatives of Ethiopian wolves are probably grey wolves and coyotes (Gottelli *et al.* 1994, 2004; Vilà *et al.* 1999). An evolutionary hypothesis consistent with these results is that Ethiopian wolves are a relict form remaining from a Pleistocene invasion of a wolf-like progenitor into East Africa. The current extent of Ethiopian high altitude moorland habitats is only 5% of the area existing after the last Ice Age (Yalden 1983; Gottelli *et al.* 2004). Consequently, the geographic range and numerical abundance of Ethiopian wolves has likely decreased during the Holocene. More recently, habitat loss and fragmentation due to human population growth and agriculture have accelerated the decline of Ethiopian wolves.

Genetic variation, differentiation and hybridisation

Mitochondrial DNA (mtDNA) sequence analyses and microsatellite typing showed that the two populations in the Bale Mountains had very low variability. All wolves had the same mitochondrial DNA haplotype, and microsatellite loci was only 46% and mean allelic diversity 38% of that commonly found in other wolf-like canids. Such low levels of heterozygosity are consistent with an equilibrium effective population size of only a few hundred

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[1] This paper is condensed from Wayne, R.K., Geffen, E. and Vilà, C. 2004. Populations and conservation genetic of canids. Pp. 55–84 in D.W. Macdonald and C. Sillero-Zubiri, (eds). *Biology and conservation of wild canids*, Oxford University Press, Oxford, UK.

individuals (Gottelli *et al.* 1994). A recent analysis of mtDNA from six other populations identified genetic differences but found low number of haplotypes and a low sequence divergence among them, confirming the wolves' recent evolution (Gottelli *et al.* 2004). The genetic structure observed was congruent with random fixation of alleles within isolated populations as habitat contracted since late Pleistocene.

Although loss of variation and inbreeding in isolated populations are concerns for endangered species, an additional problem for Ethiopian wolves is hybridisation with domestic dogs. Genetic analysis showed that suspected hybrid individuals in a population in the Sanetti Plateau of the Bale Mountains National Park had microsatellite alleles not otherwise found in Ethiopian wolves, but were present in domestic dogs. In contrast, these individuals had mtDNA haplotypes identical to those in 'pure' Ethiopian wolves (Gottelli *et al.* 1994), a result consistent with field reports that interspecific matings only involved male domestic dogs and female Ethiopian wolves (Sillero-Zubiri 1994). Additionally, parentage analysis found that a single litter had both a wolf and dog as fathers, showing that multiple paternity occurs in wolves and can involve both species. Dogs not only hybridise with Ethiopian wolves and compete with them for food, but also are reservoirs of canine diseases (Sillero-Zubiri *et al.* 1996b).

Conservation implications

The sharply lower levels of variation in the Ethiopian wolf reflect a long history of population declines compounded by recent habitat fragmentation (Gottelli *et al.* 2004). However, perhaps a greater concern than the reduced levels of genetic variation is the vulnerability of the few remaining populations to diseases such as rabies, which is already thought to have eliminated about one-half of the Bale Mountains population (Sillero-Zubiri *et al.* 1996b; Sillero-Zubiri and Macdonald 1997) and to other stochastic demographic effects. Inbreeding depression may occur in canids (Laikre and Ryman 1991; Laikre *et al.* 1993; Fredrickson and Hedrick 2002; but see Kalinowski *et al.* 1999) and may conceivably influence the persistence of the population (e.g., Seal and Lacy 1998). Loss of genetic variation in small populations may also influence the ability of the population to adapt to changing conditions (Frankham *et al.* 2002). However, Ethiopian wolves actively avoid inbreeding (Sillero-Zubiri *et al.* 1996a) thus decreasing the rate at which genetic variation is lost and mitigating the effect of inbreeding. In one population, the loss of unique Ethiopian wolves' characteristics may result from interbreeding with dogs. However, this threat may be restricted to that locality (Wayne and Gottelli 1997). Ethiopian wolves are not being bred in captivity (Sillero-Zubiri and Macdonald 1997) and the genetic results suggest that a reservoir of pure wolves must be protected and bred in a captive setting as a source for reintroduction, should efforts to sustain the wild population fail. Finally, genetic surveys of other populations of Ethiopian wolves should continue so that a balanced programme of captive and *in situ* management can be constructed that maintains historic levels of variation within, and gene flow between, populations (Wayne and Gottelli 1997; Crandall *et al.* 2000; Gottelli *et al.* 2004).

11.2.2 African wild dog

The African wild dog (*Lycaon pictus*) once ranged over most of sub-Saharan Africa, inhabiting areas of dry woodland and savannah (Woodroffe *et al.* 1997). However, due to habitat loss, hunting and disease, many populations have vanished or are severely reduced in number. The extant populations are highly fragmented and total no more than several thousand individuals (Fanshawe *et al.* 1997; Ginsberg and Woodroffe 1997a). Importantly, the western African and Kenyan populations are nearing extinction, yet these populations are not represented in zoos as only South African wild dogs are kept in captivity. Populations in South Africa currently are stabilised in protected areas (Fanshawe *et al.* 1997).

Genetic variation and population differentiation

Analysis of mtDNA nucleotide diversity suggested that wild dog populations have historically been small relative to other large carnivores (Girman *et al.* 2001). However, recent population declines due to human induced habitat loss have not caused a dramatic reduction in genetic diversity. Levels of diversity in microsatellite loci do not show strong evidence of recent or historic population decline relative to other carnivores. Further, the levels of genetic polymorphism estimated from the microsatellite data were relatively similar in all seven populations. Although the average sample size for each population varied greatly (5.8 in the North-west Namibia population to 93.8 in the Kruger population, South Africa), the mean number of alleles per locus ranged only between 3.4 and 4.4. Heterozygosity values were also similar, ranging from 0.56 for the Kruger population to 0.67 for the Selous population. The heterozygosity of a captive South African population was lower (0.50) and the mean number of alleles per locus was only 3.3.

Mitochondrial and microsatellite loci showed significant differentiation between populations. Eastern and southern populations may have been historically isolated. One historic and eight recent mtDNA haplotypes were found that defined two highly divergent clades. In contrast to a previous more limited mtDNA analysis (Girman *et al.* 1993), sequences from these clades were not geographically restricted to eastern or southern African populations. Rather, a large admixture zone was found spanning populations from Botswana, Zimbabwe and south-eastern Tanzania. Genetic differentiation between populations was significant for both microsatellite and mitochondrial markers and unique mtDNA haplotypes and alleles characterised the populations. However, gene flow estimates (Nm) based on microsatellite data were moderate to high in the range of 1.53 to 5.88 migrants per generation. In contrast, gene flow estimates based on the mtDNA control region were lower than expected in the range of 0.04 to 2.67 migrants per generation. Given the differences in the mode of inheritance of mitochondrial and nuclear markers, the results suggest a male bias in long distance dispersal. However, dispersal distance has been found to be similar for males and females in a Botswana population (McNutt 1996a), so the genetic results could indicate a higher frequency of male dispersal. Past and present distribution of the *miombo* (*Brachystegia-Julbernardia*) woodland and grassland, as well as the barrier imposed by the rift valley are biogeographic factors that may explain the current distribution of genetic variability (Girman *et al.* 2001). However, West African populations, represented by a single sample from a museum specimen, define a distinct branch suggesting a history of genetic isolation.

Conservation implications

Two haplotype clades co-occur over much of the current geographic range of the wild dog, which likely reflects natural mixing of previously isolated populations (Girman and Wayne 1997; Girman *et al.* 2001). Consequently, genetic management should aim at mimicking observed levels of gene flow between contiguous populations within this admixture zone (Crandall *et al.* 2000; Wayne and Brown 2001). Individual-based models of wild dog population dynamics suggest that even low rates of migration between populations can demographically stabilise populations otherwise at risk of extinction (Vucetich and Creel 1999). However, in wild dogs, genetic differentiation of microsatellite loci increases with distance and eastern and southern African populations may be morphologically distinct. Consequently, translocations between geographically distant southern and eastern populations are not advised because adaptive differences may exist (Crandall *et al.* 2000). For the Masai Mara and Serengeti, where wild dogs are threatened or even locally extinct (Fanshawe *et al.* 1997), the Selous region would be an appropriate source of individuals for reintroduction at the level of a few migrants per generation (see above). Additionally, because the genetic results suggest more frequent dispersal and/or longer dispersal distances in males than in females, the population management strategy should focus on the more frequent translocation of males to replicate natural processes. West African populations should be a high priority for research and conservation, especially given evidence of genetic distinction and their perilous population status.

Finally, to ameliorate genetic decline, population sizes should be kept as large as possible given the remaining habitat area. Additionally, gene flow should be facilitated by maintaining corridors that link populations, and, when this is not possible, through translocation at historic levels as indicated by genetic data. The maintenance of genetic variation, especially the component that influences fitness, is critical to population persistence and the future evolutionary response of wild dogs to changing environmental conditions (Crandall *et al.* 2000).

11.2.3 Grey wolf

The grey wolf has the largest historical geographic range of any canid, and exists in a wide range of habitats from cold tundra to the warm deserts of the Old and New World. Because grey wolves are the most mobile canid species, genetic differentiation between populations connected by appropriate habitat is expected to be low. However, wolves vary geographically in body size and pelage suggesting selection causes differentiation despite high levels of gene flow. For example, selection for differences according to habitat type (e.g. tundra *vs*. boreal forest) or prey (migratory *vs*. resident, large *vs*. small; Kolenosky and Standfield 1975; Peterson *et al.* 1998; Carmichael *et al.* 2001) could presumably cause differentiation despite gene flow. Wolf populations need to be connected by viable corridors. Despite the high potential mobility of wolves, habitat fragmentation and habitat loss can dramatically affect the demography and genetic variability of wolf populations. For example, western European populations have reduced mitochondrial DNA variation within populations but often have unique mitochondrial DNA haplotypes (Wayne *et al.* 1992; Randi 1993; Randi *et al.* 2000; see below). Similarly, by reducing the effective population size of isolated populations, predator control programmes may cause declines in genetic variation, an increase in levels of inbreeding and a disruption of social hierarchies (Ellegren *et al.* 1996; Ellegren 1999; Vilà *et al.* 2003b). Alternatively, populations that are controlled may also become population sinks if immigration is common which may enhance genetic variation (Frati *et al.* 1998; Wang and Ryman 2001).

Genetic variation

Genetic variability within large interconnected wolf populations is generally high. With the exception of the Italian wolf population, large populations in the Old and New World have several mtDNA control region or mtDNA RFLP haplotypes (Wayne *et al.* 1992; Vilà *et al.* 1999; Randi *et al.* 2000) and have high values of nucleotide diversity. In North America, only the Mexican wolf (*Canis lupus baileyi*) has low levels of variation (Roy *et al.* 1994b). Genealogical measures of nucleotide diversity suggest that grey wolves were more abundant than coyotes in the past and that both species declined throughout the Late Pleistocene, although wolves declined more rapidly. In general, nucleotide diversity data imply a decline in grey wolves from over five million breeding females (about 33 million wolves) worldwide in the late Pleistocene to about 173,000 breeding females (1.2 million wolves) in the recent past. Today, less than 300,000 exist worldwide (Boitani 2003).

Dramatic demographic declines or historical population bottlenecks have been documented for some wolf populations and genetic studies have found them to contain less genetic variation. For example, the Italian wolf population declined dramatically in the 18th and 19th century due to habitat loss and predator-control programmes (Randi 1993; Randi *et al.* 1995, 2000; Scandura *et al.* 2001) and extensive mtDNA studies showed these wolves to have a single mitochondrial haplotype, which represents lower diversity than that in other Old World populations (Wayne *et al.* 1992; Randi *et al.* 1995, 2000; Vilà *et al.* 1999; Scandura *et al.* 2001). The Italian wolf haplotype is unique, and is otherwise found only in French wolves, a population recently founded by wolves from Italy (Taberlet *et al.* 1996; Lucchini *et al.* 2002; Valière *et al.* 2003). However, levels of microsatellite variation approach that in large wolf populations (Randi *et al.* 2000; Scandura *et al.* 2001).

Scandinavian wolves have declined over the past few hundred years to the point of near extinction in the 1970s. However, a new group of wolves was discovered in southern Sweden in the early 1980s which was thought to be the founding stock of the current Scandinavian population, estimated to be about 100 individuals in 2000 (Vilà *et al.* 2003b). Genetic studies suggested that the current population is reduced in genetic variation and that variability was being lost over time (Ellegren *et al.* 1996; Vilà *et al.* 2003b). The Scandinavian population has 71% of the variation in the large neighbouring population of Finland and Russia and is fixed for a single mtDNA haplotype. The level of inbreeding observed in the Scandinavian wolves is similar to that of the Swedish captive population (Ellegren 1999) in which inbreeding depression was detected (Laikre and Ryman 1991; Laikre *et al.* 1993). The southern Scandinavian population has a single control region haplotype, unique microsatellite alleles and Y-chromosome haplotypes, thereby excluding the possibility that it had been founded by individuals released from captivity (Sundqvist *et al.* 2001). Genetic data suggest that the Scandinavian population was founded by two individuals that successfully migrated from the Finnish-Russian population and established a breeding pack in 1983 (Vilà *et al.* 2003b). The arrival of a new male migrant, reproducing for the first time in 1991, allowed the temporary population recovery of the population and avoided extreme inbreeding (Vilà *et al.* 2003b).

The Mexican wolf has declined to extinction in the wild due to habitat loss and an extensive extermination programme in the first half of the 20th century. Two of the three captive Mexican wolf populations had fewer microsatellite alleles and reduced heterozygosity (García-Moreno *et al.* 1996; Hedrick *et al.* 1997). Moreover, only two mtDNA haplotypes were found in the three captive populations (Hedrick *et al.* 1997). The total founding population numbered about seven. In the past, only the certified lineage, founded from three individuals of known Mexican wolf ancestry, was used in the captive breeding programme. However, recent genetic analysis established a close relationship among the three captive populations and found no evidence of dog, coyote or Northern grey wolf ancestry (García-Moreno *et al.* 1996; Hedrick *et al.* 1997). Consequently, to preserve the maximum genetic diversity of the Mexican wolf, plans to interbreed the three populations were developed. Like captive Swedish wolves, Mexican wolves showed signs of inbreeding depression (Fredrickson and Hedrick 2002; see also Kalinowski *et al.* 1999).

Genetic differentiation

Grey wolves show evidence of genetic differentiation on regional and continental scales. Wolves in the Old and New World do not commonly share mtDNA haplotypes (Wayne *et al.* 1992; Vilà *et al.* 1999). The degree of genetic subdivision among populations differs in wolves of the Old and New World (Wayne *et al.* 1992; Roy *et al.* 1994b; Ellegren *et al.* 1996; Forbes and Boyd 1996; 1997; Ellegren 1999; Randi 1993; Randi *et al.*, 1995, 2000; Vilà *et al.* 1999; Scandura *et al.* 2001). In the Old World, mtDNA data suggests that most populations are genetically differentiated with the exception of neighbouring populations such as those in Spain and Portugal, or recently invaded areas such as France, where Italian wolves have migrated (Taberlet *et al.* 1996; Vilà *et al.* 1999; Randi *et al.* 2000). In Western Europe, genetic subdivision may reflect recent habitat fragmentation that occurred over the past few hundred years with the loss of forests and, more importantly, a dramatic decrease in the size of all wolf populations due to human persecution (Wayne *et al.* 1992; Vilà *et al.* 1999). Genetic subdivision in Asian populations is not well known, however, recent mitochondrial DNA studies have found two subspecies of highly distinct Himalayan and lowland Indian wolves (*C. l. pallipes* and *C. l. chanco*, respectively) (Aggarwal *et al.* 2003; Sharma *et al.* 2004).

The presence of genetic subdivision in Europe contrasts with the patterns in North America where clinal variation in microsatellite alleles may exist over short distances (Forbes and Boyd 1996, 1997) although it is less apparent at a continental scale (Roy *et al.* 1994b). Similarly, mtDNA haplotypes are shared across large distances (Wayne *et al.* 1992; Vilà *et al.* 1999) but some geographic patterns also are evident. For example, mitochondrial RFLP haplotype W3 was common in Alaska and Northwest Territories but absent from populations in eastern Canada (Wayne *et al.* 1992). Conversely, RFLP haplotype W1 was absent in

Alaskan wolves but common in eastern Canada. A similar pattern was observed for mitochondrial control region sequences (Vilà *et al.* 1999). Conceivably, these weak clinal patterns reflect prior Pleistocene isolation in southern and Alaskan refugia followed by expansion and mixing during interglacials. Water barriers and differences in prey may also result in differentiation. For example, a recent study found that wolves specialising on different caribou herds in the Canadian north-west as well as populations on Banks and Victoria Islands were differentiated (Carmichael *et al.* 2001). Finally, another level of complexity is suggested by the recent finding that the Great Lakes wolf population may have been a distinct red wolf-like canid, *Canis lycaon*, which is now interbreeding with grey wolves that have migrated into eastern Canada after the last glaciation and coyotes which have entered the region in the past 100 years (see below; Wilson *et al.* 2000). Regardless, North American grey wolves proved not to be as dramatically structured and reduced in variation as their Old World counterparts as evidenced by the observation that population variability was high and levels of differentiation were low (Wayne *et al.* 1992; Roy *et al.* 1994b, 1996; Vilà *et al.* 1999).

The most highly differentiated North American grey wolf population is the Mexican wolf. Except for a reintroduced experimental population, this subspecies was thought to be extinct in the wild and exists only in three captive populations, each initiated by a small number of founders (García-Moreno *et al.* 1996; Hedrick *et al.* 1997). Two of the captive Mexican wolf populations displayed a single divergent mtDNA haplotype found nowhere else that was more closely related to a subset of Old World haplotypes than to any New World haplotype. This suggested that Mexican wolves shared a more recent ancestry with wolves from the Old World and the basal position of the Mexican wolf sequences in phylogenetic trees and analysis of historic museum specimens suggested that the Mexican wolf was a relict form stemming from an early invasion of grey wolves from Asia (Wayne *et al.* 1992; Vilà *et al.* 1999; J. A. Leonard *et al.* unpubl.).

The red wolf and Algonquin wolf

Interbreeding between highly mobile species, such as wolves and coyotes, may result in the development of large hybrid zones. The grey wolf once ranged throughout most of North America and parts of Mexico, but over the past few hundred years, wolves have been eliminated from the USA and Mexico. Similarly, the red wolf was exterminated by about 1975 from throughout its historic distribution which included much of the south-eastern USA, although it has since been reintroduced to a refuge in North Carolina (Parker 1987). Coyotes interbred extensively with red wolves as they approached extinction (Nowak 1979) and, consequently, mtDNA haplotypes and microsatellite alleles otherwise unique to coyotes are found in red wolves (Wayne and Jenks 1991; Roy *et al.* 1994b). However, an extensive genetic analysis characterising microsatellite and mtDNA variation in coyotes, grey wolves and historic and recent red wolves found no markers unique to red wolves. Instead only haplotypes and microsatellite alleles identical or very

Adult male red wolf with pup. Museum of Life and Sciences, Durham, USA. 2002.

Greg Koch

similar to those in grey wolves and coyotes were found (Roy *et al.* 1994a, 1994b, 1996). Consequently, an origin of the red wolf through hybridisation of grey wolves and coyotes in historic times or earlier was postulated (Wayne and Jenks 1991; Roy *et al.* 1994b, 1996; Reich *et al.* 1999). Similarly, genetic evidence for hybridisation between grey wolves and coyotes from Minnesota and eastern Canada suggested a hybrid form similar to that which may have existed for the red wolf (Lehman *et al.* 1991; Roy *et al.* 1994b, 1996). Thus, the genetic data imply both that significant hybridisation has occurred between the two species and that introgression of coyote genes into the wolf population has occurred over a broad geographic region.

However, new genetic results question these conclusions (Wilson *et al.* 2000). Detailed genetic analysis of eastern Canadian wolf-like canids and coyotes has found divergent mtDNA control region haplotypes with a distribution centred at Algonquin Provincial Park, Ontario. These divergent haplotypes appear to be phylogenetically similar to those of red wolves, which in turn are grouped with haplotypes of coyotes. These results may indicate that the smallish grey wolf that formerly inhabited the Great Lakes areas and the red wolf, are the same species, designated as *Canis lycaon* (Wilson *et al.* 2000). These authors suggest that the Algonquin wolf is a native New World wolf-like form that evolved independently from North American coyote-like ancestors (see Nowak 2002 for an alternative view). Finally, a recent analysis of coyotes in the south-eastern USA has shown that one dog haplotype appeared in multiple individuals across a large area (Adams *et al.* 2003). This suggests an ancient coyote-domestic dog hybridisation event when the first coyotes were expanding into eastern habitats formerly occupied by red wolves.

Wolf-dog hybridisation

In the wild, hybridisation between grey wolves and dogs is likely to be most frequent near human settlements where wolf density is low and habitats are fragmented, and where feral and domestic dogs are common (Boitani 1983; Bibikov 1988). The genetic integrity of wild wolf populations has been a concern among some conservationists (Boitani 1984; Blanco *et al.* 1992; Butler 1994), although the majority of wolf populations show no evidence of hybridisation (Vilà and Wayne 1999). However, genetic studies have detected limited wolf-dog hybridisation in Bulgaria, Italy, Latvia, Scandinavia and Spain (Dolf *et al.* 2000; Randi *et al.* 2000; Randi and Lucchini 2002; Andersone *et al.* 2002; Vilà *et al.* 2003a; Vilà *et al.* unpubl.).

Conservation implications

Several conservation implications are suggested by the genetic results. First, because the Mexican grey wolf is genetically and physically distinct, and historically isolated from other grey wolves (Nowak 1979), the breeding of pure Mexican wolves in captivity for reintroduction into the wild is advised. Second, because most wolf populations in North America are not strongly differentiated genetically, and gene flow is high among populations, reintroduction need not include only the nearest extant populations as source material. However, the reintroduction of wolves from populations where hybridisation with coyotes has occurred is perhaps not advisable (see below). Finally, genetic analysis of recolonised populations in Montana and France has found that high levels of genetic variation can be preserved (Forbes and Boyd 1997; Scandura *et al.* 2001).

The grey wolf has been divided into as many as 32 subspecies worldwide (Hall and Kelson 1959). Nowak (1995) suggested that the 24 North American subspecies should be reduced to five. However, rates of gene flow among North American wolf populations are high, and differentiation by distance characterises the genetic variation of wolves at some geographic scales. In this sense, typological species concepts may be inappropriate because geographic variation in the wolf is distributed along a continuum rather than being partitioned into discrete geographic areas delineated by fixed boundaries. A focus on locality-specific adaptations to prey size or climate (e.g., Thurber and Peterson 1991; Carmicheal *et al.* 2001) or size variation with latitude may be a more appropriate guide to conservation rather than arbitrary boundaries of a continuously distributed and high mobile species (Crandall *et al.* 2000). However, the discovery of genetically distinct populations of Indian wolf suggests they should be the focus of immediate research and the object of conservation concern. Finally, although contemporary wolf populations in Europe appear more genetically subdivided than their North American counterparts (Wayne *et al.* 1992; Vilà *et al.* 1999; Randi *et al.* 2000), the North American pattern might well reflect the ancestral condition in western Europe prior to habitat fragmentation and population decimation. Therefore, efforts to increase gene flow among European wolf populations to levels similar to that in North America could be defended.

The possible presence of a hybrid zone between a native north-eastern wolf species, and coyotes and grey wolves (see above) complicates taxonomic and conservation recommendations. If *C. lycaon* is a distinct species, conspecific with the red wolf, then captive breeding and conservation efforts *in situ* may be urgently needed. If *C. lycaon* is a hybrid between grey wolves and coyotes that is due to human-induced habitat changes and predator control efforts, then further conservation efforts may not be warranted (Jenks and Wayne 1992; Wayne and Brown 2001). For the hybridisation process to be of conservation concern, even hybridisation between a unique North American wolf and other canids, it should be caused by human activities rather than natural processes, such as glacial induced range expansions. Additional genetic data involving multiple mitochondrial, nuclear, and Y-chromosome markers are needed to better test alternative hypotheses for the origin of the red wolf and the Algonquin wolf. Finally, wolf-dog hybridisation is a non-natural occurrence that fortunately may be of concern only in a few European populations (see above).

Perhaps of greater concern is the loss of genetic variation in isolated wolf populations in the Old World (see above). Inbreeding depression has been documented in captivity (Laikre and Ryman 1991; Laikre *et al.* 1993; Federoff and Nowak 1998; Fredrickson and Hedrick. 2002; but see Kalinowski *et al.* 1999). Italian, Scandinavian and Isle Royale wolves have levels of average relatedness approaching inbred captive populations (see above), and could conceivably suffer a decrease in fitness that would eventually affect population persistence (Wayne *et al.* 1991a; Mace *et al.* 1996; Hedrick and Kalinowski 2000). High levels of gene flow likely characterised Old World populations in the past, so there is reason to restore past levels of gene flow in parts of Europe, either through habitat restoration and protection along dispersal corridors or through translocation. Future research should be aimed at monitoring and predicting genetic changes that will occur in wolf populations and trying to determine any possible population effects.

11.2.4 Kit fox and swift fox

Small canids such as foxes may have limited dispersal ability and be less able to traverse topographic barriers. Moreover, due to shorter dispersal distances, small canids may show a more pronounced pattern of genetic differentiation with distance and population subdivision. The small arid land foxes of North America are habitat specialists and relatively poor dispersers. In California, for example, the kit fox of the San Joaquin Valley, whose range is circumscribed by the coastal mountain range to the west and the Sierra Nevada mountain range to the east, is considered a distinct subspecies (*Vulpes macrotis mutica*) and is protected by the U.S. Endangered Species Act (Hall 1981; O'Farrell 1987). Populations to the east of the Rocky Mountains are collectively referred to as swift foxes (*V. velox*), and those to the west as kit foxes (*V. macrotis*). However, the two forms hybridise in north central Texas and are recognised as conspecific by some authors (Packard and Bowers 1970; Rohwer and Kilgore 1973; Nowak and Paradiso 1983; O'Farrell 1987; Dragoo *et al.* 1990).

Population variation and differentiation

Mitochondrial DNA analyses suggests that genetic divergence is related to the distance between populations and the severity of the topographic barriers separating them (Mercure *et al.* 1993). A major genetic subdivision within the kit-swift fox complex distinguished populations from the east and west side of the Rocky Mountains, consistent with the taxonomic distinction between V. *macrotis* and *V. velox*. The divergence between these taxa was nearly as great as that between them and the Arctic fox (*Alopex lagopus*), classified in a separate genus. Furthermore, within each of the two major kit-swift fox mtDNA clades, genetic distances among populations tended to increase with geographic distance (Mercure *et al.* 1993). The distinct phylogeographic pattern in kit-swift foxes contrasts with the lack of pattern observed in coyotes and grey wolves (Lehman and Wayne 1991) and suggests that the kit and swift fox may be two distinct species. However, the two forms hybridise in a contact zone in New Mexico, and microsatellite evidence indicates hybridisation occurs freely within the hybrid zone (Dragoo and Wayne 2003; J. W. Dragoo unpubl.). Finally, mitochondrial DNA data support subspecific distinction of the San Joaquin and Mexican (*V. m. zinseri*) kit foxes (Mercure *et al.* 1993; Maldonado *et al.* 1997). The latter appears to have reduced variation relative to USA populations.

Conservation implications

The San Joaquin and Mexican kit fox are genetically distinct populations that are related to kit foxes west of the Rocky Mountains. This degree of distinction suggests a limited history of isolation and provides some support for special preservation efforts. Further, the small population size and isolation of the Mexican form and absence of conservation efforts raise concern for its persistence. Topographic barriers, such as the Colorado River, or habitat barriers appear to influence geographic differentiation, but the predominant pattern within clades is one of geographic differentiation with distance. The scale of differentiation with distance is much finer in kit-swift foxes than in large canids reflecting differences in dispersal abilities and suggesting that a larger number of genetic units of conservation concern can be defined in small canids. With respect to the design of reintroduction programmes, source stocks for small canids should in general be drawn from smaller geographic areas than the large canids. For example, given the mtDNA findings, the recent use of foxes from Colorado and South Dakota rather than New Mexico or Texas as a source for a reintroduction into Canada's Saskatchewan Province, appears to have been appropriate (Scott-Brown *et al.* 1987).

11.2.5 Island fox

The island fox (*Urocyon littoralis*) is a Critically Endangered species found only on the six Channel Islands off the coast of southern California (Gilbert *et al.* 1990; Wayne *et al.* 1991b). The island fox is an insular dwarf, about two-thirds the size of its mainland ancestor, the gray fox (U. *cinereoargenteus*) (Collins 1991a; Wayne *et al.* 1991b). As suggested by the fossil and geologic record, about 16,000 years ago the three northern islands, which at that time were connected to one another, were colonised by foxes from the mainland. As sea level rose, 9,500 to 11,500 years ago, the northern islands were separated. About 4,000 years ago, foxes first arrived on the southern Channel Islands and were probably brought there by Native Americans. Consequently, genetic variation in the island populations should correlate with island area and founding time (Wayne *et al.* 1991b).

Population variation and differentiation

In general, predictions about genetic variation, island area and colonisation time were supported by molecular genetic analyses (Gilbert *et al.* 1990; Wayne *et al.* 1991b; Goldstein *et al.* 1999). The small, late colonised, San Nicolas population was invariant in all genetic markers surveyed including multi-locus DNA fingerprints and 19 microsatellite loci (Gilbert *et al.* 1990; Goldstein *et al.* 1999; Roemer *et al.* 2001a, 2002). Only inbred mice strains show a similar lack of variation, but no other wild population except the inbred, eusocial naked mole rats (*Heterocephalus glaber*) approaches this level of monomorphism (Faulkes *et al.* 1997). Similarly, the smallest island, San Miguel, had low levels of variation. In contrast, the large islands, Santa Catalina, Santa Rosa and Santa Cruz, had higher levels of variation. However, the Santa Cruz Island population, although it was founded early, had lower levels of variation than expected and Santa Catalina, although founded last, had the highest levels of variation. Finally, mitochondrial DNA data suggested that Santa Catalina Island may have been colonised multiple times from southern and northern islands.

All populations were well differentiated (Wayne *et al.* 1991b; Goldstein *et al.* 1999). The island foxes did not share mitochondrial DNA sequences with the mainland gray fox and some populations had unique haplotypes. For example, within the southern group of islands, the small population on San Nicolas possessed a unique mtDNA haplotype. Similarly, island populations had unique multilocus fingerprint bands and microsatellite alleles and differed in allele frequencies. Consequently, foxes could be correctly classified to island of origin, and haplotype trees resolved an evolutionary history of colonisation consistent with the archaeological record (Wayne *et al.* 1991b; Goldstein *et al.* 1999).

Conservation implications

Fox populations on five of six islands have decreased dramatically over the past 10 years (Roemer *et al.* 2002). On the three northern islands, the decline was due to predation by golden eagles (*Aquila chrysaetos*) (Roemer *et al.* 2001b, 2002). On Santa Catalina Island, the decline was due to a distemper epidemic and on San Clemente, a more gradual decline likely reflected predator control efforts of the loggerhead shrike (*Lanius ludovicianus migrans*) reintroduction programme (Roemer and Wayne 2003). In each case, genetic management of the remaining population is needed. On the northern islands, captive breeding is necessary to restore the wild populations, and preliminary studies have suggested that the captive population has sampled a limited subset of variation in the wild implying additional founders would be a beneficial addition to the captive breeding programme (Aguliar *et al.* unpubl.; M. Gray *et al.* unpubl.). On San Miguel Island, the wild population may be extinct, but on the other two northern islands, a dynamic exchange of wild and captive born foxes to enrich genetic variability is conceivable. On Santa Catalina Island, foxes have disappeared from about 90% of the island and a captive breeding programme of survivors has been established to assist in replenishing the loss of populations. However, a wild reservoir of over 150 foxes exists on the far western end of the island and genetic data indicate they provide a more genetically variable source for reintroduction (Aguliar *et al.* unpubl.). On San Clemente Island, several hundred individuals remain in the wild and significant genetic loss is unlikely to have occurred. There should be immediate efforts to stabilise the population and prevent further decline (Roemer and Wayne 2003).

The genetic results suggest that each island population should be treated as a separate conservation unit. Further, low levels of genetic variation in each island population relative to mainland gray foxes imply that they may be more vulnerable to environmental changes (Frankham *et al.* 2002). In previous conservation plans, the species has been treated as a single taxonomic unit with a combined population of about 8,000 individuals (California Code of Regulations 1992). However, as is now clear, by virtue of their isolation and small size, the islands are more vulnerable than an equivalently sized mainland population. Each island should be designated an independent unit with regard to conservation and at least five populations should be considered in immediate danger of extinction (Roemer and Wayne 2003). Study of captive populations combined with careful genetic management may allow successful reintroduction and more informative management of wild populations in the future.

11.2.6 Darwin's fox

On Chiloé Island, off the west coast of Chile, Charles Darwin observed and was the first to describe a small endemic fox, *Pseudalopex fulvipes*. Darwin's fox is a unique species found principally on Chiloé Island and has the smallest geographic range of any living canid (Osgood 1943; Cabrera 1958). There are perhaps less than 500 foxes currently in existence and none in captivity. Darwin's fox was thought to be recently isolated from mainland foxes given that the channel separating Chiloé from the continent is only about five kilometres wide, and the island was likely connected to South America when sea levels were lower during the last glaciation (*c.* 13,000 years B.P., Yahnke *et al.* 1996). However, the recent discovery of Darwin's fox on the mainland in central Chile, in Nahuelbuta National Park, 350km from Chiloe (Medel *et al.* 1990), and where they are sympatric with the mainland chilla (*P. griseus*), suggested that Darwin's fox may be a distinct species.

Genetic variation and differentiation

Phylogenetic analysis of mitochondrial DNA sequences confirmed the distinct species status of Darwin's fox and showed the island and single mainland populations are conspecific. Only three haplotypes were found, and only one of the mainland implying low genetic variation. Further, modest levels of genetic distinction between mainland and island populations supports their designation as a distinct subspecies. The genetic results show that Darwin's foxes diverged early in the radiation of Chilean foxes, and are at least as divergent from the chillas and culpeos (*P. culpaeus*) as the latter two are from one another. These results indicate that Darwin's fox is a relict form, having evolved from the first immigrant foxes to Chile after the land bridge formed between North and South America about 2–3 million years ago (Webb 1985; Yanke *et al.* 1996). Finally, a recent survey of other potential mainland localities where Darwin's fox may have formerly lived has found at least one locality approximately 150km north of Chiloé Island where foxes existed historically (C. Vilà *et al.* unpubl.).

Conservation implications

Darwin's fox is genetically distinct and appears to be the progenitor of the mainland fox species. The genetic results suggest it had a previous distribution on the mainland, rather than having been introduced there by humans. Darwin's fox also has a morphology unlike mainland foxes, and occupies a restricted and unique temperate rainforest habitat. Darwin's fox needs to be considered a distinct species of urgent conservation importance. The island population needs greater protection and captive populations need to be established. Captive breeding and observation of Darwin's foxes might provide better understanding of the biology and status of this Critically Endangered species that will assist in its conservation. The recent extinction and decline of four island fox populations of similar size to that of the Darwin's fox highlight its vulnerability. Finally, the presence of Darwin's foxes on the mainland currently, and in recent history, provides a mandate for introduction, possibly using the island population as a source (C. Vilà *et al.* unpubl.).

11.3 Conclusions

In general, the smaller fox-like canids show higher levels of variation between and within populations. These differences reflect higher densities and low levels of mobility in small canids. Insular canids, such as the island fox, Darwin's fox and the Isle Royale wolf, have the lowest levels of genetic variation but high levels of differentiation from mainland populations. A similar pattern is evident when habitats have been subdivided and populations isolated by human activities. For example, Scandinavian and Italian wolves have low levels of variation within populations but high levels of differentiation reflecting a recent history of isolation and population bottlenecks (Randi *et al.* 2000; Vilà *et al.* 2003b). The Ethiopian wolf, arguably the most threatened canid (despite its downgraded status in this plan), has the lowest levels of variation of any studied canid. In contrast, African wild dog genetic patterns appear dominated by ancient vicariance events such as Pleistocene isolation of southern and eastern populations followed by intermixing. However, populations in Kruger National Park and Kenya may have recently lost genetic variation due to population bottlenecks. Finally, interspecific hybridisation may occur in disturbed populations especially if one species is rare and the other abundant and the rate of encounters is high due to the presence of concentrated resources such as refuse dumps. Hybridisation with domestic dogs may threaten preservation of the unique genetic characteristics of the largest remaining population of the endangered Ethiopian wolf, but does not appear as a consequential threat to grey wolves.

Molecular genetic analysis supports species distinction for Darwin's fox, kit and swift foxes and the island fox. Analysis of populations within species have uncovered important genetic and phenotypic units including each of the island populations of island fox, the San Joaquin and Mexican kit fox, the Mexican wolf, two subspecies of Indian wolf and the Algonquin wolf, West and South African wild dogs, and New and Old World wolves. These distinct conservation units warrant separate breeding and in situ management. Interbreeding should be avoided in the absence of evidence for inbreeding depression (e.g., Hedrick and Kalinowski 2000). The next phase in genetic research on canids should focus on study of both neutral and fitness related genes so that both history and population adaptation can be assessed. This information will be valuable to conservation programmes (Crandall *et al.* 2000).

Chapter 12

Assessing and Managing Infectious Disease Threats to Canids

M. K. Laurenson, S. Cleaveland, M. Artois and R. Woodroffe

12.1 Introduction

Infectious diseases in wildlife have attracted increased attention in recent years and can be an important and intractable extinction risk for many species. A number of reviews have highlighted how disease issues are particularly relevant to canids whether because canids are the source of human diseases such as rabies, leishmaniasis or hydatid cysts (*Echinococcus granulosus*), or because threatened canids have suffered high disease-related mortality (Young 1994; Funk *et al*. 2001; Cleaveland *et al*. 2002; Woodroffe *et al*. 2004). Examples of disease in threatened canid populations are summarised in Table 12.1, which illustrates that rabies and canine distemper (CDV) are currently of greatest concern (Macdonald 1983; Appel *et al*. 1995; Deem *et al*. 2000; Woodroffe *et al*. 2004). Other diseases such as parvovirus, anthrax or otodectic mange have caused more sporadic outbreaks or may have affected populations in less obvious ways (Creel *et al*. 1995; Steinel *et al*. 2001).

This apparent association between canids and disease may arise in several ways. First, some canid species, most specifically foxes, coyotes and jackals, are opportunistic

Table 12.1. Local extinctions and crashes of free-ranging canid populations known to have been caused by infectious disease (based on Woodroffe *et al*. 2003).

Species	Pathogen	Effect	Reference
African wild dog	Rabies	Local extirpation of population of 50–70 dogs	Gascoyne *et al*. 1993 ; Kat *et al*. 1995
African wild dog	Rabies	Pack extirpated, all four dogs died	Scheepers and Venzke 1995
African wild dog	Rabies	75% of 12 dogs	Hofmeyer *et al*. 2000
African wild dog	Rabies	50% of 10 packs	J.W McNutt, pers. comm.
African wild dog	CDV	49/52 dogs died	Van de Bildt *et al*. 2002
African wild dog	CDV	All 12 dogs in pack died	Alexander *et al*. 1996
African wild dog	Anthrax	unknown, but 4/5 dogs confirmed *B. anthracis* 4/8 affected pups died, 3/3 adults survived	Turnbull *et al*. 1991 Creel *et al*. 1995
Ethiopian wolf	Rabies	53/76 known wolves died	Sillero-Zubiri *et al*. 1996b
Ethiopian wolf	CDV	Outbreak in sympatric domestic dogs. Effect on wolf population not monitored but population slow to recover from rabies outbreak	Laurenson *et al*. 1998
Ethiopian wolf	Rabies	~75% died/missing from subpopulation of 80 wolves	Randal *et al.* submitted
Kit fox	Rabies	96% decline over four years	White *et al*. 2000
Island fox	CDV	89% of 1,340 foxes disappeared	Timm *et al*. 2000
Island fox	Heartworm	78% seroprevalence, potentially some mortality in older individuals	Crooks *et al*. 2001
Blanford's fox	Rabies	75% of four foxes died	Macdonald 1993
Mednyi Arctic fox	Otodectic mange		Goltsman *et al*. 1996
Grey wolf	CPV	Pups died: Affected recruitment in one area, although overall population not affected	Mech and Goyal 1993, 1995
Grey wolf, coyote	Sarcoptic mange	Alberta	Todd *et al*. 1981a
Red fox	Sarcoptic mange	Various countries have caused population crash/limitation	Morner 1992; Danell and Hornfeldt 1987; Lindstrom *et al*. 1994; Tsukada *et al*. 1999; Harris and Baker 2001

generalists that can flourish in human-altered landscapes. Thus, their populations may be of sufficient density and size to allow some pathogens to persist. Second, the ecology of canids may expose them to infection. They may eat infected prey (Brand *et al.* 1995; Creel *et al.* 1995; Scheepers and Venzke 1995), and they frequently live in closely-knit groups that are often intolerant of other conspecifics. Interactions with conspecifics, whether social or aggressive may therefore be frequent (Woodroffe *et al.* 1997; Haydon *et al.* 2002). All these factors facilitate the transmission of infection to-and-between individuals. Third, most wild canids are closely related to the domestic dog and, therefore, susceptibility to most pathogens is shared. Where these dogs are not routinely vaccinated against common canid pathogens there is a potentially large population that can be a pathogen reservoir. Contact between wild canids and domestic dogs may be frequent in inhabited areas where wild canids coexist with humans, where domestic dogs invade protected areas, or where wide-ranging canids leave protected areas (Woodroffe and Ginsberg 1998; Woodroffe *et al.* 2004). As free-ranging domestic dogs and wild canids may directly compete for similar communal resources, such as carcasses or human refuse, contact may be more frequent than, for example, between wild and domestic felids.

Given this context, we aim to provide essential background information on disease epidemiology for wild canid managers in this chapter, but do not provide detailed descriptions of diseases or theory that can be obtained in other texts. We also aim to provide some practical information for assessing and managing disease threats, as a starting place for the field manager contemplating this issue.

12.2 Ecology of disease

An understanding of disease dynamics in host populations is fundamental to the management of canid disease. As space here is insufficient, we refer readers to a number of reviews to provide this essential background, including Anderson and May (1991), Hudson *et al.* (2002), and Woodroffe *et al.* (2004). However, it is necessary to highlight two important points. First, all the pathogens that have caused a problem in small or threatened populations of canids have the ability to infect a wide range of species and are generalists (Cleaveland *et al.* 2002). Indeed, epidemiological theory predicts that pathogens that cause major host mortality or reduce fertility are unlikely to be able to persist in small populations (Lyles and Dobson 1993). Second, these generalist pathogens must, therefore, persist in another reservoir population (Haydon *et al.* 2002). From there, they can spill-over and cause one-off or repeated epidemics in the target, threatened population.

Wildlife Rescue Association of British Columbia

Captured coyote with mange at animal rescue facility. The disease is common in coyotes in the area, and can be a symptom of a weakened immune system or other illness. Burnaby, British Columbia, Canada, 2003.

12.2.1 What is the disease reservoir?

Identifying the reservoir host for the disease is often crucial when considering the management of disease threats to canids, as it determines the options available and their likelihood of success. Identifying the reservoir is rarely a trivial task: the ultimate test of the identity of the reservoir is in some way to remove the pathogen agent from the putative reservoir community and then monitor incidence of disease in other target species in the community (Haydon *et al.* 2002). Unfortunately, this is often difficult if not impossible to carry out for reasons of scale, logistics or, for example, when the environment is the reservoir (as for Anthrax *B. anthracis*). However, other strands of evidence can be pieced together which, although not providing unequivocal proof, will suffice in most situations where practical decisions have to be made. First, epidemiological evidence in the form of case-control and cohort studies (Thrusfield 1995) may identify risk factors, such as contact with a particular species. Second, evidence of infection in putative host species, through antibody detection (serology) or the isolation of the infectious agent is a useful step, but must be interpreted with caution: not all natural hosts are reservoir hosts and may be ‘spill-over’ hosts. However, the same genetic or antigenic character of the pathogens from target and putative reservoir species should be identified. Note also that the level of incidence or seroprevalence in a one-off cross sectional study does not give any additional evidence. Pathogens may persist in reservoirs at high or low prevalence: the critical issue is persistence and this can only be determined through longitudinal studies (Haydon *et al.* 2002).

The major pathogens of concern for canids can infect a wide spectrum of carnivores and even other mammal orders. Different host species may be reservoirs in different ecological and epidemiological situations. Thus, it is often inappropriate to extrapolate from one situation to another. Due consideration must be given to the carnivore community of interest, their relative density and the likelihood of intra- and interspecies contact.

12.3 Assessing the type and severity of disease threat

Assessing the presence and severity of a disease threat, before potential threats become a reality, is both a key issue for managers of wild canids and another thorny problem (Wobeser 1994). In some situations, the potential for a disease outbreak was identified in general terms before epidemics struck (e.g., Gottelli and Sillero-Zubiri 1990), but in many others, an epidemic was unforeseen (Gascoyne *et al.* 1993). In only a few cases, had management actions been put in place before the epidemic struck. Unfortunately, in many cases the management actions, for one unforeseen reason or another, did little to ameliorate the situation (see Woodroffe *et al.* 2004).

Clearly, the severity of the disease threat depends on a number of factors: first, the incidence of each potential disease in the reservoir; second, the potential impact of the disease on target individuals and the population; and third, the probability of that disease being transmitted from the reservoir to the target species. Assessing and quantifying all these aspects is a considerable challenge. The potential methods of assessment and surveillance will depend on the disease in question, the type of reservoir (if known) and the ecology of the system.

12.3.1 Rabies

Rabies is probably the disease of the greatest concern to managers of wild canids. Rabies has an impact on public health and livestock economies and thus data on its presence and incidence is invariably of better quality than that for other pathogens. However, in many areas, particularly as distance to the laboratory increases and veterinary and transport infrastructure declines, samples from suspected rabies cases are not collected by veterinary services and sent for laboratory diagnosis. For example, in Ethiopia, although rabies is found in a large proportion of the country, laboratory diagnosed rabies cases are almost always confined to the capital city and nearby areas.

Hospital records are another source of information in rabies prevalent areas. People bitten by suspected rabid animals will often seek treatment at clinics and hospitals and thus data on the incidence of dog bites and human rabies cases can be valuable (Cleaveland *et al.* 2002). However, hospital records will invariably underestimate the severity of the problem, as many people may not seek treatment, particularly where traditional medical practices are strong (Cleaveland *et al.* 2002).

However, where rabies is prevalent, the knowledge of the presence of the disease and its clinical signs are relatively well known in local communities. For example, in Tanzania, 80% of samples submitted by local people from suspected rabies cases were positive on laboratory analysis and thus more accurate than diagnostic tests for many diseases such as tuberculosis (Cleaveland *et al.* 2003). Thus, reports of suspected rabies cases can yield valuable data on occurrence and incidence if questionnaires are done in a systematic way and detailed information on suspected rabies cases is obtained.

12.3.2 Other diseases

The presence of other diseases can be more difficult to assess, as clinical signs are less well recognised and laboratory diagnoses are less likely to have been obtained. This is particularly true for endemic diseases, those with low mortality rates, or those affecting fertility or recruitment rather than causing mortality. When a major epidemic occurs, however, the probability of it being identified as a separate disease with accurate descriptions of clinical signs by local informants is increased (e.g., CDV, Laurenson *et al.* 1998). Screening of blood samples from putative reservoir hosts for antibodies to potential pathogens (indicating previous infection by the pathogen) can be instructive for microparasites. This approach has some drawbacks and will be less successful if the disease occurs in a more epidemic pattern in the reservoir hosts or if mortality rates are high, leaving few survivors with serological evidence of infection. In addition, antibodies to some pathogens have a short half-life (e.g., rabies) and thus will decline with time, leaving no serological evidence. Examination of faecal samples or post-mortem samples can be useful to determine the occurrence of macroparasite infection (see Box 12.1).

12.3.3 Type of reservoir

When domestic carnivores, principally dogs, are the reservoir, the presence of pathogens circulating in the reservoir population disease will be easier to identify. Surveillance for all diseases is obviously more straightforward in a domestic host, as will be obtaining blood samples for serological screening. Obtaining information on the occurrence and incidence of disease in wildlife reservoirs is more problematic, not least because post-mortem samples are difficult to obtain as carcasses disappear and decompose quickly (Gulland 1995). However, reports from local communities, wildlife officers, researchers, farmers, and hunters may provide valuable information. Maximum advantage should be taken of any carcasses found (see Box 12.1 for guidance on necropsy techniques). Even if carcasses are relatively decomposed, appropriate samples should still be taken, as modern techniques such as PCR are extremely powerful (Table 12.2). Serum can also be obtained from frozen lung or muscle tissues after freezing. When major epidemics in wildlife occur, there is clearly an improved chance of carcass detection and collecting fresh samples.

Where wild species are the reservoir, obtaining blood samples for serological analysis requires trapping and handling animals and is clearly difficult. Thus, when handling occurs for other reasons, such as fitting radio-collars, it is imperative that these rare opportunities are not wasted: blood samples should always be taken and serum stored for future analyses. Similarly, samples may be obtained from species that are hunted for trophies, or harvested or culled as problem animals. Results of laboratory analyses, even if not published, should be willingly shared with management and other interested parties.

12.3.4 Pathogen and host ecology

The ecology of both the pathogen and host population are also important in determining the severity of threat. From a pathogen perspective, aside from the fundamental issue of pathogen pathogenicity, both transmission mode and

Table 12.2. Collection and storage of carnivore post-mortem samples for disease diagnosis. Note that CITES permits from both exporting and importing countries are required for shipping samples from most canids internationally. Tissue samples should be treated gently and those to be stored in formalin should be 5–10mm thick and placed in about 10 times their volume of 10% buffered formalin. Hollow organs should be opened and their contents (e.g., faeces) removed before fixation. Once the tissue is fixed, one can drain away most of the formalin, leaving just enough to keep them moist, and submit them for examination by post if local experts are unavailable. It is always wise to split samples into at least two (but preferably more) sub-samples or aliquots which are separately stored and transported. Catastrophic equipment failures or losses in transit are not uncommon.

Tissue	Storage	Temperature	Test
Brain Salivary Gland	Straw sample (glycerol saline)	-20°C (but can be stored at ambient temperature for several weeks)	Rabies (FAT, Virus isolation)
Brain Salivary Gland	Plain (cryotubes)	Liquid nitrogen (-20°C if liquid nitrogen not available, but CDV not well preserved)	Rabies (FAT, virus isolation) CDV (virus isolation from brain)
Brain	10% buffered formalin	Ambient temperature (do NOT freeze)	Histopathology – rabies, CDV and other infections
Lymph nodes (all)	Plain (cryotubes)	Liquid nitrogen -20°C	CDV isolation, particularly bronchial and pulmonary nodes
Lymph nodes (all)	10% buffered formalin	Ambient temperature (do NOT freeze)	Histopathology
Faecal samples	Plain	Freeze -20°C	CPV virus/antigen detection
Faecal samples	High-grade ethanol	Ambient temperature	Molecular genetic analyses (population genetic), PCR diagnostics
Faecal samples	5% formalin	Ambient temperature	Hydatid coproantigen assays
All tissues – including brain, salivary gland, lymph nodes, lung, liver, kidney, spleen, small intestine	10% formalin	Ambient temperature (do NOT freeze)	Histopathology – all diseases
All tissues – including brain, salivary gland, lymph nodes, lung, liver, kidney, spleen, small intestine	High-grade ethanol	Ambient temperature	PCR diagnosis – rabies, CDV, CPV, CAV, hydatid, other pathogens
Blood smear	Microscope slide – air-dried	Ambient temperature	Haemoparasites, anthrax
Blood, exudates, tissue fluids or homogenates	FTA filter-paper cards*	Ambient temperature (keep DRY)	PCR diagnosis
Blood	Tris Buffer – 'Easy Blood'**	+4°C	PCR diagnosis of haemoparasites

*FTA® Classic Card – Whatman Bioscience
Place drop of fluid onto an FTA-treated card, allow to dry and place card into sealed pouch with drying sachet. The FTA card lyses all cells and inactivates bacteria and viruses (rendering samples non-hazardous), but allows clean DNA to be retained and easily transferred to PCR reaction vessels for performing amplifications. Samples on cards can be stored for up to 10 years at room temperature.
** 'Easy Blood'

Box 12.1. Post-mortem examination of canids (adapted from Woodroffe *et al*. 1997).

Post-mortem examinations are best carried out by vets or other qualified personnel but as the collection of fresh tissue samples as soon after death as possible is of critical importance in obtaining a diagnosis, fieldworkers should carry these out immediately if these personnel are not available. Photographs or video footage should be taken throughout the examination. Observers doing necropsies should wear protective clothing, particularly gloves, and disinfectant measures taken on completion. It is often possible to have samples examined by local veterinary laboratories, but ensure duplicate samples are taken (see Table 12.2). (Linda Munson at UC Davis may be available to give advice on sample analysis – lmunson@green.ucdavis.edu).

Equipment that should be held for post-mortem examination and sample collection
Post mortem: Strong, sharp knives, a sharpening steel or stone, scissors, forceps, scalpel handles and blades, a hacksaw or rib cutters, and possibly a small hatchet.
Sample collection: Formalin (10%), glycerol saline, drinking straws (5mm diameter), various sized leakproof containers, sterile swabs.

Carrying out the post-mortem

1. Begin with a visual examination of the animal, and then palpate any abnormalities. Record the nutritional state (body condition) of the animal.
2. Cut into the right axilla (armpit) and coxofemoral (hip) joint, and turn back both right legs. Then make a shallow incision along the ventral midline, cutting through the skin from the chin to the pelvis. Do not cut across hair: instead, roll the skin back after making the first incision, and cut underneath, which preserves the edge of the knife. Peel the skin back from the underside of the dog.
3. Open the abdomen cavity by carefully cutting through the abdominal wall from the xiphoid cartilage along the last rib – avoid cutting into the intestines. Extend the incision so that you can view the abdominal organs in place. Note any abnormal contents in the peritoneal cavity, and take bacterial swabs if appropriate. Determine whether the organs are in their appropriate positions, but leave them in place at this point.
4. Cut through the diaphragm and remove the right half of the ribcage with the rib cutters or hacksaw. Examine the organs of the thorax, but leave them in place at this point, taking bacterial swabs if relevant.
5. Make cuts along the inside of the lower jaw, grasp and pull back the tongue. Cut the hyoid apparatus and draw back the tongue, oesophagus and trachea together to the level of the thoracic cavity. Remove the lungs and heart attached to the tongue, oesophagus and trachea, cutting attachments as you go. Sever the oesophagus and large blood vessels at the diaphragm. This group of organs is called the pluck – you must now examine it.
    i) Examine the tongue and oral cavity.
    ii) Dissect out the thyroid and parathyroids, and take tissue samples.
    (ii) Palpate the oesophagus before opening it, looking especially under the mucosa in the part of the oesophagus that passes through the thorax for nodules caused by *Spirocerca lupi*, a nematode worm, which may sometimes grow large enough to obstruct the oesophagus.
    iv) Examine the thymus, and take tissue samples.
    v) There are also lymph nodes in the partition between the lungs, near the thymus: find one by palpation and take a tissue sample.
    vi) Palpate the lungs, and note their colour and texture. Take a sample from the dorsal part of one of the apical lobes.
    vii) Open the trachea and examine the contents. Extend the incision into the lung and through the bronchi.
    viii) Open the pericardium (the fibrous sac that encloses the heart) and look for any abnormalities in the fluid. Take swabs if appropriate.
    ix) Now examine the heart. There are several ways of doing this. The most important points are to examine all of the surfaces for haemorrhages, and all cut surfaces for pale patches. Look for lesions on the valves, and determine whether the size and shape of the heart is normal. Take samples from the septum between the ventricles, and from the papillary muscle (of the left ventricle).
6. Next, examine the organs of the abdomen. It is extremely important that you leave examining the intestines until last, because their contents are topologically outside the body and will, therefore, contaminate other tissues with bacteria from the outside world.
    i) Remove and examine the spleen. Make multiple cuts through the parenchyma and take tissue samples.
    ii) Remove and examine the liver. Make multiple cuts through the parenchyma and take tissue samples. Open up the gall bladder last, as the bile that it contains will damage the tissues. If the gall bladder appears thickened, sample it.
    iii) Locate both kidneys and adrenal glands and remove them together. Cut the kidneys sagitally, peel off the capsule and examine all of the surfaces. Take tissue samples, ensuring that your samples include both the cortex and the medulla. Cut the adrenal glands in half, examine the cortex and the medulla, and take samples.
    iv) Examine the bladder in situ before you open it. Have a vial ready to catch any urine, but only keep the sample if it appears abnormal. Take a tissue sample from the bladder.
    v) Remove the stomach and the intestines, and cut all the attachments to separate the loops from one another. Take tissue samples from the pancreas and mesenteric lymph nodes. Then open the stomach and continue down the length of the gut to the rectum, taking tissue samples of the gut as you go. Bear in mind that the mucous membranes of the intestines are very easily damaged, so be careful, and never scrape the surfaces.
    vi) Examine the reproductive tracts and take samples as necessary. Older domestic dogs often have tumours in the testicles which can be seen with the naked eye if you make repeated cuts through them.

Box 12.1 ... continued. Post-mortem examination of canids (adapted from Woodroffe *et al*. 1997).

7. It is always a good idea to look at the articulating surfaces of some of the joints. Open up the coxofemoral (hip) joints and look for abnormalities. The knees and the joints of the ankles and toes are also easy to look at.
8. Take samples of bone marrow by cracking one of the femurs near one end, and extracting a bit of the gelatinous marrow along with spicules of bone.
9. Perhaps the most crucial organ to sample in any dead canid is the brain, because many of the most important diseases that affect canid populations attack the brain.
   i) Cut the skin and the neck muscles over the joint between the back of the skull and the first vertebra (the atlas).
   ii) Bend the head forward to give access to the occipital foramen (the hole in the back of the skull).
   iii) Push a drinking straw into the foramen and towards one of the eyes. In this way the brain stem, the base of the cerebellum, the hippocampus and parts of the cortex are all sampled.
   iv) Before drawing back the straw, pinch it between your fingers to ensure that the brain sample does not fall back out of the straw. Then carefully withdraw the straw.
   v) If you are storing your brain samples in 10% formalin, squeeze the brain sample out of the straw and into the formalin solution. If you are using glycerin solution, plunge the straw into the solution and cut the straw into pieces as necessary, but *do not remove the sample from the straw*.
10. Do not forget to collect samples for genetic analysis from the remains of the carcass.

patterns of infection are important. Closer and more direct contact between reservoir hosts and target species may be required for directly transmitted pathogens such as CDV or rabies, whereas indirectly transmitted pathogens such as canine adenovirus (CAV, urine-oral) or canine parvovirus (CPV, faecal-oral) can be transmitted when ranges overlap. When a pathogen (e.g., leishmania) is vector borne, the distribution and range of the vectors as well as host must be considered. The threat from diseases that tend to occur in epidemics is particularly difficult to assess. Even if reservoir surveys reveal no or low levels of disease, a large devastating epidemic could still occur.

The ecology of the carnivore system must also be considered. At one extreme, even if a disease that causes significant mortality occurs at high incidence in the reservoir, if there is no possibility of direct or indirect contact between reservoir and target species, then the risk of disease transmission and spill-over is effectively non-existent. Assessing the probability of transmission is surprisingly difficult, but a first step is to assess the geographical distribution of the different species and their degree of overlap (taking into account pathogen transmission mode). Inter-specific contact rates between members of the Carnivora have rarely been estimated (Rhodes *et al.* 1998). One exception is a study by Courtenay *et al.* (2001), in which they estimated contact rates between sympatric populations of domestic dogs and crab-eating foxes (*Cerdocyon thous*) in Brazil using radio-telemetry. The contact rate of individual foxes with the peri-domestic environment was calculated, as was the contact time in minutes. Potential exposure of each fox to the dogs in a village was calculated from this village contact rate and the mean density of dogs in the village. This approach found that foxes had a high level of contact with the peri-domestic habitats and that the probability of potential spill-over infections from dogs to foxes is high (Courtenay *et al.* 2001)

It is important to note, however, the uncertainty of extrapolating contact rates from healthy to diseased animals, particularly of directly transmitted pathogens. Changes in the behaviour of sick animals could in some cases either increase or decrease contact rates and transmission probability (e.g., rabies, Butler 1998). Further research is clearly required to explore this phenomenon.

12.3.5 Putting the seriousness of the threat into context

Wide-scale disease-related mortality in a population may clearly make a population vulnerable to extinction either directly or as part of the extinction vortex, through causing a population decline (Caughley and Gunn 1996). Disease may also be a limiting factor on population densities (for example, sarcoptic mange in red foxes in Scandinavia, and rabies in foxes in France/Germany), and thus depress population size (Lindström *et al.* 1994). A disease effect on fertility or recruitment rates could have a similar effect as one causing direct mortality (Caughley *et al.* 1992). Disease may thus cause a more insidious decline or prevent a population recovery after a perturbation, both of which are relatively hard to detect.

Although disease-related mortality is clearly catastrophic for the individual concerned, at the population level this mortality may be unimportant and have relatively little effect on the probability of population extinction. Thus, sporadic deaths may have little significance at the population level. That said, even sporadic deaths may affect population viability in very small populations, where pack sizes are small, where key members are affected or where the Allee effect might be important (Courchamp *et al.* 2000; Haydon *et al.* 2002).

By extrapolation, one-off epidemics, whilst clearly undesirable, may have little effect on long-term extinction probabilities, although they may have consequences for loss of genetic diversity. The high reproductive capacity and short generation time of many canid species means that populations may recover relatively quickly (Lindström *et al*. 1994). In Botswana, when around 3% of ~70 packs of African wild dogs (*Lycaon pictus*) died out from rabies, the overall population size quickly recovered (J.W. McNutt pers. comm.). Similarly (although not canids), lions in the Serengeti recovered in four years from a 30% population decline due to CDV (C. Packer pers. comm.). However, recovery times may be hampered when the formation of new packs is a difficult and rare event.

When considering and prioritising management action to reduce the impact of disease, we need to try to quantify the risk that disease poses through mortality or through its effect on fertility or recruitment. A number of population viability assessments have attempted to incorporate disease mortality into their analyses (Ginsberg and Woodroffe 1997a; Vucetich and Creel 1999; Roemer *et al.* 2000b; Haydon *et al*. 2002). In general, these models have concluded that pathogenicity and canid population size are critical factors in determining whether disease has an effect at the population level. This inherent population resilience of larger populations reinforces the desirability of management strategies to maintain canids at the highest population size possible. Highly pathogenic infections such as rabies threaten the persistence of small- and medium-sized populations, with less pathogenic infections affecting only smaller populations. Other risk factors may include fragmentation (and thus where there is little possibility of recolonisation by dispersal from other areas) and populations with a high edge-to-area ratio, which will increase the probability of transmission from the reservoir species. In addition, species with low reproductive rates, low recruitment rates, where breeding units must be of a critical size to be viable, or where new breeding units rarely form, may also be more vulnerable to the effects of disease (Woodroffe and Ginsberg 1998; Courchamp *et al.* 2000; Haydon *et al.* 2002; Hudson *et al.* 2002).

12.4 Management of disease threat for threatened populations

The decision on whether to intervene when disease threatens canid populations will depend on a wide range of factors such as the prevailing conservation philosophy, logistical and financial issues, local cultural perceptions, and, of course, the degree of threat posed by a pathogen. Ultimately, this decision rests with local managers. If the decision to intervene is taken, a range of management options are available that have been outlined in various forms in a range of publications (summarised in Table 12.3, and adapted from Laurenson *et al*. 1997b and Woodroffe *et al.* 2004; see also Wobeser 1994). There is no universal panacea for managing disease threats to canids, and wildlife managers should consider all options in their specific situation and weigh up cultural, logistical and financial considerations against the potential effectiveness of each approach Here we discuss some of the issues surrounding the most important approaches in Table 12.3.

12.4.1 Direct protection and reduced transmission in target species

Direct intervention to cure or protect the target individuals has taken place in a number of situations. This approach may be one of the few options available to managers when the reservoir species is unknown or where a relatively intractable wild reservoir population is involved. As well as providing direct protection or treatment to individuals, this approach may also reduce transmission within the host population.

Treatment of individual Arctic foxes (*Alopex lagopus*) and foxes against sarcoptic mange has been carried out with apparent success (Morner 1992; Goltsman *et al.* 1996). In addition to the myriad logistical problems involved in administering treatments, particularly when a course of treatment is required, there may be relatively few situations where direct treatment can be used as few therapies are available for viral diseases, or that have been tested in wildlife.

Direct protection of target hosts through vaccination has also been used as a conservation tool in a number of outbreak situations, including African wild dogs, island foxes (*Urocyon littoralis*) and during the recent 2003/4 outbreak of rabies in Ethiopian wolves (*Canis simensis*) (Hall and Harwood 1990; Woodroffe 1999; Randall *et al.* submitted). Where vaccines are safe, effective and require little intervention to administer, when used prophilactically rather than in an outbreak situation, they have the potential to improve the viability of canid populations severely threatened by infectious disease. Population viability modelling suggests that vaccinating 20–40% of an Ethiopian wolf population against rabies could markedly reduce extinction risks, although in very small populations (25 animals) higher coverage is required to completely remove extinction risk (Haydon *et al.* 2002). This theoretical level of coverage is quite low in comparison with that required to eliminate rabies in reservoir hosts (70%, Coleman and Dye 1995). In this situation, rabies may cause an epidemic in a wolf population but vaccination protects a core of wolves that provide the basis for breeding and population recovery.

Attempts to protect wild dogs from rabies and canine distemper, acute threats to the persistence of small African wild dog populations, by direct parenteral vaccination have met with mixed success. The issues and controversy surrounding these attempts are extensively reviewed in Woodroffe and Ginsberg (1998) and Woodroffe *et al.* (2004), but the efficacy of rabies vaccines, particularly

Table 12.3. Management options for disease control for wild canids (taken from Woodroffe *et al*. 2003, which is modified from Laurenson *et al*. 1997b).

Option	Options	Advantages	Disadvantages	Likely benefits/ chance of success
Do nothing		Cheap, easy, evades controversy	Population viability not guaranteed	Depends on degree of threat
Reduce disease in **reservoir** species		No intervention with target	Must know reservoir. No guarantee of protection in target	
	1. Vaccination	1. Effective vaccines often available, particularly for domestic reservoir	1. May be extensive and expensive, logistical challenge if wild reservoir	1. May be high if wide *cordon sanitaire* and properly managed
	2. Culling		2. Cost, welfare, logistics	2. Low
	3. Limit reproduction/ ownership	3. May get to root of limitation of domestic reservoir population	3. Long lasting effect and species specificity not yet available. Difficult to change cultural attitudes to dog ownership	3. Reasonable adjunct in theory, but difficult to change attitudes. Other methods not currently feasible
	4. Treatment	4. Therapy availability depends on pathogen	4. Effective methods not yet available over large areas for most situations	4. Will depend on therapy availability and logistic resources, but low overall
Reduce disease in **target** species		Direct protection of target individuals	Handling sometimes required	Last chance in emergency situation
	1. Vaccination		1. Proven effective and safe vaccines for wildlife not always available	1. Can be high in some situations
	2. Treatment		2. Often unavailable or unfeasible	2. Depends on pathogen, better for sarcoptic mange
Prevent **transmission** between target and reservoir		No direct intervention	Must know reservoir	Higher on islands
	1. Fencing/ physical barrier		1. Often unfeasible	1. May be good if fences carnivore-proof
	2. Restraining domestic animal reservoir		2. Cultural constraints/conflict with dog function	2. Moderate to low
	3. Buffer zone (e.g., limit humans activities in protected areas)		3. Feasibility, cultural acceptability	3. Variable depending on feasibility

after a single dose, is questionable in this species and now the subject of further research. As with Ethiopian wolves, the feasibility of using oral vaccines warrants further investigation. Live oral rabies vaccines have been extensively used to control rabies in red foxes (*Vulpes vulpes*) in Europe and have been tested for potential use on both African wild dogs and jackals in southern Africa, although no field trial has yet been carried out (Bingham *et al.* 1999, Knobel *et al*. unpubl.). Preliminary trials suggest that an effective baiting system can be designed (Knobel *et al*. 2002). However, live vaccines present some safety concerns in both target and non-target species and it is difficult to carry out safety trials on all species that might consume the baits. For example, one strain (SAD, Street-Alabama-Dufferin) was protective for jackals, but induced clinical rabies in baboons (*Papio* spp., Bingham *et al.* 1995), although other strains such as SAG2 are much more stable and have never caused disease in any species. The use of recombinant rabies vaccines, which incorporate only part of the rabies virus genome and cannot cause rabies in target or non-target species, present a safer alternative from a rabies perspective for both target and non-target species (Kieny *et al*. 1984; Blancou *et al*. 1986). However, concerns over using genetically modified organisms or inadvertent contact with immunosupressed humans and the vaccinia carrier may mean that some countries approach this method with caution.

Direct vaccination has also been used to protect island foxes from canine distemper in California's Channel Islands. Very high mortality associated with a distemper outbreak on Santa Catalina Island in 1999 demonstrated the need for a tool to protect recovering populations from distemper on this and the three other islands that had experienced major declines for other reasons (Timm *et al.* 2000). A new recombinant distemper vaccine, vectored by the canary pox virus (Timm *et al.* 2000) was tested, as this vaccine cannot replicate or shed CDV or pox virus in mammals. Trials on six captive foxes showed that the vaccine caused seronconversion with no observed side effects. Vaccination protocols were then trialed on the western part of Santa Catalina Island not reached by the epidemic, which by then had faded out (S. Timm pers. comm.). Although, in the absence of challenge experiments, it is impossible to be 100% certain that vaccination confers protection from canine distemper, the existence of a distemper vaccination protocol known to be safe and likely to be effective for use in free-ranging island foxes is a valuable addition to the toolkit for the conservation of this Critically Endangered species (Woodroffe *et al.* 2004).

More recently, an emergency trial parenteral vaccination campaign was carried out to control an outbreak of rabies in Ethiopian wolves in the Bale Mountains (Randall *et al.* submitted). As permission had not been granted to test the efficacy of oral vaccines, wolves were trapped and vaccinated by injection with an inactivated rabies vaccine. Although this represented a huge logistical effort, preliminary results suggest good seroconversion rates but the trial is still ongoing. Only extensive monitoring work will enable the success or failure of this approach to be assessed.

This example notwithstanding, demonstration of the effectiveness of direct vaccination of target animals this approach has been limited (but see Hofmeyr *et al.* 2000, where vaccinated African wild dogs survived a rabies outbreak that killed other members of the pack), In most cases where direct vaccination has been employed, it has been a 'crisis' intervention dealing with acute disease risks where it has not been possible to leave unvaccinated controls. Overall, although this approach has some clear advantages (Table 12.3), vaccine and treatment availability is currently a severe constraint as few vaccines or treatments have been tested for safety and efficacy in wildlife. In addition, in the absence of challenge experiments in captivity, only situations where target hosts are naturally challenged will ultimately enable the efficacy of vaccines to be assessed. Feasibility studies are also needed to assess the population coverage levels that can be achieved using oral vaccines (Knobel *et al.* 2002). Nevertheless, during most disease outbreak this approach was essentially the conservation manager's only potentially feasible intervention option. Irrespective of their success, these interventions have yielded invaluable information on the logistics involved and efficacy of this approach.

12.4.2 Management of infection in reservoir hosts

Threatened canid species may also be protected from infectious disease through a reduction in the number of susceptible animals in the reservoir population, which will lead to a reduction or elimination of the disease and thus also a reduction in the chance of disease being transmitted to target hosts A reduction in the number of susceptible animals can be achieved in several ways. First the overall number of animals in the reservoir population can be reduced through limiting the population by culling or fertility control or, where domestic dogs are involved, by reducing dog ownership levels. Second, animals can be removed from the susceptible population by vaccination them. Clearly, we need to know which species is the reservoir of infection for this approach to be used. For many diseases affecting wild canids, domestic dogs are the reservoir host but wild canids have also been implicated in a number of cases. For example red foxes (Europe), yellow mongooses (*Cynictis penicillata*) (South Africa), raccoons (*Procyon* spp.), and skunks (*Mephitis* spp.) (North America) are examples of wild reservoirs for rabies, whereas a suite of wild carnivores may be involved in sustaining endemic canine distemper infection in Europe and North America. Control of diseases of public health concern, such as rabies or visceral leishmaniasis, has traditionally been carried out with this approach. The successes and failures of past culling and vaccination efforts thus provide important lessons for the conservation of rare canids threatened by infectious disease (Aubert 1994; Brochier *et al.* 1996).

Limiting host density by culling or fertility control

Where domestic dog populations are involved as a disease reservoir, culling or fertility control, although superficially attractive solutions, will not address the underlying demand for domestic dogs as these populations are usually limited by human decisions (Perry 1993). However, it ought to be possible, at least theoretically if not practically, to limit domestic dog densities to levels at which pathogens such as rabies cannot persist (e.g., Cleaveland and Dye 1995). However, cultural attitudes towards dogs vary widely, but in most developing countries their usefulness is acknowledged, for example as guards and cleaners. Limiting the number of dogs owned per family (either by law or changing social attitudes) may thus be culturally challenging to implement. Indeed, we know of no such successful programme. Moreover, where human densities are high, even comparatively low dog:human ratios may generate populations large enough to represent a disease risk to local wildlife and thus the success of this approach can be limited.

Culling wild canids such as foxes to control rabies, although sometimes successful in the short term in a limited area, has otherwise met with failure due to the rapid recovery of fox populations and the continued (expensive) culling effort required (Macdonald 1993; Aubert 1994). In addition, changing moral attitudes are rendering this approach obsolete. Culling domestic dogs, although frequently used to remove problem or un-owned urban dogs in many countries, is also becoming less acceptable, at least in the north.

Fertility control could also be used to manage canid population densities and, in theory at least, show some promise (Barlow 1996). In practice, given that female dog sterilisation by surgery is expensive and culturally and logistically difficult, and that dog populations are rarely closed, this approach may be limited in its success. Fertility control would be even more difficult to achieve among wild canids, although initial investigations of immuno-contraceptive vaccines, which target the release of reproductive hormones, have shown encouraging results for red foxes in France and Australia, and are being developed for domestic dogs (Fayer-Hosken *et al.* 2000). Oral chemical contraceptives are available for use in wildlife (reviewed in Tuyttens and Macdonald 1998) but, like poisons, their use in areas occupied by threatened populations would be inappropriate. Despite these concerns, immuno-contraception – especially if it could be combined with vaccination – may be a feasible option if technology can be developed for the future management of disease reservoirs.

Vaccination of reservoir hosts

Experience from the control of rabies risks to humans and livestock suggest that vaccination of both domestic dogs and wild canids may be powerful tools for the protection of threatened species from acute disease threats. Direct vaccination of wild reservoir hosts (foxes, raccoons, coyotes, skunks) has successfully reduced the incidence of rabies on a large scale in Europe and in the United States (Brochier *et al.* 1996). Moreover, large-scale vaccination of domestic reservoirs is commonly conducted for a variety of reasons in the animal health sector. In the last decade this approach has been adopted in several situations in an effort to protect wild canids. Programmes have attempted to create a *cordon sanitaire* in the reservoir around threatened populations. In theory the area to be covered will vary considerably with the density of the canid of interest: the same size population of African wild dogs (home range 400–1,200km^2 per pack, Woodroffe *et al.* 1997) than Ethiopian wolves (home range 6–11km^2 per pack, Sillero-Zubiri and Gottelli 1995a). As threatened canids are generally are surrounded by a sea of reservoir hosts, whether wild or domestic, regional eradication is near-impossible without a wide-scale coordinated rabies control programme. As such, without national or international control programmes, it is likely that vaccination cover would have to be maintained in perpetuity to control the disease threat. However, a coordinated rabies control programme with both public health and livestock authorities would reduce the cost borne by the conservation community and both financial (primarily from a reduction in livestock losses) and public health benefits would accrue to local populations. Vaccination of domestic dogs by wildlife managers also provides benefits that may improve protected area-community relations as both parties may cooperate and spend time in a mutually beneficial activity (Sillero-Zubiri and Laurenson 2001). As such it can be a powerful tool for wildlife managers looking for opportunities for cooperation and communication.

In rural Tanzania, vaccination of domestic dogs has shown that that a simple central-point vaccination strategy, resulting in vaccination of 60–65% of dogs against rabies and distemper adjacent to Serengeti National Park, has significantly reduced the incidence of rabies in dogs and risk of exposure to people, with opportunities for transmission to wildlife also decreasing (Cleaveland *et al.* 2003). Dog vaccination campaigns have also been carried out around other national parks in Tanzania such as Ruaha, Arusha and Tarangire. In the Bale Mountains National Park in Ethiopia, intensive dog vaccination against rabies and CDV started in 1998 within the park and where resources allowed, in neighbouring communities. No case of these diseases was reported between 1998 and August 2003 Rabies cases in dogs and other species still occurred at the edge of vaccination zones, although the overall incidence in dogs and humans very much reduced (Ethiopian Wolf Conservation Programme unpubl.). However in September 2003, rabies broke out in Ethiopian wolves in one area of the park, thought to have been brought in by an unvaccinated immigrant domestic dog (Randall *et al.* submitted). It is thus apparent that a wide *cordon sanitaire* is required, particularly when transhumance of humans and their domestic animals occurs. This outbreak also illustrates a disadvantage of this approach: there is no direct protection of the target species and success cannot be guaranteed if intervention is carried out on too small a scale and where there are inadequate resources to cover such areas. Furthermore where payment for vaccination is expected or where dogs are used for illegal hunting are not presented for vaccination, the success of the approach may be curtailed.

Concern has been expressed that vaccination of disease reservoirs – especially domestic dogs – could remove an agent of population limitation and lead to increased host density (Moutou 1997). This could be potentially damaging, especially if vaccine cover were to be halted (Woodroffe 2001). However, dog populations are thought to be limited by humans (Perry 1993) and preliminary studies indicate that, while dog vaccination in northern Tanzania has led to a significant decline in mortality rates, population growth rates have not increased (S. Cleaveland unpubl.). It appears that the reduced demand for pups has lowered recruitment rates, resulting in a much more stable population which is protected against rabies. However, data are still required to assess longer-term demographic impacts and the demographic impact of mass vaccination in different settings.

Overall, although this approach is not without its problems and requires considerable financial and logistical resources (Table 12.3), it is currently the most feasible method available to managers where a domestic reservoir is involved.

12.4.3 Reducing disease transmission between host species

In theory, limiting disease transmission between reservoir and threatened hosts should be effective in reducing the threat of disease. Reduced transmission could be achieved by eliminating range overlap between the species; that is by clear physical separation. Indeed bighorn sheep (*Ovis canadensis*) have been protected from pneumonia and scabies transmitted from domestic sheep (*O. aries*) by barring domestic sheep from buffer zones surrounding bighorn populations (Jessup *et al.* 1991).

In gazetted national parks there are few reasons to tolerate domestic dogs and unaccompanied dogs are usually captured or extirpated. In areas where separation is not possible, the control of free-ranging domestic dogs presents a substantial challenge and may be near-impossible in many situations. For example, game fences around wildlife areas in South Africa should reduce contact between wild canids inside and wild or domestic canids outside. Indeed, fences around Kruger National Park may partially explain the absence of evidence of exposure to CDV and canine parvovirus among wild dogs (Van Heerden *et al.* 1995). However, small carnivores are notoriously adept at crossing such fences and a game fence did not prevent rabies killing wild dogs in Madikwe Game Reserve, probably transmitted across the fence by jackals (Hofmeyer *et al*. 2000).

Where ranges of target and reservoir hosts do overlap, there may still be measures that can be taken to reduce disease transmission. Limitation of contact between Ethiopian wolves and sympatric dogs inside wolf habitat has been attempted through community education programmes that encourage people to tie up their dogs at home. Collars and chains were supplied, but older dogs were adept escape artists and collars and chains were very useful for other purposes, such as tying up calves or horses (Sillero-Zubiri and Laurenson 2001) is probably almost impossible to accustom older dogs to accept being tied up, thus training would have to start with the next generation of pups. In addition, cultural resistance from dog owners is likely to hinder such efforts, not least because restricting dogs may reduce their usefulness as guards and cleaners, and their ability to forage when people cannot afford to provision them. In addition, cultural taboos against close contact with dogs are present in some areas, again increasing cultural resistance to handling and tying. Overall, the success of this approach may be limited and it must be recognised that cultural change occurs slowly, both in terms of the generational times of humans and dogs.

12.5 Which approach is best?

Infectious disease is a threat to wild canids that conservationists are ill-equipped to manage. Lack of information hinders management of this newly recognised threat – there are no established models to follow, and some early and unsurprising failures have attracted damaging controversy (Woodroffe 2001). This makes it difficult to assess which approach is most likely to meet with success. However, it is important to recognise that the decision not to intervene is in itself a conscious decision and not a lack of consideration. In general, intervention will be most warranted in small and isolated populations with a high edge-to-area ratio and for highly pathogenic infections (Woodroffe *et al.* 2004). Intervention may be less warranted in larger populations and for less virulent infections. However, the decision to intervene may be taken due to local political and cultural considerations or where additional public health or economic benefits accrue to local communities. Where intervention is warranted, vaccination of threatened hosts or of domestic reservoir hosts presents the most feasible options in our disease management toolkit at present, particularly when safe, effective and practicable vaccination protocols are available. Vaccination of wildlife reservoirs is more problematic. In all situations, the specific conditions in the area will determine what action or actions are taken as there is no universal panacea to mitigate the threat of disease for canids.

12.6 Conclusions

Disease threat assessment and management for wild canids often presents a challenging issue for managers with the apparently complex ecology and epidemiology sometimes involved. Field managers must take a multi-disciplinary approach and bring in the expertise of veterinarians, ecologists, theoreticians and others. The Canid Specialist Group's Disease & Epidemiology Working Group is also always available and willing to give advice. Improved surveillance is fundamental to improving management and further testing of alternative management options is required. Informed decisions cannot be made without such background information. Although management options may often ultimately depend on non-biological factors such as feasibility, the cultural or political environment or the availability of finance, we should strive to take objective and scientific management decisions with the best information available.

Chapter 13

Management of Wild Canids in Human-Dominated Landscapes

C. Sillero-Zubiri and D. Switzer

13.1 Introduction

Whereas some canid species are declining globally under the pressure of habitat degradation and fragmentation, disease and persecution, other have managed to survive and even thrive in human-dominated landscapes. This overlap with people results in competition for resources, which is at the heart of the conflict between many wild canids and man.

Canids prey upon a range of livestock, game stock, and threatened wildlife, and a few of the larger species may also attack, and on rare occasions, fatally injure humans. As a result of this and innate human prejudice, canids have frequently been vilified by people, classed as vermin and actively sought out and killed. Control may be occasional and opportunistic, such as when a farmer shoots a fox attacking his chickens, or targeted and systematic, such as with control programmes to reduce or eradicate problematic species. Harassment notwithstanding, canids have survived in many areas where other carnivores have gone extinct. Their resilience is principally due to their relatively high reproductive rate (i.e., large litter sizes and early sexual maturity), which compensates for increased human-inflicted mortality rates, and their adaptability to new environments. Canids can often quickly recover from population decreases and range contraction, and rates of re-colonisation are often high due to high levels of dispersal (Gittleman 1989).

This chapter examines the reasons why canids frequently find themselves in conflict with humans, and the ways in which conservation biologists and managers have tried to solve these problems. Data for this chapter are derived from original research, literature reviews, and from a preliminary analysis of the information provided in the species accounts of Part I of this action plan. This paper borrows several ideas first developed by Sillero-Zubiri and Laurenson (2001) for carnivores in general. For additional information on managing conflict in canids, see Sillero-Zubiri *et al*. (2004b).

13.2 Why do canids come into conflict with humans?

Given the long tradition of canid persecution, it is pertinent to ask what the reasons are behind human-canid conflict. Although in recent times public perception of canids has improved, historically, the majority of people have held negative views towards wild canids, with these views being handed down through the generations, and then carried with them as they migrate. These views have often been generated by an ingrained fear of the larger species, and by the recurrent issue of wild canids predating on livestock and valuable game species. Europeans, for instance, took their intolerance of carnivores with them when they colonised other regions of the world, notably Africa and America. In North America, grey wolves (*Canis lupus*) and coyotes (*Canis latrans*) were actively hunted by the colonists upon their arrival, and by the 1930s wolves had been extirpated from most of the USA, with only Minnesota and Alaska harbouring viable populations (Mech 1970). Elsewhere, Europeans were responsible in 1876 for the last known canid extinction, namely that of the Falklands wolf or Malvinas fox (*Dusicyon australis*) (Macdonald and Sillero-Zubiri 2004b). Similarly, African wild dogs (*Lycaon pictus*) were considered vermin by European farmers and deliberately killed on farmland and protected areas (Woodroffe *et al*. 1997).

Intriguingly, Africans' perceptions may differ from those of Europeans; for example, wild dog kills are considered a useful source of meat by the Shona in Zimbabwe (G. Rasmussen pers. comm.), and the Maasai people of East Africa regard them as an asset as they prey on wildebeest (*Connochaetes taurinus*), which they regard as competition for grazing with their cattle (Fuller and Kat 1990).

13.2.1 Attacks on humans

The larger canids are often considered a direct threat to human life. Grey wolves and wild dogs, and to a lesser extent dholes (*Cuon alpinus*) are portrayed as villains in the myths and folklore of many cultures (Landau 1993). Attacks on humans are quite rare though, and deaths are even less frequent (Linnell *et al*. 2000), yet many people still hold a deep-rooted fear of wild canids and this contributes to the overall negative view held in many societies. For instance, attacks by wolves are still feared by people in the USA, even though, in contrast to other predators like bears and mountain lions (*Felis concolor*), there have been no verified attacks in the last century

(Mech 1970; Kellert *et al.* 1996). African wild dogs are often described as 'ruthless killers' (e.g., Bere 1955), although attacks on humans rarely, if ever, occur (Creel and Creel 2002). In situations where canids do attack people it is often due to an individual rabid animal in 'furious' phase, attacking people repeatedly over the short time period they survive (Linnell *et al.* 2000). With the eradication or reduction of rabies in many parts of the wolf's range, the incidence of wolf attacks has dropped dramatically, but cases are still reported from Asia and the Middle East (see Chapter 12).

The majority of present-day predatory (non-rabies) wolf attacks seem to occur in highly modified environments, with little or no natural prey, with wolves habituated to people presence and relying heavily on human refuse and livestock as an alternative source of food. As many as 273 children have been reported killed by wolves in the last 20 years in northern India, where wolves come into close contact with shepherd children due to their dependence on villages for food (Jhala and Sharma 1997). Wolf attacks may result from habituation, with wolves loosing their fear of humans and increasing the likelihood of encounters. Furthermore, attacks may also result from provocation when wolves are cornered, trapped or a den with pups is breached.

Although attacks are very rare, when they occur they attract a disproportionately large amount of sensationalist media coverage, and have the potential to be very damaging to canid conservation efforts. For example, the recent killing of a young boy by a dingo (*Canis lupus dingo*) on Australia's Fraser Island has led to calls for a dingo cull, even though this population is considered one of the most genetically pure dingo populations remaining (Queensland Parks and Wildlife Service 2001). Thankfully, it appears that the efforts of conservation groups are proving increasingly successful at overturning this inherent human fear of canids, and conservation support for wild canids is gaining in popularity.

13.2.2 Competition for resources

Ever since our ancestors began herding livestock, many carnivore species have been persecuted for their role as predators of domestic animals. Throughout Europe there were, and in some instances still are, deliberate policies to reduce the numbers of predatory species to safeguard livestock and poultry, and also to promote human safety and to benefit game species. Certain canid species have experienced a long history of organised persecution; for example, in 6th century BC Greece, the city of Athens issued state bounties for the killing of wolves in an attempt to protect livestock from predation (Reynolds and Tapper 1996). Grey wolves were also deliberately exterminated from the islands of Japan, except Sahkalin, even though other large mammalian carnivores were allowed to remain extant (Dobson 1994). In some areas predator reduction was so effective that canids survived only in very low numbers or were completely extirpated. For example, in Britain grey wolves, brown bears (*Ursus arctos*) and lynx (*Felis lynx*) were all extinct by the middle of the 19th century (Harris 1989).

Unlike the exaggerated problem of attacks on humans, canid predation on livestock and game is a harsh reality difficult to deal with. In many countries large-scale control policies have traditionally been deployed to reduce livestock predation, and are often written into state law, and rewarded by bounty schemes (Childes 1988). Yet, the resources and expense invested in control campaigns have often been disproportionate with the damage perpetrated. For example, in South Africa £400,000 (currency of the period) was spent between 1915 and 1925 to extirpate predators (Pringle 1977).

More recently, conservationists have led a re-examination of the costs to farmers, hunters and society as a whole, of preserving viable carnivore populations (e.g., Clark *et al.* 2001; Sillero-Zubiri and Laurenson 2001). Although the general public is no longer willing to see wild canid populations reduced simply because they come into conflict with certain sectors, this change is not necessarily taking place among people living near wild carnivores. As a result, canids still face substantial persecution, particularly in those areas where they spill-over from the edges of protected areas (Woodroffe and Ginsberg 1998). Meanwhile, conflict has not been a problem for many decades in agricultural landscapes where carnivores have been extirpated, but this situation is changing as many carnivore populations, especially wolves and coyotes, have been increasing and reclaiming some of their historical ranges (Mladenoff *et al.* 1995).

Predation on livestock

Every domestic species, from chickens to cattle, is affected by canid predation. Indeed, livestock predation was the most frequently cited reason for problems between humans and canids in part 1 of this volume. Due to selective breeding and protection, domestic animals exhibit little effective anti-predator behaviour, making them particularly vulnerable to predators (Kruuk 2002), with domestication effectively breeding out the "wildness" of these animals. Changes in livestock husbandry and a decrease in the manpower employed in livestock production, most rapid and advanced in the developed world, have resulted in animals rarely herded (e.g., Rasmussen 1999) or guarded by dogs and thus more vulnerable to predation. In addition, livestock compete with wild herbivores for resources and, subsequently, they can either reduce the abundance or alter the distribution or behaviour of wild prey, thus changing the pattern of predation to include more livestock (Yalden 1996). Although farmers consistently express the most negative attitudes toward large canids, such as grey wolves and African wild dogs, they often constitute a minor problem compared with smaller canids such as jackals, coyotes, and feral dogs (e.g., Ciucci and Boitani 1998).

Livestock losses can be significant. Estimates of sheep losses to wild canids in the USA, for example, ranged from US$19–150 million between 1977 and 1999, and cattle losses represented US$52 million in 2000 (Knowlton *et al*. 1999). Although these losses represent only a fraction of the total income generated by the USA livestock industry, often they are not spread out evenly over the farmer community but rather are borne by a few individual farmers who endure the majority of the damage. In developing countries high livestock losses can have a serious impact on farmers' livelihoods. In India's Spiti Region losses to predators averaged US$128 per family per year in three villages, which equates to half the average annual per capita income (Mishra 1997).

Predation on game species

Throughout history, canids have been seen as competitors for prey and this remains the second most significant cause of human-canid conflict today. In Europe, gamekeepers target red foxes and other predators in an attempt to increase the population of partridges, pheasants, and grouse that are available for hunters to shoot (e.g., Macdonald *et al*. 2000). In North America, carnivore populations have traditionally been controlled in order to increase game species, in particular wild ungulates. This strategy was prevalent even amongst conservationists, and predator removal was the National Parks' policy until the latter half of the 20th century (Clark *et al*. 1999). Although carnivores are increasingly valued as an integral part of the ecosystem, and in spite of the fact that canids mostly target the sick and infirm animals that are not sought after by hunters, there is still great pressure from the hunting lobby to reduce their numbers. In Alaska, for example, grey wolves are blamed by hunters for declining moose and caribou populations and the resulting reduction in hunting quotas (Gasaway *et al*. 1992).

Predation on threatened wildlife

Wild canids can also have a detrimental effect on other wildlife, particularly where they have been introduced to isolated islands, where ground-nesting seabirds have often not developed any defence mechanisms to avoid predation. Arctic foxes (*Alopex lagopus*), for instance, have been responsible for large reductions on several Arctic seabird colonies, due to either being introduced by man (Bailey 1993) or where they have naturally invaded islands (Birkhead and Nettleship 1995). See Courchamp *et al*. (2003) for a review of mammal invaders on islands.

In a few exceptional circumstances, there may be a novel conservation dilemma when a threatened canid species has had a significant impact on another threatened species. In the Alas Purwo National Park, Java, Indonesia, dholes were deemed responsible for the decline in the Endangered banteng (*Bos javanicus*) (Indrawan *et al.* 1996), and consequently a reduction in their numbers was recommended. Asian wolves (*Canis lupes pallipes*) in Velavadar National Park, India, may play a part in limiting the population size of the Vulnerable blackbuck antelope (*Antilope cervicapra*) (Jhala 1994). While these conflicting situations might only pose a localised threat, they do create a conservation quandary when ecosystem conservation, practical management and animal welfare must all be balanced with existing land-use.

In a reversal of the above scenario, threatened canid populations can also be under threat from other species, such as African wild dogs facing competitive exclusion from spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*) in some protected areas (Creel and Creel 1996). Canid populations can also be threatened through intra-guild competition, such as with coyotes preying heavily on sympatric swift foxes (*Vulpes velox*) (e.g., Carbyn *et al.* 1994).

13.3 Solving problems: approaches to canid-human conflict

The traditional way to deal with conflict between humans and wild canids was to attempt to remove the threat simply through extermination. This approach of blanket predator control has traditionally been the backbone of canid management, with farmers and wildlife managers trapping or poisoning canids wholesale. However, the outcome of indiscriminate control is not always straightforward, both in technical terms and due to widespread resistance amongst the general public.

Widespread killing seldom delivers effective long-term predation reduction and the preferred approach is now one that focuses on changing the behaviour of the individuals directly involved in damage, and also addresses the behaviour of the people that are facing the problem. Non-lethal methods are increasingly favoured to prevent, or at least reduce, the incidence of predation, and the management goal is slowly shifting to minimise impact on innocent individuals, while minimising human-canid conflict (Treves and Karanth 2003). Indeed, in some instances the predation problem can be exacerbated where culling allows the immigration of problem animals into vacant territories (Sacks *et al*. 1999). Consequently, removing culprit individuals from a canid population may be more efficient than attempting population control (Conner *et al*. 1998; Blejwas *et al*. 2002).

In the next section, various lethal and non-lethal methods are examined, followed by a review of approaches that attempt to reduce or eliminate human-canid conflict by increasing human tolerance towards wild canids.

13.3.1 Predation control and reduction

Trapping

Trapping is perhaps the oldest method used to reduce predator numbers and a wide variety of cage, box, leg-hold traps and snares have been used, either killing the malefactor directly or holding it until it can be destroyed by a returning hunter. Traps are often unselective and may kill non-target species (see Conover 2002). Traps have been made illegal in many parts of the world due to concerns over the high level of stress, pain and suffering on the animals that are caught. Notwithstanding this, trapping is still a major method for canid reduction, most notably in the control of coyotes in the USA and Patagonian foxes. Most countries where commercial trapping for furbearers still occurs, e.g., Canada, the European Union and the Russian Federation, have regulated open and closed seasons and restrictions on methods of capture, under an agreement on international trapping standards signed in 1997. Recently, an ISO standard was developed for mammal trap testing (ISO 1999), and there are efforts to research and disseminate best trapping practices (e.g., IAFWA 2003).

Shooting

Perhaps the most widely used method to kill canids, shooting is labour intensive but species-specific. For certain species, e.g., red fox, shooting with a rifle is usually regarded as offering the best combination of efficiency and humaneness, and is often carried out at night with a spotlight and vehicle (Reynolds and Tapper 1996). Shooting on a large scale has been used in North America to control canid populations, including aerial hunting from helicopters; this technique is commonly used by agriculture agencies in the western USA to reduce coyote predation on sheep (Wagner and Conover 1999). Used in combination with expert tracking, or stalking at a kill site, shooting becomes a good method for targeting problem animals, although it requires experienced personnel.

Denning

Farmers often resort to trapping canids in their dens, digging them out and euthanising them, or fumigating the den and asphyxiating the occupants. Although still legal as a means to control pest species in the USA and elsewhere, both methods are considered inhumane and their use is strongly discouraged.

Poison baiting

Baits containing poison are often used in schemes to eradicate canids from a large area, and were one of the chief methods by which wolves were exterminated from large parts of Europe and North America (e.g., wolf poison campaigns to increase wild ungulate populations in Alberta, Canada in the 1950s and 1960s; Gunson 1992). Among population culling techniques, poisoning exemplifies a necessary trade-off between utility (cost-efficiency), conservation (target-specificity) and humaneness, with no one method satisfying all criteria (see Sillero-Zubiri *et al.* 2004b). In addition to widespread opposition on welfare grounds, there are serious concerns about the effects of toxins on other wildlife and livestock, since poison baits are not discriminatory. This is of particular concern to conservationists where the intended target species is sympatric with populations of a threatened species. In order to circumvent the specificity shortfall, coyotes in the USA have been targeted by a spring-powered device called M-44 that delivers a lethal dose, and that is selective by using bait designed only to attract canids (Beasom 1974).

Livestock protection collars

This collar consists of a sachet of poison attached to the neck of the domestic animal needing protection. It operates on the premise that many canids kill by a neck bite, and they would thus puncture the sachet, release and swallow the deadly poison. These collars are particularly effective as they target only the individual canids that are responsible for killing livestock, sparing those that do not engage on livestock predation, and take individuals that have evaded other capture methods (Burns *et al.* 1996). One study in California showed a halving of lamb losses to coyotes from 15.8 % to 7% of the flock (Timm 1999). The main advantages of this method are its high specificity, its potential application on other livestock including cattle and goats, and protection against a number of predator species. Unfortunately, the need to equip most of the herd or flock with collars renders it impractical and expensive. Additionally, there has been objection over the use of the compound 1080 (sodium fluoroacetate) in the collars and the effect it may have on non-target species, as collars may accidentally fall off and subsequently come in contact with other wildlife.

Sport hunting

Hunting canids for sport remains a traditional pastime in Europe, Asia, North America, Patagonia and Australia. It may include hunting with firearms, bows or crossbows, or large organised hunts using horses and packs of dogs. From a management perspective, sport hunting can be used to offset livestock losses or dispose of known 'problem' animals, while it may also be useful in conserving populations of canids since it can increase their value. For example, some foxhunts in Britain have actually invested in management policies that conserve a certain population level of red foxes, such as habitat creation, artificial den sites, and artificial feeding, in order that there is sufficient quarry to hunt (Reynolds and Tapper 1996). Notwithstanding this, it is unlikely that sport hunting would deliver a viable alternative for mitigating human-canid conflict, as most canid species are not sought after by sports hunters.

13.3.2 Non-lethal alternatives

The search for non-lethal alternatives to manage canid conflict has intensified over the last few decades due to increasing conservation and welfare concerns. Non-lethal approaches should not be thought of as a completely novel area, as many such methods (for example, suitable husbandry, guarding dogs and barriers) were traditionally used to reduce canid predation on livestock and game. Unfortunately, the traditional methods declined in use with the intensification of agriculture, but there is now a move back towards some of these traditional techniques and also a search for new non-lethal techniques. The most important aspect to realise with the development of these alternatives is that there is no one method that would be applicable in all situations, and often several may be needed in combination to significantly reduce conflict.

Use of fencing as a barrier for predation

Fencing can be employed either to keep predators out of a particular pasture, field or enclosure containing valuable stock, or to keep them confined within a particular area, such as a wildlife reserve. In Africa there is widespread use of traditional *bomas* or *kraals*, small enclosures built from dense thickets of Acacia bush (*Acacia* spp.), to protect livestock from predators when they are most vulnerable (e.g., at night or during calving). Kruuk (2002) showed that a simple thorn-bush boma could make a large difference to subsistence shepherds in northern Kenya, where 90% of all losses to predators took place outside enclosures. In Europe and Asia, livestock has traditionally been fenced in by hedges, stone-walls, wooden fences and more recently, barbed wire. Although these barriers are effective in preventing animals from straying, they offer little protection from predation, as they are permeable to discerning carnivores.

Small predator-proof fences have been used to protect ground-nesting birds (Bailey 1993), and have successfully excluded Arctic foxes from the nests of Alaskan pectoral sandpipers (*Calidris melanotos*) (Estelle *et al*. 1996). Installation costs and maintenance of predator-proof fences tend to be prohibitive at a large scale, and fencing would be impractical to prevent canid predation on sheep production systems in the western USA and Argentine Patagonia (Knowlton *et al*. 1999). In Australia, however, a 5,614km fence excludes dingoes from sheep farming lands in South Australia, Queensland, and New South Wales (Reynolds and Tapper 1996), and it is deemed that sheep farming would not be viable without this fence.

Electric fences provide a promising non-lethal predation avoidance/protection system that also protects the carnivores involved, and can be cost-effective for some species in some situations (Balharry and Macdonald 1999). In the Rumanian Carpathos, tests of mobile night corrals were successful at significantly reducing losses to wolves and bears (Mertens *et al* 2002). As a cheaper alternative to wire fences, Musiani and Visalberghi (2001) propose “fladry”, a line of red flags hanging from ropes traditionally used to hunt wolves in eastern Europe, which in tests showed captive wolves avoiding the flags even when the daily food ration was placed on the other side.

Fencing reserves and their wildlife has been used as a way of reducing conflict with the surrounding communities. Although this is an outdated conservation approach and antagonised with modern ‘open’ conservation systems, in many places it has proved very effective. Several public and private areas in South Africa are prime examples, such as Kruger or Pilanesberg National Parks. Unfortunately, permanent fence construction and upkeep are costly, thus precluding their use in poorer countries. More importantly fencing effectively cuts wildlife movement and may result in catastrophes during droughts or bushfires, and the small size of many fenced reserves means that populations of canids with a small genetic pool will require active management.

Improving livestock husbandry

Predation risk tends to increase with herd size, distance from people and buildings, proximity to thick cover, and carcasses left in the open (e.g., Mech *et al*. 2000; Kruuk 2002); many of these attributes are brought about by the extensification of livestock farming.

Diligent husbandry is essential to prevent unnecessary losses, such as improved vigilance, preventing livestock from straying and returning herds to enclosures at night (e.g., Kruuk 2002). It has also been argued that in certain economies, utilising additional manpower is justified because it has economic benefits beyond those accrued simply through reduced predation. Most of these are resultant from improved stock tractability and herder vigilance, and include reduced stock theft, increased weaning weights because calves spend more time with their dams, and sick animals or cows with calving difficulties are noticed earlier. In addition, as cattle become more manageable with the continual handling there is a reduction in losses to physical injuries from breakouts and they benefit from fewer stress-related problems (Rasmussen 1999).

Specific husbandry practices, however, must be developed for the particular situation of each producer’s group, and evaluated accordingly, to prevent the use of practices that may only delay predation or have undesirable side effects (Knowlton *et al*. 1999). At a larger land-use scale, diversification has been proposed to reduce conflict (Johnson *et al*. 2001), such as shifting from sheep to cattle husbandry (e.g., Patagonia).

Livestock guarding animals

Livestock guarding dogs (LGDs) have been used by shepherds to guard their flocks from predator attacks in Europe and Asia as early as the 6th century (Rigg 2001). With the foregoing of traditional livestock techniques, the use of LGDs had been in decline in much of Europe, and flocks were left unprotected in many areas. However, the recovery of predator populations in many areas has lead to a re-awakening of interest in using LGDs to protect livestock. For instance, the reintroduction of LGDs is currently underway in several southern and Eastern European countries to prevent wolf predation. LGDs have also been extensively trialed in the USA and are now in use in a number of western states to help reduce coyote predation on sheep.

A good LGD is usually large, independent, intelligent, attentive and gentle towards livestock, but aggressive towards predators (Knowlton *et al*. 1999). The dogs are placed with a flock or herd of animals from an early age and bond with them, effectively becoming part of the herd. They remain with the herd at all times, even when humans are absent, alerting the flock and shepherds to the presence of predators and will themselves attempt to drive predators away from the flocks. Overall, the economics of using LGDs is dependent on a number of factors including the annual rate of predation, the ability and longevity of the dog, and the costs of purchase and maintenance (Green *et al*. 1984). To be effective LGDs must be able to see predators approaching easily, and, therefore, it is best to use them in flocks of 100–200 sheep in large open pastures, or instead in small fenced areas (Rigg 2001).

Although the most frequently used, dogs are not the only animals that can be used for livestock guarding. Llamas have proved to be effective livestock guards in certain situations and since the early 1980s have been increasingly used in the USA to defend against predation on sheep by wolves and coyotes (Meadows and Knowlton 2000). Llamas have an inherent dislike of canids, and when pastured away from other llamas will bond with sheep becoming part of the flock. They have several advantages over LGDs, namely they live longer, require less training, have a faster acquisition of guardian status, have fewer special management considerations such as food and maintenance, and are more compatible with other depredation techniques (Meadows and Knowlton 2000). However, their ability to guard the sheep depends on the ability to see the whole pasture and the sheep within it, and, therefore, it may be better for them to be used in relatively small, flat, open pastures (Timm 1999). They can also cause trouble if dogs are used to herd the sheep, as they will often behave aggressively towards these dogs (Timm 1999).

Donkeys were often used to defend livestock from predators in Namibia when European-owned farms developed there a century ago, and are now making a comeback (Rigg 2001). In Switzerland, donkeys have been used to guard sheep since 1995. Donkeys are capable of providing a high level of protection at a relatively low cost and level of maintenance (Rigg 2001), and their use could be very beneficial in developing countries where the cost of maintaining LGDs may be too high to be economically viable for most farmers.

Translocation of problem animals

Translocation has been used in North America to manage individual grey wolves involved in livestock depredation. It has also had limited application with African wild dogs, involving the relocation of whole packs from problem farmland areas. In Zimbabwe such translocations have showed high survival of the new founder stock (90% survival), followed by successful reproduction in the new area. This experience has showed promise for similar translocations in the future, as it delivers a face saving excuse to farmers that otherwise would have illegally killed the dogs. Even though new dogs have slowly filled the artificial vacuum created by the translocation, the latter has assisted to maintain an '*entente cordiale*' with landowners (G. Rasmussen pers. comm.).

There are concerns that the survival of translocated animals may be poor, particularly in an ecosystem with a high density of conspecifics where a translocated animal could get an opportunity to fit into the social system (Linnell *et al*. 1997). For example, of 107 wolves translocated in northern Minnesota following depredation or harassment of livestock, 17% were shot, or recaptured at least once, for re-offending (Fritts *et al.* 1984). Although the mortality of translocated wolves was not higher than that of resident wolves, pack mates failed to stay together and travelled long distances with some animals returning home. It would appear that unless there are large areas available with a low density of conspecifics and where conflict potential is low, this strategy is unlikely to work (Linnell *et al.* 1997) (see Chapter 15 for a more detailed discussion of canid translocations).

Conditioned taste aversion

The principle of conditioned taste aversion (CTA) relies on taste and olfactory agents that cause a deep and lasting aversion to associated tastes and create a negative association between eating a particular food and sickness. Gustavson *et al*. (1976) first suggested that lacing lithium chloride on baits could be a useful management tool for problem predators and extensive trials have been conducted since, but because of poor experimental design, results have been equivocal and, therefore, controversial (Reynolds 1999). Unfortunately, CTA does not seem to be viable as a canid deterrent (Andelt *et al*. 1999; Linnell 2001); predators do not seem to associate the illness with killing behaviour, and, therefore, they often continue to kill livestock. Furthermore, there are practical problems with CTA application, in that it requires the predator to be treated several times, and as new individuals are recruited into the population treatment would need to be repeated regularly.

Direct, generalised aversion to foul-tasting substances, such as Bitrex™, has an advantage over CTA in that because the experience of foul taste on sampling is immediate it involves no ambiguity as to which prey is associated with the negative experience, and it may, therefore, effectively confer protection upon untreated prey. This has been shown with a family of captive red foxes successfully conditioned to avoid untreated milk after drinking treated milk (Macdonald and Baker 2003), and may hold some potential as a predation deterrent.

Aversion and disruptive stimuli

Undesirable stimuli such as sonic and light deterrents have been tested to scare canids away from livestock and game. These can include strobes, sirens or pyrotechnics that aim to startle or frighten a predator, forcing them to retreat from an area of livestock or disrupting their predatory attempts (Shivik and Martin 2001; Shivik *et al.* 2003). Sounds are alleged to repel animals by several mechanisms including, pain, fear, communication jamming, and disorientation (Bomford and O'Brien 1990). Explosive bangs deliver sound loud enough to cause pain, but often are a nuisance to humans and the use of pain for animal control tends to draw animal welfare objections. Another disadvantage to these sound repellents is that animals quickly become habituated to them, rendering them ineffective in the long-term.

A more advanced and novel use of disruptive stimuli is to coordinate the activation of the stimuli with the actual predation behaviour. Disruptive stimuli could be triggered by collars worn by individual canids, so that the stimuli are activated on the approach of the predator toward a certain area, i.e., a pasture containing livestock (Shivik *et al.* 2003). Collars can also be fitted that will give a canid an electric shock if they attempt to attack livestock, causing pain and discomfort and hence repelling the individual (Shivik *et al.* 2002). These collars could be placed on target animals by using automated collaring devices (Rasmussen 1997; Shivik *et al*. 2000), and by placing these collaring devices in the vicinity of livestock herds it may be possible to target collaring to those animals which are most likely to attack livestock. The potential for this approach is somewhat limited due to high costs of equipment and the level of expertise needed to set up the systems. However, they may prove useful in areas where the conservation of a threatened predator is paramount, thereby justifying the high cost.

Fertility control

In theory, canid populations could be manipulated by controlling their reproductive capacity, and fertility control via immunocontraception and chemosterilants have been proposed for such population control (e.g., Asa 1992). In Australia, immunocontraception of red foxes has been tested to deliver protection from predation to marsupials (Newsome 1995). This approach could prove useful for many common canid species involved in conflict, but current technology has the disadvantage that a high 'hit rate' is required to achieve population control, as well as the need of handling, and the ensuing high cost and effort. Baiting with birth control chemicals may become a viable option in the future, pending the development of easy to use, reliable and safe birth control compounds.

13.3.3 Approaches to increase tolerance of canids

The traditional approach to dealing with troublesome predators is giving way to a more compassionate one that also focuses on changing human perceptions and behaviour in an attempt to reduce conflict while coexisting with wild species. For this to happen, a greater awareness of the views of all the relevant stakeholders (e.g., livestock producers, wildlife managers, hunters, conservationists, the public at large), and a willingness to work together toward solutions is essential if we are to be successful at reducing conflict. By changing the attitudes of those affected and increasing the threshold of what people are prepared to tolerate, an otherwise insurmountable conflict may become manageable. In addition, economic benefits may be accrued from conserving canids and other wildlife, such as from tourism and employment, or the broader society may bear a share of the costs, through compensation and insurance schemes.

Recognising the problem

One of the first steps in reducing human-canid conflict is to acknowledge that there is a problem and to view it with objectivity (Sillero-Zubiri and Laurenson 2001). The negative impact of canids on a local economy tends to affect well-defined communities, be it small-scale shepherds in Africa or the Carpathian mountains, gamekeepers on the British moorlands, Argentine and Australian sheep farmers or Rocky Mountains cattle ranchers. Often these groups feel they are marginalised or ignored by government officials, particularly conservationists. As in many walks of life, simply listening to a grievance and recognising a community's problem can alleviate the problem through reducing underlying tension.

Community participation and sharing revenue

Novel ideas for the co-management of habitat and wildlife with local communities are increasingly seen as the way forward for conservation, particularly outside protected areas. These frequently involve improving the economic benefits the community may derive from wildlife. Community participation in wildlife management might involve the design and management of a protected area, such as the Afroalpine grasslands of Menz that afford protection to Ethiopian wolves (*Canis simensis*) (Malcolm and Ashenafi 1997), or the actual transfer of land and resource rights to local communities. In Canada's Western Arctic, polar bears (*Ursus maritimus*) have benefited from a co-operative wildlife management process established by the Inuvialuit Land Claim, which indirectly reflects on wolf and Arctic fox conservation (Bailey *et al.* 1995). An interesting by-product of this initiative is that it overcame the mutual distrust existing between government biologists and the Inuvialuit.

There are a number of ways in which programmes have endeavoured to transfer economic benefits to local communities, particularly through ecotourism, hunting, employment and compensation for any livestock losses. Clearly, where economic benefits are substantial, this is one of the most powerful ways of reducing negative perceptions of wild carnivores and wildlife in general. The philosophy that local communities should directly benefit financially from conservation underpins many of the recent strategies for community-based conservation, although it is not without its critics.

One example of community conservation that indirectly benefited African wild dogs in a few areas is the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE) in Zimbabwe. This programme was set up to promote conservation of wildlife through utilisation by allowing communal landholders to receive direct income generated by hunting fees, game-viewing and curio sales (Child 1996). Large predators, previously persecuted for livestock losses, now have enhanced value for the local people as they command substantial hunting fees. Probably of greater value, however, are conservation projects that become significant employers in the local community (e.g., the Ethiopian Wolf Conservation Programme), and may also provide additional social benefits such as supporting schools and providing healthcare.

Compensation and other cost-sharing schemes

The cost of tolerating wild canids tends to be unevenly spread, and there is a case for the broader society to share the burden with the few afflicted individuals through public funding. Compensation schemes are one such mechanism, but they have faced many limitations and may soon give way to better alternatives.

Direct compensation for livestock losses has proven to be a relatively widespread and sometimes inexpensive, but not always effective, means for relaxing opposition to canid conservation. In Italy, for example, the local government compensates 100% of the value of livestock killed by wolves, bears and even feral dogs (Cozza *et al.* 1996). This amounted to a modest 0.4–2.8% of total livestock subsidies in the region. It is vital that the criteria for compensation are clearly laid out, to avoid abuses in the claim system. For example, a few farmers may take advantage of the situation to gain other subsidies. In Italy, farmers sometimes keep old or infirm sheep for headage payments, but these are more likely to be killed by predators (Cozza *et al.* 1996). The opposite of compensation is a bounty scheme, such as that in place with a group of Argentine sheep producers, the majority of whom get 5–10 fox bounties every year, effectively subsidising some of their losses (Novaro *et al.* 2004).

Although compensation schemes may alleviate direct losses to farmers, they do nothing to alleviate the problem, rarely deal with full costs, are open to corruption, can involve expensive bureaucracy, and tend to encourage a state of constant conflict. Furthermore, they often do not identify and improve situations where only a few farmers suffer the vast majority of losses, nor do they encourage the improvement of management systems (though these shortfalls may be alleviated if compensation criteria are modified). Crucial components of a successful compensation scheme include quick and accurate verification of damage, prompt and fair payment, sufficient and sustainable funds, and measures of success (Nyhus *et al.* 2003). As compensation schemes are costly to administer and are open to corruption, a scheme could be considered whereby rather than paying owners for each kill, they are paid a lump sum to tolerate predators. This approach would positively benefit those that have good husbandry practices and hopefully promote others to follow suit.

Some of the difficulties inherent in compensation may be circumvented by community-based insurance schemes, where the community has a vested interest in the transparency of the system and legitimacy of claims, and where producers sustaining least losses may derive some benefit analogous to a "no-claim" bonus. Commercial livestock growers may insure valuable stock against predation, particularly with pedigree herds, using established commercial insurance brokers. Premiums could then be reflected by parameters such as management strategies and risk of predation due to proximity to the wildlife area. As a result, rather than 'managing the predator', in order to meet regulations set by insurers, such a system would encourage ranchers to adopt an active herd management strategy (e.g., Rasmussen 1999).

In the USA, Defenders of Wildlife has created an innovative programme called the Proactive Carnivore Conservation Fund with the objectives of reducing conflicts between predators and humans, keeping predators from being unnecessarily killed by agencies in response to human conflicts, and increasing general tolerance for carnivores across the landscape. They cost-share with ranchers actions to prevent livestock depredation from occurring, such as buying livestock guardian dogs, erecting electric fencing to keep wolves away from sheep, hiring "wolf guardians" to monitor wolves in sheep territory by radio telemetry, and chasing them away when they get close to livestock (N. Fascione pers. comm.). Defenders of Wildlife has also paid more than US$250,000 in compensation to ranchers for losses due to wolf attacks since 1995.

Other alternatives include providing tax incentives to landowners and transferring user fees from recreation to landowners. A novel way of sharing the cost of living with carnivores is to add a premium price to goods labelled and marketed as produced by "predator-friendly" farms (e.g., Cheetah Conservation Fund, L. Marker pers. comm.), and "wolf-friendly" and "wild dog-friendly" beef would be the next natural step for this approach.

Recreational use

Ecotourism has been a major growth industry over the last 20 years and there is no doubt that some canid species are becoming an attraction for tourists planning a traditional wildlife safari. Traditionally, tourism has been a source of revenue for established conservation areas, with parts of Africa, India and the Rocky Mountains abounding with examples where safari tourism has become a major source of income. In southern Africa, commercial farmers, whose precarious income from cattle farming has always been susceptible to drought, are increasingly turning to tourism as well as consumptive trophy hunting as an alternative source of income (Lambrechts 1995).

Although ecotourism appears to be a potent tool for canid conservation, it is perhaps only the high profile and visible canid species (e.g., African wild dogs, grey wolves, Ethiopian wolves, dholes and maned wolves) that may draw tourists, and hence may be partially capable of supporting a sustainable tourist trade. This approach may be unsuitable to other more secretive species or those extremely sensitive to human pressure. However, it is not necessarily seeing the animal that is important, as many visitors to areas renowned for their predators are attracted by the knowledge of the presence of these animals, even if the chance of sightings may be minimal. But expectations may surpass reality and tourists and experienced naturalists alike may become disappointed if they do not see the elusive focus of their interest during their visit.

However, a note of caution is needed as the economic rewards of ecotourism may be low or not reach the expectations of the local community. For example, in the Bale Mountains in Ethiopia, where income from tourism is often given as a justification to the local community for the presence of a park, the number of tourists visiting each year is numbered only in the hundreds, many visitors hire vehicles rather than local horses or guides to see the area, and the amount of money that goes into the local community is relatively small. Tourism may also be susceptible to changes in the global economy or political stability of a given country. This was dramatically displayed by the recent crash in Zimbabwe's substantial tourism trade (with African wild dogs a significant attraction), due to ongoing political instability. Thus, it would be unwise to hinge carnivore conservation purely on the economic benefits accrued from tourism, particularly as only a proportion of these benefits may go to local communities. It is also salient to point out that many regions do not necessarily lend themselves to ecotourism, and, furthermore, many rural communities may not welcome the intrusion of paying visitors.

Conservation education

In many situations it is impossible to provide sufficient economic benefit to local communities to compensate for the resources that are lost to wildlife (see Chapter 18). In these circumstances the most important way that public support can be gained for large canids and their conservation is through educational programmes, so that local people can relate positively to the species or habitats in question. Perceptions of predator problems often exaggerate the reality (e.g., Rasmussen 1999), and education programmes can target this by delivering accurate information and increase people's tolerance and appreciation for wildlife (Conover 2002).

Recommendations to involve the local community include targeting key groups with education campaigns, building support through the use of spokespeople within the target groups, integrating human and ecological

Signage for city residents regarding urban-dwelling coyotes as part of "Co-existing with Coyotes" programme. The programme works to reduce conflict between people, pets and coyotes through education. It targets elementary school children, day care facilities, park users and pet service businesses as audiences as well as providing situation specific advice and information to individuals who have encountered a coyote. Vancouver, British Columbia, Canada, 2003.

Coyotes have large ears that point up. They can hear a mouse under 20cm of snow.

Coyotes rarely fight with each other. They use gestures and sounds to communicate.

The majority of coyotes that have bitten children have been fed by adults.

Coyotes have bushy black tipped tails which they carry low while in motion.

Coyotes are active day and night.

Coyotes eat a wide range of foods including rodents, fruit, insects and fish.

Lower Mainland coyotes weigh between 9-16kg (20-35lbs).

COYOTE ALERT

Think you saw a coyote?

You probably did. Coyotes are very adaptable creatures and are commonly found in cities across North America. They moved into Vancouver in the late 1980s.

Pet safety:

- Keep your dog in sight and under control
- Avoid bushy areas or neglected properties
- Never let large dogs interact with a coyote
- Never feed coyotes

If a coyote approaches:

Appear as aggressive as possible

- Shout in a loud and deep voice
- Throw objects at the coyote
- Do not run, maintain eye contact
- Move towards an area of activity

Coyote attractants in your neighborhood:

- Accessible garbage, compost, fallen tree fruit
- Rat habitat - neglected sheds and properties
- Outdoor pet food (stored or fed)

Coyote Info-line:604 681 WILD (9453)

www.stanleyparkecology.ca

Report aggressive coyotes or the feeding of coyotes to the Ministry of Water, Land and Air Protection at 604 582 5200.

Stanley Park Ecology Society

concerns and, if possible, designing species-specific education initiatives using the species as a flagship for other conservation concerns. Some canid species can act as such flagships to gain public support for habitat conservation – grey and Ethiopian wolves being good examples, with comparable potential for African wild dogs, dholes and perhaps even Darwin's or island foxes. Conservation projects may engender a local pride so that the community see the target species as "their" animal, and this is more often than not the root of the problem.

In the recent past educational activities have been seen as the first step in outreach programmes around protected areas, and indeed are increasingly becoming an integral part of the activities of conservation agencies, but their success is still open to question and not often evaluated. In a few cases involving canids that we reviewed, however, there was an obvious improvement in the situation. For example, in northern Kenya the killing of wild dog pups at dens stopped (K. Doherty pers. comm.) and in Canada an education programme made farmers aware of the presence and conservation importance of swift foxes and the farmers became involved in monitoring foxes (A. Moehrenschlager pers. comm.). For education programmes to reach their full potential as formal undertakings, it is imperative that adequate funding, resources, and trained personnel are available, as opposed to being additions "tagged" onto existing research programmes.

13.4 Conclusions

Increasingly, farmers are re-examining traditional anti-predation methods and, with the use of new technology, adapting and developing them to fit into modern livestock production systems. Simple husbandry practices, such as keeping livestock in pens at night, extra surveillance by herdsmen and shepherds, the provision of alternative pastures away from canid dens, the proper disposal of livestock carcasses, and the use of livestock guarding dogs (particularly breeds with more developed anti-predator instincts), may all help to reduce livestock losses.

In some cases, it may be difficult to change livestock husbandry, either because farmers are resistant to change or because management options are too difficult or expensive to put into practice. There may also simply be little incentive for farmers to change, if losses are relatively low, or else farmers may not be keen to take on perceived extra work. Thus, it is important that the local community is involved by any process seeking to address human-canid conflict through the various conservation approaches reviewed, in the hope of reverting traditionally, deeply based, negative views of wild canids in younger generations. Community involvement, however, requires strong partnerships, shared goals for both wildlife and human communities, and shared responsibility.

Realistically, in human-dominated landscapes where canids and people coexist there will only be, at best, an uneasy tolerance. Thus, to conserve wild canids, conservation policy must encompass a mixture of strategies, including protectionism, conservation education, public relations, community involvement and revenue sharing. While some of the examples in this review have illustrated how steps have been taken along this path, future conservation efforts must expand the use and variety of innovative and imaginative solutions to canid-human conflicts.

Chapter 14

Evaluating and Predicting the Impacts of Exploitation and Trade on Canid Populations

W.E. Johnson

14.1 Introduction

Canid exploitation and trade forms an integral part of our cultural heritage, and, to a large extent, reflects the full range of our contradictory attitudes and responses to wildlife in general. Canids, having been exploited for subsistence, medicinal, commercial profit, and recreational purposes, have also been domesticated for the purposes of pets, companions, co-workers, and service providers. While large investments of time and money have been employed to persecute individuals and populations as pests, because of concerns over personal safety, disease transmission, or depredation on livestock and pets, substantial resources have also been spent on protecting and restoring canid populations.

The exploitation of canids often elicits strong feelings and disagreements. However, given that harvest and trade of wildlife, is not, in and of itself, inherently intolerable, it becomes easier to find commonly accepted approaches and links between the exploitation of canids and conservation. Market regulation, if structured correctly, can be easier, more effective, and less expensive than their elimination. For many species there is growing support for the concept that providing viable commercial outlets for wildlife products can be a powerful incentive for the conservation of these populations, provided that resource ownership and profit benefits are equitably distributed.

The steps needed to monitor population health and the effects of harvest or persecution, through the utilisation of increasingly sophisticated methods to examine population dynamics, predator-prey relationships, and habitat requirements, are generally agreed upon. However, the task of analysing the costs and benefits of wildlife trade is substantially more complicated. A significant issue is the difficulty (technically, economically, and politically) of obtaining sufficient data on the level of trade, and in obtaining appropriate biological and demographic data from elusive canid species. Although there have been substantial improvements in population sampling and estimation techniques (see Chapter 15), as well as an increased understanding of the parameters that are important in maintaining viable populations, for most species and populations, neither the needed baseline data have been collected, nor have populations been monitored for sufficient periods of time to make broad conclusions about how to distinguish between detrimental and non-detrimental impacts.

14.2 The positive impacts

There are numerous examples of the positive impacts of trade in canids. Several canid populations have successfully sustained varying levels of harvest and trade for extended periods of time without long-term deleterious effects, while supporting viable economic enterprises. The red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), coyote (*Canis latrans*), and Arctic fox (*Alopex lagopus*) are the best examples of how exploitation over an extended period of time can be biologically and economically sustainable (Geist 1994). The long-term success and sustainability of this exploitation has been attributed to several factors, including public ownership of wildlife, elimination of a commercial market for the parts of vulnerable wildlife species, centralisation of wildlife laws, and prohibition of indiscriminate killing (Geist 1988). The sustainability of exploitation also appears to be facilitated when the commercial value of the wildlife products is low relative to alternative sources of income, and when the investment by the hunter or trapper in terms of time and money is high (Lavigne *et al.* 1996). The sustainability of exploitation can also be self fulfilling as the increased monitoring, scrutiny, and regulation that accompanies legal exploitation activities provides additional data and science that promotes better population management of these populations.

Utilisation is also more likely to be sustainable when supported by increased economic benefits derived from related activities. In North America, the Arctic fox is also a prime example of the economic benefits that canid exploitation can bring to local communities, as it remains the single most important terrestrial game species in the Arctic and an important source of income for the First Nations peoples. In addition, a large percentage of the trade in canids has historically been for fur derived from captive populations, especially for Arctic fox and raccoon dog (*Nyctereutes procyonoides*) furs farmed in Scandinavian countries and Poland.

14.3 The negative impacts

Humans can also negatively affect canid populations in a direct manner. These impacts often lead to local extirpations of species, and more rarely, to their extinction, as exemplified with the Falkland Island wolf (*Dusicyon australis*). The legal market of wildlife products, either nationally or internationally, especially when valuable, can promote overexploitation and illegal poaching. However, one of the most common factors leading to large reductions in numbers and distribution is human exploitation and predator control. For example, grey wolves (*Canis lupus*) have cohabitated with humans for thousands of years, and have invariably been extirpated through direct persecution and indirectly by the loss of habitat and prey. Due to their threat on humans and livestock, wolves were totally eradicated from large parts of North America and most of Europe by 1900 (Delibes 1990; Young and Goldman 1994) through hunting and poisoning, and were deliberately removed from all of the Japanese islands, except Sakhalin, in the 19th century (Dobson 1994). However, heavy exploitation does not always lead to extinction. In contrast with wolves, coyotes have managed to expand their numbers and distribution in spite of tremendous efforts to eradicate them. Coyotes, which benefited from the removal of wolves throughout much of North America, thrive in most human-inhabited areas where other carnivores do not.

14.4 Case studies

The primary motivations behind the wide-scale exploitation or persecution of canids have generally been commerce and population control, with intensity or effort varying predictably on supply and demand. Major differences in the commercial exploitation of canids are seen among species, populations, and administrative divisions (regions, countries, etc.), many of which are illustrative of how canids respond to commercial harvest, and how exploitation and conservation are often linked. An illustrative example of the many issues relating to canid trade and harvest is the case of three common fox species found in the southern cone of South America. Each has been persecuted to varying degrees in large portions of their ranges, primarily for economic and commercial purposes: the culpeo (*Pseudalopex culpaeus*) and the chilla (*P. griseus*) in Chile, Argentina, Bolivia, and Peru, and Pampas fox (*P. gymnocercus*) in southern Brazil, Uruguay, Paraguay, and northern Argentina. Although some of these foxes are exploited for subsistence purposes, predator control, or recreation, historically, the major factors motivating their harvest have been economic.

During the 1970s, foxes were among the most commonly traded species in South America. From 1976 to 1979, around 3,600,000 'grey' fox pelts (chilla and Pampas fox combined) and 32,000 culpeo fox pelts were exported from Buenos Aires, Argentina, with a total value of over US$80 million (Mares and Ojeda 1984). From 1982 to 1984 these figures had dropped to around 70,000 'grey' and 4,500 culpeo fox pelts (Ojasti 1993). This decline was probably the result of a combination of reduced demand in the foreign markets of the United States, Germany, and the rest of Europe, stricter enforcement of regional wildlife legislation, and reductions in population densities in the most readily accessible areas (see sections 3.4 and 3.6).

In South America, as with elsewhere in the world, fox exploitation is also related to the trade of other species, such as wild cats (McMahan 1986; Bowles 1996), and to the dynamics of national and international markets, laws and regulations for these species, and the strength of local enforcement agencies. Trade in carnivore skins in South America focused initially on the jaguar (*Panthera onca*). Later, it shifted to foxes and smaller cats such as the ocelot (*Leopardus pardalis*), margay (*L. wiedii*), oncilla (*Oncifelis tigrina*), and eventually to the Geoffroy's cat (*O. geoffroyi*), as laws regulating exploitation and trade shifted both nationally and internationally in the 1960s and 1970s. Traders and professional trappers were motivated to develop new wildlife products for trade and to find commercial routes through countries with the least enforcement and the most relaxed laws. Since the inception of the CITES agreement, the Appendix status of several species of cats and foxes had to be changed because of unsustainable trade or the difficulty in distinguishing products from protected and unprotected species (Bowles 1996).

Although the international pelt trade has, by most accounts, continued to decline during the last two decades, trade still occurs, especially in Argentina (e.g., Iriarte and Jaksic 1986; Johnson and Franklin 1994a; Novaro 1995). However, small farmers, ranchers or herdsmen have generally replaced the professional hunts or trappers, often harvesting foxes as "by-catch" while spotlighting or trapping for other economically important species such as the European hare (*Lepus capensis*). Significant economic incentives still exist for the continued exploitation of these carnivores. The money derived from the sale of a few pelts a year can represent an important contribution to the annual income of many rural residents (Novaro 1995). These factors, along with cultural traditions, sustain trapping throughout most of southern South America, despite restrictions. Culpeo hunting, in particular, continues in an effort to reduce sheep depredation (Bruggers and Zaccagnini 1994). A limited amount of trade in fox pelts still occurs in southern South America, including a small number of farmed animals. However, exports have declined from the levels of the early and mid-1980s, probably due to lower international demand. For example, from 1997 to 1999 around 8,000 fox pelts were

Ranch worker with culpeo skins. Neuquen province, Argentina, 2000.

Andrés Novaro

exported from Argentina annually (A. Novaro and M. Funes pers. comm.).

Although the legal trade of pelts in South America has been credited with leading to overexploitation of target and non-target populations and species, the impact of harvest on the South American fox populations is unknown, mostly because there have never been any broad estimates of population sizes. Many of these fox species appear to tolerate high levels of exploitation (Broad *et al*. 1988). The ability of South American foxes, like other canid species, to tolerate such high mortality is not only due in part to their generally high intrinsic growth rate and large reproductive capacity, but may also be a function of the heterogeneous spatial distribution of hunting pressure. This in effect creates "source" populations of non-exploited foxes and "sink" populations of exploited animals (Pulliam 1988). Novaro (1995) concluded that in spite of unsustainable trapping levels on some ranches (46 to 73%), fox densities remained relatively stable because of recruitment from other areas. Although fox populations have also benefited from the establishment of National Parks and other protected areas, this does not always guarantee their protection. In Torres del Paine National Park, 45% of the documented chilla and culpeo mortality resulted from poaching (Johnson and Franklin 1994a).

Largely because of difficulties in regulating and limiting the legal hunting, trapping, and trade of foxes in South America, in many areas the most effective conservation tool for maintaining carnivore populations has been to completely ban these activities. In contrast, the characteristics and history of carnivore exploitation in North America have been somewhat different. In Canada and the United States a combination of greater monetary resources, stronger governmental agencies, broader and stricter enforcement of hunting and trapping limits, and better population estimates have led to the management of carnivore populations through legal harvest. Hunters and trappers, as well as a large segment of the general public, are often active participants in the process of managing populations to ensure long-term viability. This has led to the maintenance of legal hunting and trapping of numerous carnivore species including foxes, cats, bears, and mustelids, as well as a wide range of ungulates and birds.

Among the northern hemisphere canids, Arctic foxes, red foxes, and raccoon dogs are the most economically important furbearers and all three are seasonally trapped, and to a lesser extent raised in captivity. The current distributions of red fox and raccoon dogs have both been influenced by human introductions. Red foxes from Britain were released into north-eastern North America during the late 1600s and early 1700s, perhaps contributing to a range expansion across much of the continent around that period (see section 5.3). Raccoon dogs were originally restricted to north-eastern Asia, but after the release of several thousand individuals into western Russia from the late 1920s through the 1950s, they are now found throughout much of northern and eastern Europe (see section 5.4).

14.5 Predicting the impacts

There is much that can be applied to canid conservation that comes from studies of their exploitation and population biology. The impacts of exploitation on the demographics of canid populations can be complex, and are affected by numerous ecological, economic, social, and legal factors. Harvest levels tend to fluctuate greatly over time and vary considerably from one area to another. Historically, the largest impact has been on species exploited for commercial gain for their pelts, although no canid species appears to have been driven to extinction from economic trade alone. The impact of exploitation has been especially acute on species with low densities and birth rates, such as the grey wolf and African wild dog (*Lycaon pictus*), during times when they have had high economic value. Species with larger population sizes, higher birth rates, lower economic value, and/or more elusiveness have fared better. Canid species in the latter category that have been heavily exploited or persecuted species include red fox, culpeo and coyote. For some species, such as the coyote, dingo and red fox, it is clear that extraordinary efforts are required to completely eliminate the species from an area. In these species, moderate harvest rates can easily be compensated for by reproduction rate or immigration. Broad, sustained control efforts are needed to maintain reduced populations (Harris and Saunders 1993; Reynolds and Tapper 1996).

Populations respond to human-induced mortality from harvest or control in many different ways. One of the most common responses is to increase recruitment. In red foxes, increasing total reproductive output more often depends on changes in pregnancy rates, especially among juveniles, and not on changes in litter size (Pils *et al.* 1981; Allen 1984; Harris and Smith 1987). Immigration and emigration are also important mechanisms that can compensate for heavy exploitation, especially in mobile species. In heavily harvested populations, emigration may become insignificant or be delayed due to the increased availability of resources (Harris and Smith 1987). Conservation efforts to increase carnivore populations might thus benefit from actions that shorten generation times or increase reproduction rates. Carnivore populations can also respond to exploitation through compensatory mortality, where harvest simply replaces other forms of death, thereby limiting its effect on populations (Errington 1956), although some degree of additive mortality has been shown in a few carnivore species (Bailey *et al.* 1986; Clark *et al.* 1989). For population managers managing species for which additive mortality is operative, even low levels of mortality from harvest or poaching can be detrimental.

In addition to affecting population size directly, demographic changes can also result from the preferential harvest of certain sex and age classes of carnivores. Trapping of canids during certain periods of year, when the young are dispersing for example, can disproportionately affect different segments of the population. Males disperse farther and in greater numbers in many canid species than females, perhaps resulting in additional differences in genetic and demographic patterns (see review by Waser 1996). In a study of urban red fox, 73% of male juveniles dispersed compared with 32% of females (Harris and Trewhella 1988) and over greater distances (Trewhella *et al.* 1988).

The effects of exploitation and control vary among species and responses may be hard to predict because of complex interactions among the various population parameters. For example, most forms of exploitation are spatially non-random. The heavy harvest of certain populations, areas, or habitats can affect the demographic connectivity of populations and the ability of individuals to disperse, creating or exacerbating the complexity of a metapopulation structure and increasing the probability that harvest mortality may be additive instead of compensatory. Aspects of this scenario have been studied by some authors with source and sink population models incorporating differing rates of productivity, survival, and dispersal (Pulliam 1988; Danielson 1991). This approach has not often been tested empirically; however, it has been proposed that dingo populations experience a cycle based on food supply and control. When food resources are scarce in the safe source areas, they disperse to agricultural areas where fewer dingoes and intense persecution and control efforts (e.g., poisoning, trapping, shooting) create demographic sinks (Thomson *et al.* 1992). In south-eastern Australia, this cycle has been disrupted by the maintenance of almost 6,000km of fence separating areas of intense control from areas where dingo populations are tolerated.

There are numerous examples where certain canid populations receive protection, while adjacent populations are harvested or persecuted. For example, the Pampas fox is hunted legally and controlled by a bounty system in portions of Argentina. However, in Brazil, Uruguay and Paraguay, populations are legally protected, although persecution still occurs from sheep ranchers. The grey wolf, while common in Canada, Alaska, and Russia, where the species is harvested for furs and persecuted for perceived threats against livestock, game species, and humans, is under threat elsewhere in the world. As with other species, although it is unlikely that harvest and trade of wolves in Canada, Alaska and Russia threaten those populations, the effects of legal trade on other less stable populations are not well understood.

The lack of sufficient data by which to anticipate the impact of exploitation, population control, or conservation efforts is one of the largest problems facing wildlife managers (Harris and Saunders 1993; Weber and Rabinowitz 1996). Field research is crucial to understanding the basic ecological requirements of exploited species. However, it is as important to monitor the results of management plans, not only to be able to modify these actions, but also to learn from them. To this end, long-term data sets are particularly valuable. Good data has an additional value when enacting management plans in that some of the paralysing debates over policy decisions can sometimes be avoided when discussing facts instead of dealing with opinions. Since we will probably be making active management decisions about all carnivore populations in the future, we must accept the responsibility to do this as well as possible. This implies being able to collect the data with which to make these decisions.

To improve our ability to manage canid populations, both for harvest and conservation, research is needed in several areas. Some of the needed research efforts are species-specific while others are more broadly applicable. For many canids, basic information on life-history parameters and population ecology is still unknown, much less how they will respond to exploitation. The management of many canids would benefit from research similar to that which has been conducted on wolves, which has allowed simple models to be written estimating sustainable mortality rates, and estimating the sizes of wolf populations given available ungulate biomass (Fuller 1989). These data would then allow managers to predict the resiliency of populations to exploitation, factoring in their aptitude to alter their behavioural patterns, their capacity to compensate demographically to increased exploitation levels, and their ability to disperse across different habitats, distances, and barriers (Weaver *et al.* 1996). More research is also needed on the importance of heterogeneous harvest levels and the role of refugia, which leads to source-sink dynamics.

More research is needed comparing the effects of different exploitation techniques on different species. For example, the timing and location of harvest could theoretically influence the age and sex of individuals killed. Often only the number of animals harvested is taken into consideration when assessing whether populations are threatened. However, harvest based on reproductive potential, but which does not consider behavioural aspects might severely disrupt relationships in regard to territories or social groups, as with wolves (Haber 1996). More research is also needed comparing exploited and non-exploited populations of the same species, in similar environments.

The difficulty in obtaining reliable population estimates is one of the most fundamental tools missing for managers. Increased emphasis needs to be placed on the development of both direct and indirect methods of monitoring populations using new technologies. This should not only include demographic characteristics, but also genetic aspects such as reliable estimates of effective population size and the amount of gene flow among areas, as well as approaches that assess the prevalence of pathogens and their impact on the population. It is important to maintain the integrity of a functional ecosystem, since exploitation can change the ecological relationships in a community. For example, small carnivores have been shown to benefit from the loss of larger ones (see Johnson *et al.* 1996).

14.6 Conclusions

The canid family includes a diverse range of species, each with a unique set of conservation issues. In addition, the populations of many canid species experience a wide range of pressures. These differences lead to the necessity of developing coherent international, national, and local management plans for most canid species. To ensure the survival of some canids, even species such as the island fox (*Urocyon littoralis*), Darwin's fox (*Pseudalopex fulvipes*), Ethiopian wolf (*Canis simensis*), and African wild dog, for which there has never been a large commercial interest, complete protection and active monitoring and management may always be necessary. Species requiring constant attention will generally be found in small, isolated populations and have specialised ecological requirements and/or low intrinsic growth rates. These may or may not require large amounts of contiguous habitat, depending on their density, ecological requirements and dispersal abilities. Other canids are species that will require a certain amount of control in addition to thorough protection. They will include some of the larger species such as wolves, which in most portions of their range are unlikely to ever be common enough to permit controlled harvest, but which may require selective culling in certain populations, especially of "problem animals" (see Mech 1995b). Since predator control is also expensive, these activities will generally be restricted to agricultural areas.

A second group of canids will have very heterogeneous distributions and needs. In some areas populations may allow sustainable harvest, but in other areas exploitation leading to trade may be impractical or detrimental. These populations will generally be large and distributed over broad geographic areas, and present rapid growth rates and some economic value. Not all of these species will necessarily be harvested. However, for ecological, political or social reasons, any exploitation activity will surely require concurrent research, monitoring, and regulatory efforts. The species most often included in large economic trade enterprises include the red fox, Arctic fox, coyote, grey wolf, swift fox (*Vulpes velox*), kit fox (*V. macrotis*), gray fox, culpeo, chilla, Pampas fox, black-backed jackal (*Canis mesomelas*), Blanford's fox (*Vulpes cana*), raccoon dog, and dhole. Some of these, including the red fox, Arctic fox, coyote, grey wolf, gray fox, culpeo, chilla, Pampas fox and black-backed jackal, are killed locally primarily during predator control operations, and, like the dingo, have no large intrinsic economic value.

A final group of species is composed of those that generally are not exploited and for which there is limited commercial use or trade. This group includes the short-eared dog (*Atelocynus microtis*), Sechuran fox (*Pseudalopex sechurae*), bush dog (*Speothos venaticus*), pale fox (*Vulpes pallida*), Indian fox (*V. bengalensis*), corsac fox (*V. corsac*), Tibetan fox (*V. ferrilata*), golden jackal (*Canis aureus*), Ethiopian wolf, maned wolf (*Chrysocyon brachyurus*), crab-eating fox (*Cerdocyon thous*), and hoary fox (*Pseudalopex vetulus*).

The conservation, harvest, exploitation and trade of canids are not always incompatible activities. The goals of minimising the potential adverse effects of carnivores, maximising the benefits that they provide, and also ensuring their long-term conservation, are all fundamentally related by the science of population management (Shea *et al*. 1998). The successful reestablishment and conservation of many carnivores will eventually require varying degrees of control of these same species. Inclusion of the local human community is one of the most crucial steps in promoting the successful maintenance or reintroduction of carnivore species. The debate over sustainable use of canids can also add a scientific framework to the discussions of wildlife management. The process of regulated exploitation and harvest may help enlist public support for conservation efforts, foster local participation in finding solutions to conservation and management problems, and provide monetary compensation to the community for the presence of a carnivore population.

Exploitation of wild animals is an emotional issue that has been the subject of intense debate on moral, pragmatic, and economic grounds (see Robinson and Redford 1991; Swanson and Barbier 1992; Taylor and Dunston 1996). Humans affect all wildlife species and all wildlife management has animal welfare implications (Taylor and Dunston 1996). Successful wildlife utilisation and trade must be compatible with conservation, and generally has been based on broad ecosystem and cultural approaches. This includes the development of the necessary infrastructure and trained personnel for the management and preservation of all species in a multi-use, multi-species approach. Canid conservation will ultimately depend on the collective education of consumers of carnivore products (both extractive and non-extractive), resource managers, and those communities living in closest proximity to, and interacting most directly with these animals.

Chapter 15

Survey and Census Techniques for Canids

E.M. Gese

15.1 Introduction

We already know that the status and distribution of canid populations throughout the world is of growing concern for biologists and the public alike. Habitat loss, fragmentation and degradation, human persecution, decreases in prey, disease, poaching, and increased competition with other carnivores due to reduced space and habitat, have led to some canid species facing extinction, while others occupy only a fraction of their former range. While reintroductions of some species have been successful (e.g., grey wolves *Canis lupus* to the Northern Rockies of the U.S.), other species face an uncertain future (e.g., African wild dogs *Lycaon pictus*). Paramount to canid recovery, reintroduction, or management, is acquiring accurate information regarding the status of a species, or a particular population. Reliable methods that provide accurate data on the distribution, abundance, and population trend of a species are required. These parameters are also fundamental for helping to determine the conservation status of a species according to the IUCN Red List Categories and Criteria (for example, the B criterion relies on knowledge of geographic range size, where a species with a range of less than 20,000km² could qualify in one of the categories of threat). However, because many canids are secretive, nocturnal, wide ranging, in densely vegetated habitats or remote areas, or at extremely low densities, surveys of a canid species or population can be very difficult.

Abundance may be assessed in two ways: relative and absolute. Relative abundance uses indices of animal abundance (e.g., track counts, dens) that can be compared over time or between areas. Absolute abundance involves actually counting animals and estimating the number or density of animals in the population. With repeated sampling over time, both relative indices and absolute estimates can be used to monitor population trends. This chapter reviews techniques useful for censusing canids, and is adapted from Gese (2001). For techniques related to determining demographic parameters (birth, death, emigration, immigration), readers are referred to Caughley (1977), White and Garrott (1990), Royama (1992), and Thompson *et al.* (1998). Methods for censusing or surveying wild canids vary in accuracy, reliability and cost. Many of the techniques described herein require in-depth evaluation as to their accuracy and reliability in monitoring population trends (Gese 2001). As an example, a recent study by Schauster *et al.* (2002a) compared six survey techniques for monitoring abundance of swift foxes (*Vulpes velox*) in Colorado, USA. This study found that mark-recapture estimates ($r = 0.711$) were the best predictor of fox density, followed by scat deposition surveys ($r = 0.697$), scent-post surveys ($r = 0.608$), spotlight surveys ($r = 0.420$), trapping surveys ($r = 0.326$), and lastly, activity index surveys ($r = 0.067$). Combinations of techniques increased prediction capabilities. Other studies that used, or attempted to use, the techniques described in this chapter have been included as examples.

Some considerations before implementing a survey
Prior to surveying any canid population, the precision, accuracy, power, sample size, survey design, and statistical assumptions of each method should be considered (Skalski and Robson 1992). In addition, for each method the observer must address problems pertaining to "observability" or "catchability" of the species, the size of area to be sampled, costs, logistics, manpower, and time constraints (Lancia *et al.* 1994).

15.2 Methods employed to determine species distribution

Sometimes it may only be necessary to determine the presence and distribution of a species. Methods typically used to determine species distribution include habitat mapping, questionnaires, interviews, sighting reports, or confirmation of sign. Any survey method that provides an estimate of animal abundance provides distribution information as well.

15.2.1 Habitat mapping

Time can be saved by considering the type of habitat required for a species and examination of habitat maps or aerial photos. Habitat suitability models have been developed for many wildlife species (e.g., Boyle and Fendley 1987; Rogers and Allen 1987), but have not been developed for canids. With the continued development of satellite imagery, remote sensing, and Geographic Information Systems (GIS), areas containing suitable habitat for a species can be identified allowing for maximisation of survey efforts. Surveys can then be stratified by habitat types or land classes (Macdonald *et al.* 1998).

15.2.2 Questionnaires, interviews, and sighting reports

Many agencies compile status reports using questionnaires to assess the relative abundance and distribution of canid species. Sightings and general impressions from people in the field can determine species distribution, and gain a subjective estimate of animal abundance. More in-depth questionnaires or interviews of persons with knowledge of the area and who spend considerable time in the field provide not only a range report, but may also provide an estimate of abundance (e.g., Allen and Sargeant 1975; Harris 1981). Questionnaires, interviews, and sighting reports have been used to determine distribution, and sometimes abundance of several species (e.g., Allen and Sargeant 1975; Harris 1981; Fuller *et al.* 1992; Fanshawe *et al.* 1997). Problems with this method include misidentification of species, low response levels to the questionnaire, a bias for animal sightings concentrated along roads or near human habitation, and the reliability of the respondents.

15.2.3 Presence of sign

In the absence of visual confirmation of the species itself, surveys of animal sign may be used to determine presence. Several different methods of sign surveys have been used, including documentation of tracks, scats, scratches, burrows or dens, and hair samples (often obtained through the use of hair snares or hair tubes). The use of track plates to determine species presence has proven useful (e.g., Zielinski and Truex 1995). A full description is provided by Zielinski (1995), but track surfaces may generally be produced from smoked or carbon-sooted aluminum plates, contact paper, chalk, or ink. A visual and/or olfactory lure is used as an attractant and while investigating the attractant, the animal leaves tracks on the tracking surface. Identification of tracks, getting the animal to step on the plate, transportation of the plates, and protecting the track plates from weather are just a few of the common problems that require prior planning (Zielinski 1995; Zielinski and Truex 1995). This technique provides a reliable measure of species distribution or presence, but may be unreliable for determining relative animal abundance.

A common problem with using sign to determine canid distribution is the consistent identification of tracks, scats, burrows, and hair samples. Species identification from scats can be facilitated by using faecal bile acid patterns (e.g., Major *et al.* 1980). Examination of hair samples with a light microscope and comparison to a hair key or reference collection can aid species identification (e.g., Adorjan and Kolenosky 1969; Moore *et al.* 1974). DNA techniques allow for more accurate identification from scat or hair samples (Foran *et al.* 1997a,b; Paxinos *et al.* 1997), and can also be used to identify individual animals allowing for estimation of population size (e.g., Kohn *et al.* 1999). When using scat surveys, the seasonal decay rate of the scats may need to be considered, as well as whether scats are being consumed by scavengers. Also, the amount of sign left behind by an animal does not always correlate with animal density, nor does failure to find sign necessarily indicate species absence.

In their most rudimentary form, sign surveys provide distribution information. When standardised, these sign surveys may be used as an index of animal abundance. If certain areas or habitats are repeatedly surveyed over time and the number of hours of searching (or some measure of effort) is recorded, then surveys may be standardised to allow for trends over time or comparisons between areas.

15.2.4 Remote cameras

The use of remote cameras set along trails, near bait stations, or nests has been used mainly to detect forest carnivores. The cameras, commercially available from several manufacturers (Kucera *et al.* 1995), can be triggered by an animal tripping a line, or activated remotely by pressure-sensitive plates, motion or heat detectors, or breaking of an infrared beam.

15.3 Methods for estimating animal abundance

After determining species distribution, data on animal abundance and population trends may be required. Animal abundance may be monitored indirectly by counting animal sign, or by direct methods of counting the animals themselves. Estimating animal abundance requires consistent and standardised application of a technique to be able to detect changes or differences with some degree of accuracy, precision, and power. Therefore, for the following techniques one must maintain a standardised protocol for the survey and consistently apply it to all future surveys. Whether sign surveys, indices of relative abundance, or measures of absolute animal abundance are used, caution should be exercised when examining population trends. Assessing rates of increase or decrease from trend data should take into account the precision and accuracy of the methods used. The influence of other variables on survey results should also be taken into consideration, such as characteristics of the animals themselves, topography and vegetation, temporal factors, observer experience, ability, and fatigue, and spatial distribution of the species. One should examine the assumptions and power of the technique to determine its ability to detect population changes (Gerrodette 1987; Eberhardt and Simmons 1992).

15.3.1 Indirect methods

Scent-station surveys

One of the most common sign surveys used for indexing canid abundance is scent-post or scent-station surveys (Linhart and Knowlton 1975; Roughton and Sweeny 1982; Schauster *et al.* 2002a). Scent-station surveys involve placing a scented tablet or other attractant within a circular area of sifted dirt. Tracks left by an animal are identified and recorded. Typically, stations are spaced at predetermined intervals along roads or trails and then visited for 3–4 consecutive nights to record tracks; the sifted area is swept smooth after each night. The frequency of animal visitation to operable stations (i.e., those not disturbed by wind, rain, vehicles) is used as an index of abundance. Scent-post surveys have been used to estimate the relative abundance of many canid species (e.g., Linhart and Knowlton 1975; Travaini *et al.* 1996; Sargeant *et al.* 1998; Schauster *et al.* 2002a). Seasonal changes in habitat use and visits to multiple stations by a single animal can contribute to invalid correlations of animal density and visitation rates; see Smith *et al.* (1994) and Sargeant *et al.* (1998) for recommendations on how to use these methods apropriately. Misidentification of tracks, weather (wind, precipitation), wariness of animals, and manpower should also be considered with scent-station surveys.

Activity index

A variation of the scent-station survey that has been used to index dingo populations is the activity index (Allen and Engeman 1995; Allen *et al.* 1996). This index of animal visitation uses a sifted dirt area on a road without any scent or lure to attract animals (Schauster *et al.* 2002a). The number of track sets crossing the sifted area is used to assess relative abundance and calculate a variance estimate (Engeman *et al.* 1998).

Scat deposition transects

The rate at which scats are deposited along established roadways or trails has been used to estimate relative abundance of canids (e.g., Andelt and Andelt 1984; Crête and Messier 1987; Beltrán *et al.* 1991; Schauster *et al.* 2002a). This method involves designating transects or routes along a roadway or trail, clearing all scats from the road, then returning and collecting all scats encountered two weeks later. If transects vary in length, or the time between collections varies, then the index can be standardised to scats/km/day. A study by Knowlton (1984) found that scat deposition rates for coyotes were correlated with estimates of animal density derived from mark-recapture techniques using radio-isotope tagging of faeces. For long-term monitoring, scat transects should be conducted along the same routes at the same time of year to avoid introducing biases associated with differential prey digestibility and seasonal changes in food items consumed (Andelt and Andelt 1984). Misidentification of scats and heavy vehicle traffic on roadways can be problematic when using scat counts. Use of DNA techniques for identifying species from scats may alleviate the problems of misidentification (Foran *et al.* 1997a,b) and identification of individual animals collected during scat deposition transects could be used to estimate population size (Paxinos *et al.* 1997; Kohn *et al.* 1999). A recent study by Harrison *et al.* (2002) compared survey techniques for estimating relative and absolute abundances of swift foxes in New Mexico. This study found that for relative abundance surveys, the most efficient technique was collection of scats followed by verification of species depositing scats with DNA analysis, while for absolute abundance surveys, trapping and re-sighting with remote cameras at bait stations was more accurate than counting unique microsatellite DNA genotypes from collected scats.

Track counts along a transect

Tracks left by canids along river beds, dry washes, sandy fire breaks or roads, or on snow-covered roads and trails have been used as a relatively simple, efficient, and inexpensive measure of relative abundance for canids (e.g., Crête and Messier 1987; Servin *et al.* 1987). Canids which occupy regions that receive snow can be monitored by counting tracks along established transects one to two days after fresh snowfall. Some pitfalls when attempting transect counts of tracks should be noted. Misidentification of tracks and low power to detect population changes can occur with track counts (Ballard *et al.* 1995). Precision can be increased by increasing sampling effort, or increasing the length of transects if censusing highly nomadic species. Much of the power of this estimator is dependent upon a high rate of encountering sign along the transects (Kendall *et al.* 1992). When working in areas with snowfall, one must also consider the condition, consistency and depth of the snow, ambient temperature, and the time of year. As is typical for any survey technique involving sign, observer experience at interpreting tracks is also crucial for consistent and reliable monitoring.

Den and burrow surveys

Ground and aerial surveys for active dens have been conducted along transects to index relative abundance of some canids, mainly foxes (e.g., Trautman *et al.* 1974; Garrott *et al.* 1983; Hersteinsson *et al.* 2000). The key to this survey technique is relatively open habitat with little vegetative cover and a species that makes conspicuous dens or burrows. These surveys can be relatively expensive (aerial searches) and/or labor intensive (ground searches). The presence of faeces or tracks at the burrow or den can assist in species identification. Ground surveys along transects can also be used to calculate the density of dens if the perpendicular distance from the transect to the den is recorded. This technique does not work well for indexing canids with large social units. For animals that exist in packs, the number of active dens would more likely indicate the number of social units present across an area, but not the size of the social unit.

Vocalisation response surveys

For canids that utilise howls to communicate, the response rate to simulated vocalisations has been used as an index of relative abundance (e.g., Wenger and Cringan 1978; Okoniewski and Chambers 1984; Fuller and Sampson 1988; Robbins and McCreery 2003). Howling surveys typically employ recorded vocalisations, although human imitation can be used. Travelling along roads or trails and stopping at predetermined intervals, howls are produced and then observers listen for a specified amount of time for a response from the target species. A recent study using both playbacks and human simulations of long distance calls of African wild dogs recorded that dogs would approach from distances of as much as 2km, and found that playbacks are an effective conservation tool particularly where road networks are limited and/or thick vegetation restrict off-road driving (Robbins and McCreery 2003). Surveys may be conducted over several nights using the vocalisation response to estimate relative abundance. Standardisation and consistency of this method is needed for reliable and comparable results for trend analyses. The seasonal, social, temporal, and spatial factors that influence vocalisation rates also need to be noted (Harrington and Mech 1982; Walsh and Inglis 1989; Gese and Ruff 1998). For an accurate population census, the area of interest needs to be intensively surveyed to obtain adequate coverage (Fuller and Sampson 1988).

Frequency of depredation complaints

The frequency of livestock depredation complaints may be useful as an indicator of relative abundance under the general belief that animal abundance is correlated with rates of livestock predation. Because this relationship has not been explicitly tested, caution should be exercised when using this technique as depredation rates are subject to changes in livestock stocking rates, habitat type, size of area used, husbandry practices, and environmental variables (Knowlton *et al*. 1999).

Some considerations when using indirect methods

Indirect methods provide only relative abundance and must be applied consistently for any reliable comparisons between areas, habitats, or time. Whenever indices of relative abundance are used, it should be determined whether relative indices and absolute abundance are positively and linearly related. Comparison of an inexpensive indirect method to a more expensive direct method could prove worthwhile for calibration of the less expensive technique. During calibration, the techniques should be performed concurrently and conducted on a species-specific, habitat-specific, and seasonal basis. Unfortunately, few indices of relative abundance have been tested with a known population estimate.

15.3.2 Direct counts

Direct counts involve actually counting the animals themselves, in contrast to counting sign. These counts may use either dead animals (e.g., harvest reports, mortality samples) or live animals (e.g., trapping, sightings). The assumptions of direct counts and the estimators used to determine population size should be reviewed (Caughley 1977; Burnham *et al*. 1980; Skalski and Robson 1992). Counts may involve total counts of the area, or a subsample of the area with extrapolation to the rest of the area of concern. Stratification of subsamples by habitat type can increase the validity, usefulness, and precision of the survey (Macdonald *et al*. 1998).

Harvest reports and pelt registration

One method of estimating abundance (and distribution) of a species is using historical and current harvest or trapping records (e.g., Clark and Andrews 1982). In the Canadian provinces, mandatory pelt sealing reports have been used to estimate furbearer population trends (Novak 1987). While information from harvested animals can be used to construct models for population estimation (Clark and Andrews 1982), harvest data alone is generally not a reliable estimate of population trends. Pelt prices, trapper behaviour and memory recall, differential harvest methods, and environmental and social factors all influence harvest rates (Clark and Andrews 1982). For rare species, harvest reports are generally unreliable for population trends, while harvest reports for abundant furbearers may be reliable measures of population trend. However, little in-depth testing has been conducted to confirm the relationship between population density and harvest statistics.

Road mortality samples

The frequency of carcasses found on roads has been proposed as a measure of population trend, usually as an index of relative abundance (e.g., Clark and Andrews 1982). However, differences in animal behavior and movements, habitat, traffic density, road surface, and road density likely influence kill rates of some canids. The relationship between population density and road kill rate also has not been adequately examined. Road mortality samples can confirm species presence.

Drive counts

In certain habitats, animals may be driven into an area and counted as they cross the observer's line (e.g., Beltrán *et al*. 1991). This technique is labour intensive, due to the use of counters, beaters, and possibly hounds, and sample sizes may be difficult for statistical analyses and comparison.

Spotlight surveys

Spotlight surveys are a cost effective method typically used for assessing the relative abundance of nocturnal canids (e.g., Ralls and Eberhardt 1997; Schauster *et al.* 2002a). These surveys involve two observers standing in the back of a truck driven slowly along roadways, scanning the road and sides using spotlights. When an animal is detected, usually by eye shine, the driver stops and the observers identify the animal (sometimes using binoculars or a spotting scope). The mileage and time of detection is recorded for each sighting. An index of animals/km is then calculated. Spotlight counts can be used to estimate population size with line-transect methodology if the perpendicular distance to the sighted animal is recorded (Thompson *et al.* 1998). Transects need to be fairly lengthy, and because vegetative cover and topography influences visibility, these variables should be considered in survey design (Ralls and Eberhardt 1997). Surveys can be conducted over several nights (repeated counts) to obtain a measure of sampling error. Large samples with replication are needed to detect changes in population size with any statistical power (Ralls and Eberhardt 1997). Surveys can be conducted seasonally and annually for population trend analysis (Schauster *et al.* 2002a). Spotlight counts do not work well in areas with low densities of canids. A recent study by Ruette *et al.* (2003) has noted that a number of methodological improvements are necessary before spotlight distance sampling can become a routine monitoring tool for fox species.

Remote camera traps

While camera systems have been used to detect species presence and identify animals at bait stations or nests, they can also be used to determine abundance if individuals can be identified by artificial tags (e.g., ear tags, radio collars) or natural features (pelage, etc.) and then apply mark-recapture estimators. Harrison *et al.* (2002) found that re-sighting with cameras at bait stations was more accurate for estimating swift fox abundance than counting unique microsatellite DNA genotypes from collected scats. Remote cameras also provide a permanent photographic record. Disadvantages of remote cameras include their expense (although the technology is becoming increasingly affordable), getting animals to trigger the camera, non-target species activating the camera, and the delay between photo acquisition and development (although digital cameras may negate this concern).

Catch-per-unit-effort

Live-trapping gives a positive confirmation of species presence (distribution) and the number of animals captured per trap night can also be used as an index of relative abundance (e.g., Knowlton 1984; Crooks 1994; Schauster *et al.* 2002a). Trapping is expensive and labour intensive, and can be ineffective in areas with low density. In addition, standardisation of capture procedures and variation among individual trappers can cause problems.

Capture-mark-recapture

While mark-recapture is fairly time consuming, labour intensive, and costly, it has proved useful for estimating population size in canids (e.g., Roemer *et al.* 1994; Hein and Andelt 1995; Schauster *et al.* 2002a). Mark-recapture can provide relatively accurate estimates of population size if sample sizes are adequate, collection techniques are unbiased, and the basic assumptions for the population estimator are not violated (see Caughley 1977; Thompson *et al.* 1998, and references therein). This method involves capturing and marking individuals, then recapturing a number of the marked individuals again and estimating population size based upon the ratio of marked to unmarked animals recaptured using one of several models (e.g., Pollock 1981; Seber 1982). Marks employed to tag the animal include ear tags, radio collars, dyes, and physiological markers such as radioactive isotopes (Kruuk *et al.* 1980), iophenoxic acid (Knowlton *et al.* 1988), or chlorinated benzenes (Johnston *et al.* 1998). Recapture may involve physical recapture, re-sighting or photographs, returns from trappers or hunters, recapture via fecal analysis for a physiological marker, faecal DNA analysis, or a combination of these. If the extent of the area of interest is known, density estimates can be derived. Several models for population estimation (e.g., the Petersen, Jolly-Seber, and Schnabel asymptotic methods) can be used to calculate population size (Caughley 1977; Jolly 1982; Seber 1982; Thompson *et al.* 1998). Many of these models are available on computer software, such as CAPTURE (White *et al.* 1982), NOREMARK (White 1996), and EAGLES (Arnason *et al.* 1991).

Direct counts by removal

For some species that are considered pests, the removal method has been used to estimate animal abundance (e.g., Skalski *et al.* 1984). Disadvantages of this technique is the lack of knowledge of what proportion of the population was missed or not captured, and how large an area was affected by the removal. Due to the economic importance of the species, intrinsic values, and/or the social and ethical ramifications, the removal method is rarely employed.

Transect, strip, or area sampling

In certain circumstances, it may be possible to count the number of animals along transects, strips, in quadrants, or within a defined area and estimate animal population size or density (e.g., Burnham *et al.* 1980). Trends in relative abundance can be compared from direct counts; absolute abundance may be estimated if correction factors can account for problems with 'sightability'. Population estimates can also be calculated by distance methods along line-transects (Burnham *et al.* 1980). Software programs that estimate population size using distance data along transects include DISTANCE (Buckland *et al.* 1993, Laake *et al.* 1993) and TRANSECT (Burnham *et al.* 1980). Aerial surveys typically require a large species occupying sparsely vegetated habitat allowing for maximum 'sightability'. The number of animals sighted can be affected by animal behaviour, weather, vegetation, visibility, and observer experience and fatigue. The use of ultraviolet, infrared, or thermal imagery photography may enhance "sightability" (e.g., Havens and Sharp 1998). Ground surveys are practical for animals readily viewed in open habitats. In certain situations, the entire area of interest may be surveyed, and through repeated sampling, the entire population may be counted. However, the ability to count all individuals in an area is rare, but correction factors from a radio-marked sample allow determination of a more accurate estimate of population size. For transect and sighting surveys, it is important that the different habitats within the area be sampled, not just the areas with good visibility.

Identification of individual animals

While the opportunity to directly observe canids may be considered rare, there are certain species living in national parks or reserves with open habitats that allow for direct observation and identification of all individuals in the study area. Maddock and Mills (1993) censused African wild dogs by collecting photographs from tourists and other field personnel. They were able to identify 357 wild dogs from 26 packs by examining more than 5,000 photographs. Studies using identification of individuals are usually conducted in relatively open habitat and with a species that is observable and tolerant of human presence. Also, the animals do not necessarily need to be marked for individual identification, as individuals may be re-sighted and identified indirectly. Track characteristics have been used in which tracks of individual animals were separated on the basis of characteristics and location. The main advantage of using characteristics of individual tracks for identification is that it entails less effort than a large-scale trapping programme, although the accuracy of this method in relation to changes in population size remains untested. While individual identification allows for a relatively complete count, the time and effort necessary means that this method is useful only in particular situations and is often conducted in conjunction with behaviour studies (e.g., Gese *et al.* 1996c). Again, the use of hair snares to acquire hair samples can be used with DNA sequencing to identify individuals in the population.

Radio-telemetry

The advent of radiotelemetry increased the ability to monitor secretive canids. Using this method, one can estimate the home range or territory size of an animal. It is now widely accepted that combining territory size (and overlap) with the number of members of the social unit, plus the percentage of radio-collared transients sampled from the population, density estimates can be derived for the population (e.g., Mech 1973; Fuller 1989). For more solitary species, estimates of home-range size, the extent of inter- and intrasexual home-range overlap, and the proportion of transients in the population are used to estimate population density. While radiotelemetry is labour intensive and costly, this technique provides one of the best and most reliable estimates of population density for many species. With the advent of satellite and GPS technology, more intensive monitoring of large and medium-sized canids will be possible (e.g., Ballard *et al.* 1998; Merrill *et al.* 1998), but the technology is still somewhat expensive and systems for smaller species will require further technological development.

Águas Emendadas Ecological Station is one of the most important regions to conservation in Distrito Federal, Brazil, but is threatened by urban expansion. It is a protected area, devoted solely for preservation purposes, and is home to many ecologically important native species being monitored, including the maned wolf (*Chrysocyon brachyurus*), crab-eating fox (*Cerdocyon thous*) and hoary fox (*Pseudalopex vetulus*). This radio-collared adult female maned wolf vocalises when a researcher approaches her cub. Águas Emendadas Ecological Station, Distrito Federal, Brazil, 1997.

Flávio Rodrigues

15.4 Conclusions

The methods and techniques available for determining the presence and abundance of canid species are varied, and this chapter has attempted to illustrate by means of examples some of the instances where these techniques have been applied to studies on canid populations (or other similar large predators) and the advantages and disadvantages of each. While a combination of methods is always likely to provide the best results (see, for example, Schauster *et al*. 2002a), the feasibility and application of the appropriate methodology will always depend on factors such as the species, habitat, costs, manpower, time constraints (Lancia *et al*. 1994), and also on the kind of questions that are being addressed and the consequent accuracy and power of the statistical assumptions of each method (Skalski and Robson 1992).

Chapter 16

Captive Canid Conservation

K.L. Bauman, C.S. Asa, J. Grisham and W. Verberkmoes

16.1 History of canids in captivity

Wild animals have been kept in captivity for thousands of years. Military conquests and trade with foreign lands created large royal collections of exotic animals in countries including China, Egypt, and England. In the 18th and 19th centuries, several large European collections were opened to the public for the first time. These menageries or zoological parks became places of public entertainment where strange and unusual animals could be seen. The Austrian Royal collection became the Tiergarten Schonbruun (1752) and the British Royal family formalised their menagerie as the Zoological Society of London in 1828. This increase in popularity in the 19th century resulted in the opening of hundreds of new zoological parks worldwide, including the Royal Melbourne Zoological Gardens (1857), Zoological Society of Philadelphia (1874) and Jardín Zoológico Municipal de Buenos Aires (1874).

Many early zoological collections included wolves and foxes, well known to the visitors from legend and livestock predation. The Zoological Society of London (ZSL) held grey wolves (*Canis lupus*), coyotes (*C. latrans*) and raccoon dogs (*Nyctereutes procyoniodes*) prior to 1900 (Crandall 1964), while the Philadelphia Zoo received their first fennec fox (*Vulpes zerda*) in 1900 (Bauman 2002). Most canid species proved to be quite adaptable to captivity and longevity was high. For example, a grey wolf captured as a pup lived for more than 15 years at the Bronx Zoo (Crandall 1964). Many canid species reproduced quite readily, including the raccoon dog (ZSL 1877), grey wolf (Bronx Zoo 1902, and ZSL 1903), coyote (Bronx Zoo 1900), and dhole (*Cuon alpinus*) (ZSL, late 19th century) (Crandall 1964). Captive breeding success came later for some of the more sensitive canid species with the birth of the first litter of African wild dogs (*Lycaon pictus*) in 1942 (M. Quick pers. comm.), fennec foxes in 1954 (Bauman 2002) and maned wolves (*Chrysocyon brachyurus*) in 1967 (Crandall 1964).

Despite these strides in captive breeding, overall success was still limited and unable to meet the demand for animals, resulting in the continuing capture of wild animals to fill exhibits. However, by the mid-20th century it had become clear that nature did not have an inexhaustible supply of animals, and the days of easy importation of wildlife for zoos were rapidly diminishing. This knowledge, combined with the increasing awareness of the responsibilities of zoos for managing wildlife, made clear the importance of accurate record keeping. Studbooks (or pedigrees) became prevalent in the late 1960s and early 1970s, and the International Species Information System (ISIS) was founded in 1973.

Michelle Nelson

Captive bred African wild dog pups, born at the Mountain View Conservation and Breeding Society facility. Fort Langley, British Columbia, Canada, 2003.

Zoos began to take a more active role in species conservation in the early 1970s with the passage of the U.S. Endangered Species Act and establishment of the Convention on the International Trade of Endangered Species of Flora and Fauna (CITES). The first opportunity for zoos to directly participate with the recovery of a canid species came when the United States listed the red wolf (*Canis rufus*) as endangered in 1967. The passage of the Endangered Species Act resulted in the creation of the United States Fish and Wildlife Service's (USFWS) Red Wolf Recovery Program, which listed captive breeding as a priority (Parker 1988). The Point Defiance Zoo was selected to develop the captive breeding programme, which included providing the space and expertise to develop the resources critical for the reintroduction programme. In 1981, the continued decline of wildlife populations led the American Zoo and Aquarium Association (AZA) to focus captive breeding efforts and to form the Species Survival Plan (SSP7) programme. The SSP7 concept was based on long-term management of a species, wherein all animals in AZA accredited zoos form a large, cooperative breeding programme. The red wolf was one of the first AZA SSP7s (1984), with 63 wolves in four zoos. In other regions of the world, conservation programmes similar to SSP7s were developed. In Europe, the European Endangered Species Programme (EEP) developed captive conservation programmes for carnivore species, while Australia, Japan, China, South Africa, and Central and South America developed similar programmes.

Established in the 1990s, Taxon Advisory Groups (TAGs) became responsible for coordinating the captive efforts for the entire taxonomic group by developing a Regional Collection Plan. The TAG also facilitates captive conservation efforts through a network of field researchers associated with universities, conservation, and governmental agencies. Data from the IUCN Canid Specialist Group are now routinely incorporated into collection management decisions. For example, the publication of the 2002–2005 AZA Canid and Hyaenid TAG Regional Collection Plan was timed to take advantage of the recommendations from the Canid Biology and Conservation Conference hosted by the Canid Specialist Group in Oxford, UK, in September 2001. Modern day zoos and zoo-based programmes for canid species provide support for canid conservation in a variety of ways including captive breeding, education programmes, research and the funding of field initiatives.

16.2 Contributions of captive canids to conservation

The history of canids in captivity provides an excellent framework from which the evolution of zoos can be seen. The contributions captive canids have made to conservation are often overlooked, while the benefit of captive breeding continues to be debated among some conservationist biologists. For example, without captive space and expertise, neither the red wolf nor the Mexican wolf (*Canis lupus baileyi*) recovery programmes would have had the resources necessary for their reintroduction and educational programmes. Additionally, research on captive canids in the areas of reproductive physiology, genetics, veterinary medicine, nutrition and behaviour have increased our understanding of canid biology.

16.2.1 Genetic reservoirs

Captive breeding is the basic function of every zoo. This requires an understanding of the species' natural history, appropriate husbandry, proper animal health and diet, plus skilled staff, an accurate pedigree, and the space to house multiple individuals. The decisions of which animals to breed, with whom, and how often are pivotal to every captive breeding programme (Ballou and Foose 1996). It takes many years and, in most cases, many institutions working cooperatively to create a viable captive population numbering in the hundreds. In the extreme, captivity is the last refuge for a species, as has been the case for the Mexican wolf, red wolf and island fox (*Urocyon littoralis*). Ideally, captive breeding is utilised as an *ex situ* conservation tool in a proactive rather than reactive manner, and preferably always in conjunction with *in situ* conservation actions.

Zoos are often criticised for having breeding programmes for non-threatened species, yet there are justifications for this approach. If captive breeding is done properly, managing for genetic diversity, then these populations serve as genetic reservoirs (Ryder and Fleischer 1996), if needed, for reintroduction, re-stocking or genetic exchange. Clearly, not all species will require these techniques, yet the status of wild populations are often tenuous, and unforeseen stochastic events have made many species that were common not too long ago, threatened today. For example, the wild population of maned wolves, which was previously considered stable, has shown recent evidence of decline and field research has begun to determine the scope of the problem. The captive population of maned wolves represents a source of animals if needed. Similarly, the fennec fox currently is listed as Data Deficient on the IUCN Red list (Appendix 1), as are many other fox species. Since the status of these wild populations is completely unknown, it is possible that the captive population of fennec foxes may be needed in the future as a source of unrelated individuals. Additionally, the husbandry techniques utilised for captive breeding of fennec, swift (*Vulpes velox*) and island foxes may someday prove a valuable tool for saving other fox species.

16.2.2 Educational programmes

All conservation organisations work to raise public awareness of the issues facing wildlife conservation through various communication channels, such as magazine articles, posters and television documentaries. Zoos have the advantage of being able to provide people a direct connection with animals. The opportunity to see a Mexican wolf pup's antics or touch a fennec fox while learning about its desert home provides a lasting connection. Collectively, AZA zoos in the USA receive over 130 million visitors per year, more than professional baseball and football games combined. This provides a tremendous opportunity to teach visitors about the importance of the conservation of wild dogs, wolves, foxes and jackals. Many canids need the good public relations of educational programmes to bring attention to their conservation needs. Often portrayed as ravenous predators, little would be known about canids and their conservation dilemma if it were not for zoos helping spread the message to countless visitors.

Zoos also have begun to educate visitors about local conservation issues. The Santa Barbara Zoo in California has taken a leadership role in educating the public about the island fox. They are one of only six zoos in the U.S. currently exhibiting island foxes. Graphical displays explain the reasons for the decline, what biologists are doing to address the problems and actions that can be taken to save the species (for example, not bringing unvaccinated domestic dogs to the Channel Islands). They participate in the Island Fox Recovery Team run by the U.S. National Park Service, lending staff and equipment to the project. A similar programme has been proposed for swift fox. Since all captive swift fox in AZA zoos are within the native range, the educational impact on the local level could be very high. However, not all education programmes are directed at zoo visitors; the need for educational efforts in range countries is also important. The Maned Wolf SSP7 has worked with Brazilian biologists to produce and distribute a poster about maned wolves to local villages. Written in Portuguese and Spanish, the poster not only provides species information, but also strives to inspire national pride.

16.2.3 Reintroduction*

Reintroduction attempts to establish a species in an area which was once part of its historical range, but from which the species has been extirpated (Kleiman and Beck 1994). It has been well accepted that reintroductions are complex undertakings with a multitude of biological, ecological and social factors that require long-term commitment of resources. Reintroductions of canids have occurred using both wild-born (e.g., grey wolves in Yellowstone) and captive-born animals (e.g., red and Mexican wolves). There was a brief period in the late part of the last century when zoos billed themselves as 'modern arks', a concept that promoted the idea that animals bred in captivity existed as sources for reintroduction programmes. It is now recognised that providing animals for reintroduction is merely one of many roles of a modern zoo. A study examining the use of captive-bred animals (all taxa) as sources for reintroduction suggested these releases were successful 11% of the time (Beck *et al.* 1994). Reintroduction programmes for canids have had success using captive-born individuals in red (Waddell 1996) and Mexican wolves (Lindsey and Siminski 2003), African wild dogs (Mills 1999) and swift foxes (Boitani *et al*. 2004). In African wild dogs, released packs were comprised of both wild- and captive-born individuals, whereas the red and Mexican wolf recovery programmes released only captive-bred animals. The swift fox programme utilised both captive-bred and translocated animals and did find a higher survival rate in the translocated individuals (Boitani *et al*. 2004).

Zoos have greatly contributed to the success recovery programmes, including captive breeding and reintroduction of red and Mexican wolves. These programmes have benefited from the partnership between the zoos and USFWS by building on the respective strengths of each partner. In addition, captive breeding forms the basis of island fox recovery, for which reintroduction is the ultimate goal.

Red wolf

Declared endangered by the USA in 1967, the red wolf officially became extinct in the wild in 1980 after eight years of intense trapping effort by the USFWS (Parker 1988). The decision to remove all red wolves from the wild, while aggressive, was justified by the goals of the Recovery Programme. The goal was to establish a captive breeding colony of genetically pure red wolves, as determined by genetic testing, and supply animals for the release programme (Parker 1988). The breeding colony was established through a cooperative agreement between USFWS and the Point Defiance Zoo. Forty wolves were moved to the Point Defiance Zoo for breeding and further genetic testing, and of those 17 were certified as 'pure' (Parker 1988; Bergman 1997). Infanticide occurred in the first several litters, but husbandry modifications resulted in successful reproduction from 14 of the certified wolves (Bergman 1997).

In 1984, when the red wolf programme became an SSP7, the population had grown to 63 animals at five zoos (Waddell 1995); in 2003 there were 153 animals living in 35 institutions in addition to those in the wild (Waddell 1995, 1996). Since the release of four captive pairs of red wolves in eastern North Carolina in September 1987, red wolves have formed family groups, established territories and

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* Note: Additional information relating to reintroduction programmes for canids can be found in Chapter 17.

produced young. Since the beginning of the project, 69 animals have been released and more than 127 pups have been born in the wild. Currently, 90% of the free-ranging wolves in eastern North Carolina at Alligator River Wildlife Refuge are wild-born, which illustrates the biological success of the restoration efforts (Phillips 1997; Waddell 1997). Pup mortality has been higher in litters born to captive-born females than to wild-born females, 25% and 6%, respectively (Bergman 1997). To continue genetic exchange, new techniques such as cross-fostering captive-born pups to wild litters have been developed at the Point Defiance Zoo and show promise (W. Waddell pers. comm.). The programme has had its share of problems and controversies, including the question of the genetic purity of the red wolves released into the wild (Wayne *et al.* 1998), but the success of the reintroduction programme has paved the way for additional programmes.

Mexican wolf

The Mexican wolf is the rarest and most genetically distinct subspecies of the grey wolf in North America. Endangered in both the USA (1976) and Mexico (1974), the Mexican wolf was considered extirpated from the USA in 1970. It is considered extremely rare or extinct in Mexico, where it has not been seen in the wild since 1980. The USFWS conducted trapping efforts in Mexico between 1977 and 1980, capturing five individuals, considered to be the last Mexican wolves in the wild (Siminski 2002). Three zoos in the USA volunteered to provide space for the wolves (Lindsey and Siminski 2003) and a captive breeding programme was begun in collaboration with the USFWS Mexican Wolf Recovery Team. Management of the breeding programme became the responsibility of the holding institutions in 1985, with the formation of the Mexican Wolf Captive Management Committee (Lindsey and Siminski 2003). The Captive Management Committee worked in collaboration with the governmental agencies in both countries, the Instituto Nacional de Ecología de la Secretaria del Medio Ambiento Recursos Naturales y Pesca in Mexico and the USFWS in the United States.

In 1993, the Captive Management Committee reorganised as an SSP7, becoming the first bi-national SSP7 programme. The mission of the Mexican Wolf Programme has been to support the re-establishment of the Mexican wolf in the wild through captive breeding programmes, public education, and research (Siminski 2002). Extensive genetic testing resulted in two additional captive populations of Mexican wolves to be certified as 'pure', one population originated from the Chapultepec Zoo in Mexico City and the other from private ownership in the USA (Shields *et al.* 1987; Weber-Rodriguez 1989; Fain *et al.* 1995; Hedrick 1996; Garcia-Moreno *et al.* 1996). These two populations were integrated into the breeding programme, which in 2002 consisted of 241 individuals in 47 institutions (USA and Mexico).

All holding institutions follow captive management techniques that were designed for the goal of reintroduction: decreased human contact and large exhibits with natural conditions to increase the chance of exposure to prey. Immediately prior to release, selected wolves are moved to pre-conditioning pens that are not open to the public, for acclimatisation and further evaluation (Lindsey and Siminski 2003). The first reintroduction of Mexican wolves in the USA occurred in 1998 at the Apache National Forest in Arizona when 11 captive-born wolves were released from their acclimation pens into the wild. Additional releases have occurred on the reservation of the White Mountain Apache Tribe in Arizona on land contiguous with the Apache National Forest. The initial releases were not without problem, and several wolves were shot by hunters. However, as of 2003 there are at least 32 free-ranging Mexican wolves in Arizona and New Mexico. Releases in Mexico are planned for 2004.

Island fox

The primary justification for establishing captive populations of island foxes was protection. Dramatic declines in the numbers of free-ranging foxes on four of the California Channel Islands resulted in recommendations that foxes be captured and maintained in pens on the islands until the cause(s) of decline could be determined and mitigated. Captive breeding was a secondary objective, meant to increase the number of animals until release would be feasible (Coonan 2002). Captive breeding of the wild-caught animals has been generally successful, although some genetically important individuals have not reproduced (Coonan and Rutz 2003).

The foxes in captive facilities on the islands cannot be transferred to mainland zoos due to regulations against them being moved back to the islands later for release after being held on the mainland. The concern centres on the potential for diseases or parasites being introduced to the islands, which could hinder recovery efforts. There are, however, island foxes from San Clemente Island in six mainland zoos. This exception highlights the different histories of the foxes from the various islands. First, the foxes inhabiting each of the six islands are considered separate subspecies, so are being managed separately, and only four of the six subspecies are currently considered endangered by the USFWS. The foxes on San Clemente Island are not among the four considered endangered, but were found predating on the endangered San Clemente loggerhead shrike. To protect the shrikes, foxes were captured, and some were transferred to mainland zoos where they serve primarily an educational function as the focus of a programme to inform Californians about the plight of their cousins on the other islands.

However, unless reintroductions can proceed in the near future, the growing number of foxes in the island captive facilities may necessitate the transfer of at least some individuals to mainland zoos. A recommendation from the most recent Island Fox Working Group Meeting (Coonan 2002) is to establish goals for the San Clemente foxes in mainland zoos. Possible outcomes might be phasing out San Clemente Island foxes to create space for other subspecies for a breeding programme or to house surplus non-breeding foxes from the islands. The Canid and Hyaenid TAG will participate in these discussions.

16.2.4 Research

Although we may never be able to reintroduce maned wolves, bush dogs (*Speothos venaticus*) or the other canid species back into nature, studies of captive animals can provide insight into their biological processes that can inform conservation programmes. Many techniques, such as hormone assays, and medical treatments, such as vaccine regimes, can be tested and validated in captivity for later transfer to the field. Knowledge of husbandry techniques can also be of direct benefit to wild populations. When the decision was made by the National Park Service Island Fox Recovery Team to remove animals from the wild, information on pen design, shift doors and nest box design developed for fennec and swift foxes were used to design the captive facilities.

The behavioural needs of canids in captivity present a challenge due to limited space and the need to manage the genetics of the small population, which results in the creation of artificial pack situations. Research documenting responses to introductions of related and non-related individuals are being monitored in African wild dogs as a method to improve reintroduction outcomes (K. McCreery pers. comm.). Basic information on mating behaviour and parturition can be recorded in the captive setting with time-lapse infrared video cameras capable of recording 24hrs without the need for human presence. These systems have been used to provide valuable data on parturition success in the Mexican wolf (S. Lindsey pers. comm.) and are being used to study courtship and mating behaviour of the island fox.

Genetic management

Zoo populations are small even when managed collectively, and small populations require intensive effort to manage genetic diversity. The effort by zoos to keep accurate studbooks and manage their captive populations for retention of genetic diversity creates opportunity for studies of theoretical population management (Ryder 2003). Although there may be a great deal of debate regarding this concept, wildlife reserves and sanctuaries are becoming more isolated and the insight gained from zoos in the management of small population genetics can greatly assist the management of free-ranging wildlife in the future.

Reproductive physiology

Captive populations have also been the focus of studies of reproductive physiology and the development of assisted reproductive techniques, such as semen cryopreservation and artificial insemination. Very little is known about basic reproductive parameters for most canids. Grey wolves, coyotes, and red (*Vulpes vulpes*) and Arctic foxes (*Alopex lagopus*) are the exceptions, primarily because reproductive tracts were often examined when animals were killed as part of predator control programmes. In addition, because the two fox species are also bred for fur production, some aspects of their reproductive physiology have been thoroughly studied. Data on basic reproductive parameters, such as the number of oestrous cycles per year, the extent of reproductive suppression of subordinates, and other life history data, have not been systematically documented for most other canid species. Such information is important not only for managing captive and free-ranging populations, but forms the basis of Population and Habitat Viability Analyses (PHVA).

Captivity can provide the ideal setting for reproductive studies, because the animals are likely to be habituated to human presence. Also, samples for hormone monitoring can be more easily obtained than from wild individuals. Hormone patterns during reproductive cycles have been published for fennec fox (Valdespino 2000; Valdespino *et al.* 2002) and red wolf (K. Goodrowe pers. comm.), are ongoing for bush dog (K. DeMatteo pers. comm.), island fox and New Guinea singing dog (C*anis hallstromi* – see section 9.1, p. 223) (C. Asa and J. Bauman pers. comm.) and have begun in maned wolf (N. Songsasen pers. comm.). Semen traits have been characterised and extensive development of semen cryopreservation techniques has been conducted for both red (Goodrowe *et al.* 1998, 2001) and Mexican wolves (Asa 2001; Musson 2001; C. Zindl unpubl.). Semen from genetically valuable individuals is maintained in semen banks for both of these species as part of the captive management plan.

Although records from ISIS and studbooks are not collected as part of prospective research, they do provide a source for some basic life history data, such as age of first reproduction, reproductive life span, inter-birth interval, seasonality and litter size. However, caution must be used when examining these data as captive management practices may affect results. For example, in most cases data on mate access are not recorded so inter-birth interval could be over-estimated.

In addition, if small isolated populations are to be managed genetically, basic assisted reproductive techniques such as artificial insemination could be an important substitute for translocating animals. Unfortunately, manipulation of the canid reproductive cycle has proven more difficult than in most other species. Improvements in the success rate of artificial insemination in the domestic dog are encouraging, but the extensive handling required to determine the time of oestrus and ovulation plus repeated inseminations make the technique impractical or even unacceptable for application to wild canids. However, recent success with inducing oestrus and ovulation with a short-acting GnRH agonist (Ovuplant7: ZooPharm, Ft. Collins, Colorado) in grey wolves, followed by either natural mating or artificial insemination, resulted in the birth of live pups (C. Asa and K. Bauman unpubl.). This technique provides an alternative to monitoring the hormonal changes associated with ovulation and permits inseminations to be properly timed.

More advanced methods of assisted reproduction, such as embryo transfer and in vitro fertilisation, are also more difficult in canids than in other species and require even more handling and manipulation than does artificial insemination. For assisted reproduction beyond semen cryopreservation or artificial insemination to become part of recovery or management programmes, considerable research and development are necessary. However, such advanced methods may not contribute substantially more than artificial insemination.

Another challenge to reproductive management or monitoring in canids has been detecting pregnancy, because of the obligate pseudopregnancy that follows ovulation in females that do not conceive (Asa 1996). This pseudopregnancy has previously been indistinguishable from pregnancy with assays for progesterone, the steroid hormone characteristic of pregnancy. However, an assay for relaxin, a peptide hormone elevated by mid-gestation in pregnant but not pseudopregnant females, has recently been validated for generic grey and Mexican wolves and for island foxes (J. Bauman pers. comm.). Developed for domestic dogs (WitnessRelaxin, Synbiotics Corp. USA), this assay may also be accurate for pregnancy detection in other canids.

Contraception and population control

Contraception has been used successfully in zoos for more than 25 years for genetic management and to limit production of surplus animals, but attempts to extend the application of contraceptive or sterilisation techniques to free-ranging populations have been problematic. Difficulties include delivery and species specificity, but application to canids presents problems beyond those encountered with other mammalian taxa. The commonly used progestin-based contraceptives are effective but are associated with potentially lethal side effects (reviewed in Asa 1996). The zona pellucida vaccines that have proven successful in some free-ranging ungulates appear to cause irreversible damage to the ovaries of canids (Mahi-Brown *et al.* 1988). However, hopes that a single injection of the vaccine might be effective as a chemosterilant have not been successful (J. Kirkpatrick pers. comm.).

Although administration of contraceptives or sterilants to free-ranging animals presents additional challenges, the results of research and monitoring efforts in captive populations can provide basic information on efficacy and safety. Currently, a promising new contraceptive alternative for canids is being tested in zoos. The GnRH agonist implant Suprelorin7 (Peptech Animal Health, Australia), which appears to be safe and effective for up to one year in both domestic (Trigg *et al.* 2001) and African wild dogs (Bertschinger *et al.* 2001, 2002), may provide an alternative for free-ranging as well as captive canids. Trials with two other canid species (grey wolves and bush dogs) have been less successful, although failures are believed to be due to inadequate dose (Bertschinger *et al.* 2001). As an alternative to reversible contraceptives, a technique for chemical vasectomy developed in domestic dogs (Pineda *et al.* 1977) can achieve permanent sterilisation in the field without surgery.

Immobilisation

Although small canids can often be manually restrained for quick procedures, large canids must be chemically restrained for safe handling. The dissociative anaesthetics ketamine and Telazol (tiletamine plus zolazepam) are most frequently used with captive canids (for reviews see Kreeger 1999 and Kennedy-Stoskopf 2003). Many immobilisation drugs or drug combinations are often first tested in captivity, especially on species where little field research has occurred, such as bush dogs. Some modification may be needed to decrease the induction time for free-ranging animals, but should be determined on a species-by-species basis.

16.2.5 Animal health and nutrition

Captive canids are routinely vaccinated for disease, and data on reactions are recorded in the medical records. New vaccines or vaccine regimes can be tested in the captive setting as well, since animals can be closely monitored and blood samples taken at intervals to evaluate serological titers. One of the outcomes from the 1996 African Wild Dog Master Plan meeting was the recommendation from regional coordinators, as well as representatives of the Canid Specialist Group, to utilise the captive population for vaccine testing for distemper and rabies. Distemper vaccine testing has also been requested for the island fox, perhaps using the generic gray fox (*Urocyon cinereoargenteus*) as a model.

In addition to data on vaccination and immobilisation protocols, results of blood chemistries are recorded and submitted to ISIS to the physiological reference database. Examples of these reference values for both serum chemistries and haematological parameters can be found in Kennedy-Stoskopf (2003).

Nutrition is an important component of animal health. Recent advances in the formulation of meat-based diets have decreased bacterial load and increased palatability in carnivore diets (Allen *et al.* 1999). Specific nutrition concerns of canids in captivity are rare, but maned wolves have been problematic, with poor body condition and coat, dental problems and a poor reproductive rate (Bush 1980). Cystinuria, or excessive levels of cystine in the urine, has been documented in maned wolves. Originally cystinuria was thought to be linked to diet in captive maned wolves, but it has also been found in wild maned wolves (M. Rodden pers. comm.). Research on dietary factors and the formulation of new diets are ongoing (Childs *et al.* 2001).

16.2.6 Funding

The financial contribution zoos make to canid conservation in the form of support of captive breeding programmes and direct support for *in situ* projects is substantial. The Red Wolf SSP7 programme was the subject of a study by a Cornell University economist William Rosen, who estimated that zoos spend about $351,000 per year on facilities, food and staff (Bergman 1997). If that figure is multiplied by the other SSP7 programmes managed at AZA facilities, then that would suggest that AZA zoos spend more than $1,404,000 per year on canids alone. Additionally, zoos fund numerous field research and educational initiatives each year, although no figure exists for the amount spent directly on canid programmes. AZA zoos have contributed over $10,000 in support of African wild dog field projects and $11,000 for the Ethiopian Wolf Population and Habitat Viability Analysis (PHVA) meeting.

16.3 Structure of captive canid programmes

The programmatic structure of all captive conservation programmes is dictated by the regional zoo associations. Three of these, the American Association of Zoos and Aquariums (AZA), the European Association of Zoos and Aquariums (EAZA) and the Australasian Regional Association of Zoological Parks and Aquaria (ARAZPA), have well-organised and active programmes for canids. All have recently published Regional Collection Plans for canids. It should be noted that other programmes do exist in zoos in other places of the world (for example, Brazil, details of which are not published and, therefore, could not be included in this chapter). Since the movement to organise individual zoos into cooperative components of a conservation network began in North America, we will rely heavily on the AZA model to describe how the organisation of captive programmes facilitates the support of canid conservation.

The studbook forms the foundation for all captive programmes. Accurate pedigree data are vital to genetic management of the captive population, and breeding decisions are based on the genetic and demographic information contained in the studbook.

16.3.1 Species Survival Plans

The SSP focuses captive breeding and conservation efforts at the species level. The main function of an SSP is coordination of captive efforts. For example, the AZA Mexican Wolf SSP meets annually with the counterpart Mexican zoo team to discuss progress and problems. Captive wolves in the two countries are managed as one population, with international transfers becoming more common as genetic pairings are recommended between wolves residing on different sides of the border. Representatives from USFWS also attend these meetings, as well as similar ones for the red wolf, to coordinate reintroduction efforts. Although educational programmes can be targeted at the taxon level, the majority are facilitated through the individual SSP programmes. These programmes typically include an explanation of the conservation need and the status of both the wild and captive populations. Educational materials, especially *ex situ* programmes are also vital for schools in range countries. All information necessary to maintain a SSP species in captivity is published in husbandry manuals. These manuals are updated every few years and contain recommendations for housing, nutrition, veterinary care, social groupings, contraception and behavioural needs. Funding for species-specific research and *ex situ* projects is also facilitated through the SSP.

Species level management exists at the highest level for: Iberian wolf (*C. l. signatus*) (EAZA), maned wolf (EAZA, AZA, ARAZPA), bush dog (EAZA), African wild dog (EAZA, AZA), fennec fox (AZA, ARAZPA), red wolf (AZA) and Mexican wolf (AZA). Species-level management also exists for: fennec fox (EAZA), dhole (ARAZPA), African wild dog (ARAZPA) and island fox (AZA). Both EAZA and AZA have dedicated space for the Ethiopian wolf (*Canis simensis*) if the Ethiopian authorities request future support.

16.3.2 Taxon Advisory Group

Zoos have made great strides in efforts to ensure that each species in captivity has a role to play in canid conservation. Decisions regarding which species are kept in captivity are made by the TAG during the creation of the Regional Collection Plan by evaluating all the based on an objective set of criteria.

The AZA Canid and Hyaenid TAG Regional Collection Plan (RCP) was published in 2002. The scope of the RCP includes all canid species, even though some of the species have no history of being in captivity. Taxonomic classifications were adopted from the Canid and Wolf Specialist Groups and excluded subspecies, with the exception of the Mexican wolf, which is of specific conservation concern in North America.

Since zoos have limited space to hold canids, it is vital that the RCP take into account the current number of spaces available for each species, in addition to the number of projected new spaces. Additionally, captive populations in other regions were assessed, where relevant, to reduce duplication of effort.

Conservation status was taken from three sources: *The 2000 IUCN Red List of Threatened Species* (see http://www.redlist.org for the most recent Red List); *Foxes, Wolves, Jackals and Dogs: An Action Plan for the Conservation of Canids* (Ginsberg and Macdonald 1990); and the U.S. Fish and Wildlife Service web site (http://www.fws.gov). Two decision trees were constructed, one for species currently held (Figure 16.1) and another for those not currently held in AZA zoos (Figure 16.2). The conservation status of the species in the wild was the most important selection criterion. Key elements included listing the specific programme contribution, e.g., genetic reservoir for reintroduction purposes, fund-raising or research and whether there was a recommendation for captive programme from field scientists. Priority was given to programmes already established, resulting in lower ranks for populations not in captivity. Discussions after the decision-tree ranking regarding the perceived costs and benefits to each captive programme included existing husbandry skills and interest from member zoos in the species.

Then, based on rank, each species was placed in one of six categories: Species Survival Plan (SSP) with intense, captive management; Population Management Programme

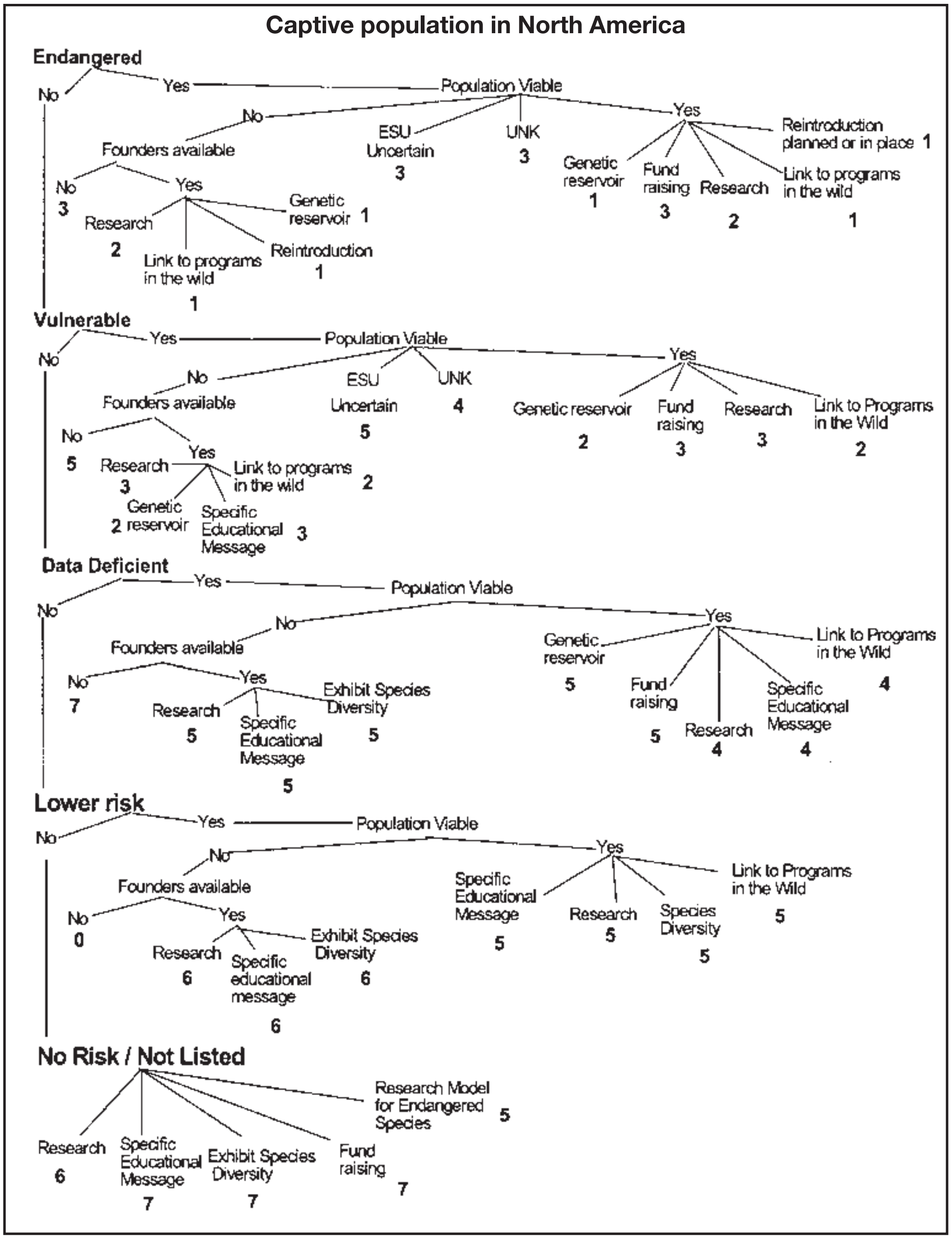


Figure 16.1. Decision tree for canid species currently held in AZA zoos. The decision tree model places selection criteria with the highest priority on the top 'branches'; the lower the 'branch', the lower priority.

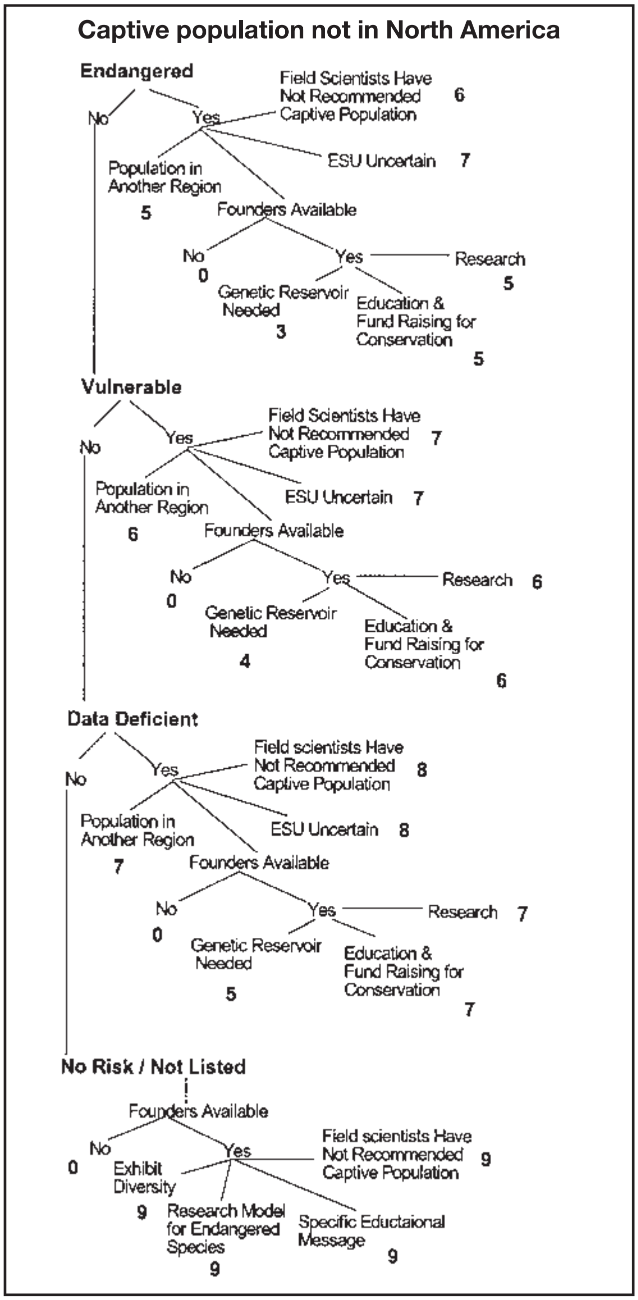


Figure 16.2. Decision tree for those canid species not held in AZA zoos. The decision tree model places selection criteria with the highest priority on the top 'branches'; the lower the 'branch', the lower priority.

(PMP) with long-term captive management, but less intensely managed genetically than an SSP; Display/ Education/Research Population (DERP), for species where no genetic or demographic management is needed; Phase-in Population (PIP), for any new species requiring a management programme; Phase-out Population (POP), for species with low conservation status, and whose space could be better utilised to house species of higher conservation status; and No Recommended Programme (NRP), for species with no current management programme and that, despite threatened status, are not recommended for management. The inclusion of the category for phasing out a species acknowledges that a greater contribution to conservation can be made with fewer, higher quality programmes rather than the more traditional approach of exhibiting the greatest diversity of species within a taxon.

16.4 Conclusions

In his book the *Management of Wild Mammals in Captivity*, Crandall (1964) described the evolution of zoos well by stating that "...the zoological garden is a fluid, moving entity, changing so constantly in concept and execution...". Indeed, zoos have been transformed from places for the public to view the strange and the unusual, to organisations that contribute resources directly to conservation efforts. Today, zoos have realised that captive programmes support conservation in many ways: education, captive breeding, reintroduction, scientific research and funding are all tools that zoos provide.

However, due to limited resources in zoos worldwide and the importance of captive breeding to the conservation of canids, the captive breeding community will need to work even closer with conservation biologists to identify where to prioritise their activities and research. Increased communication between the canid TAG programmes of all zoo associations and the Canid Specialist Group is essential. There has been much effort on the part of zoos to better integrate captive efforts with the needs of conservation in the wild, but work must continue in this area. Continued support of field research initiatives is essential, and not only of species held by zoos in their collections. In addition, there should be increased communication among the TAG programmes of the various zoo associations to further reduce duplication of effort, and to facilitate exchange of ideas and techniques. An important action over the coming years will be to assist zoos in regions of the world with high wild canid density, and/or not covered by a zoo association, through the formation or support of captive programmes.

While it is essential that zoos continue to support basic research in the areas of husbandry, behaviour, genetics, reproductive physiology, contraception and population control, immobilisations, vaccines, animal health and nutrition, and genome resource banks, an important recommendation is the need to create a process in which captive canid programmes can be objectively evaluated. The evaluation should cover the genetic and demographic goals of the captive population, research efforts and contribution and link to field conservation efforts. This will assist zoos in remaining focused on the relationship between the captive population and the conservation needs of wild canids.

Chapter 17

Canid Reintroductions and Metapopulation Management

A. Moehrenschlager and M.J. Somers

17.1 Introduction

Human-induced habitat loss, habitat fragmentation, hunting, poisoning, and trapping have led to the extirpation of small canid populations or, in extreme cases, species. However, if sufficient captive or wild animals of a species persist, the potential for the restoration of extirpated populations still remains. Here we examine the successes or failures of canid reintroductions around the world and aim to identify lessons from these programmes that might aid future reintroduction attempts.

In 2002, the IUCN/SSC Reintroduction Specialist Group held a Strategic Planning Workshop where reintroductions were shown to be growing in conservation significance because they:

- are increasing in number;
- attract public attention;
- are regionally important; and
- can use flagship species to facilitate habitat conservation.

Certainly, canids are generally charismatic, ecologically significant, and often sufficiently wide-ranging to be adequate umbrella species for habitat preservation, but the restoration of many species can still be ecologically or politically problematic.

Successful reintroductions require that a number of species-specific, environmental, and bio-political criteria be met (Kleiman and Beck 1994). There should be a need to augment the wild population, sufficient founder stock should be available, and extant wild populations should not be jeopardised by the reintroduction (Kleiman and Beck 1994; Woodford and Rossiter 1994). The species' biology should be well understood, appropriate reintroduction techniques should be known, and sufficient resources should be available for the programme. The original causes for the species' extirpation should be removed and sufficient unsaturated, protected habitat should be available. Reintroductions should conform to legal requirements, be supported by both government and non-government agencies, and have minimal negative impacts on local people (Kleiman and Beck 1994).

Compared to smaller and less wide-ranging species, many canids could be ill-suited for reintroduction because:

- their large home range requirements can only be satisfied in extensive protected areas which might not be available (Woodroffe and Ginsberg 1998);
- local people frequently oppose the reintroduction of species that prey on domestic livestock or threaten humans (Phillips 1995; Woodroffe and Ginsberg 1999b); and
- the extensive planning and implementation required for reintroductions (Fritts *et al.* 1997) is prohibitively expensive.

In this chapter we aim to delineate aspects of metapopulation theory that have been incorporated into the recovery planning of threatened canids. We also review canid reintroductions to delineate some crucial taxonomic, political, and biological factors that may determine restoration success. Finally, we outline issues that we see as action plan priorities for canid reintroductions in the future.

17.2 Metapopulation management from theory to practice

A metapopulation is a set of spatially isolated groups of individuals that share individuals among them (Wells and Richmond 1995). Numerous canid species are threatened by habitat loss or habitat degradation. One of the main consequences of this is increased fragmentation (Saunders *et al.* 1991) which increases the likelihood of extinctions (Gilpin and Hanski 1991). When habitat is limited, extant and reintroduced canid populations must be managed as a metapopulation to ensure their long-term persistence.

When individuals are moved from one location to another and released to re-establish populations or metapopulations, the scope of such activities may differ depending on programme goals, release techniques, and geographic aspects. We adopt the definition of a **reintroduction** as an attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct (IUCN 1998b). We include wild or captive animals, or a combination of these in our definition. A **translocation** is a deliberate and mediated movement of wild individuals or populations from one part of their range to another with existing conspecifics. **Supplementation** is the addition of individuals to an existing population of conspecifics. **Soft releases** are those releases where the animals are housed in an enclosure at the place of release for some time before being set free. **Hard releases** are those where the animals are released directly from vehicles or crates without any acclimatisation phase at the place of reintroduction.

Species respond differently to fragmentation and, therefore, an autecological approach has been suggested to the maintenance of metapopulations (Laurance 1991). Differential responses can be due to the landscape pattern, levels of habitat loss (Harrison and Fahrig 1995), life-history, and ecological traits such as diet or vulnerability to predators and competitors (Laurance 1991). The persistence of patchy distributions is related to a number of factors, including rates of local extinction within habitat patches, as well as the frequency of immigration and recolonisation (Lindenmayer and Lacy 1995). It has been shown that seemingly low levels of dispersal can be sufficient to create a stable metapopulation structure (e.g., Simberloff and Cox 1987), which may also allow the viability of canid populations despite relatively small exchange rates between isolated sub-populations.

Four metapopulation parameters have been identified (Hanski 1999) that would characterise canid metapopulation dynamics:

- habitat patches can support locally breeding populations;
- all patches are at risk of extinction;
- recolonisation must be able to occur; and
- the dynamics between patches are asynchronous.

The successful management of sub-populations depends on the minimum viable metapopulation size (Hanski *et al.* 1996). This is the minimum number of interacting local populations necessary for the long-term persistence of a metapopulation in a balance between local extinctions and recolonisations (Hanski *et al.* 1996). Genetic and demographic management of canid sub-populations is essential. Demographic management should aim to control possible negative detrimental factors (e.g., sex ratio variation) as well as declines in population size due to stochastic demographic processes (Foose and Ballou 1988). Genetic management aims to reduce the effects of inbreeding and genetic drift to allow for genetic population viability over time (Lande 1988; Lacy 1997). While metapopulations are governed by extinction and recolonisation rates, reintroduction practitioners have the luxury of artificially choosing immigration sites and numbers through sound metapopulation planning.

17.3 Metapopulation planning

17.3.1 Ethiopian wolf

Ethiopian wolf (*Canis simensis*) surveys by Marino (2003) confirm that the population consists of around 500 subadult and adult individuals, of which half are found in the Bale Mountains. The survey has also revealed the presence of several other Ethiopian wolf populations in Afroalpine habitat north of the Rift Valley. Newly found populations in Wollo are small in size (between 25 and 50 wolves) and almost all small habitat patches in the Afroalpine units are occupied. Recently the species was extirpated from a 20km² habitat patch in Gosh Meda and with the exception of Bale, and possibly Arsi, all Ethiopian wolf populations may be vulnerable to extinction due to their small population and habitat patch sizes. However, their continued persistence in small populations suggests the species may be relatively resilient (Gottelli *et al.* 2004), although there are no recent examples of recolonisation and recovery after local extinctions (Sillero-Zubiri *et al.* 2000). A metapopulation management approach has been proposed for Ethiopian wolves, although reintroductions are not recommended at this time (Sillero-Zubiri and Macdonald 1997).

17.3.2 Grey wolf

After grey wolf (*Canis lupus*) populations began to recover in southern Canada and after the U.S. Endangered Species Act protected wolves as of 1974, wolves began to recolonise northern Montana naturally. The first case of wolves reproducing in this area was documented in 1986, and by 1993 the population had grown to 88 wolves in seven packs (Fritts *et al.* 1995).

The U.S. Fish and Wildlife Service appointed a Northern Rocky Mountain Wolf Recovery Team to further recover this wolf population (Fritts *et al.* 1997). The subsequent recovery plan identified north-western Montana, central Idaho, and the greater Yellowstone area, totalling about 69,000km², as potential release areas based on prey numbers, sufficient publicly owned land, and a low potential of conflicts between wolves and humans (USFWS 1987). Assessments suggested that the restoration of 10 breeding pairs per release area would create a viable metapopulation (USFWS 1994; Fritts and Carbyn 1995; Fritts *et al.* 1997), if subsequent dispersal connected the release sites and the Canadian wolf population (Boyd *et al.* 1995). Haight *et al.* (1998) modelled wolf subpopulations and concluded that wolves can survive in sub-populations if there is genetic connectivity between them, human persecution is not excessive, and prey is abundant. They used 16 sub-populations and found that as few as two immigrants a year helped maintain high (>80%) site occupancy. The recovery plan suggests that, if recovery-level populations totalling about 300 wolves were reached and maintained for three consecutive years, the species would be removed from ESA protection to be managed by state and tribal wildlife agencies.

Two other grey wolf recovery programmes, guided by their own recovery plans, exist outside the northern

William Campbell

A nine month old male grey wolf watches biologists after being captured and fitted with a radio collar in Yellowstone National Park. This park is the site of the successful Yellowstone Wolf Restoration Project, made possible by conservation policy and government, as well as private, funding. For example, the United States National Park Service called for restoring the human extirpated wolf population under its native species policy. The U.S. Congress provided funds to the Fish & Wildlife Service, National Park Service and U.S. Forest Service, to prepare a statement on restoring wolves to Yellowstone and central Idaho. The Yellowstone Wolf Restoration Project was started in the park, and has become a model in successful reintroduction and canid conservation. Yellowstone National Park, Wyoming, USA, 2003.

Rockies; one in the upper Midwest (USFWS 1992) and the other in the south-western states (Parsons and Nicholopoulus 1995).

17.3.3 Red wolf

Red wolves (*Canis rufus*) were extirpated from almost all of the eastern United States at the beginning of the 1900s because of persecution and habitat loss. Remaining red wolves were trapped in Texas and Louisiana from 1973 to 1980 to establish a captive-breeding programme, which subsequently led to reintroduction attempts in two mainland and three island populations since 1987 (Phillips 1995).

A metapopulation has been proposed for the red wolf. A population viability analysis indicated that to meet metapopulation management objectives, the USFWS would have to establish a population of 550 red wolves. These 550 would be distributed between a captive population of 330 and a free-ranging population of 220 at three or more sites (Phillips 1995; Reading and Clark 1996).

17.3.4 African wild dog

African wild dogs (*Lycaon pictus*) disappeared from 25 of the 39 former range countries in the last 30 years. Only six populations, found in southern and eastern Africa, had more than 100 animals by 1997 (Woodroffe *et al.* 1997). Many reintroductions have been attempted, most of them unsuccessful (Woodroffe and Ginsberg 1999b). Following recommendations in the IUCN Wild Dog Action Plan (Woodroffe *et al.* 1997) a metapopulation approach to African wild dog conservation in South Africa was proposed by Mills *et al.* (1998). The primary objective was to establish a second South African, artificially managed metapopulation consisting of eight packs in small conservation areas by 2007. Potential reintroduction sites were identified and an adaptive management model was created to implement metapopulation recommendations.

The South African Wild Dog Action Group (WAG-SA) (renamed as the South African Wild Dog Advisory Group in 2003) has been meeting 3–4 times per year since 1997 to oversee the formation of new subpopulations such as those in Venetia-Limpopo, Pilanesberg and Karongwe. Mills (2003) argued that wild dog restoration is only feasible in sufficiently large reserve areas and only if biodiversity conservation is a primary objective for these sites. He suggests that potential metapopulation reserves should be ranked according to their willingness and/or ability to allow ecological processes to occur that would benefit African wild dogs. In priority reserves, metapopulation management should simulate natural conditions as closely as possible. Since wild dog numbers naturally fluctuate (Maddock 1999), subpopulation viability assessments must also incorporate reproductive rates, genetic status, and the potential effects of supplementing single-sex juvenile groups (Mills 2003).

17.4 Review of canid reintroduction programmes to date

Canid species comprised 13% of carnivore reintroductions and translocations reported by 2000, compared to mustelids (58%), felids (22%), ursids (4%) and hyaenids (3%) (Breitenmoser *et al.* 2001). Here we review the current status of canid translocation and reintroduction attempts.

17.4.1 Grey wolf

In at least three attempts grey wolves have been released for purposes other than reintroduction. Experimental releases of four captive wolves in Alaska (Henshaw *et al.* 1979) and five translocated wolves in Michigan (Weise *et al.* 1979) were unsuccessful. In Minnesota, 107 grey wolves were captured at or near farms and successfully translocated into forested areas where other wolves may have been resident already (Fritts *et al.* 1984).

In Georgia (western Asia) 22 wolves were pre-conditioned to avoid humans and to avoid livestock before a reintroduction attempt. Over four years of monitoring, survival rates were high and two generations of descendents were produced (Badridze 1999).

Grey wolf reintroduction to Idaho has been successful after 15 translocated wolves were released in 1995, 20 in 1996, and one in 1998. Extirpated from the state before 1995, $\geq$ 122 wolves including 10 reproductive packs were estimated to exist in the wild by 1998 (Bangs *et al.* 1998). The reintroduction of wolves to Yellowstone National Park has also been successful. From 1995 to 1997, 44 wolves were soft-released and by 1998 the Greater Yellowstone population consisted of 116 wolves with seven packs that produced 10 litters of pups (Bangs *et al.* 1998). Within four years of the reintroduction programme, 133 pups had been born in 29 litters in the greater Yellowstone area. In the summer of 2002, at least 216 free-ranging wolves could be found in this region with about 14 packs (132 individuals) holding territories primarily within the park and 14 packs (84 individuals) primarily outside its boundaries (Smith *et al.* 2003). Despite the short interval since reintroductions began, the success of the Yellowstone programme is already initiating debates about the potential de-listing of Yellowstone-area wolves under the U.S. Endangered Species Act (Pyare and Berger 2003).

17.4.2 Red wolf

Analyses of 320 red wolf releases indicated that release success was primarily dependent on the degree of wolf habituation in captivity and landscape manipulation by humans (Van Manen *et al.* 2000). Eight years of reintroduction releases in Great Smoky Mountains National Park of North Carolina and Tennessee were unsuccessful, as juvenile survival was low and wolves failed to establish home ranges within the protected area.

Red wolf restoration to the Alligator River National Wildlife Refuge in north-eastern North Carolina has been successful to date with an estimated population size of 100 individuals of which 63 were still radio-collared in December 2002. At that point, approximately 160 red wolves also existed in 37 captive facilities. Recently, reintroduction methods have been further refined as captive pups have now been successfully fostered by wild parents at the release site (American Zoo and Aquarium Association 2003). Currently, red wolves range across an area of approximately 6,000km^2 in North Carolina including private and public lands (Phillips *et al.* 2003). One of the greatest remaining threats to red wolves is hybridisation with coyotes, but plans are being implemented to reduce interbreeding and remove hybrids (Kelly 1999).

17.4.3 Mexican wolf

The probable historic range of the Mexican wolf (*Canis lupus baileyi*) included portions of central and northern Mexico, western Texas, southern New Mexico, and south-eastern and central Arizona. The Mexican wolf was extirpated from the wild in the United States by the mid-1900s (Parsons 1998), fewer than 50 adult breeding pairs were estimated to exist in Mexico in 1978 (McBride 1980), and it appears unlikely that viable populations, if any wolves at all, currently remain in the Mexican wilderness (Parsons 1998). The primary factors responsible for this decline were extermination campaigns using traps, digging pups from dens, shooting, and poisoning, which were often encouraged by public or private bounties.

Five Mexican wolves captured in Durango, Mexico, between 1977 and 1980 were used to found a captive-breeding population. Subsequent breeding efforts (reviewed in Chapter 16) led to a captive population of over 200 individuals in 40 zoos and wildlife sanctuaries throughout the USA and Mexico by 1999 (Parsons 1999). The primary goal of the reintroduction effort is to restore a self-sustaining population of about 100 Mexican wolves distributed across 12,950km^2 in the Blue Range Wolf Recovery Area of south-eastern Arizona and south-western New Mexico (Paquet *et al.* 2001).

In March 1998, 11 wolves representing three family groups were soft-released into Arizona's Apache National Forest on 29 March 1998 (Parsons 1998). Two adults and three subadults were shot and three wolves were captured and returned to captivity. By 1999, the free-ranging population consisted of at least 24 Mexican wolves in five packs, and one wild-born litter whose size was not known (Parsons 1999). Subsequently 45 additional individuals were released by March 2001 (Paquet *et al.* 2001). In May 2001, 28 individuals were reported to exist in the wild and five litters had been produced during that spring. Paquet *et al.* (2001) recommended that releases should continue with major alterations to the goals, procedures, and organisational aspects of the programme.

17.4.4 African wild dog

The first successful wild dog reintroduction was into Hluhluwe-Umfolozi Park (HUP) from 1980–1981 (Maddock 1999). A mixture of 24 wild-caught and hand-reared wild dogs were released, which persisted with a mean annual density of 19.9 wild dogs in the 960km^2 reserve. In 1986, four semi-tame wild dogs were released into HUP, which left the park (Maddock 1999). As numbers declined after 1993, another three wild-caught males and one female were introduced in 1997. The pack produced 12 pups in 1998 but it split up in 1999 after the alpha female died. The two adult males left the park and roamed widely in other reserves and game ranching areas before one was found dead and the other disappeared (Somers 2001). Of the 1997 reintroduction, only one male (brought in as a yearling of the alpha female) still survived in 2003. In 2000, two females were introduced which bonded with two existing males from the original pack. As of March 2003 there were two packs, both of which have had pups in 2001 and 2002. A third pack, consisting of two males and two females from the Limpopo Province, is currently awaiting release with an unrelated adult female and three juvenile males. This introduction will be the first where unrelated animals of the same sex have been combined and released.

There were three attempts to reintroduce wild dogs into Etosha National Park, Namibia, from 1978 to 1990 (Scheepers and Venzke 1995). In 1978, six hand-reared yearlings were released which died within four months, mainly due to starvation (Scheepers and Venzke 1995). In 1989, five adult captive-bred wild dogs were released, but all died of unknown causes within three months. After the success of the reintroduction of wild dogs into Hluhluwe-Umfolozi Park, it was decided to try again in 1990. Five captive-bred males (including three adults) and eight females (three adults) were to be released. One adult male and female escaped while being transported to Etosha. The female was shot a week later on a farm. The male formed a pack with two domestic dogs which hunted together until the wild dog was trapped in a reserve 350km away. He was returned to the released wild dog pack, which subsequently killed him with bites on the spine and neck. The remaining animals struggled to hunt and lost body condition. Four died of rabies, six were killed by lions and one disappeared.

Six wild dogs were reintroduced into Tsavo West National Park, Kenya, in 1997. They disappeared after eight days, and eventually all animals were killed (Kock *et al.* 1999). In 1986, nine captive-raised wild dogs were released into the Matetsi Safari Area in Zimbabwe and then shot by a local farmer. In Zimbabwe wild dogs have been captured and released successfully in safer areas (G. Rasmussen pers. comm.).

In 1975, three males and two females were reintroduced into South Africa's Kalahari National Park which soon split up and disappeared (Frame and Fanshawe 1990; cited in Woodroffe and Ginsberg 1999b). In 1992, seven male and seven female wild dogs were reintroduced via soft release to Venetia-Limpopo Nature Reserve, South Africa. They bred that year but later left the reserve and some were found poisoned on farmland (Van Heerden 1992; Woodroffe and Ginsberg 1999b). In January 2002 nine wild dogs were reintroduced, which subsequently bred.

In 1995, three wild-caught and three captive-bred individuals were reintroduced via soft release into Madikwe Game Reserve, South Africa. They produced two litters of pups, however, 18 of 21 wild dogs died of rabies in 1997. In January 1998 three captive-bred females and two wild-caught juvenile males were reintroduced, and in July 1998 two captive-bred and two wild-caught males were added to the wild population. In 2000 new males were added and have since disappeared. In February 2000 another rabies outbreak killed eight of 11 unvaccinated pups but none of the vaccinated adults. There are now three successfully breeding packs in Madikwe, and some individuals have been removed to supplement other release areas, including Hluhluwe-Umfolozi Park.

Nine wild dogs were reintroduced by soft release into Pilanesberg National Park, South Africa, in 1999 (van Dyk and Slotow 2003). This release again demonstrated that a combination of wild-caught and captive-bred wild dogs could successfully be used for wild dog reintroductions. In 2002 another two females were bonded with two present males and two packs now exist in the park. These packs have bred on numerous occasions.

In 2001, one wild-caught male and two captive-bred females were reintroduced by soft release into Karongwe Nature Reserve, South Africa. The three successfully bred in 2002.

Captive wild dogs are presently awaiting reintroduction into Marakele National Park and reintroductions are being planned for other areas such as Addo Elephant National Park and Greater St Lucia Wetland Park, South Africa.

17.4.5 Swift fox

The swift fox (*Vulpes velox*) is native to shortgrass and mixed-grass prairies of the Great Plains in North America (Egoscue 1979). Historically, the swift fox was considered an abundant predator of the prairies, but numbers were severely depleted by the late 1880s and early 1900s. On the northern limit of its range, swift foxes were present in the Canadian provinces of Alberta, Saskatchewan, and Manitoba. The southern species' boundary was New Mexico and Texas in the United States. Historical records also exist for areas in Montana, Wyoming, North Dakota, South Dakota, Nebraska, Kansas, Colorado, and Oklahoma. Current estimates for the USA suggest that swift foxes are located in 39–42% of their historic range depending on conservative *vs.* liberal estimates of historic range and the time span of records that are considered (Sovada and Scheick 1999). In Canada, the last recorded specimen was collected in 1928 and a single sighting was made in 1938 (Soper 1964), after which the species was considered nationally extirpated.

As part of a national reintroduction programme, 942 swift foxes were released in Canada from 1983 until 1997 (see section 4.6). Translocated foxes that were monitored from 1994–1998 had higher survival rates than previously monitored captive-bred foxes, and similar survival rates to resident, wild-born foxes (Moehrenschlager and Macdonald 2003). In 1997, the Canadian population was estimated to have approximately 192 and 89 in respective subpopulations. Of foxes that were live-captured from 1994 –1998, 88% were born in the wild within the reintroduced population (Moehrenschlager 2000; Moehrenschlager *et al*. 2003). By 2001, the number of individuals trapped on replicated townships had increased significantly, and the known distribution of swift foxes increased three-fold since the previous census. While the population was previously fragmented in Canada and sparse in Montana, the population is now connected because gaps within the known distribution are smaller than maximum dispersal distances of this species (Moehrenschlager and Moehrenschlager 2001). This increased connectivity might decrease the likelihood of extinction through coyote predation or red fox competition, which are the primary threats (Tannerfeld *et al.* 2003; Moehrenschlager *et al*. 2004), but increases the possibility of disease transmission throughout the population.

17.5 Lessons learned

17.5.1 Socio-political factors can make or break canid reintroduction programmes

Several authors have pointed out that valuational and organisational aspects are at least as critical for carnivores as biological parameters (Beck *et al*. 1994; Reading and Miller 1995; Miller *et al*. 1996; Reading and Clark 1996; Breitenmoser *et al.* 2001). Since many canids require large home ranges in protected habitats and many prey on livestock or commercially hunted species, stakeholders such as landowners, hunters, the resource-extraction industry, indigenous communities, regional and federal governments, and conservation organisations may have special interests surrounding the protection of canids. Recovery planning that is inclusive, interdisciplinary, and effective is difficult to achieve, but critical to the protection of canids (Boitani *et al*. 2004).

One of the most crucial aspects determining the success of canid reintroductions is the support of affected landowners, or mitigation measures to placate those that resist such efforts. Support for a possible reintroduction of wolves to New Brunswick, Canada, was lowest for sampled individuals that were hunters, feared wolves, or had low levels of formal education. The primary reason for opposing reintroductions was that deer availability for hunting would decline (Lohr *et al*. 1996). Opponents to a possible reintroduction of wolves into Colorado, USA, expressed concern about wolf attacks on livestock, financial losses to ranchers, wolves threatening residential areas, and large losses of deer or elk. Proponents believed wolf reintroduction would control deer, elk and rodent populations, restore the environment, and help educate the public about wilderness (Pate *et al*. 1996).

Strong opposition from some factions stalled the reintroduction of wolves to Yellowstone National Park and central Idaho for two decades, until a proposal to reintroduce wolves was accepted as long as it was deemed 'non-essential-experimental' under the United States Endangered Species Act (Fritts *et al*. 1997). Nevertheless, a group comprised mostly of farmers and ranchers filed a lawsuit to stop this reintroduction. Similarly, the New Mexico Cattle Growers Association filed a lawsuit in the U.S. District Court of New Mexico to stop the reintroduction of Mexican wolves (Parsons 1999).

Careful management of released red wolves and the emerging population involved close public consultation, which has led many landowners to allow wolves on their properties (Phillips *et al*. 1995). Defenders of Wildlife, a non-governmental organisation, has compensated ranchers for livestock losses caused by reintroduced Mexican wolves and grey wolves in Yellowstone. In assessing the future of the Mexican wolf, Paquet *et al*. (2001) concluded that human attitude is the primary factor that will determine the viability of this species.

17.5.2 The taxonomy of historical and potential source populations may determine the feasibility and magnitude of reintroduction programmes

As we attempt to discern which species or subspecies require conservation action, taxonomic classification is of paramount importance. Imperilled species are more likely to receive funding, research, and political protection than subspecies, which in turn are more likely to receive protective measures than geographically-depleted populations of generally abundant species. The likelihood that reintroduction or translocation programmes will be implemented depends directly on the resolution of genetic questions. This, however, is at present usually of more concern in developed countries where detailed genetic data are available for most threatened species.

At the beginning of the swift fox reintroduction programme in Canada, critics cautioned that animals from the central USA should not be used to re-establish northern populations because of a possible mixing of subspecies (Stromberg and Boyce 1986). Reintroductions continued because others doubted such subspecies existed (Herrero *et al*. 1986), and later testing illustrated that these original subspecies designations are likely unwarranted (Mercure *et al*. 1993). The designation of San Joaquin kit foxes as a distinct subspecies (*Vulpes macrotis mutica*) led to federal listing under the United States Endangered Species Act. This increased protective measures and resulted in a regional reintroduction attempt, which was unsuccessful as 97% of released animals died (Scrivner *et al*. 1993).

Reintroduction and conservation efforts to protect Mexican wolves are taxonomically supported by the fact that Mexican wolves are a genetically distinct subspecies (Garcia-Moreno *et al*. 1996). Mexican wolves were found to have a unique Bgl restriction-site polymorphism and, contrary to distance tree analyses, mitochondrial DNA analysis suggests that Mexican wolves are more similar to Old World wolves than North American conspecifics (Wayne *et al*. 1992). By comparison, the classification of red wolves has been problematic. Mitochondrial DNA analyses demonstrated that the red wolf is either a hybrid form, or that it is a distinct taxon that hybridised with grey wolves or coyotes over much of its geographical range (Wayne and Jenks 1991). Further mtDNA and nuclear DNA analyses support the former hypothesis that red wolves originated through coyote-grey wolf hybridisation (Roy *et al*. 1996), likely in the last 2,500 years (Reich *et al*. 1999). Although some proponents still use morphometric analyses to argue that red wolves are not wolf-coyote hybrids (Nowak 2002), the genetic evidence has presented a conundrum for reintroduction efforts. Recent genetic evidence suggesting that wolves in south-eastern Ontario and southern Quebec, Canada, be classified as a new species, *Canis lycaon* (Wilson *et al*. 2000), may be the beginning of similar conservation challenges for these populations.

Through taxonomic reclassification a seemingly abundant population can suddenly be found to be a Critically Endangered species that requires captive breeding, translocation, or reintroduction. The fact that island foxes (*Urocyon littoralis*), previously thought to be gray foxes, are in fact a distinct species composed of six distinct subspecies (Wayne *et al*. 1991b; Wilson and Reeder 1993), has had immediate conservation consequences which have resulted in captive-breeding and translocation programmes. Nevertheless, the island fox is not yet recognised as an imperilled species under the United States Endangered Species Act. Similarly, Darwin's fox (*Pseudalopex fulvipes*) was thought to be a subspecies of chilla (*P. griseus*), but subsequent genetic evaluation has shown that they are a distinct species, and recently listed as Critically Endangered. Given disease and demographic threats to the population, it is now likely that captive breeding will be initiated.

17.5.3 Soft-releases and translocations are effective reintroduction techniques

Captive-bred swift foxes that were released in autumn had higher survival rates than those released in spring (Brechtel *et al*. 1993; Carbyn *et al.* 1994,), but translocated swift foxes were more successful than both captive-release treatments (Carbyn *et al*. 1994; Ginsberg 1994). Survival and reproductive rates were compared between 56 swift foxes that had been born in the Canadian release area to those of 29 Wyoming swift foxes that were translocated from Wyoming between 1994 and 1996 and tracked for up to 850 days after release (Moehrenschlager and Macdonald 2003). Translocated juveniles dispersed less far but survived and reproduced as well as translocated adults, suggesting that juveniles can be used to establish translocated foxes in small, protected areas, while minimising demographic effects on source populations. The fact that survival rates and litter sizes of translocated foxes were similar to those of resident animals indicates that translocation can be an effective reintroduction tool for this species, and possibly other foxes (Moehrenschlager and Macdonald 2003).

Soft releases were used from 1983–1987 and hard releases from 1987 onwards (Herrero *et al*. 1991) because they were less expensive. Radio-telemetry revealed that survival and reproductive success were highest for swift foxes with small dispersal distances, suggesting that measures should be taken to acclimate animals to release sites through soft releases (Moehrenschlager and Macdonald 2003). In Idaho, hard-released grey wolves also ranged widely and did not reproduce in the first year, while soft-released wolves in Yellowstone National Park remained close to the release site and bred successfully (Smith 1999). Survival rates were highest for red wolves that had been wild-reared with a short acclimation period at the release site (Van Manen 1999).

17.5.4 Released canids can adapt quickly to local conditions

Reintroduced canids only establish populations if individuals can establish territories, hunt, avoid predators, find mates, and reproduce. Depending on body size, guild structure, and predator occurrence, the challenges canids face after release differ between species. Pack hunters such as African wild dogs need to develop social and cooperative hunting skills to kill large prey and resist competitive carnivores, while solitary hunters do not. However, comparatively small solitary foragers, such as island, swift, kit, and Arctic foxes that are preyed upon by predators such as golden eagles (*Aquila chrysaetos*) may need to develop predator avoidance strategies.

Red wolf releases that consisted of adults accompanied by young pups tended to form cohesive groups, exhibit fewer wide-ranging movements, and were less likely to experience vehicle-related mortalities (Van Mannen 1999). Released grey wolves can adapt their hunting skills to local conditions. Only two of 41 studied wolves that had been translocated from Alberta and British Columbia, Canada, to Yellowstone National Park had been previously exposed to bison. Eight one-year-old wolves killed an emaciated bison calf 21 days after release, the first adult bison was killed after 25 months during a 9.5-hour-long hunt, and subsequently 14 bison kills were documented over a period of four years (Smith *et al*. 2000). Captive-bred Mexican wolves had no previous hunting experiences in the wild when the first three family groups were released in

1998. Nevertheless, three weeks after their release, three subadult members of one family killed a mature cow elk and evidence was found to suggest that the other two families had also killed adult elk or elk calves (Parsons 1998).

17.5.5 Disease can hamper reintroduction attempts

In the planning of any translocations or reintroductions, the risk of accidental transmission of disease into unaffected populations via released animals must be carefully assessed. Woodford and Rossiter (1994) recommend that veterinary involvement in reintroduction projects should begin as early as possible. They point out instances of inadequate disease risk assessment resulting in expensive failures, and the introduction of destructive pathogens into resident wildlife populations by captive-bred and wild-caught animals. Infectious diseases may have short-term or long-term effects on population size and viability by affecting rates and patterns of mortality or reproduction. Assessment procedures should address infectious agents that released animals may be exposed to, or that they might carry to conspecifics and other susceptible species at the release site (Nowell and Jackson 1996). Although the risk of disease may be deemed higher where domestic dogs are sympatric, in Madikwe Game Reserve wild dogs were killed by a strain of rabies from black-backed jackals (*Canis mesomelas*) (M. Hofmeyr pers. comm.).

17.5.6 Canid restoration can have profound ecosystem effects

Carnivores are thought to be crucial to the maintenance of healthy ecosystems, but the scale of their function is often difficult to evaluate within extant populations. Reintroductions provide unique opportunities to test the impacts of different types of carnivores. While ecosystem impacts of swift fox reintroduction have not been thoroughly explored, the reintroduction of Yellowstone Park wolves elucidates that the re-establishment of a top carnivore can be felt on all ecosystem levels.

The number of coyotes in Yellowstone Park's Northern Range dropped from 80 individuals in 12 packs before wolf reintroduction, to 36 coyotes in nine packs. Within three years of wolf reintroduction, 25–33% of annual coyote mortality was due to wolves, mean coyote pack size dropped from 6 to 3.6 adults, and coyote population size dropped by 55% (Crabtree 1998). Functionally, surviving coyotes have increased vigilance behaviours and altered foraging patterns since wolf reintroductions began (Switalski 2003). While male behaviour was not affected, the vigilance of female bison and elk increased significantly. Among elk this was true for both females with calves, which increased vigilance rates from 20% to 43%, and females that did not have calves, which increased vigilance from 11.5% to 30.5% (Laundré *et al.* 2001). Changes in elk foraging patterns can even be detected on a plant community level. Elk pellet counts were significantly lower in habitats that wolves used frequently than in rarely used areas. Consequently, aspen sucker height was significantly higher in areas of high wolf-use than regions that wolves used rarely.

17.6 Conclusions

Despite extinction in the wild, taxonomic controversies, ongoing hybridisation with coyotes, and potential conflicts with landowners, the red wolf reintroduction programme is showing ongoing signs of success. Similarly, the grey wolf reintroduction to Yellowstone has been an ecological triumph despite numerous political and legal battles. Reintroduced swift foxes have been de-listed from 'extirpated' to 'endangered' in Canada. Reintroduction attempts of Mexican wolves and African wild dogs are showing increasing promise and the integration of sound metapopulation planning will facilitate population viability in the future. The diversity of biological and organisational challenges that have been successfully overcome to restore canids should truly be celebrated. That said, numerous challenges still lie ahead.

Ginsberg (1994) determined that although breeding success in canids is highly variable and captive populations of many imperilled species are too small, some can be successfully reintroduced if adequate animals, habitat, and funds are available. Since that time only the island fox, for which releases may begin soon, has been added into reintroduction programmes (Timm *et al.* 2002). Although only nine of the world's 35 canid species exist in the USA or Canada, five of the six species involved in reintroductions are from these countries. This raises the question whether canid reintroductions are primarily aimed at species in wealthy countries, while species that are imperilled in poorer regions receive less attention. Reintroductions can be used as a powerful conservation tool to restore canids (Boitani *et al.* 2004), but it is unclear which canids require such assistance in the future. Hence, we propose that the status, restoration need, and feasibility of reintroductions should be addressed for all canid species in the next five years.

Captive-bred animals and, to a lesser extent, translocated individuals, need to develop hunting- and predator-avoidance skills that are pertinent to their release locations. Successful mixed releases of captive-bred and translocated African wild dogs and the recent success of red wolf fostering in the wild, suggest that such techniques can improve the effectiveness of captive-bred animals. While soft-releases have been successfully combined with pre-conditioning experiments in other carnivores (Reading and Clark 1996), canid restoration programmes often have not. Experimental designs that rigorously test success differences between fostering practices, pre-release conditioning, and release techniques should become integral programmes of canid reintroduction programmes in the future. Moreover translocations of African wild dogs, grey wolves, and swift foxes have been used with great success, but none have thoroughly evaluated the impact of these activities on source populations. If future translocations are used to restore canids, impact evaluations should not only be required in the release areas but also in the source populations.

In the planning phase, or as reintroductions show signs of success, the question continually arises as to how many individuals need to be restored for the programme to be deemed successful (Pyare and Berger 2003). While the answer hinges largely on demographic parameters that determine effective population size, minimum viable population size estimates are also dependent on genetic parameters. Some argue that a population of 50 individuals is sufficient to avoid short-term deleterious effects of inbreeding depression (Franklin 1980; Soulé 1980), others believe that 500 is sufficient to maintain genetic variability in quantitative characters (Reed and Bryant 2000), while some believe that 1,000–5,000 individuals may be a safer number to strive for (Lynch and Lande 1998). Tremendous resources are required for canid restorations, many stakeholders are affected, and the viability of reintroduced canids needs to be adequately secured over time. For ecological and political purposes, future minimum viable population size targets need to be more specifically defined for canids in general or, ideally, for specific canid taxa. At the least, future canid conservation efforts would benefit from refined estimates of minimum viable population sizes in pack-living versus solitary canids.

Chapter 18

Conservation Education and its Relevance to Wild Canids

D. Taylor

"It is not education, but education of a certain kind that will save us." (Orr 1994)

18.1 Introduction

Conservation education is an extremely complex and varied subject. The issues involved often raise more questions than answers, and the task of developing and implementing education programmes is a daunting one, especially when you consider that some programmes may take decades to achieve their goals. Education, however, is now becoming more widely recognised as one of a number of effective conservation strategies.

One of the key issues in wild canid conservation is conflict mitigation (see Chapter 13), and trying to implement strategies to foster co-existence. Education has a key role in conflict mitigation, but what is less clear is how to develop, implement and evaluate effective conservation education strategies. There is a dearth of practical information available on this subject, and a lack of multidisciplinary cooperation between all the stakeholders involved.

A further problem is that education programmes are often developed and implemented by people who have no formal training in education as a discipline. Biologists working with individual species may have expertise in their chosen field, but are not usually specialised in both the disciplines of science and education. Non-governmental organisations (NGOs) rely heavily on volunteers who also may not have any formal academic qualifications as educators.

When developing conservation strategies, a number of moral and ethical issues also need to be considered. Not least of these is the reason(s) for conserving a certain species and/or habitat, which species should be given priority, and who should make the decisions – conservationists, politicians, the international community or the indigenous people.

Some of these issues might at first seem beyond the scope of a chapter on conservation education, but the key issue here is: *Who needs educating, and why?*

- Is it the hunters and farmers with the aim of fostering co-existence in human/carnivore conflict situations?
- Is it the policy-makers in order to lobby for legislation to protect wild canids?
- Is it the general public in order to bring about attitude and behaviour changes at a societal level?
- What about education and training programmes for conservationists – again with the aim of fostering co-existence?

The purpose of this chapter is to highlight some of the issues that need to be considered when developing a wild canid conservation education programme, and to provide some general practical guidelines.

18.2 Defining education

As conservationists, we need to be clear on what we mean when we use the term *education*? It is a term that is frequently cited in conservation literature and at biology conferences and symposia, and often without any clear definitions being offered. For instance, is a communication or awareness-raising initiative really an 'education' programme?

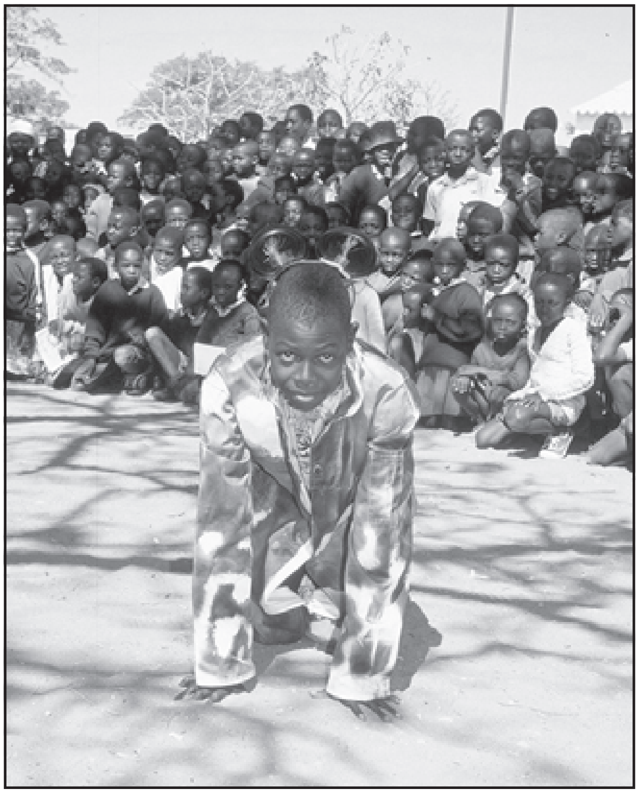
'Education' is an abstract concept difficult to define. There are numerous education theories, but there is no universally agreed or unchanging definition (Jarvis 1993). It is, therefore, often described through criteria used or through the processes of education. One example of defining education is that it equips the learner with knowledge, skills and experience at a level where insight and criticality are achieved. Peters (1966) argues that a person can be extremely knowledgeable or well informed, but this does not necessarily mean they are 'educated', they must also have some understanding of the 'reason why' of things. In other words, a level of cognitive perspective must be achieved. It is this cognitive perspective that conservation educators aim for when attempting to change attitudes or influence behaviour.

In order for sustainable education strategies to work in wild canid conservation, the different concepts, criteria and processes of education need to be understood. Changing the negative views of of some people for canids will require a shift in attitudes at a societal level, which will involve 'educating' younger generations through the formal school system.

Below are brief descriptions of some of the terms used in education and communication:

- **Formal education** – the highly institutionalised, chronologically graded and hierarchically structured 'education system' spanning lower primary school and upper reaches of the university (Coombs and Ahmed 1974), often referred to as 'front end education'. Formal education frequently refers to teaching method rather than to the structure of the educational provision (Jarvis 1993).
- **Non-formal education** – any organised systematic, educational activity carried on outside the framework of the formal system to provide selected types of learning to particular subgroups in the population (Coombs and Ahmed 1974). This structured education, delivered over a period of time would include community programmes, adult education programmes, and programmes run by voluntary organisations which are not primarily set up to provide education, but do so as part of their wider function.
- **Informal education** – generally defined as unorganised and often unsystematic, although it accounts for the great bulk of any person's total lifetime learning (Jarvis 1993).

Young students engage in an African wild dog (*Lycaon pictus*) educational workshop, featuring costumes for role-playing exercises, such as the suit this young man demonstrates. Experiential learning techniques are used to illustrate behaviours and research methods, such as predator-prey chase simulations between groups of children, and exercises wherein the children become "hiding" wild dogs while the researcher (facilitator) uses tracking gear to find them. Painted Dog Conservation, Hwange, Zimbabwe, 2001.



Peter Blinston

- **Conservation education** – according to Orr (1994), all education is 'environmental education', but most conservation education programmes usually fall within the two categories of non-formal and informal education.

  The World Conservation Union (IUCN) defines conservation education as: "a long-term process which seeks to modify the behaviour and attitudes of people by heightening their awareness of the natural environment and all its components."

  It should be borne in mind, however, that there are groups of people who are more aware of conservation and the natural environment, but they may not be disposed to protecting those parts of it that threaten their own livelihoods or welfare. Certain types of hunters and farmers may fall into this category, and may be resistant to any attempt to change or modify their behaviour.
- **Indoctrination** – the concept of indoctrination is particularly relevant in conservation education when dealing with different cultures and, therefore, different beliefs and value systems. Snook (1972) gives a simple definition: "The inculcation of a proposition or set of propositions in the pupil that are said to be certain when the teacher knows they are uncertain and with a lack of regard for any evidence to the contrary."

  Conservation educators need to be aware of the dangers of indoctrination by taking into account the beliefs, values and cultures of indigenous people. There may well be situations where we should ask ourselves whether it is morally or ethically right to impose our own values and beliefs, when implementing conservation strategies, on people in other societies? This may be particularly relevant when considering human-canid conflict mitigation, or where certain restrictions are placed on human activities in order to protect individual species or habitats. Conservationists may decide that hunters, trappers, ranchers or livestock owners pose the main threat to canids through their practices or behaviour. What is less straightforward is how to achieve canid conservation through education strategies without this leaning towards indoctrination, bearing in mind that attitudes toward canids are often entrenched in centuries of culture and tradition.
- **Communication** – the exchange and imparting of ideas and information, and the combination of effective sending and effective receiving. Communication as a conservation tool includes a wide range of activities, strategies, and approaches, of which some of these may be defined as being 'educational'. In other words, effective communication brings about behaviour modification through a process of reflection and criticality. Others may simply impart information to raise awareness. When developing a conservation education programme, a whole range of education and communication strategies may be employed.

Table 18.1. Elements of success for conservation education programmes (Jacobson and McDuff 1997).

Planning
Have clear goals
Identify measurable objectives
Adopt an interdisciplinary approach
Assess participants' social/education/economic backgrounds
Ensure programme relevance to local populations
Build necessary support (govt/community/industry)
Maintain a budget plan
Develop an organisational plan
Plan for potential problems and resolution of conflicts
Implementation
Follow an integrated approach
Use existing organisations/groups
Encourage active/voluntary participation
Involve reluctant participants creatively
Be sensitive to the audience
Provide direct contact with the environment/resource
Use key ecosystems/resources/species in programme
Select appropriate educational media
Use mass media
Focus on economic/cultural values
Provide conservation incentives
Maintain informality/entertainment value of programme
Be flexible
Evaluation
Evaluate programme components/monitor programme
Use more than one method of evaluation
Collect feed back for programme modification/creation of new programmes
Transfer programmes to local control and support
Develop specific long-term plans for sustainability
Disseminate programme results

18.3 Developing a conservation education programme

Conservation education is extremely complex and varied, and there is no 'one size fits all' solution. However, there are a number of generic stages in developing an education programme, which, no matter how complex the conservation goals are, will apply to most programmes, and which can then be applied with some adaptation.

Jacobson and McDuff (1997) reviewed 15 successful conservation education programmes and identified 28 programme elements of success (Table 18.1).

The following sections take these 'elements of success' into account for the development and implementation of a conservation education programme focusing on any wild canid species.

18.3.1 Planning

Good planning will aid implementation and will also be a contributing factor in the overall success of the programme. Planning is required at every stage:

- Strategic action planning
- Research planning
- Operational planning
- Financial planning
- Evaluation and monitoring

Defining the conservation goal(s)

Primary conservation goals are usually straightforward – for example, to protect and conserve wild canid populations and/or their habitat. However, there may also be a number of secondary conservation goals, perhaps including the protection and conservation of prey species in the programme goals. Although it may be stating the obvious, it is a useful exercise to have the primary conservation goals as a starting point and to ensure that all programme goals are very clearly defined. Poorly defined goals will lead to problems when quantifying the criteria for success of the conservation goals, in terms of both the biological and social measures, and later when evaluating whether the criteria for success have been met. For long-term programmes, there will inevitably be a turnover in project staff. New staff joining a project will need to have a clear understanding of the conservation goals.

One of the main conservation problems for wild canids is human-canid conflict mitigation, especially in the case of humans and grey wolves (*Canis lupus*), where depredation of livestock is one of the major factors affecting wolves and conservation efforts. One of the key themes at the 2003 World Wolf Congress in Banff, Canada, was controlling wolf populations where predation on livestock and game species was perceived to be a problem. In this case, conflict mitigation may be the primary goal that underpins the education programme.

It is easy to see the contentious issues that arise, and the difficulties that may be encountered, in trying to develop an effective education programme to satisfy this goal when there is a polarisation of the different groups involved. Many hunters, ranchers and outfitters would like to see lethal control methods used, while conservationists favour non-lethal methods that would raise tolerance levels towards increasing wolf populations, such as livestock guardians, fencing, 'scare' devices and aversion conditioning. In such situations a number of primary and secondary conservation goals would be required.

Identifying threats and barriers to the conservation goal(s)

This is the key to solving the conservation problem or issue. In our modern world environmental problems are often anthropogenic:

- Habitat loss or fragmentation
- Human/carnivore conflict
- Predator-prey relationships – e.g., over-harvesting of prey species
- Political – legislation and policy

- Prevailing attitudes – often negative for wild canids
- Pollution
- Economics versus ethics – often there is a focus on ‘worth’ and ‘value’ in anthropocentric terms rather than biocentric terms

This list is not exhaustive, and a number of threats may occur simultaneously. Ethiopian wolves (*Canis simensis*), for example, are threatened by habitat loss and continued fragmentation, canid related diseases, overgrazing of highland pasture, human interference and persecution (due to livestock losses), hybridisation with domestic dogs, road kills, and accidental poisoning (which was aimed at other predators Williams 2003).

Simply identifying the threats and barriers is not enough. The exact nature of the threat needs to be clearly understood and the underlying reasons for the threat or barrier existing need to be clarified.

Note: In the case of grey wolves, the problem is exacerbated in countries where wolves have returned after a long absence, either through natural migration or recovery programmes. France provides such an example, since wolves and other large carnivores have been absent from the landscape for some time and the arrival of wild wolves from Italy in 1992 caused a great deal of hostility, especially from sheep farmers. Once wolves started to prey on sheep, farmers took to demonstrating with their flocks through the streets of Nice – an event that was also widely reported by the media throughout the world. Negative perceptions of the wolf have been ingrained over many centuries. Indeed, the stories such as Little Red Riding Hood and The Beast of Gevaudan originated in France. These ingrained attitudes, together with little or no experience of dealing with large predators, have left French farmers and local people ill-equipped to deal with the situation, and the result has been conflict.

The conservation problem and possible solutions also need to be placed into a wider geo-political and cultural context. Conservationists often carry out their work in other countries where there may be different languages spoken and a variety of different cultures. Identifying the threats and barriers to conservation (both direct and indirect), evaluating the underlying reasons and placing them in context will help when identifying and defining the target group(s) causing the problem.

Identifying and defining the target groups

For any conservation education programme to be successful in achieving both the conservation and education goals, it is vital that the target groups are clearly defined and understood. The ‘general public’ does not exist (Jacobson 1999), and the term ‘community’ is too general. A geographical community (town, city, neighbourhood) is usually defined by physical boundaries. Another concept of community is ‘community of interest’ where the members share a common goal, purpose or interest. Furthermore, it may be necessary to divide target groups into subcategories, depending on the education strategy being formulated and the ‘messages’ that need to be delivered.

In wild canid conservation, often the main threats are those groups who, for one reason or another, are in conflict with the aims of the conservationists. These may include:

- Hunters
- Farmers/livestock owners
- NGOs with conflicting agendas
- Local people

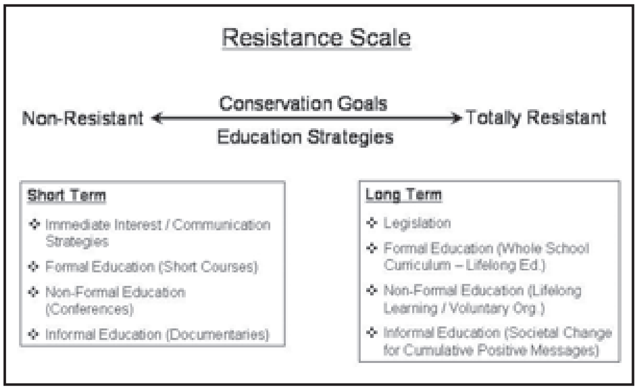
Aside from understanding the ‘who’ and ‘what’ of the conservation problem and its causes, the target group’s motivation(s) for their behaviour also needs to be clarified:

- economic survival
- livelihood protection
- physical protection
- competition for game or prey species
- attitudes and perceptions
- sport / recreational hunting

Understanding the target groups and what motivates their behaviour makes the task of effective education and/or conservation strategies much easier to apply. One method is to measure levels of resistance to the primary conservation goals. Target groups can be placed on a Resistance Scale (Figure 18.1) to help ascertain the quantity and level of ‘education’ needed, as well as the approximate time required to achieve the conservation goals. This is a very simple model, but it demonstrates the need to look very carefully at the target groups that the education programme is aimed at.

The more resistant the target group is to the primary conservation goal, the more difficult it will be to influence a change in behaviour that will help achieve the

Figure 18.1. Resistance Scale – a simple model to identify levels of resistance to primary conservation and education goals in order to aid the implementation of appropriate education strategies.



conservation goals. At the lower (non-resistant) end of the Resistance Scale there are those groups who may simply be unaware of the conservation problem and who are, on the whole, in favour of conservation. Raising awareness of the problem through communication and public relations is more likely to influence a change in perception, attitude and behaviour. However, it is these groups who are least likely to have their lifestyles affected by the conservation problems or issues and who will find it easier to support a conservation programme. In Norway, for example, local people were initially very negative towards the natural reintroduction of wolves into the area. In this case, all that was required to change negative perceptions was to increase local knowledge of large predators and ecology (see Box 18.1).

Groups who are totally resistant to the conservation goals, however, will have no motive for modifying their behaviour. In some human-canid conflict situations, certain target groups may be openly hostile to conservationists. A farmer or hunter whose very survival may depend on killing wild canids is unlikely to change this behaviour unless there is an incentive or disincentive to do so. People tend to make decisions that maximise their self-interest in the short term (Norgaard 1997).

Wild canids have the additional barrier of negative perceptions and attitudes. In a study of public perceptions of predators, particularly the wolf and coyote, Kellert (1985) found that livestock producers expressed very negative attitudes toward the wolf, although wolves constitute a negligible factor in livestock predation.

Note: It must be borne in mind, however, that farmers and hunters do not fit neatly into homogenous target groups when applying conservation strategies. There are some farmers and hunters who are not intolerant of canids, and who actively engage in their conservation. For example, the Thirteen Mile Lamb and Wool Company in Montana, USA has adopted a 'predator friendly' policy and practises non-lethal methods of predator control using llamas to protect livestock. Thirteen Mile produces knitwear from its sheep's wool depicting wolves which they sell to supplement their income, even though their livestock have been threatened by wolves.

It is clear that the problem at the higher end of the Resistance Scale becomes much more complex, and can have a knock-on effect. Hunting and farming groups also have a powerful political voice in some countries and may influence policy-makers. In these situations, other conservation strategies are needed, which may require some form of education for other groups of people in order to ultimately achieve the conservation goals. This comes back to the question of whom needs educating and why? Awareness of such complexities, however, will help formulate education strategies which can be used in conjunction with other conservation strategies, and will hopefully promote some form of unity and cohesion in working towards the overall goals of the project.

Box 18.1. From fear to curiosity – a conservation education programme in Norway.

In 1997, a grey wolf pack established itself in southern Norway. The presence of wolves, in an area where they had been absent for many years, provoked an acute fear and insecurity among the local people. In November 2000, the Ministry of the Environment and the local municipality started a two-year, non-formal education and communication programme in the Stor-Elvdal community, which has 3,000 inhabitants spread throughout the countryside. The programme comprised of carnivore news bulletins being sent to every household six times *per annum*, together with a range of outdoor education activities delivered through local schools for 500 children, for 30 days each semester. Activities included radio-tracking, snow-tracking, howling events, investigating carcasses and dens. A website for the project was also developed (http://www.rovdyrkunnskap.net) which attracted children from all over the country who wanted to learn more about the programme.

At the start of the project, there was a negative reaction from the community. However, as soon as the children became involved in the activities, attitudes started to change. The children were enthusiastic about the discoveries they were making and the new knowledge they were acquiring. This enthusiasm was then generated on to the parents, who then expressed interest and a willingness to learn more about the activities. A range of 20 activities was then arranged for the adults, with between 30 to 150 participants in each event. The aim of the education programme was to increase both theoretical and practical knowledge through 'self-experience'.

After two years, the initial evaluations show that the programme has achieved some success, with local people demonstrating greater curiosity about wolves and other large carnivores, and the fear of wolves has been greatly reduced. People have subsequently asked for more information and further activities related to large carnivores, and have even become involved in population estimation research on wolves in the area.

For further reading about the programme (only available in Norwegian at present), please see:
NOVA Rapport 9:2003 Evaluering av "Prosjekt rovdyrkunnskap" i Stor-Elvdal commune by Mette Svenningsen & Ketil Skogen (report available from http://www.nova.no)

Further information about the project may be obtained from:
Kristin Evensen Gangaas
The Ministry of the Environment
Stor-Elvdal kommune
2480 Koppang
Norway
Email: kristin.evensen.gangaas@stor-elvdal.kommune.no

Defining the education aims and objectives

The education goals will usually be aimed at modifying the behaviour of target groups in order to achieve the overall conservation goals. Jacobson (1997) suggests several goals of conservation education, including:

- Increasing public knowledge and consequent support for the development of appropriate environmental management and conservation policies.
- Fostering a conservation ethic that will enable responsible natural resource stewardship
- Altering patterns of natural resource consumption.
- Enhancing the technical capabilities of natural resource managers.
- Incorporating resource management concerns into private sector and government policy-making processes.

The reasons for and type of education (formal, informal, and non-formal or simply a public relations or communications programme) needed by certain groups and sub-groups need to be ascertained. Some groups may simply need to be made aware of a particular problem to change their perceptions, others may require attitude or behaviour changes. The first is less problematic. There are fewer ethical and philosophical considerations. Providing information and raising awareness may not require the recipients to take action or to make any radical changes to their lifestyle. The degree of behaviour modification will depend on the degree of resistance to the primary conservation goal and will determine the nature of the education programme. Education aimed at changing attitudes and behaviours, on the other hand, requires a great deal of reflection and consideration of the complexities involved. Canid biologists and conservationists are well aware of the hostility faced when the species they are trying to conserve come into direct conflict with human activities, such as hunting, livestock farming, etc. At this level, a number of conservation strategies may be required, e.g., education, legislation, and incentives or disincentives. In Bulgaria, for example, a campaign that provides breeding pairs of livestock guarding dogs to local shepherds has been combined with a number of non-formal education and communication initiatives. These include courses provided at local schools, widely distributed brochures, posters, photo exhibitions, calendars, and media coverage (working with local television). Legal action was also taken to lobby for changes in hunting laws, which was successful (Tsingarska-Sedefcheva 2003).

Education strategies as a conservation tool should not be used in isolation. If behaviour modification is required at a societal level, and a variety of strategies are to be applied, then this will require a multidisciplinary approach that might also require a change in attitude or behaviour on the part of biologists and conservationists.

18.3.2 Implementing a strategic action plan

A strategic action plan will provide an overview of what needs to be achieved, and will allow benchmarks to be incorporated to aid the monitoring and evaluation process (see Table 18.2).

Table 18.2. Some suggestions on headings for the strategic action plan are given below, although these may vary from programme to programme.

- **Background Information/Introduction**
  - — Define the "problem"
- **Aims and Objectives of the Programme**
  - — Primary Conservation Goal(s)
    - Short, Medium, Long Term
  - — Education Aims and Objectives
    - Short, Medium, Long Term
- **Research**
  - — Target Group Research
  - — Methodologies
  - — Research Results
- **Conservation Education Strategy/Plan**
  - — Define the Target Groups
  - — Define Methods of Education to be Used
    - Formal Education – school curricula
    - Non Formal Education – adult education, structured programmes
    - Informal Education
      - — NGOs
      - — Community Education
      - — Communication/Awareness Programmes
      - — Mass Media
- **Resources Required**
  - — Human Resources
    - Project Leaders/Directors
    - Educators/Trainers
    - Administrative Staff
    - Volunteers
    - Researchers
  - — Financial
  - — Capital Equipment
  - — Operational
    - Premises – for project staff
    - Locations for delivery of education (where applicable)
    - Vehicles
    - Operational Systems and Procedures
- **Legal Issues**
  - — Conventions and Treaties
  - — Licences and Permits
  - — Local, National and International Legislation
  - — Employment Law
  - — Health and Safety Legislation
  - — Company/Organisation Structure – legal entity
- **Financial Plan**
  - — Budgets
  - — Income and Expenditure Forecasts
  - — Cashflow Forecasts
  - — Balance Sheets
  - — Management Accounts/Internal Financial Information

18.3.3 Evaluating the education programme

Evaluation is an important stage in a conservation education programme, and yet constraints on resources (financial, available staff and time) may lead to this part of the process being given less attention. In an analysis of successful wildlife conservation education programmes, Pomerantz and Blanchard (1992) reveal that few of the case studies found in a literature search included an evaluation component. Similarly, of the 56 reports included in Norris and Jacobson's (1998) analysis, fewer than half reported using some type of evaluation. However, in the same analysis, there were significantly higher rates of success for the programmes that did include evaluation.

Kleiman *et al*. (2000) describe three important aspects of effective evaluation:

1. Having an individual with leadership ability and considerable expertise to organise the format and oversee the review process;
2. Ensuring, at the outset, that there is agreement among the programme participants and the review committee on the goals and objectives of the conservation programme, what is to be evaluated, and the criteria for defining success; and
3. Ensuring that the programme is inclusive and involves all participants and stakeholders.

When incorporating evaluation into a programme consideration needs to be given to the following key elements:

- Measuring success – what the programme has accomplished. Have the criteria been met for both the conservation and education goals?
- How effectively has the programme functioned as a process?
- How are changes going to be made to the programme as a result of evaluation findings?
- How will information obtained from the evaluation be disseminated?

Evaluation should be integrated into every conservation programme, and it is important that it is included as part of the process when planning for resources. Otherwise it is difficult to evaluate the impact of a programme, as well as the effective features of successful conservation education programmes (Jacobson and McDuff 1997).

18.4 Resources required

18.4.1 Human resources

Human resources will probably be multi-agency and involve several stakeholders such as scientists, researchers, educators and trainers, conservationists, funders and sponsors, administrators, volunteers, policy-makers, community groups, local businesses, NGOs, and the media. The various roles will need to be clearly defined, and good communication between the various agencies or stakeholders is extremely important.

Effective project leaders are vital to the success of the programme and will need to be identified and accepted as they will be the driving force behind the project. Strong, effective leaders will also help to deal with any conflict resolution that may potentially threaten the programme.

18.4.2 Financial resources

Obtaining the necessary funding for any conservation project requires a great deal of time and energy. For conservationists this is a part of the process that is often the least welcome, and one that few people are trained to undertake. Financing a project is often seen as a 'necessary evil' and for this reason can often be undertaken half-heartedly. It is also a continuous process, especially if the project is long term.

Wherever possible, a professional fundraiser should be recruited – someone who has the necessary expertise in approaching potential funders and sponsors and who can prepare the necessary documentation, grant proposals and funding bids. Some fundraisers may offer to help on a voluntary basis until the project is more established. Others operate on a 'commission' basis whereby if they obtain the funding the project requires, they are paid a percentage.

Prepare a detailed financial plan. This can be done using spreadsheets or simple accounting software packages.

The first step of this process is to establish how much finance will be required and what this will be for:

- Salaries and staff expenses
- Capital equipment
- Premises
- Educational materials
- Research expenses
- Travel expenses
- Operational expenses and other overheads

Accessing funding can be a long, difficult and dispiriting process. However, even a cursory internet search will demonstrate that there is a lot of money available for conservation projects in the form of grants, awards and prizes, and sponsorships. Some conservation projects may also attract legacies and bequests, and donations. The key is to match your programme objectives to the funders' criteria. Be creative, and don't forget that there are two angles to conservation education programmes – the conservation angle and the education angle. There is funding available for both.

18.5 Conclusions

Education has an important role in conserving canids. This includes changing perceptions and attitudes in order to increase tolerance and foster co-existence. A recurring theme is conflict mitigation and addressing the issues that arise as a result of human/canid conflict – livestock depredation, competition for game species, negative perceptions and attitudes that provoke a ‘fear’ response, etc. It should also be recognised, however, that the issues involved are extremely complex and varied. Trying to quantify conservation education raises far more questions than it answers. But understanding the concepts of education, and how education can be applied in conjunction with a number of other conservation strategies will help to make the task of developing a conservation education programme much easier.

At present, there is still very little practical conservation education information available. There is also a lack of cohesive information with regard to conservation education programmes that are taking place worldwide. There are many excellent and successful initiatives, and we can also learn lessons from the ones that are not so successful. This information needs to be made more widely available. There needs to be a lot more cohesion with regard to conservation education that cuts across all boundaries and promotes a sense of unity and common purpose. If the target groups requiring the education are the policy-makers, then conservationists (in the broadest sense – encompassing everyone who works for the protection of species and habitats) need to have a stronger voice to be able to lobby at the highest levels.

Conservation education should be developed with a long-term view. Some of the attitudinal shifts and behavioural changes required are at societal level. This will mean implementing a combination of strategies, starting with early years education through the formal school system right through to adult education through non-formal, informal and communication programmes.

And finally, it is important to understand the problems and the target groups in great depth. It is this detailed knowledge and understanding that should underpin any conservation education programme.

PART 4

Action Plan for Canid Conservation into the 21st Century

Chapter 19

Some Considerations for Setting Priorities and Measuring Success for Canid Conservation

M.G.L. Mills

19.1 Introduction

One of the major challenges in conservation is the setting of priorities and measuring the success of the actions. There is the temptation when developing a conservation action plan to draw up a wish list of projects and actions, many of which have little chance of being funded. As a result many projects and actions in action plans are not implemented. An objective approach that sets priorities is clearly worth striving for. A method of auditing progress towards achieving the goals set out is equally important. In this section, some simple guidelines and principles for setting priorities and measuring their success are suggested.

19.2 Selecting priority species

The conservation status of a species, as determined by applying the IUCN Red List Categories and Criteria, is obviously the most important criterion when prioritising species for conservation action (Appendix 1). While all threatened species (i.e., those classed as Critically Endangered, Endangered and Vulnerable) deserve to be the focus of concerted conservation efforts, Critically Endangered and Endangered species should receive immediate attention, and separate and unique action plans. The IUCN Red List remains the most important tool for prioritising species on a global basis (Lamoreux *et al.* 2003).

Fifteen member dhole pack (*Cuon alpinus*) in pre-hunt bonding ritual. From top left: Alpha male, second male, alpha female. Bandipur National Park, Karnataka State, India, 1997.

Krupakar Senani

However, a problem arises when a species is Endangered globally, but not uncommon regionally; for example, the African wild dog (*Lycaon pictus*). At first thought, most of the action would seem to be needed where the species is most threatened. However, pouring resources into an area where the chances of success are low may not be as prudent as applying resources in areas where the species is doing well in order to ensure its continued survival there. Synthesis of action plans with a focus on regional or local conservation priorities is important. It is worth noting here that the IUCN, recognising the value and importance placed in the Red Listing process of species at a national or regional level by governments and other policy-making institutions, has developed guidelines for applying the IUCN Red List Categories and Criteria at the regional level (IUCN 2003). Consequently, species whose threat status has been assessed nationally or regionally could be prioritised on a comparable scale by local or regional conservation groups. However, globally threatened species remain the top conservation priorities.

In addition to the IUCN Red List status, Mills *et al.* (2001), in their analysis of geographic priorities for carnivore conservation in Africa, also applied a number of other criteria, such as taxonomic distinctiveness and degree of endemism and extent of occurrence, in an attempt to strengthen the evaluation of priority scores for African carnivores. They also included body size, as an estimator of the potential for human conflict, on the premise that larger carnivores would be more likely to attack livestock and, therefore, potential for human-wildlife conflict would be greater. This analysis gave rise to some rather unexpected results, although it did identify the Ethiopian wolf (*Canis simensis*) and the African wild dog as the first and second highest priority species requiring conservation action for the African continent. Nowell and Jackson (1996) applied a similar approach to the Felidae.

Not surprisingly, many projects represent the personal bias of the individuals involved. We often tend to focus on the local, abundant, problematical and economically valuable species, or the charismatic large ones (Ginsberg 2001). This is not always necessarily a bad thing as long as the motivation is transparent and the goals serve the interests of conservation. Local buy-in and involvement is very important and is likely to enhance the chances of success of plans and actions.

The most widely applied priority-setting approach in conservation is the hotspots model first developed by Myers (1988; see Myers *et al.* 2000), which attempts to focus conservation on areas of high species endemism and threat. By combining hotspot models with the use of iterative selection algorithms where representation is achieved using the principle of complementarity, as has been provisionally applied by Mills *et al.* (2001) for African carnivores, it might be possible to highlight areas of importance for canids. However, the basic problem of knowing the distribution patterns of the species concerned may often inhibit such a process and would appear to be a priority in many cases.

19.3 What to do

Priority-setting exercises tell us what to save first, not how to do it. Operational strategies need to be implemented in order to address the conservation issues. These can be broadly identified as research and management actions.

Perhaps one of the most fundamental differences in approach towards conservation issues is the species versus ecosystem approach. By definition, the IUCN Species Survival Commission (SSC) is based on a species approach. A major criticism of the species approach is that it is not holistic and does not necessarily take into account ecosystem functioning. While this is true, species projects, particularly those on threatened species, are often essential, and when strategic can achieve unprecedented success. There is also the argument that some charismatic species such as the Ethiopian wolf or African wild dog can be used as umbrella species to help conserve an ecosystem. However, we should never lose sight of the fact that a species is only a part of an ecosystem and that the final goal of conservation must be not only to conserve species, but also viable natural ecosystems and the patterns and processes that make them. Species conservation should not undermine ecosystem functioning.

In order to evaluate the conservation status of a species it is imperative to be able to say something about its distribution, abundance and population trends, its taxonomic status, and the threats facing the species. Surveys and population monitoring, therefore, are an extremely important aspect of species conservation. However, for many species, even highly visible ones like African wild dogs, it is often extremely difficult to obtain accurate figures of abundance and trends. Indeed, there may be too much importance attached to numbers as opposed to population viability, which, although linked, are not necessarily the same thing. Numbers *per se* and even short-term population trends are less important than the long-term viability of a population.

This action plan, like all SSC action plans, is concerned with only one small component of the rich biodiversity that makes up the planet, in this case the family Canidae. The considerable advantage of this approach is that specialists can focus in on their particular area of expertise. However, there are limited resources that can be channeled into conservation and, wherever possible, collaboration between specialists in different fields is desirable. For example, if a survey of wild dogs is to be undertaken in Nigeria, those responsible should contact other specialist groups such as the Cat and the Hyaena specialist groups to discuss with them the possibility of including additional species in the survey. This might be possible to achieve at little extra cost or output. An integrative approach would also promote guild-level studies and further elucidate the conservation importance of guild shifts and mesopredator release (Ginsberg 2001).

Detailed field studies investigating particular issues, or in an attempt to identify a species' role and needs in the ecosystem, are often required in order to draw up management strategies. In this regard an adaptive management approach, whereby the consequences of actions or conditions are studied, is likely to be particularly rewarding.

Ensuring the ecological integrity of an area and including full habitat representation is important. If suitable habitat is available, animals will survive if poaching is controlled. In the case of Data Deficient species, especially the small cryptic canids, habitat preservation is probably the best approach rather than detailed and difficult attempts at surveys. The greatest challenge in implementing ecoregional conservation plans is to ensure sufficient areas of contiguous habitat to be set aside for wildlife. Where this is not possible, more manipulative metapopulation management strategies could be applied (Mills *et al.* 1998).

19.4 Measuring success

Maintaining an objective and up-to-date measure of success is difficult to implement and requires discipline and time. Progress reports are very important and useful, but from time to time a wider overall evaluation of the action plan programme is needed. Perhaps a steering or core committee of the Canid Specialist Group should be constituted which could meet, say every two to three years, to evaluate progress. At a longer time scale, regular updating of action plans at ten-year intervals is essential for keeping abreast of developments and issues. Most importantly, species need to be assessed according to the IUCN Red List Categories and Criteria, using the most recent and up-to-date information available, on a regular basis.

Chapter 20

Action Plan for Canid Conservation into the 21st Century

C. Sillero-Zubiri, D. W. Macdonald and the Canid and Wolf Specialist Groups

In this section we list the projects and actions that we believe are priorities for canid conservation over the next ten years, chiefly focusing on threatened species (see Appendix 1). Given that canids are present throughout the world, and that many of the range countries do not have appropriate scientific and conservation infrastructure, we have attempted to identify the most essential projects and actions to improve the conservation status of threatened canid species, rather than present a wish list of projects per country as other IUCN action plans attempt. We aim to achieve a realistic list of projects and actions that would have a good chance of being implemented.

We take advantage from the individual Action Plans that have already been published for the Ethiopian wolf and African wild dog. For these two species we incorporate a mix of proposed and new projects and actions needed prepared by the relevant panel of experts from their Working Groups. Projects that have already been successfully implemented are excluded. Detailed projects for dholes, island, kit and swift foxes were also prepared by the experts of the relevant Working Groups.

Projects and actions are presented in a simple summary form and are organised into two sections. Section I consists of general projects affecting all canids, which address major issues in canid conservation, many covered in Part 3 of this document. Section II includes a larger group of single species projects and actions, laid out in the same geographical order as the Species Accounts. Threatened species are listed first (their IUCN Category indicated in square brackets), followed by Data Deficient species. Whenever possible, the projects for a given species are listed in order of priority. To locate projects for a certain region or species, see the summary list which follows. Although these projects are numerous, they do not address all species, nor all the general recommendations made for future work in Part 3 of this volume.

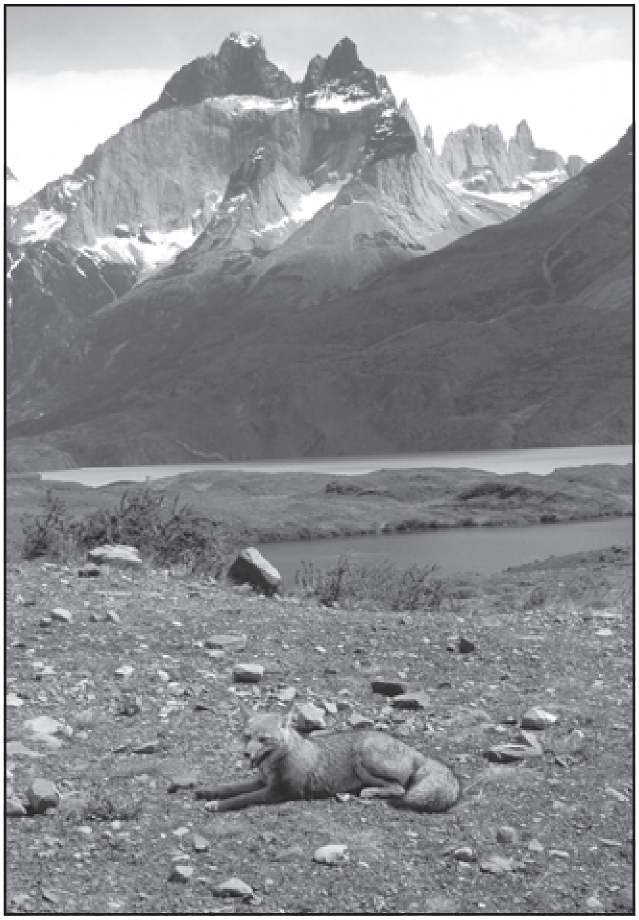
A ***project*** is defined as a research activity with objectives. It involves data collection, analysis and interpretation, followed by the making of recommendations.

An ***action*** entails doing something that is not focused on research, but that will in some measure improve the conservation status of the species involved.

We have included both ongoing and proposed projects in the Action Plan. Existing projects have received varying amounts of their budgeted funding, and a contact address is provided for donors and other interested parties. They are distinguished from the second group by the placement of an asterisk (*) following the title.

The second type of project consists of those proposed by Regional Sections and Canid Specialist Group members-at-large. These projects need detailed proposals, funding and, in many cases, workers. Donors and other interested parties should use the suggested contact and email (full mail addresses in Appendices 3 and 4) or contact the CSG directly for details. The CSG maintains a database of contacts for the executors of existing projects, and asks that the CSG be informed of contacts and progress related to these projects.

Chilla (*Pseudalopex griseus*) in Torres del Paine National Park, Chile, 2002.



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Budgetary needs are considered, but the cost information provided here is for planning purposes only. This aspect of the action plan will be refined as funding or management constraints dictate. Projects are categorised as follows in terms of approximate annual budget (all figures in US$):

I $10,000 or less
II $10,000 to $20,000
III $20,000 to $50,000
IV $50,000 to $100,000
V over $100,000
? Not known

List of Priority Projects and Actions

I. Project and actions involving all species

Implementation of Canid Action Plan

1.1 [Action] Employ a Programme Officer to act as liaison between the Canid Specialist Group, project managers and potential donors

Canid Project Database

1.2 [Action] Maintain a database of existing and planned projects on wild canid species*

Status surveys

1.3 [Action] Promote short field surveys of Data Deficient canid species
1.4 [Project] Develop standardised survey methodology
1.5 [Action] Support the development of non-invasive population monitoring methodology

Education and public relations

1.6 [Action] Raise support for Canid News and http://www.canids.org*
1.7 [Project] Investigate methods for initiating effective education campaigns at local level*

II. Species projects and actions

South America (Chapter 3)

2. Darwin's fox [CR]

2.1 [Project] Biology of Darwin's foxes in Chiloé Island*
2.2 [Project] Finding the missing links: uncovering additional mainland populations of the Darwin's fox
2.3 [Project] Local attitudes and conservation education in Chiloé Island*
2.4 [Project] Presence of canine infectious diseases and the risk of transmission to the Darwin's fox population*
2.5 [Project] Reproductive success of Darwin's foxes in fragmented versus intact forest*

3. Bush dog [VU]

3.1 [Project] Bush dog ecology in Paraguay*
3.2 [Project] Survey the population status of bush dogs within protected areas
3.3 [Project] Evaluate the historical distribution and current status of bush dogs at country level*

4. Maned wolf [NT]

4.1 [Project] Maned wolf population survey and habitat assessment throughout the species range
4.2 [Project] Mammal communities on the rainforest-savanna boundary in Bolivia*
4.3 [Project] Environmental and human factors affecting maned wolf conservation in Argentina*
4.4 [Action] Involving local people in the conservation of maned wolves in Argentina*

5. Short-eared dog [DD]

5.1 [Project] Distribution and status of short-eared dog
5.2 [Project] Ecology and conservation of short-eared dogs in south-eastern Peru*

6. Sechuran fox [DD]

6.1 [Project] Natural history, distribution and status of Sechuran fox
6.2 [Project] Epidemiology of disease in Sechuran fox populations

6.3 [Action] Sechuran fox utilisation and conservation education in rural areas of Peru

Central and North America (Chapter 4)

7. Red wolf [CR]

7.1 [Action] Promote support and funding for the Red Wolf Coalition's education activities on behalf of the red wolf restoration effort in north-eastern North Carolina*
7.2 [Project] Determine the effectiveness of the U.S. Fish and Wildlife Service's Adaptive Management Plan to reduce hybridisation between red wolves and coyotes*

8. Island fox [CR]

8.1 [Project] An assessment of mate choice in captive island foxes*
8.2 [Project] Enhancing reproduction in captive island foxes on San Miguel Island*
8.3 [Project] An assessment of non-invasive techniques for monitoring wild island foxes*
8.4 [Project] An assessment of variation at the major histocompatibility complex in the island fox*
8.5 [Project] An exploration into the factors causing population decline in the San Clemente Island fox*
8.6 [Action] Complete removal of golden eagles from the Northern Channel Islands
8.7 [Action] Captive island foxes to remain in captivity until the threat of golden eagle predation is completely mitigated
8.8 [Action] An evaluation of cryogenic storage of sperm and artificial insemination as a means to increase reproduction in captive island foxes
8.9 [Action] Cessation of trapping of island foxes on San Clemente Island as part of the San Clemente Loggerhead Shrike Recovery Program
8.10 [Action] Development of educational outreach to inform public of the decline of the island fox

9. Arctic fox [LC]

9.1 [Action]. Establish and promote legal protection for the endemic subspecies of Arctic fox (*Alopex lagopus pribilofensis*) on Pribilof Islands, Bering Sea, Alaska*

10. Kit fox [LC]

10.1 [Action] Monitor kit fox populations throughout their range
10.2 [Project] Distribution and strongholds of the kit fox in the southern portion of its range*
10.3 [Action] Monitor populations of San Joaquin kit foxes in central California, USA*
10.4 [Project] Investigate mitigation strategies for San Joaquin kit foxes
10.5 [Project] Investigate interactions between San Joaquin kit foxes and non-native red foxes

11. Swift fox [LC]

11.1 [Project] Determine habitat selection of reintroduced swift foxes in Canada and Montana
11.2 [Project] Determine serology and health of swift foxes and sympatric canids in Canada and Montana
11.3 [Project] Determine gene flow and connectivity within the reintroduced Canadian/Montana swift fox population
11.4 [Action] Develop a swift fox recovery strategy that is compatible with Canada's Species at Risk Act
11.5 [Action] Monitor the reintroduced swift fox population in Canada and Montana
11.6 [Project] Role of parental attendance and habitat heterogeneity in the reproductive success of swift fox under different disturbance regimes*

12. Grey wolf [LC]

12.1 [Action] Revise the U.S. Fish and Wildlife Service's Mexican Wolf Recovery Plan*
12.2 [Action] Revise the federal rules governing management of wolves that travel outside the Blue Range Wolf Recovery Area in south-eastern Arizona and south-western New Mexico*
12.3 [Project] Spatial analysis of restoration potential and population viability of the Mexican wolf in the south-western United States and northern Mexico*
12.4 [Project] Utility of an experience centre for improving the survival of captive-born Mexican wolves released to the wild
12.5 [Action] Promote support and funding for the Wolf Forum for the Southern Rockies*
12.6 [Action] Promote support and funding for the Southern Rockies Wolf Restoration Project*

13. Gray fox [LC]

13.1 [Project] Evolution and conservation of the Cozumel Island gray fox*

Europe and North and Central Asia (Chapter 5)

14. Arctic fox [LC]

14.1 [Project] Conservation of insular Arctic fox populations endemic to Bering Sea Islands in Alaskan and Russian waters
14.2 [Action] Saving the Endangered Fennoscandian *Alopex lagopus* [SEFALO+]*

15. Grey wolf [LC]

15.1 [Project] Conservation and management of grey wolves in Finland*

16. Raccoon dog [LC]

16.1 [Project] The spatial ecology of small carnivores in south-east Finland and the control of rabies*

Sub-Saharan Africa (Chapter 6)

17. Ethiopian wolf [EN]

17.1 [Action] Coordination of Ethiopian wolf conservation*
17.2 [Project] Ethiopian wolf population surveys*
17.3 [Project] Monitoring wolf populations, their Afroalpine ecosystem and human activities within the ecosystem*
17.4 [Project] Prioritisation of areas for conservation*
17.5 [Project] Social structure and ecology of wolf populations in northern Ethiopia
17.6 [Project] Wolf MHC gene variability
17.7 [Project] Screening wolf populations for dog genes
17.8 [Project] Ethiopian wolf phylogeography*
17.9 [Action] Disease prevention*
17.10 [Project] Test methods to reduce disease transmission and incidence in domestic dogs and Ethiopian wolves*
17.11 [Project] Control of domestic dog populations within and surrounding Ethiopian wolf ranges
17.12 [Action] Hybrid management*
17.13 [Action] Inform and educate the people of Ethiopia about the Ethiopian wolf and its Afroalpine ecosystem*
17.14 [Action] Inform and lobby organisations in Ethiopia of the importance of the environment as a cross-cutting issue*
17.15 [Action] Build the capacity of Ethiopia in the fields of ecology, conservation, epidemiology, conservation education and conservation policy*
17.16 [Project] Attitudes of local people to the Ethiopian wolf and its Afroalpine ecosystem*
17.17 [Action] Secure the protection of the Bale Mountains National Park*
17.18 [Action] Secure the protection of other areas of Afroalpine ecosystem in Ethiopia*
17.19 [Action] Promote tourism and other methods of generating revenue in wolf ranges*
17.20 [Action] Financial sustainability of the Ethiopian Wolf Conservation Programme*
17.21 [Action] Feasibility of establishing a captive breeding population
17.22 [Action] Preservation of Ethiopian wolf genetic material

18. African wild dog [EN]

18.1 [Action] Maintenance and expansion of very large wildlife areas, including Corridors and Transfrontier Conservation Area Development
18.2 [Project] Develop specific, low-cost methods and techniques for reducing human and livestock conflict
18.3 [Project] Develop tools to foster coexistence of wild dogs with livestock farmers in Kenya*
18.4 [Project] Develop tools to foster coexistence of wild dogs with livestock farmers in the Kalahari region
18.5 [Project] Develop tools to foster coexistence of wild dogs with people in Zimbabwe*
18.6 [Project] Coexistence between game farmers and wild dogs in South Africa
18.7 [Project] Develop tools to evaluate disease threats to wild dogs and determine whether intervention is necessary
18.8 [Project] Vaccine trials on wild dogs held in captivity*
18.9 [Project] Monitoring population and pack dynamics of wild dogs in Kruger National Park, South Africa*
18.10 [Project] Monitoring population and pack dynamics of wild dogs in the Okavango region, Botswana*
18.11 [Project] Monitoring of the distribution, density, and mortality of wild dogs in Zimbabwe*
18.12 [Project] Monitoring and evaluation of management strategies for wild dogs in the Rungwa-Ruaha ecosystem, Tanzania
18.13 [Project] Ecology of wild dog populations in dryland areas of the Kalahari region
18.14 [Project] Status and ecology of the African wild dog in central and northern Mozambique*
18.15 [Project] Status, distribution, and ecology of an unprotected wild dog population in north-eastern Kenya*
18.16 [Project] Status of African wild dog populations in West Africa
18.17 [Project] Establish distribution and status of wild dogs in southern Sudan
18.18 [Project] Establish distribution and status of wild dogs in central Africa
18.19 [Project] Determine status of wild dogs in Teffedest Mountains, Algeria
18.20 [Project] Develop low-tech methods for surveying and monitoring wild dogs
18.21 [Action] Establish a second wild dog population in South Africa by setting up a series of smaller populations and managing them as a meta-population*
18.22 [Action] Development of a viable community conservation programme in Zimbabwe*

North Africa and the Middle East (Chapter 7)

19. Desert canid community

19.1 [Project] Natural history, distribution and status of the pale fox, Rüppell's fox and fennec fox
19.2 [Project] Distribution and status of Rüppell's fox and Blanford's fox in south-west Saudi Arabia, Yemen and Oman
19.3 [Project] Survey of canid species in the central Sahara Desert

20. Blanford's fox [VU]

20.1 [Project] Distribution and status of the Blanford's fox in Egypt, Sudan and the Horn of Africa

21. Rüppell's fox [DD]

21.1 [Project] Causes for local extinction of Rüppell's fox in Israel

22. Grey wolf [LC]

22.1 [Project] Status of little known populations of the grey wolf in Iran, Iraq and Syria
22.2 [Project] Status of populations of the grey wolf in the southern Arabian Peninsula
22.3 [Project] Status and taxonomic elucidation of *Canis aureus lupaster*

South Asia, South of the Himalaya [Chapter 8]

23. Dhole [VU]

23.1 [Project] Development and evaluation of survey methods
23.2 [Project] Genetic studies
23.3 [Project] Ecological and behavioural studies
23.4 [Action] Surveys and monitoring
23.5 [Action] Prioritisation of populations for conservation action
23.6 [Action] Understanding the epidemiology of disease in dholes
23.7 [Action] Protection of dholes and their habitat
23.8 [Action] Management of the prey base
23.9 [Action] Conflict with people
23.10 [Action] Conflict with other threatened species
23.11 [Action] Captive breeding of dholes
23.12 [Action] Reintroduction and translocation of dholes
23.13 [Action] Legislative issues affecting dhole conservation

Australia and Oceania [Chapter 9]

24. Dingo [VU]

24.1 [Project] Status and taxonomic elucidation of New Guinea singing dog
24.2 [Action] Identify suitable reference material to assess dingo genetic introgression
24.3 [Project] Assess the conservation implications of dingo genetic introgression

I. Projects and actions involving all species

Implementation of Canid Action Plan

1.1 [Action] Employ a Programme Officer to act as liaison between the Canid Specialist Group, project managers and potential donors

Objectives: To run the everyday business of the Specialist Group and implement activities proposed in the Canid Action Plan.

Implementation details: A full-time Programme Officer will run the everyday business of the specialist group, including membership, communication, publication of Canid News, liaison, maintenance of Canid Project Database and oversee implementation of the Canid Action Plan. The Project Manager will respond to request for information, documentation, contacts and other assistance in connection with the implementation of Canid Action Plan activities.

Annual budget: III

Time frame: Long-term

Contact: Canid Specialist Group, canids@zoo.ox.ac.uk

Canid Project Database

1.2 [Action] Maintain a database of existing and planned projects on wild canid species*

Objectives: To assist the implementation of the Canid Action Plan by further developing the existing Canid Project Database, in order to facilitate communication between project managers and potential donors; communication of project results and dissemination of information on canid conservation for public education and awareness.

Implementation details: The Canid Specialist Group has already established an online Canid Project Database (Appendix 5) of existing and planned projects on all wild canid species. The database will be expanded to incorporate project outputs and links to other useful information, as well as to manage contacts and grey literature (e.g., unpublished reports and thesis). The Canid Project Database will be instrumental in ensuring that conservation successes can be duplicated elsewhere and failures avoided.

Annual budget: II

Time frame: Ongoing, needs funding

Contact: Canid Specialist Group, canids@zoo.ox.ac.uk

Status surveys

1.3 [Action] Promote short field surveys of Data Deficient canid species

Objectives: Facilitate planning and funding of field surveys on little known canid species; encourage wildlife biologists in range countries to collect data on distribution and status of Data Deficient species.

Implementation details: Relatively inexpensive short-term surveys would help provide needed information on the lesser-known canid species. The Canid Specialist Group will help channel relevant information on any suitable small-grant programme to those in the field better able to undertake necessary surveys.

Annual budget: II

Time frame: Long-term

Contact: Canid Specialist Group, canids@zoo.ox.ac.uk

1.4 [Project] Develop standardised survey methodology

Objectives: To develop a standard for short survey methodology.

Implementation details: Canids can be difficult to survey, particularly rare species or those occurring at very low densities (see Chapter 15). Questionnaires can be important to obtain a coarse-scale evaluation of presence/absence, habitat preference and trends, and may also include assessment of threats. A standard, simple to use questionnaire, should be made available to those likely to undertake field surveys in areas of interest. Questionnaires may be supplemented with spot-light transect counts, selective live trapping and opportunistic collection of tissue samples and faeces, and standard protocols would be provided for these methods as well. Calibration at specific locations of known canid density can help test whether information and trends estimated with questionnaires at a larger scale are reliable. Any data derived from short surveys should be submitted to the Canid Specialist Group and stored in the database.

Annual budget: I

Time frame: 6 months

Contact: Canid Specialist Group, canids@zoo.ox.ac.uk

1.5 [Action] Support the development of non-invasive population monitoring methodology

Objectives: To promote the investigation of novel approaches for long-term estimation of trends on threatened canid populations; prepare adequate field protocols.

Implementation details: For threatened species that require monitoring to assess the effects of threats over a certain period (i.e., ten years) a relative measure of population status can be more informative (and cheaper) than estimates of total population size. Monitoring does not need to cover the entire distribution range of a species, but rely on 'sentinel' populations as a surrogate. Trends are also a good parameter to evaluate the success or failure of conservation measures applied during a given period.

New non-invasive techniques are emerging (see Chapter 15), which offer the potential to monitor populations without disturbance, and would make evaluating population trends much simpler and cheaper in the future. These include using genetic identification of individual animals using systematic collection of hair or faeces and capture-mark-recapture techniques for estimating population size and structure (See Projects 8.3, 15.2, 16.20). For low density species domestic dogs may be trained to recognise and locate canid faeces and other sign. Calibration at specific locations of known canid density can help test new approaches. Techniques based on photographic records and spoor surveys have been developed in the past, but may only be applicable for conspicuous diurnal species and open, sandy habitats respectively.

Annual budget: II

Time frame: 1 year

Contact: Canid Specialist Group, canids@zoo.ox.ac.uk

Education and public relations

1.6 [Action] Raise support for Canid News and http://www.canids.org*

Objectives: To secure funding for the Canid Specialist Group peer-reviewed online journal and CSG website.

Implementation details: The Canid Specialist Group produces an online peer-review journal Canid News (Appendix 5), which replaced the CSG's original newsletter. Canid News is hosted in the CSG website, which in itself is an instrumental communication tool and information exchange between the CSG, people involved in canid conservation and other interested parties. Funds are required to maintain the hardware and keep software up-to-date, redesign the site and cover annual server fees.

Annual budget: II

Time frame: Ongoing, needs funding

Contact: Canid Specialist Group, canids@zoo.ox.ac.uk

1.7 [Project] Investigate methods for initiating effective education campaigns at local level*

Objectives: Investigate education strategies commensurate with canid conservation goals such as lessening human-canid conflict, reducing disease transmission and explaining the ecological role of carnivores. Provide a framework to help plan and implement effective conservation campaigns to improve public under-standing.

Implementation details: Through a literature review, interviews and questionnaire surveys define primary conservation goals, target groups, geo-political, social and cultural contexts affecting peoples attitude to wild canids. Develop education and communication strategies (non-formal, informal, formal); identify and source appropriate levels of funding, human resources, materials and equipment; identify ways to foster multi-disciplinary and multi-agency cooperation; train conservation project personnel on the basics of conservation education.

Annual budget: II

Time frame: 1–2 years

Contact: Canid Specialist Group, canids@zoo.ox.ac.uk, and E4C Education for Conservation, Denise Taylor, denise.taylor@btinternet.com

II. Species projects and actions

South America [Chapter 3]

2. Darwin's fox [CR]

2.1 [Project] Biology of Darwin's foxes in Chiloé Island*

Objectives: To obtain basic information on the ecology and genetic structure of the Darwin's fox on Chiloé Island.

Implementation details: A multidisciplinary team supported by local agencies and NGOs are conducting research at a few intensive sites and several rapid-assessment sites throughout Chiloé Island. A combination of intensive trapping and non-invasive techniques are used to monitor foxes, determine population size and relative abundances, map the vegetation and study the genetic structure of all the sub populations in the island. A predictive model will be constructed to better understand the factors affecting fox distribution and abundance.

Annual budget: IV (funded by the UK Department of Agriculture and Rural Affairs)

Time frame: 3 years

Contact: Jaime E. Jiménez, jjimenez@ulagos.cl, http://www.darwinfox.org

2.2 [Project] Finding the missing links: uncovering additional mainland populations of the Darwin's fox

Objectives: To search for additional populations of the Darwin's fox on Chile's mainland, targeting the dense, virgin forests between Maullin and Nahuelbuta Mountains, and remaining coastal forest north of Chiloe.

Implementation details: With only two, widely separated, populations of Darwin's foxes known in Chile, there is great interest in discovering information on or actual populations of Darwin's foxes in other areas on the mainland. Recent evidence indicates that there might be populations of Darwin's foxes persisting on the mainland in remaining pockets of forests. This project will seek to locate additional populations and to determine potential threats to these populations. Field searches will use extensive remote camera systems, trapping, and collection of droppings to identify fox presence using molecular techniques.

Annual budget: II

Time frame: 1 year

Contact: Canid Specialist Group (South America Regional Section), canids@zoo.ox.ac.uk

2.3 [Project] Local attitudes and conservation education in Chiloé Island*

Objectives: To sensitise Chiloé Island's population toward fox conservation and sustainable use of biodiversity through an education programme; build up capacity of local conservation biologists to further the conservation of Darwin's foxes.

Implementation details: Rural and urban local peoples' attitudes to wildlife and native forest conservation are determined using a questionnaire survey. Using the Darwin's fox as a flagship for forest conservation slide shows, posters, fliers, courses, and a website are used to educate and improve the awareness of the local communities on the unique and rapidly declining island biodiversity. Using the project resources, priority will be given to train local biologists that would take on future Darwin's fox conservation initiatives.

Annual budget: II

Time frame: 3 years

Contact: Jaime E. Jiménez, jjimenez@ulagos.cl, http://www.darwinfox.org

2.4 [Project] Presence of canine infectious diseases and the risk of transmission to the Darwin's fox population*

Objectives: Evaluate presence of canine infectious diseases in local domestic dog and fox communities in Chiloé and Nahuelbuta National Park; determine possible modes of disease transfer that may affect the Darwin's fox.

Implementation details: Domestic dogs are found in and around Darwin's fox populations in Chiloé and Nahuelbuta National Park. Small populations are potentially at risk if they come into contact with infected dogs, and there have been recent outbreaks of rabies and canine distemper in wild canids in nearby Argentina. Two separate site-specific projects seek to identify which canine diseases are present in the area and to what extent. Blood samples are collected from foxes and domestic dogs (including park visitors' dogs that are frequently allowed in the park). In Nahuelbuta samples will also be collected from sympatric chilla and culpeo, to establish their role as carriers.

Annual budget: I

Time frame: 1 year

Contact: Nahuelbuta: Elise McMahon, emcmahon@forwild.umass.edu;
Chiloe: Jaime E. Jiménez, jjimenez@ulagos.cl

2.5 [Project] Reproductive success of Darwin's foxes in fragmented versus intact forest*

Objectives: Determine reproductive success of the Darwin's fox population in Nahuelbuta National Park, comparing pairs living outside and on the borders of the park to those living within the park.

Implementation details: Darwin's foxes on the mainland are protected within the boundaries of the Nahuelbuta National Park. However, there are breeding pairs whose home ranges lie beyond the park on privately owned land. This land of highly fragmented forest is used for cattle grazing and wood extraction, heavily used by both humans and their dogs, and has a higher density of culpeos, a potential predator of Darwin's foxes. Breeding pairs will be radio-collared, monitored and their breeding success measured, the latter determined by number of pups and/or juveniles trapped within the parental home range and confirmed by DNA analysis.

Annual budget: III

Time frame: 3 years

Contact: Elise McMahon, emcmahon@forwild.umass.edu

3. Bush dog [VU]

3.1 [Project] Bush dog ecology in Paraguay*

Objectives: To investigate bush dog ecology within a diverse carnivore community in Atlantic Forest.

Implementation details: Bush dogs are one of 16 confirmed mammalian carnivore species in the Mbaracayú Forest Biosphere Reserve, a fragment of Interior Atlantic Forest in eastern Paraguay. This project evaluates the ecological role of bush dogs within this community using non-invasive methods. Permanent camera-trapping grids, coupled with baited tracking stations and hair snares, will be established throughout the reserve during wet and dry seasons. Individual bush dogs will be identified from faeces via molecular techniques. Current diet-based indices of interactions between bush dogs and other carnivores from the reserve (i.e., overlap, niche breadth) will be tested for long-term consistency, diet analyses and the examination of habitat patterns will continue. Bush dog locations will be entered in a GIS to evaluate habitat and land use by all carnivore species; spatial comparisons will be made between bush dogs and other species.

Annual budget: IV

Time frame: Ongoing, 5–8 years

Contact: Gerald L. Zuercher, geraldz@ksu.edu, http://www.ksu.edu/kscfwru/

3.2 [Project] Survey the population status of bush dogs within protected areas

Objectives: To survey key protected areas in Paraguay, Brazil and elsewhere within bush dog range, and attempt to estimate population status and trends.

Implementation details: Although bush dogs are widely distributed and known to occur in several locations of Brazil and Paraguay, they are confirmed for only a few sites and there are no estimates of population numbers and trends. Furthermore, there is little idea as to their status in most protected natural habitat throughout their range. A number of selected protected areas will be surveyed using replicates of 1km^2 camera grids, coupled with baited tracking stations and hair snares. Faeces from bush dogs will be collected both opportunistically and in deliberate search efforts. Collected faeces will be tested by molecular techniques for both species and individual identification. Confirmed bush dog faeces will serve as exact locations for habitat analyses and examined for diet content. Land-owners and indigenous peoples, in and around sites, will be interviewed for information of recent dog sightings. Results will be extrapolated to derive some idea of country-wide population distribution and sizes.

Annual budget: III (country projects require independent funding)

Time frame: 3–5 years

Contact: Canid Specialist Group (South America Regional Section), or Brazil: Tadeu G. de Oliveira, tadeu4@yahoo.com, http://www.procarnivoros.org.br, Paraguay: Claudia Mercolli, cmercolli@mbertoni.org.py, http://www.mbertoni.org.py

3.3 [Project] Evaluate the historical distribution and current status of bush dogs at country level*

Objectives: To evaluate the historical distribution of bush dogs and assess current status and trends at a country level using a mail questionnaire.

Implementation details: Knowledge of population status and trends is needed for the development of long-term conservation plans. Unfortunately this information is largely missing for the secretive bush dogs. Using a mail questionnaire sent to rangeland countries this project will compile information of historical and current presence/absence data, opportunistic sightings, habitat preferences, records of mortality and disease. Additional information will be obtained from the literature of previous surveys and museum specimens. The information collated will be combined with GIS maps of potentially available habitat to prioritise regions for research and conservation.

Annual budget: I

Time frame: 1–2 years

Contact: Karen DeMatteo, KDeMatteo@aol.com

4. Maned wolf [NT]

4.1 [Project] Maned wolf population survey and habitat assessment throughout the species range

Objectives: To develop population and habitat surveys within and around protected natural areas throughout the species range; estimate population status and trends in specific areas to assess whether protection within those areas is successful.

Implementation details: Current estimates of maned wolf populations are very rough and often mere extrapolations on the size of what is thought to be suitable habitat. Estimates of population trends over a time period can be more important than estimates of total population size in providing information to assess the effects of threats and the success or failure of conservation measures applied during that period.

An assessment of suitable habitat throughout the species range is also needed. This should include:

a) defining what constitutes suitable habitat for the maned wolf, and
b) determining how much habitat remains, and the degree of connectivity and threats between remnants of suitable habitat.

Methods need to be developed and tested to reliably assess long-term population trends of maned wolves in specific locations with different degrees of protection.

Annual budget: III

Time frame: 2 years

Contact: Canid Specialist Group (South America Regional Section), canids@zoo.ox.ac.uk

4.2 [Project] Mammal communities on the rainforest-savanna boundary in Bolivia*

Objectives: To study the ecology, behaviour, and habitat use of maned wolf in a complex habitat mosaic at the pampa/forest boundary in Parque Nacional Noel Kempff Mercado, Santa Cruz, Bolivia.

Implementation details: This study forms part of a larger project aimed at understanding the ecology of mammal communities in Bolivias rainforest-savanna boundary. Radio-tracking, diet, health and genetic studies of maned wolves are in progress. Inter-annual variation in small mammal prey is being followed by yearly, standardised trapping (now in 5th year). This may be the only current study of the species in seasonally flooded grasslands.

Annual budget: II

Time frame: Ongoing

Contact: Louise Emmons, emmons.louise@nmnh.si.edu

4.3 [Project] Environmental and human factors affecting maned wolf conservation in Argentina*

Objectives: To study the ecological requirements of maned wolves in the southern end of their range and evaluate human impacts threatening their conservation.

Implementation details: Agricultural expansion and conflicts with humans appear to be the most important threats to the maned wolf in Argentina. Interviews with local people are being done to detect problems and attitudes toward the maned wolf and to map land use.

Annual budget: III

Time frame: 2002–2005

Contact: Lucía Soler, luengos@criba.edu.ar, http://www.oikoveva.org

4.4 [Action] Involving local people in the conservation of maned wolves in Argentina*

Objectives: Contribute to change attitudes of local people towards maned wolf conservation.

Implementation details: An education conservation programme is being developed in collaboration with local people to highlight the importance of biodiversity conservation and to plan different actions to promote conservation. The National Park Administration, Private Reserves, and social leaders are involved in conservation efforts. National and international workgroups are promoted to develop integrative conservation action plans for maned wolves.

Annual budget: II

Time frame: 2002–2005

Contact: Lucía Soler, luengos@criba.edu.ar

5. Short-eared dog [DD]

5.1 [Project] Distribution and status of short-eared dog

Objectives: To conduct basic presence/absence surveys in key parts of the species range, including western Brazil, Ecuador, Bolivia, Colombia, and northern Peru; to map their distribution and evaluate species status.

Implementation details: Although widespread, the short-eared dog is arguably the least-known canid species in South America. Detailed information on population abundance or status is missing. This project will seek to clarify, through a series of mail questionnaires and subsequent presence/absence field surveys in selected locations, the current distribution and status of the species. Survey techniques will be carefully designed to avoid confusion between sympatric species. Biological samples for morphological and genetic studies will also be collected if possible.

Annual budget: II–III

Time frame: 2–3 years

Contact: Canid Specialist Group (South America Regional Section), or M.R.P. Leite Pitman, mrpl@duke.edu

5.2 [Project] Ecology and conservation of short-eared dogs in south-eastern Peru*

Objectives: To study the ecology and implement basic conservation measures to protect short-eared dogs in Cocha Cashu Biological Station and the Alto Purus Reserved Zone, south-eastern Peru.

Implementation details: Simple presence/absence surveys and a radio-tracking study have yielded some information on this little-known species, suggesting that the Peruvian Amazon may represent one of the best enclaves for this species. Concern exists that disease transmitted by domestic dogs may be the main threat to this low-density forest specialist. The project is seeking funding to establish a domestic dog vaccination programme in the protected areas of Amazonian Peru and to expand field work to other sites within the species' range.

Annual budget: III–IV
Time frame: Ongoing
Contact: M.R.P. Leite Pitman, mrpl@duke.edu

6. Sechuran fox [DD]

6.1 [Project] Natural history, distribution and status of Sechuran fox

Objectives: To study the basic biology and ecological requirements of the Sechuran fox; determine distribution range, population size and status; determine existence of subspecies.

Implementation details: The Sechuran fox is one of the least-known canid species. Just a few studies about this species have been undertaken, principally in northern Peru. Its distribution, population size, existence of subspecies, reproductive ecology and other aspects of its behaviour are unknown. Sechuran foxes appear to tolerate traditional human land use but may be threatened in some parts of their range. Therefore, it is important to increase our knowledge of the species and design and implement a conservation action plan. The project should include field surveys in southern Ecuador, northern and central Peru (to 14°S), using tracking, sightings, camera traps, collection of genetic material, and an interview survey on interactions with local people.

Annual budget: II
Time frame: 1–2 years
Contact: Canid Specialist Group (South America Regional Section), canids@zoo.ox.ac.uk

6.2 [Project] Epidemiology of disease in Sechuran fox populations

Objectives: To study disease transmission in foxes and domestic animals and evaluate its importance in Sechuran fox conservation.

Implementation details: The Sechuran fox inhabits areas with high rural human density and predominantly agricultural land use. The parasites and diseases affecting the species are unknown, but individuals with disease symptoms are regularly observed. The project will include field surveys, collection of blood, ectoparasites, faeces and any carcasses found opportunistically for laboratory analysis, and evaluation of domestic dogs for disease in the surveyed areas.

Annual budget: I
Time frame: 1 year
Contact: Canid Specialist Group (South America Regional Section), canids@zoo.ox.ac.uk

6.3 [Action] Sechuran fox utilisation and conservation education in rural areas of Peru

Objectives: To reduce the use of Sechuran fox parts to make amulets; mitigate livestock predation by Sechuran fox and other sympatric carnivores; introduce a carnivore and habitat conservation ethic in rural areas of northern Peru and southern Ecuador.

Implementation details: Sechuran fox parts are priced to make amulets and foxes are sometimes caught and their tails cut, but the extent of this practice is not known. Wildlife product trade (primarily for carnivores) needs to be assessed and local authorities supported in controlling such trade. One way of changing peoples' perception for predators in Peruvian and Ecuadorian rural areas is to deliver education programmes, including child education, to mitigate the impact of predation on livestock.

Annual budget: II
Time frame: 2–3 years
Contact: Canid Specialist Group (South America Regional Section), canids@zoo.ox.ac.uk

Central and North America [Chapter 4]

7. Red wolf [CR]

Compiled by the Wolf Specialist Group

7.1 [Action] Promote support and funding for the Red Wolf Coalition's education activities on behalf of the red wolf restoration effort in north-eastern North Carolina*

Objectives: The Red Wolf Coalition promotes red wolf recovery by: fostering public-private partnerships; increasing public awareness; raising funds and other contributions; and advocating for the species as an integral component of the south-eastern United States.

Implementation details: Promote red wolf recovery by educating and involving the public in the restoration effort in north-eastern North Carolina. Seek additional funding to implement more education programmes and to construct a red wolf education centre in Columbia, North Carolina. Liaise with other conservation and community projects to seek new ideas for improving the effectiveness of the Coalition and for resolving conflicts between local residents and red wolves.

Annual budget: V
Time frame: Ongoing, long-term
Contact: Aubrey White Remige, redwolf@coastalnet.com, http://www.redwolves.com

7.2 [Project] Determine the effectiveness of the U.S. Fish and Wildlife Service's Adaptive Management Plan to reduce hybridisation between red wolves and coyotes*

Objectives: Investigate the feasibility, effectiveness, and repeatability of an Adaptive Management Plan to reduce (or prevent) hybridisation between red wolves and coyotes in north-eastern North Carolina, so that the red wolf can be restored to a significant portion of the species' historic range.

Implementation details: From 1987 through 1994 efforts to restore a population of red wolves via the reintroduction to the Alligator River National Wildlife Refuge were successful. During the mid-1990s the status of the project changed as hybridisation between red wolves and coyotes became increasingly common. In response the U.S. Fish and Wildlife Service developed an Adaptive Management Plan that called for hybridisation to be eliminated or reduced through intensive fieldwork to euthanise or sterilise coyote and hybrids and promote the formation and maintenance of red wolf pairs. Implementation of the plan began in April 1999 and some progress has been recorded. Additional fieldwork and analysis of data need to be completed to assess the plan's overall feasibility, effectiveness, and repeatability. This assessment is requisite to determining the likelihood of recovering the red wolf given that coyotes are widespread throughout the red wolf's historic range.

Annual budget: V

Time frame: Ongoing, 3–5 years needed

Contact: Buddy Fazio, buddy_fazio@fws.gov, http://alligatorriver.fws.gov/redwolf.html

8. Island fox [CR]

Compiled by the CSG Island Fox Working Group (Gary Roemer, Tim Coonan, Linda Munson, Robert Wayne and Rosie Woodroffe)

The projects and actions proposed for conservation of the island fox reflect the species extremely restricted island distribution and recent population decline. Found only on the six largest California Channel Islands, the total number of island foxes has dropped from over 6,000 to less than 1,200 individuals (Roemer 1999; Roemer *et al.* 2001a, 2002). Current management actions to save the island fox from extinction include:

i) live-capture and translocation of golden eagles;
ii) the reintroduction of bald eagles as a potential deterrent to golden eagles;
iii) the establishment of four captive breeding facilities;
iv) the application of an experimental vaccine to confer immunity to canine distemper virus;
v) continued disease surveillance and a determination of mortality factors;
vi) continued population monitoring of wild fox populations; and
vii) the eradication of feral pigs.

8.1 [Project] An assessment of mate choice in captive island foxes*

Objectives: To develop a methodology that will allow unpaired female island foxes to choose an unrelated mate to improve captive propagation.

Implementation details: Island fox reproduction in some captive breeding facilities has been poor and there is a need to improve reproductive output for eventual release back into the wild. Determination of relatedness based on microsatellite profiles will be used to select unrelated males that will then be introduced to captive females. Female hormone levels will be monitored and female behavioural response to urine from the selected males along with behavioural cues to introduced males will be interpreted. The male 'selected' by the female will then be used to establish a pair for future captive propagation or release. Implementation of the project would need to occur on three islands (San Miguel, Santa Rosa and Santa Cruz) administered by the National Park Service.

Annual budget: III

Time frame: Long-term

Contact: Gary Roemer, groemer@nmsu.edu, or Cheri Asa, ASA@slu.edu

8.2 [Project] Enhancing reproduction in captive island foxes on San Miguel Island*

Objectives: To enhance reproduction in paired island foxes in the San Miguel Island captive breeding facility.

Implementation details: Since its initiation in 1999, the captive population on San Miguel Island has doubled, from 14 to 28, but few pairs have contributed to this growth. This past breeding season only 3 of 10 pairs produced litters. Island fox reproduction in the San Miguel captive breeding facility has been less than optimal and there is a need to improve reproductive output for eventual release back into the wild. Methods may include but are not limited to: hormonal assays to evaluate female oestrous cycle; behavioural studies of mate choice (See Project 20.11.1 above) and artificial insemination (See Action 20.11.8. below). In addition, there is a reproductive skew within two of the captive facilities, Santa Rosa and San Miguel that may prove useful for breeding purposes. On Santa Rosa there is an excess of females and on San Miguel there is an excess of males. An inter-island transfer of females from Santa Rosa to San Miguel would provide additional pairings that could bolster reproduction in the San Miguel facility. However, this suggested hybridisation between two distinct subspecies has both genetic and disease related concerns.

Annual budget: III
Time frame: Long-term
Contact: Tim Coonan, Tim_Coonan@nps.gov

8.3 [Project] An assessment of non-invasive techniques for monitoring wild island foxes*

Objectives: To develop microsatellite markers and DNA extraction methods from non-invasively collected samples (faeces or hair) to monitor released foxes during the breeding season.

Implementation details: Trapping of foxes during the breeding season can influence reproduction. Non-invasive methods offer the potential to monitor populations during this critical period without disturbance. DNA will have to be extracted from faeces or hair collected in a systematic manner. Microsatellite profiles generated from non-invasive samples will be compared to DNA extracted from white blood cells. Captive populations offer a convenient avenue for such exploration. This work would be a collaborative effort between the National Park Service and UCLA's Conservation Genetics Lab.

Annual budget: III
Time frame: Long-term
Contact: Robert Wayne, rwayne@ucla.edu,
or Tim Coonan, Tim_Coonan@nps.gov

8.4 [Project] An assessment of variation at the major histocompatibility complex in the island fox*

Objectives: To assay for variation at the major histocompatibility complex (MHC) in the island fox to locate alleles that may confer resistance to disease and to use this information in the development of a captive breeding strategy.

Implementation details: Documenting variation at fitness related genes in the Island fox is useful in identifying functionally relevant genetic loci for the current captive breeding programmes. These data will be incorporated into developing breeding strategies for the maintenance of genetic diversity within the captive populations on San Miguel, Santa Rosa, Santa Cruz and Santa Catalina Islands. Variation has already been assessed at three MHC loci across all island fox populations.

Annual budget: I
Time frame: 2 years
Contact: Robert Wayne, rwayne@ucla.edu

8.5 [Project] An exploration into the factors causing the population decline in the San Clemente Island fox*

Objectives: To determine the factors contributing to the population decline of the San Clemente Island fox and to implement management actions to reverse the decline.

Implementation details: Over the past decade, the population size of the San Clemente Island fox has declined by 40–60% owing, in part, to a predator control programme aimed at protecting the San Clemente loggerhead shrike (see Action 20.11.9 below). Other factors, including habitat conversion, vehicular collision and disease may be playing a role in this decline.

Annual budget: III
Time frame: Long-term
Contact: Jan Larson, Larson.Jan.K@ni.cnrsw.navy.mil

8.6 [Action] Complete removal of golden eagles from the Northern Channel Islands

Objectives: To completely remove the threat posed by golden eagles to wild island foxes remaining on Santa Cruz Island and to captive-reared foxes that are to be released on San Miguel, Santa Rosa and Santa Cruz Islands.

Implementation details: Predation by golden eagles has been the principal factor in the decline of island foxes on the Northern Channel Islands. An eagle live-capture and translocation programme implemented since 1999 has been very successful: 31 golden eagles have been removed from the islands. This programme has been unable to remove all of the golden eagles, however, because some are wary of being trapped. The remaining eagles, estimated to be between 6 and 10 birds, are continuing to prey on foxes preventing their recovery. Other means, including lethal control of the eagles that cannot be trapped need to be explored to remove this mortality factor. This is an urgent action that needs immediate attention.

Annual budget: III
Time frame: Long-term
Contact: Gary Roemer, groemer@nmsu.edu,
Rosie Woodroofe, rwoodroffe@ucdavis.edu,
Brian Latta, blatta@cats.ucsc.edu,
Devra Kleiman, dgkleiman @aol.com,
or Katherine Ralls, rallsk@thegrid.net

8.7 [Action] Captive island foxes to remain in captivity until the threat of golden eagle predation is completely mitigated

Objectives: To minimise the threat posed by golden eagles to captive-reared foxes by maintaining the foxes in captivity until golden eagles are removed.

Implementation details: Two of three captive-reared foxes released on Santa Cruz Island in 2002 were killed by golden eagles with 16 of 19 fox mortalities attributed to predation by golden eagles between 2000 and 2003. Because of their naïve nature, it is likely that captive-reared foxes released back into the wild would suffer high mortality owing to predation by golden eagles. Releases conducted while golden eagles are present would potentially waste valuable reintroduction stock and the funds that supported the rearing of those released animals. A release conducted in the presence of golden eagles may hamper the recovery effort and should be avoided.

Annual budget: III
Time frame: Short-term
Contact: Tim Coonan, Tim_Coonan@nps.gov,
Rosie Woodroofe, rwoodroffe@ucdavis.edu,
Gary Roemer, groemer@nmsu.edu,
Devra Kleiman, dgkleima n@aol.com,
or Katherine Ralls, rallsk@thegrid.net

8.8 [Action] An evaluation of cryogenic storage of sperm and artificial insemination as a means to increase reproduction in captive island foxes

Objectives: To develop techniques to obtain and store sperm and inseminate receptive female island foxes to improve captive propagation.

Implementation details: There is a need to improve reproductive output of island foxes in captive facilities for eventual release back into the wild and the need to store gametes for protection of genetic stock. Cryogenic methods of sperm storage should be implemented and a semen bank created at the Saint Louis Zoo. Methods of artificial insemination need to be developed as a safeguard to bolster poor reproduction within captive facilities.

Annual budget: IV
Time frame: Long-term
Contact: Cheri Asa, ASA@slu.edu

8.9 [Action] Cessation of trapping of island foxes on San Clemente Island as part of the San Clemente Loggerhead Shrike Recovery Program

Objectives: To formalise discussions with the U.S. Navy and U.S. Fish and Wildlife Service for the express purpose of evaluating the impact on foxes of current management actions aimed at protecting the San Clemente loggerhead shrike. If necessary, stop management actions that are adversely affecting the San Clemente Island fox.

Implementation details: Management actions directed at predators of the San Clemente loggerhead shrike appear to be adversely impacting the San Clemente Island fox. Actions aimed at capturing and confining island foxes during the fox breeding season need to be re-evaluated. Discussions and meetings between recovery teams for both species should be held and alternative methods for protecting the shrike that do not impact the fox developed.

Annual budget: I
Time frame: 5 years
Contact: Gary Roemer, groemer@nmsu.edu, or Robert Wayne, rwayne@ucla.edu

8.10 [Action] Development of educational outreach to inform public of the decline of the island fox

Objectives: To develop informational brochures that can be mailed to the general public and especially boat owners that frequent the Channel Islands, to inform them of the dangers of introducing diseases via domestic dogs to the island fox.

Implementation details: Hire a person whose specific task will be the development of the information brochure and its subsequent dissemination. Part-time assistance would be needed with funds funnelled to Channel Islands National Park and/or the Santa Catalina Island Conservancy.

Annual budget: II
Time frame: 2 years
Contact: Tim Coonan, Tim_Coonan@hps.gov

9. Arctic fox [LC]

9.1 [Action]. Establish and promote legal protection for the endemic subspecies of Arctic fox (*Alopex lagopus pribilofensis*) on Pribilof Islands, Bering Sea, Alaska*

Objectives: To establish legal protection for the endemic Pribilof fox. Designate the Pribilof Islands, Alaska, as a distinct game management unit (GMU), to allow for implementation and enforcement of state game management regulations that more accurately reflect the origin and taxonomic status of the islands' Arctic fox populations (at present, the Pribilof Islands fall within a GMU in which there is no closed season and no limit on the number of arctic foxes that may legally be killed).

Implementation details: Provide recommendations to the Alaska Department of Fish and Game (ADFG) that the Pribilof Islands be designated as a distinct GMU. Within that GMU, provide legal protection for the endemic Pribilof fox. Utilise recent data (1990–2002) on population estimates and trends to set a sustainable limit on annual fox harvesting on the Pribilof Islands. Broaden public education programmes that provide factual information regarding the origin and status of the Pribilof Islands fox populations. Both locally and globally, promote conservation of these unique insular canids.

Annual budget: I
Time frame: ongoing, 1–2 years
Contact: Paula A. White, PAW@carnivoreconservation.com

10. Kit fox [LC]

10.1 [Action] Monitor kit fox populations throughout their range

Objectives: Monitor the presence and abundance of kit foxes throughout their range, particularly in marginal regions such as the northern and southern parts of the range.

Implementation details: Kit fox populations should be monitored so that profound population declines in any region can be identified and addressed in a timely manner. Such monitoring may be particularly important in marginal areas in the northern and southern portions of the range where kit fox abundance may be naturally low.
Annual budget: V
Time frame: Long-term, continuous
Contact: Canid Specialist Group (Central and North America Regional Section)
Mexico: Rurik List, rlist@prodigy.net.mx,
USA: Brian Cypher, bcypher@esrp.org

10.2 [Project] Distribution and strongholds of the kit fox in the southern portion of its range*

Objectives: Determine the current distribution of the kit fox in Mexico. Identify areas important for kit fox conservation.
Implementation details: The precise distribution of the kit fox in the southern portion of its range is not well defined, but is necessary for effective conservation. The project intends to use probability distribution models and ground-truthing to define the distribution. Land conversion, urban development and overgrazing within the Chihuahuan desert are affecting native vegetation throughout, thus the identification and protection of areas important for the conservation of the species are of prime concern. To achieve this, interviews with biologists within the southern range of the kit fox and field surveys will be used to obtain this information.
Annual budget: I
Time frame: 1 year
Contact: Rurik List, rlist@prodigy.net.mx

10.3 [Action] Monitor populations of San Joaquin kit foxes in central California, USA*

Objectives: Monitor presence and abundance of the subspecies *Vulpes macrotis mutica* throughout its range.
Implementation details: San Joaquin kit foxes continue to be subject to a variety of threats including continuing habitat loss and degradation, rodenticides, and larger competitors such as expanding populations of non-native red foxes. Population monitoring has been either local or inconsistent, and a more systematic annual monitoring programme should be implemented through out the range of this subspecies.
Annual budget: IV
Time frame: Long-term, continuous
Contact: Brian Cypher, bcypher@esrp.org

10.4 [Project] Investigate mitigation strategies for San Joaquin kit foxes

Objectives: Identify strategies to mitigate adverse impacts to San Joaquin kit foxes from urban, agricultural, and industrial development.
Implementation details: San Joaquin kit foxes are threatened by continuing urban, agricultural, and industrial development. Strategies to mitigate such impacts warrant further investigation, especially impacts associated with urban development and highway construction.
Annual budget: V
Time frame: 3–6 years
Contact: Brian Cypher, bcypher@esrp.org

10.5 [Project] Investigate interactions between San Joaquin kit foxes and non-native red foxes

Objectives: Investigate interspecific interactions between San Joaquin kit foxes and non-native red foxes.
Implementation details: Non-native red foxes are expanding in distribution and abundance within the range of the San Joaquin kit fox. Observed impacts by red foxes on kit foxes include predation, competition for den sites, and competition for food resources. The severity and implications of these impacts are not well understood, and additional impacts such as disease transmission have not been investigated. A rigorous investigation of this potentially significant threat to kit foxes is warranted.
Annual budget: IV
Time frame: 5–10 years
Contact: Brian Cypher, bcypher@esrp.org

11. Swift fox [LC]

11.1 [Project] Determine habitat selection of reintroduced swift foxes in Canada and Montana

Objectives: Determine GIS habitat suitability model, based upon habitat-specific trapping rates; predict ideal sites for future swift fox reintroductions.
Implementation details: The reintroduced swift fox population in Canada and Montana is isolated from swift foxes elsewhere. The habitat model, which is based on systematic trapping censuses, will be updated every 5 years as additional data are obtained through replicated surveys. The initial model will be available in 2004/2005. Model results will be integrated into population viability analyses, for demographic projections.
Annual budget: II
Time frame: Model development:1–2 years, Model refinement continuous
Contact: Axel Moehrenschlager, axelm@calgaryzoo.ab.ca

11.2 [Project] Determine serology and health of swift foxes and sympatric canids in Canada and Montana

Objectives: Determine the prevalence and likelihood of disease transmission between swift foxes, red foxes, coyotes, and domestic dogs; determine the haematology and parasite load of swift foxes and sympatric canids.

Implementation details: The reintroduced swift fox population in Canada and Montana is isolated from swift foxes elsewhere. Initial surveys revealed a high prevalence of canine parvovirus and canine distemper in the swift fox population. Swift foxes are in frequent contact with potential disease reservoirs, such as domestic dogs that have not been vaccinated. Blood analyses will be conducted on swift foxes in different age classes as well as on the sympatric canids.

Annual budget: III

Time frame: 2004–2006

Contact: Axel Moehrenschlager, axelm@calgaryzoo.ab.ca

11.3 [Project] Determine gene flow and connectivity within the reintroduced Canadian/ Montana swift fox population

Objectives: Determine whether the population, which was primarily created through the establishment of two isolated subpopulations, is now connected; determine the potential spread of disease outbreaks in the population.

Implementation details: The reintroduced swift fox population in Canada and Montana is isolated from swift foxes elsewhere. Hair samples have been collected from over 20,000km^2 over a five-year period, and 88 have been analysed with 12 polymorphic loci. Additional samples will be analysed, and interpreted using appropriate software to identify kin, dispersal, and gene flow questions.

Annual budget: IV

Time frame: 2004–2007

Contact: Axel Moehrenschlager, axelm@calgaryzoo.ab.ca

11.4 [Action] Develop a swift fox recovery strategy that is compatible with Canada's Species at Risk Act

Objectives: Compile the current scientific and jurisdictional knowledge regarding swift foxes in Canada; identify and prioritise strategies that will lead to the downlisting of swift foxes from 'endangered' status (on the U.S. Endangered Species Act) to a 'least concern' status in the next 15 years; set specific targets within defined time frames that can be achieved through the collaboration of provincial agencies.

Implementation details: The reintroduced swift fox population in Canada and Montana is isolated from swift foxes elsewhere. This recovery strategy is spearheaded by the Calgary Zoo staff in conjunction with the Canadian swift fox recovery team. The final strategy will be approved by Canada's Environment Minister, and actions will largely be implemented by responsible agencies in Alberta and Saskatchewan.

Annual budget: I

Time frame: 2004–2005

Contact: Shelley Pruss, spruss@calgaryzoo.ab.ca, or Axel Moehrenschlager, axelm@calgaryzoo.ab.ca

11.5 [Action] Monitor the reintroduced swift fox population in Canada and Montana

Objectives: Sample a portion of the swift fox population annually to obtain trend information; conduct a comprehensive census across the population every five years to assess trend, abundance, and habitat selection changes.

Implementation details: The Canadian population was comprehensively surveyed in 1996/1997 and Montana was included in a similar survey in 2000/2001. The primary survey tool has been live-trapping, supplemented with snow-tracking surveys. These will continue, but genetic censusing techniques are also being refined.

Annual budget: 2004, 2007–2009, 2012–2014: II; 2005/2006 and 2010/2011: V

Time frame: 2004 onwards, long-term

Contact: Axel Moehrenschlager, axelm@calgaryzoo.ab.ca

11.6 [Project] Role of parental attendance and habitat heterogeneity in the reproductive success of swift fox under different disturbance regimes*

Objectives: Monitor swift fox populations under different disturbance regimes in Colorado; determine the impacts of grazing, military training, and no grazing on community structure (vegetation, prey base, predator guild, swift fox demographics); examine parental care of pups at the den.

Implementation details: Swift foxes are being monitored across six study areas (2 replicates of grazing/no military training; 2 replicates of military/no grazing; 2 replicates with no grazing/no military). At each site, vegetation, small mammals, and fox demographics (density, survival, reproduction, movements, dispersal, space use) are being documented. Parental care, den attendance, and behaviours are being recorded at several swift fox dens to examine behavioural budgets of adults attending pups.

Annual budget: V

Time frame: 3–5 years

Contact: Eric Gese, egese@cc.usu.edu

12. Grey wolf [LC]

Compiled by the Wolf Specialist Group

12.1 [Action] Revise the U.S. Fish and Wildlife Service's Mexican Wolf Recovery Plan*

Objectives: Ensure long-term survival of wild Mexican wolves (*Canis lupus bailey*) through restoration and conservation measures outlined in a federally approved Recovery Plan

Implementation details: Promote recovery of the Mexican wolf by revising the federal Recovery Plan for the species. The existing plan was authorised in 1982 and is now obsolete. Effort needs to be expended to assemble the logistical, fiscal, and intellectual resources to develop a new Recovery Plan that will guide future activities to recover the Mexican wolf.

Annual budget: II

Time frame: 2–4 years

Contact: Brian Kelly, brian_t_Kelly@fws.gov, http://mexicanwolf.fws.gov

12.2 [Action] Revise the federal rules governing management of wolves that travel outside the Blue Range Wolf Recovery Area in south-eastern Arizona and south-western New Mexico*

Objectives: Ensure the success of the Mexican wolf restoration project being implemented in the south-western USA.

Implementation details: Promote survival of Mexican wolves in the south-western USA by eliminating the need for management actions catalysed by the wolf crossing an imaginary/arbitrary boundary. Currently federal rules governing the restoration project require wolves that wander outside the restoration area to be captured and returned or placed in captivity. This provision runs counter to the dispersal abilities of the species and management of grey wolves elsewhere. The provision ignores the presence of suitable habitat outside the restoration area and the importance of genetic exchange between subpopulations of Mexican wolves that must eventually be restored to recover the species. Consequently, the rules need to be modified to allow wolves to inhabit areas outside the restoration area in the absence of a valid management concern. Local, state, and federal officials need to be lobbied so they endorse the changes. Conservation organisations need to be supported so they can catalyse the necessary changes.

Annual budget: II

Time frame: 1–2 years

Contact: Brian Kelly, brian_t_kelly@fws.gov, http://mexicanwolf.fws.gov

12.3 [Project] Spatial analysis of restoration potential and population viability of the Mexican wolf in the south-western United States and northern Mexico*

Objectives: Assess potential habitat, landscape-level threats, and population viability for Mexican wolves across the south-western U.S. and northern Mexico.

Implementation details: The potential for recovering the Mexican wolf throughout a significant portion of the species historic range needs to be assessed before future restoration activities can be initiated.

Methods useful for the assessment include:

1. Combining habitat suitability modelling with population viability analyses to allow mapping of restoration priority areas;
2. Determination of subpopulation persistence within a larger metapopulation (e.g., through dispersal and consequent demographic rescue effect); and
3. Consequent insight into "how much is enough?" habitat to ensure population viability and eventual species recovery.

This assessment is critical to future recovery planning for the Mexican wolf.

Annual budget: III

Time frame: 2 years

Contact: Carlos Carroll, carlos@sisqtel.net, http://www.conservationresearch.org

12.4 [Project] Utility of an experience centre for improving the survival of captive-born Mexican wolves released to the wild

Objectives: Investigate the feasibility and effectiveness of improving the survival of captive-born Mexican wolves released in a restoration area by first subjecting them to life in the wild at an experience centre.

Implementation details: Management approaches need to be developed that maximise the survival of captive-born animals released to the wild. One approach calls for captive-born animals to first be subjected to the rigors of life in the wild at an experience centre (encompassing about 1,500km² of wildlands) before being released in a restoration area. Such an approach could advance recovery of Mexican wolves by providing naïve, captive-born animals with opportunities to enhance behaviours critical to survival, allowing some to produce wild-born pups for reintroduction, and by providing the U.S. Fish and Wildlife Service an opportunity to 'preview' the survival abilities of wolves that are being considered for release in a restoration area.

Annual budget: IV

Time frame: 5–10 years

Contact: Mike Phillips (Turner Endangered Species Fund), tesf@montana.net, http://www.tesf.org

12.5 [Action] Promote support and funding for the Wolf Forum for the Southern Rockies*

Objectives: Promote educational initiatives designed to ensure that a proper decision is made about restoring grey wolves to the Southern Rockies Ecoregion in the U.S. (mostly western Colorado and northern New Mexico).

Implementation details: Supporting the Wolf Forum for the Southern Rockies will help promote proper

decision-making about wolf recovery in the Southern Rockies Ecoregion. The Forum is dedicated to providing scientific information and diverse viewpoints on wolf restoration to the Southern Rockies. It encourages input from diverse organisations both opposing and favouring wolf restoration efforts. The Forum does not advocate any position relating to wolf recovery, but rather serves as a balanced resource for accurate information, and a forum for all perspectives relative to wolf restoration to the Southern Rockies. Seek additional funding to support Forum activities. Liaise with other conservation and community projects to maximise the effectiveness of the Forum's efforts.
Annual budget: IV
Time frame: Ongoing, long-term
Contact: Walter Medwid (International Wolf Center), wmedwid@wolf.org, http://www.wolf.org

12.6 [Action] Promote support and funding for the Southern Rockies Wolf Restoration Project*

Objectives: Promote science-informed advocacy concerning wolf restoration to the Southern Rockies Ecoregion in the United States (mostly western Colorado and northern New Mexico).
Implementation details: Promote the restoration of the grey wolf to the Southern Rockies Ecoregion by supporting the efforts of the Southern Rockies Wolf Restoration Project. The Project is dedicated to restoring wolves to the Southern Rockies. The Project will use science-informed advocacy to advance its mission. Seek additional funding to support Project activities. Liaise with other conservation and community projects to maximise the effectiveness of the Project's efforts.
Annual budget: V
Time frame: Ongoing, long-term
Contact: Mike Phillips (Turner Endangered Species Fund), tesf@montana.net, http://www.rockywolf.org

13. Gray fox [LC]

13.1 [Project] Evolution and conservation of the Cozumel Island gray fox*

Objectives: Gain insights on the taxonomy and phylogenetics of the dwarf gray fox population in Cozumel Island, Mexico; evaluate current population status and assess conservation priorities.
Implementation details: Every aspect of the biology of the population of gray foxes on Cozumel Island Mexico is poorly known. We know gray foxes still exist on the island, but no living specimens have ever been closely examined in a research context, and the taxonomic status of the population has never been assessed. Subfossil specimens currently being analysed suggest the population is of reduced stature (dwarfed) and has inhabited the island for at least several thousand years. Field reports suggest a very small (probably far less than 50 individuals) population persists, although exact numbers are unknown. We are currently assessing the taxonomic status based on the subfossil specimens. Field-work is carried out when possible in tangent to other studies of the dwarf carnivore fauna on Cozumel.
Annual budget: I–II
Time frame: Ongoing; 2–3 yrs
Contact: Matthew Gompper, gompperm@missouri.edu

Europe and North and Central Asia [Chapter 5]

14. Arctic fox [LC]

14.1 [Project] Conservation of insular Arctic fox populations endemic to Bering Sea Islands in Alaskan and Russian waters

Objectives: To compare current conservation status and threats facing the three subspecies of Arctic foxes endemic to the Bering Sea Islands (*Alopex lagopus semenovi*, Mednyi Island, Commander Islands, Russia; *A. l. beringensis*, Bering Island, Commander Islands, Russia; *A. l. pribilofensis*, Pribilof Islands, Alaska).
Implementation details: Collaboration study comparing existing data on Bering Sea Island fox populations. A comparison of the natural history and ecology of Arctic foxes living on the Pribilof Island and Commander Island groups. Identification of threats to specific populations, including an assessment of disease transfer from domestic pets to insular arctic foxes. Investigation of an existing disease currently afflicting foxes on the Pribilof Islands, which may be contributing to the Pribilof fox population decline. Promotion of public awareness as to the conservation issues facing these insular fox populations.
Annual budget: III
Time frame: 2 years
Contact: Paula A. White, PAW@carnivoreconservation.com, in collaboration with Mikhail Goltsman (Commander Islands)

14.2 [Action] Saving the Endangered Fennoscandian *Alopex lagopus* [SEFALO+]*

Objectives: To protect the Arctic fox in Sweden, Finland and Norway, where it is threatened with extinction, using a dynamic management approach to monitor and allocate conservation actions efficiently.
Implementation details: The Arctic fox in Sweden, Finland and Norway is considered a priority species by the EU Habitat directive. There are less than 150 individuals in mainland Europe, even a small demographic change may dramatically affect the risk

of extinction. Large areas within the previous range of the Arctic fox are empty today and many young foxes have difficulties finding a non-related partner. The main threat is small population size, constrained by low food availability, and the foxes are highly dependent on a regular pattern of population cycles of small rodents (*Clethrionomys* sp., *Microtus* sp., *Lemmus* sp.). The red fox is a dominant competitor and a predator on juveniles and is currently increasing its range, taking over dens and excluding arctic foxes from parts of their breeding range.

The project will use a supplementary feeding programme to increase reproductive output and juvenile survival, and a red fox control programme to safeguard the best Arctic fox territories. In Sweden, areas around dens with Arctic fox cubs will be excluded from ptarmigan hunting, to decrease disturbance from hunting dogs. An information plan at local, regional and European level will promote public cooperation and understanding for the actions needed to support the Fennoscandian Arctic fox population.

Annual budget: V (EU LIFE-Nature 2003)
Time frame: 2003–2008
Contact: Anders Angerbjörn,
Anders.angerbjorn@zoologi.su.se,
http://www.zoologi.su.se/research/alopex/

15. Grey wolf [LC]

Compiled by the Wolf Specialist Group

15.1 [Project] Conservation and management of grey wolves in Finland*

Objectives: To promote expansion of the wolf population from its limited eastern range so that wolves may establish themselves in parts of in central and western Finland.

Implementation details: Wolf attacks on dogs and livestock that are likely to impair public acceptance of wolf recolonisation to central Finland. The impact of wolves on livestock is mitigated by gathering information on the movements of wolves using radio-tracking and consequently informing hunters and farmers of the likely presence in their area. The main study area (*c*. 10,000km²) is located in eastern Finland, adjacent to Russian core regions. Dispersal patterns, space use and wolf-human conflicts are examined by means of radio- and satellite-tracking. Since 1998, 36 wolves from six territories located in east-central Finland have been equipped with transmitters and monitored.

Annual budget: V
Time frame: 10 years (1998–2007)
Contact: Ilpo Kojola, ilpo.kojola@rktl.fi

16. Raccoon dog [LC]

16.1 [Project] The spatial ecology of small carnivores in south-east Finland and the control of rabies*

Objectives: To build models for rabies spread in south-east Finland and to prevent the disease from spreading from Russia to Finland. To demonstrate to hunters the effectiveness of oral vaccination for rabies control, rather than culling foxes and raccoon dogs.

Implementation details: Data on home ranges, movements and habitat use will be collected on the small carnivore community (chiefly red fox and raccoon dog) in south-east Finland by radio tracking, and contact rates between individuals, both within and between species, will be determined. Population densities are monitored. The study will be expanded to the Russian part of the border in cooperation with Russian researchers. The resulting model will assist planning of oral vaccination campaigns (i.e., where/when/how to vaccinate raccoon dogs and foxes to minimise the risk of rabies transmission and to minimise the costs of vaccinations).

Annual budget: IV
Time frame: 3–4 years
Contact: Kaarina Kauhala, kaarina.kauhala@rktl.fi

Sub-Saharan Africa [Chapter 6]

17. Ethiopian wolf [EN]

Compiled by the CSG Ethiopian Wolf Working Group (Stuart Williams, Karen Laurenson, Jorgelina Marino, Dada Gottelli, James Malcolm, Lucy Tallents, Zelealem Tefera Ashenafi and Claudio Sillero-Zubiri)

The following projects and actions are necessary for the conservation of Ethiopian wolves and their Afroalpine habitat to achieve the minimum population level to ensure their long-term survival. Overall, the actions and projects as described in the Ethiopian Wolf Action Plan (Sillero-Zubiri and Macdonald 1997) are further supported here. There are a number of projects and actions recommended in Sillero-Zubiri and Macdonald (1997) that have already been carried out and are, therefore, obsolete. To prevent the need to cross-reference that document, the actions that are still relevant are listed here, with the exception of the detailed actions necessary for the establishment of a captive breeding facility.

17.1 [Action] Coordination of Ethiopian wolf conservation*

Objectives: To ensure coordinated efforts for the conservation of the Ethiopian wolf and its Afroalpine ecosystem.

Implementation details: Efforts to conserve the Ethiopian wolf and its Afroalpine ecosystem need to be prioritised, agreed and coordinated. This includes not only the members of the CSG Ethiopian Wolf Working Group, but also, pertinently, the efforts within Ethiopia. This is done through the Ethiopian Wolf Conservation Committee, which is comprised of key stakeholders and decision-makers within Ethiopia.

Annual budget: I

Time frame: Ongoing, long-term

Contact: Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org

17.2 [Project] Ethiopian wolf population surveys*

Objectives: To improve the information about the size and structure of wolf populations.

Implementation details: Examine the possibility of using genetic identification of individual animals from faecal matter as a means for carrying out capture-mark-recapture techniques for estimating the size and structure of wolf populations. If the technique is successful and once baseline information has been collected, populations could then be monitored using genetic techniques.

Annual budget: III

Time frame: Initially 3–4 years, thereafter ongoing and long-term

Contact: Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org

17.3 [Project] Monitoring wolf populations, their Afroalpine ecosystem and human activities within the ecosystem*

Objectives: Continual assessment and monitoring of the threats to the Ethiopian wolf and their habitats; monitor the wolf demography, reproductive success, use of space and population trends in known wolf packs in all wolf ranges; monitor human activities in all wolf ranges, including use of habitats by domestic livestock and the areas used for subsistence agriculture; monitor for the presence or emergence of dog-wolf hybrids; monitor the changes in extent and quality of the wolf ranges; and monitor the prevalence of diseases among domestic dog and wolf populations.

Implementation details: These activities are ongoing in most wolf ranges at present including the BMNP, Guassa-Menz, South Wollo, North Wollo and Simien. Annual or bi-annual visits are made to the remaining wolf ranges – Arsi and Mt Guna. The monitoring of human activities should be underpinned by the assessment of changes in the vegetation, particularly degradation. The rate of habitat loss should be quantified from these assessments.

Annual budget: III

Time frame: Long-term. Monitoring should continue *ad infinitum*.

Contact: Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org

17.4 [Project] Prioritisation of areas for conservation*

Objectives: To prioritise the areas for the conservation of the Ethiopian wolf and its Afroalpine ecosystem.

Implementation details: There is a need to prioritise the areas on which to focus efforts for the conservation of the Ethiopian wolf and its Afroalpine ecosystem. The assessment should include consideration of the distribution of the genetic variability among wolf populations to ensure that 90% of the genetic variation of the wolf is conserved for the forthcoming 100 years. In addition, the assessment should consider the ecological importance of each wolf range.

Annual budget: I

Time frame: 2 years

Contact: Stuart Williams (Ethiopian Wolf Conservation Programme), s.williams@telecom.net.et,
http://www.ethiopianwolf.org

17.5 [Project] Social structure and ecology of wolf populations in northern Ethiopia

Objectives: Initiate research to determine the social structure and ecology of the small, isolated wolf populations in northern Ethiopia.

Implementation details: Seek funding for doctoral/post-doctoral research; prioritise areas for research, taking into account logistic constraints.

Annual budget: IV

Time frame: 4–5 years

Contact: Wildlife Conservation Research Unit (Oxford University), wcru@zoo.ox.ac.uk,
http://www.wildcru.org, http://www.ethiopianwolf.org

17.6 [Project] Wolf MHC gene variability

Objectives: Determine the variation of the MHC gene complex within and among wolf populations.

Implementation details: Determination of the variation of the MHC gene complex within and among wolf populations would have two functions:

i) to determine the variability within a part of the genome on which selection takes place; and
ii) to give important information about the ability of wolves to respond to the disease threats.

If detailed information were collected on the Bale population, this would also determine the effects of the bottleneck that resulted from disease episodes during the early 1990s.

The implementation would be dependent on:

i) funding;
ii) sample collection from the field (in collaboration with the EWCP); and

iii) having a genetics laboratory to run the analyses.

Annual budget: IV

Time frame: 3 years

Contact: Wildlife Conservation Research Unit (Oxford University), wcru@zoo.ox.ac.uk, http://www.wildcru.org, http://www.ethiopianwolf.org

17.7 [Project] Screening wolf populations for dog genes

Objectives: Screen all Ethiopian wolf populations for dog genes and, therefore, determine the degree of hybridisation and consequent dilution of the Ethiopian wolf genome.

Implementation details: The implementation would be dependent on:

i) funding;
ii) sample collection from the field (in collaboration with the EWCP); and
iii) having a genetics laboratory to run the analyses.

Annual budget: III

Time frame: 3 years

Contact: Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org

17.8 [Project] Ethiopian wolf phylogeography*

Objectives: To continue to examine wolf phylogeography.

Implementation details: The data would be used for further population viability analyses and to assess whether the data support the development of a metapopulation management plan; these data could be compared with other, closely related, sympatric species such as common jackals and domestic dogs that are distributed (albeit contiguous unlike the wolves) over the same broad area.

Annual budget: III

Time frame: 3–5 years

Contact: Jorgelina Marino, jorgelina.marino@zoo.ox.ac.uk, http://www.ethiopianwolf.org; or Dada Gottelli, dada.gottelli@ioz.ac.uk

17.9 [Action] Disease prevention*

Objectives: To prevent disease transmission from domestic dogs to Ethiopian wolves through parenteral vaccination of dog populations living within and surrounding selected wolf ranges.

Implementation details: In order to prevent the transmission of canine diseases from domestic dogs to Ethiopian wolves, the dogs within wolf ranges where the threat of disease is most acute (i.e., domestic dog densities are high within and surrounding the wolf range) need to be vaccinated against rabies, parvovirus and canine distemper, and those living in the areas surrounding the wolf ranges against rabies alone. Requires training of local veterinarians.

Annual budget: III

Time frame: Long-term, ongoing at present and no exit strategy envisaged

Contact: Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org; or Karen Laurenson, karenlaurenson@fzs.org

17.10 [Project] Test methods to reduce disease transmission and incidence in domestic dogs and Ethiopian wolves*

Objectives: To determine the efficacy of oral vaccination of domestic dogs and Ethiopian wolves as a means of preventing disease outbreaks.

Implementation details: Despite the ongoing success of the EWCP's vaccination campaign, parenteral vaccination of domestic dogs can be challenging and, in areas where domestic dog densities are low, not the most cost-effective means of preventing disease among Ethiopian wolf populations. Research is necessary to determine the efficacy of oral delivery of vaccine among domestic dog and Ethiopian wolf populations, including determination of an effective method or bait for vaccine delivery, the rate of sero-conversion, the rate of non-target species consumption, the effect of multiple vaccination in individuals. Thereafter, test the cost-effectiveness of the different methods of disease prevention.

Annual budget: IV

Time frame: 4–5 years

Contact: Karen Laurenson, karenlaurenson@fzs.org; or Darryn Knobel, d.l.knobel@sms.ed.ac.uk, http://www.epi.vet.ed.ac.uk

17.11 [Project] Control of domestic dog populations within and surrounding Ethiopian wolf ranges

Objectives: To investigate effective methods of reducing domestic dog populations within and surrounding wolf ranges.

Implementation details: Reduced dog populations within and surrounding wolf ranges would lead to reduced risk of disease transmission from dogs to wolves, and reduced risk of hybridisation, and the reduction of interference competition between dogs and wolves.

Methods of dog control need to be considered and tested, including removing the functional need for dogs by:

i) encouraging people to build wildlife-proof enclosures for their livestock;
ii) encouraging people to dig pit latrines; and
iii) encouraging people to use inaccessible refuse pits.

The use of contraceptives and autoimmune techniques also need to be investigated.

Annual budget: IV

Time frame: 5–7 years

Contact: Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org

17.12 [Action] Hybrid management*

Objectives: To manage dog-wolf hybrid animals when they are born.

Implementation details: Dog-wolf hybrids occur when female wolves mate with male dogs. If the fertile hybrid remains within the wolf population, the dog genes may spread to threaten the genetic integrity of the wolf population. When hybrid animals are recorded through the monitoring or surveys carried out by the EWCP, hybrid animals should be humanely killed, or caught and sterilised.

Annual budget: I

Time frame: Ongoing, long-term.

Contact: Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org

17.13 [Action] Inform and educate the people of Ethiopia about the Ethiopian wolf and its Afroalpine ecosystem*

Objectives: To provide factual information on the Ethiopian wolf and its Afroalpine ecosystem, including their importance and conservation requirements.

Implementation details: The people of Ethiopia must embrace the Ethiopian wolf and its Afroalpine ecosystem as a symbol of the wildlife, and as part of the living heritage of the country. In order to do so, they must be informed and educated about the importance of the Ethiopian wolf and the Afroalpine ecosystem, and their conservation requirements. As such, an education campaign targeting Ethiopians at all levels, including local communities (farmers, pastoral people, school children, local authorities and traditional authorities), the general populous, and federal and regional governments. Informing and educating should also use local, national and international scientific and popular media. Where possible, the media should be provided with appropriate film, graphic and written information on the Ethiopian wolf and its Afroalpine ecosystem. The Ethiopian wolf should be promoted as a flagship species (together with the gelada baboon, *Theropithecus gelada* – an endemic primate genus) for Ethiopian fauna and flora, and for the Afroalpine ecosystem of the Ethiopian highlands, in particular. When targeting local communities, negative attitudes to the wolf should be counteracted through education. Where they exist, negative local beliefs about the Ethiopian wolf should be dispelled. This should include the production of road signs that work to dispel the local belief that an Ethiopian wolf crossing one's path is bad luck. The need for sustainable use of natural resources should underpin the education campaign. Local people should be informed about the need to reduce the number of domestic dogs coupled with education about the means that they might do this (see Project 17.11 above).

Annual budget: III

Time frame: Ongoing, long-term

Contact: Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org

17.14 [Action] Inform and lobby organisations in Ethiopia of the importance of the environment as a cross-cutting issue*

Objectives: To promote the paramount importance of the environment as an issue cutting across all sectors and to encourage policy development and implementation in the environmental sector.

Implementation details: Despite the link between the chronic problems faced by Ethiopia and the environment, this sector is being largely marginalised. This undermines the sustainability of solutions being considered by organisations in Ethiopia. There is a need to inform, lobby and advise organisations in Ethiopia, including government, non-government and donors, at both federal and regional levels, on the environment, and to advise and assist with the development and implementation of policy and strategies in this sector. This should also include contributing to the development of school and college curricula within Ethiopia so that they include the environment, and wildlife and ecosystem conservation in particular.

Annual budget: I

Time frame: Ongoing, long-term

Contact: Stuart Williams, s.williams@telecom.net.et, http://www.ethiopianwolf.org

17.15 [Action] Build the capacity of Ethiopia in the fields of ecology, conservation, epidemiology, conservation education and conservation policy*

Objectives: To train Ethiopians in the fields necessary to sustain management solutions, and activities necessary for the conservation of the Ethiopian wolf and its Afroalpine ecosystem.

Implementation details: Training Ethiopians in the fields of ecology, conservation biology, conservation education, conservation policy and epidemiology is necessary for the sustainability of conservation solutions for the Ethiopian wolf and its Afroalpine ecosystem. This includes the development of Ethiopian institutions, both governmental and non-governmental, that are involved in the field of wildlife conservation or environmental development.

Annual budget: III

Time frame: Ongoing, long-term

Contact: Stuart Williams, Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org

17.16 [Project] Attitudes of local people to the Ethiopian wolf and its Afroalpine ecosystem*

Objectives: To determine the attitudes of local people to the Ethiopian wolf and its Afroalpine ecosystem as a means of developing education campaigns, and thereafter to test the efficacy of the education campaigns.

Implementation details: An assessment of the attitudes of local people is necessary for the development and design of an appropriate education campaign with the aim of counteracting negative attitudes to the Ethiopian wolf and its Afroalpine ecosystem. The assessment can thereafter act as a baseline for continual assessments to examine the effectiveness of an education campaign.

Annual budget: II

Time frame: Ongoing, long-term

Contact: Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org

17.17 [Action] Secure the protection of the Bale Mountains National Park*

Objectives: To secure the conservation of the Bale Mountains National Park and its ecological processes as the key area of the conservation of the Ethiopian wolf and its Afroalpine ecosystem.

Implementation details: The Bale Mountains is the stronghold of the Ethiopian wolf and is the largest area of Afroalpine ecosystem on the continent. Securing this area is essential for the conservation of the Ethiopian wolf. This can be best done by:

i) facilitating the processes and projects necessary to strengthen the management and operation of the park;
ii) assisting with the process of gazetting the park by the government of Ethiopia;
iii) seeking international recognition of the area as a UNESCO World Heritage Site;
iv) facilitating the processes and projects that enhance the social and economic well-being of local human communities by ensuring the sustainable use of natural resources.

Annual budget: III

Time frame: Ongoing, long-term.

Contact: Stuart Williams, s.williams@telecom.net.et, http://www.ethiopianwolf.org; or Belgian Technical Cooperation (Ethiopia) btc.eth@telecom.net.et

17.18 [Action] Secure the protection of other areas of Afroalpine ecosystem in Ethiopia*

Objectives: To secure the conservation of other areas of Afroalpine in Ethiopia.

Implementation details: Lack of space is the ultimate limiting factor for Ethiopian wolves and it is essential that what habitat remains at present is protected. Only two areas of Afroalpine ecosystem are protected at present: the Bale Mountains National Park (see above) and the Simien Mountains National Park (SMNP). The boundaries of the SMNP should be expanded to include adjacent and more important Afroalpine habitat, and activities by the national park, NGOs and multilateral organisations working in the area should be assessed to ensure that the conservation of the Ethiopian wolf and its habitat are being adequately addressed in their work. In other areas, there is a need to assess the possibility of assigning an appropriate protected area status, such as that which is being considered for the Guassa-Menz area at present. Legislation would have to be appropriate, allowing access and use of the area by local communities, but preventing the unsustainable exploitation that is the norm at present. The involvement of the local human community is essential to ensure the success of projects to assign protected area status.

Annual budget: IV

Time frame: Ongoing, long-term

Contact: Stuart Williams, s.williams@telecom.net.et, http://www.ethiopianwolf.org

17.19 [Action] Promote tourism and other methods of generating revenue in wolf ranges*

Objectives: To ensure that all means of generating revenue from wolf ranges are realised and that the revenue is shared with local communities.

Implementation details: Reduction of dependency of local human communities on unsustainable exploitation of natural resources of the Afroalpine ecosystem to conserve Ethiopian wolf habitat. This includes development of tourism. The link between the income-generating scheme and the Ethiopian wolf and the Afroalpine ecosystem must be ensured in the understanding of the beneficiaries of the projects. This includes lobbying the federal and regional governments to develop and implement appropriate policy and legislation, to allow local communities to share revenue generated from national parks and other government institutions accrued as a result of the Ethiopian wolf, its Afroalpine ecosystem and/or other wildlife derived economic benefits.

Annual budget: II

Time frame: Ongoing, long-term

Contact: Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org

17.20 [Action] Financial sustainability of the Ethiopian Wolf Conservation Programme*

Objectives: To ensure the financial sustainability of the Ethiopian Wolf Conservation Programme (EWCP) for the forthcoming 15 years.

Implementation details: The Ethiopian Wolf Conservation Programme was established as the primary vehicle for the conservation of the Ethiopian wolf and its Afroalpine ecosystem in 1995 and has the mandate to implement the *in situ* actions described in Sillero-Zubiri and Macdonald (1997) and those herein described. The EWCP is necessarily a long-term programme and, therefore, optimum mechanisms to ensure that funding is not a constraint to the implementation of conservation actions should be sought. The funding should span the forthcoming 15 years with moral engagements for 15 years beyond that. This should be facilitated by the development of a 15-year strategic plan for the EWCP.

Annual budget: I

Time frame: Ongoing, long-term

Contact: Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org

17.21 [Action] Feasibility of establishing a captive breeding population

Objectives: To ensure the survival of the Ethiopian wolf in the event of a catastrophe in Ethiopia.

Implementation details: Consider the best means of achieving the conservation of the Ethiopian wolf to prevent extinction in the event of a catastrophe in Ethiopia, whether political or climatic. Options may include a captive breeding facility, for which details of the necessary actions can be found in Sillero-Zubiri and Macdonald (1997), or intensely managing a selected area of Afroalpine habitat, probably in the Bale Mountains, to favour the persistence of the Ethiopian wolf. A precondition to this is to determine the political and financial ramifications of establishing a captive breeding facility; *in situ* conservation is deemed the priority and any form of captive breeding should not replace, hinder or compromise the goals or funding base of the *in situ* conservation efforts as these are deemed to be the priority.

Annual budget: I

Time frame: Long-term

Contact: Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org

17.22 [Action] Preservation of Ethiopian wolf genetic material

Objectives: To preserve the genetic material of the Ethiopian wolf.

Implementation details: Examine the possibility of preserving the genetic diversity of the Ethiopian wolf using 'cryopreservation' technology within the gene bank facilities being established within Ethiopia but with expertise that is being developed with partners such as Saint Louis Zoo, USA. Implementation of the actions is dependent on the technology being perfected. The capture of wolves for the collection of gametes should be done opportunistically and not as an end in and of itself. As with captive breeding, funding should not be diverted from the *in situ* work. A precondition would be to determine the political and financial ramifications of establishing an Ethiopian wolf 'gene bank' for similar reasons to those discussed above. If all the above conditions are acceptably met, carry out a pilot study and tests of the efficacy of the methods in this species.

Annual budget: IV

Time frame: 4–5 years and then in perpetuity

Contact: Ethiopian Wolf Conservation Programme, ewcp@zoo.ox.ac.uk, http://www.ethiopianwolf.org; or Cheri Asa, ASA@slu.edu

18. African wild dog [EN]

Compiled by the CSG African Wild Dog Working Group (J.W. McNutt, Kim McCreery, Gus Mills, Gregory Rasmussen, Bob Robbins, Claudio Sillero-Zubiri and Rosie Woodroffe)

The actions proposed for conservation of the African wild dog reflect the serious extinction threats that the species faces. Wild dog populations require very large areas to persist. Populations occupying small areas or fragmented habitats are at risk of extinction through conflict with human activities, and infectious diseases shared with domestic dogs. As in Woodroffe *et al*. (1997), our primary recommendation is to seek creative ways to maintain and, where possible, expand large wildlife-friendly areas available to wild dogs. Resolution of conflicts between people and wild dogs requires further investigation, but several studies are planned or in place. Strategies for evaluating and managing disease threats to wild dogs remain severely limited by the available data; this issue requires urgent attention.

18.1 [Action] Maintenance and expansion of very large wildlife areas, including Corridors and Transfrontier Conservation Area Development

Objectives: To identify and establish corridors prioritising transfrontier wildlife protected areas throughout sub-Saharan Africa to promote conservation of wide ranging wildlife populations, international cooperation and a broad wildlife conservation ethic among African nations.

Implementation details: Identify habitats and geographic corridors of importance for *Lycaon* that could link protected areas across southern Africa. Specific corridors include:

i) from the Okavango in northern Botswana north through Namibia and into south-eastern Angola and south-western Zambia;
ii) Kruger National Park, South Africa and south-eastern Zimbabwe;
iii) western Zimbabwe with north-eastern Botswana; and

iv) Selous Game Reserve with Niassa Game Reserve in northern Mozambique.

Corridor linkages necessarily include political and policy development for cooperation among governments, NGO's and local communities. Monitoring, poaching abatement and outreach programmes are required.

Annual budget: IV
Time frame: 4–8 years
Contact: John Hanks, hanksppt@iafrica.com

18.2 [Project] Develop specific, low-cost methods and techniques for reducing human and livestock conflict

Objectives: To develop and implement techniques for limiting ranging in wild dog packs into areas where they are at high risk of mortality, such as livestock areas, roads and villages.

Implementation details: Wild dog numbers can be severely reduced near villages, roads, and livestock areas by poaching, automobiles, and disease transfer from domestic dogs. Wild dog pack ranges, even those associated with protected areas, often border and include at least one type of these high-risk areas within their territories. Protected area populations would benefit by avoiding these particular sites. Wild dogs use chemical communication through scent marking to advertise and delineate territorial boundaries with neighbouring packs. Areas beyond these boundaries tend to be avoided by other wild dogs. It may be possible to construct artificial boundaries, using the species' own chemical and olfactory communication system. Such boundaries could be expected to affect the ranging behaviours of resident packs near identified high-conflict areas. Reducing ranging even temporarily into an area, coupled with outreach programmes and education about improved animal husbandry could affect greater human tolerance for wild dogs ranging occasionally into livestock areas.

Annual budget: III
Time frame: 2–3 years
Contact: Megan Parker or J.W. McNutt (Botswana Predator Conservation Program), lycaon@info.bw

18.3 [Project] Develop tools to foster coexistence of wild dogs with livestock farmers in Kenya*

Objectives: To reduce human impact on wild dogs by understanding the causes of wild dog depredation on livestock, and developing alternatives to lethal control of wild dogs.

Implementation details: Monitoring of five radio-collared packs of wild dogs living outside protected areas in Samburu and Laikipia Districts, northern Kenya. Comparison of stocking density, wildlife abundance and level of wild dog activity in areas with and without a history of depredation on livestock. Case-control study comparing husbandry of herds that are and are not attacked by wild dogs.

Annual budget: IV
Time frame: 3 years
Contact: Rosie Woodroffe, rwoodroffe@ucdavis.edu

18.4 [Project] Develop tools to foster coexistence of wild dogs with livestock farmers in the Kalahari region

Objectives: To understand:

i) the impact of wild dogs on commercial livestock farms in the Kalahari region, and
ii) the impact of farmers on dogs, and to develop approaches to reducing both wild dog predation and the need for lethal control by farmers.

Implementation details: Such a project would involve monitoring of wild dog packs in central Botswana (Ghanzi, Heineveldt, and Makalamabedi are candidate districts) and eastern Namibia (e.g., Herreroland). Natality and mortality of collared packs will provide a measure of farmer impact on wild dog populations, while monitoring losses of mainly free-ranging cattle, as well as smaller stock, will give a measure of wild dog impact. These projects will complement ongoing work in East Africa, which has an entirely different system of livestock husbandry and land use.

Annual budget: III
Time frame: 4 years
Contact: Botswana: Matthew Swarner,
mjswarner@ucdavis.edu;
Namibia: Robin Lines, wilddog@mweb.com.na

18.5 [Project] Develop tools to foster coexistence of wild dogs with people in Zimbabwe*

Objectives: To reduce human impact on wild dogs by:

i) establishing the true impact of wild dogs on livestock and managed game;
ii) ameliorating negative attitudes towards wild dogs by providing reliable information on their true impact; and
iii) developing non-lethal management tools to assist the species to reside in non-protected areas.

Implementation details: Monitoring the survival of packs resident in all areas contiguous with Hwange National Park and interacting with all the stakeholders where *Lycaon* is found to be present. Methods of ameliorating conflict and high mortality factors are researched for their usefulness and adopted. Tools researched include fitting protective collars to dogs in areas of high snare risk, evaluating methods of capture from a welfare angle, and developing efficient methods to translocate family units where necessary. Capture methodology is in its last phase with the use of 'fladry' being tested to effect boma capture without the aid of a helicopter which research showed to be stressful.

Annual budget: IV
Time frame: Ongoing
Contact: Gregory Rasmussen (Painted Dog Conservation Trust), phdr@mweb.co.zw

18.6 [Project] Coexistence between game farmers and wild dogs in South Africa

Objectives: With the proliferation of game farms in the northern regions of South Africa, wild dogs are reappearing, yet they are not welcome by the game farmers. Ways need to be established whereby coexistence between game farmers and wild dogs can be achieved.

Implementation details: Surveys of the most important wild dog areas are needed. The ecological role of the wild dog in these areas and their movement patterns should then be established, as well as the development of wild dog ecotourism. Communication with and education of game farmers is needed.

Annual budget: II
Time frame: 3 years
Contact: Gus Mills, gusm@sanparks.org

18.7 [Project] Develop tools to evaluate disease threats to wild dogs and determine whether intervention is necessary

Objectives: To develop tools to evaluate disease threats to wild dogs and determine whether intervention is necessary.

Implementation details: Infectious disease has contributed to the extinction of at least one well-studied population and thwarted two reintroduction attempts. While it appears that small populations, and those in close contact with domestic dogs, are most at risk, there are insufficient data available to determine the circumstances under which extinction risks are so high that intervention might be warranted.

This study will combine:

i) screening of wild dogs and other disease hosts at a number of sites;
ii) studies of wild dog movements relative to domestic dogs; and
iii) spatial epidemiological modelling to evaluate disease risks to wild dog populations both inside and outside protected areas.

Annual budget: V
Time frame: 3–5 years
Contact: Rosie Woodroffe, rwoodroffe@ucdavis.edu

18.8 [Project] Vaccine trials on wild dogs held in captivity*

Objectives: To develop safe, effective protocols for vaccination of African wild dogs that would be suitable for use in the field if and when necessary.

Implementation details: Both rabies and distemper have caused whole-pack deaths of wild dogs and may threaten certain populations. At present there is no protocol known to be both safe and effective to protect free-ranging wild dogs from either disease. Wild dogs given a single dose of inactivated rabies vaccine are known to have died from wild strains of rabies in the field. Likewise, captive wild dogs given inactivated distemper vaccines have suffered catastrophic mortality from a wild strain of distemper. Worse, a number of wild dog pups given modified live distemper vaccines have died from vaccine-induced distemper. This study will build on existing work to investigate the role that multiple doses of inactivated rabies vaccine, orally-delivered live rabies vaccine, recombinant *Vaccinia*-vectored rabies vaccines, and subunit canarypox-vectored distemper vaccines, might play in protecting wild dogs from infection.

Annual budget: III
Time frame: 3 years
Contact: Rosie Woodroffe, rwoodroffe@ucdavis.edu

18.9 [Project] Monitoring population and pack dynamics of wild dogs in Kruger National Park, South Africa*

Objectives: To monitor population trends and to understand the factors responsible for the large population and pack fluctuations in wild dogs in Kruger.

Implementation details: Monthly monitoring of a sample of five radio-collared packs and photographic surveys every four year of the entire park.

Annual budget: I (monthly monitoring), II (photographic surveys)
Time frame: Ongoing
Contact: Gus Mills, gusm@sanparks.org

18.10 [Project] Monitoring population and pack dynamics of wild dogs in the Okavango region, Botswana*

Objectives: Continuous monitoring of one of the last remaining large populations of wild dogs.

Implementation details: The Botswana Wild Dog Project, begun in 1989, continues to monitor the wild dog population in the Northern Conservation Zone and represents the longest continuous life-history dataset for the species in the wild. The population is largely dependent on the Moremi Game Reserve and Chobe National Park, and the numerous wildlife management areas associated with the Okavango Delta, a World Heritage Site. An average of 10 wild dog packs each year are monitored using VHF and GPS/satellite radio telemetry. Direct observations include recording of reproductive efforts and success, dispersal and territorial behaviours.

Annual budget: IV
Time frame: Continuous, ongoing
Contact: J.W. McNutt (Botswana Predator Conservation Program), lycaon@info.bw

18.11 [Project] Monitoring of the distribution, density, and mortality of wild dogs in Zimbabwe*

Objectives: To identify population trends as well as hotspots where attention may be required to safeguard the wild dog population.

Implementation details: Sightings and causes of mortality are continually sought by liaison with wildlife societies, farmers' unions and the Department of National Parks and Wildlife Management. Every five years, questionnaires are sent out countrywide. Provide results and recommendations to relevant national authorities to enable the species to be beneficially managed.

Annual budget: I

Time frame: Ongoing

Contact: Gregory Rasmussen, phdr@mweb.co.zw

18.12 [Project] Monitoring and evaluation of management strategies for wild dogs in the Rungwa-Ruaha ecosystem, Tanzania

Objectives: To assess the status and local distribution of the Rungwa-Ruaha wild dog population, and identify management practices affecting their density and distribution in the Rungwa-Ruaha Landscape.

Implementation details: Preliminary implementation would focus on identifying the local area occupied by wild dogs within the landscape. Subsequent activities will focus on population assessment and establishing baselines for monitoring and surveillance. These activities will form the foundation for evaluation of existing and proposed management activities, including hunting of other carnivores and disease management in domestic dogs surrounding the protected area complex.

Annual budget: IV

Time frame: 3–5 years (monitoring to be ongoing)

Contact: Peter Coppolillo, PCoppolillo@WCS.org

18.13 [Project] Ecology of wild dog populations in dryland areas of the Kalahari region

Objectives: To determine the size and distribution of wild dogs in the drier habitats of central and southern Botswana.

Implementation details: Estimates of the wild dog population in the Central Kalahari Game Reserve (CKGR) and associated wildlife management areas in what is called the Southern Conservation Zone (164,000km^2, National Predator Strategy, 2003) indicate a potentially important population for the species. The population estimate of 621 wild dogs in the zone is based on spoor sampling in the CKGR (0.8 dogs/100km^2, DWNP, Botswana) and, therefore, gives a wide confidence range (approximately 100–1,200 wild dogs). The possibility that such a large population, contiguous with the northern population exists in and around wildlife habitats in central and southern Botswana merits more intensive investigation. Study would emphasise detailed observations of a sample of the population (4 to 6 packs) to determine density and ranging behaviours through the use of GPS and satellite radio telemetry. Detailed data on this sample population would provide greater confidence in the population estimates given for the entire region.

Annual budget: III

Time frame: 3 years

Contact: Matthew Swarner or J.W. McNutt (Botswana Predator Conservation Program), lycaon@info.bw

18.14 [Project] Status and ecology of the African wild dog in central and northern Mozambique*

Objectives: To assess current conservation status of African wild dog populations in Mozambique and promote conservation efforts.

Implementation details: Little is known of the distribution and status of the wild dog in Mozambique, with no information published since the account by Smithers and Lobão-Tello (1976). Mozambique's is potentially a key population since it would link Tanzanian wild dogs with those occurring in Zimbabwe and north-eastern South Africa.

Collect and analyse baseline ecological information on distribution and relative abundance of the African wild dogs, habitat availability, prey and competitor species (lion and spotted hyaena) and people's attitudes to dogs. Provide training on complementary skills, research results and recommendations to state authorities and research institutions responsible for the conservation of wild dogs and other large carnivores in Mozambique. This project will seek to clarify, through a series of mail questionnaires and subsequent presence/absence field surveys in selected locations, the current distribution and status of all three species.

Annual budget: III

Time frame: 6–12 months

Contact: Claudio Sillero-Zubiri, claudio.sillero@zoo. ox.ac.uk

18.15 [Project] Status, distribution, and ecology of an unprotected wild dog population in north-eastern Kenya*

Objectives: To provide baseline data on status and distribution, predator-prey relationships with special reference to the Critically Endangered hirola (*Beatragus hunteri*) and domestic livestock, habitat utilisation, disease, and human/wild dog interactions, and promote community-based conservation efforts.

Implementation details: Nothing is known about the conservation status of wild dogs in the Ijara/Garissa Districts of north-eastern Kenya. This population may provide an important link with wild dogs in the Horn of Africa. The project will be conducted in partnership with a locally-based environmental organisation. Baseline information will be collected and analysed from reported sightings, playback surveys, and routine monitoring of radio-collared packs. Community participants will be trained in applied field research including monitoring techniques and data collection. Ongoing assessment of local attitudes and concerns is an integral part of this project.

Annual budget: IV

Time frame: 3–5 years

Contact: Kim McCreery and Bob Robbins, lycaonpictus@earthlink.net

18.16 [Project] Status of African wild dog populations in West Africa

Objectives: To assess current conservation status of African wild dog populations in West Africa and promote conservation efforts.

Implementation details: Collect and analyse baseline ecological information on distribution and relative abundance of the African wild dog, habitat availability, prey and competitor species (lion and spotted hyaena) and people's attitudes to dogs. Particular attention will be paid to monitoring wild dog status in and around Niokola-Koba National Park, Sénégal, which holds the only potentially viable wild dog population known in West Africa.

Provide training on complementary skills, research results and recommendations to state authorities and research institutions responsible for the conservation of wild dogs and other large carnivores.

This project will seek to clarify, through a series of mail questionnaires and subsequent presence/absence field surveys in selected locations, the current distribution and status of African wild dogs.

Annual budget: II

Time frame: 1–2 years

Contact: Canid Specialist Group (Sub-Saharan Africa Regional Section), canids@zoo.ox.ac.uk

18.17 [Project] Establish distribution and status of wild dogs in southern Sudan

Objectives: To determine the status and distribution of wild dogs in southern Sudan, a potentially important area where a significant population may remain

Implementation details: Initial surveys would be carried out by interviewing people in and around Boma, Dinder and Southern National Parks and the Bengagai Game Reserve. Additional interviews would be carried out in other areas, particularly the Nile floodplain. Interviewing could be targeted using remotely sensed data to identify areas where wild dogs might persist.

Annual budget: I

Time frame: 1 year

Contact: Canid Specialist Group (Sub-Saharan Africa Regional Section), canids@zoo.ox.ac.uk

18.18 [Project] Establish distribution and status of wild dogs in central Africa

Objectives: To assess the distribution and status of wild dogs in central Africa, where important populations may remain.

Implementation details: Interviews to:

i) add to Breuer's (2003) survey of wild dog distribution and status in Cameroon;
ii) confirm the status of the populations in and around Manovo-Gounda-St Floris and Bamingui-Bangoran National Parks (Central African Republic); and
iii) confirm the status of the populations in and around Ouadi-Rimé-Ouadi-Achim and Siniaka-Minim Game Reserves (Chad).

Annual budget: II

Time frame: 1 year

Contact: Canid Specialist Group (Sub-Saharan Africa Regional Section), canids@zoo.ox.ac.uk

18.19 [Project] Determine status of wild dogs in Teffedest Mountains, Algeria

Objectives: To determine whether wild dogs are present in the Teffedest Mountains, Algeria.

Implementation details: Wild dogs have been reported as present in the Teffedest Mountains, Algeria, but this has never been confirmed. If wild dogs are present here they are almost certainly both genetically and ecologically highly distinct from all other populations and have a high conservation value. A preliminary survey would require interviewing local people. If wild dogs are still reported, interviews could be followed up with surveys for tracks, scats and other signs of wild dog presence.

Annual budget: II

Time frame: 1 year

Contact: Canid Specialist Group (North Africa and Middle East Regional Section), canids@zoo.ox.ac.uk

18.20 [Project] Develop low-tech methods for surveying and monitoring wild dogs

Objectives: To develop methods for surveying and monitoring wild dogs that can be used extensively and inexpensively.

Implementation details: Because wild dogs never occur at high densities, it is difficult to monitor their numbers. In many areas, wild dog extinctions were unknown for several years after the fact. Techniques are, therefore, needed to monitor wild dogs in 'sentinel' areas. Because these techniques need to be used over large and often remote areas, they need to be inexpensive. Techniques based on track surveys have been developed in the past, which is of value in flat, rather homogeneous environments but may be less applicable areas with a variety of substrates. Tracking might be supplemented by the use of domestic dogs trained to recognise and locate wild dog sign and faeces. Both approaches could be adopted in areas of known wild dog density, used to calibrate density estimates derived from other areas.

Annual budget: II
Time frame: 2 years
Contact: Megan Parker, mnparker@igc.org

18.21 [Action] Establish a second wild dog population in South Africa by setting up a series of smaller populations and managing them as a metapopulation*

Objectives: There is presently no protected area in South Africa large enough to contain a second viable wild dog population. There are several fenced areas in suitable habitat large enough to contain one or two packs, but without corridors between them. A strategy to manage and conserve wild dogs in these reserves is being developed.

Implementation details: Wild dogs are being introduced into these reserves. The various subpopulations in each reserve are being monitored and managed as part of a single metapopulation by simulating the natural processes of immigration and emigration in natural populations.

Annual budget: I
Time frame: 10 years
Contact: Gus Mills, gusm@sanparks.org

18.22 [Action] Development of a viable community conservation programme in Zimbabwe*

Objectives: To demonstrate that wild dogs can have value other than through ecotourism, but that is not appropriate in many areas of the species' range. It is intended this project will enable rural communities to benefit from having an active research and conservation programme in their region, and consequently see the dogs as 'their' flagship species.

Implementation details: Building of a conservation education and environmentally friendly crafts centre where all stakeholders can participate and appreciate conservation as well as gain educational and developmental skills. Building of a children's bush camp with a conservation curriculum that highlights the ecological value and links between all species and in particular top predators that are most often targets of prejudice and misconception. This programme will see a throughput of 80 local children per week.

Annual budget: IV (establishment), II (running)
Time frame: Indefinite
Contact: Gregory Rasmussen phdr@mweb.co.zw

North Africa and the Middle East [Chapter 7]

19. Desert canid community

Since most canid species in North Africa and the Middle East live in the desert, where resources are limited, studying the interaction between species can be valuable for conservation purposes. Disturbance by people (e.g., agriculture, hunting) may easily change the canid community by allowing the larger species to invade and exclude the smaller ones. The initial processes can be local, but will spread out in time and with development.

19.1 [Project] Natural history, distribution and status of the pale fox, Rüppell's fox and fennec fox

Objectives: To study basic biology and ecological requirements of three African desert foxes, the pale, Rüppell's and fennec foxes; to conduct presence/absence surveys in key parts of their range to map their distribution and evaluate species status.

Implementation details: Although widespread, the desert foxes are arguably the least-known canid species in the world. Detailed information on population abundance or status is missing. This project will seek to clarify, through a series of mail questionnaires and subsequent presence/absence field surveys in selected locations, the current distribution and status of all three species. Survey techniques will be carefully designed to avoid confusion between sympatric species. Biological samples for morphological and genetic studies will also be collected where possible.

Annual budget: II
Time frame: 2–3 years
Contact: Canid Specialist Group (North Africa and Middle East Regional Section), canids@zoo.ox.ac.uk

19.2 [Project] Distribution and status of Rüppell's fox and Blanford's fox in south-west Saudi Arabia, Yemen and Oman

Objectives: To undertake surveys of the distribution of two desert foxes in the southern sector of the Arabian Peninsula in order to determine range and conservation status.

Implementation details: Both foxes are widespread in this area, but with a few localised exceptions nothing is known of either population abundance or conservation status. This project will serve to establish the current distribution and status of the two species through field surveys in selected locations. Apart from direct observations methods to be used would include: recording of tracks and other signs, camera traps, box traps, and scent posts.

Annual budget: II
Time frame: 6 months
Contact: Chris and Tilde Stuart, aawrc@yebo.co.za

19.3 [Project] Survey of canid species in the central Sahara Desert

Objectives: To survey areas of the central Sahara Desert (e.g., Haggar Mountains) for canids and other carnivores.

Implementation details: Several reports of unidentified canids have been received from this region, where there has been very little research. Field surveys in suitable locations will use spoor tracking, scent posts, camera and box traps to record presence.

Annual budget: II

Time frame: 2 months

Contact: Canid Specialist Group, (North Africa and Middle East Regional Section), canids@zoo.ox.ac.uk

20. Blanford's fox [VU]

20.1 [Project] Distribution and status of the Blanford's fox in Egypt, Sudan and the Horn of Africa

Objectives: This species was considered one of the rarest mammals in Asia and was discovered in the Middle East only 20 years ago, and more recently in Egypt. The project seeks to map the distribution of this species in Africa.

Implementation details: The proposed survey will provide knowledge on the distribution and status of the species in north-eastern Africa. Potential habitat in eastern Egypt, eastern Sudan, Eritrea and Ethiopia will be scanned for tracks, and automated cameras and box traps will be used to record presence. DNA will be sampled from trapped individuals, skins, and other remains. The data will be later use to assess radiation patterns and population subdivision.

Annual budget: II

Time frame: 2 years

Contact: Canid Specialist Group (North Africa and Middle East Regional Section), canids@zoo.ox.ac.uk

21. Rüppell's fox [DD]

21.1 [Project] Causes for local extinction of Rüppell's fox in Israel

Objectives: To study whether competitive exclusion by red foxes is the main cause for local extinction of the Rüppell's fox in Israel.

Implementation details: The Rüppell's fox was the most abundant fox species in the Negev Desert up until the 1960s. Thereafter an increase in human presence and agriculture has allowed red foxes to follow and settle in those arid regions. A sharp decrease in the population of Rüppell's fox was documented in the following years. The project composes two parts: an extensive survey of red and Rüppell's foxes over the Negev Desert, and a study on the interaction between these two species. The results have conservation implications for other regions where both species coexist.

Annual budget: III

Time frame: 2–3 years (ongoing, but needs more funding)

Contact: Eli Geffen and Reuven Hefner, geffene@ccsg.tau.ac.il

22. Grey wolf [LC]

Compiled by the Wolf Specialist Group

22.1 [Project] Status of little known populations of the grey wolf in Iran, Iraq and Syria

Objectives: To determine the status of the grey wolf in Iran, Iraq and Syria

Implementation details: The grey wolf is under intense hunting pressure in many Middle-Eastern countries, where no legal protection for this vulnerable species is provided. Iran previously had a large wolf population, but there are concerns that numbers have declined. The current status of wolves in Iran, Iraq and Syria is unknown and field surveys in suitable locations where wolves were known to occur are urgently needed.

Annual budget: II

Time frame: 2–3 years

Contact: Wolf Specialist Group, mechx002@tc.umn.edu

22.2 [Project] Status of populations of the grey wolf in the southern Arabian Peninsula

Objectives: To determine the distribution and conservation status of the grey wolf in southern Saudi Arabia, Oman and Yemen

Implementation details: The grey wolf is under serious threat in the southern Arabian Peninsula and virtually no recent information is available on the region's largest canid. Hunting pressure on the wolf and other large carnivores in the area is considerable and no effective conservation measures are in place anywhere in the region. Field surveys to be undertaken in selected locations where wolves most recently reported.

Annual budget: II

Time frame: 6 months

Contact: Wolf Specialist Group, mechx002@tc.umn.edu

22.3 [Project] Status and taxonomic elucidation of *Canis aureus lupaster*

Objectives: To survey the population of *Canis aureus lupaster* in southern Egypt; map its distribution, evaluate status and determine taxonomic affiliations.

Implementation details: It has been argued that *C. a. lupaster* is actually a small wolf, rather than a large jackal, and it might represent a distinct canid form. It has been reported in Egypt and Libya, but its distribution and status is unknown. A field expedition will compile information on population range and abundance. Biological samples will be collected, from the field and museum specimens, for morphological and molecular studies to elucidate taxonomic affiliation.

Annual budget: II

Time frame: 6 months

Contact: Canid Specialist Group (North Africa and Middle East Regional Section), canids@zoo.ox.ac.uk

South Asia, South of the Himalaya [Chapter 8]

23. Dhole [VU]

Compiled by the CSG Dhole Working Group (Simon Hedges, Leon Durbin, Arun Venkataraman, A. J. T. Johnsingh, Will Duckworth, Martin Tyson and Arati Iyengar)

23.1 [Project] Development and evaluation of survey methods

Objectives: To evaluate and adapt survey methods for detecting dhole presence and estimating abundance.

Implementation details: The feasibility of the following methods for detecting dhole presence and estimating abundance needs to be evaluated and further adapted:

i) camera trap-based survey methods;
ii) track identification based methods for indicating dhole presence;
iii) track count-based methods for the production of indices of relative abundance (paying particular attention to the problem of domestic and feral dogs);
iv) use of faecal genetics (i.e., genetic fingerprinting individual dholes from their scats to census pack and population size);
v) call-based survey methods, i.e. calling-up packs of dholes using playback of whistle calls, pup sounds, and prey sounds for detecting and counting dhole packs (additional information could be gained by video filming any dholes that approach close enough); and
vi) production of a short illustrated identification guide showing dhole footprints, scats, and the animals (could be given to reserve managers, surveyors, etc.).

Annual budget: II

Time frame: 1 year

Contact: Canid Specialist Group (Dhole Working Group), canids@zoo.ac.uk

23.2 [Project] Genetic studies

Objectives: To assess genetic variability within and between populations and to identify appropriate conservation/management units.

Implementation details: Genetic studies focused on determining levels of genetic variability within and between populations are needed to assess appropriate conservation/management units and help set priorities. These studies should also aim to assess the validity of current taxonomic groupings and determine whether there exist hybrid forms within regions of mainland Asia. Information is also needed about the effects of fragmentation and levels of inbreeding. A study addressing many of these issues is currently underway at the University of Southampton.

Annual budget: III

Time frame: 2 years

Contact: Canid Specialist Group (Dhole Working Group), canids@zoo.ac.uk

23.3 [Project] Ecological and behavioural studies

Objectives: Promotion of ecological and behavioural studies focussed on developing conservation strategies for the species.

Implementation details: Little is known of dhole behaviour and ecology. Conservation of the species requires a greater understanding of the population dynamics and the likely significance of kleptoparasitism and intra-guild predation and competition (e.g., the likely consequences of the tiger's decline on dhole population abundance and the significance of competition between dholes and feral/domestic dogs). Ongoing genetic work being conducted at the University of Southampton should contribute to understanding of dhole population dynamics by providing information on population structure, levels of gene flow and rates of dispersal. Once this project is complete, we will need to reassess gaps in knowledge, and determine what additional data need to be collected in order to design and implement an appropriate conservation strategy for dholes.

Predator-prey interactions are also in need of study (e.g., likely prey base sizes necessary to support viable numbers of packs). In addition, we need to investigate the likely minimum reserve size and quality (e.g., prey abundance, habitat quality) for population viability.

Any studies involving the capture and immobilisation of dholes should use the opportunity to screen animals caught for diseases. All dhole carcasses should be necropsied and screened for disease. Standard protocols should be distributed to field workers in areas with dholes. Domestic and feral dogs and other carnivores living in and around dhole habitat should be screened for disease wherever possible.

Annual budget: IV

Time frame: 5 years

Contact: Canid Specialist Group (Dhole Working Group), canids@zoo.ac.uk

23.4 [Action] Surveys and monitoring

Objectives: The accurate delineation of present dhole distribution within its speculated range through the use of questionnaires and targeted field surveys

Implementation details: Establishing the presence or likely absence of dholes (particularly in protected areas) throughout much of their range is a high priority. Current information is often anecdotal, vague or of poor resolution. There is presently little information on population trends. A way of tackling this is through better coordination between surveyors and their respective organisations and the CSG Dhole Working Group. However, targeted surveys for estimating relative abundance in potential sites and monitoring programmes of both dhole and prey abundance within key populations are still required. These areas are being identified as part of Dhole Action Plan (DAP) process.

Annual budget: IV

Time frame: 2 years

Contact: Canid Specialist Group (Dhole Working Group), canids@zoo.ac.uk

23.5 [Action] Prioritisation of populations for conservation action

Objectives: The development of a framework for prioritising dhole populations and conservation action within populations.

Implementation details: An assessment and review of the relative merits of genetic approaches versus more ecology-based approaches in setting priorities is needed. For example, would it be a good idea to modify the Tiger Conservation Unit approach of Dinerstein *et al*. (1997) and use it for dholes? There is also a need to discuss whether one should prioritise for protection those populations that are fragile or disappearing or those that are more robust. Appropriate priority setting requires information on dhole abundance and distribution, prey base, habitat utilisation and habitat integrity, levels of persecution, human abundance in surrounding areas and socio-political background. It is also necessary to evaluate how feasible, important, and useful such an exercise would be. Consequent to the prioritisation of populations there is a need to rank conservation action within sites in accordance to their importance, cost of implementation, political problems within target sites, and approximate time to achieve the projects' goals.

Annual budget: II

Time frame: 2 years

Contact: Canid Specialist Group (Dhole Working Group), canids@zoo.ac.uk

23.6 [Action] Understanding the epidemiology of disease in dholes

Objectives: Studying the epidemiology and effect of diseases and their control in dhole populations.

Implementation details: Disease has often been said to play a major role in dhole population dynamics, but as most 'evidence' is anecdotal a study is long overdue. An important component of such a study is a survey to investigate the status of domestic and feral dogs within the dhole's range and their role as disease reservoirs and vectors. Studies to assess the value of vaccinating domestic dogs and other reservoir hosts are needed. The possibility of (and likely value of) establishing vaccinated buffer zones around important dhole populations should be investigated. Elimination of feral dogs within protected areas should be carried out wherever possible, since feral dogs are both a source of disease and a source of interspecific competition for prey species. We also need pre-emptive studies of the feasibility of vaccinating dholes against rabies. Appropriate vaccination protocols need to be developed (many lessons can be learnt from the work on the African wild dog and Ethiopian wolf). The threat posed by canine distemper virus and other diseases need to be assessed too.

Annual budget: IV

Time frame: 5 years

Contact: Canid Specialist Group (Dhole Working Group), canids@zoo.ac.uk

23.7 [Action] Protection of dholes and their habitat

Objectives: Identify threats to dholes and promote actions that both reduce direct persecution of dholes and protect their habitat and prey bases.

Implementation details: It is quite evident that dholes require complete protection from persecution, initially within designated protected areas but eventually outside the protected area network. In many cases, this will mean enforcement of existing legislation. There is a need to identify those countries or regions where dholes are most at risk from direct persecution and initiate measures to reduce persecution. Reasons for persecution need to be identified and education campaigns initiated where necessary and appropriate. Protection of the dholes' prey base is a priority (in many areas the work would best be done in conjunction with other programmes). The protection of dens, which are often seriously persecuted by humans in some areas, is a high priority. Den sites need to be identified and patrolling increased in these areas. An additional tactic could be enforcing penalties for entering marked exclusion zones around den sites. Other strategies need to be discussed. Methods to reduce indirect killing (e.g., road kills and snares) should be developed. Actions such as increasing linkage between parks, creation of buffer zones, and encouraging land use favourable to wildlife around parks, need to be addressed on a case-by-case basis. These actions will often be best addressed in

collaboration with existing conservation projects and thus a list of existing and relevant projects throughout the range of the species needs to be compiled.
Annual budget: III
Time frame: 3 years
Contact: Canid Specialist Group (Dhole Working Group), canids@zoo.ac.uk

23.8 [Action] Management of the prey base

Objectives: Augmenting dhole prey base through management and protection.
Implementation details: In areas where dholes are threatened by low prey abundance, habitat management to boost prey numbers is required. In addition to the obvious need to protect prey species from poaching and disturbance, other projects could include elimination of feral dogs living in dhole habitat, the creation of artificial water sources, and the regular burning of grassland areas and scrub clearance to boost prey carrying capacity. Such projects need careful management as they may cause problems for other species, but conversely, they may also be of value in their own right if specific prey species themselves are of conservation concern. In some parts of the dhole's range, notably India, many conservationists and wildlife managers strongly believe that exotic weed infestation is reducing the carrying capacity of prey species' habitat. There is a possibility that as a result of this infestation, dhole foraging patterns have changed, but this has to be scientifically substantiated. A thorough scientific investigation which could, if necessary, lead to a weed management/habitat improvement programme, is needed.
Annual budget: IV
Time frame: 3 years
Contact: Canid Specialist Group (Dhole Working Group), canids@zoo.ac.uk

23.9 [Action] Conflict with people

Objectives: Identifying patterns and levels of conflict within range states and designing policy and actions to mitigate conflicts.
Implementation details: A survey is needed to identify levels of conflict between people and dholes in all range states. This work should be linked to ecological field studies wherever possible to allow us to investigate under what circumstances dholes kill livestock. A policy is needed (in all range states) for dealing with stock predation. Attitudes to dholes need to be evaluated to determine whether peoples' perception of problems reflects the real situation. The relative merits and the feasibility of compensation and insurance schemes need to be evaluated for each country or region. Domestic animal husbandry techniques need to be assessed for potential modifications that would reduce losses to dholes and other predators. Surveys of domestic and feral dogs will also be useful to help assess likely culprits in cases of stock predation.
Annual budget: III
Time frame: 3 years
Contact: Canid Specialist Group (Dhole Working Group), canids@zoo.ac.uk

23.10 [Action] Conflict with other threatened species

Objectives: Formulation of a policy for dealing with predation of dholes by other threatened predators. Similarly, policies for dealing with dhole predation on threatened prey species need to be developed.
Implementation details: Predation of dholes by tigers needs to be studied to assess its prevalence. More generally, discussion is needed to develop suitable protocols for dealing with the problems caused if dholes are found to be preying on important populations of threatened prey species at unsustainable rates.
Annual budget: I
Time frame: 1 year
Contact: Canid Specialist Group (Dhole Working Group), canids@zoo.ac.uk

23.11 [Action] Captive breeding of dholes

Objectives: A review of the status of the existing captive populations.
Implementation details: The role of captive breeding as part of a dhole conservation strategy (ongoing DAP process) should be evaluated. Particular emphasis should be given to the issue of hybridisation between dholes belonging to different subspecies. The promotion of zoo exhibits such as the highly educational African wild dog exhibit in the Brookfield Zoo in Chicago should be a high priority.
Annual budget: II
Time frame: 2 years
Contact: Canid Specialist Group (Dhole Working Group), canids@zoo.ac.uk

23.12 [Action] Reintroduction and translocation of dholes

Objectives: An assessment of the necessity and feasibility of reintroducing or translocating dholes.
Implementation details: Potential sites where dholes once existed or where present populations are threatened through genetic isolation or small population sizes need to be identified. The desirability and possibility of re-establishing or augmenting such populations needs to be assessed.
Annual budget: I
Time frame: 1 year
Contact: Canid Specialist Group (Dhole Working Group), canids@zoo.ac.uk

23.13 [Action] Legislative issues affecting dhole conservation

Objectives: A review of the current legal protection for dholes within in their range states, with a view to recommending further legal protection if necessary.

Implementation details: The legal protection conferred on dholes throughout their range needs to be reviewed (ongoing as part of the DAP process), and where necessary measures should be taken to improve protection afforded under national laws. Other issues which need to be addressed include: mechanisms for enhancing enforcement of legal protection and strategies through which governments can be persuaded to provide legal protection where absent, or increase existing protection if it is found to be lacking. The feasibility of restricting the availability of poisons needs to be assessed in countries like India where poisons such as strychnine are easily available over the counter.

Annual budget: I

Time frame: 1 year

Contact: Canid Specialist Group (Dhole Working Group), canids@zoo.ac.uk

Australia and Oceania [Chapter 9]

24. Dingo [VU]

24.1 [Project] Status and taxonomic elucidation of New Guinea singing dog

Objectives: To conduct presence/absence surveys for remnant populations of singing dogs in mountain areas of Papua New Guinea, including Dokfuma, Mt. Capella, Star Mountains, Sanduan Province and Mt. Keriokambu, Morobe Province; to collect whenever possible droppings of wild canid and domestic dogs from near villages for eventual molecular analysis in order to elucidate the taxonomy of this canid and whether it hybridises with domestic dogs; to interview local people for information on historical and current distribution of singing dogs and collate traditional stories concerning the dogs.

Implementation details: There is no recent evidence for the persistence of any wild populations of dingoes (or singing dogs) in New Guinea, although residents of remote mountain areas report seeing or hearing wild dogs at the higher elevations. This project will seek to determine the presence of wild dogs in those areas and hopefully elucidate their taxonomic provenance. From local reports and past literature reports, two remote areas have been selected as likely to harbour wild dogs. Field personnel will visit each area and look for positive sign of dog presence and visit the nearest villages to gather information and domestic dog samples.

Annual budget: II

Time frame: 6 months

Contact: Canid Specialist Group (South Asia and Australasia Working Group), canids@zoo.ac.uk, New Guinea Singing Dog Conservation Society, Lehr Brisbin, brisbin@srel.edu, or Janice Koler-Matznick, jkoler@ccountry.com

24.2 [Action] Identify suitable reference material to assess dingo genetic introgression

Objectives: To study the levels of introgression between dingoes and domestic dogs throughout the species range.

Implementation details: There is a need to assess the genetic make-up of dingo populations throughout their distribution in order to identify the prevalence of hybrid forms and inform dingo conservation planning. Careful attention needs to be given to the provenance of reference material. Recent studies have used modern dingoes as reference material (i.e., material sampled in recent decades from captive populations that are known – from skull measurements and coat colour – to be hybrid or have a high potential to be hybrid). Arguably a better source for reference material could be obtained from fossils and cave deposits in Australia that are dated 200–3,000 years BP, pre-dating European settlement (and hence domestic dogs). Locations and catalogue numbers of some material are indicated by Corbett (2003).

Annual budget: II–III

Time frame: 1–2 years

Contact: Canid Specialist Group (South Asia and Australasia Working Group), canids@zoo.ac.uk

24.3 [Project] Assess the conservation implications of dingo genetic introgression

Objectives: To study the behavioural ecology of dingo-dog hybrids in Australia and compare their ecological role with that of pure dingoes.

Implementation details: Field studies are needed in south-eastern Australia to assess whether the ecological role of dingo-dog hybrids is similar to dingoes. There are differences in breeding behaviour between dingoes and hybrids – such as biannual oestrous cycling in hybrid bitches and thus the potential for hybrids to raise two litters per year or to whelp pups in the summer. This may have implications on conservation of rare or threatened species, as well as for sheep and cattle farmers where there is increased stock killing by canids. Also, if dingo populations are replaced by hybrids (as is the case in eastern Australia), then arguably the conservation of dingo-like hybrids can only be justified if their ecological role is similar to dingoes (see Daniels and Corbett 2003).

Annual budget: IV–V

Time frame: 3 years

Contact: Canid Specialist Group (South Asia and Australasia Working Group), canids@zoo.ac.uk

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Appendix 1

List of Canids on the 2004 IUCN Red List of Threatened Species

Assessments were made using the IUCN Red List Categories and Criteria: Version 3.1 (IUCN 2001), which can be found in Appendix 2. Evaluations for 1996 (as listed in Baillie and Groombridge 1996) used version 2.3 (IUCN 1994). The status of all canid species listed on the 2000 IUCN Red List, was unchanged from 1996. The current assessment and evaluation process was overseen by Claudio Sillero-Zubiri, Red List Authority for the Canidae. CITES status (http://www.cites.org).

Scientific Name	**Common Name(s)**	**Red List 1996**	**Red List 2004**	**CITES 2003**
Alopex lagopus	Arctic fox	**LR**(lc)	**LC**	
Atelocynus microtis	Short-eared dog	**DD**	**DD**	
Canis adustus	Side-striped jackal	**LR**(lc)	**LC**	
Canis aureus	Golden jackal	**LR**(lc)	**LC**	**III**
Canis lupus dingo	Dingo	**LR**(lc)	**VU**: A2e	
Canis lupus	Grey wolf	**LR**(lc)	**LC**	**II**[1]
Canis latrans	Coyote	**LR**(lc)	**LC**	
Canis mesomelas	Black-backed jackal	**LR**(lc)	**LC**	
Canis rufus	Red wolf	**CR**: D	**CR**: D	
Canis simensis	Ethiopian wolf	**CR**: A1b+2be,C1,E	**EN**: C2a(i), D	
Cerdocyon thous	Crab-eating fox	**LR**(lc)	**LC**	**II**
Chrysocyon brachyurus	Maned wolf	**LR**(nt)	**NT**	**II**
Cuon alpinus	Dhole	**VU**: C2a	**EN**: C2a(i)	**II**
Dusicyon australis	Falkland Island wolf	**EX**	**EX**	
Lycaon pictus	African wild dog	**EN**: C1	**EN**: C2a(i)	
Pseudalopex culpaeus	Culpeo	**LR**(lc)	**LC**	**II**
Pseudalopex fulvipes	Darwin's fox	Not listed	**CR**: C2a(ii)	
Pseudalopex griseus	Chilla	**LR**(lc)	**LC**	**II**
Pseudalopex gymnocercus	Pampas fox	**LR**(lc)	**LC**	**II**
Pseudalopex sechurae	Sechuran fox	**DD**	**DD**	
Pseudalopex vetulus	Hoary fox	**DD**	**DD**	
Nyctereutes procyonoides	Raccoon dog	**LR**(lc)	**LC**	
Otocyon megalotis	Bat-eared fox	**LR**(lc)	**LC**	
Speothos venaticus	Bush dog	**VU**: C2A	**VU**: C2a(i)	**I**
Urocyon cinereoargenteus	Gray fox	**LR**(lc)	**LC**	
Urocyon littoralis	Island fox	**LR**(cd)	**CR**: A2be+3e	
Vulpes bengalensis	Indian fox	**DD**	**LC**	**III**
Vulpes cana	Blanford's fox	**DD**	**VU**: C1	**II**
Vulpes chama	Cape fox	**LR**(lc)	**LC**	
Vulpes corsac	Corsac	**DD**	**LC**	
Vulpes ferrilata	Tibetan fox	**LR**(lc)	**LC**	
Vulpes macrotis	Kit fox	**LR**(cd)[2]	**LC**	
Vulpes pallida	Pale fox	**DD**	**DD**	
Vulpes rueppellii	Rüppell's fox	**DD**	**DD**	
Vulpes velox	Swift fox	**LR**(cd)[2]	**LC**	
Vulpes vulpes	Red fox	**LR**(lc)	**LC**	**III**[3]
Vulpes zerda	Fennec fox	**DD**	**DD**	**II**

Notes:

[1] Except the populations of Bhutan, India, Nepal and Pakistan, which are included on Appendix I.

[2] *Vulpes macrotis* and *V. velox* evaluated as a single taxon.

[3] Only subspecies *V. v. griffithii*, *V. v. montana* and *V. v. pusilla*.

Appendix 2

IUCN Red List Categories and Criteria Version 3.1

Prepared by the IUCN Species Survival Commission
As approved by the 51st meeting of the IUCN Council, Gland, Switzerland, 9 February 2000

I. Introduction

1. The IUCN Red List Categories and Criteria are intended to be an easily and widely understood system for classifying species at high risk of global extinction. The general aim of the system is to provide an explicit, objective framework for the classification of the broadest range of species according to their extinction risk. However, while the Red List may focus attention on those taxa at the highest risk, it is not the sole means of setting priorities for conservation measures for their protection.

Extensive consultation and testing in the development of the system strongly suggest that it is robust across most organisms. However, it should be noted that although the system places species into the threatened categories with a high degree of consistency, the criteria do not take into account the life histories of every species. Hence, in certain individual cases, the risk of extinction may be under- or over-estimated.

2. Before 1994 the more subjective threatened species categories used in IUCN Red Data Books and Red Lists had been in place, with some modification, for almost 30 years. Although the need to revise the categories had long been recognised (Fitter and Fitter 1987), the current phase of development only began in 1989 following a request from the IUCN Species Survival Commission (SSC) Steering Committee to develop a more objective approach. The IUCN Council adopted the new Red List system in 1994.

The IUCN Red List Categories and Criteria have several specific aims:

- to provide a system that can be applied consistently by different people;
- to improve objectivity by providing users with clear guidance on how to evaluate different factors which affect the risk of extinction;
- to provide a system which will facilitate comparisons across widely different taxa;
- to give people using threatened species lists a better understanding of how individual species were classified.

3. Since their adoption by IUCN Council in 1994, the IUCN Red List Categories have become widely recognised internationally, and they are now used in a range of publications and listings produced by IUCN, as well as by numerous governmental and non-governmental organisations. Such broad and extensive use revealed the need for a number of improvements, and SSC was mandated by the 1996 World Conservation Congress (WCC Res. 1.4) to conduct a review of the system (IUCN 1996). This document presents the revisions accepted by the IUCN Council.

The proposals presented in this document result from a continuing process of drafting, consultation and validation. The production of a large number of draft proposals has led to some confusion, especially as each draft has been used for classifying some set of species for conservation purposes. To clarify matters, and to open the way for modifications as and when they become necessary, a system for version numbering has been adopted as follows:

Version 1.0: Mace and Lande (1991)
The first paper discussing a new basis for the categories, and presenting numerical criteria especially relevant for large vertebrates.

Version 2.0: Mace *et al.* (1992)
A major revision of Version 1.0, including numerical criteria appropriate to all organisms and introducing the non-threatened categories.

Version 2.1: IUCN (1993)
Following an extensive consultation process within SSC, a number of changes were made to the details of the criteria, and fuller explanation of basic principles was included. A more explicit structure clarified the significance of the non-threatened categories.

Version 2.2: Mace and Stuart (1994)
Following further comments received and additional validation exercises, some minor changes to the criteria were made. In addition, the Susceptible category present in Versions 2.0 and 2.1 was subsumed into the Vulnerable category. A precautionary application of the system was emphasised.

Version 2.3: IUCN (1994)
IUCN Council adopted this version, which incorporated changes as a result of comments from

IUCN members, in December 1994. The initial version of this document was published without the necessary bibliographic details, such as date of publication and ISBN number, but these were included in the subsequent reprints in 1998 and 1999. This version was used for the *1996 IUCN Red List of Threatened Animals* (Baillie and Groombridge 1996), *The World List of Threatened Trees* (Oldfield *et al.* 1998) and the *2000 IUCN Red List of Threatened Species* (Hilton-Taylor 2000).

Version 3.0: IUCN/SSC Criteria Review Working Group (1999)
Following comments received, a series of workshops were convened to look at the IUCN Red List Criteria following which, changes were proposed affecting the criteria, the definitions of some key terms and the handling of uncertainty.

Version 3.1: IUCN (2001)
The IUCN Council adopted this latest version, which incorporated changes as a result of comments from the IUCN and SSC memberships and from a final meeting of the Criteria Review Working Group, in February 2000.

All new assessments from January 2001 should use the latest adopted version and cite the year of publication and version number.

4. In the rest of this document, the proposed system is outlined in several sections. Section II, the Preamble, presents basic information about the context and structure of the system, and the procedures that are to be followed in applying the criteria to species. Section III provides definitions of key terms used. Section IV presents the categories, while Section V details the quantitative criteria used for classification within the threatened categories. Annex I provides guidance on how to deal with uncertainty when applying the criteria; Annex II suggests a standard format for citing the Red List Categories and Criteria; and Annex III outlines the documentation requirements for taxa to be included on IUCN's global Red Lists. It is important for the effective functioning of the system that all sections are read and understood to ensure that the definitions and rules are followed. (**Note:** Annexes I, II and III will be updated on a regular basis.)

II. Preamble

The information in this section is intended to direct and facilitate the use and interpretation of the categories (Critically Endangered, Endangered, etc.), criteria (A to E), and subcriteria (1, 2, etc.; a, b, etc.; i, ii, etc.).

1. Taxonomic level and scope of the categorisation process

The criteria can be applied to any taxonomic unit at or below the species level. In the following information, definitions and criteria the term 'taxon' is used for convenience, and may represent species or lower taxonomic levels, including forms that are not yet formally described. There is sufficient range among the different criteria to enable the appropriate listing of taxa from the complete taxonomic spectrum, with the exception of micro-organisms. The criteria may also be applied within any specified geographical or political area, although in such cases special notice should be taken of point 14. In presenting the results of applying the criteria, the taxonomic unit and area under consideration should be specified in accordance with the documentation guidelines (see Annex 3). The categorisation process should only be applied to wild populations inside their natural range, and to populations resulting from benign introductions. The latter are defined in the IUCN *Guidelines for Re-introductions* (IUCN 1998) as '... an attempt to establish a species, for the purpose of conservation, outside its recorded distribution, but within an appropriate habitat and eco-geographical area. This is a feasible conservation tool only when there is no remaining area left within a species' historic range'.

2. Nature of the categories

Extinction is a chance process. Thus, a listing in a higher extinction risk category implies a higher expectation of extinction, and over the time-frames specified more taxa listed in a higher category are expected to go extinct than those in a lower one (without effective conservation action). However, the persistence of some taxa in high-risk categories does not necessarily mean their initial assessment was inaccurate.

All taxa listed as Critically Endangered qualify for Vulnerable and Endangered, and all listed as Endangered qualify for Vulnerable. Together these categories are described as 'threatened'. The threatened categories form a part of the overall scheme. It will be possible to place all taxa into one of the categories (see Figure 1).

3. Role of the different criteria

For listing as Critically Endangered, Endangered or Vulnerable there is a range of quantitative criteria; meeting any one of these criteria qualifies a taxon for listing at that level of threat. Each taxon should be evaluated against all the criteria. Even though some criteria will be inappropriate for certain taxa (some taxa will never qualify under these however close to extinction they come), there should be criteria appropriate for assessing threat levels for any taxon. The relevant factor is whether *any one* criterion is met, not whether all are appropriate or all are met. Because it will never be clear in advance which criteria are

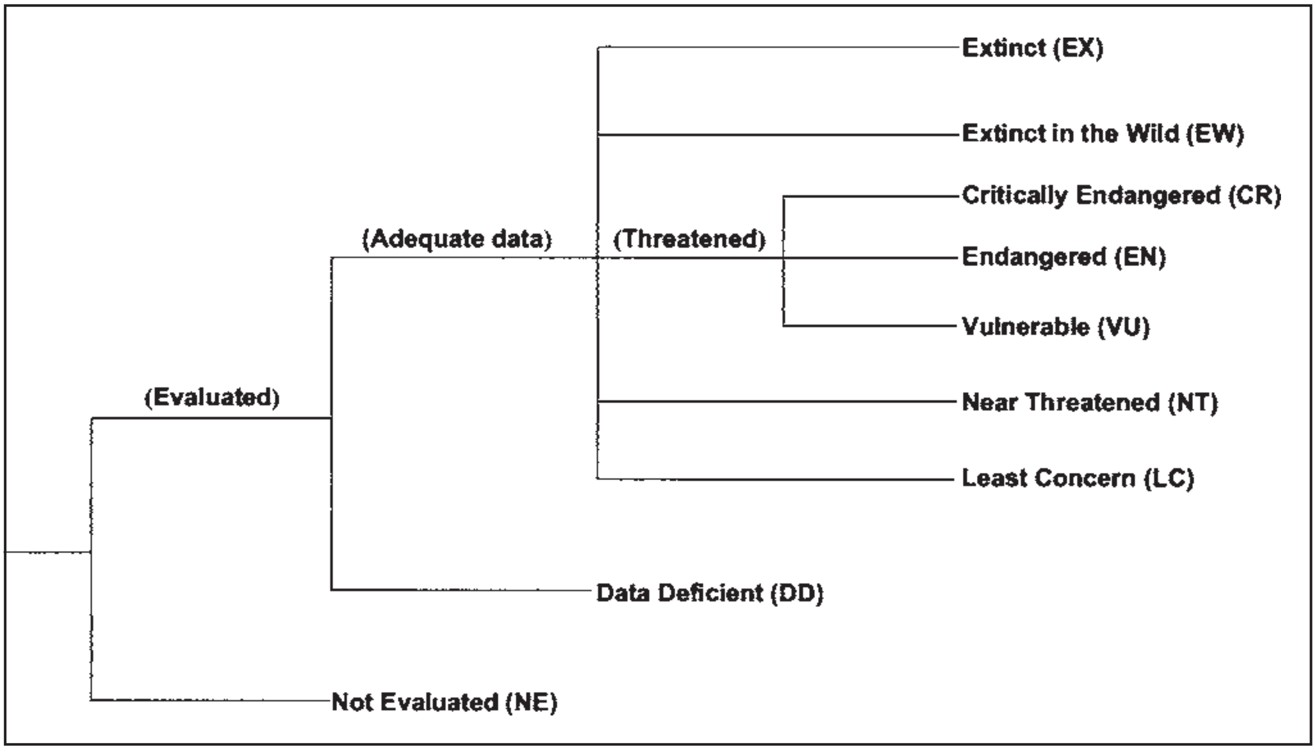


Figure 1. Structure of the categories.

appropriate for a particular taxon, each taxon should be evaluated against all the criteria, and *all* criteria met at the highest threat category must be listed.

4. Derivation of quantitative criteria

The different criteria (A–E) are derived from a wide review aimed at detecting risk factors across the broad range of organisms and the diverse life histories they exhibit. The quantitative values presented in the various criteria associated with threatened categories were developed through wide consultation, and they are set at what are generally judged to be appropriate levels, even if no formal justification for these values exists. The levels for different criteria within categories were set independently but against a common standard. Broad consistency between them was sought.

5. Conservation actions in the listing process

The criteria for the threatened categories are to be applied to a taxon whatever the level of conservation action affecting it. It is important to emphasise here that a taxon may require conservation action even if it is not listed as threatened. Conservation actions which may benefit the taxon are included as part of the documentation requirements (see Annex 3).

6. Data quality and the importance of inference and projection

The criteria are clearly quantitative in nature. However, the absence of high-quality data should not deter attempts at applying the criteria, as methods involving estimation, inference and projection are emphasised as being acceptable throughout. Inference and projection may be based on extrapolation of current or potential threats into the future (including their rate of change), or of factors related to population abundance or distribution (including dependence on other taxa), so long as these can reasonably be supported. Suspected or inferred patterns in the recent past, present or near future can be based on any of a series of related factors, and these factors should be specified as part of the documentation.

Taxa at risk from threats posed by future events of low probability but with severe consequences (catastrophes) should be identified by the criteria (e.g. small distributions, few locations). Some threats need to be identified particularly early, and appropriate actions taken, because their effects are irreversible or nearly so (e.g. pathogens, invasive organisms, hybridisation).

7. Problems of scale

Classification based on the sizes of geographic ranges or the patterns of habitat occupancy is complicated by problems of spatial scale. The finer the scale at which the distributions or habitats of taxa are mapped, the smaller the area will be that they are found to occupy, and the less likely it will be that range estimates (at least for ‘area of occupancy’: see Definitions, point 10) exceed the thresholds specified in the criteria. Mapping at finer scales reveals more areas in which the taxon is unrecorded. Conversely, coarse-scale mapping reveals fewer unoccupied areas, resulting in range estimates that are more likely to exceed the thresholds for the threatened categories. The choice of scale at which range is estimated may thus, itself, influence the outcome of Red List assessments and could be a source of inconsistency and bias. It is impossible to provide any strict but general rules for mapping taxa or habitats; the most appropriate scale will depend on the taxon in question, and the origin and comprehensiveness of the distribution data.

8. Uncertainty

The data used to evaluate taxa against the criteria are often estimated with considerable uncertainty. Such uncertainty can arise from any one or all of the following three factors: natural variation, vagueness in the terms and definitions used, and measurement error. The way in which this uncertainty is handled can have a strong influence on the results of an evaluation. Details of methods recommended for handling uncertainty are included in Annex 1, and assessors are encouraged to read and follow these principles.

In general, when uncertainty leads to wide variation in the results of assessments, the range of possible outcomes should be specified. A single category must be chosen and the basis for the decision should be documented; it should be both precautionary and credible.

When data are very uncertain, the category of 'Data Deficient' may be assigned. However, in this case the assessor must provide documentation showing that this category has been assigned because data are inadequate to determine a threat category. It is important to recognise that taxa that are poorly known can often be assigned a threat category on the basis of background information concerning the deterioration of their habitat and/or other causal factors; therefore the liberal use of 'Data Deficient' is discouraged.

9. Implications of listing

Listing in the categories of Not Evaluated and Data Deficient indicates that no assessment of extinction risk has been made, though for different reasons. Until such time as an assessment is made, taxa listed in these categories should not be treated as if they were non-threatened. It may be appropriate (especially for Data Deficient forms) to give them the same degree of attention as threatened taxa, at least until their status can be assessed.

10. Documentation

All assessments should be documented. Threatened classifications should state the criteria and subcriteria that were met. No assessment can be accepted for the IUCN Red List as valid unless at least one criterion is given. If more than one criterion or subcriterion is met, then each should be listed. If a re-evaluation indicates that the documented criterion is no longer met, this should not result in automatic reassignment to a lower category of threat (downlisting). Instead, the taxon should be re-evaluated against all the criteria to clarify its status. The factors responsible for qualifying the taxon against the criteria, especially where inference and projection are used, should be documented (see Annexes 2 and 3). The documentation requirements for other categories are also specified in Annex 3.

11. Threats and priorities

The category of threat is not necessarily sufficient to determine priorities for conservation action. The category of threat simply provides an assessment of the extinction risk under current circumstances, whereas a system for assessing priorities for action will include numerous other factors concerning conservation action such as costs, logistics, chances of success, and other biological characteristics of the subject.

12. Re-evaluation

Re-evaluation of taxa against the criteria should be carried out at appropriate intervals. This is especially important for taxa listed under Near Threatened, Data Deficient and for threatened taxa whose status is known or suspected to be deteriorating.

13. Transfer between categories

The following rules govern the movement of taxa between categories:

A. A taxon may be moved from a category of higher threat to a category of lower threat if none of the criteria of the higher category has been met for five years or more.
B. If the original classification is found to have been erroneous, the taxon may be transferred to the appropriate category or removed from the threatened categories altogether, without delay (but see Point 10 above).
C. Transfer from categories of lower to higher risk should be made without delay.

14. Use at regional level

The IUCN Red List Categories and Criteria were designed for global taxon assessments. However, many people are interested in applying them to subsets of global data, especially at regional, national or local levels. To do this it is important to refer to guidelines prepared by the IUCN/SSC Regional Applications Working Group (e.g. Gärdenfors *et al.* 2001). When applied at national or regional levels it must be recognised that a global category may not be the same as a national or regional category for a particular taxon. For example, taxa classified as Least Concern globally might be Critically Endangered within a particular region where numbers are very small or declining, perhaps only because they are at the margins of their global range. Conversely, taxa classified as Vulnerable on the basis of their global declines in numbers or range might be Least Concern within a particular region where their populations are stable. It is also important to note that taxa endemic to regions or nations will be assessed globally in any regional or national applications of the criteria, and in these cases great care must be taken to check that an assessment has not already been undertaken by a Red List Authority (RLA), and that the categorisation is agreed with the relevant RLA (e.g. an SSC Specialist Group known to cover the taxon).

III. Definitions

1. Population and Population Size (Criteria A, C and D)

The term 'population' is used in a specific sense in the Red List Criteria that is different to its common biological usage. Population is here defined as the total number of individuals of the taxon. For functional reasons, primarily owing to differences between life forms, population size is measured as numbers of mature individuals only. In the case of taxa obligately dependent on other taxa for all or part of their life cycles, biologically appropriate values for the host taxon should be used.

2. Subpopulations (Criteria B and C)

Subpopulations are defined as geographically or otherwise distinct groups in the population between which there is little demographic or genetic exchange (typically one successful migrant individual or gamete per year or less).

3. Mature individuals (Criteria A, B, C and D)

The number of mature individuals is the number of individuals known, estimated or inferred to be capable of reproduction. When estimating this quantity, the following points should be borne in mind:

- Mature individuals that will never produce new recruits should not be counted (e.g. densities are too low for fertilisation).

- In the case of populations with biased adult or breeding sex ratios, it is appropriate to use lower estimates for the number of mature individuals, which take this into account.

- Where the population size fluctuates, use a lower estimate. In most cases this will be much less than the mean.

- Reproducing units within a clone should be counted as individuals, except where such units are unable to survive alone (e.g. corals).

- In the case of taxa that naturally lose all or a subset of mature individuals at some point in their life cycle, the estimate should be made at the appropriate time, when mature individuals are available for breeding.

- Re-introduced individuals must have produced viable offspring before they are counted as mature individuals.

4. Generation (Criteria A, C and E)

Generation length is the average age of parents of the current cohort (i.e. newborn individuals in the population). Generation length therefore reflects the turnover rate of breeding individuals in a population. Generation length is greater than the age at first breeding and less than the age of the oldest breeding individual, except in taxa that breed only once. Where generation length varies under threat, the more natural, i.e. pre-disturbance, generation length should be used.

5. Reduction (Criterion A)

A reduction is a decline in the number of mature individuals of at least the amount (%) stated under the criterion over the time period (years) specified, although the decline need not be continuing. A reduction should not be interpreted as part of a fluctuation unless there is good evidence for this. The downward phase of a fluctuation will not normally count as a reduction.

6. Continuing decline (Criteria B and C)

A continuing decline is a recent, current or projected future decline (which may be smooth, irregular or sporadic) which is liable to continue unless remedial measures are taken. Fluctuations will not normally count as continuing declines, but an observed decline should not be considered as a fluctuation unless there is evidence for this.

7. Extreme fluctuations (Criteria B and C)

Extreme fluctuations can be said to occur in a number of taxa when population size or distribution area varies widely, rapidly and frequently, typically with a variation greater than one order of magnitude (i.e. a tenfold increase or decrease).

8. Severely fragmented (Criterion B)

The phrase 'severely fragmented' refers to the situation in which increased extinction risk to the taxon results from the fact that most of its individuals are found in small and relatively isolated subpopulations (in certain circumstances this may be inferred from habitat information). These small subpopulations may go extinct, with a reduced probability of recolonisation.

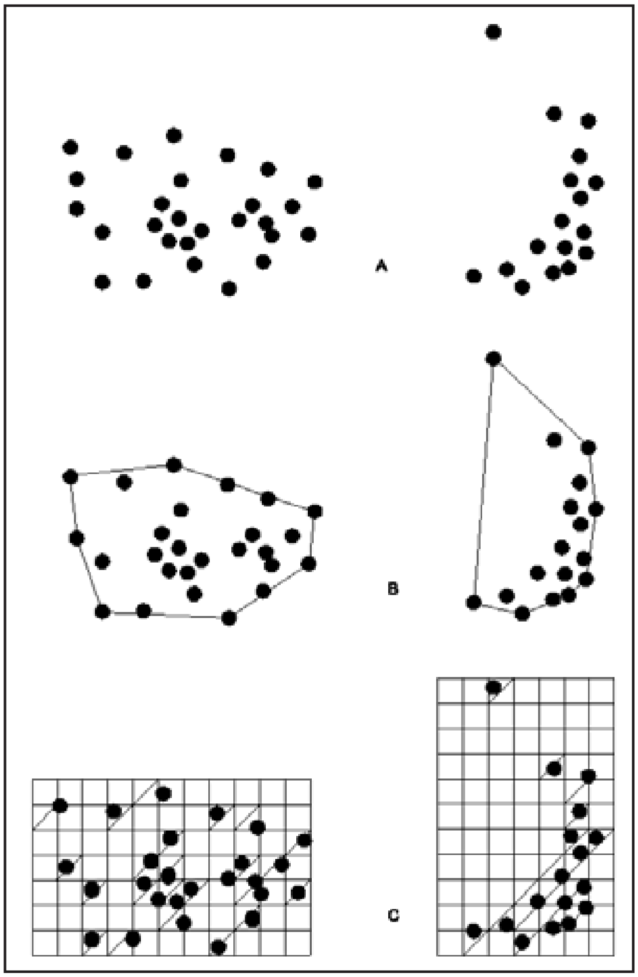
9. Extent of occurrence (Criteria A and B)

Extent of occurrence is defined as the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy (see Figure 2). This measure may exclude discontinuities or disjunctions within the overall distributions of taxa (e.g. large areas of obviously unsuitable habitat) (but see 'area of occupancy', point 10 below). Extent of occurrence can often be measured by a minimum convex polygon (the smallest polygon in which no internal angle exceeds 180 degrees and which contains all the sites of occurrence).

10. Area of occupancy (Criteria A, B and D)

Area of occupancy is defined as the area within its 'extent of occurrence' (see point 9 above) which is occupied by a taxon, excluding cases of vagrancy. The measure reflects the fact that a taxon will not usually occur throughout the area of its extent of occurrence, which may contain unsuitable or unoccupied habitats. In some cases (e.g. irreplaceable colonial nesting sites, crucial feeding sites for migratory taxa) the area of occupancy is the smallest area essential at any stage to the survival of existing populations of a taxon. The size of the area of occupancy will be a function of the scale at which it is measured, and should be at a scale appropriate to relevant biological aspects of the taxon, the nature of threats and the available data (see point 7 in the Preamble). To avoid inconsistencies and bias in assessments caused by estimating area of occupancy at different scales, it may be necessary to standardise estimates by applying a scale-correction factor. It is difficult to give strict guidance on how standardisation should be done because different types of taxa have different scale-area relationships.

Figure 2. Two examples of the distinction between extent of occurrence and area of occupancy. (A) is the spatial distribution of known, inferred or projected sites of present occurrence. (B) shows one possible boundary to the extent of occurrence, which is the measured area within this boundary. (C) shows one measure of area of occupancy which can be achieved by the sum of the occupied grid squares.



11. Location (Criteria B and D)

The term 'location' defines a geographically or ecologically distinct area in which a single threatening event can rapidly affect all individuals of the taxon present. The size of the location depends on the area covered by the threatening event and may include part of one or many subpopulations. Where a taxon is affected by more than one threatening event, location should be defined by considering the most serious plausible threat.

12. Quantitative analysis (Criterion E)

A quantitative analysis is defined here as any form of analysis which estimates the extinction probability of a taxon based on known life history, habitat requirements, threats and any specified management options. Population viability analysis (PVA) is one such technique. Quantitative analyses should make full use of all relevant available data. In a situation in which there is limited information, such data as are available can be used to provide an estimate of extinction risk (for instance, estimating the impact of stochastic events on habitat). In presenting the results of quantitative analyses, the assumptions (which must be appropriate and defensible), the data used and the uncertainty in the data or quantitative model must be documented.

IV. The Categories[1]

A representation of the relationships between the categories is shown in Figure 1.

EXTINCT (EX)

A taxon is Extinct when there is no reasonable doubt that the last individual has died. A taxon is presumed Extinct when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time frame appropriate to the taxon's life cycle and life form.

EXTINCT IN THE WILD (EW)
A taxon is Extinct in the Wild when it is known only to survive in cultivation, in captivity or as a naturalised population (or populations) well outside the past range. A taxon is presumed Extinct in the Wild when exhaustive surveys in known and/or expected habitat, at appropriate times (diurnal, seasonal, annual), throughout its historic range have failed to record an individual. Surveys should be over a time frame appropriate to the taxon's life cycle and life form.

CRITICALLY ENDANGERED (CR)
A taxon is Critically Endangered when the best available evidence indicates that it meets any of the criteria A to E for Critically Endangered (see Section V), and it is therefore considered to be facing an extremely high risk of extinction in the wild.

ENDANGERED (EN)
A taxon is Endangered when the best available evidence indicates that it meets any of the criteria A to E for Endangered (see Section V), and it is therefore considered to be facing a very high risk of extinction in the wild.

VULNERABLE (VU)
A taxon is Vulnerable when the best available evidence indicates that it meets any of the criteria A to E for Vulnerable (see Section V), and it is therefore considered to be facing a high risk of extinction in the wild.

NEAR THREATENED (NT)
A taxon is Near Threatened when it has been evaluated against the criteria but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for or is likely to qualify for a threatened category in the near future.

LEAST CONCERN (LC)
A taxon is Least Concern when it has been evaluated against the criteria and does not qualify for Critically Endangered, Endangered, Vulnerable or Near Threatened. Widespread and abundant taxa are included in this category.

DATA DEFICIENT (DD)
A taxon is Data Deficient when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status. A taxon in this category may be well studied, and its biology well known, but appropriate data on abundance and/or distribution are lacking. Data Deficient is therefore not a category of threat. Listing of taxa in this category indicates that more information is required and acknowledges the possibility that future research will show that threatened classification is appropriate. It is important to make positive use of whatever data are available. In many cases great care should be exercised in choosing between DD and a threatened status. If the range of a taxon is suspected to be relatively circumscribed, and a considerable period of time has elapsed since the last record of the taxon, threatened status may well be justified.

NOT EVALUATED (NE)
A taxon is Not Evaluated when it is has not yet been evaluated against the criteria.

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1 Note: As in previous IUCN categories, the abbreviation of each category (in parentheses) follows the English denominations when translated into other languages (see Annex 2).

V. The Criteria for Critically Endangered, Endangered and Vulnerable

CRITICALLY ENDANGERED (CR)
A taxon is Critically Endangered when the best available evidence indicates that it meets any of the following criteria (A to E), and it is therefore considered to be facing an extremely high risk of extinction in the wild:

A. Reduction in population size based on any of the following:

1. An observed, estimated, inferred or suspected population size reduction of ≥90% over the last 10 years or three generations, whichever is the longer, where the causes of the reduction are clearly reversible AND understood AND ceased, based on (and specifying) any of the following:
    a) direct observation
    b) an index of abundance appropriate to the taxon
    c) a decline in area of occupancy, extent of occurrence and/or quality of habitat
    d) actual or potential levels of exploitation
    e) the effects of introduced taxa, hybridisation, pathogens, pollutants, competitors or parasites.

2. An observed, estimated, inferred or suspected population size reduction of ≥80% over the last 10 years or three generations, whichever is the longer**,** where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible**,** based on (and specifying) any of (a) to (e) under A1.

3. A population size reduction of ≥80%, projected or suspected to be met within the next 10 years or three generations, whichever is the longer (up to a maximum of 100 years), based on (and specifying) any of (b) to (e) under A1.

4. An observed, estimated, inferred, projected or suspected population size reduction of ≥80% over any 10 year or three generation period, whichever is longer (up to a maximum of 100 years in the future), where the time period must include both the past and the future, and where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on (and specifying) any of (a) to (e) under A1.

B. Geographic range in the form of either B1 (extent of occurrence) OR B2 (area of occupancy) OR both:

1. Extent of occurrence estimated to be less than 100km^2 and estimates indicating at least two of a–c:
   a. Severely fragmented or known to exist at only a single location.
   b. Continuing decline, observed, inferred or projected, in any of the following:
      i) extent of occurrence
      ii) area of occupancy
      iii) area, extent and/or quality of habitat
      iv) number of locations or subpopulations
      v) number of mature individuals.
   c. Extreme fluctuations in any of the following:
      i) extent of occurrence
      ii) area of occupancy
      iii) number of locations or subpopulations
      iv) number of mature individuals.

2. Area of occupancy estimated to be less than 10 km^2, and estimates indicating at least two of a–c:
   a. Severely fragmented or known to exist at only a single location.
   b. Continuing decline, observed, inferred or projected, in any of the following:
      i) extent of occurrence
      ii) area of occupancy
      iii) area, extent and/or quality of habitat
      iv) number of locations or subpopulations
      v) number of mature individuals.

   c. Extreme fluctuations in any of the following:
      i) extent of occurrence
      ii) area of occupancy
      iii) number of locations or subpopulations
      iv) number of mature individuals.

C. Population size estimated to number fewer than 250 mature individuals and either:

1. An estimated continuing decline of at least 25% within three years or one generation, whichever is longer (up to a maximum of 100 years in the future) OR

2. A continuing decline, observed, projected, or inferred, in numbers of mature individuals AND at least one of the following (a–b):
   a) Population structure in the form of one of the following:
      i) no subpopulation estimated to contain more than 50 mature individuals, OR
      ii) at least 90% of mature individuals in one subpopulation.
   b) Extreme fluctuations in number of mature individuals.

D. Population size estimated to number fewer than 50 mature individuals.

E. Quantitative analysis showing the probability of extinction in the wild is at least 50% within 10 years or three generations, whichever is the longer (up to a maximum of 100 years).

ENDANGERED (EN)
A taxon is Endangered when the best available evidence indicates that it meets any of the following criteria (A to E), and it is therefore considered to be facing a very high risk of extinction in the wild:

A. Reduction in population size based on any of the following:

1. An observed, estimated, inferred or suspected population size reduction of ≥70% over the last 10 years or three generations, whichever is the longer, where the causes of the reduction are clearly reversible AND understood AND ceased, based on (and specifying) any of the following:
   a) direct observation
   b) an index of abundance appropriate to the taxon
   c) a decline in area of occupancy, extent of occurrence and/or quality of habitat
   d) actual or potential levels of exploitation
   e) the effects of introduced taxa, hybridisation, pathogens, pollutants, competitors or parasites.

2. An observed, estimated, inferred or suspected population size reduction of ≥50% over the last 10 years or three generations, whichever is the longer, where the reduction or its causes may not have

ceased OR may not be understood OR may not be reversible, based on (and specifying) any of (a) to (e) under A1.

3. A population size reduction of ≥50%, projected or suspected to be met within the next 10 years or three generations, whichever is the longer (up to a maximum of 100 years), based on (and specifying) any of (b) to (e) under A1.

4. An observed, estimated, inferred, projected or suspected population size reduction of ≥50% over any 10 year or three generation period, whichever is longer (up to a maximum of 100 years in the future), where the time period must include both the past and the future, and where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on (and specifying) any of (a) to (e) under A1.

B. Geographic range in the form of either B1 (extent of occurrence) OR B2 (area of occupancy) OR both:

1. Extent of occurrence estimated to be less than 5,000 km^2, and estimates indicating at least two of a–c:
   a. Severely fragmented or known to exist at no more than five locations.
   b. Continuing decline, observed, inferred or projected, in any of the following:
      i) extent of occurrence
      ii) area of occupancy
      iii) area, extent and/or quality of habitat
      iv) number of locations or subpopulations
      v) number of mature individuals.

   c. Extreme fluctuations in any of the following:
      i) extent of occurrence
      ii) area of occupancy
      iii) number of locations or subpopulations
      iv) number of mature individuals.

2. Area of occupancy estimated to be less than 500 km^2, and estimates indicating at least two of a–c:
   a. Severely fragmented or known to exist at no more than five locations.
   b. Continuing decline, observed, inferred or projected, in any of the following:
      i) extent of occurrence
      ii) area of occupancy
      iii) area, extent and/or quality of habitat
      iv) number of locations or subpopulations
      v) number of mature individuals.
   c. Extreme fluctuations in any of the following:
      i) extent of occurrence
      ii) area of occupancy
      iii) number of locations or subpopulations
      iv) number of mature individuals.

C. Population size estimated to number fewer than 2,500 mature individuals and either:

1. An estimated continuing decline of at least 20% within five years or two generations, whichever is longer, (up to a maximum of 100 years in the future) OR

2. A continuing decline, observed, projected, or inferred, in numbers of mature individuals AND at least one of the following (a–b):
   a) Population structure in the form of one of the following:
      i) no subpopulation estimated to contain more than 250 mature individuals, OR
      ii) at least 95% of mature individuals in one subpopulation.
   b) Extreme fluctuations in number of mature individuals.

D. Population size estimated to number fewer than 250 mature individuals.

E. Quantitative analysis showing the probability of extinction in the wild is at least 20% within 20 years or five generations, whichever is the longer (up to a maximum of 100 years

VULNERABLE (VU)
A taxon is Vulnerable when the best available evidence indicates that it meets any of the following criteria (A to E), and it is therefore considered to be facing a high risk of extinction in the wild:

A. Reduction in population size based on any of the following:

1. An observed, estimated, inferred or suspected population size reduction of ≥50% over the last 10 years or three generations, whichever is the longer, where the causes of the reduction are: clearly reversible AND understood AND ceased, based on (and specifying) any of the following:
   a) direct observation
   b) an index of abundance appropriate to the taxon
   c) a decline in area of occupancy, extent of occurrence and/or quality of habitat
   d) actual or potential levels of exploitation
   e) the effects of introduced taxa, hybridisation, pathogens, pollutants, competitors or parasites.

2. An observed, estimated, inferred or suspected population size reduction of ≥30% over the last 10 years or three generations, whichever is the longer, where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on (and specifying) any of (a) to (e) under A1.

3. A population size reduction of ≥30%, projected or suspected to be met within the next 10 years or three generations, whichever is the longer (up to a maximum of 100 years), based on (and specifying) any of (b) to (e) under A1.

4. An observed, estimated, inferred, projected or suspected population size reduction of ≥30% over any 10 year or three generation period, whichever is longer (up to a maximum of 100 years in the future), where the time period must include both the past and the future, and where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible, based on (and specifying) any of (a) to (e) under A1.

B. Geographic range in the form of either B1 (extent of occurrence) OR B2 (area of occupancy) OR both:

1. Extent of occurrence estimated to be less than 20,000 km^2, and estimates indicating at least two of a–c:
   a. Severely fragmented or known to exist at no more than 10 locations.
   b. Continuing decline, observed, inferred or projected, in any of the following:
      i) extent of occurrence
      ii) area of occupancy
      iii) area, extent and/or quality of habitat
      iv) number of locations or subpopulations
      v) number of mature individuals.
   c. Extreme fluctuations in any of the following:
      i) extent of occurrence
      ii) area of occupancy
      iii) number of locations or subpopulations
      iv) number of mature individuals.

2. Area of occupancy estimated to be less than 2,000 km^2, and estimates indicating at least two of a–c:
   a. Severely fragmented or known to exist at no more than 10 locations.
   b. Continuing decline, observed, inferred or projected, in any of the following:
      i) extent of occurrence
      ii) area of occupancy
      iii) area, extent and/or quality of habitat
      iv) number of locations or subpopulations
      v) number of mature individuals.
   c. Extreme fluctuations in any of the following:
      i) extent of occurrence
      ii) area of occupancy
      iii) number of locations or subpopulations
      iv) number of mature individuals.

C. Population size estimated to number fewer than 10,000 mature individuals and either:

1. An estimated continuing decline of at least 10% within 10 years or three generations, whichever is longer, (up to a maximum of 100 years in the future) OR

2. A continuing decline, observed, projected, or inferred, in numbers of mature individuals AND at least one of the following (a–b):
   a) Population structure in the form of one of the following:
      i) no subpopulation estimated to contain more than 1,000 mature individuals, OR
      ii) all mature individuals are in one subpopulation.
   b) Extreme fluctuations in number of mature individuals.

D. Population very small or restricted in the form of either of the following:
   1. Population size estimated to number fewer than 1,000 mature individuals.
   2. Population with a very restricted area of occupancy (typically less than 20 km^2) or number of locations (typically five or fewer) such that it is prone to the effects of human activities or stochastic events within a very short time period in an uncertain future, and is thus capable of becoming Critically Endangered or even Extinct in a very short time period.

E. Quantitative analysis showing the probability of extinction in the wild is at least 10% within 100 years.

Annex 1: Uncertainty

The Red List Criteria should be applied to a taxon based on the available evidence concerning its numbers, trend and distribution. In cases where there are evident threats to a taxon through, for example, deterioration of its only known habitat, a threatened listing may be justified, even though there may be little direct information on the biological status of the taxon itself. In all these instances there are uncertainties associated with the available information and how it was obtained. These uncertainties may be categorised as natural variability, semantic uncertainty and measurement error (Akçakaya *et al.* 2000). This section provides guidance on how to recognise and deal with these uncertainties when using the criteria.

Natural variability results from the fact that species' life histories and the environments in which they live change over time and space. The effect of this variation on the criteria is limited, because each parameter refers to a specific time or spatial scale. Semantic uncertainty arises from vagueness in the definition of terms or lack of consistency in different assessors' usage of them. Despite attempts to make the definitions of the terms used in the criteria exact, in some cases this is not possible without the loss of generality. Measurement error is often the largest source of uncertainty; it arises from the lack of precise information about the parameters used in the criteria. This may be due to inaccuracies in estimating the values or a lack of knowledge. Measurement error may be reduced or eliminated by acquiring additional data. For further details, see Akçakaya *et al.* (2000) and Burgman *et al.* (1999).

One of the simplest ways to represent uncertainty is to specify a best estimate and a range of plausible values. The best estimate itself might be a range, but in any case the best estimate should always be included in the range of plausible values. When data are very uncertain, the range for the best estimate might be the range of plausible values. There are various methods that can be used to establish the plausible range. It may be based on confidence intervals, the opinion of a single expert, or the consensus opinion of a group of experts. Whichever method is used should be stated and justified in the documentation.

When interpreting and using uncertain data, attitudes toward risk and uncertainty may play an important role. Attitudes have two components. First, assessors need to consider whether they will include the full range of plausible values in assessments, or whether they will exclude extreme values from consideration (known as dispute tolerance). An assessor with a low dispute tolerance would include all values, thereby increasing the uncertainty, whereas an assessor with a high dispute tolerance would exclude extremes, reducing the uncertainty. Second, assessors need to consider whether they have a precautionary or evidentiary attitude to risk (known as risk tolerance). A precautionary attitude will classify a taxon as threatened unless it is certain that it is not threatened, whereas an evidentiary attitude will classify a taxon as threatened only when there is strong evidence to support a threatened classification. Assessors should resist an evidentiary attitude and adopt a precautionary but realistic attitude to uncertainty when applying the criteria, for example, by using plausible lower bounds, rather than best estimates, in determining population size, especially if it is fluctuating. All attitudes should be explicitly documented.

An assessment using a point estimate (i.e. single numerical value) will lead to a single Red List Category. However, when a plausible range for each parameter is used to evaluate the criteria, a range of categories may be obtained, reflecting the uncertainties in the data. A single category, based on a specific attitude to uncertainty, should always be listed along with the criteria met, while the range of plausible categories should be indicated in the documentation (see Annex 3).

Where data are so uncertain that any category is plausible, the category of 'Data Deficient' should be assigned. However, it is important to recognise that this category indicates that the data are inadequate to determine the degree of threat faced by a taxon, not necessarily that the taxon is poorly known or indeed not threatened. Although Data Deficient is not a threatened category, it indicates a need to obtain more information on a taxon to determine the appropriate listing; moreover, it requires documentation with whatever available information there is.

Annex 2: Citation of the IUCN Red List Categories and Criteria

In order to promote the use of a standard format for citing the Red List Categories and Criteria the following forms of citation are recommended:

1. The Red List Category may be written out in full or abbreviated as follows (when translated into other languages, the abbreviations should follow the English denominations):

Extinct, EX
Extinct in the Wild, EW
Critically Endangered, CR
Endangered, EN
Vulnerable, VU
Near Threatened, NT
Least Concern, LC
Data Deficient, DD
Not Evaluated, NE

2. Under Section V (the criteria for Critically Endangered, Endangered and Vulnerable) there is a hierarchical alphanumeric numbering system of criteria and subcriteria. These criteria and subcriteria (all three levels) form an integral part of the Red List assessment and all those that result in the assignment of a threatened category must be specified after the Category. Under the criteria A to C and D under Vulnerable, the first level of the hierarchy is indicated by the use of numbers (1–4) and if more than one is met, they are separated by means of the '+' symbol. The second level is indicated by the use of the lower-case

alphabet characters (a–e). These are listed without any punctuation. A third level of the hierarchy under Criteria B and C involves the use of lower case roman numerals (i–v). These are placed in parentheses (with no space between the preceding alphabet character and start of the parenthesis) and separated by the use of commas if more than one is listed. Where more than one criterion is met, they should be separated by semicolons. The following are examples of such usage:

EX
CR A1cd
VU A2c+3c
EN B1ac(i,ii,iii)
EN A2c; D
VU D1+2
CR A2c+3c; B1ab(iii)
CR D
VU D2
EN B2ab(i,ii,iii)
VU C2a(ii)
EN A1c; B1ab(iii); C2a(i)
EN B2b(iii)c(ii)
EN B1ab(i,ii,v)c(iii,iv)+2b(i)c(ii,v)
VU B1ab(iii)+2ab(iii)
EN
A2abc+3bc+4abc;B1b(iii,iv,v)c(ii,iii,iv)+2b(iii,iv,v)c(ii,iii,iv)

Annex 3: Documentation Requirements for Taxa Included on the IUCN Red List

The following is the **minimum** set of information, which should accompany every assessment submitted for incorporation into the *IUCN Red List of Threatened Species*™:

- Scientific name including authority details
- English common name/s and any other widely used common names (specify the language of each name supplied)
- Red List Category and Criteria
- Countries of occurrence (including country subdivisions for large nations, e.g. states within the USA, and overseas territories, e.g. islands far from the mainland country)
- For marine species, the Fisheries Areas in which they occur should be recorded (see http://www.iucn.org/themes/ssc/sis/faomap.htm for the Fisheries Areas as delimited by FAO, the Food and Agriculture Organisation of the United Nations)
- For inland water species, the names of the river systems, lakes, etc. to which they are confined
- A map showing the geographic distribution (extent of occurrence)
- A rationale for the listing (including any numerical data, inferences or uncertainty that relate to the criteria and their thresholds)
- Current population trends (increasing, decreasing, stable or unknown)
- Habitat preferences (using a modified version of the Global Land Cover Characterisation (GLCC) classification which is available electronically from http://www.iucn.org/themes/ssc/sis/authority.htm or on request from redlist@ssc-uk.org)
- Major threats (indicating past, current and future threats using a standard classification which is available from the SSC web site or e-mail address as shown above)
- Conservation measures, (indicating both current and proposed measures using a standard classification which is available from the SSC web site or e-mail address as shown above)
- Information on any changes in the Red List status of the taxon, and why the status has changed
- Data sources (cited in full; including unpublished sources and personal communications)
- Name/s and contact details of the assessor/s
- Before inclusion on the IUCN Red List, all assessments will be evaluated by at least two members of a Red List Authority. The Red List Authority is appointed by the Chair of the IUCN Species Survival Commission and is usually a sub-group of a Specialist Group. The names of the evaluators will appear with each assessment.

In addition to the minimum documentation, the following information should also be supplied where appropriate:

- If a quantitative analysis is used for the assessment (i.e. Criterion E), the data, assumptions and structural equations (e.g. in the case of a Population Viability Analysis) should be included as part of the documentation.
- For Extinct or Extinct in the Wild taxa, extra documentation is required indicating the effective date of extinction, possible causes of the extinction and the details of surveys which have been conducted to search for the taxon.
- For taxa listed as Near Threatened, the rationale for listing should include a discussion of the criteria that are nearly met or the reasons for highlighting the taxon (e.g. they are dependent on ongoing conservation measures).
- For taxa listed as Data Deficient, the documentation should include what little information is available.

Assessments may be made using version 2.0 of the software package RAMAS® Red List (Akçakaya and Ferson 2001). This program assigns taxa to Red List Categories according to the rules of the IUCN Red List Criteria and has the advantage of being able to explicitly handle uncertainty in the data. The software captures most of the information required for the documentation above, but in some cases the information will be reported differently. The following points should be noted:

- If RAMAS® Red List is used to obtain a listing, this should be stated.
- Uncertain values should be entered into the program as a best estimate and a plausible range, or as an interval (see the RAMAS® Red List manual or help files for further details).
- The settings for attitude towards risk and uncertainty (i.e. dispute tolerance, risk tolerance and burden of proof) are all pre-set at a mid-point. If any of these settings are changed this should be documented and fully justified, especially if a less precautionary position is adopted.
- Depending on the uncertainties, the resulting classification can be a single category and/or a range of plausible categories. In such instances, the following approach should be adopted (the program will usually indicate this automatically in the Results window):
  - If the range of plausible categories extends across two or more of the threatened categories (e.g. Critically Endangered to Vulnerable) and no preferred category is indicated, the precautionary approach is to take the highest category shown, i.e. CR in the above example. In such cases, the range of plausible categories should be documented under the rationale including a note that a precautionary approach was followed in order to distinguish it from the situation in the next point. The following notation has been suggested e.g. CR* (CR–VU).
  - If a range of plausible categories is given and a preferred category is indicated, the rationale should indicate the range of plausible categories met e.g. EN (CR–VU).
- The program specifies the criteria that contributed to the listing (see Status window). However, when data are uncertain, the listing criteria are approximate, and in some cases may not be determined at all. In such cases, the assessors should use the Text results to determine or verify the criteria and sub-criteria met. Listing criteria derived in this way must be clearly indicated in the rationale (refer to the RAMAS® Red List Help menu for further guidance on this issue).
- If the preferred category is indicated as Least Concern, but the plausible range extends into the threatened categories, a listing of 'Near Threatened' (NT) should be used. The criteria, which triggered the extension into the threatened range, should be recorded under the rationale.
- Any assessments made using this software must be submitted with the RAMAS® Red List input files (i.e. the *.RED files).

New global assessments or reassessments of taxa currently on the IUCN Red List, may be submitted to the IUCN/SSC Red List Programme Officer for incorporation (subject to peer review) in a future edition of the *IUCN Red List of Threatened Species*™. Submissions from within the SSC network should preferably be made using the Species Information Service (SIS) database. Other submissions may be submitted electronically; these should preferably be as files produced using RAMAS® Red List or any of the programs in Microsoft Office 97 (or earlier versions) e.g. Word, Excel or Access. Submissions should be sent to: IUCN/SSC Red List Programme, IUCN/SSC UK Office, 219c Huntingdon Road, Cambridge, CB3 0DL, United Kingdom. Fax: +44-(0)1223-277845; Email: redlist@ssc-uk.org

For further clarification or information about the IUCN Red List Criteria, documentation requirements (including the standards used) or submission of assessments, please contact the IUCN/SSC Red List Programme Officer at the address shown above.

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Appendix 5

Canid Specialist Group Resources

How do we communicate?

http://www.canids.org

The official IUCN/SSC Canid Specialist Group (CSG) website, with relevant information on the CSG membership and *modus operandi*. The site hosts all CSG publications, including action plans, species accounts, complete bibliographies, bulletins, short news and announcements. The CSG maintains a substantial collective library, and access to many titles is available through the site. Other CSG resources listed below are also hosted at the site.

Canids-L

Canids-L is a free, rapid channel for communication among CSG members and other people directly involved in canid research, management or policy setting. The mailing list is open to anybody actively involved in canid conservation and research and other wild canid enthusiasts, providing a forum for discussion of new emerging conservation topics. Canids-L is moderated, and its traffic is kept relatively light, with postings not exceeding 100 per year. Types of news items appropriate for this list include, but are not limited to:

- News of new discoveries, outbreaks of disease or other mayor threats affecting canids
- Discussion of methodologies, techniques, and research equipment
- Inquiries from researchers regarding management and conservation strategies
- Reporting of rare events and comparison of experiences
- Abstracts of recent publications of interest to canid scientists
- News of scientific and conservation meetings.

Subscribe to Canids-L for the latest canid news. To subscribe simply send an empty email from your email account to: canids-l-subscribe@maillist.ox.ac.uk

Canid News Online

An electronic, peer-reviewed, scientific journal devoted to the dissemination of current research on all species of the Canidae. Its aim is to provide a forum for the exchange and publication of information, ideas and opportunities among all those concerned for the study, conservation and welfare of wild canids. Our goal is that Canid News should include high quality articles that not only convey the excitement of canid biology, but also inform upon conservation problems, and hopefully contribute towards their resolution. Manuscript submissions and peer review are handled by email and the content is posted exclusively on the internet, mirrored in another two sites.

Action Plans

An important output of the CSG is the production of action plans for the conservation of canid species. In addition to this global canid action plan, and the original action plan published in 1990, the CSG has embarked in the production of detailed action plans for all threatened canid species. Plans on dholes and kit foxes will soon be added to the already published plans for the Ethiopian wolf and African wild dog:

— **Foxes, Wolves, Jackals and Dogs (1990)**
http://www.canids.org/1990CAP/90candap.htm
— **African Wild Dog Action Plan (1997)**
http://www.canids.org/PUBLICAT/AWDACTPL/wldogtoc.htm
— **Ethiopian Wolf Action Plan (1997)**
http://www.canids.org/PUBLICAT/EWACTPLN/ewaptoc.htm

Canid Project Database (CPD)

An online information resource for canid conservation, providing detailed information of planned, on-going, or recently completed conservation projects on all canids. The CPD will be instrumental to the implementation of this action plan, by seeking to facilitate exchange of information between field projects, and develop contacts with potential sponsors and collaborators. The CPD is managed by Oxford University's Wildlife Conservation Research Unit. Projects can be concerned with any aspect of canid biology and/or conservation. This resource will soon be expanded to provide a searchable database of canid conservation practitioners. http://www.canids.org

How can you help?

- Reporting any information of interest on threatened canid species
- Providing financial support to the CSG
- Assistance with the implementation of any of the Action Plans' projects.

For further information contact:

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Wildlife Conservation Research Unit,
Zoology Department, South Parks Road,
Oxford OX1 3PS, UK
E-mail: canidsg@zoo.ox.ac.uk
Visit our site at http://www.canids.org

IUCN/SSC Action Plans for the Conservation of Biological Diversity

Action Plan for African Primate Conservation: 1986-1990. Compiled by J.F. Oates. IUCN/SSC Primate Specialist Group, 1986, 41 pp. (out of print)

Action Plan for Asian Primate Conservation: 1987-1991. Compiled by A.A. Eudey. IUCN/SSC Primate Specialist Group, 1987, 65 pp. (out of print)

Antelopes. Global Survey and Regional Action Plans. Part 1. East and Northeast Africa. Compiled by R. East. IUCN/SSC Antelope Specialist Group, 1988, 96 pp. (out of print)

Dolphins, Porpoises and Whales. An Action Plan for the Conservation of Biological Diversity: 1988-1992. Second Edition. Compiled by W.F. Perrin. IUCN/SSC Cetacean Specialist Group, 1989, 27 pp. (out of print)

The Kouprey. An Action Plan for its Conservation. Edited by J.R. MacKinnon and S.N. Stuart. IUCN/SSC Asian Wild Cattle Specialist Group, 1988, 19 pp. (out of print)

Weasels, Civets, Mongooses and their Relatives. An Action Plan for the Conservation of Mustelids and Viverrids. Compiled by A. Schreiber, R. Wirth, M. Riffel and H. van Rompaey. IUCN/SSC Mustelid and Viverrid Specialist Group, 1989, 99 pp. (out of print.)

Antelopes. Global Survey and Regional Action Plans. Part 2. Southern and South-central Africa. Compiled by R. East. IUCN/SSC Antelope Specialist Group, 1989, 96 pp. (out of print)

Asian Rhinos. An Action Plan for their Conservation. Compiled by Mohd Khan bin Momin Khan. IUCN/SSC Asian Rhino Specialist Group, 1989, 23 pp. (out of print)

Tortoises and Freshwater Turtles. An Action Plan for their Conservation. Compiled by the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, 1989, 47 pp.

African Elephants and Rhinos. Status Survey and Conservation Action Plan. Compiled by D.H.M. Cumming, R.F. du Toit and S.N. Stuart. IUCN/SSC African Elephant and Rhino Specialist Group, 1990, 73 pp. (out of print)

Foxes, Wolves, Jackals, and Dogs. An Action Plan for the Conservation of Canids. Compiled by J.R. Ginsberg and D.W. Macdonald. IUCN/SSC Canid and Wolf Specialist Groups, 1990, 116 pp. (out of print)

The Asian Elephant. An Action Plan for its Conservation. Compiled by C. Santiapillai and P. Jackson. IUCN/SSC Asian Elephant Specialist Group, 1990, 79 pp.

Antelopes. Global Survey and Regional Action Plans. Part 3. West and Central Africa. Compiled by R. East. IUCN/SSC Antelope Specialist Group, 1990, 171 pp.

Otters. An Action Plan for their Conservation. Edited P. Foster-Turley, S. Macdonald and C. Maso. IUCN/SSC Otter Specialist Group, 1990, 126 pp. (out of print)

Rabbits, Hares and Pikas. Status Survey and Conservation Action Plan. Compiled and edited by J.A. Chapman, J.E.C. Flux. IUCN/SSC Lagomorph Specialist Group, 1990, 168 pp.

African Insectivora and Elephant-Shrews. An Action Plan for their Conservation. Compiled by M.E. Nicoll and G.B. Rathbun. IUCN/SSC Insectivore, Tree-Shrew and Elephant-Shrew Specialist Group, 1990, 53 pp.

Swallowtail Butterflies. An Action Plan for their Conservation. Compiled by T.R. New and N.M. Collins. IUCN/SSC Lepidoptera Specialist Group, 1991, 36 pp.

Crocodiles. An Action Plan for their Conservation. Compiled by J. Thorbjarnarson and edited by H. Messel, F.W. King and J.P. Ross. IUCN/SSC Crocodile Specialist Group, 1992, 136 pp.

South American Camelids. An Action Plan for their Conservation. Compiled and edited by H. Torres. IUCN/SSC South American Camelid Specialist Group, 1992, 58 pp.

Australasian Marsupials and Monotremes. An Action Plan for their Conservation. Compiled by M. Kennedy. IUCN/SSC Australasian Marsupial and Monotreme Specialist Group, 1992, 103 pp.

Lemurs of Madagascar. An Action Plan for their Conservation: 1993-1999. Compiled by R.A. Mittermeier, W.R. Konstant, M.E. Nicoll, O. Langrand. IUCN/SSC Primate Specialist Group, 1992, 58 pp. (out of print)

Zebras, Asses and Horses. An Action Plan for the Conservation of Wild Equids. Edited by P. Duncan. IUCN/SSC Equid Specialist Group, 1992, 36 pp.

Old World Fruit Bats. An Action Plan for their Conservation. Compiled by S. Mickleburgh, A.M. Hutson and P.A. Racey. IUCN/SSC Chiroptera Specialist Group, 1992, 252 pp. (out of print)

Seals, Fur Seals, Sea Lions, and Walrus. Status Survey and Conservation Action Plan. Peter Reijnders, Sophie Brasseur, Jaap van der Toorn, Peter van der Wolf, Ian Boyd, John Harwood, David Lavigne and Lloyd Lowry. IUCN/SSC Seal Specialist Group, 1993, 88 pp.

Pigs, Peccaries, and Hippos. Status Survey and Conservation Action Plan. Edited by William L.R. Oliver. IUCN/SSC Pigs and Peccaries Specialist Group. IUCN/SSC Hippo Specialist Group, 1993, 202 pp.

Pecaries. Extraido de *Pigs, Peccaries, and Hippos: Status Survey and Conservation Action Plan (1993)* . Editado por William L.R. Oliver. IUCN/CSE Groupo de Especialistas en Puercos y Pecaries, 1996, 58pp.

The Red Panda, Olingos, Coatis, Raccoons, and their Relatives. Status Survey and Conservation Action Plan for Procyonids and Ailurids. (In English and Spanish) Compiled by Angela R. Glatston. IUCN/SSC Mustelid, Viverrid, and Procyonid Specialist Group, 1994, 103 pp.

Dolphins, Porpoises, and Whales. 1994-1998 Action Plan for the Conservation of Cetaceans. Compiled by Randall R. Reeves and Stephen Leatherwood. IUCN/SSC Cetacean Specialist Group, 1994, 91 pp.

Megapodes. An Action Plan for their Conservation 1995-1999. Compiled by René W.R.J.Dekker, Philip J.K.McGowan and the WPA/Birdlife/SSC Megapode Specialist Group, 1995, 41 pp.

Partridges, Quails, Francolins, Snowcocks and Guineafowl. Status survey and Conservation Action Plan 1995-1999. Compiled by Philip J.K. McGowan, Simon D. Dowell, John P. Carroll and Nicholas J.A.Aebischer and the WPA/BirdLife/SSC Partridge, Quail and Francoliln Specialist Group. 1995, 102 pp.

Pheasants: Status Survey and Conservation Action Plan 1995-1999. Compiled by Philip J.K. McGowan and Peter J. Garson on behalf of the WPA/BirdLife/SSC Pheasant Specialist Group, 1995, 116 pp.

Wild Cats: Status Survey and Conservation Action Plan. Compiled and edited by Kristin Nowell and Peter Jackson. IUCN/SSC Cat Specialist Group, 1996, 406 pp.

Eurasian Insectivores and Tree Shrews: Status Survey and Conservation Action Plan. Compiled by David Stone. IUCN/SSC Insectivore, Tree Shrew and Elephant Shrew Specialist Group. 1996, 108 pp.

African Primates: Status Survey and Conservation Action Plan (Revised edition). Compiled by John F. Oates. IUCN/SSC Primate Specialist Group. 1996, 80 pp.

The Cranes: Status Survey and Conservation Action Plan. Compiled by Curt D. Meine and George W. Archibald. IUCN/SSC Crane Specialist Group, 1996, 401 pp.

Orchids: Status Survey and Conservation Action Plan. Edited by Eric Hágsater and Vinciane Dumont, compiled by Alec Pridgeon. IUCN/SSC Orchid Specialist Group, 1996, 153 pp.

Palms: Their Conservation and Sustained Utilization. Status Survey and Conservation Action Plan. Edited by Dennis Johnson. IUCN/SSC Palm Specialist Group, 1996, 116 pp.

Conservation of Mediterranean Island Plants. 1. Strategy for Action. Compiled by O. Delanoë, B. de Montmollin and L. Olivier. IUCN/SSC Mediterranean Islands Plant Specialist Group, 1996, 106 pp.

Wild Sheep and Goats and their Relatives. Status Survey and Conservation Action Plan for Caprinae. Edited and compiled by David M. Shackleton. IUCN/SSC Caprinae Specialist Group, 1997, 390 + vii pp.

Asian Rhinos. Status Survey and Conservation Action Plan (2nd Edition) . Edited by Thomas J. Foose and Nico van Strien. IUCN/SSC Asian Rhino Specialist Group, 1997, 112 + v pp. (out of print)

The Ethiopian Wolf. Status Survey and Conservation Action Plan. Compiled and edited by Claudio Sillero-Zubiri and David Macdonald. IUCN/SSC Canid Specialist Group, 1997, 123pp. (out of print)

Cactus and Succulent Plants. Status Survey and Conservation Action Plan. Compiled by Sara Oldfield. IUCN/SSC Cactus and Succulent Specialist Group, 1997, 212 + x pp.

Dragonflies. Status Survey and Conservation Action Plan. Compiled by Norman W. Moore. IUCN/SSC Odonata Specialist Group, 1997, 28 + v pp.

Tapirs. Status Survey and Conservation Action Plan. Edited by Daniel M. Brooks, Richard E. Bodmer and Sharon Matola. IUCN/SSC Tapir Specialist Group, 1997, viii + 164pp.

The African Wild Dog. Status Survey and Conservation Action Plan. Compiled and edited by Rosie Woodroffe, Joshua Ginsberg and David Macdonald. IUCN/SSC Canid Specialist Group, 1997, 166pp.

Grebes. Status Survey and Conservation Action Plan. Compiled by Colin O'Donnel and Jon Fjeldså. IUCN/SSC Grebe Specialist Group, 1997, vii + 59pp.

Crocodiles: Status Survey and Conservation Action Plan, 2nd Edition. Edited by James Perran Ross. IUCN/SSC Crocodile Specialist Group, 1998, viii + 96pp. (out of print)

Hyaenas: Status Survey and Conservation Action Plan. Compiled by Gus Mills and Heribert Hofer. IUCN/SSC Hyaena Specialist Group, 1998, vi + 154 pp.

North American Rodents: Status Survey and Conservation Action Plan. Compiled and edited by David J. Hafner, Eric Yensen, Gordon L. Kirkland Jr.. IUCN/SSC Rodent Specialist Group, 1998, x + 171pp.

Deer: Status Survey and Conservation Action Plan. Edited by C. Wemmer. Compiled by Andrew McCarthy, Raleigh Blouch and Donald Moore. IUCN/SSC Deer Specialist Group, 1998, vi + 106pp.

Bears: Status Survey and Conservation Action Plan. Compiled by C. Servheen, S. Herrero and B. Peyton. IUCN/SSC Bear and Polar Bear Specialist groups, 1998, x + 306pp. (out of print)

Conifers: Status Survey and Conservation Action Plan. Compiled by A. Farjon and C.N. Page. IUCN/SSC Conifer Specialist Group, 1999, ix + 121pp.

African Rhino: Status Survey and Conservation Action Plan. Compiled by R. Emslie and M. Brooks. IUCN/SSC African Rhino Specialist Group, 1999, ix + 92pp. (out of print)

Curassows, Guans and Chachalacas: Status Survey and Conservation Action Plan for Cracids 2000–2004. Compiled by Daniel M. Brooks and Stuart D. Strahl (with Spanish and Portuguese translations). IUCN/SSC Cracid Specialist Group, 2000, viii + 182pp.

Parrots: Status Survey and Conservation Action Plan 2000–2004. Edited by Noel Snyder, Philip McGowan, James Gilardi, and Alejandro Grajal, 2000, x + 180pp.

West Indian Iguanas: Status Survey and Conservation Action Plan. Compiled by Allison Alberts. IUCN/SSC West Indian Iguana Specialist Group, 2000, vi + 111pp.

Grouse: Status Survey and Conservation Action Plan 2000–2004. Compiled by Ilse Storch. WPA/BirdLife/SSC Grouse Specialist group, 2000, x + 112pp.

Mosses, Liverworts, and Hornworts: Status Survey and Conservation Action Plan for Bryophytes. Compiled by T. Hallingbäck and N. Hodgetts. IUCN/SSC Bryophyte Specialist Group, 2000, x + 106pp.

Pheasants: Status Survey and Conservation Action Plan 2000–2004. Edited by Richard A. Fuller and Peter J. Garson. WPA/BirdLife/SSC Pheasant Specialist group, 2000, vii + 76pp.

Megapodes. Status Survey and Conservation Action Plan 2000–2004. Edited by René W.R.J. Dekker, Richard A. Fuller, and Gillian C. Baker on behalf of the WPA/BirdLife/SSC Megapode Specialist Group, 2000, vii + 39pp.

Partridges, Quails, Francolins, Snowcocks, Guineafowl, and Turkeys. Status Survey and Conservation Action Plan 2000–2004. Edited by Richard A. Fuller, John P. Carroll, and Philip J.K. McGowan on behalf of the WPA/BirdLife/SSC Partridge, Quail, and Francolin Specialist Group, 2000, vii + 63pp.

Microchiropteran Bats. Status Survey and Conservation Action Plan. Compiled by Anthony M. Hutson, Simon P. Mickleburgh, and Paul A. Racey. IUCN/SSC Chiroptera Specialist Group, 2001, x + 258pp.

Antelopes. Part 4: North Africa, the Middle East, and Asia. Global Survey and Regional Action Plans. Compiled by D.P. Mallon and S.C. Kingswood. IUCN/SSC Antelope Specialist Group, 2001, viii + 260pp.

Equids. Zebras, Assess and Horses. Status Survey and Conservation Action Plan. Edited by Patricia D. Moelman. IUCN/SSC Equid Specialist Group, 2002, ix + 190pp.

Dolphins, Whales and Porpoises. 2002–2010 Conservation Action Plan for the World's Cetaceans. Compiled by Randall R. Reeves, Brian D. Smith, Enrique A. Crespo and Giuseppe Notarbartolo di Sciara. IUCN/SSC Cetacean Specialist Group, 2003, ix + 139pp.

Cycads. Status Survey and Conservation Action Plan. Edited by John Donaldson. IUCN/SSC Cycad Specialist Group, 2003, ix + 86pp.

West African Chimpanzees. Status Survey and Conservation Action Plan. Edited by Rebecca Kormos, Christophe Boesch, Mohamed I. Bakarr and Thomas Butynski. IUCN/SSC Primate Specialist Group, 2003, ix + 219pp.

European Bison. Status Survey and Conservation Action Plan. Edited by Zdzisław Pucek. Compiled by Zdzisław Pucek, Irina P. Belousova, Małgorzata Krasińska, Zbigniew A. Krasiński and Wanda Olech.IUCN/SSC Bison Specialist Group, 2004, ix + 54 pp.

Other IUCN/SSC Publications

IUCN Policies and Guidelines
Policies and Guidelines are published as booklets and offer scientifically-based conservation principles and guidelines to aid decision-making at both the global and national level.

Monographs (arranged by topic)
- CITES
- Crocodiles
- Educational Booklets on Mammals
- Marine Turtles
- Plants
- Trade
- Others

Occasional Papers Series
SSC Occasional Papers cover a broad range of subjects including conservation of groups of species in a particular geographical region, wildlife trade issues, and proceedings of workshops.

A more detailed list of IUCN/SSC publications is available from the SSC office, Rue Mauverney 28, CH 1196 Gland, Switzerland. Tel: +41 22 999 0000, Fax: +41 22 999 0015, E-mail: mcl@iucn.org

IUCN/Species Survival Commission

The Species Survival Commission (SSC) is one of six volunteer commissions of IUCN – The World Conservation Union, a union of sovereign states, government agencies and non-governmental organisations. IUCN has three basic conservation objectives: to secure the conservation of nature, and especially of biological diversity, as an essential foundation for the future; to ensure that where the Earth's natural resources are used this is done in a wise, equitable and sustainable way; and to guide the development of human communities towards ways of life that are both of good quality and in enduring harmony with other components of the biosphere.

A volunteer network comprised of some 8,000 scientists, field researchers, government officials and conservation leaders from nearly every country of the world, the SSC membership is an unmatched source of information about biological diversity and its conservation. As such, SSC members provide technical and scientific counsel for conservation projects throughout the world and serve as resources to governments, international conventions and conservation organisations.

IUCN/SSC Action Plans assess the conservation status of species and their habitats, and specifies conservation priorities. The series is one of the world's most authoritative sources of species conservation information available to natural resource managers, conservationists, and government officials around the world.

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