Status Survey and Conservation Action Plan

Hyaenas

Compiled by
Gus Mills and Heribert Hofer

IUCN/SSC Hyaena Specialist Group

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Executive Summary

Gus Mills

This Action Plan deals with the four living species of the carnivore family the Hyaenidae: the striped hyaena *Hyaena (Hyaena) hyaena*, the brown hyaena *Hyaena (Parahyaena) brunnea*, the spotted hyaena *Crocuta crocuta*, and the aardwolf *Proteles cristatus*. Notwithstanding their low species diversity, hyaenas are unique and vital components of most African and some Asian ecosystems. Being large carnivores they clash with the interests of humans to a greater extent than do many other groups of animals. Perhaps the most important challenge facing those of us committed to the conservation of this group of animals is to overcome the very strong negative feelings many people have towards hyaenas. Until they are viewed in a more positive light it will be difficult to effectively implement management plans for hyaenas.

To achieve our objective we have addressed what we consider to be the most important issues in hyaena conservation in 11 chapters plus six appendices and a comprehensive bibliography. The introductory chapter provides a synopsis of the Action Plan. In chapter 2 the taxonomy and systematics of living hyaenids is reviewed. It concludes that: a) the aardwolf should be included in the Hyaenidae family; b) the brown hyaena and striped hyaena are each other's closest relative; c) the case for subspecific distinction for the aardwolf is sound because of its disjunct distribution; d) the subdivision of striped hyaena into five subspecies should be maintained, although this needs to be reviewed.

Chapter 3 gives summaries of the major ecological and behavioural characteristics of each species. This is done to give the reader a basic insight into the biology of each and a glimpse of the complexities of their societies. In Chapter 4 the distribution of the four species is described, and in Chapter 5 population assessments, threats and the conservation status of each species are reviewed on a country by country basis. This fundamental information is needed before any kind of conservation action can be taken. Much of the information in Chapters 4 and 5 was obtained through a questionnaire survey circulated to over 250 prospective respondents, who were chosen because of their knowledge of the animals and/or local conditions in the distribution range of each species.

The species accounts are followed by Chapter 6 on the management of hyaenas in protected areas. This chapter is particularly relevant to the spotted hyaena as this species is most dependent on large conservation areas for its long term survival. Chapter 7 addresses the management of hyaenas outside conservation areas, where they frequently live in close contact with people. This is an important subject demanding innovative solutions. Survey and census techniques are reviewed in Chapter 8 because distribution and status surveys of hyaenas in many areas are badly needed. Chapter 9 addresses the question of captive breeding of hyaenas and analyses the role this can play in the conservation of the family members.

In light of the distorted public perception of hyaenas, Chapter 10 on education and public awareness is of particular importance, as it provides some guidelines to rectify this situation.

The final chapter (11) is the most important one. It discusses appropriate conservation approaches and suggests projects that could enhance the conservation status of the various members of the family. Of course discussing the actions is one thing, implementing them is quite another. It is up to the members of the Hyaena Specialist Group in conjunction with governments, conservation bodies in the relevant countries, NGOs, local communities, and others to initiate and implement the necessary projects and actions to improve the conservation status of these fascinating and important animals.

Appendix 1 is a preliminary Population and Habitat Viability Analysis (PHVA) for hyaenas. In this analysis the results of a study using simulations of population persistence are presented to assess the impact of various human actions on hyaena populations. Appendix 2 gives scientific names of mammals mentioned in the text, Appendix 3 lists the Hyaena Specialist Group Members, Appendix 4 lists the respondents to the questionnaire survey, Appendix 5 reprints the questionnaire for the survey and Appendix 6 describes the IUCN Red List Categories. Finally, the Action Plan ends with a hyaena bibliography including all references cited in the text.

Chapter 1

Introduction
Synopsis of the Action Plan

This Status Survey and Conservation Action Plan deals with the four living species of the family Hyaenidae: the striped hyaena *Hyaena (Hyaena) hyaena*, the brown hyaena *Hyaena (Parahyaena) brunnea*, the spotted hyaena *Crocuta crocuta* and the aardwolf *Proteles cristatus*. Hyaenas are important and influential components of most African and some Asian ecosystems. Unfortunately, human interests often conflict with those of hyaenas to a greater extent than with many other groups of animals, and as a result they suffer the effects of strong negative feelings towards them.

Chapter 2: Taxonomy and Systematics of Living Hyaenas (Family Hyaenidae)

A review of palaeontological studies and new data from a molecular study clarify a number of previously contentious issues in hyaenid systematics and taxonomy:

1. The aardwolf belongs to the family Hyaenidae; it is not appropriate to place it into a separate family.
2. The striped and the brown hyaena are each other's closest relatives.
3. The aardwolf diverged from other hyaenas about 15–32 million years ago, the spotted hyaena separated from the brown and the striped hyaena 10 million years ago, and the striped and the brown hyaena split six million years ago. As the generic rank of the striped and the brown hyaena continues to be unresolved, they are provisionally placed in the genus *Hyaena*. However, the long separation of the two lineages suggests that the two species should be placed into different subgenera, *Hyaena* (*Hyaena*) in the case of the striped and *Hyaena* (*Parahyaena*) in the case of the brown hyaena.
4. The case for subspecific distinction is stronger in the aardwolf than in the other three species because of its disjunct distribution. Provisionally two subspecies are retained: *P. c. cristatus* in southern Africa and *P. c. septentrionalis* in eastern Africa and north Africa.
5. On the basis of skull size, the five currently recognised subspecies of the striped hyaena probably form two larger groups, a northeast African-Arabian group composed of *Hyaena hyaena dubbah* and *H. h. sultana* and a northwest African-Asian group composed of *H. h. barbara*, *H. h. syriaca* and *H. h. hyaena*.
6. Neither the spotted hyaena nor the brown hyaena are currently recognised to have subspecies.

Chapter 3: Species Accounts

3.1 Aardwolf. This smallest member of the family is slightly larger than a jackal, with long, slender legs, a long neck, and a sloping back. It is considered an indicator species for the Somalia-Kalahari semi-desert axis and occurs in Africa in two discrete populations separated by wetter woodlands in Zambia and southern Tanzania. It feeds primarily on one local species of nasute harvester termite (genus *Trinervitermes*). It is a nocturnal, solitary forager, but socially monogamous; a mated pair occupying a perennial territory with their most recent offspring. Like all hyaenids, the aardwolf maintains its territory by means of depositing (pasting) secretions from the anal gland on grass stalks. The species is a seasonal breeder and mating takes place during the first two weeks of July. It is promiscuous, as dominant males often gain copulations with the females of subordinate males in neighbouring territories. The denning period lasts four months. In southern Africa the majority of aardwolves occur on farm land outside conservation areas. Here the greatest threat to the species comes from indirect poisoning aimed at periodic outbursts of locust plagues.

3.2 Striped hyaena. This medium-sized, dog-like animal has a sloping back and black vertical stripes on its sides. In most of its range it occurs in open habitat or light thorn bush country. In addition to scavenging carrion and the remains of kills of other predators, it feeds on a wide variety of vertebrate, invertebrate, vegetable, and human-associated organic matter. It may also kill large vertebrates including livestock, but records suggest that such attacks are rare. The least well studied of the hyaenas, it is nocturnal, a solitary forager, and lives in small groups of unknown composition. It is a non-seasonal breeder which prefers to den in caves. The striped hyaena has one to four cubs which are fed with meat carried back to the den by both sexes. Where they are sympatric, the striped hyaena is dominated by the spotted hyaena. Humans are the most important source of mortality. Striped hyaenas appear to be very susceptible to poisoning, as they will readily accept strychnine-poisoned bait.

3.3 Brown hyaena. This medium-sized, dog-like animal has a sloping back and a pelage that is shaggy and dark brown to black, except for the neck and shoulders, which are white. It is an inhabitant of the South West Arid Zone of Africa. Although primarily a scavenger of a wide range of vertebrate remains, it supplements its diet with wild fruits, insects, birds' eggs, and occasionally small animal prey. The impact of the brown hyaena on domestic animals is usually small. A nocturnal, solitary forager, it lives in clans ranging in size from a solitary female and her cubs, to groups containing several females and their offspring of different ages. Adult males either remain with their natal clan, leave their clan and become nomadic, or immigrate into a new clan. The brown hyaena is a non-seasonal breeder. Its den is normally a single hole in the ground, and it usually has only a single litter of one to four cubs, although two or more females may share a den in territories where more than one female breeds. For the first three months of their lives the cubs are nursed by their mother, after which the milk diet is increasingly supplemented with food carried to the den by all clan members. Where sympatric, the spotted hyaena is dominant over the brown hyaena and may have a detrimental effect on the latter's numbers and distribution in certain areas.

3.4 Spotted hyaena. This largest member of the family has a spotted coat and slightly sloping back. A particular feature of this species is that the secondary sexual organs are very similar in males and females. The female clitoris is of the same size and shape as the penis and she possesses pseudo-testes. The spotted hyaena inhabits semi-desert, savannah, open woodland, dense dry woodland and mountainous forest. It is a hunter-scavenger capable of killing large prey, which it runs down after a long and fast chase, often by hunting in groups. Highly social, it lives in clans of up to 80 individuals in a society characterised by a strict dominance hierarchy. Females are dominant over males, and even the lowest ranking female is dominant over the highest ranking male. Females usually remain in their natal clan, while males disperse at about two and a half years of age. Its highly social nature has led to the evolution of a wide variety of vocalisations. It is a non-seasonal breeder and the one to two cubs per female are kept at a communal den and suckled by their mother until they are about a year old. Unlike the brown and striped hyaenas the adults do not carry food to the den. The spotted hyaena's major competitor is the lion. Humans are the most important source of mortality, through persecution and meat poaching with snares. The most important natural source of mortality is predation by lion and conspecifics.

Chapter 4: World-wide Distribution of Hyaenas

Information on the occurrence and distribution of the four extant hyaena species was extracted from the literature, while individual records were obtained from members of the Hyaena Specialist Group and other knowledgeable people, as well as the respondents to the Hyaena Action Plan questionnaire. In most cases only records made since 1970 were considered. Maps summarising distribution records on a one-degree grid system were prepared. With the new form of government and constitution in South Africa the provincial system has been revised. The old four-province system with "independent" homelands has given way to a nine-province system. Since the questionnaire survey and most of the relevant literature from South Africa refer to the old four-province system, we have decided to follow this system for the purposes of analysing the regional status of the relevant hyaenids.

4.1 Aardwolf. The aardwolf occurs in two discrete populations (Fig. 4.1). The southern population ranges over most of southern Africa, extending into southern Angola, southern Zambia and southwestern Mozambique. A 1,500km gap occurs between this population and the northern one which extends into central Tanzania, to northeastern Uganda, Somalia and parts of Ethiopia, then narrowly along the coast of Eritrea and Sudan, to the extreme southeast of Egypt.

4.2 Striped hyaena. The distribution of the striped hyaena is now patchy in most places (Fig. 4.7), suggesting that it occurs in many small isolated populations. This is particularly so in most west African countries, most of the Sahara desert, parts of the Middle East, the Caucasus, and central Asia. It has a continuous distribution over larger areas in Ethiopia, Kenya, and Tanzania. The current distribution pattern is virtually unknown for Pakistan, Iran and Afghanistan, where it may be more widespread than current records indicate.

4.3 Brown hyaena. The brown hyaena is confined to southern Africa where it is still widespread, particularly in the drier western parts of the region (Fig. 4.19).

4.4 Spotted hyaena. The distribution of the spotted hyaena is now patchy in many places, especially in West Africa (Fig. 4.22), with populations concentrated in protected areas and surrounding land. It still enjoys continuous distributions over large areas in Ethiopia, Kenya, Tanzania, Botswana, Namibia, and the Transvaal Lowveld areas of South Africa.

Chapter 5: Population Size, Threats and Conservation Status of Hyaenas

From the questionnaire survey and published and unpublished studies, the total world population sizes of striped, brown, and spotted hyaenas were estimated within each range country. This was not done for the aardwolf because of a lack of data. The results are summarised for the striped hyaena in Table 5.2, the brown hyaena in Table 5.4, and the spotted hyaena in Table 5.6. These estimates provide a first approximation of the order of magnitude of the likely population sizes. The main threats as well as the historical and current country-specific threats facing each species are discussed.

An assessment of the conservation status of each species in each country was made. Using the 1994 IUCN Red List Categories (Appendix 6) as the basis for a simplified list of categories, the national status of each species was assessed (Fig 5.1, Box 5.2).

5.1 Aardwolf. Although the aardwolf may be harvested as a food source and is purposefully or accidentally killed in predator control programmes, these mortalities appear to be of little significance in areas with well established populations. The greatest threat to the aardwolf is from spraying poisons on swarms of locusts, which it eats. The Population and Habitat Viability Analysis (Appendix 1) suggests that aardwolf populations are likely to tolerate many factors, yet population isolation may have a more detrimental effect on population viability than other factors.

Although there is little information from most northern range states, the overall status of the aardwolf is currently described as **Lower Risk: Least Concern**.

5.2 Striped hyaena. Evidence suggests that the striped hyaena is already extinct in many localities and that populations are generally declining throughout its range. The striped hyaena evokes many superstitious fears, and is widely exploited as an aphrodisiac as well as for traditional healing. It is also killed because of suspected or real damage inflicted on agricultural crops and livestock. A tentative estimate of the total world-wide population size is 5,000 to 14,000 individuals (Table 5.2).

Fragmentation of the world population into many subpopulations is suspected although the actual degree of fragmentation, rate of habitat loss and population decline are unknown. A minimum population estimate is less than 10,000 individuals. This suggests that the present classification of Lower Risk: Least Concern is now inappropriate. We therefore suggest that the status be changed to **Lower Risk: Near Threatened.**

5.3 Brown hyaena. Because of its secretive nature and nocturnal habits, the brown hyaena, like the striped hyaena, is not easy to encounter and is often overlooked; even in stock farming areas. Poisoning, trapping and hunting have had a detrimental effect on populations and are a threat to the species in some areas. Intolerance and ignorance by commercial stock farmers in Namibia, South Africa and Zimbabwe have led to the killing of many non-harmful individuals. Although used in traditional medicine and rituals, it is not nearly so sought after in this regard as the spotted hyaena. It also has very little demand as a trophy. The Population and Habitat Viability Analysis (Appendix 1) suggests that deterioration of habitat quality (i.e. a decline carrying capacity of the habitat) is the most important factor for population viability.

A tentative estimate of the total world-wide population is a minimum of between 5,000 to 8,000 individuals (Table 5.4). Because the global population size is estimated to be below 10,000 and the species is prone to deliberate and incidental persecution, it is no longer appropriate to classify the brown hyaena as Lower Risk: Least Concern. Therefore, it is recommended that the status be changed to **Lower Risk: Near Threatened.**

5.4 Spotted hyaena. Viable populations still exist in a number of countries and the total world population is calculated at between 27,000 and 47,000 (Table 5.6).

The spotted hyaena has been and still is widely shot, poisoned, trapped and snared, even inside some protected areas. Persecution most often occurs in farming areas after confirmed or assumed damage to livestock, or as a preventative measure to protect livestock. Most populations in protected areas in southern Africa are considered to be stable, whereas populations in eastern and western Africa, including in protected areas, are considered to be declining, mostly due to incidental snaring and poisoning. The Population and Habitat Viability Analysis (Appendix 1) suggests that both a decline in habitat quality (i.e. carrying capacity) and population isolation would detrimentally affect the viability of spotted hyaena populations.

The total world population size of the spotted hyaena is well above 10,000 individuals, with several subpopulations exceeding 1000 individuals, and its range is well over $20,000km^2$. Despite these figures, the rapid decline of populations outside conservation areas due to persecution and habitat loss makes the species increasingly dependent on the continued existence of protected areas. We therefore agree with the latest classification of the spotted hyaena as **Lower Risk: Conservation Dependent.**

Chapter 6: Role and Management of Hyaenas in Protected Ecosystems

Management plans for protected areas should take the presence of hyaenids into account, as they are important elements in ecosystems. This is particularly true given the fact that the effects of hyaenas on other species cause many problems.

6.1 Interactions with prey species. The spotted hyaena is the only hyaenid species which has the potential to play an important role in population regulation of ungulates. Whether this potential is realised in any given area depends on many factors. Before conclusions can be drawn about its regulatory role in any particular area a detailed study is required.

6.2 Effects of prey on hyaenids. Variation in prey populations have been shown to affect diet, foraging behaviour and success, population density and composition, social dynamics, reproduction, and spatial and social organisation in hyaenids.

6.3 Competition with other carnivores. In the management of protected areas, the competition between spotted hyaenas and species of special concern, such as cheetah, wild dog, leopard and lion should be taken into account.

Competition between the various species of hyaenas may also be important. For example, the spotted hyaena is dominant over other hyaenas and possibly affects the density and distribution of the striped and brown hyaenas in some areas.

6.4 Major management considerations

1. Of all hyaena species, the spotted hyaena is most in need of attention within protected areas. Because of its dependence on protected areas of high productivity, it is arguable that the spotted hyaena is the species presently most likely to become extinct. Threats of disease (especially rabies) should be closely monitored, and if necessary, immunisation should be considered. Similarly, threats from poachers (snaring, trapping, shooting) should be taken seriously.
2. There is a need for bringing the scientific interest and the ecological role of hyaenas to the attention of decision makers and the public. Scientists should play an important role in this.
3. Before interfering with any interactions between populations of hyaenas and their prey, a detailed study should be carried out to establish likely consequences. Much more information and research is needed about the effects of hyaenids on prey populations and vice versa.

Chapter 7. Hyaenas Living Close to People: Predator Control, Attacks on People and Translocations

7.1 Predator control. The spotted hyaena is most often implicated in stock losses, although both the brown hyaena and the striped hyaena may also be involved at times. The aardwolf is exclusively an insect eater.

Predator control is an essential management practice in stock farming areas. However, the aim should be to seek methods to reduce predator damage, rather than to increase predator mortality. Where it is necessary to reduce hyaena numbers in a particular area, shooting is the best way; the generalised use of poisons is the worst as this method is unselective. The cost of control should not exceed losses through predation.

It is difficult to reconcile the conservation of spotted hyaenas with commercial stock farming. In less developed agricultural areas and on game ranches where spotted hyaenas still survive, the management emphasis should be on damage control. The brown hyaena and the striped hyaena are less likely to kill large domestic stock and should be able to co-exist with humans. Research is needed on how farmers can obtain maximum ecological benefits from hyaenas. Once effective measures have been developed they need to be properly implemented through education and training campaigns.

7.2 Compensation. The question of paying compensation for livestock losses as a way of encouraging land owners or local communities to tolerate the presence of predators needs to be carefully considered. It may be an effective tool when properly instituted and not abused.

7.3 Attacks on humans. Hyaenas will eat humans, but most of the victims are people sleeping outside at night, – usually children. Traditionally, many African tribes put corpses out in the bush for spotted hyaenas to dispose of.

7.4 Translocation. Instead of killing carnivores in areas where they are regarded as a nuisance, they may be caught and translocated to conservation areas. However, the relocation of large carnivores is a complicated management procedure. A translocation should only be attempted if a species is extinct in an area, the causes of its extinction are known and rectified in the new area, and conditions to support a viable population are available. Furthermore, the genetic consequences must be considered. With social carnivores like spotted hyaenas, mixing animals from different groups further complicates the problem. Whenever a translocation is carried out, adequate follow up observations to assess the success of the exercise are essential.

Chapter 8: Survey and Census Techniques for Hyaenas

It is important to be able to assess the status and distribution of animals and to monitor population trends, especially in the case of rare or endangered species. Several methods can be used.

8.1 Questionnaire Surveys. Questionnaire surveys have been used as a first step in documenting the status and distribution of a species. Questionnaires have the advantage of reaching a large number of people, of covering a large area (i.e. several continents), and are relatively inexpensive. However, the amount and quality of information that is accumulated is limited and usually inadequate.

8.2 Extrapolation. Population densities by extrapolation have been calculated for a range of species including hyaenas. This is done by making observations of home range and group size from known or radio collared individuals and extrapolating these over a defined area. The data used are usually obtained during studies not primarily concerned with monitoring population trends.

8.3 Line transects. A daytime line transect survey was used to census spotted hyaenas on the short grass plains of the Serengeti. The high density of hyaenas on the plains at this time and the extreme openness and flatness of the habitat make this area one of the few places in the world where it is possible to obtain reasonable data on hyaena population densities by this method.

8.4 Lincoln index. The Lincoln index, a mark-recapture method, is a widely used and most helpful method for estimating animal abundance. Several workers have successfully used a modified Lincoln index for censusing spotted hyaenas in different habitats. It could be used on other hyaena species as well, although species which live at low densities will require a high level of effort to obtain an adequate number of resightings of marked animals. However, most users of the Lincoln index have only produced a population estimate without calculating a variance. This makes it difficult to compare census estimates.

8.5 The use of sound. Spotted hyaenas have been surveyed by playing amplified tape recordings of sounds that are known to attract spotted hyaenas to calling stations. From experiments to measure the response of hyaenas to these sounds, a probability model can be used to estimate the expected number of hyaenas per unit area. The possibility of using sound to attract brown and striped hyaenas exists, but because of their solitary habits and generally low densities, this method is only likely to produce satisfactory results with intensive sampling, or in areas where the species occur in unusually high densities.

8.6 Identification of individuals. It is possible to use physical characteristics such as pelage patterns, nicks in ears, etc., to identify individuals and to build up a reference collection of animals in a particular area. In this way an idea of the population numbers may be obtained.

8.7 Tracks and signs. It is also possible, under very special conditions, to identify individual animals by their tracks. Where the substrate allows, a less ambitious application of this technique might be the conducting of an initial survey by driving along a transect and counting the number of tracks crossing it. The prominent white scats left by hyaenas are another useful sign for documenting relative densities, or at least the presence of hyaenas, although differentiating between species and between hyaenids and feral dogs is difficult.

Chapter 9: Hyaenids in Captivity and Captive Breeding: Aims and Objectives

Although hyaenas have been commonly kept in captivity, they have often not been kept well and are now facing "extinction" in many of the world's captive collections. As competition for cage space increases hyaenids are losing out to large felids and canids. Although they are easily kept in captivity, propagation in zoos has been limited.

9.1 ISIS data. Data contained within the International Species Information System (ISIS) revealed that there are approximately 145 living hyaenas and 40 aardwolves within participating zoos. If 25% of the world's captive wildlife within the world's 1100 zoos is entered into ISIS, then there is a conservative possibility of 300 spaces for hyaenas, and 100 spaces for the aardwolf in zoos world-wide.

9.2 Extant programs. The level of regional and international captive management programs for hyaenids is low in comparison to other carnivore families. Hyaenas are included within the American Zoo and Aquarium Association's (AZA) Canid and Hyaena Taxon Advisory Group (TAG), because of the similarity of husbandry needs for both families.

9.3 North American cage space allocation. The AZA Canid and Hyaena TAG's Conservation Assessment Management Plan (CAMP) recommended that existing hyaena and aardwolf spaces be divided between aardwolves and spotted hyaenas and that brown and striped hyaenas should be phased out of AZA zoos and other collections in North America through natural attrition.

9.4 International captive objectives. The CAMP's recommendations for captive management of hyaenid species world-wide are that the brown hyaena should be managed as a Nucleus I species (a captive nucleus of 50-100 individuals to represent 98% of the wild gene pool), and that the other three species should be managed as Nucleus II species (a captive nucleus of 25–100 individuals of taxa either of little conservation concern, or pending review of population estimates). However, the north

African subspecies of the striped hyaena should be managed as 90/100 I species (a population sufficient to preserve 90% of the average genetic diversity of the wild gene pool) if founders become available. These programs should preferably be undertaken by zoos within the species' natural range.

Chapter 10: Cultural and Public Attitudes: Improving the Relationship between Humans and Hyaenas

One of the aims of this action plan is to promote a better understanding of the four existing hyaena species. This is a major task given the ingrained prejudices that exist towards hyaenas in many cultures.

10.1 Cultural significance of hyaenas: many cultures, many views. Hyaenas are important animals in many cultures. They are frequently associated with witchcraft; their body parts are used as ingredients in traditional medicinal treatments and they are viewed with contempt and fear. They are thought to influence people's spirits, snatch children, rob graves, and steal livestock.

10.2 Attitudes. Official attitudes towards hyaenas vary widely among countries. There is often a discrepancy between the legal classification of a species and the attitude displayed towards it by officials.

Neutral or negative attitudes to the various hyaena species dominate amongst people living in close contact with hyaenas. A key issue for farmers is the loss of livestock due to predation by hyaenas. Farmers assume that the predators feeding on a carcass are the ones that made the kill. Thus they sometimes mistakenly assign responsibility for livestock losses to predators that are incapable of killing livestock, such as the aardwolf and, in the case of large livestock, the brown hyaena.

Tourists also do not rate hyaenas very highly and they still suffer from a bad public image. Appropriate education and encounters with hyaenas in the wild might improve attitudes.

Articles in the press and television films can have an enormous impact on a large number of people. Unfortunately, even recently, some wildlife film makers have presented incorrect information about hyaenas. Other films feed on the combination of ignorance and prejudices that have dominated the views of western people about hyaenas for a long time. On the positive side, Hyaena Specialist Group members have been quite active in recent years and a number of popular articles in a variety of magazines and countries have contributed to portraying a more accurate picture of hyaena behaviour. Scientifically accurate, interesting films on hyaenas are also beginning to be made.

10.3 A campaign to modify current attitudes. In spite of some progress, prejudices rather than knowledge about hyaenas still dominate the views of many people. Many common prejudices could be overcome if the behaviour and ecology of hyaenas was more widely appreciated. There is still a need for scientists working on hyaenas to communicate their research findings through popular articles and books. There is also a need for concerted education campaigns through the use of fact sheets, displays and posters, and films and videos.

Chapter 11: Action Plan for Hyaenid Conservation into the 21st Century

The data collected during the compilation of the Action Plan suggest that of the four hyaenid species the striped hyaena is the one in most need of conservation attention. It is also the least well studied of the four species. The spotted hyaena is also in need of conservation attention in many countries and its future mainly depends on the maintenance of large conservation areas.

The following are priority projects and actions for hyaena conservation over the next ten years, as well as ongoing projects:

11.2 Projects and actions involving all species

Database

1. (Project). Establish and maintain a database on the conservation status and state of knowledge of the four hyaena species.

Status surveys

2. (Project). Design a data sheet for basic surveys of hyaenids and distribute it as widely as possible to improve knowledge of the distribution and conservation status of each species.
3. (Action). Encourage and provide assistance to wildlife researchers and managers to collect data on the population status of hyaenids in all range states, particularly those in which the status of a population is Threatened or Data Deficient (see Table 5.8).

Education and public relations

4. (Action). Produce a Hyaena Specialist Group Newsletter at least once every two years.
5. (Action). Initiate a campaign through IUCN and other NGOs to establish a policy of limiting or reducing damage to livestock by wild carnivores, by concentrating efforts on improving livestock protection rather than implementing control of predators.
6. (Action). Reprint and update the colour poster "Why conserve hyaenas?". Investigate the possibility of translating it into other major range state languages

and prioritise these. Circulate it as widely as possible.

7. (Project). Investigate methods for initiating effective education campaigns directed at local people to explain the ecological role of scavengers in key areas, ways of lessening pastoralist/predator conflicts and ways to prevent possible attacks of hyaenas on people.
8. (Project). Review the relationship between rural people and hyaenas.
9. (Action). Initiate and support efforts to improve public perceptions of hyaenas.
10. (Action). Promote hyaenas as tourist attractions, particularly where this might generate revenue for local communities. To this end, investigate the possibility of setting up of feeding sites (hyaena restaurants), particularly in urban or semi-urban areas, and encouraging people to visit these in order to view hyaenas.
11. (Project). Identify and assess the effects of incentives on hyaeana conservation.

11.3 Species projects and actions

Striped hyaena

12. (Action). Update the IUCN global status of the striped hyaena from Lower Risk: Least Concern to Lower Risk: Near Threatened.
13. (Project). Assess the potential viability of striped hyaena populations in countries where the population is classified as Threatened and Data Deficient.
14. (Action). Campaign for increased protection of the striped hyaena throughout its range. Wanton killing of this species should be banned in those countries where it occurs.
15. (Project). Review the classification of the subspecies of the striped hyaena and the distribution and status of each.
16. (Project). Document basic aspects of the population dynamics of the striped hyaena.
17. (Project). Investigate the diet and foraging behaviour of the striped hyaena.
18. (Project). Conduct a behavioural and ecological study of the striped hyaena.

Brown hyaena

19. (Action). Change the global status of the brown hyaena from Lower Risk: Least Concern to Lower Risk: Near Threatened.
20. (Project). Survey the status and distribution of the brown hyaena in the urban areas of Gauteng Province in South Africa.

Spotted hyaena

21. (Action). Change the global status of the spotted hyaena from Lower Risk: Least Concern to Lower Risk: Conservation Dependent.
22. (Project). Assess the potential viability of spotted hyaena populations in countries where the population is Threatened and Data Deficient.

11.4 Currently running projects

Striped hyaena

23. (Project). Assessment of the status of the striped hyaena in Georgia and bordering territories, and a program for its recovery.

Brown hyaena

24. (Project). Foraging behaviour of brown hyaenas at seal colonies on the Namibian Coast.

Spotted hyaena

25. (Project). Behavioural ecology and population dynamics of spotted hyaenas in the Serengeti, Tanzania.
26. (Project). Behavioural ecology of spotted hyaenas in the Ngorongoro Crater, Tanzania.
27. (Project). Long-term ecological monitoring of a hyaena clan in the Masai Mara National Reserve, Kenya.
28. (Project). Behavioural endocrinology of free-living spotted hyaenas.
29. (Project). Behavioural development in the spotted hyaena.
30. (Project). The evolution of intelligence in response to social complexity.
31. (Project). A multidisciplinary investigation of the proximate mechanisms of female masculinization in the spotted hyaena.
32. (Project). The behavioural ecology of the spotted hyaena in a high density population in southwestern Kenya.
33. (Project). The Laikipia Large Carnivore Study

Chapter 2

Taxonomy and Systematics of Living Hyaenas (Family Hyaenidae)

Susan M. Jenks and Lars Werdelin

2.1 Introduction

The Hyaenidae is the least diverse of the living carnivore families, with a mere four extant species placed in three or four genera. Despite this, there has historically been considerable controversy regarding some aspects of their taxonomy and systematics (Fig. 2.1). This is particularly the case with regard to the aardwolf, *Proteles cristatus*, whose specific relationship to the other species in the family Hyaenidae has been subject to regular scrutiny.

Hyaenas are very common in the fossil record; they were the dominant carnivores in the Middle and Upper Miocene of Eurasia. They also presented quite a different ecological picture than modern hyaenas do, with the majority of forms being generalised, dog-like carnivores rather than the hunter-scavenger and bone-cracker forms of today. The fossil record of hyaenas has recently been extensively revised by Werdelin and Solounias (1991, 1996). The fossil record indicates that the splits between the lineages leading to the extant forms are all old, some going back at least to the early Late Miocene, more than nine million years ago.

2.2 Phylogenies: hypotheses

The striped hyaena was the first hyaenid species described by Linnaeus (*Canis hyaena*, 1758). It was subsequently recognised as belonging to a new genus *Hyaena* by Brisson (1762). Linnaeus thus established the existence of morphological similarities between hyaenas and canids very early, and although subsequent studies have demonstrated that hyaenas are feloids, the similarities between hyaenas and canids indicate morphological convergence in a suite of characters. Linnaeus' description of *Hyaena hyaena* was followed by descriptions of the spotted hyaena as *Canis crocuta* by Erxleben (1777), the aardwolf as *Viverra cristata* by Sparrman (1783) and the brown hyaena as *Hyaena brunnea* by Thunberg (1820). The genus *Crocuta* for the spotted hyaena was established by Kaup (1828), and the genus *Proteles* for the aardwolf by Geoffroy (1824). The first fossil hyaenid taxon was described by Croizet and Jobert (1828).

In subsequent decades, many new hyaena species were named that are now recognised as synonyms of the four species of hyaenids living today, although occasionally the striped hyaena is still referred to as *Hyaena striata* instead

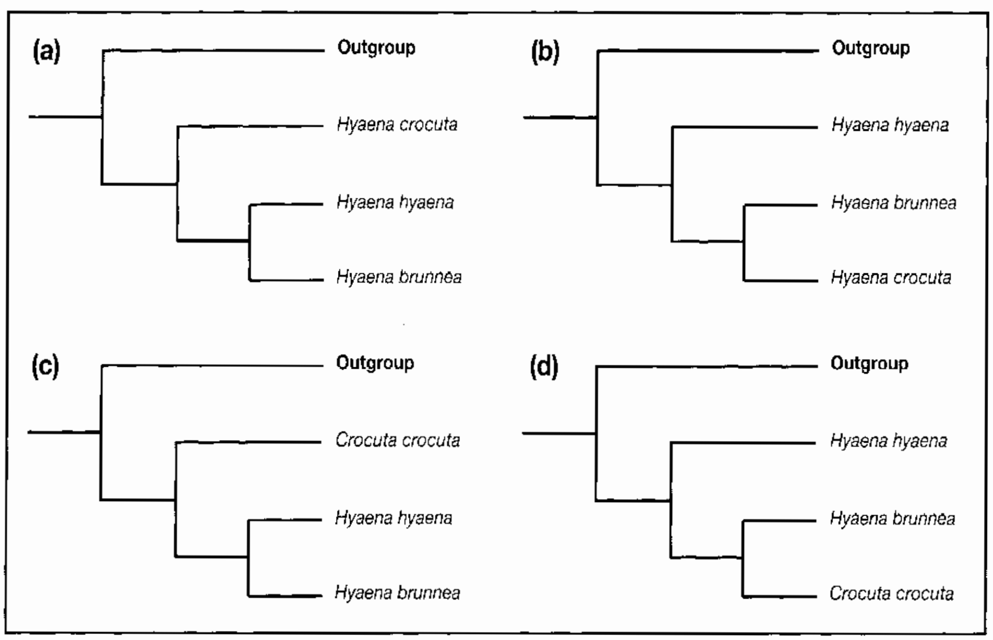


Figure 2.1. Hypotheses of interrelationships between extant species of Hyaenidae proposed during the past century. The original schemes included fossil taxa. These have been removed from the trees shown here. **(a)** Hypothesis of Gaudry (1862–1867). **(b)** Hypothesis of Schlosser (1890). **(c)** Hypothesis of Pilgrim (1932). **(d)** Hypothesis of Galiano and Frailey (1977).

of *Hyaena hyaena*. Systematic zoologists concluded that *Hyaena hyaena* and *Hyaena brunnea* were closely related and that these two in turn were related to *Crocuta crocuta*. *Proteles cristatus* was seen as a very distant relative of the other three species and was often placed in a subfamily (Protelinae) or even family (Protelidae) of its own. With this scheme firmly established, zoologists largely abandoned the study of hyaenid systematics, leaving it to palaeontologists to classify fossil hyaenid forms and to consider the taxonomic relationship of fossil and extant forms. Box 2.1 describes the historical development of the major hypotheses by palaeontologists over the past 100 years regarding the phylogenetic relationships between *H. hyaena*, *H. brunnea* and *C. crocuta*. These may be summarised in the following way:

1. *H. hyaena* and *H. brunnea* are closely related, as has always been suggested by zoologists, and should be placed in the same genus.
2. *H. brunnea* is more closely related to *C. crocuta* than either is to *H. hyaena*. A consequence of this second hypothesis is that *H. hyaena* and *H. brunnea* should be placed in distinct genera, although not a single author went this far in their taxonomies.
3. The lineages leading to *H. hyaena* and *H. brunnea* have been distinct since the Upper Miocene and therefore deserve distinct genus-level names, regardless of their relationship to each other or to *Crocuta crocuta*.

Box 2.1. The three hypotheses of phylogenetic relationships amongst extant hyaenas.

Over the past 100 years, paleontologists advanced a variety of phylogenetic schemes on the relationship between *H. hyaena*, *H. brunnea* and *C. crocuta*. They can be categorised as belonging to one of three hypotheses.

The first study presenting a phylogeny of hyaenas was that of Gaudry (1862–1867). His cladogram (Fig. 2.1a) expressed the standard pattern of phylogenetic relationships between the four extant species as reflected in the zoological nomenclature, with *H. hyaena* and *H. brunnea* being more closely related to each other than either is to *C. crocuta*. Pilgrim (1932) continued with Gaudry's idea of *H. hyaena* and *H. brunnea* being closely related but separated *C. crocuta* as a distant relative of these two (Fig. 2.1c). Like Pilgrim (1932), Ewer (1955) considered *H. hyaena* and *H. brunnea* to be closely related. Thenius (1966) agreed with the close relationship between *H. hyaena* and *H. brunnea* and the exclusion of *C. crocuta*, although he considered *H. hyaena* and *H. brunnea* to be more distantly related than either Pilgrim (1932) or Ewer (1955).

The second hypothesis was first proposed by Schlosser (1890) who argued that *H. brunnea* is more closely related to *C. crocuta* than either is to *H. hyaena* (Fig. 2.1b). Schlosser (1890) also thought that either *H. brunnea* or *C. crocuta* or both are closely related to the large Plio-Pleistocene Eurasian hyaenas, *Pliocrocuta perrieri* and *Pachycrocuta brevirostris*. Galiano and Frailey (1977) published the first explicitly cladistic analysis of hyaenid phylogeny. They returned to Schlosser's hypothesis that *H. brunnea* is more closely related to *C. crocuta* than it is to *H. hyaena* (Fig. 2.1d), but retained the congeneric status of *H. hyaena* and *H. brunnea*, and a separate genus for *Crocuta*.

Hendey (1974) did not comment on the relationship of *H. hyaena* and *H. brunnea* to *C. crocuta* but suggested that *H. hyaena* and *H. brunnea* were only distantly related. He placed *H. brunnea* into a new subgenus called *Parahyaena*.

2.3 Phylogenies: morphological and palaeontological data

Werdelin and Solounias (1990, 1991) have addressed the issue of hyaenid interrelationships from a palaeontological and morphological perspective. Despite a thorough survey of the skull, dentition and selected areas of the postcranial skeleton, very few phylogenetically informative characters were found. This is because most characters with more than one character state within the Hyaenidae are uniquely derived features of *C. crocuta* (mainly using *P. cristatus* as the outgroup). The highly autapomorphic nature of this species is what lies at the heart of traditional classifications of hyaenids into the genera *Proteles*, *Hyaena*, and *Crocuta*. The two species of *Hyaena* are then grouped together because they look much more similar to each other than either does to *C. crocuta*. However, modern theory shows that similarity *per se* is not a sufficient indicator of phylogenetic relationships, and therefore we must instead look for shared derived characters, of which there are very few in the morphology of hyaenas.

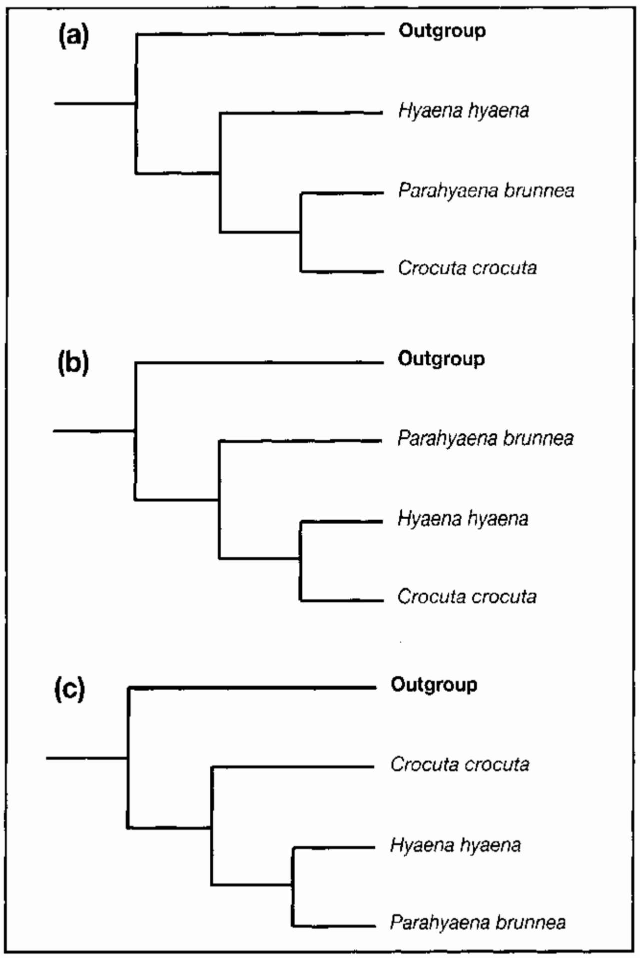
The study by Werdelin and Solounias (1991) took two approaches. In the first, an attempt was made to polarise characters on an *a priori* basis, using various types of information, including outgroup and ontogenetic. This yielded the following results:

- The shortest of the three possible rooted trees for *H. hyaena*, *H. brunnea*, and *C. crocuta* is that which unites *H. brunnea* and *C. crocuta* as sister taxa. This tree is 28 steps long and had the following characters as synapomorphies of *C. crocuta* and *H. brunnea* (for character definitions, see Werdelin and Solounias 1991): M1 reduced, P4 metastyle long, supramastoid crest strong, overlap between atlas and axis long.
- The second best tree is that which unites *C. crocuta* and *H. hyaena* as sister taxa, with the following synapomorphies: anterior position of the infraorbital foramen, scapular spine straight in caudal view.
- The third tree, which has the traditional topology with *H. brunnea* and *H. hyaena* as sister taxa, is the poorest (31 steps) and has only one synapomorphy for these taxa: presence of a second inferior oblique muscle fossa at the maxillary-lacrimal-frontal juncture.

In the second approach, Werdelin and Solounias (1991) explicitly introduced *P. cristatus* as the outgroup. This led to a reduced data set, as many dental characters are not applicable to the latter taxon. The results showed that:

- The trees with either *H. brunnea* or *H. hyaena* as sister taxon to *C. crocuta* are equally long, 32 steps (Fig. 2.2a,b). Synapomorphies uniting *C. crocuta* and *H. brunnea* were: supramastoid crest strong, overlap between atlas and axis long. Synapomorphies uniting *C. crocuta* and *H. hyaena* were: anterior position of infraorbital foramen, presence of premaxillary-frontal suture, scapular spine straight in caudal view.
- The poorest tree (Fig. 2.2c, 33 steps) was once again the traditional one with *H. brunnea* and *H. hyaena* as sister taxa. The synapomorphies uniting these two taxa were: presence of a second inferior oblique muscle fossa at the maxillary-lacrimal-frontal juncture, premaxillary-maxillary suture near the middle of the incisive fossa.

Figure 2.2. Results of morphological studies of hyaenid interrelationships as detailed in Werdelin and Solounias (1991).
TL indicates tree length; CI indicates consistency index.
(a,b) Equally parsimonious hypotheses (TL=32, CI=0.76).
(c) Least parsimonious hypothesis (TL=33, CI=0.72).



Thus, these morphological studies of hyaenas are not conclusive. If anything can be suggested by these studies, it is that the traditional scheme of including two species within the genus *Hyaena* is the least supported. Topologies with either *H. hyaena* or *H. brunnea* as the sister taxon to *C. crocuta* are about equally supported. Even when data from fossils are added, it is difficult to choose between these two competing hypotheses of relationships, although perhaps *H. brunnea* is slightly better supported as a sister taxon to *C. crocuta* (Werdelin and Solounias 1991). As a consequence of these results, Werdelin and Solounias (1991) elevated *Parahyaena* to generic rank and classified the brown hyaena as *Parahyaena brunnea*.

In summary, the most recent morphological studies indicate that *P. cristatus* is unambiguously placed as the sister taxon to the other three living hyaenas. The studies do not exclude any specific hypothesis on the relationships between the other three species. The least support was generated for the traditional hypothesis of a close relationship between the striped and brown hyaena. This analysis and stratigraphic data strongly indicate that regardless of the exact interrelationships between the extant hyaenas, the lineages leading to them split well down into the Miocene. Such deep splits would tend to confirm the distinct generic status of the living forms.

2.4 Phylogenies: molecular data

In a further attempt to resolve the evolutionary relationships amongst extant hyaena species, we have sequenced 1140 base pairs of the mitochondrial DNA cytochrome b genes from all four species. Mitochondrial DNA (mtDNA) has been used extensively in molecular phylogenetic studies as a tool to ascertain the relationships among species, populations and individuals. The cytochrome b gene has proven useful for investigating the relationships of organisms over a wide range of divergence times and appears to be particularly useful for divergences less than 50 million years old (Wilson *et al.* 1985, Moritz *et al.* 1987, Irwin *et al.* 1991). Additionally, cytochrome b is a protein coding gene with well-defined structure-function relationships, enhancing alignment and subsequent evolutionary analyses (Irwin *et al.* 1991). Box 2.2 describes the sources of tissue samples and the molecular methods employed in this analysis.

The cytochrome b sequences yielded 163 informative sites (characters of which at least two nucleotides are

Box 2.2. Molecular methods.

The DNA of two individuals of each hyaena species was extracted and sequenced for this study. Samples were obtained courtesy of the FSBR hyaena project, UC-Berkeley: *C. crocuta* (blood) and CRES, the San Diego Zoological Park: *H. hyaena* (cells), *H. brunnea* (spleen/liver) and *P. cristatus* (spleen/liver). CRES, the San Diego Zoological Park, also provided DNA samples from a civet (*Nandinia binotata*) and binturong (*Arctictis binturong*) as outgroup taxa.

Hyaena DNA was extracted by the standard proteinase K, phenol-chloroform methods. DNA was amplified by the polymerase chain reaction (PCR) using universal primers (Kocher *et al.* 1989; Meyer and Wilson 1990; Irwin *et al.* 1991). PCR products were purified and were directly sequenced using either a manual double-stranded sequencing protocol with Sequenase (USB) and/or by cycle sequencing using Taq polymerase and an ABI automatic sequencer (Model 377). Preliminary outgroup sequences from the civet and the binturong were obtained by PCR and direct manual sequencing of cloned products.

Complete cytochrome b sequences for the additional outgroups: cat (*Felis catus*) and harbour seal (*Phoca vitulina*) were obtained from genbank (accession numbers: X82296 and X82306 respectively). Partial meerkat (*Suricata suricatta*) sequence, also used as an outgroup, was obtained from genbank (accession number: D28 906). The 1140 base pair sequences from each species were aligned to each other for direct comparison of sequence differences. All sequences were aligned by eye. The aligned sequences were then subjected to phylogenetic analyses using the computer programs PAUP 3.1.1 (Swofford 1993) and MacClade 3.0 (Maddison and Maddison 1992). We used the exhaustive search parsimony algorithm in PAUP to create phylogenetic trees. A single tree resulted from each search using this algorithm.

represented at least twice each). The spotted hyaena sequence was more similar (lower percent sequence divergence) to the striped and brown hyaena sequences than to the aardwolf sequence, and the aardwolf sequence was more similar to the spotted than to the striped or brown (Table 2.1).

The most significant result to emerge from the parsimony search algorithm for a phylogenetic tree is the grouping of the striped hyaena with the brown hyaena. Fig. 2.3a shows the single most parsimonious tree derived from the cytochrome b sequence data. The brown and striped hyaenas are placed as a sister group to a clade uniting the spotted hyaena and aardwolf. The tree length is 566 steps; altering the tree topology to unite the brown and spotted or to unite the striped and spotted hyaenas results in longer trees (592 and 594 steps respectively). Note that the bootstrap value for the brown/striped clade is 100%. The grouping of the spotted hyaena and aardwolf is most likely due to "long lineage" (branch) effects in parsimony analysis. Such effects can result from homoplasy (similarity not due to common ancestry, such as when a character state evolves more than once in different branches of the tree) in lineages that have been separate for some time. Adding additional outgroup information, especially from closely related groups, may eliminate the long lineage effect. However, adding 402 base pairs of meerkat cytochrome b sequence and 1140 base pairs of preliminary viverrid sequence (civet) did not significantly alter the tree topology.

DNA code is read in triplets of bases, and mutations at third positions are more frequently "silent" (do not result in amino acid changes) and so accumulate more rapidly than those occurring at first or second positions. Thus, building a tree with only first and second positions can provide a more conservative estimate of phylogenetic relationships. When this was done with our data set, a tree with a topology similar to the tree derived from the entire data set was obtained (Fig. 2.3b). Once again, long lineage effects are probably responsible for uniting the spotted hyaena with the aardwolf.

Because of the biochemistry of DNA, certain types of nucleotide substitutions occur more frequently than others and are therefore more likely to be subject to homoplasy. Transversions (change from a purine to a pyrimidine or vice versa) occur less frequently than transitions (change from one type of purine to another or from one pyrimidine

Table 2.1. Matrix showing percent sequence divergence above the diagonal and number of nucleotide differences below the diagonal for 1140 bp of the cytochrome b gene.

	Striped hyaena	Brown hyaena	Spotted hyaena	Aardwolf	Cat	Seal
Striped hyaena	-	8	11	14	17	19
Brown hyaena	88	-	11	14	17	20
Spotted hyaena	130	132	-	12	17	17
Aardwolf	163	158	139	-	19	20
Cat	196	193	189	203	-	19
Seal	215	223	199	226	214	-

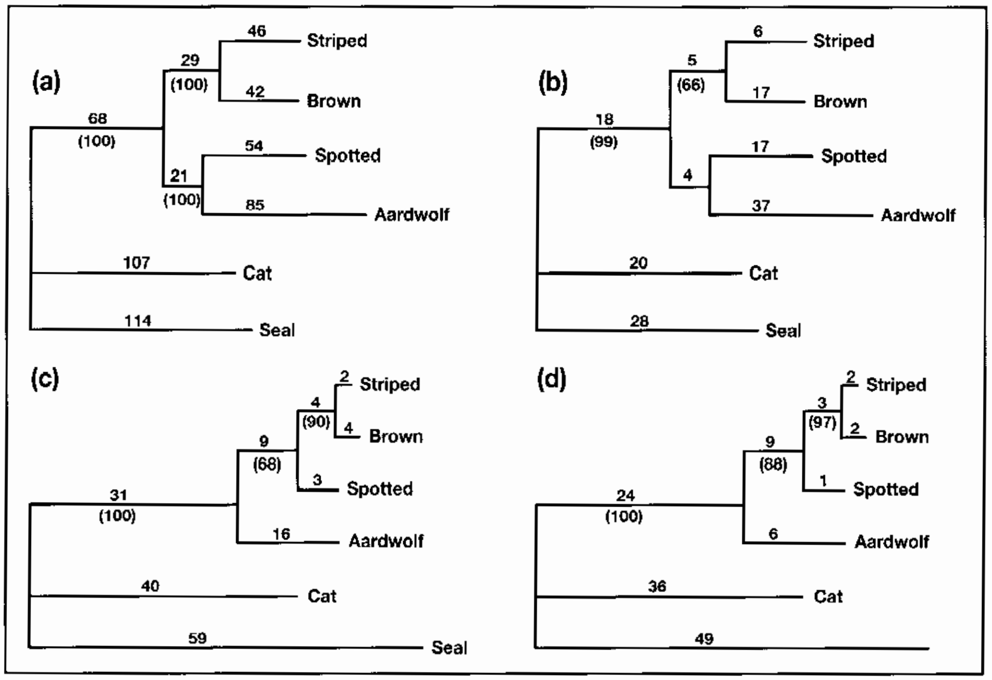


Figure 2.3. Numbers on branches indicate branch lengths, numbers in parentheses indicate bootstrap values for 100 replications. TL indicates tree length; CI indicates consistency index. **(a)** Single most parsimonious tree derived from 1140bp of cytochrome b using the Exhaustive Search option in Paup. TL=566; CI=0.825; g1=-1.05. **(b)** Single most parsimonious tree using first and second positions only in an Exhaustive Search. TL=152; CI=0.836; g1=-0.961. **(c)** Single most parsimonious tree found in Exhaustive Search using transversions only. TL=167; CI=0.928; g1=-1.639. **(d)** Single most parsimonious tree found in Exhaustive Search using third position transversions only. TL=132; CI=0.932; g1=-1.483.

to another pyrimidine). Therefore, the use of transversions alone in an analysis can provide a more conservative and perhaps "real" estimate of phylogenetic relationships. Fig. 2.3c presents the single most parsimonious tree using transversions alone in an exhaustive search. When transversions alone were used, the spotted hyaena and aardwolf grouping was no longer supported and each was placed on its own branch, with the aardwolf diverging earlier. The topology of this tree most likely reflects the "true" tree with regard to the placement of the aardwolf because the long lineage effects were eliminated by filtering the characters with the highest potential for "noise" (homoplastic transitions). The bootstrap values for the branches of this tree were all high. Using transversions and transitions, with transversions weighted three times as important as transitions (the transition:transversion ratio), a tree was produced with the same topology as using transversions alone.

Using the percent sequence divergences presented in Table 2.1, derived from the analysis of the entire cytochrome b sequence, and an estimated 2–4% sequence divergence per million years for vertebrate mtDNA (Li and Graur 1991), we can calculate approximate divergence times for the four extant hyaena species: Striped/brown: 2–4 million years ago (Mya); brown, striped/spotted: 3–6 Mya; striped, brown/aardwolf: 4–7 Mya; spotted/aardwolf: 3–6 Mya. Morphological analyses, however, suggest earlier divergence times (see above). Irwin *et al.* (1991) have shown that transversions at the third positions of mammalian cytochrome b genes accumulate nearly linearly, at a rate of 0.5% per Mya. If we use only third position transversions to construct a tree, the tree topology is the same as that for all transversions only and is well supported by bootstrapping (Fig. 2.3d). Estimation of divergence dates using these data (Table 2.2) yields dates that are somewhat more congruent with those derived

Table 2.2. Matrix showing percent sequence divergence above the diagonal and number of nucleotide differences below the diagonal for third position transversions only.

	Striped hyaena	Brown hyaena	Spotted hyaena	Aardwolf	Cat	Seal
Striped hyaena	-	3	5	16	57	64
Brown hyaena	4	-	5	16	56	63
Spotted hyaena	6	6	-	10	51	57
Aardwolf	20	20	12	-	51	61
Cat	70	68	62	62	-	70
Seal	78	77	69	74	85	-

from morphological analyses, ranging from 6 Mya (striped/brown) to 32 Mya (striped, brown/aardwolf), but appear inflated for the more distantly related groups (aardwolf/striped and brown; hyaenas/outgroups).

In summary, our phylogenetic analyses of the cytochrome b gene currently support the traditional hypothesis of a close relationship between the extant striped and brown hyaenas. The small number of living taxa available for analysis is unfortunate and limits our understanding of their evolution. Obtaining DNA from fossil material such as *Pachycrocuta brevirostris* could be informative, although perhaps impossible. It is also worth noting here that molecular data could be very useful for subspecies determination in the widespread striped hyaena. At the same time, we also note that our data support the placement of the aardwolf, *Proteles cristatus*, in the Hyaenidae.

2.5 Phylogenies: conclusions

The systematics and taxonomy of hyaenas has been the subject of some debate over the past 100 years. Most of this debate has taken place among paleontologists faced with the extensive fossil record of hyaenas. Zoologists, who only deal with four species in the extant fauna, have adhered to a scheme of interrelationships that closely relates striped and brown hyaenas and more distantly relates spotted hyaenas. The most recent morphological analysis (Werdelin and Solounias 1991) suggested another scheme, with brown hyaenas more closely related to spotted hyaenas than to striped hyaenas. However, the data supporting this assertion have never been strong. New data from molecular studies as presented herein contradict this morphologically and paleontologically based hypothesis of relationships and instead support the traditional scheme. These molecular data provide a much stronger case than hitherto available from morphological data, and a scheme of relationships that closely relates striped and brown hyaenas must be considered firmly established for the present. Advocates of other hypotheses must present new and better data to support their claims. Exactly what this means in terms of the phylogeny of the family as a whole, including both living and fossil representatives, remains to be seen. At the very least, a number of characters will have revised polarities, which might suggest interesting new avenues in character evolution.

The fact that a consensus has been reached regarding the scheme of interrelationships among extant hyaenas does not mean that the question of taxonomy has been settled. Uniting striped and brown hyaenas into a common genus *Hyaena* simply because they are the two most closely related species can be considered naive as such a criterion can lead to an infinite regress. One alternative is to rank taxa by their age, as espoused by Hennig (1966). In the present case this means providing the nodes separating the species with minimum ages, relating these ages to similar ages reported for related groups of taxa, such as Felidae, and then correlating the ranks of the taxa involved. This is difficult in the present case, because our estimates of divergence times derived from molecular data lack consistency.

The dates derived from total sequence differences (Table 2.1) are manifestly too low, especially for the outgroups. A divergence date between striped hyaena and cat of 4–8 million years represents at best a fourth of the estimated age of the latter family as derived from paleontological and molecular sources and must be considered spurious. It also suggests that the rate of sequence divergence in these families is lower than the average for vertebrate mtDNA. These data must be disregarded for the time being. On the other hand, the data on third position transversions (Table 2.2) give divergence dates that are too high for the distantly related taxa (over 100 million years for the example above). However, the divergence dates for spotted, striped and brown hyaenas obtained from Table 2.2 are very close to those obtained from the fossil record. These data suggest that the cytochrome b molecule does not behave in a clock-like fashion in the group under investigation. Instead, the rate of sequence divergence may have slowed over the time-span studied, such that for the last 15 million years or so a divergence rate of 0.5% per million years is a reasonable mean, but beyond this time frame the rate was an unknown number of percentage points higher.

The consensus position from combining paleontological and molecular data is that aardwolf diverged from other hyaenas about 15–32 million years ago. Spotted hyaenas diverged from brown and striped about 10 million years ago and striped and brown hyaenas diverged about 6 million years ago. These dates do not contradict any well established data. How does this compare with felids? Currently available dates for felids (Collier and O'Brien 1985) indicate times of divergence to be on the order of 3–6 million years (equal to or less than between striped and brown hyaenas) between species never seriously considered to belong to the same genus (such as lynxes and pantherine cats or cheetah and pantherines). However, there is no reason to assume that rates of divergence are necessarily congruent between taxonomic groups and there are many examples of the same molecule evolving at different rates in different species (Gillespie 1991). Thus, using age as a criterion for ranking can be misleading.

Thus, in the absence of clear-cut data regarding rank among hyaenas and because the cytochrome b data unite striped and brown hyaenas as sister taxa relative to *Crocuta* and *Proteles*, we place the former two together in the genus *Hyaena*. At the same time, we note that the evidence

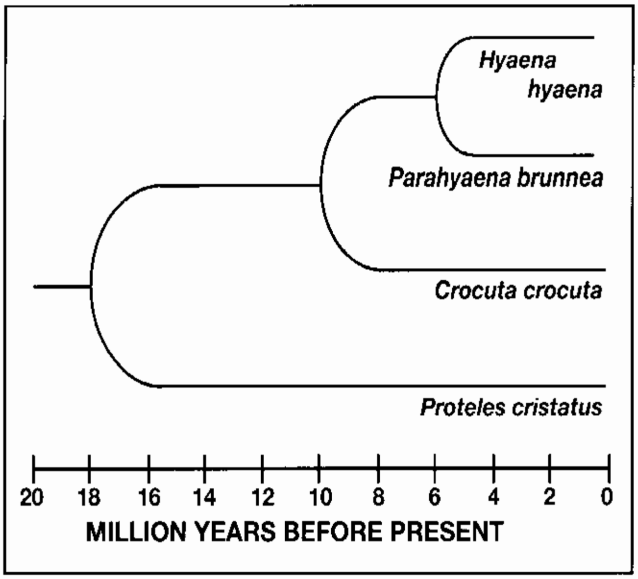


Figure 2.4. Hypothesis of interrelationships and divergence times of hyaenid lineages as reported in this chapter.

suggests that the timing of the split between striped and brown hyaena is relatively old (down into the Miocene). We acknowledge this by placing the two in different subgenera, *Hyaena* (*Hyaena*) and *Hyaena* (*Parahyaena*), respectively. This mirrors the original intent of Hendey (1974) in erecting *Parahyaena*. We further note that the philosophy underlying biological nomenclature and what the relationship should be between nomenclature and the evolution of taxonomic groups, especially for the practice of conservation biology, is currently a matter of much needed debate.

The phylogeny and divergence dates of hyaenas as derived from the current paleontological and molecular information is shown in Fig. 2.4.

2.6 Taxonomy and nomenclature

This section provides a list of synonyms of the four extant hyaena species and discusses the evidence for recognition of subspecies.

Genus *Hyaena* Brünnich, 1771

Hyaena Brisson, 1762:13, 168. Type species: *Canis hyaena* Linnaeus, 1758. Not available.

Hyaena Brünnich, 1771:34, 42, 43. Type species: *Canis hyaena* Linnaeus, 1758.

Euhyaena Falconer in Murchison, 1868:464. Type species: *Canis hyaena* Linnaeus, 1758.

Parahyaena Hendey, 1974:149 (as subgenus). Type species: *Hyaena brunnea* Thunberg, 1820.

Subgenus *Hyaena* Brünnich, 1771

Hyaena Brisson, 1762:13, 168. Type species: *Canis hyaena* Linnaeus, 1758. Not available.

Hyaena Brünnich, 1771:34, 42, 43. Type species: *Canis hyaena* Linnaeus, 1758.

Euhyaena Falconer in Murchison, 1868:464. Type species: *Canis hyaena* Linnaeus, 1758.

Hyaena (Hyaena) hyaena (Linnaeus, 1758): striped hyaena

Canis hyaena Linnaeus, 1758:40. Type locality: Benna Mountains, Laristan, southern Persia.

Hyaena striata Zimmerman, 1777:366. Renaming of *hyaena* Linnaeus.

Hyaena dubbah Meyer, 1793:94. Type locality: Atbara, Anglo-Egyptian Sudan.

Hyaena orientalis Tiedemann, 1808:59. Renaming of *hyaena* Linnaeus.

Hyaena fasciata Thunberg, 1820:59. Renaming of *hyaena* Linnaeus.

Hyaena antiquorum Temminck, 1820:51. Renaming of *hyaena* Linnaeus.

Hyaena vulgaris Desmarest, 1820:215. Type locality: La Barbarie, l'Egypte, l'Abyssinie, La Nubie, La Syrie, La Perse.

Hyaena dubia Schinz, 1821:509. Type locality: Dongola, Sudan.

Hyaena virgata Ogilby, 1839: lxiv. Renaming of *hyaena* Linnaeus.

Hyaena barbara Blainville, 1844:81. Type locality: Oran, western Algeria.

Hyaena indica Blainville, 1844:82. Renaming of *hyaena* Linnaeus.

Hyaena suilla Filippi, 1853:127. Type locality: Gabes, southern Tunisia.

Hyaena syriaca Matschie 1900:54. Type locality: Antiocha, Syria.

Hyaena schillingsi Matschie, 1900:55. Type locality: Kilimanjaro, East Africa.

Hyaena zarudnyi Satunin, 1905:7. Type locality: Karun River, Iraq.

Hyaena bokcharensis Satunin, 1905:8. Type locality: Bokhara, Turkestan.

Hyaena bilkiewiczi Satunin, 1905:9. Type locality: Ashabad, Turkestan.

Hyaena bergeri Matschie, 1910:261. Type locality: Eljego Escarpment, Kenya.

Hyaena satunini Matschie, 1910:363. Type locality: Caucasus.

Hyaena rendilis Lönnberg, 1912:64. Type locality: Guaso Nyiro, Kenya.

Hyaena hyaena sultana Pocock, 1934:636. Type locality: Mt. Qara, 1500 ft., Ain, southeastern Arabia.

Hyaena makapani Toerien, 1952:293. Type locality: Makapansgat, Transvaal. (Fossil)

The striped hyaena has a relatively large distribution across several continents, and has perhaps more for this reason than for any inherently great variability been split into a number of species over the past centuries. None of these species can be considered valid today. Perhaps the best indication of the relatively homogeneous nature of this species is the fact that only one fossil species has been described, the large *H. makapani* from South Africa (an area which lies outside the present range of the species). *H. makapani* can today be referred to as *H. hyaena*.

At one time or another, the various taxa listed in the synonymy for *H. hyaena* have been downgraded to subspecies, but Pocock (1934) revised these, leaving five that are still recognised (Rieger 1979a, 1981). They are defined mainly on metric and pelage characters and are *H. h. barbara* from northwest Africa, *H. h. dubbah* from northeast Africa, *H. h. syriaca* from Syria, Asia Minor and the Caucasus, *H. h. hyaena* from India, and *H. h. sultana* from Arabia; the last mentioned being new to Pocock's work. Rieger (1979a) suggested that these five subspecies can be placed into two larger groups, a northeast African-Arabian group composed of *H. h. dubbah* and *H. h. sultana* and a northwest African-Asian group composed of *H. h. barbara*, *H. h. syriaca*, and *H. h. hyaena*. The two groups are differentiated on the basis of the size of the skull.

From a morphological point of view, the subspecies of striped hyaena are inadequately characterised. No detailed investigation of morphological variability within the species has been carried out since Pocock (1934) and is urgently needed in order to evaluate the status of the subspecies. At present it is clear that the population status of the recognised subspecies cannot form an acceptable basis for possible conservation measures.

Subgenus *Parahyaena* Hendey, 1974

Parahyaena Hendey, 1974:149. Type species: *Hyaena brunnea* Thunberg, 1820.

Hyaena (Parahyaena) brunnea (Thunberg, 1820): brown hyaena

Hyaena brunnea Thunberg, 1820:59. Type locality: Cape of Good Hope.

Hyaena fusca E. Geoffroy, 1825:444. No locality given.

Hyaena striata A. Smith, 1826:14 (*non* Zimmerman, 1777). Type locality: South Africa.

Hyaena villosa A. Smith, 1827:461. Type locality: South Africa.

Hyaena brunnea melampus Pocock, 1934:824. Type locality: Otjitundua, central Kaokoveld, northern Namibia.

The subspecies of brown hyaena were revised along with those of striped hyaena by Pocock (1934). He recognised two subspecies, *H. b. brunnea* and *H. b. melampus* (newly erected by Pocock). These two subspecies are distinguished solely on the basis of the markings on the legs. He gave the distributions as follows. *H. b. brunnea*: "South and southeast Africa as far north as the Kalahari, the northern Transvaal and Gasaland." *H. b. melampus*: "Kakaoveld, Damaraland, and the Upington district, about 500 miles inland from the coast, in S.W. Africa." From a morphological point of view, the characters used to distinguish these two forms are entirely inadequate given their great variation, and unless new data are forthcoming the two subspecies of *H. brunnea* must be rejected.

Genus *Proteles* I. Geoffroy, 1824

Proteles I. Geoffroy, 1824:139. Type species: *Proteles lalandii* I. Geoffroy (= *Viverra cristata* Sparrman).

Geocyon Wagler, 1830:30. Type species: *Proteles lalandii* I. Geoffroy (= *Viverra cristata* Sparrman).

Proteles cristatus (Sparrman, 1783): aardwolf

Viverra cristata Sparrman, 1783:581. Type locality: Near Little Fish River, Somerset East, eastern Cape Province.

Viverra hyaenoides Desmarest, 1822:538. Type locality: Cape of Good Hope.

Proteles lalandii I. Geoffroy, 1824:139. Type locality: Near Algoa Bay, eastern Cape Province.

Proteles typicus A. Smith, 1833:96. Renaming of *lalandii*.

Proteles cristatus harrisoni Rothschild, 1902:443. Type locality: Umpata, Mossamedes district, southwestern Angola.

Proteles cristatus septentrionalis Rothschild, 1902:444.

Proteles cristata transvaalensis Roberts, 1932:6. Type locality: Roodekuil, Pretoria district, Transvaal.

Proteles cristatus canescens Shortridge and Carter, 1938:285. Type locality: Eselfontein (Kamiesberg), Little Namaqualand, northwestern Cape Province.

Proteles has a disjunct distribution that has been related to the distribution of its secondary prey genus, *Hodotermes*. This disjunct distribution has been the motivation for recognising two subspecies, *P. c. cristatus* in southern Africa and *P. c. septentrionalis* in eastern Africa and north to the northernmost part of Sudan (Coetzee 1977, Meester *et al.* 1986). However, this distinction has not been followed up by studies of either morphological or genetic variation and the extent of gene flow between the two regions has therefore not been ascertained. Clearly, however, the case for subspecific distinction is stronger within *P. cristatus* than in any of the other species of Hyaenidae.

Genus *Crocuta* Kaup, 1828

Crocuta Kaup, 1828:1145. Type species *Canis crocuta* Erxleben, 1777.

Crocotta Kaup, 1829:78. Respelling of *Crocuta*.

Crocuta crocuta (Erxleben, 1777): spotted hyaena

Canis crocuta Erxleben, 1777:578. Type locality: Guinea, Ethiopia, Cape of Good Hope. Designated as Senegambia by Cabrera (1911).

Hyaena maculata Thunberg, 1811:302. Type locality: South Africa.

Hyaena capensis Desmarest, 1817:499. Type locality: Cape of Good Hope,

Hyaena rufa Desmarest, 1817:499. Type locality: Cape of Good Hope.

Hyaena spelaea Goldfuss, 1823:4.56. Type locality: Gailenreuth, Germany. (Fossil)

Hyaena cuvieri Boitard, 1842:233. Type locality: Cape of Good Hope.

Hyaena crocuta habessynica Blainville, 1844:82. Type locality: Ethiopia (implied).

Hyaena sivalensis Falconer and Cautley in Falconer, 1868:548. Type locality: Siwaliks, India. (Fossil)

Hyaena (Crocotta) wissmanni Matschie, 1900:22. Type locality: Epikuro, Namibia.

Hyaena (Crocotta) gariepensis Matschie, 1900:25. Type locality: Bamboesberg, 31°30' S, 26°20' E, near Molteno, eastern Cape Province (Ellerman *et al.* 1953).

Hyaena (Crocotta) germinans Matschie, 1900:26. Type locality: Lake Rukwa, Tanzania.

Hyaena (Crocotta) thierryi Matschie, 1900:30. Type locality: Sansanne Mangu, Togo.

Hyaena (Crocotta) togoensis Matschie 1900:31. Type locality: Kete Krachi, Togo.

Hyaena (Crocotta) noltei Matschie, 1900:211, 215. Type locality: Yoko, upper Sanaga, south Cameroon.

Hyaena (Crocuta) leontewi Satunin, 1905:556. Type locality: Ethiopia.

Crocotta kibonotensis Lönnberg, 1910:16. Type locality: Kibonoto Steppe, Kilimanjaro, Tanzania.

Crocotta panganensis, Lönnberg, 1910:18. Type locality: Kibonoto Steppe, Kilimanjaro, Tanzania.

Crocuta rufopicta Cabrera, 1911a:97. Type locality: Odweina, 160km south of Berbera, Somalia.

Crocuta thomasi Cabrera, 1911a:98. Type locality: Ankole, Uganda.

Crocuta nyasae Cabrera, 1911a:99. Type locality: Mlanje Mountain, southern Malawi.

Crocuta nzoyae Cabrera, 1911b:200. Type locality: Nzoia River, Guas Ngishu Plateau, Kenya.

Crocuta crocuta fisi Heller, 1914:5. Type locality: Merelle Waterholes, Marsabit road, northern Kenya.

Hyaena ultima Matsumoto, 1915:2. Type locality: Sechuan, China. (Fossil)

Crocuta crocuta fortis Allen, 1924:214. Type locality: Faradje, Kibali-Ituri district, northeastern Democratic Republic of Congo.

Crocuta ultra Ewer, 1954:570. Type locality: Kromdraai, Transvaal. (Fossil)

Crocuta venustula Ewer, 1954:828. Type locality: Swartkrans, Transvaal. (Fossil)

Unlike *H. hyaena*, for which a number of specific nomina have been erected mainly on the basis of its relatively extensive modern range, this is an extremely variable species, both temporally and spatially. Although limited today, its geographic range once covered almost all of Africa and Eurasia (Werdelin and Solounias 1991). Within this enormous range the species has displayed a bewildering array of morphologies leading to an equally bewildering set of specific and subspecific epithets.

Gradually, taxonomists began to realise that all of this variation could be included within a single species. The seminal work in this area is Matthews (1939a), who showed on the basis of a large series of skulls from Tanzania that all of the variation seen in the then recognised subspecies could also be found within a single population. Only two sets of characters stood out: pelage variation, which is notoriously subject to ecophenotypic variation, and size, which is highly variable within *C. crocuta* and also subject to Bergmann's rule (according to which equatorial populations are smaller than populations further away from the equator). Matthews (1939a) rejected all the subspecies of *C. crocuta*, a decision which has been amply confirmed since then.

When fossils are added, *C. crocuta* can be perceived as even more variable than it is at present, and a number of fossil species have also been named that are today considered synonymous with *C. crocuta*. In fact, firm evidence for more than one species within *Crocuta* is still lacking (Werdelin and Turner 1996).

2.7 Summary

The systematics and taxonomy of hyaenas has been the subject of some debate over the past 100 years. Most of this debate has taken place among paleontologists faced with the extensive fossil record of hyaenas. The extant species are the striped hyaena, *Hyaena hyaena*, the brown hyaena, *Hyaena brunnea*, the aardwolf, *Proteles cristatus*, and the spotted hyaena, *Crocuta crocuta*. A review of paleontological studies and new data from a molecular study reported here for the first time clarifies a number of previously contentious issues (see Fig. 2.4): (1) The aardwolf belongs to the family Hyaenidae; it is not appropriate to place it into a separate family. (2) The striped and the brown hyaena are each other's closest relative. (3) The extant species are the endpoints of evolutionarily old lineages. Within the Hyaenidae, the aardwolf diverged from other hyaenas about 15–32 million years ago, the spotted hyaena separated from the brown and the striped hyaena 10 million years ago, and the striped and the brown hyaena split six million years ago. As the generic rank of the striped and the brown hyaena continues to be unresolved, they are provisionally placed in the genus *Hyaena*. However, the long separation of the two lineages suggests that the two species should be placed in different subgenera, *Hyaena* (*Hyaena*) in the case of the striped and *Hyaena* (*Parahyaena*) in the case of the brown hyaena.

The case for subspecific distinction is stronger in the aardwolf than in the other three species because of its disjunct distribution. Provisionally two subspecies are retained: *P. c. cristatus* in southern Africa and *P. c. septentrionalis* in eastern Africa and north to the northernmost part of Sudan. However, genetic and morphological studies have not been done to verify this. Five currently recognised subspecies of the striped hyaena are inadequately defined: *H. h. barbara* (northwest Africa), *H. h. dubbah* (northeast Africa), *H. h. syriaca* (Syria, Asia Minor and the Caucasus), *H. h. hyaena* (India), and *H. h. sultana* (Arabia). On the basis of skull size, these subspecies probably form two larger groups, a northeast African-Arabian group composed of *H. h. dubbah* and *H. h. sultana* and a northwest African-Asian group composed of *H. h. barbara*, *H. h. syriaca* and *H. h. hyaena*. The population status of the five subspecies cannot, at present, form an acceptable basis for possible conservation measures. Neither the spotted nor the brown hyaena are currently recognised to have subspecies.

Chapter 3

Species Accounts

3.1 Aardwolf *Proteles cristatus* (Sparrman, 1783)

Philip Richardson

Box 3.1. Common and indigenous names for the aardwolf.

Afrikaans – aardwolf, erdwolf, maanhaarjakkals
Amharinja – kamer-djibb
Arabi – dabóuh
English – aardwolf
French – protéle
Galla – ia
German – Erdwolf
kiswahili – fisi ndogo, fisi ya mkole.
Ndebele – inthuhu, isanci
Portuguese – protelo
seTswana – thukwe, thukwi, thukgwi, mMabudu
siSwati – ngci
Shona – mwena
Southern Sotho – thikhoi
Somali (general Somalia) – abalcùf, abalhot
Somali (Nogal) – abacùf, uèr
Somali (central Somalia) – uer dauà, schambel
Spanish – lobo de tierra
Northern Sotho – sethukhu
T (Zambia) – kasuntula
Venda – tshivingwi
Xhosa – inchi, nehi

Physical description

The aardwolf is slightly larger than a jackal or a fox and has long, slender legs and a long neck. Its sloping back is not as pronounced as in the three other hyaena species. The background colour of the body varies from yellowish-white to rufous. The throat and underparts are paler and can reach a greyish-white colour. There are three vertical black stripes on the body and one or two diagonal stripes across the fore- and hindquarters. Irregular horizontal stripes run across the legs, which are darker towards the feet. Sometimes black spots or stripes are present on the neck. Having stripes on the body, the aardwolf superficially resembles the striped hyaena, but it is less than half the size and its stripes are much more regular than those of the hyaena. There are five digits on the front feet (the other members of the Hyaenidae have only four), and four on the hind feet.

In southern Africa, adult body mass varies seasonally with the availability of termites, and averages around 8–10 kg (Anderson 1994) with little variation between sexes. Kingdon (1977) lists body masses of up to 14kg in east Africa. Head to tail the aardwolf measures 0.95m (0.85–1.05m) and stands 0.475m (0.45–0.5m) at the shoulder (Smithers 1983, Koehler and Richardson 1990).

Habitat

The aardwolf is considered an indicator species for the Somalia-Kalahari semi-desert axis, although it now occurs in two discrete populations separated by wetter woodlands in Zambia and southern Tanzania (Kingdon 1977). In southern Africa the prime habitat appears to be open, grassy plains but it still occupies most habitats which have a mean annual rainfall of between 100 and 800mm. It is most common in the 100–600mm range and does not occur in forests or pure desert (Smithers 1983). In east Africa it also occurs in open country. It is independent of drinking water. It makes extensive use of springhare and aardvark burrows for refuge during the day, but can also dig its own burrows (Richardson 1985, Anderson 1994).

Diet and foraging behaviour

Diet

Throughout its distribution range the aardwolf feeds primarily on one local species of nasute harvester termite (genus *Trinervitermes*). The preferred species are: *T. bettonianus* in east Africa (Kruuk and Sands 1972); *T. rhodesiensis* in Zimbabwe and Botswana (Smithers 1971); and *T. trinervoides* in South Africa (Cooper and Skinner 1979, Richardson 1987a). In South Africa the diet is supplemented in winter by the pigmented harvester termite *Hodotermes mossambicus* (Richardson 1987a) and in east Africa during the rainy season by a number of other termites belonging mainly to the genera *Odontotermes* and *Macrotermes* (Kruuk and Sands 1972).

Foraging behaviour

The aardwolf is a solitary forager. Its termite prey forages in dense concentrations, completely exposed on the soil surface while browsing or collecting dry grass (Kruuk and Sands 1972, Richardson 1987a). Unlike most other ant- or termite-eating mammals, such as the aardvark (*Orycteropus afer*), which have to dig to access their prey, the aardwolf licks termites from the soil surface.

Photo 3.1. An aardwolf feeding on termites.

It is primarily nocturnal, and its activity periods seem to be determined largely by the activity of termites. The termite species, *Trinervitermes trinervoides*, cannot tolerate direct sunlight (Hewitt *et al.* 1972) so it is primarily active at night. However, during cold nights in winter these termites are inactive, so the aardwolf becomes active earlier in the afternoon in order to feed on the heavily pigmented termite *Hodotermes mossambicus*, a diurnal species (Hewitt *et al.* 1972, Richardson 1987a). The aardwolf nevertheless experiences a period of food deprivation during the southern African winter and loses up to 20% of its body weight (Richardson 1987a, Anderson 1994). This is a critical period for the cubs and many die during particularly dry years (Richardson 1987a). Although there is no winter in east Africa, *T. bettonianus* appears to be less active during the wet season, so the aardwolf has to feed on a wider variety of termites (Kruuk and Sands 1972). It is unknown whether this is also a period of food deprivation for the aardwolf in this region.

Social behaviour

The aardwolf is socially monogamous; a mated pair occupying a perennial territory with their most recent offspring. The offspring stay in their natal territory for one year, and disperse around the time when the next litter is born. Territory sizes vary from about 1–4km^2, the size being determined by the availability of termites. In the Northern Cape Province of South Africa each territory has approximately 3,000 *T. trinervoides* mounds.

Apart from aggressive encounters, territories are maintained by means of depositing (pasting) secretions from the anal gland on grass stalks (Richardson 1987b, 1991), as is the case with other members of Hyaenidae. Both sexes scent mark (paste), although males mark more than females. Pasting occurs on average more than two times per 100m moved and about 200 times per night. Scent marks are concentrated along the territory boundary and at dens and middens (Richardson 1987b,1991).

When intruders are encountered within the territory the resident immediately raises the long mane along its back and, particularly if the intruder is of the same sex, chases it to the border. Intruders are seldom caught, and fights only rarely occur between males during the mating season. Fighting may be highly aggressive and accompanied by deep roars, with animals being bitten on the neck and sometimes the rump. Fatal fights have been recorded (unpublished observations). The aardwolf has no long distance call (Peters and Sliwa 1997).

Reproduction and denning behaviour

In the North Cape Province of South Africa females come into pro-oestrus during the last weeks of June (mid-winter). Mating usually takes place during the first two weeks of July. The aardwolf is highly promiscuous with dominant males often gaining copulations with the females of subordinate males in neighbouring territories. Copulation may last up to four hours although there is no copulatory tie. Females remain receptive for one to three days, but are normally not receptive after a copulation lasting more than three hours. A female will recycle if she is not fertilised (Richardson 1985,1987b).

The gestation period is approximately 91 days and mean litter size is 2.5 (range 1–4) (Anderson pers. comm., Richardson 1985, Koehler and Richardson 1990). In South Africa the young are born from October through December (Shortridge 1934, Stuart 1977, Richardson 1985), although with the warmer winters further north in Botswana and Zimbabwe the breeding season seems to be less restricted (Smithers 1983).

The cubs are born in dens, from which they first emerge after about a month. The den usually has a single entrance measuring about 25cm high and 30cm wide (Anderson 1994). The denning period lasts four months, with dens being changed about once a month. After about nine weeks the cubs start foraging for termites near the den. After 12 weeks cubs will go foraging with the adults, but still stay within 300–500m of the den. After four months they have been weaned and forage mostly independently throughout the territory (Richardson 1985, Koehler and Richardson 1990).

Males help in rearing the young by guarding the den against jackals, which are probably their greatest natural enemy. Although paternal care varies, during the first three months some males may spend up to six hours a night guarding the cubs while the female is away foraging (Richardson 1985, 1987b). The reproductive success of females which have males guarding the den is about 1.5 cubs per year, which is about three times greater than that of solitary females.

Competition

The aardwolf is a highly specialised carnivore and appears to be unable to feed efficiently on anything other than social insects (Anderson *et al.* 1992). It also appears to be the only African ant- or termite-eater that can tolerate the terpene defence secretions of *Trinervitermes* soldiers (Richardson and Levitan 1994). Although both the aardwolf and bat-eared fox may feed on *Hodotermes* during the winter and the aardvark occasionally opens *Trivitermes* mounds (Richardson and Levitan 1994), the aardwolf appears to experience very little competition for food.

Mortality and pathogens

In southern Africa the majority of aardwolves occur on farm land outside conservation areas. Here the greatest threat to the species appears to come from indirect poisoning aimed at periodic outbursts of locust plagues. These poisoning events have the potential of killing off half the local adult population and all the cubs. Males appear to be more susceptible to poisoning, thus depriving females of paternal care for their cubs and lowering their reproductive success. After one such incident in the North Cape the population took four years to recover, and because of lack of emigration by the surviving cubs the population became highly inbred although without any obvious inbreeding depression (Richardson in prep).

Probably the most important natural mortality factors inside conservation areas are predation by jackals on cubs (see above) and severe drought. Although drought does not appear to affect adults, it can reduce cub survival from 70% to 45%. Intraspecific fighting and diseases appear to be minor causes of death. Inside conservation areas predation by large carnivores like the lion and leopard probably occur, although we have no data on this. In the Serengeti aardwolves have frequently been seen foraging close to spotted hyaena dens, but have been ignored by the hyaenas (H. Hofer pers. comm.). Mills (1990) recorded a brown hyaena attempting to dig out aardwolf cubs.

Another mortality factor outside conservation areas is persecution by humans, either due to the mistaken belief that the aardwolf takes lambs, incidentally while persecuting jackals, or as a source of food. Aardwolves are also occasionally run over by vehicles at night as they stand dazzled in the lights. Road kills are most common during early summer in southern Africa when the one-year-olds are emigrating from their natal territories. However, none of these mortality factors appear to be significant when compared with poisoning, jackal predation and drought.

Rabies and rabies-related viruses have been recorded in 43 specimens from southern Africa (Swanepoel *et al.* 1993). Two subspecies of mallophagus louse *Felicola intermedius intermedius* and *Felicola i. hyaenae* have been found only on the aardwolf and the brown hyaena respectively (Hopkins 1960), which provides further evidence for including the aardwolf in the Hyaenidae (Ledger 1968).

Current or planned research projects

No aardwolf studies are known to be going on at present.

3.2 Striped Hyaena *Hyaena (Hyaena) hyaena* (Linnaeus, 1758)

Heribert Hofer

Physical description

This medium-sized, dog-like animal has a back sloping downwards towards the tail, and black vertical stripes on the sides. Its general colour is pale grey or beige. It has a black patch on the throat, five to nine more or less distinct vertical stripes on the flanks and clearer black transverse and horizontal stripes on the fore and hind legs. The head is roundish with a pointed muzzle and pointed ears. It has a mane along the mid-dorsal line which can be held erect. Its black and white tail is long and bushy, with hair that is generally coarse and long. The feet have four toes and short, blunt, non-retractable claws.

Five subspecies are distinguished, mainly by their differences in size and pelage, although this classification is provisional (see Chapter 2):

H. h. barbara from northwest Africa
H. h. dubbah from northeast Africa
H. h. sultana from Arabia
H. h. syriaca from Syria, Asia Minor and the Caucasus
H. h. hyaena from India

H. h. sultana on the Arabian peninsula has an accentuated blackish dorsal mane, with mid-dorsal hairs reaching 20cm in length, a ground colour grey to whitish grey, a dusky grey muzzle, and buff yellow below the eyes (Gasperetti *et al.* 1985). In Israel, *H. h. syriaca* has a dorsal crest that is not predominantly black but rather mixed grey and black (Mendelssohn 1985, Mendelssohn and Yom-Tov 1988).

Body mass varies between 26 and 41kg for males and 26 and 34kg for females. Total body length excluding tail varies between 1.0 and 1.15m and shoulder height between 0.66 0.75m. Amongst the provisional subspecies, body mass and body size are only well studied in *H. h. syriaca* in Israel (Mendelssohn 1985, Mendelssohn and Yom-Tov 1988).

A detailed description of locomotion and anatomy can be found in Spoor and Badoux (1986, 1988) and Spoor and Belterman (1986). The functional morphology of the head is considered by Buckland-Wright (1969) and Biknevicius and Ruff (1992).

Habitat

In most of its range the striped hyaena occurs in open habitat or light thorn bush country. In North Africa it prefers open woodlands and bushy and mountainous regions. Both the centre of the Arabian desert and the Sahara are avoided (Rieger 1979a). In central Asia it also avoids high altitudes and dense thickets and forests (Heptner and Sludskij 1980). The maximum altitudes recorded are 2,250m in Iran, 2,500m in India (sources in

Box 3.2. Common and indigenous names for the striped hyaena.

The name of each language is given first, followed by the local name for the striped hyaena; the languages are listed in alphabetical sequence.

Amharinja – djibb
Arab (CAR) – karaïng
Arab (Chad) – marfaïn
Arab (North Africa) – d'ba, debba
Arab (High) – zalab
Arab (Ethiopia) – dibb
Baguirmien – niougo kisserné
Bambara) – nama koro
Berber: Rif – ifis
Bornouan – boultou guechi
Danakil – jangóula
Dioula – suruku, namakoro
English – striped hyaena
Fulbe – fouru
French – hyène rayée
Galla – wårabéssa
German – Streifenhyäne
Gouragi – woraba
Gourmantche – namuno
Harari – worábba
Haoussa – sayaki, kure-kure
Hassaniya – gougouh-raïguett
Hebrew – tzavoa
Hindi (northern India) – hundar, lakkar, baghar
Hindi (southern India) – teras
Italian – iena striata
Kiswahili (east Africa) – fisi
Kotoko – machi n'chamé
Malinké – souloukou
Moore – katre, swasa
Ngambaye – riguen'ndah
Ouolof – boukki
Peuhl (Fouta Djalon) – boronou
Peuhl (Burkina Faso, Cameroon, Mali) – fowrou, fouru
Russian – polosataya giena
Somali (Ethiopia) – worábbo
Somali (Somalia general) – didthir, whera
Somali (Migiurtinia) – uaraba ueri, uaraba uèr, didier, dider
Sonhraï – chabo-diano, koro
Tamacheq – chabo diano
Tamil – kalada koratu, kaluthai puli
Tigrinja – zibb-i
Uzbek – srtlon, dulta

Photo 3.2. Large striped hyaena cubs at a den in the Serengeti.

Rieger 1979a) and 3,300m in Pakistan (Roberts 1977). In the Caucasus region, Turkmenistan, Tadzhikistan, and Uzbekistan, prime habitats include savannah and semi-desert regions up to an altitude of 2,100m, mountain areas with a strong relief and valleys and slopes (even with little or no vegetation) with plenty of caves or other resting sites and riverine areas. Other preferred habitats are thickets of tamarisks, the periphery of sand deserts, and the special pistachio (*Pistacia vera*) savannahs characteristic of the Badhyz area of southeast Turkmenistan (Heptner and Sludskij 1980). Because of its limited ability to thermoregulate, the striped hyaena stays south of the January isotherms of 1°C, and avoids areas with minimum temperatures of less than -15 to -20°C and more than 80–120 days of frost per year (Heptner and Slodskij 1980).

In Israel it is present even close to dense human settlements. Individuals have recently been recorded 19km south of Tel Aviv, 5km east of the international airport and on the Tel Aviv-Haifa highway near Mount Carmel (Mendelssohn 1985, Mendelssohn and Yom-Tov 1988). In India it used to be common in open country especially where low hills and ravines were available. (Prater 1948).

In west Africa the striped hyaena occurs in the Sahel and Sudan savannas.

Diet and foraging behaviour

Diet

The striped hyaena scavenges carrion and the remains of kills of other predators (wolf, spotted hyaena, cheetah, leopard, lion, tiger). It also consumes a wide variety of vertebrates, invertebrates, vegetables and fruits, including the fruits of *Balanites* trees, and human-associated organic matter (Kruuk 1976, Rieger 1979a, Heptner and Sludskij 1980, Osborn and Helmy 1980, Kerbis-Peterhans and Horwitz 1992). The massive cheek teeth and supporting musculature easily permit the gnawing and breaking of bones and carapaces. The striped hyaena may also kill smaller vertebrates including livestock (see section on Damage to agriculture and livestock, below).

The proportion of scavenged and killed prey items is still a matter of debate as there are no detailed studies on the diet of the striped hyaena. Rieger (1979a) suggests that only individuals from the three larger subspecies *H. h. barbara*, *H. h. syriaca* and *H. h. hyaena* (Middle East, Asia minor, central Asia and the Indian subcontinent, and North Africa) kill larger prey animals including livestock, as there is no evidence that the smaller subspecies *H. h. dubbah* and *H. h. sultana* (east Africa and Arabian peninsula) attack larger herbivores. In Turkmenistan it has been recorded to feed on wild boar, kulan, porcupine, and particularly tortoises. In Uzbekhistan and Tadzhikistan, seasonal abundance of oil willow fruits (*Eleagnus angustifolia*) is an important contribution to their diet, while in the Caucasus region it is grasshoppers (Heptner and Sludskij 1980). In Israel it feeds on garbage, carrion, and fruits, particularly dates and melons (Macdonald 1978, Mendelssohn 1985, Mendelssohn and Yom-Tov 1988). In eastern Jordan near the Azraq oasis, the main sources of food are carcasses of feral horses and water buffalo, and refuse from local villages (Al Younis 1993). The striped hyaena is able to drink water of very variable quality, from freshwater to soda and salt water, but it may also fulfil its water requirements with melons (Heptner and Sludskij 1980).

Foraging behaviour

Less is known about the sensory capacities, prey location and hunting behaviour of the striped hyaena than of either the spotted or brown hyaena. Seasonal influxes of striped hyaenas accompanying migrations of large herds of domestic and wild ungulates in Turkmenistan suggest that it may cover long distances on foraging trips, or at least part of the time live a nomadic existence in this region (Heptner and Sludskij 1980). In Egypt it was known to move along ancient caravan roads where the chance of locating a dead camel is high (Osborn and Helmy 1980). In the Serengeti, the greater part of its nocturnal activity is spent searching for food or moving between established foraging sites. It covers a total of 7–27km (mean 19km) per night, either following established animal tracks or zig-zagging cross-country (Kruuk 1976). While walking at a speed of two to four km/h (Kruuk 1976), it stops to investigate the bases of tree trunks, dense shrubs, clumps of grass, old holes, etc. It is apparently able to memorise the location of fruiting trees, garbage dumps and other established feeding sites. It is able to locate tortoises in their hiding places during periods of aestivation and hibernation (Kullman 1965, Gaisler *et al.* 1968); one hyaena was observed locating and digging out three tortoises in two and a half hours in one night (Heptner and Sludskij 1980). Observed hunts were a simple chase and grab procedure (Kruuk 1976). Food storage is practised commonly; the relevant food item may be stored in tall bushy or marshy clumps or at the base of dense shrubby vegetation (Kruuk 1976).

Damage to agriculture and livestock

Table 3.1 presents a summary of the information from the Action Plan questionnaires on damage to agricultural produce and livestock killed by the striped hyaena. Goats, sheep, dogs, and poultry are the most commonly recorded items. Larger animals are also occasionally reputed to be killed, although the possibility cannot be excluded that cases of scavenging were mistakenly identified as kills. In most cases of damage to larger livestock it is unclear whether the targeted individual was adult or young, healthy or sick. The records suggest that attacks typically occur at low frequencies (Table 3.1). Exceptions of more frequent livestock damage are reputed to occur in Egypt, Ethiopia, India, Iraq, and possibly Morocco (Table 3.1).

In Turkmenistan the striped hyaena is known to kill dogs, whereas in the Caucasus region it is reported to kill

Table 3.1. Damage to agricultural produce and livestock (species and frequencies of kills: O often; R rarely) by striped hyaenas as reported in the questionnaire survey.

Country	Number of cases/year	Cattle	Sheep	Goat	Others	Remarks
Algeria	< 5	R	yes	-	poultry	
Burkina Faso	6-10	some, young	young (R)	young (R)	-	
Egypt	> 50	-	yes	yes	date palms	
Ethiopia	> 50	O	O	O	donkey, horse	by repute all species often; stock keeping techniques poor
India	> 50	-	R	R	poultry, dog	not usually near villages
Iraq	11-50	-	R	-	dog (O)	horses and donkeys in the 1950s
Israel	yes	R	yes	-	poultry, palm dates, melons	damage to irrigation hoses
Kenya	> 50	-	O	O	camel (R)	camel by repute
Morocco	11–50	R	R	R	dog, donkey	
Niger	< 5	-	R	R	-	
Nigeria	yes	-	R	R	-	
Oman	rare	-	-	R	-	very rarely reported as a problem
Saudi Arabia	< 50	-	yes	yes	donkey, horse	maybe camel
Tanzania	some	-	R	R	-	unlikely to be reported
Turkmenistan	< 5	R	R	-	dog, melon	records unreliable since 1990

dogs, sheep and other small domestic animals (Heptner and Sludskij 1980). In Iraq reports from the 1950s indicate that the striped hyaena may attack horses and donkeys (Hatt 1959). In Africa, dogs, sheep and goats are occasionally at risk (Ronnefeld 1969). Records of attacks on sheep and goats originate from North Africa, Israel, Iran, Pakistan, and India, on donkeys from North Africa, Israel, Iran, Pakistan, and India, on horses in Iran, and on dogs in India (Roberts 1977, Rieger 1979a, Johnson 1987). Older records of attacks on sheep and goats also come from the Sinai and Somalia (Osborn and Helmy 1980).

The striped hyaena also occasionally causes damage to melon fields and to date palms in date plantations in Israel (H. Mendelssohn unpublished data) and Egypt (Osborn and Helmy 1980), and to water and honey melon plantations in Turkmenistan (Heptner and Sludskij 1980).

Social behaviour

Rieger (1979a, 1981) has argued that across subspecies, differences in body size, proportion of killed prey items in the diet, and group sizes (sociality) co-vary. The two smaller subspecies, *H. h. dubbah* and *H. h. sultana*, formerly sympatric with the spotted hyaena, are supposed to be more solitary and are not known to kill larger wild or domestic herbivores. The larger subspecies *H. h. syriaca*, *H. h. hyaena* and *H. h. barbara*, however, kill larger herbivores and have been repeatedly observed in small groups. Current information is inadequate to test this idea.

Typical group sizes are one or two in all subspecies (Rieger 1979a), although groups of up to seven animals have been reported in *H. h. dubbah* in Libya (Hufnagl 1972). In Israel, *H. h. syriaca* is generally solitary, but occasionally several are seen together at a carcass, apparently males and females, or females and large cubs (Macdonald 1978). *H. h. syriaca* has been recorded as monogamous in central Asia (Heptner and Sludskij 1980).

Home range sizes of one female and one male in the Serengeti were 44km^2 and 72km^2 respectively, with little evidence of territorial behaviour (Kruuk 1976). Van Aarde *et al.* (1988) calculated a home-range size for a single female in the Negev desert in Israel to be approximately 61km^2 over a period of seven months, which partly overlapped with two other individuals.

When striped hyaenas fight they bite at the throat and legs, not the mane. The mane serves as a signalling device during social interactions. During meetings, striped hyaenas investigate and lick the mid-back region where the mid-dorsal crest is situated. Greetings also involve sniffing of the nose and extruded anal pouch, and repeated pawing of the throat of the greeting partner (Fox 1971, Rieger 1978, Macdonald 1978). In aggressive encounters, the black patch near the thoracic and lumbar vertebrae is erected (Rieger 1979a). The striped hyaena scent marks (pastes) on grass stalks, stones, tree trunks and other objects with the anal pouch (Kruuk 1976). The striped hyaena uses a smaller variety of calls than the spotted hyaena (Kruuk 1976, Peters 1984).

Reproduction and denning behaviour

In the wild litter size varies from one to four (median of three) throughout the year, after a gestation period of 90–91 days (Pocock 1941, Ronnefeld 1969, Heptner and Sludskij 1980), although H. Mendelssohn (pers. comm.) reported a peak of births in spring in Israel. Average litter size in captivity is 2.4, with a range of one to five (Rieger 1979a). Parturition is preceded by intensive digging behaviour by the female and often followed by a one-day post-partum oestrus three weeks later (Rieger 1981).

Cubs are born blind, with closed ear tubes and white to grey fur with clear black stripes. Eyes first open after seven to eight days, and teeth erupt from day 21 onwards. Cubs begin to eat meat at the age of 30 days (Rieger 1979a). Weaning in captivity takes place after eight weeks (Heptner and Sludskij 1980). In the wild cubs have been observed suckling until four to five months of age (Rieger 1981), or up to 10–12 months (Kruuk 1976). Both the male and female bring food to the cubs (Kruuk 1976, Davidar 1985, 1990).

Various ages of sexual maturity have been reported. A striped hyaena was four years old when she gave birth to her first litter in the zoo of Tashkent (Heptner and Sludskij 1980), but most females mature by the age of two to three years in other zoos (Rieger 1979a). Mendelssohn (1985) reported three free-living individuals in Israel of approximately 15 months of age with three large embryos.

The striped hyaena prefers to den in caves. Den entrances are fairly narrow and may be hidden by large boulders. Measurements of two dens in the Karakum desert yielded a width of 0.67m and 0.72m for the entrance. The dens lead 3m and 2.5m down and extended over a distance of 4.15m and 5m. There were no lateral extensions or special chambers (Heptner and Sludskij 1980). These simple constructions contrast with much more elaborate designs exceeding 27m in length discovered in Israel (Kerbis-Peterhans and Horwitz 1992).

Competition

In Israel the striped hyaena may encounter wolves, red foxes and caracals at carcasses. On a one-to-one basis it is dominant over the wolf, but a group of four wolves has been observed driving a single hyaena from a carcass (H. Mendelssohn unpublished data). A caracal may drive a subadult striped hyaena away from a carcass (Skinner and Ilani 1979). Competitors in central Asia include leopards, wolves, golden jackals, red and corsac foxes and vultures (Heptner and Sludskij 1980). The striped hyaena frequently scavenges from kills of tiger, leopard, cheetah, and wolf – a major component of the striped hyaena's diet in central Asia are scavenged carcasses killed by wolves (Heptner and Sludskij 1980, Lukarevsky 1988). In India, the striped hyaena usually wins one-to-one encounters over carcasses with leopards, tiger cubs and domestic dogs but may be dominated by adult tigers (observations in Action Plan questionnaires, Pocock 1941, Rieger 1979 and references therein). In east Africa, the striped hyaena is dominated by the spotted hyaena and sometimes the leopard, yet in turn it may dominate the leopard and the domestic dog (Kruuk 1976). When attacked by domestic dogs or dug out by humans, the striped hyaena may use "shamming", i.e. the animal pretends to be dead, even if repeatedly bitten (Pocock 1941, Heptner and Sludskij 1980).

Mortality and pathogens

Humans are the most important source of mortality. Throughout the Arabian peninsula and North Africa it is loathed as a grave robber and severely persecuted through baiting, tracking and trapping.

Persecution

A bounty system operating in Algeria during the 1880s contributed to a decline in population size; in 1881 and 1882 alone, 196 individuals were killed (Kowalski and Rzebik-Kowalska 1991). In the Arabian peninsula, the majority of museum specimens were collected dead, hanging in trees and on sign posts (Gasperetti *et al.* 1985).

The striped hyaena appears to be very susceptible to poisoning as it readily accepts strychnine-poisoned bait. In many cases it is not the target, as the bait is laid out for other carnivores such as wolves or leopards suspected of killing livestock, or because wolves are wanted by fur trappers in central Asia (Heptner and Sludskij 1980). Along the Mediterranean coast in Israel, the striped hyaena was exterminated by strychnine poisoning during the rabies eradication campaign administered by the British government between 1918 and 1948. The striped hyaenas ate poisoned donkey carcasses that were provided to control golden jackals, then the main carrier of rabies. Further large-scale poisoning occurred here between 1950 and 1970. Today, large-scale reduction by strychnine poisoning also threatens the striped hyaena throughout Niger (Millington and Tiega 1990, 1991).

In the Caucasus and in central Asia, a major source of mortality over the past 100 years has been persecution, as the striped hyaena was held responsible for the disappearance of unattended small children. In the 1880s alone the striped hyaena was held responsible for the kidnapping or injuring (biting) of 25 children and three adults who slept outside in the district of Jerewan in the Caucasus. The government paid a substantial bounty (100 rubles) for every hyaena killed. Further cases of striped hyaenas killing or kidnapping children in this area were reported in the 1890s and 1900s, as well as in Azerbaidjan in the 1930s and 1940s (Heptner and Sludskij 1980). Today in India, the government still organises killings of wolves and striped hyaenas (even in conservation areas) in places where carnivores are suspected of child lifting. In recent times this has happened in Karnataka, Bihar state. Attacks on children have been reported as recently as 1974 when 19 children up to the age of four years were reported to be killed at night (Rieger 1979a).

Hunting and trapping for fur

Striped hyaenas have rarely been hunted for their fur (for instance in the Caucasus countries), but have incidentally been caught in traps set by fur trappers for other species. In Russia, the striped hyaena was not even considered a fur species but was bought and sold as "minor quality wolf" and "fox". Nevertheless, in the areas covered by the Commonwealth of Independent States (i.e. the Caucasus region, Tadzhikistan, Turkmenistan and Uzbekistan) a total of 200 skins were bought by the government in the 1930s. In the 1950s less than 100 were bought and none have been bought since 1970. In Turkmenistan alone between 1931 and 1937 up to 130 skins were offered by trappers every year. However, since 1948 this number has been reduced to a few dozen and since 1970 none have been offered (Heptner and Sludskij 1980).

Road accidents

In Israel today the major mortality factor is traffic accidents (H. Mendelssohn, pers. comm.). About 20 to 30 hyaenas (roughly 15–20% of the population) are killed each year on the roads. For instance, on the Arara road (from the Dead Sea to Eilat) 20 were reported to have been killed between 1982 and 1985, and 24 between 1988 and 1991. Nissim (1985, 1986) observed that all the cubs reared by three females in several litters were killed on roads before they were one year old. Striped hyaenas are apparently attracted to the roads by the smell of small animals that have been run over (H. Mendelssohn pers. comm.). These high losses imply that the population is very young and can only be sustained because females mature early and manage to rear a litter before being hit by a car. Evidence of a shift in age distribution over the past 50 years comes from the observation that in the 1940s old hyaenas with worn teeth were found, whereas today no hyaenas are found that are older than 5–6 years (H. Mendelssohn pers. comm.).

Natural sources of mortality

In central Asia natural enemies are the wolf and were, until recently, tiger and leopard. Some hyaenas die by breaking through ice on lakes (Heptner and Sludskij 1980).

In captivity, social factors, (i.e. death due to injuries from conspecifics) comprised 9% of all deaths, and experience has shown that two females older than 15 months cannot be kept together without one being killed (Rieger 1979a). In captivity, striped hyaenas may reach 23–24 years of age (Rieger 1979a).

Pathogens

Little is known about pathogens and their impact on the striped hyaena, or the role of the species as a vector for pathogens that may affect humans (Israel: Loos-Frank 1990; Iran: Sadighian *et al.* 1973; Tadzhikistan: Borgarenko and Khokhlova 1978; Yemen: Stanley 1990). In Libya, the striped hyaena has been ruled out as a vector for the tapeworm (which causes serious cysts in humans), as it is rarely carried by the species (Hufnagl 1972, Gebreel *et al.* 1992).

Current or planned research projects

1. A conservation project in Georgia is currently underway (J. Badridze, Noah's Ark Center for the Recovery of Endangered Species, Georgia). It will collect data from Georgia and neighbouring areas (Armenia, Azerbaidjan) on population size and distribution. A detailed study will focus on habitat use, diet, and factors that may affect current population dynamics, including competition with other carnivores, habitat destruction, and other forms of human impact. The results will be used to set up a recovery program that may include the establishment of protected areas to safeguard key populations and the reintroduction of individuals or pairs if deemed suitable.
2. A research project on predator-prey dynamics in semi-arid ecosystems in Kutch in India is due to start shortly (Y. Jhala, Wildlife Institute of India). It will assess the role of predation in a carnivore community comprised of the striped hyaena, the Indian wolf and the golden jackal, and focus on habitat utilisation, diet and interactions with people and their livestock.
3. A study of the ecology of the striped hyaena in the Nilgiri Biosphere Reserve of the western ghats area in South India is also soon to be started (R. Arumugam, Indian Institute of Science).

3.3 Brown hyaena *Hyaena (Parahyaena) brunnea* (Thunberg, 1820)

Gus Mills

Box 3.3. Common and indigenous names for the brown hyaena.

Afrikaans – bruin hiëna, strandwolf, strandjut
English – brown hyaena
French – hyène brune
German – braune Hyäne, Schabrackenhyäne
Ndebele – impisi
Portuguese – hyena castanha
Southern Sotho – phiribjokwane
Spanish – hiena parda
Northern Sotho – sephiribjôkwane
Tsonga – shimisani
seTswana – phiritshwana
Xhosa – inchuka, ingqawane

Physical description

This medium-sized, dog-like animal has long forelegs and well developed forequarters, but weak hindquarters and a sloping back. The pelage is shaggy and dark brown to black, except around the neck and shoulders which are white. The underparts are light coloured and the lower forefeet and hindfeet have white stripes. The ears are long and pointed.

Adults usually weigh around 40kg (28–47kg) (Mills 1982a), with little variation between the sexes. Exceptionally large brown hyaenas include a female from the Eastern Cape, South Africa which was recorded to have weighed 67.6kg (P. Swanepoel pers. comm.) and two of unrecorded sex from the Eastern Transvaal Lowveld, which weighed 72.6 and 59.9kg (Roberts 1954). Head to tail the brown hyaena measures 1.4m (1.26–1.61m) and stands 0.79m (0.72–0.88m) at the shoulder.

Habitat

The brown hyaena inhabits the South West Arid Zone of Africa (Smithers 1983). It is found in desert areas with annual rainfall less than 100mm, particularly along the coast, semi-desert, open scrub and open woodland savannah with a maximum rainfall up to about 650mm. It shows an ability to survive close to urban areas. It is independent of drinking water, but needs some type of cover in which to lie up during the day. For this it favours rocky, mountainous areas with bush cover in the bushveld areas of South Africa (Skinner 1976).

Diet and foraging behaviour

Diet

The brown hyaena is primarily a scavenger of a wide range of vertebrate remains, which is supplemented by wild fruits, insects, birds' eggs and the occasional small animal which is killed. In the southern Kalahari vertebrate prey killed by brown hyaenas made up only 4.2% of the food items eaten (Mills 1990). These were all small animals such as springhare, springbok lamb, bat-eared fox and korhaan species. Along the Namib Desert coast it feeds predominantly on Cape fur seal pups, of which only 2.9% were killed by the brown hyaena (Goss 1986). It also scavenges other marine organisms washed up on the shore. In agricultural areas of the Transvaal, South Africa, cattle (in the form of carrion) and medium-sized and small indigenous animals were most commonly eaten (Skinner 1976).

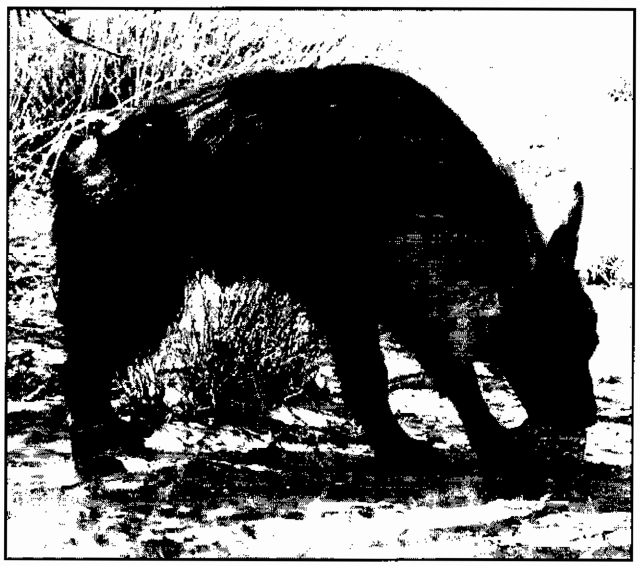


Photo 3.3. Brown hyaena eating a tsama melon in the Kalahari.

G. Mills

Foraging behaviour

The brown hyaena is a strictly solitary, predominantly nocturnal forager, covering large distances in its search for food. In the southern Kalahari the brown hyaena spent on average 80% of the hours of darkness active and covered 31.1km per night, with the maximum recorded being 54.4km (Mills 1990). Its sense of smell is well developed and carrion is mainly detected by smell. Even fairly old and dry carcasses can be detected from 2km downwind. Hunting is unspecialised and opportunistic, directed at small animals only and largely unsuccessful. Of 128 hunts observed in the southern Kalahari, only six (4.7%) were successful, with the most often hunted animals being springhare, springbok lamb and bat-eared fox (Mills 1990).

Damage to livestock

The impact of the brown hyaena on domestic animals is usually small (Table 3.2). However, when specifically asked about this impact, nearly all respondents to the Action Plan questionnaire mentioned that in particular sheep and goats were sometimes killed by the brown hyaena, as well as calves of cattle, poultry, and domestic dogs and cats. Stock killing is often carried out by a particular individual. Removal of this individual solves the problem, according to Skinner (1976), who reported two cases of stock killing over several months which ceased once the culprit was removed, even though there were other brown hyaenas in the area. Finding a brown hyaena on a carcass is not evidence that this individual was the killer, as brown hyaenas are habitual scavengers.

Table 3.2. Damage to livestock (species and frequencies of kills: O often; R rarely) by brown hyaenas as reported in the questionnaire survey.

Country	Number of cases/year	Cattle	Sheep	Goat	Others	Remarks
Botswana	R	-	-	(R) mainly young	-	
Mozambique	R	R	-	-	-	Said not to kill, but to maim
Namibia	< 5	-	R	R	Poultry	Probably often confused with spotted hyaena
South Africa						
Cape Province	11-50	(R) calves	O	O		
Natal	<5	(R) calves	R	R		
Free State	11-50	-	O	R	Dogs	
Transvaal	11-50	R	R	R	Poultry, dogs, cats	

Social behaviour

Brown hyaenas live in clans ranging in size from a solitary female and her cubs to groups containing several females and their offspring of different ages. Adult males either remain with their natal clan, become nomadic or immigrate into a new clan.

Although members of a clan forage on their own, several may come together at a large food source. Clan members also join together to defend a common territory. In the southern Kalahari clan territories varied in size from 235 to 480km² (Mills 1990), and along the Namib Desert coast a group territory was measured to cover 220km² (Goss 1986). In the Transvaal agricultural areas the range of a translocated adult male was only 49km², suggesting that agricultural development may in some instances be advantageous to the brown hyaena (Skinner and van Aarde 1987). Clan size is determined by the type of food in the territory and territory size by the manner in which the food resources are distributed.

Territorial ownership, and also probably information between group members, is communicated by defecating at latrines and particularly by depositing anal gland secretions onto grass stalks in a scent marking behaviour called pasting (Photo 3.4). Each time a brown hyaena pastes, two distinct substances are secreted: a thin, black smear consisting mainly of lipo-fuschin from apocrine tissue and, below it, a thick, white blob, rich in lipid, the smell of which lasts for over 30 days. Brown hyaenas distribute pastings throughout the territory, on average 2.6 times per kilometre travelled, although they paste with a higher frequency near territory boundaries than in the hinterland of the territory. Pastings are so well distributed over a brown hyaena territory that an individual is hardly ever more than 500m from an active pasting (Gorman and Mills 1984).

Territorial fights are usually ritualised neck-biting bouts between two animals of the same sex, accompanied by loud yelling and growling by the submissive animal. The brown hyaena has no long distance calls.

Reproduction and denning behaviour

The brown hyaena is a polyoestrous, non-seasonal breeder with anoestrous occurring during lactation. The gestation period is approximately 97 days and mean litter size is 2.3 (range: 1–5) (Mills 1982b). Both nomadic and immigrant males may mate and all adult females in a clan may reproduce, although the matriarch apparently produces more cubs than other female clan members.

The den is usually a single hole in the ground with a narrow entrance of about 30cm height and 50cm width (Mills 1982b), although in some areas caves are used (Skinner 1976, Goss 1986). At most dens a single litter of cubs is raised, but two or even more females may share a den in territories where more than one female breeds (Owens and Owens 1979a, Mills 1990). The breeding females are usually a mother and her grown up daughters and the females may even suckle each other's cubs, although they give priority to their own. The denning period lasts 15 months, during which time the cubs use several different dens. In the southern Kalahari each den is occupied for an average of 3.6 months (Mills 1990). For the first three months of their lives the cubs are nursed by their mother, typically at sunset and sunrise, after which the milk diet is supplemented to an increasing degree by food which is carried to the den by all clan members. Consequently brown hyaena dens often become littered with bones and other food remains (Mills and Mills 1982a). The cubs are weaned at about one year of age, but from

G. Mills

Photo 3.4. Brown hyaena depositing a secretion from its anal gland onto a grass stalk in a scent marking behaviour known as pasting.

about ten months of age they also begin to forage for themselves.

Competition

Over much of its range, the brown hyaena lives in association with other carnivorous animals and benefits from many of them by scavenging from their kills. Lion kills provide many scavenging opportunities for brown hyaenas, although they are dominated and even sometimes killed by lions. The brown hyaena is usually dominant over the leopard, cheetah, caracal, and black-backed jackal. Competition for food between the brown hyaena and black-backed jackal can at times be severe, and vultures too can deprive it of food. The spotted hyaena is dominant to the brown hyaena and in certain areas deprives it of a significant amount of food. This may have a detrimental effect on brown hyaena numbers in certain areas and may even affect its distribution, as where the spotted hyaena is common the brown hyaena is usually absent or very rare (Mills 1990).

Mortality and pathogens

In conservation areas the highest mortality rates are amongst subadults and old adults. Starvation and wounds inflicted during both inter and intra-specific fights are the main causes of natural mortality. Starvation can be caused by a severe wearing down of the teeth, which results in an inability to consume bones. There is little evidence suggesting that disease is an important cause of mortality.

Outside national parks and protected areas, the brown hyaena may run into conflict with humans. Brown hyaenas have been shot, poisoned, trapped, and hunted with dogs in predator eradication or control programmes in Botswana, Namibia, South Africa, and Zimbabwe (Smithers 1983). Often brown hyaenas are inadvertently killed in non-selective control programmes. They are also occasionally run over by vehicles in South Africa.

Little is known about parasites and pathogens in the brown hyaena. A tapeworm *Taenia hyaenae*, a nematode *Spirocerca lupi*, and a pentastomid *Armillifer armillatus* have been recorded to affect hyaenas (Greve and Russel 1974, Mills 1982b). Rabies or a rabies-related viral infection has only been recorded in three individuals (Swanepoel *et al.* 1993).

Current or planned research projects

A study of the foraging behaviour of the brown hyaena at seal colonies on the Namib Coast is due to commence in the latter half of 1997 (I. Wiesel, University of Hamburg).

3.4 Spotted hyaena *Crocuta crocuta* (Erxleben, 1777)

Heribert Hofer

Physical description

Appearance

This large, dog-like animal has a spotted coat and is heavily and strongly built. Its general colour is sandy, ginger or dull grey to greyish brown, with blackish or dark brown spots on the back, flanks, rump, and legs. Spots may turn brown and fade with age. The forelegs are longer than the hind legs so that the back slopes downwards to the base of the tail. The long, thick neck provides a highly muscular structure that complements the powerful cutting and ripping movements of the massive jaws. The head is large, rounded and powerful with a short and blunt muzzle. The ears are rounded, in contrast to the pointed ears of other hyaena species. The hair is short, coarse and woolly, and is composed of moderately fine underfur with a length of 15–20mm, and longer, stouter, flat-sectioned bristle hairs with a length of 30–40mm. Their four-toed feet have short, blunt, non-retractable claws and broad and flat pads. They have a short tail, comprised of approximately 24cm of bone with an added 12cm of hair only. The tail is narrow and fairly thin and ends in a black, bushy tip. Total body length is around 1.3m and front shoulder height is 0.75m. Body mass ranges from 45kg for males and 55kg for females in the Serengeti (H. Hofer and M.L. East, unpublished data) to more than 70kg in southern Africa (see Mills 1990).

A detailed description of the skull, musculature and locomotion can be found in Buckland-Wright (1969), Spoor and Badoux (1989), and Spoor and Belterman (1986).

Scent glands, situated on either side of the rectum, discharge secretions into a sac situated between the tail and the anus. During scent marking the sac is everted and the secretions are deposited in a semi-crouched position while walking or standing over a grass stalk or small bush (further details see section on Territories, below).

Sexing individuals

The spotted hyaena has been considered a hermaphrodite in many cultures because the secondary sexual organs appear to be very similar in males and females. The female clitoris is of the same size and shape as the penis, can be erected and it is situated at exactly the same position as the penis would be in a male. Through the clitoris runs the urogenital canal, with an exit in a narrow slit at the tip, similar to the penis. The similarity to the male is further enhanced by two swellings simulating a scrotum. These

Box 3.4. Common and indigenous names for the spotted hyaena.

Afrendile – walaba
Afrikaans – gevlekte hiëna
Amharinja – djibb
Arab (CAR) – marfaïn
Arab (Chad) – marfaïn
Arab (North Africa) – d'ba
Arabi (Ethiopia) – dibb
Ateso – ibuin
Avukaia – labagu
Babouté – mangou
Baguirmien – niougo
Baka – libagu
Bakola – massobé
Bambara – namakoro, souroukou
Banda – bongo
Baya – bongo
Bechuana – piri, phiri
Bemba (Zambia) – chimbwi
Bornouan – boultou
Creole – lobo
Danakil – jangóula
Dioula – suruku, namakoro
Elkoni – makatiet nyenegea
English – spotted hyaena
French – hyène tachetée
Fula – bonoro
Futa – bonoro
Fulbe – fourou
Gallaorabéjsa – wårabéssa, orabéjsa
Gambe – mangili
German – Tüpfelhyäne, Fleckenhyäne
Gouragi – woraba
Gourmantche – namlino
Harari – worábba
Hassaniya – guervave
Haoussa – koura
Herero – mbúngu-mbidíwa
Ila (Zambia) – kabwenga
Jita – imembe
Kalenjin – kimatet
Kaonde (Zambia) – mungolwe
Karamojong – ebu, etutui
Kichagga – ingurunju, ifulu
Kigogo – misi
Kikamba – mbiti
Kikondo – mbulu
Kikuyu – hiti
Kiliangulu – warabes
Kiluba – kimburi
Kimaragoli – mbiti
Kimeru – mbitingaau
Kinyarwanda – impyisi
Kinyaturu – mpiti
Kinyiha – ipatama
Kipare – ibau
Kirangi – mbichi
Kisukuma – mbiti
Kisungwa – fifi
Kiswahili – fisi, nyangao
Kitaita – mbisi
Kizigua – ibau
Koniagui – iriguni
Kota – massoba
Kotoko – machi
Kunda (Zambia) – tika
Luzi (Zambia) – sitongwani
Luganda – empisi
Lugbara – rar
Luhya – namunyu
Lunda (Zambia) – kangolu, kaubi
Luo – otoyo
Luvale (Zambia) – chimbungu, munguli
Lwo – lagwara
Madi – ebowu
Malinké – namakoro, souroukou
Mambakushu – dimbúngurúmba
Manding – tourouma
Mangbetu – neunga
Masai – ondilili, oln'gojine
Maure – chertat, gaboune, gougouh
Mboko – assoba
M'boum – baglak
Mondo – lepagu
Mongom – massobé
Moore – katre, swasa
Ngambaye – riguen ndah
Nkoya (Zambia) – muntambwi
Nsenga (Zambia) – chimbwe
Nyanja (Zambia) – fisi
Ouolof – bouki
Ovambo – kafúkambúngu, mbúngu-omaníni
Ovacuangari – divúndu
Ovadirico – divúndu
Peuhl (Fouta Djalon) – fowru, bonorou
Peuhl (Burkina Faso, Cameroon, Mali) – fowrou, fouru
Portuguese – hiena machada
Runyoro – empisi
Sambara – namakoro, souroukou
Sara – nyéyi
Sarakolé – tourougué
Sebei – mangatiet
Serere – omone
seTswana – phiri, leHolo
Shona – bere
Somali (Ethiopia) – worábbo
Somali (central Somalia) – uaraba
Somali (Migiurtina) – duruà
Somali (Nogal) – drueh
Songhai – koro
Sotho (northern and southern) – phiri
Tigrinja – zibb-i
Tonga (Zambia) – suntwe
Toucouleur – Foorou
Tsonga – mhisi
Tumbuka (Zambia) – chimbwi
Twi – pataku
Xhosa – impisi, mpisi, isAndawane
Yoruba – kòríkò, ikoókò
Zande – ngini, nzege

Further names in a number of Southern African click languages were recorded by Shortridge (1934).

swellings are slightly smaller than a male's scrotum, but are similar in form and colour and are located where the male organs can be found. There is no vagina as the outer labiae are fused.

Diagnostic traits that reliably distinguish males from females in the field are:

1. The shape of the glans of the penis and its equivalent in an erect clitoris are different (Photo 3.5a & b). This can be seen in cubs from approximately the third month onwards and permits a simple, reliable method of sexing in the field. The male glans is more likely to be pointed backwards towards the hind legs, continuing the arch of the erect penis, and has a pronounced incision at its base. The shape of the glans is asymmetric and terminates in a tapering tip (Photo 3.5a). In contrast, the incision at the base of the "glans" of the clitoris is less pronounced, its shape symmetric, and its termination blunt, not tapered. The clitoris is also more likely to point forward towards the stomach (Frank *et al.* 1990, H. Hofer unpublished data) (Photo 3.5b). Other sexing methods require hair or tissue samples and employ histological (Wurster-Hill *et al.* 1970, Yost 1977) or molecular methods (Schwerin and Pitra 1994).
2. When females are lactating, their hairless udder, comprised of two large, black or partially pink nipples, is clearly visible and diagnostic.
3. Older males are likely to have a convex stomach shape – the line of the stomach descends from the front legs and ascends again to the hind legs, and if pronounced makes the belly look almost like a "V". In females the stomach line remains flat towards the hind legs where it ends in the udder. In older females, the udder is stretched and the belly line gives the appearance of descending towards the hind legs. Males also have a slighter build than females. The outline of the stomach is distorted when animals have recently fed, so this criterion works reliably only with animals with a normal belly size.
4. It is also possible to distinguish males from females in social situations by their behaviour. Males often approach females in a hesitant way with submissive gestures, such as positioning their ears backwards. Cubs and subadult immature females are very difficult to distinguish from similarly aged males unless the erect clitoris or penis can be well observed.

Habitat

The spotted hyaena inhabits semi-desert, savannah and open woodland, dense dry woodland, and mountainous forest up to 4,000m altitude (Kruuk 1972a). It is absent from or occurs in only very low densities in tropical rainforests and along coasts (e.g. Namibia). In west Africa, preferred habitats include the Guinea and Sudan savannahs. It does not occur in the belt of dense forest along the coast (Happold 1973). In the Namib Desert, it is found in riverine growth along seasonal rivers, the subdesertic pro-Namib and the adjoining inland plateau (Coetzee 1969). In prime habitat, densities of the spotted hyaena are higher than those of other large carnivores, including those of both the striped hyaena and brown hyaena. In desert and semi-desert regions, however, the brown hyaena and striped hyaena can occur at higher densities than the spotted hyaena (Mills 1990).

Diet and foraging behaviour

The spotted hyaena is still widely regarded as a scavenger that picks up leftovers at the kills of other carnivores (cheetah, leopard, lion) or feeds on carrion. However, this is not correct. All studies demonstrate that the spotted

Photo 3.5. The glans of a male penis – left **(a)** and female clitoris – right **(b)** of the spotted hyaena, showing the difference in shape of this organ in the two sexes.

H. Hofer and M. East

hyaena is a predator in its own right and in natural ecosystems kills the majority of the animals it feeds on. The spotted hyaena is impressively versatile in its choice of prey, as its food varies greatly between ecosystems. In addition, it has developed a wide diversity of hunting techniques.

The misconception of the spotted hyaena being primarily a scavenger may have arisen for the following reasons:

- Very little is left behind at spotted hyaena kills because carcasses are completely dismembered and everything except horns can be eaten. Often the only remaining evidence of a hyaena kill is a wet patch of vegetation and the stomach contents of the victim. Thus, even experienced naturalists are likely to miss signs of hyaena predation.
- Spotted hyaenas feed with great speed. For instance Kruuk (1972a) observed 38 spotted hyaenas completely demolishing an adult zebra in 15 minutes. Thus, chance observations of hyaena predation and feeding are likely to be rare.
- Few people have observed spotted hyaenas hunting, as this behaviour usually takes place at night. Many people have observed them at kills where lions are feeding at dawn. Here the impression is that the spotted hyaenas are waiting for their turn after the lions have finished eating. In such situations it is possible that the hyaenas made the kill and were chased off by the lions. If spotted hyaenas are present around a lion-occupied kill and have blood on their faces and necks, while the lions show none or little, then the kill was almost certainly made by the hyaenas.

Prey species

The spotted hyaena primarily kills and scavenges mammalian herbivores. This includes small, medium and large-sized antelope, Cape buffalo, and other herbivores such as zebra, warthog, and the young of giraffe, hippopotamus and rhinoceros. It can be very opportunistic and has been recorded eating almost any mammal, bird, fish or reptile, irrespective of size or species (see Brown and Root 1971, Pienaar 1969, Kruuk 1972a, Eloff 1975, Kingdon 1977, Kruuk 1980, Tilson *et al.* 1980, Stelzner and Strier 1981, Hitchins and Anderson 1983, Mills 1984, 1990, Henschel and Skinner 1990a, Sillero-Zubiri and Gottelli 1992a). It may also pick up carrion and human-associated organic material, including cooked porridge, offal, garbage, a variety of vegetable matter, and buffalo and wildebeest dung. The spotted hyaena has a reputation of killing and scavenging domestic stock, mostly cattle, sheep and goats, but also poultry, cats, dogs, horses, donkeys, and camels (see below). These predatory activities have actually been observed.

Diet in different ecosystems

Detailed studies on diet have been conducted in the Kruger ecosystem (South Africa), the Etosha and the Namib (Namibia), the Kalahari and the Chobe (Botswana), the Serengeti (Tanzania), and the Masai Mara and the Aberdare Mountains (Kenya).

In Kruger National Park the most important prey items are blue wildebeest, buffalo, Burchell's zebra, greater kudu and impala (Henschel and Skinner 1990a), whereas in the nearby Timbavati area the major food species are giraffe, impala, wildebeest and zebra (Bearder 1977). In Namibia, the main prey are springbok and kudu in the Etosha National Park, gemsbok, mountain zebra, and springbok in the Namib (Tilson *et al.* 1980, Skinner and van Aarde 1981), and wildebeest in other places (Action Plan questionnaire). In the southern Kalahari their principal prey are gemsbok, wildebeest, and springbok (Mills 1984b, 1990). In Chobe spotted hyaenas principally hunt migratory zebra and resident impala (Cooper 1990). In the Serengeti ecosystem and the Ngorongoro Crater in northern Tanzania, spotted hyaenas primarily hunt wildebeest, Thomson's gazelle and zebra (Kruuk 1972a, Hofer and East 1993a, 1995a). In the Masai Mara (Kenya) more than 80% of prey are topi and Thomson's gazelle, except for the four months when the migratory herds of wildebeest and zebra are present (K.E. Holekamp and L. Smale unpublished data). In the Aberdare Mountains (Kenya) the dominant prey items are bushbuck, suni and buffalo (Sillero-Zubiri and Gottelli 1992a). In northern Kenya spotted hyaenas are likely to live on Grant's gazelle, gerenuk, sheep, goats, and cattle (Kruuk 1980).

Little is known about the spotted hyaena's diet in west Africa. Although it is considered to be primarily a scavenger on wildlife and human rubbish, the spotted hyaena also attacks domestic stock and at least in some areas is thought to kill small to medium-sized antelopes. In Cameroon spotted hyaenas are commonly seen feeding on small antelopes like kob, but may also scavenge reedbuck, kongoni, buffalo, giraffe, elephant, topi and roan antelope. In Malawi it has been recorded to feed on medium to large-sized ungulates such as waterbuck and impala. In the Selous Game Reserve (Tanzania) it has been recorded to feed primarily on wildebeest, followed by buffalo, as well as zebra, impala, giraffe, reedbuck, and kongoni (S. Creel unpublished data). In Uganda it is believed to eat primarily birds and reptiles and in Zambia it is believed to concentrate on carrion.

Diet choice and prey preferences

In the southern Kalahari and Kruger National Park migratory species are taken less often than expected, and the most common resident herbivore species more often than expected. In the southern Kalahari, the principal prey is gemsbok, the most common resident herbivore, and wildebeest, the most common migratory herbivore (Mills 1990). Gemsbok are preferred, whereas wildebeest are killed less often than expected (Mills 1990, Hofer and East 1995a). In Kruger the preferred prey are also resident herbivores (kudu, impala and warthog), whereas migratory herbivores are killed less often than expected (Henschel and Skinner 1990a).

In Chobe and the Serengeti, migratory species are taken more often than expected, and the principal resident herbivores less often than expected. In Chobe the principal prey is impala, the most common resident herbivore, and zebra, the most common migratory herbivore (Cooper 1990). Zebra are preferred, whereas impala are killed less often than expected (Hofer and East 1995a). In the Serengeti, wildebeest, the most common migratory herbivore, is the principal prey (Kruuk 1972a) and killed more often than expected, whereas impala, the most common resident herbivore, is not an important prey species (Kruuk 1972a, Hofer and East 1993a) and is killed less often than expected (Hofer and East 1995a).

Thus, it appears that the spotted hyaena has prey preferences but that these do not follow simple rules. Prey preferences depend on whether herbivore prey is resident or migratory, but the preferences change between southern African and more northern ecosystems.

Foraging behaviour

The spotted hyaena detects live prey by sight, hearing, and smell. It detects carrion by smell, the noise of other predators feeding on the carcass, or, during daytime, by watching vultures descending on a carcass. Its hearing is acute enough to pick up noises emanating from predators killing prey or feeding on carcasses over distances of up to 10km (Mills 1990).

Typically the spotted hyaena hunts solitarily or in small groups of two to five, although larger parties have been observed (Kruuk 1972a). During a hunt, individuals often run at moderate speeds through a herd of ungulates apparently looking at herd members before deciding which individual to attack. The spotted hyaena chases its prey over long distances, often several kilometres, at speeds of up to 60km/h (Kruuk 1972a, Mills 1990). The maximum distance recorded was 24km in pursuit of an eland in the Kalahari (Mills 1990). It has also been observed to run down flamingoes in shallow soda lakes (Brown and Root 1971) and to drown lechwe in flood plains by swimming after the fleeing prey (Child and Robbel 1975). Ambush attacks on resting wildebeest in the Serengeti (H. Hofer and M.L. East unpublished data) or solitary, standing topi in the Masai Mara in Kenya may also occur (Rainy and Rainy 1989).

The spotted hyaena travels long distances in search of prey. In the Kalahari, the average distance travelled between significant food items varied between 42 and 80km (Eloff 1964, Mills 1990). In the Namib Desert the maximum distance between the core area of a clan's range and distant carcasses was 30km (Tilson and Henschel 1986). In Chobe hyaenas walked up to 28km between a clan range and a permanent source of water. In the Serengeti all clan members frequently leave their territory during periods when migratory herds are absent from the clan territory, and go on foraging (commuting) trips to the nearest concentrations of migratory wildebeest, zebra and Thomson's gazelles (Hofer and East 1993a,b,c). These trips last on average three days for lactating females, who need to return to the clan territory to nurse their young, and nine to ten days for non-lactating females and males. Lactating females commute between clan territory and migratory herds 40 to 50 times per year, other adults undertake fewer trips. As the average one-way distance between clan territory and the nearest migratory herds is 40km, lactating females commute at least 2,880–3,680km per year (Hofer and East 1993c). This is three times the annual distance covered by the migratory herds (Sinclair and Norton Griffiths 1979).

Hunting success

Hunting success varies with group size, prey species, prey defence tactics, prey size and age, and habitat (Mills 1985a, 1990). Several hyaenas are required to kill buffalo and zebras because of their large size and sharp hooves and because zebra groups defend attacked conspecifics (Kruuk 1972a, Sillero-Zubiri and Gottelli 1992a, H. Hofer and M.L. East unpublished data). Hunts of ungulate calves are more successful than hunts of adults of the same species (Mills 1990). Pregnant ungulate females and injured, sick or old prey are easier to hunt than healthy adults in their prime (Kruuk 1972a, Mills 1990). A strong and experienced hyaena may kill an adult wildebeest on its own (Mills 1990, H. Hofer and M.L. East unpublished data). Gemsbok are probably more easily caught on sandy substrates in the Namib desert (Skinner and van Aarde 1981) and lechwe are more easily caught in water (Child and Robbel 1975).

Food intake

In one sitting, adult spotted hyaenas are able to eat up to 18kg (Bearder 1977), which is equal to one-third of their own body weight. They can endure more than a week without food without any obvious negative consequences. Cubs show a remarkable resilience to lack of regular food. In both the Kalahari (Mills 1990) and the Serengeti (Hofer and East 1993c), spotted hyaena cubs regularly go without food or drink for several days without displaying obvious consequences. Average daily food consumption for an adult was estimated at 2.0kg/day in the Ngorongoro Crater

(Kruuk 1972a), 3.8kg/day in Umfolozi (Green *et al.* 1984) and the Kruger National Park (Henschel and Skinner 1990a), and 4.0kg/day in the Namib (Henschel and Tilson 1988).

Damage to domestic stock

Damage to domestic stock mainly involves cattle, sheep and goats and varies widely in intensity (Table 3.3). However, reports of damage are often not substantiated and a hyaena scavenging at a carcass may be mistaken for having killed the animal. The importance of domestic stock as a food item may depend on accessibility; i.e. stock keeping practices (Kruuk 1980, Chapter 7), availability of alternative prey, and availability of human-associated sources of rubbish and other organic material (information from Action Plan questionnaires). "Surplus" – killing of small domestic stock, has been reported in eastern Cape Province, South Africa (Stuart 1981). The presence of domestic dogs and the use of thorn fences to coral livestock are efficient in reducing attacks on domestic stock by spotted hyaenas and other predators (see Chapters 5 and 7). In a study of livestock damage by spotted hyaenas in northern Kenya, 90% of all kills were made outside the protection of thorn fences (Kruuk 1980).

Social behaviour

The spotted hyaena is the most social species of all carnivores in that it has the largest group sizes and the most complex social behaviour. The spotted hyaena lives in social groups called clans that defend group territories. The society is characterised by a strict dominance hierarchy.

Table 3.3. Species and frequencies of domestic stock taken by spotted hyaenas as reported in the Action Plan questionnaire survey (O often R rarely).

Country	Number of cases/year	Cattle	Sheep	Goat	Others	Remarks
Botswana	> 50	R	O	O	-	may cause quite a lot of stock loss when people do not look after stock properly; often blamed for stock losses when scavenging at dead carcasses
Burkina Faso	11-50	some, young	young (R)	young (R)	-	
Cameroon	rarely	R	R	R	donkey?	
Central African Republic	rarely	yes	-	-	-	Chadian cattle herds that come to graze inside reserves
Ethiopia	> 50	O	O	O	donkey, horse	by repute all species often; stock keeping techniques poor
Guinea-Bissau	> 50	O	O	O	donkey	frequently by repute. In Canquelifa, hyaenas are said to move in massively for a month and kill, herds suffering large damages
Kenya	> 50	R	O	O	donkey, camel	donkey and camel by repute
Malawi	> 50	yes	yes	yes	poultry, cat, dog	
Namibia	> 50	O	O	O	dog (O), horse (R), donkey (O)	in western Caprivi some herdsmen claim major losses but these are unsubstantiated
Niger	6-10	-	R	R	-	
Nigeria	yes	poss.		R	poultry	
Senegal	< 5	yes	yes	yes	-	
Sierra Leone	no	-	-	-	-	
South Africa	few	R	R	R	donkey (R)	
Tanzania	some	R	R	R	-	unlikely to be reported; see Mchitika (1996)
Uganda	< 5	-	yes	yes	poultry	
Zambia	very limited	yes	-	yes	-	very little livestock present

Females are dominant over males, and even the lowest ranking female is dominant to the highest ranking male. Females usually remain in their natal clan and thus large clans may contain several matrilines. Males typically disperse from their natal clan when about two and a half years of age.

The society is a "fission-fusion" society; thus clan members do not remain together, but frequently forage alone or in small groups. Clan members co-operate in communal defence of the territory, of food resources, and the clan den. As with the social monkeys and apes, spotted hyaena female cubs normally acquire a dominance immediately below that of their mother. There is much "social politics" among clan members, with individuals regularly forging alliances and coalitions. Overall, spotted hyaena society is characterised by its flexible nature, as demonstrated by impressive variation in group size, territorial behaviour, foraging tactics, and nursing behaviour.

Clan size

Unlike many other social species where all group members are usually seen together, spotted hyaena clan members frequently wander alone or in small groups and only sometimes meet in large numbers. This occurs at kills, at the communal den, or when clan members rally together to defend group territories (Kruuk 1972a, Tilson and Hamilton 1984, Henschel 1986, Frank 1986a, Cooper 1989, Mills 1990, Hofer and East 1993a).

The average number of adults and subadults in a clan varies from three in desert and semi-desert areas of southern Africa, to 54 (maximum 80 individuals) in the savannah areas of east Africa. Territory size and the density of prey inside a clan's communal territory usually limit clan size, with one interesting exception. In the Serengeti, an ecosystem dominated by migratory herbivores, hyaena density and clan size are not limited by resident herbivore density, as Serengeti spotted hyaenas regularly undertake foraging trips to feed on nearby migratory herds (Hofer and East 1993a,b, 1995a).

Territories

Territory size in the spotted hyaena is very variable, ranging from less than 40km^2 in the Ngorongoro Crater (Kruuk 1972a) to over 1,000km^2 in the Kalahari (Mills 1990). Clans defend communal territories through vocal displays (East and Hofer 1991b), scent marking (Gorman and Mills 1984) and boundary patrols (Kruuk 1972a). Clan members also co-operate in defending territories during boundary disputes with neighbouring clans. Long-distance calls, particularly whoops, are used to quickly rally clan members to such sites of conflict (Kruuk 1972a, Henschel and Skinner 1991, East and Hofer 1991b). Spotted hyaenas scent mark their territories by pasting a secretion from the anal gland onto grass stalks, and by depositing a secretion from interdigital glands when they scratch the ground (Kruuk 1972a, Mills 1990). Spotted hyaenas also scent mark their territories by defecating in communal latrines (Kruuk 1972a, Mills 1990). Pasting sites and communal latrines are normally scattered throughout a clan's territory and this "hinterland" scent marking strategy (Gorman and Mills 1984) may be a way of optimising the distribution of scent marks over a large area with a limited amount of scent and time (Mills 1990).

In the Serengeti, clans defend territories against neighbouring clans but individual animals may move in transit through other clan territories when they commute to distant migratory herds (Hofer and East 1993b). When migratory herds are present inside a clan territory, many non-residents also enter the territory to feed. Non-residents typically signal submission and retreat when detecting residents, and at kills non-residents usually wait at a distance and feed after residents have departed. Aggression between residents and non-residents is rare when commuters are in transit. Aggression is more common when residents encounter intruders searching for food, and most intense at kills where agonistic encounters may escalate into fights causing serious damage (Hofer and East 1993b). The commuting system of Serengeti hyaenas and the flexible response of territory owners to intruders illustrate the flexible nature of the social behaviour of spotted hyaenas (see also Knight *et al.* 1992).

Female dominance

Spotted hyaena society is female-dominated (Kruuk 1972a), with a clear, linear dominance hierarchy amongst first the female and then the male clan members (Frank 1986b). Top-ranking females have priority of access to large carcasses and this provides increased reproductive success in comparison with low-ranking females (Frank *et al.* 1995a). Apart from males dispersing from natal territories, clans may split (fission) if current clan size exceeds a threshold above which the food base of the territory is insufficient (Mills 1990), or if a territory in the neighbourhood has become vacant (Holekamp *et al.* 1993).

Vocalisations

The highly social nature of the spotted hyaena has led to the evolution of a wide variety of vocalisations (Kruuk 1972a, Henschel 1986, Mills 1990). The best known spotted hyaena vocalisation is the whoop, which can be heard over several kilometres. Spotted hyaenas can recognise each other individually by their whoops, at least within their clan (East and Hofer 1991a). Whoops can function as a rallying call to gather scattered clan members together to defend territory boundaries, food resources, and the communal den. Mothers whoop to locate their wandering cubs and some animals whoop to recruit hunting partners. Whoops are also used as a form of individual display, particularly by animals of high rank (East and Hofer 1991b). Adult males whoop more frequently than females, and top-ranking males put more effort into vocal displays than lower ranking males (East and Hofer 1991b).

Another well-known vocalisation is the laugh or giggle, which is a signal of submission. A submissive individual laughs to signal to its partner that it accepts a lower status.

Greeting ceremonies

The spotted hyaena has a ritualised greeting or meeting ceremony during which two individuals stand parallel and face in opposite directions. Both individuals usually lift the hind leg nearest to the other and sniff or lick the anogenital region of the other. The unique aspect of greetings between individuals is the prominent role of the erect "penis" in animals of both sexes. This is used to signal submission. Greetings occur between all ages and both sexes, although greetings between adult females and males are uncommon and restricted to males above median rank, principally the alpha male. Cubs can erect their penis or clitoris and engage in greeting ceremonies as early as four weeks after birth (East *et al.* 1993).

Reproduction and denning behaviour

Denning

The social life of a clan is centred around the communal den. Some clans use particular den sites for years whereas others may use several different dens within a year or even several den sites simultaneously. These may be separated by up to 7km (Hofer and East 1993a). The dens are not excavated by hyaenas but taken over from other species, mostly warthog, aardvark and bat-eared fox (Kruuk 1972a). The structure of dens does not normally permit the access of adult animals, thus cubs must emerge at the den entrance to have contact with their mother. This structure of small channels underground has been considered an effective anti-predator device which protects cubs during the absence of their mother (Kruuk 1972a). Circumstantial evidence suggests that predation on cubs by other hyaenas (infanticide) or other carnivores may occur but is considered rare (Mills 1990). Infanticide has only been observed in the Serengeti (Hofer and East 1995a) where high-ranking females were observed killing the offspring of low ranking females in the same clan (H. Hofer and M.L. East, unpublished data).

Females may give birth at the communal den or in a private birth den (East *et al.* 1989, Henschel and Skinner 1990b). Mothers with low social status probably use birth dens away from the communal den to ensure that they can maintain continuous access to their cubs. Mothers may also use isolated birth dens to ensure they become acquainted with their cubs before they transfer them to the communal den (East *et al.* 1989). As there are often several animals present at the communal den, cubs probably benefit from the vigilance of adults that can alert young to the presence of predators. Social interactions at the communal den between cubs and adult members of the clan probably play an important role in helping cubs to integrate themselves into the dominance structure of the clan (Holekamp and Smale 1991, 1993, East *et al.* 1993). Cubs are reared at the communal den for a period of approximately 12 months when their major source of food is milk provided by their mother (Hofer and East 1993c, Frank *et al.* 1995a).

Female reproduction

Females give birth through their penis-like clitoris. During parturition, the clitoris ruptures to permit the passage of the young, creating a large bleeding wound of several centimetres that takes weeks to heal. Females usually have a litter size of two, although singletons and triplets have also been observed (Frank *et al.* 1991). Age at first parturition varies substantially between two and five years (Frank *et al.* 1995a, Hofer and East 1996). As all females reproduce and females rear their young together in the communal den, occupied dens may contain up to 30 young of different ages from up to 20 litters. Females usually nurse only their own cubs and reject approaches by other cubs. An exception to this rule was observed during a difficult period in the Kalahari when several mothers suckled offspring communally (Knight *et al.* 1992). Cubs are nursed for a prolonged period and not weaned until they are between 14 and 18 months of age (Hofer and East 1993c). The milk of Serengeti spotted hyaenas has the highest protein content (mean 14.9%) recorded for any terrestrial carnivore, a fat content (mean 14.1%) exceeded only by that of palaearctic bears and the sea otter, and a higher gross energy density than the milk of most terrestrial carnivores (Hofer and East 1995a). Due to their milk's high energy content and the long nursing period, spotted hyaenas have the highest energetic investment per litter of any carnivore (Oftedal and Gittleman 1989).

Reproductive success is related to dominance status in that high-ranking females have a higher reproductive success because they have a shorter interbirth interval and a better chance of rearing young successfully (Frank *et al.* 1995a). Sex ratios amongst adults are usually even or slightly female-biased (Mills 1990, Hofer and East 1993a, Frank *et al.* 1995a). Significant deviations in offspring sex ratios in singleton and twin litters are observed when cubs can first be sexed at the age of two to three months (Frank *et al.* 1991) and remain until weaning (Hofer and East

1997). Such deviations in the sex ratio from the expected distribution are either due to changes in the sex ratio at conception (Holekamp and Smale 1995) or are the consequence of sex-specific siblicide after birth (Hofer and East 1997).

Siblicide

Siblicide occurs when the death of a cub is caused by a litter mate (sibling). At birth spotted hyaena eyes are open and the teeth fully erupted – two characteristics which are rare amongst carnivores. Litter mates engage in aggressive interactions within minutes after birth (Frank *et al.* 1991). These quickly lead to the establishment of a dominance hierarchy between siblings (Golla 1993, Smale *et al.* 1995) and allow the dominant cub to control access to maternal milk. Siblicide in the spotted hyaena is facultative in that it occurs only in some twin litters. A cub that manages to kill its sibling obtains significant benefits. Growth rates of singletons are higher than those of twins and cubs with a higher growth rate have a better chance of surviving to the age of independence at two years (Hofer and East 1993c). It is possible that high maternal investment in litters, lack of communal suckling, and the substantial benefits associated with being a singleton have favoured selection for high neonatal aggression leading to siblicide (East *et al.* 1993).

Male reproductive tactics

Males disperse from their natal clan when they are at least two years old, thus reproductive males are usually immigrants. Newly immigrant males join the male dominance hierarchy at the bottom. Males increase in social status as their tenure in the clan increases (Frank 1986a, Mills 1990, East *et al.* 1993). Males invest considerable time in developing amicable relationships with clan females. They do this by forming consortships and following females for periods of days or weeks. Males that have devoted many years to developing relationships with females are probably favoured by females and thus these males may father more cubs than immigrants with short-term tenure in a clan.

Competition

The spotted hyaena most frequently competes with the lion for kills (Kruuk 1972a, Schaller 1972a, Bearder 1977, Eaton 1979). Dominance relations between the spotted hyaena and competing species are not absolute but depend on the numerical presence of both parties. For instance, lions usually displace spotted hyaenas at kills. However, if hyaena group size is large and the ratio of the number of spotted hyaenas to the number of female and subadult lions exceeds four, hyaenas are able to displace lions from kills unless a male lion is present (Cooper 1991). A single spotted hyaena usually dominates a cheetah, leopard (but not always), striped hyaena, brown hyaena, any species of jackal, and an African wild dog (but not a pack) (Kruuk 1972a, Eaton 1979, Mills 1990, H. Hofer and M.L. East unpublished data).

The proportion of diet that the spotted hyaena scavenges from kills of other predators, or loses to other predators, varies substantially between ecosystems. When spotted hyaenas outnumbered lions ten to one in the Ngorongoro Crater, lions usually scavenged from kills made by spotted hyaenas (Kruuk 1972a). In the Serengeti and in Timbavati, where lion and spotted hyaena numbers are much more even, both species scavenge approximately the same proportion of their diet from each other's kills (Kruuk 1972a, Schaller 1972a, Bearder 1975). In the Kruger National Park spotted hyaenas scavenge far more from lions than vice versa (Mills and Biggs 1993).

Mortality and pathogens

Adult mortality

Average annual mortality rates in conservation areas are around 13–15% (Mills 1990, Hofer *et al.* 1993, Frank *et al.* 1995a). The most important source of mortality is humans, through shooting, trapping and poisoning. A detailed case study from the Serengeti illustrates this. Within the Serengeti population of more than 7,000 hyaenas, approximately 400 per year die due to snares or traps (Hofer *et al.* 1996). These snares are responsible for more than 50% of all adult spotted hyaena deaths (Hofer *et al.* 1993, Hofer and East 1995a). Game meat hunters have killed commuting hyaenas by snaring since the early 1960s (Kruuk 1972a, Schaller 1972a). Apparently only since the mid-1970s has game meat hunting rapidly expanded, as more people have moved within walking distance of the boundaries of protected areas north and west of the Serengeti (Campbell and Hofer 1995, Hofer *et al.* 1996).

The impact of game meat hunters on the demography of this Serengeti population of spotted hyaenas has been substantial. First, the distribution of ages at the time of death has significantly changed since 1966–1969 (Kruuk 1972a), a time when presumably the impact of game meat hunters was below the current level. Between 1987 and 1991 relatively more medium-aged individuals died than were represented amongst the skulls of Serengeti hyaenas collected by Kruuk (1972a). Second, instead of a potential positive population growth in excess of 4%, the population declined annually between 1987–91 by 2.4%, suggesting that game meat hunters reduced the annual rate of population increase by as much as 7% (Hofer *et al.* 1993, Hofer and East 1995a).

Sources of natural adult mortality include predation by lions (Kruuk 1972a, Schaller 1972a, Mills 1990), violent encounters between conspecifics at kills or in clan wars (Kruuk 1972a, Henschel and Skinner 1991), injuries associated with giving birth for the first time (Frank *et al.* 1995b, Hofer and East 1995b), and prey-originated injuries when hunting large animals (Eloff 1975, H. Hofer and M.L. East unpublished data).

Cub mortality

Fifty to sixty percent of hyaena cubs survive their first 12 months (Mills 1990, Frank *et al.* 1995a, Hofer and East 1995a). Intraspecific social factors in the form of observed and presumed infanticide by adult clan members and observed and presumed siblicide are important sources of cub mortality (Henschel 1986, Mills 1990, Hofer and East 1995a). Cubs may also starve to death when their mothers fail to return to the communal den. In the Serengeti all but two cases of cub starvation occurred when the mother was known to have died, the majority of them killed by game meat hunters during the dry season (Hofer *et al.* 1993). Other sources of mortality include predation by lions and the collapse of communal dens after heavy rain storms (Kruuk 1972a, East *et al.* 1989, Mills 1990, Hofer and East 1993a).

Pathogens and disease

Adult Serengeti hyaenas have been found with antibodies against rabies, canine herpes, canine brucella, canine adenovirus, canine parvovirus, feline calysi, leptospirosis (Hofer and East 1995a), as well as bovine brucella, rinderpest, and anaplasmosis (Sachs and Staak 1966). It is unclear whether exposure to these pathogens results in disease or may be a cause of mortality; to date no carcass has been found that has provided evidence of such pathogen effects. During the recent canine distemper epizootic in the Serengeti in 1993–1994, several cubs below six months of age died from canine distemper. A molecular analysis of the virus isolated from hyaenas indicated that the viruses isolated from hyaenas and lions were more closely related to each other than to the closest domestic dog canine distemper virus (Haas *et al.* 1996). Evidence of the presence of canine distemper was also found in Masai Mara spotted hyaenas (Alexander *et al.* 1995).

In the Kalahari, rabies epizootics may play an important role in the population dynamics of the spotted hyaena (Mills 1990). Cases of hyaenas killed by rabies have also been reported from South Africa (Barnard 1979), Namibia (Swanepoel *et al.* 1993), Zambia (Röttcher and Sawchuk 1978), Malawi (Edelsten 1995), and Ethiopia (Mebatsion *et al.* 1992). In both the Serengeti and the Masai Mara, spotted hyaena populations revealed a similar, high frequency of exposure (46.6% seroprevalence) to rabies. Here, seroprevalence increased with age and lifetime home range and decreased with social status. However, exposure did not necessarily cause clinical symptoms or affect individual survival or longevity. Analysis of serial saliva samples indicated that spotted hyaenas are unlikely to be rabies vectors and thus exposure to the virus was not caused by intraspecific infection (M.L. East *et al.* unpublished data). The source of the rabies virus is still unknown, as it may either be of domestic (e.g. domestic dogs) or of wildlife-based origin (wild canids such as jackals and bat-eared foxes, or infected prey).

The spotted hyaena has been recorded to carry microfilaria of *Dipetalonema dracunculoides* in northern Kenya (Lightner and Reardon 1983), and occasionally antibodies to the horse sickness virus obtained from eating zebra carcasses (Binepal *et al.* 1992). It is known to carry at least three species of cestodes in the genus *Taenia*, none of which are infective to humans (Jones and Khalil 1982). The spotted hyaena also carries protozoan parasites of the genus *Hepatozoon* in the Serengeti (Krampitz *et al.* 1968), Kenya (Brocklesby and Vidler 1963, 1965) and South Africa (McCully *et al.* 1975). Although hyaenas act as hosts to trypanosomes, a role as a transmission agent has been discounted (Baker 1968, Geigy *et al.* 1971, Sachs *et al.* 1971, Bertram 1973, Geigy and Kauffmann 1973, Geigy *et al.* 1973, Beglinger *et al.* 1976, Awan 1979).

Current or planned research projects

1. A project in captivity focusing on aspects of behaviour and endocrinological control of behaviour (Frank, Glickman).
2. Field projects in the Masai Mara (Holekamp, Smale, Frank) and in the Serengeti and Ngorongoro Crater (Hofer, East) in east Africa continue to explore social and reproductive behaviour in relation to the ecological framework, life history and demography of individually known animals, the influence of social status on reproductive success and the flexibility of maternal behaviour and allocation on aspects such as cub growth and offspring sex ratios.
3. Studies on pathogen occurrence and prevalence, and the impact of poaching and other sources of human disturbance on population persistence and demography are being investigated by Hofer and East (Serengeti).

Chapter 4

Worldwide Distribution of Hyaenas

Heribert Hofer and Gus Mills

Information on the occurrence and distribution of the four extant hyaena species has been extracted from the literature, individual records by members of the Hyaena Specialist Group and other knowledgeable people, and from the respondents to the hyaena Action Plan questionnaire. Sources varied widely in both the time period covered and the quality of the data; ranging from systematic surveys to incidental records of specimen, sightings, acoustic evidence, or tracks. Coverage of different countries, regions within countries, and different time periods also varied substantially in quality and detail.

In most cases we only considered records from the last 25 years (since 1970). Species-specific identification can sometimes be unreliable (see Box 10.1). We considered a record reliable if the animal in question was a dead specimen, the record was provided by a colleague who was likely to be able to accurately identify the species of hyaena, or the location precluded any possible misidentification. The country by country accounts occasionally discuss problems arising from a lack of distinction of hyaena species for identification purposes.

In some countries where international or civil wars prevented research activities in the 1970s and 1980s the most recent records are from the 1960s, and thus were classified as old (see Box 4.1). This does not imply that hyaenids do not occur there anymore; it just indicates that little surveying has been done in these places recently. This applies to Afghanistan, Angola, Eritrea, Mozambique, Morocco-Western Sahara, Somalia, and Sudan.

Box 4.1. Distribution maps.

Distribution maps in many mammal identification books depict the range of a species as a more or less continuous area. Such maps have several disadvantages that make them inadequate in the context of a detailed status survey. They smooth the edge of the species range; hide discontinuities in actual population distribution due to topographic barriers or habitat preferences; rarely indicate changes in distribution over time; give no indication of differences in surveying effort or the quality of information available; and do not recognise potential differences in viability of populations inside and outside protected areas. Such maps tend to exaggerate actual distributions because they include both areas where the species might occur and those where the species actually does occur. In a sense they are hypotheses about the distribution of a species and may be considered "maximum distribution" maps.

Because of the variable quality and quantity of information we are currently unable to create maps that consider these problems in an adequate way. We have therefore chosen a compromise where we divide information between textual country-by-country accounts and the visual records in distribution maps. The textual accounts explain details of coverage and surveying effort, the quality of information available, differences between historical and recent distribution, and list all protected areas from where a definitive record for a species is available. The maps distinguish between historic and recent records and to some extent provide information on the quality of the data. Because the maps (and textual accounts) are based on actual records they provide a "minimum distribution". Thus, absence of a symbol on the map might designate one of two situations. It could reflect the genuine absence of a species from this area, or a place that has not been surveyed but where hyaenas in fact do occur. It is likely that hyaenas will occur in some of the gaps that can be recognised on the maps. The maps may therefore be helpful in that they suggest places where surveys may be particularly urgent and fruitful.

We used the following symbols to distinguish between different types of records:

● a reliable recent record for this area (sighting or specimen within the past 25 years);
○ an unverified or doubtful recent record for this area;
△ an old record for this area (sighting or specimen before 1970), or a locality where the species has been recently exterminated
□ a site where the species was recently reintroduced.

The maps summarise distribution records on a one-degree grid system over several countries in a region. Symbols were plotted in the centre of each degree square. A one-degree grid is fine enough to provide a detailed record of the distribution within the country, yet coarse enough to minimise errors associated with imprecise locality information in our sources. A grid system does not distinguish local gaps in distribution due to habitat differences but this is not such an important problem for hyaenas (except for aardwolves), as they are all opportunists and occur in a wide range of conditions. Of greater concern, the map symbols do not give an indication of abundance. A "recent record" may represent anything from an isolated record of a single nomadic individual to a large population numbering several hundred or thousand individuals. Currently we do not have information on abundance for most areas and are therefore unable to quantify distribution records. Population status and abundance are considered in detail in Chapter 5.

The textual country by country accounts cover each country within the historical range of each species and the immediate neighbouring countries. An attempt has been made to list all conservation areas with some status of protection for which confirmed sightings or records of specimen were available. The maps summarise distribution records on a one-degree grid system over several countries in a region (see Box 4.1 for a detailed discussion and an explanation for map symbols). The world distribution maps for each species are: aardwolf Fig. 4.1, striped hyaena Fig. 4.7, brown hyaena Fig. 4.19, and spotted hyaena Fig. 4.22.

4.1 Aardwolf

Historical distribution

There is no reason to believe that the historical distribution of the aardwolf is much different from its current distribution, especially in southern Africa where data are more complete. Records collected over the last 20 years indicate that the aardwolf still occurs over most of southern Africa, although historically it has always been absent from pure desert and dense forest. The aardwolf is a shy, unobtrusive animal that thrives in arid and open countryside. Thus its prime habitats are inherently areas used for extensive livestock grazing. These farming areas seldom suffer sufficient change to make it inhospitable to the aardwolf, and as a result there are few conflicts between humans and the aardwolf.

Current distribution

The aardwolf occurs in two discrete populations (Fig. 4.1). The southern population ranges over most of southern Africa, extending into southern Angola, southern Zambia and southwestern Mozambique. A 1,500km gap occurs between this population and the northern one which extends into central Tanzania, to northeastern Uganda, Somalia and parts of Ethiopia, then narrowly along the coast of Eritrea and Sudan to the extreme southeast of Egypt.

Angola. Fig. 4.3. Records from before 1974 indicate presence in the southwest where it ranges from the coast to the highlands to altitudes above 1900m (Crawford-Cabral 1989).

Botswana. Fig. 4.2. Widespread throughout the country (Smithers 1971).

Djibouti. Fig. 4.5. Unknown.

Egypt. Fig. 4.6. Records from the extreme southeast of the country on the border with Sudan (Osborn and Helmy 1980).

Eritrea. Fig. 4.5. Probably found throughout (Yalden *et al.* 1980, 1996).

Ethiopia. Fig. 4.5. Previously only found in the northeast. Two road kills in 1987 and 1990 provide the first records from the central Rift Valley of Ethiopia (Yalden *et al.* 1996).

Kenya. Fig. 4.4. Widely but sparsely distributed (Kingdon 1977).

Lesotho. Fig. 4.2. No recent records, but probably occurs throughout (Smithers 1971).

Mozambique. Fig. 4.3. Occurs in the extreme southwest and along the border region with northeast Zimbabwe (Smithers and Lobão Tello 1976).

Namibia. Fig. 4.2. Occurs throughout except along the Namib Desert coast and sand dunes (Smithers 1971, Stuart 1975, P. Stander pers. comm.).

South Africa. Fig. 4.2. (Note: because the information for South Africa was compiled before the new constitution was implemented, the old provincial basis is used here).
(a) Cape Province. Widespread throughout the province and quite common in the northern, central and eastern regions (Stuart 1981, Lloyd and Millar 1983).
(b) Natal. Uncommon, but occurs throughout the province (Rowe-Rowe 1992).
(c) Free State. Widespread and common (Lynch 1983).
(d) Transvaal. Widespread throughout, but most common in the west (Rautenbach 1982).

Somalia. Fig. 4.5. Sparsely distributed throughout (Azzaroli and Simonetta 1966).

Sudan. Fig. 4.6. Historic record from the northeast (Osborn and Helmy 1980).

Swaziland. Fig. 4.2. Recorded from Malolotja Nature Reserve in the highveld region in the northwest of the country, where numbers appear to be stable (Monadjem 1997).

Tanzania. Fig. 4.4. Swynnerton (1951) recorded it from Lolkisale, southern Masailand, Sambala, Matomondo, Mpwapwa, Itumba, Manyoni, Singida, Kiganga, Shinyanga and Tabora. Quite common on the Serengeti plains (H. Hofer and M.L. East unpublished data).

Figure 4.1. World distribution of the aardwolf.

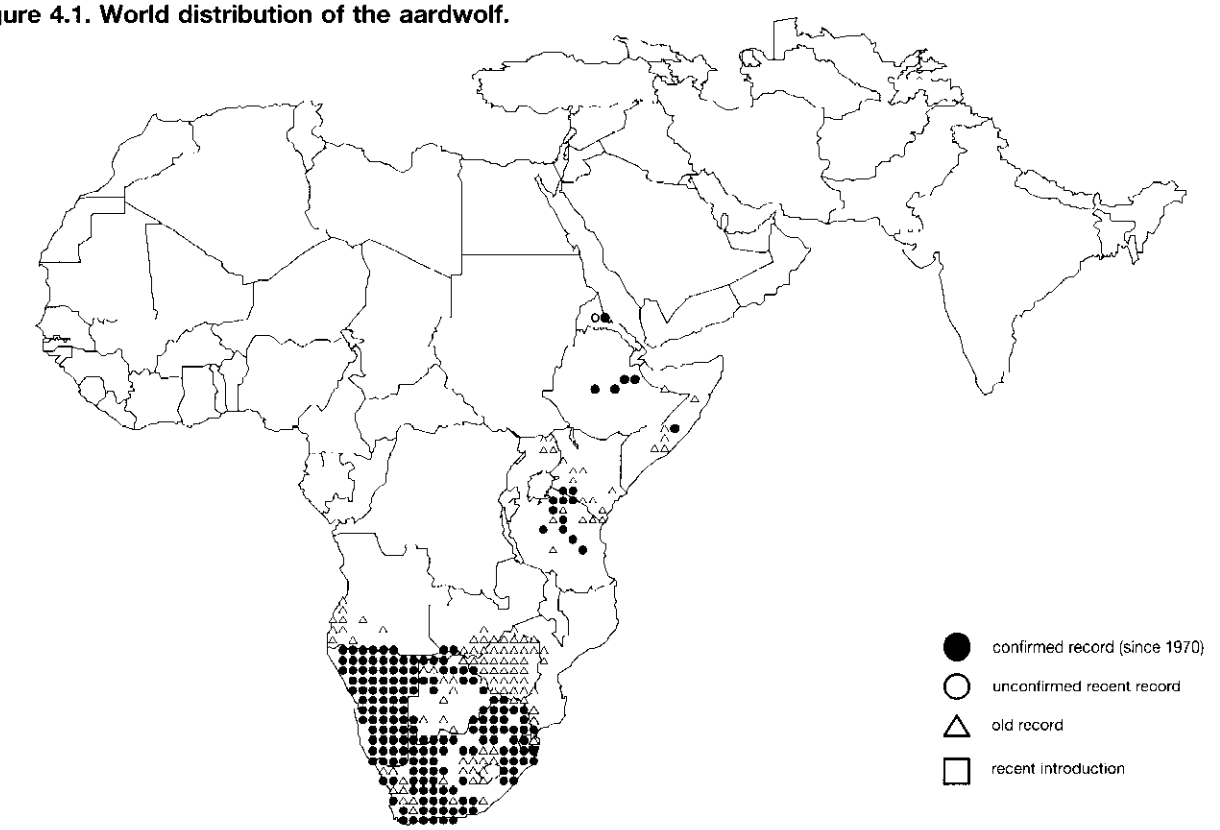


Figure 4.2. Distribution of the aardwolf in Botswana, Lesotho, Namibia, South Africa and Swaziland.

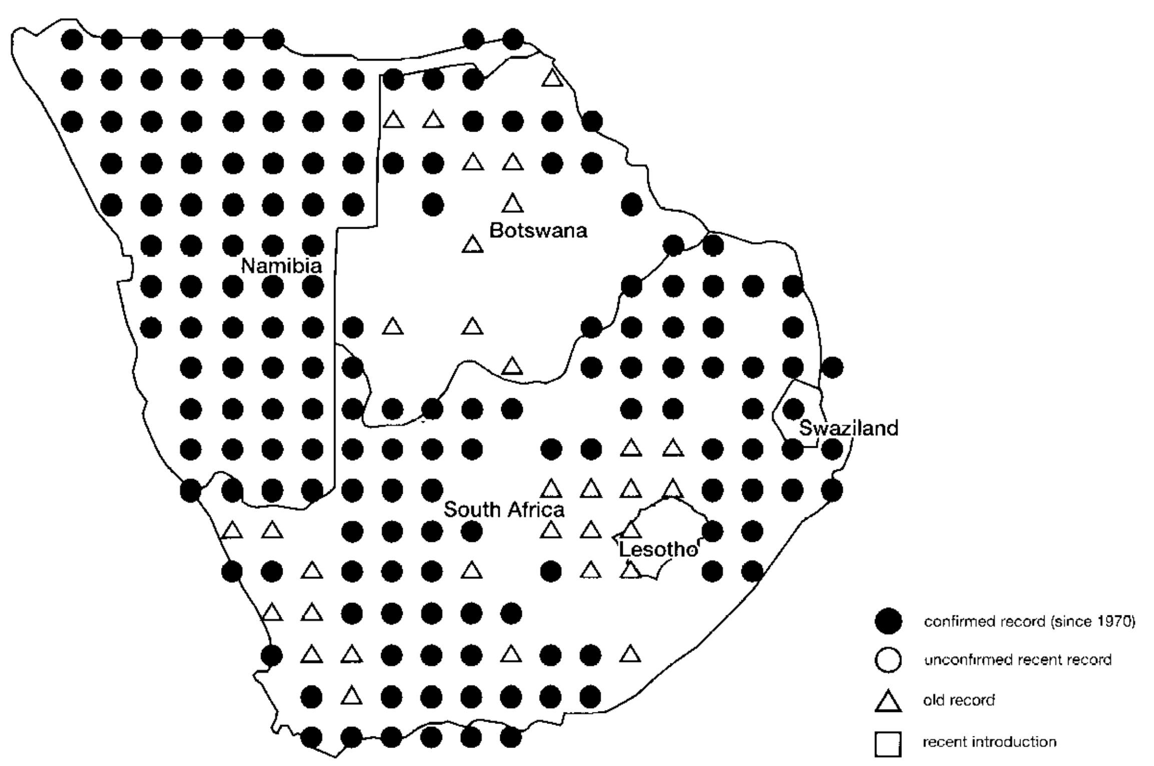


Figure 4.3. Distribution of the aardwolf in Angola, Mozambique, Zambia and Zimbabwe.

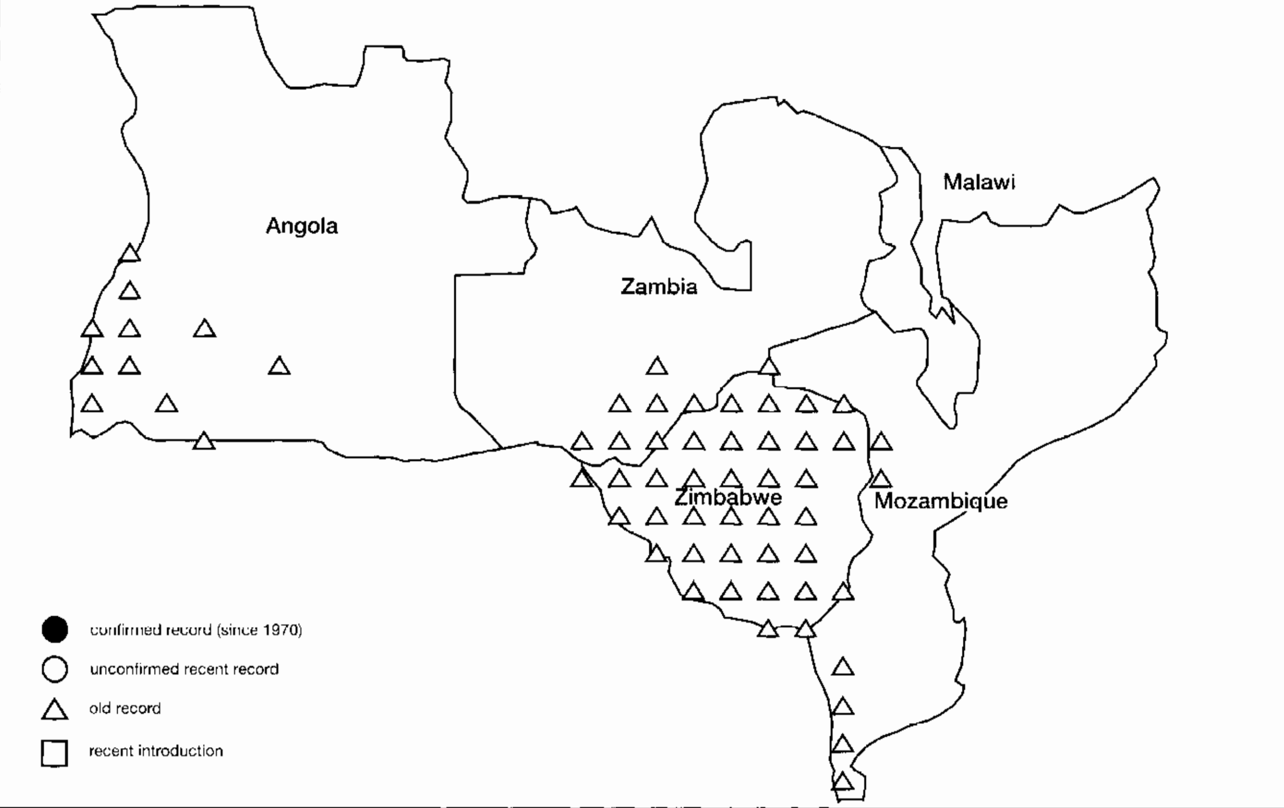


Figure 4.4. Distribution of the aardwolf in Kenya, Tanzania and Uganda.

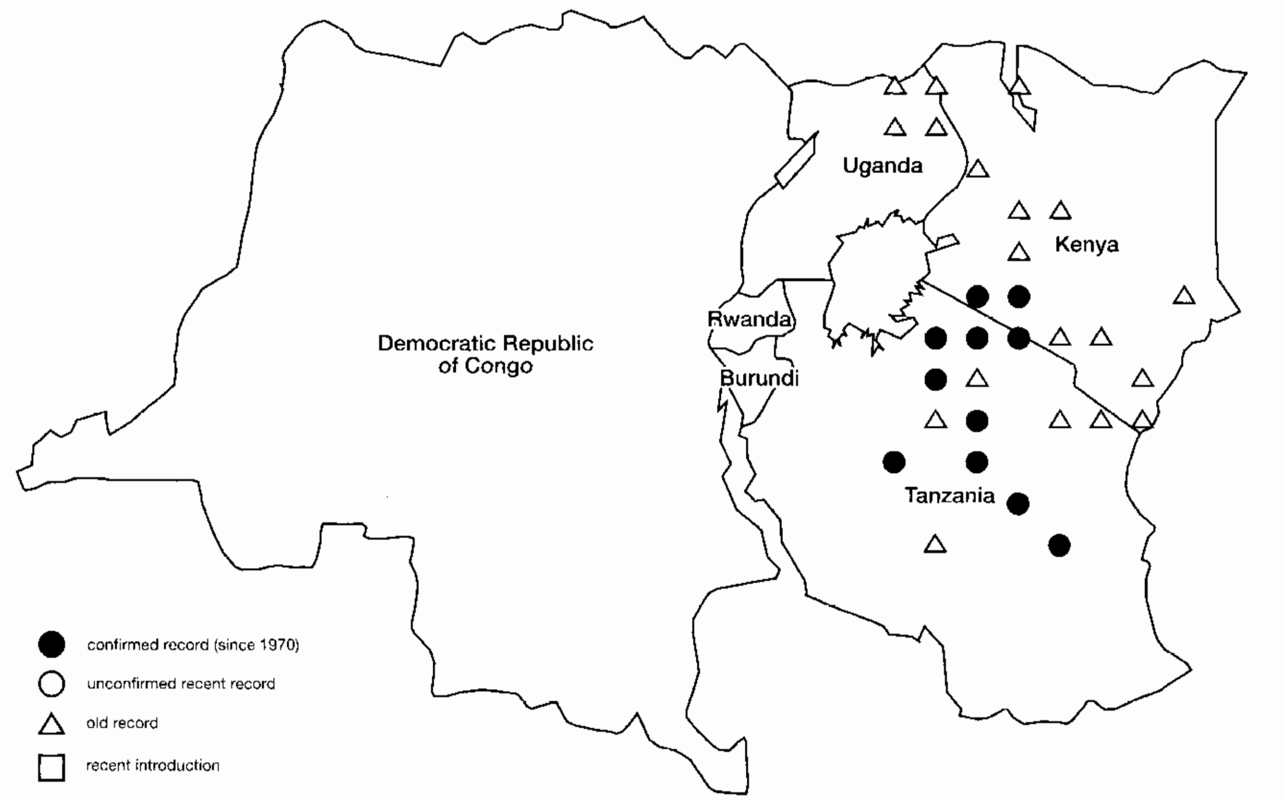


Figure 4.5. Distribution of the aardwolf in Eritrea, Ethiopia and Somalia.

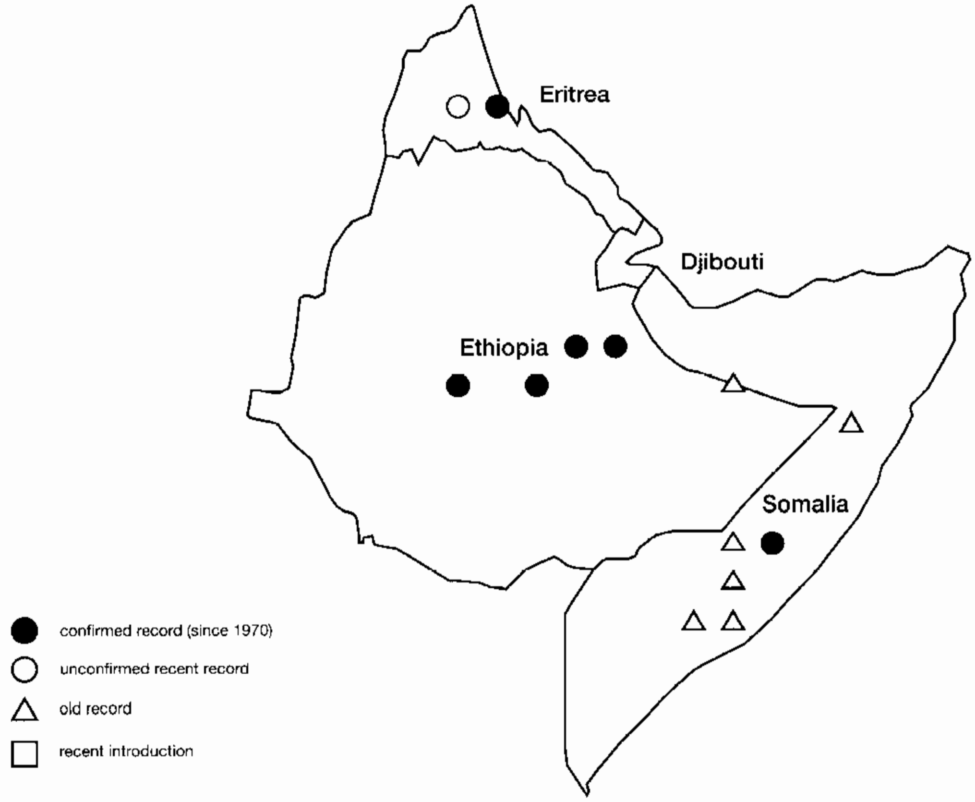
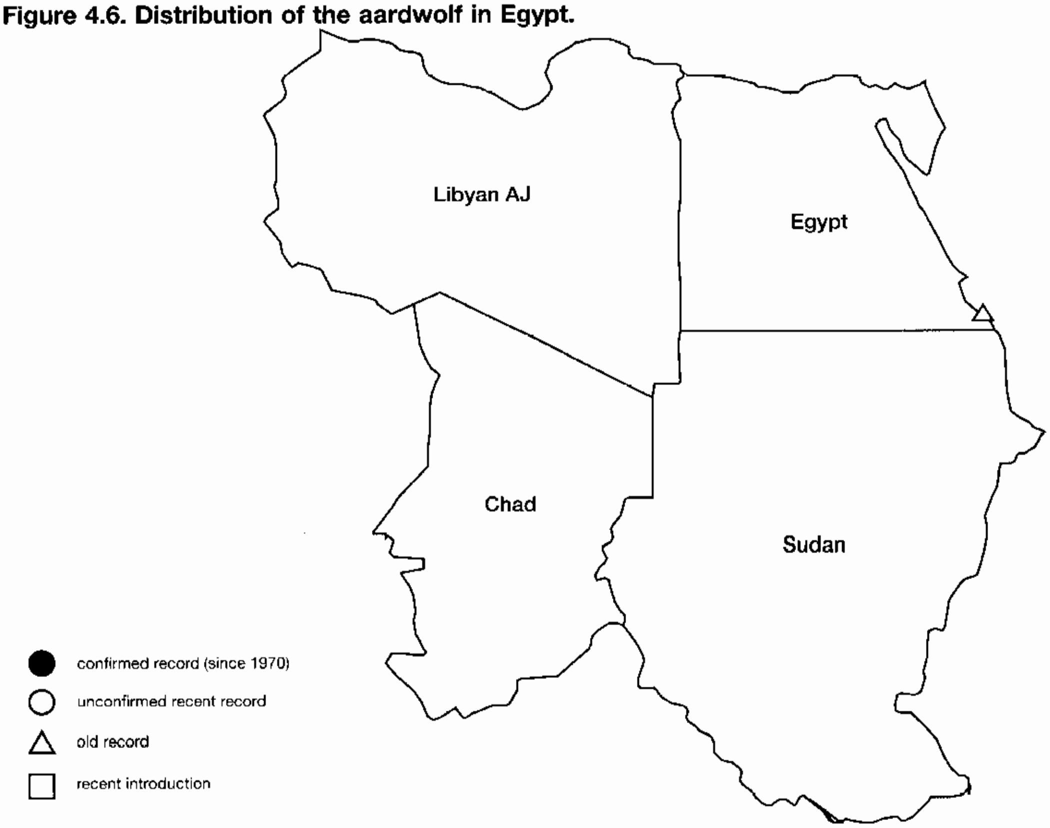


Figure 4.6. Distribution of the aardwolf in Egypt.



Uganda. Fig. 4.4. Older records from the northeast only (Kingdon 1977).

Zambia. Fig. 4.3. Recorded from Kalomo and Mazabuka in southern Zambia where it was noted to be quite common (Ansell 1960). Also recorded from Sinazongwe on Lake Kariba (Smithers 1966). It is uncertain whether aardwolves occur north of the Kafue river (Smithers 1966, Ansell 1978).

Zimbabwe. Fig. 4.3. Widespread and common, although absent from the higher levels over 2000m (Smithers 1966), but no recent records could be found.

4.2 Striped hyaena

Historical distribution

The historical distribution of the striped hyaena encompasses Africa north of and including the Sahel zone, eastern Africa south into Tanzania, the Arabian Peninsula and the Middle East up to the Mediterranean shores, Turkey, Iraq, the Caucasus (Azerbaidjan, Armenia, Georgia), Iran, Turkmenistan, Uzbekistan, Tadzhikistan, Afghanistan (excluding the higher areas of the Hindukush) and the Indian subcontinent. Striped hyaenas did not reach Assam, Bhutan or Myanmar and did not enter the Himalayan range.

Current distribution

The distribution of the striped hyaena is now patchy in most places (Fig. 4.7), suggesting that it occurs in many small isolated populations. This is particularly so in most west African countries, most of the Sahara desert, parts of the Middle East, the Caucasus, and central Asia. It has a continuous distribution over larger areas in Ethiopia, Kenya, and Tanzania. Its current distribution pattern is virtually unknown for Pakistan, Iran and Afghanistan, where the striped hyaena may be more widespread than current records indicate.

Afghanistan. Fig. 4.16. Historically widespread. Records of specimens and sightings from the 1960s and early 1970s indicate presence in the western areas near the border to Iran and the southern and eastern areas near the border to Pakistan (Kullman 1965, Gaisler *et al.* 1968, Hassinger 1973, Gasperetti *et al.* 1985), but no recent surveys or records are available.

Algeria. Fig. 4.12. Historically widespread in the northern part, from the coast to the Saharan Atlas and the northern belt of the desert, and in mountainous areas in the far south. Current records indicate that it reaches as far south as Beni Abbes in the west and probably El Golea in the east (Kowalski and Rzebik-Kowalska 1991). Present in Djurdjura National Park, El Kala National Park, Mergueb Natural Reserve, Béni-Salah Natural Reserve; may also still occur in Chréa National Park, Taza National Park and Theniet El Had National Park. Continued presence is doubtful in the Ahaggar National Park and Tassili N'Ajjer National Park in the extreme south (Kowalski and Rzebik-Kowalska 1991).

Armenia and Azerbaidjan. Fig. 4.15. Historically widespread, but now only very patchily distributed and present in only a few places (Heptner and Sludskij 1980, Gasperetti *et al.* 1985).

Benin. Fig. 4.11. No records. May occur in border areas near Burkina Faso and Niger.

Burkina Faso. Fig. 4.11. Probably occurred throughout the country. In protected areas still present in "W" National Park, Arly National Park, Kabore Tambi National Park, and Nazinga Game Ranch. Outside protected areas still occurs in Sahel burkinabé, east and southwest Burkina, Sourou, and Kassi.

Burundi. Fig. 4.8. No records.

Cameroon. Fig. 4.10. Rare but was apparently present in the northern savannah areas (Jeannin 1936), including Waza National Park and probably Kalamaloué National Park. Current records are from Waza National Park and surrounding areas (Happold 1973, 1987; Depierre and Vivien 1992) and unconfirmed records from the central parts of the country (questionnaires).

Central African Republic. Fig. 4.10. No records. May occur in the northern savannah areas.

Chad. Fig. 4.13. Historically present in the Tibesti mountains but no recent records from there (Le Berre 1990). Two recent records from the southern half of the country.

Congo. Fig. 4.10. No records.

Côte d'Ivoire. Fig. 4.11. No records; not known by local people (questionnaires).

Democratic Republic of Congo. Fig. 4.8. No records.

Djibouti. Fig. 4.9. Historically widespread but no recent records (Yalden *et al.* 1980, 1996). Because species is poorly recognised there is little reliable information from areas other than conservation areas (J.C. Hillman, pers. comm.).

Egypt. Fig. 4.13. Historically widespread throughout the country, concentrating in the western oases, the Nile valley and the Sinai (Osborn and Helmy 1980). Recent records cover most of the Nile valley, areas near oases in the west, and coastal areas near the Mediterranean and Red Seas (Osborn and Helmy 1980, Gasperetti *et al.* 1985).

Eritrea. Fig. 4.9. Historically widespread but few recent records (Yalden *et al.* 1980, 1996). Because species is poorly recognised there is little reliable information from areas other than conservation areas (J.C. Hillman pers. comm.).

Ethiopia. Fig. 4.9. Historically widespread (Yalden *et al.* 1980, 1996). Recent records include Awash National Park, Mago National Park, Omo National Park (Baba *et al.* 1982), Yangudi Rassa National Park, and Yabello Sanctuary. Probably also occurs in Babille Elephant Sanctuary. Because species is poorly recognised there is little reliable information from areas other than conservation areas (J.C. Hillman pers. comm.).

Gabon. Fig. 4.10. No records.

Gambia. Fig. 4. 11. No records.

Georgia. Fig. 4.15. Historically widespread, but now only very patchily distributed and present in only a few places in the southeast (Heptner and Sludskij 1980, Gasperetti *et al.* 1985, J. Badridze unpublished data).

Ghana. Fig. 4.11. No records. Might occur in the border area with Burkina Faso in the extreme northeast.

Guinea. Fig. 4.11. Unconfirmed records. Apparently known to local people (questionnaires). Presence and distribution unclear.

India. Fig. 4.18. Historically widespread throughout most of India except for regions of deciduous evergreen forest in the southwest. In southern India the distribution is peculiar. It is present in the dry Serus areas (<900mm rainfall) of the Deccau plateau but is not found in heavier deciduous forest (>1000mm rainfall), nor in evergreen and semi-evergreen forms of the western Ghats (1500–6000mm rainfall). Present in the northern strip of the coastal plains in Karnataka and Goa states, up to the western Ghats (4,000 6,000mm rainfall) where the original evergreen forms are now entirely replaced by cultivation (Karanth 1982, 1986). This may suggest range and habitat extension in the wake of human colonisation. In northern and eastern India it also continues to exist outside conservation areas. Present in many conservation areas throughout the subcontinent including Ranthambore, Kanha, Palamau, Mudumalai, Bandipur, Anamallai, Jawahar, and Corbet (Nair *et al.* 1977, complete list in Kothari *et al.* 1989). However, there are few confirmed recent records.

Iran. Fig.4.16. Historically widespread. Specimen and sight records mainly from the south and the Iraqi-Iranian border (Lay 1967, Gasperetti *et al.* 1985). Recent sightings in previously well-known localities (Rieger 1979a, C.M. Naumann unpublished data).

Iraq. Fig. 4.14. Common in the valley of Mesopotamia but apparently absent from the desert (Khadim *et al.* 1977, Gasperetti *et al.* 1985). Recent records include the Mesopotamian valley, the eastern side and mountainous areas of Kurdistan including Samarah and Balad (north of Baghdad), west of Tharthar Lake, Aziziya (Wasit province), Nasiriya, and Amara (questionnaires, Gasperetti *et al.* 1985, Harrison and Bates 1991).

Israel. Fig. 4.14. Historically widespread throughout the country (Mendelssohn and Ilani 1988). It still occurs in most areas of Israel, and has even returned to the densely populated coastal plain where it had been exterminated by strychnine poisoning (Ilani 1979).

Jordan. Fig. 4.14. Historically widespread (Gasperetti *et al.* 1985, Searight 1987). Recent records from the centre and the southwest (Gasperetti *et al.* 1985; Qumsiyeh *et al.* 1993; Al Younis 1993) of the country. Present in Shaumeri Wildlife Reserve, Azraq Wetland Reserve and Azraq Desert Reserve (Al Younis 1993), and Dana Nature Reserve (Amr *et al.* 1996).

Kenya. Fig. 4.8. Historically widespread in more arid habitats. Recent sightings in Masai Mara Game Reserve and surrounding Masailand, Lake Natron, the northern arid zones, Samburu, Tsavo and other conservation areas.

Kuwait. Fig. 4.14. Historically present. No recent records although little attention has been paid to the interior desert.

Lebanon. Fig. 4.14. Historically widespread. Recent records from coastal areas (Thomé and Thomé 1983, Gasperetti *et al.* 1985, Harrison and Bates 1991).

Libya. Fig. 4.13. Historically widespread in the northern part of the country. Still widely recorded in the Tripolitaine and the Cyrenaica (Hufnagl 1972, Le Berre 1990).

Mali. Fig. 4.12. Still known to be present in the Adrar des Iforas massif (Sidiyène and Tranier 1990) and in Boucle du Baoulé National Park (Happold 1973).

Mauritania. Fig. 4.12. Historically widespread throughout the country. Still occurs in the Adrar in the west (Le Berre

1990) and two recent records from the Region Première northwest of Nema (questionnaire survey).

Morocco. Fig. 4.12. Historically widespread (Panousse 1957). The questionnaire survey and published evidence give variable accounts of the current distribution. Apparently only relict populations left in the west and in the southern High Atlas, concentrated in Reserve integrale de Missour, Tazeka National Park, Parc National de l'Oriental and Iriki Hunting Reserve. It appears to have disappeared from the central plateau and the Middle Atlas (Aulagnier and Thevenot 1986).

Morocco-Western Sahara. Fig. 4.12. Widely but thinly spread along coastal areas and eastern regions bordering Mauritania (Aulagnier and Thevenot 1986). Also occurs at Rio de Oro and Seguir el Hamra (Le Berre 1990).

Nepal. Fig. 4.18. No historic records. Repeated sightings in scrubland outside conservation areas suggest a range extension into this country since the 1970s (Mitchell and Derksen 1976). Sighted at the edge of Royal Chitwan National Park in 1973 and 1980, at Narayani River in 1980, and tracks were seen in Kailali district 1987 (questionnaire survey).

Niger. Fig. 4.12. Historically widespread throughout the country. Still distributed across the Sahel zone but precise locations unavailable. Reported to have been recently exterminated in the Aïr and Ténéré National Nature Reserves (Millington and Tiega 1990, 1991).

Nigeria. Fig. 4.10. Historically present in the Sahel savannah zone in the north and east (Rosevear 1953). A few recent records along the border with Cameroon near Waza National Park in Cameroon (Happold 1987).

Oman. Fig. 4.14. Historically widespread. Still present near the southeastern coast (Gasperetti *et al.* 1985, Harrison and Bates 1991). Occurs in Dhofar, Huquf and along the coast from Dhofar to Ra's al Hadd. Unsubstantiated reports from northern Omani territory towards Strait of Hormuz, a very rugged area full of mountains and gorges. Possibly also in the area on the fringe of the great sands of the Rub-al-Khali (C. Stuart and T. Stuart pers. comm.).

Pakistan. Fig. 4.16. Historically widespread in rough, hilly country, rocky escarpments, mountain steppes, and the sand-dune areas in the Indus plains where there are few human settlements (Roberts 1977). Sightings from the 1960s and early 1970s indicate still widespread occurrence in the south and west. No recent surveys or records available.

Qatar. Fig. 4.14. No recent records.

Rwanda. Fig. 4.8. No records.

Saudi Arabia. Fig. 4.14. Historically widespread, it is now reportedly absent from the central desert regions (Nader and Büttiker 1982, Harrison and Bates 1991). Present in Asir National Park (Al-Khalili and Nader 1984), Harrat al-Harrah Protected Area and Khunfah Protected Area. Outside protected areas has been documented to occur in adequate habitat throughout northwestern Arabia and is suspected to occur also in remote regions of the northwest (Seddon 1996). Frequently encountered in the 30 km by 30 km oasis area from Sakakah to Al Jawf in Al Harrah, sparse in At Tawil in Al Hamad. Does not occur in the An Nafud sand desert (Green 1986).

Senegal. Fig. 4.11. Historically present in the north. Recent records from Boundou in the east, Ferlo Nord and Ferlo Sud Faunal Reserves in the north, and Oualo and Cayor in the northwest (Dupuy 1982, 1984, questionnaire survey).

Somalia. Fig. 4.9. Always considered rarer than the spotted hyaena although widespread. Records restricted to the northwest corner of the country, areas close to the Ethiopian border, and the coastal southeast (Drake-Brockman 1910, Azzaroli and Simonetta 1966, Gasperetti *et al.* 1985). No recent records.

Sudan. Fig. 4.13. Historically widespread throughout the country. Records are from the Nile valley, the coast, and the border with Egypt (Gasperetti *et al.* 1985, Le Berre 1990). Little information available for the south of the country and no recent records.

Syria. Fig. 4.14. Historically widespread. Records from the west, northwest, and northeast of the country (Gasperetti *et al.* 1985, Harrison and Bates 1991). No recent records.

Tadzhikistan. Fig. 4.17. Historically widespread in the southwest and northern areas (Isakov *et al.* 1988). Still present in the southwest of the country, including the Tigrovaya balka Reserve (Heptner and Sludskij 1980, Isakov *et al.* 1988).

Tanzania. Fig. 4.8. Historically widespread throughout the northern savannah ecosystems and bush country in the Serengeti, Lake Natron, Longido and Ngare Nanyuki areas, around the base of Mount Meru and Kilimanjaro mountains and the Pare mountains in the east (Swynnerton 1951). Recent sightings and records of road kills indicate that at least the northern half of the Maasai steppe in the centre of Tanzania is populated by the striped hyaena (H. Hofer unpublished data), but otherwise the distribution has changed little. An unconfirmed record from Ruaha National Park south

Figure 4.7. World distribution of the striped hyaena.

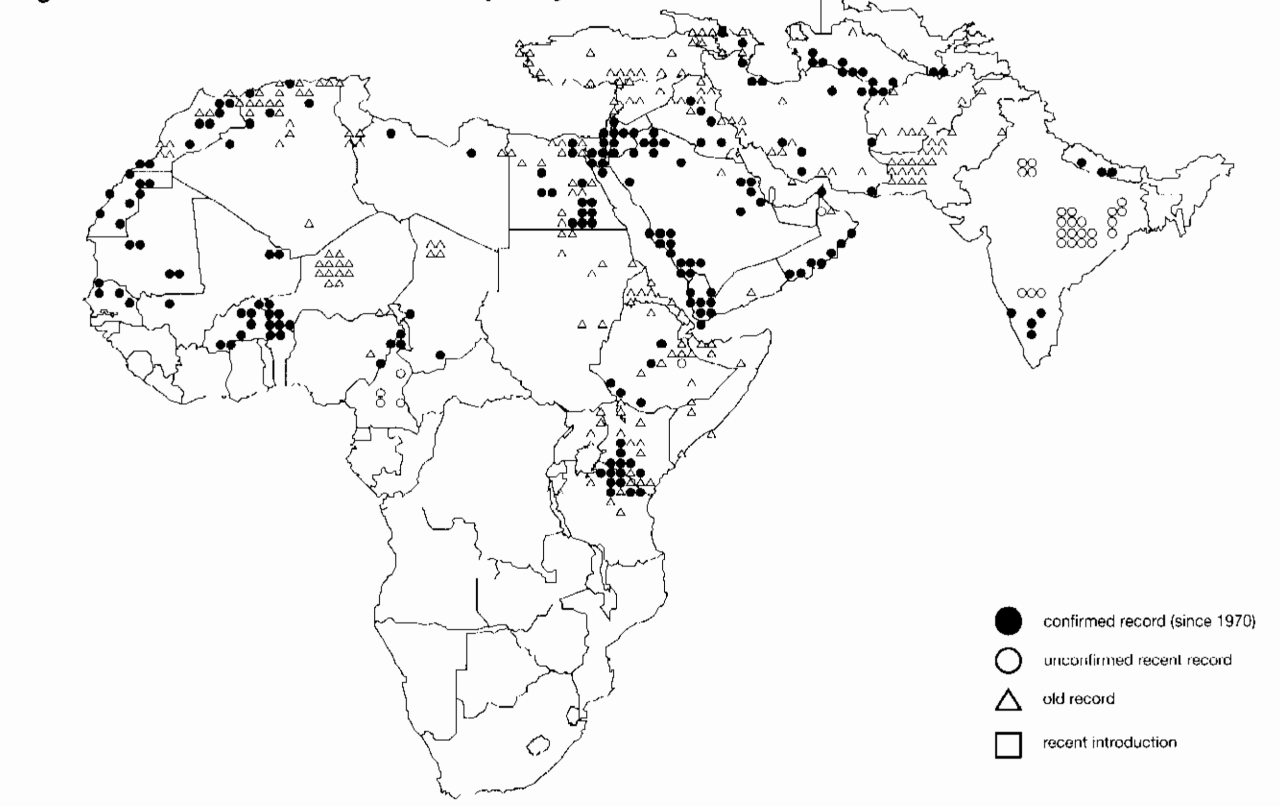


Figure 4.8. Distribution of the striped hyaena in Kenya, Tanzania and Uganda.

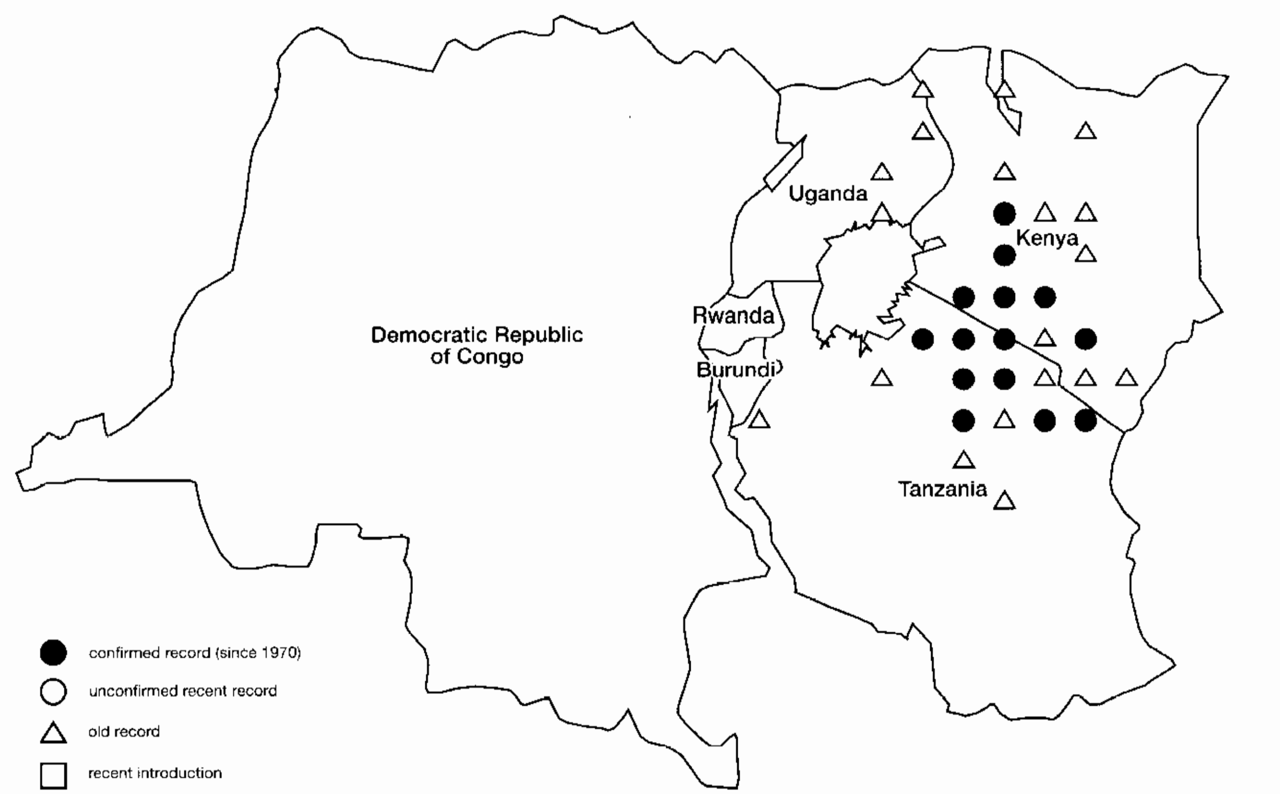


Figure 4.9. Distribution of the striped hyaena in Eritrea, Ethiopia and Somalia.

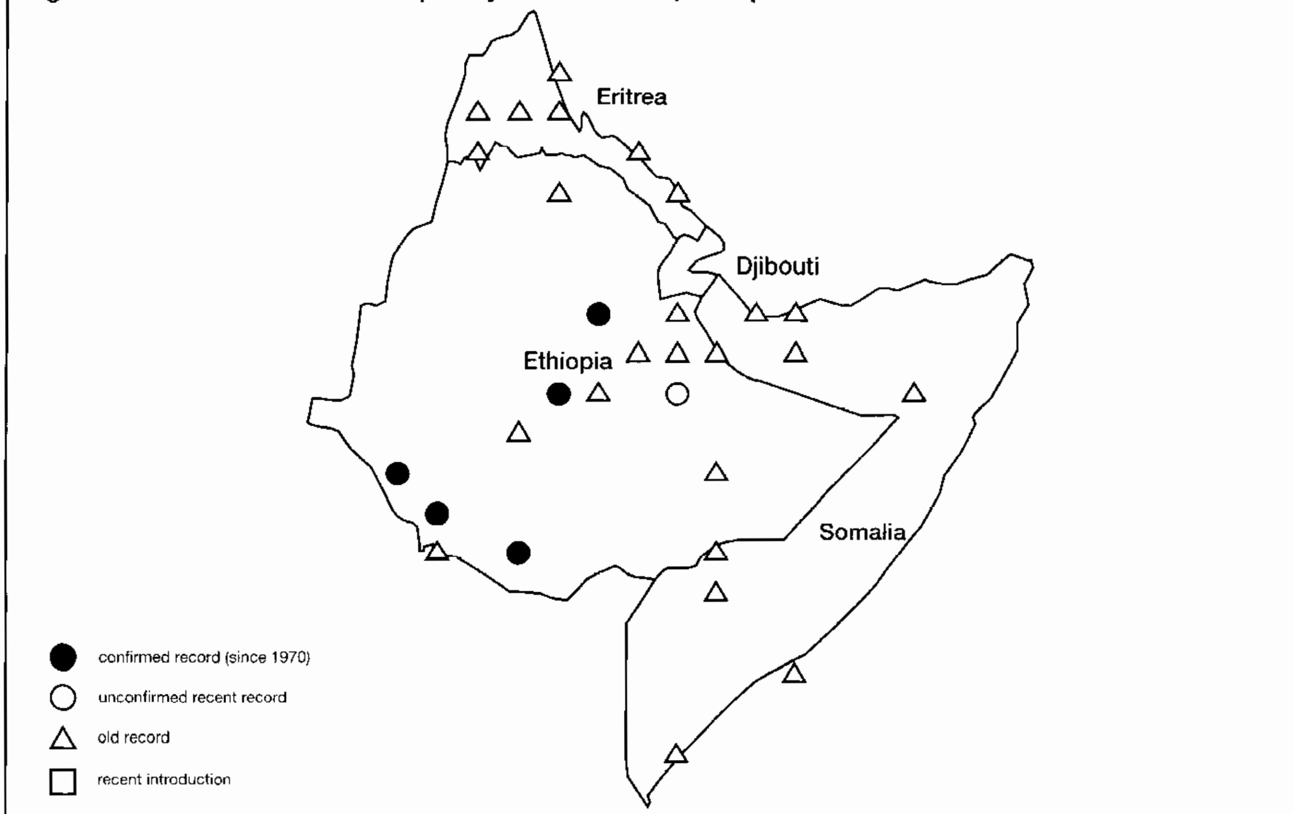


Figure 4.10. Distribution of the striped hyaena in Cameroon and Nigeria.

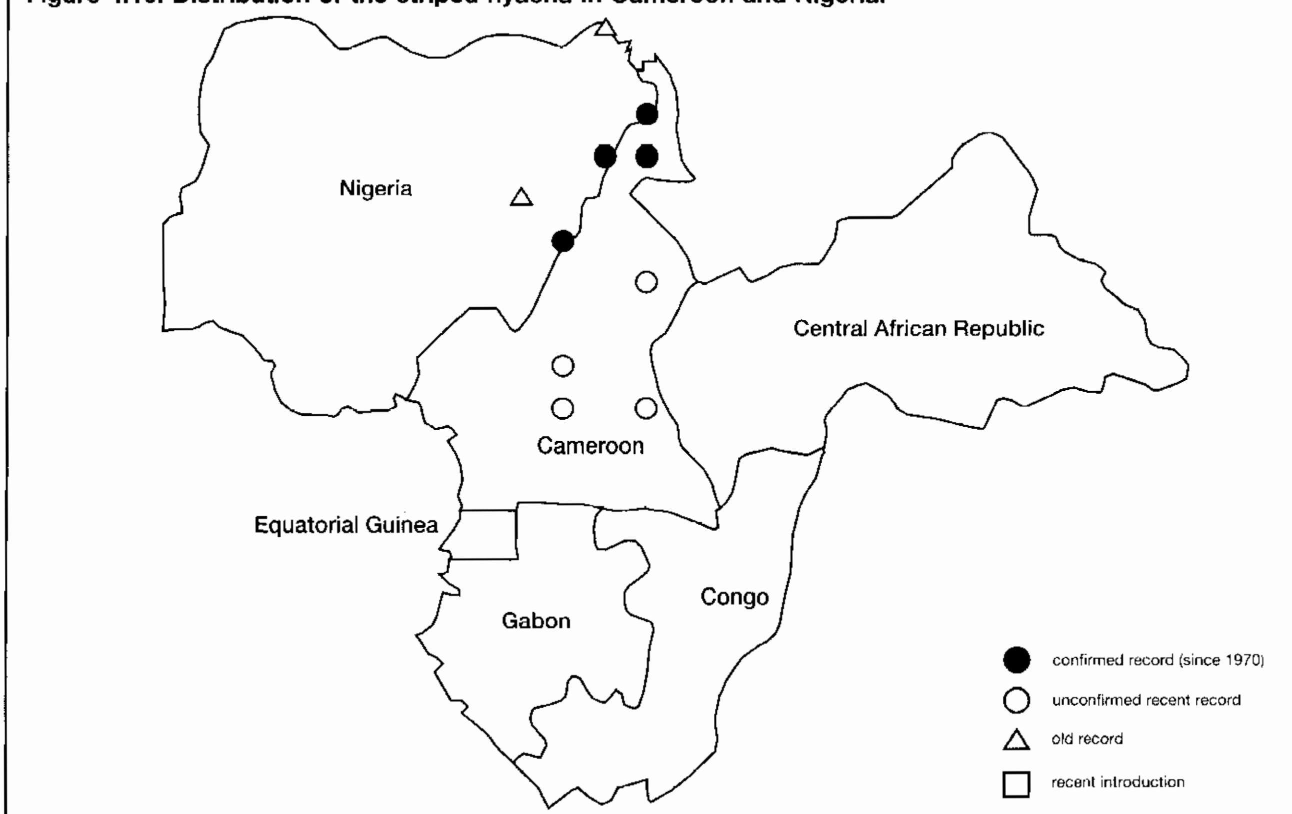


Figure 4.11. Distribution of the striped hyaena in Burkina Faso and Senegal.

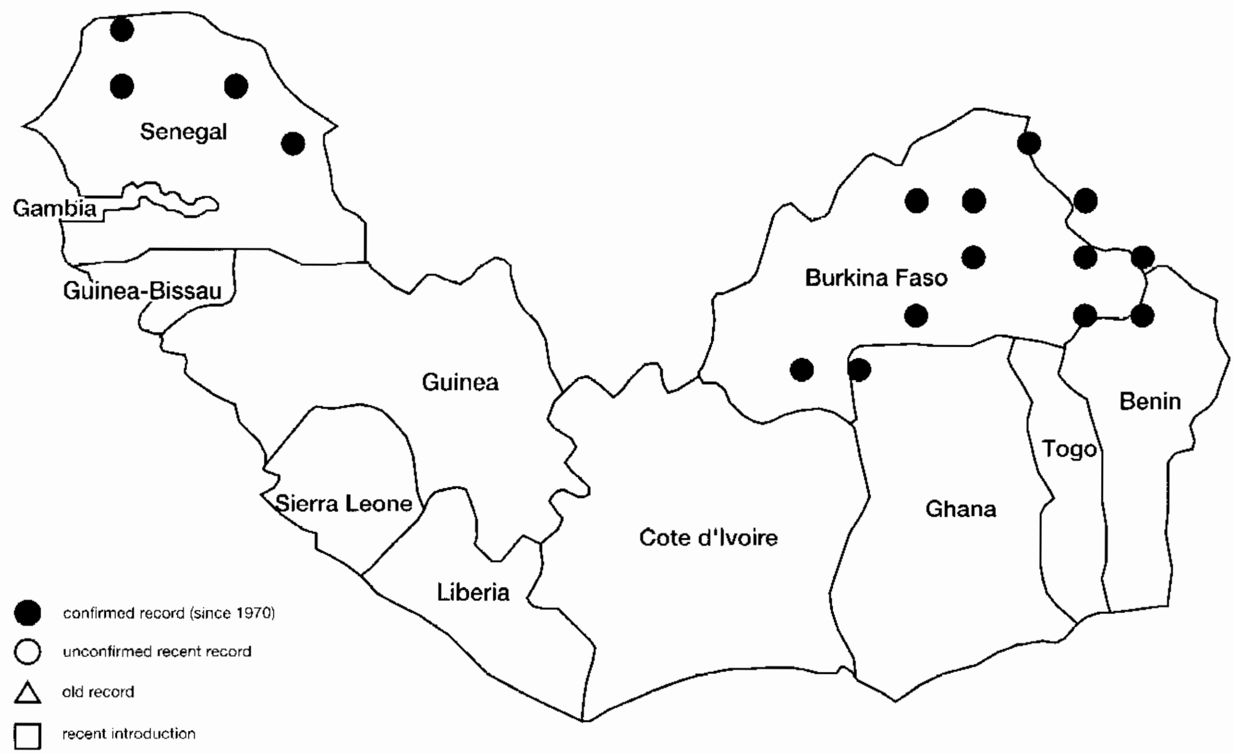


Figure 4.12. Distribution of the striped hyaena in Algeria, Mali, Mauritania, Morocco-Western Sahara, Niger and Tunisia.

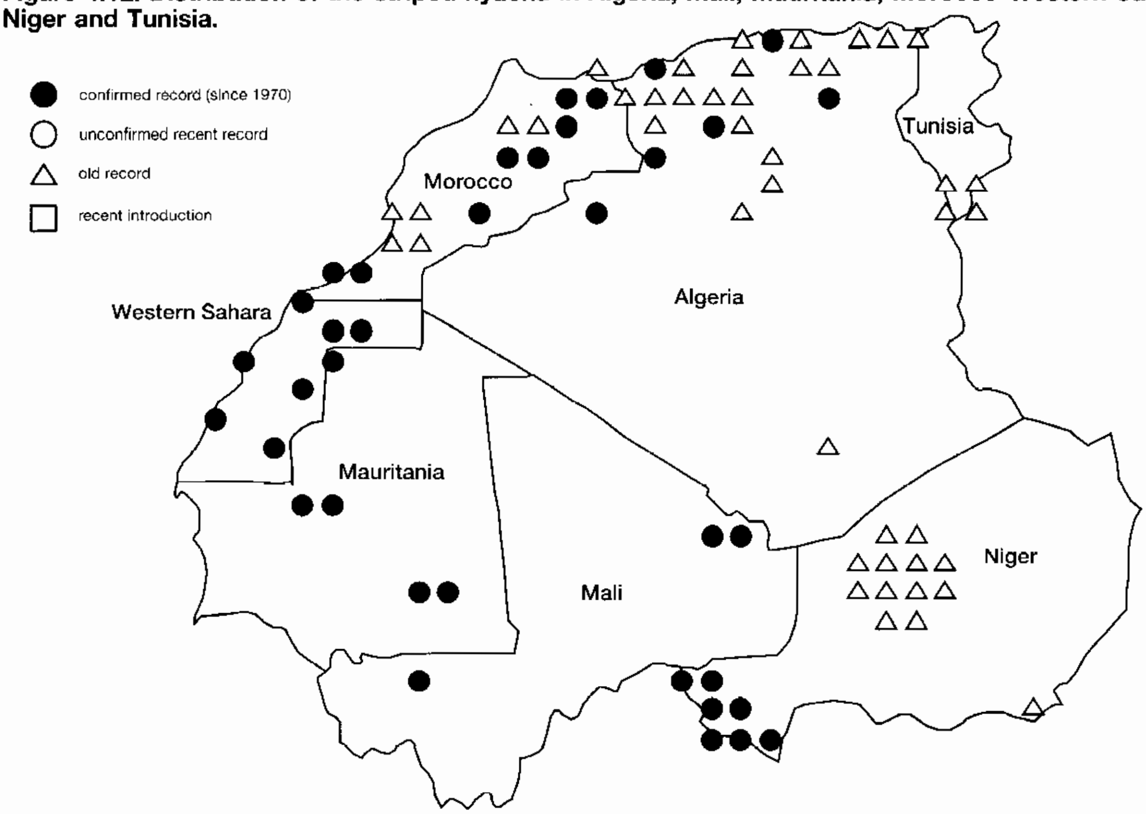


Figure 4.13. Distribution of the striped hyaena in Chad, Egypt, Libya and Sudan.

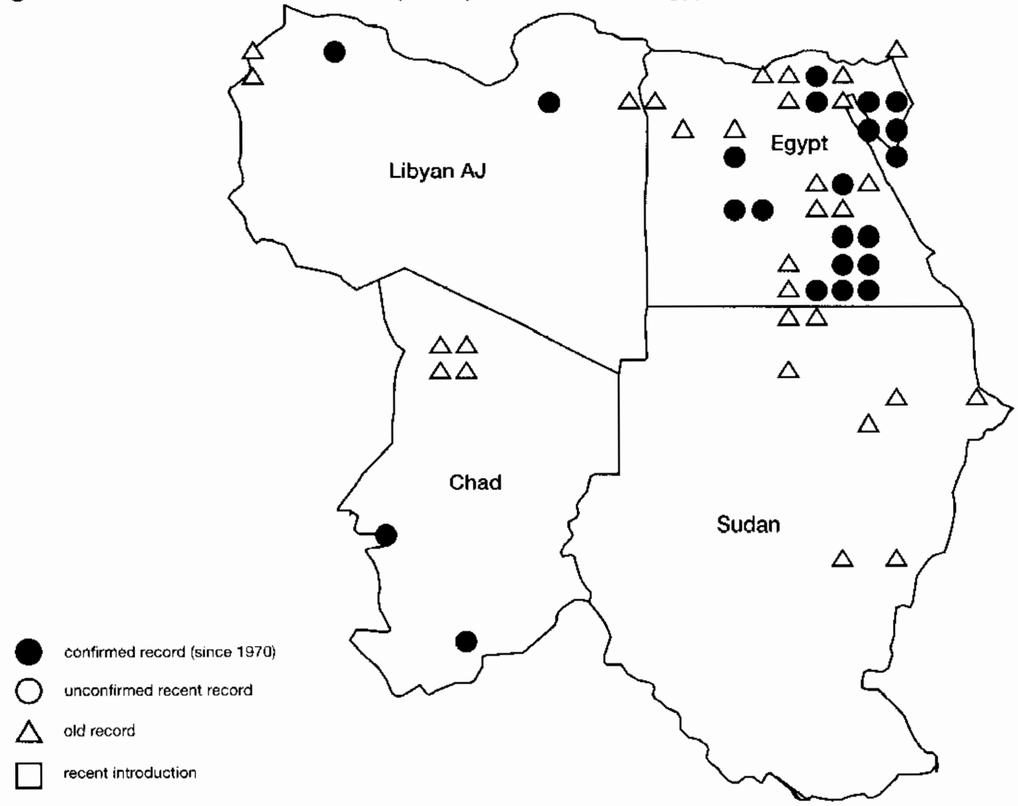


Figure 4.14. Distribution of the striped hyaena in Iraq, Israel, Jordan, Lebanon, Oman, Saudi Arabia, Syria and Yemen.

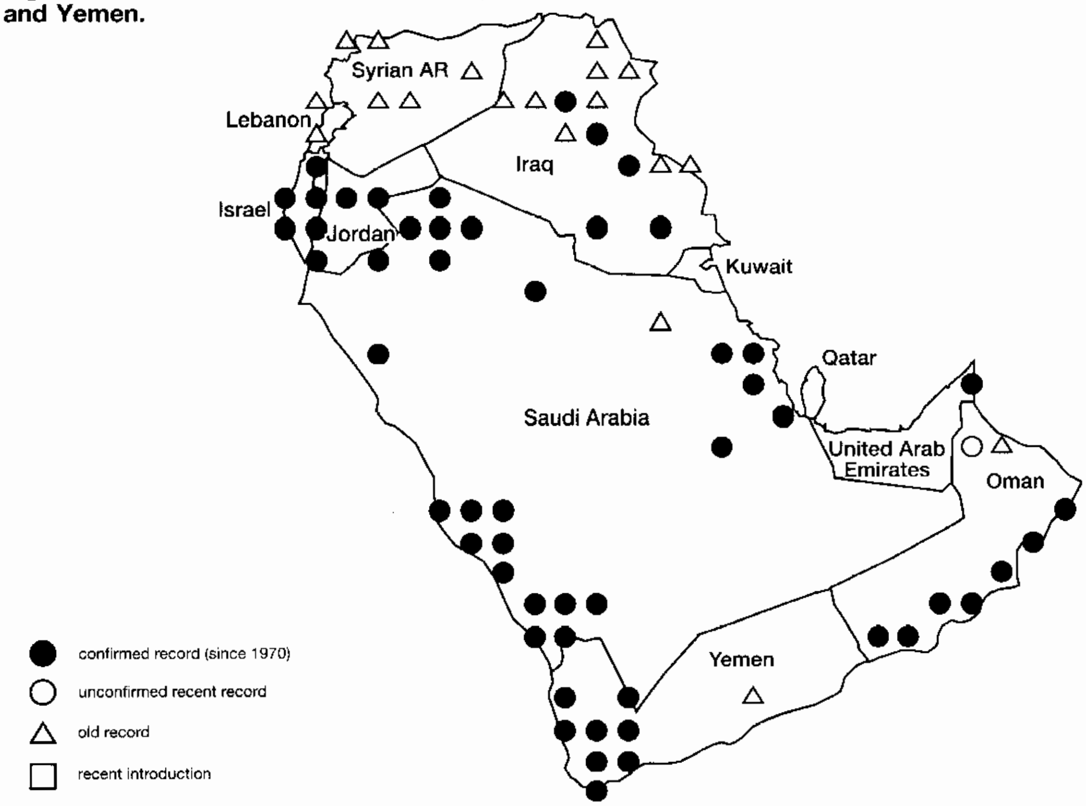


Figure 4.15. Distribution of the striped hyaena in Armenia, Azerbaidjan, Georgia and Turkey.

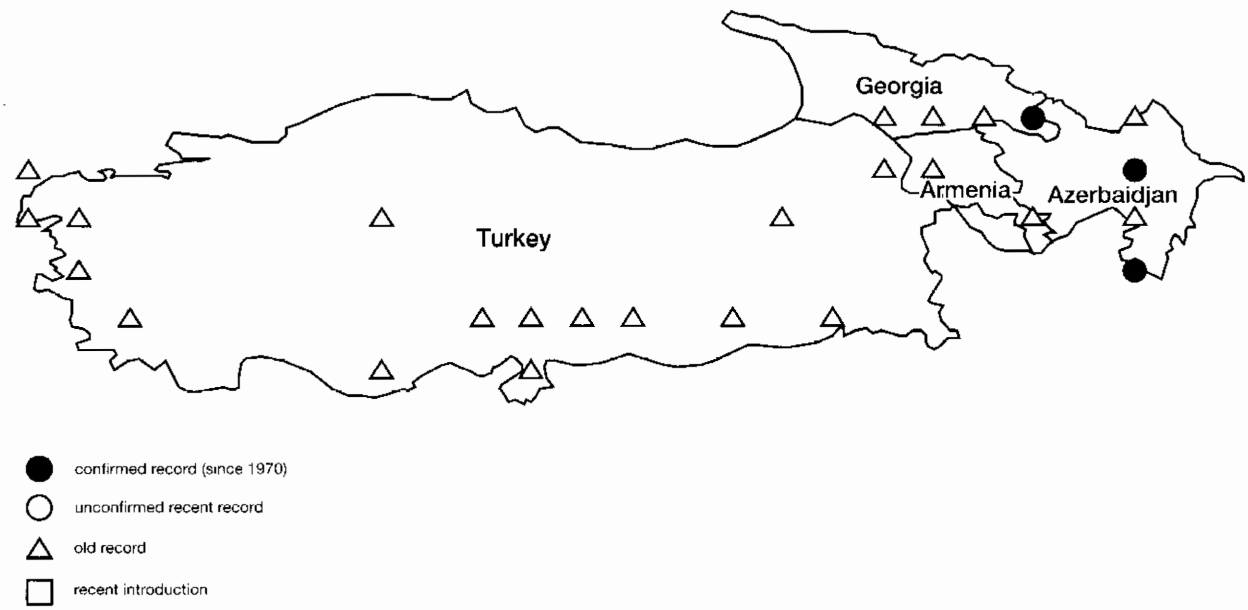


Figure 4.16. Distribution of the striped hyaena in Afghanistan, Iran and Pakistan.

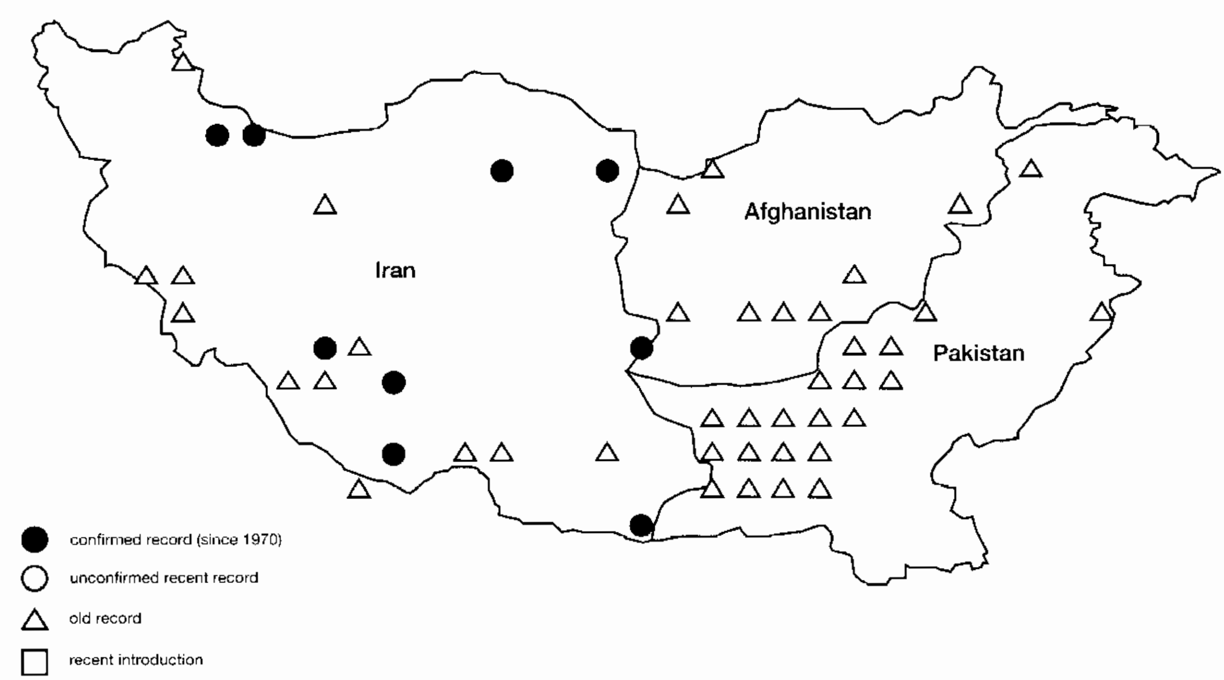
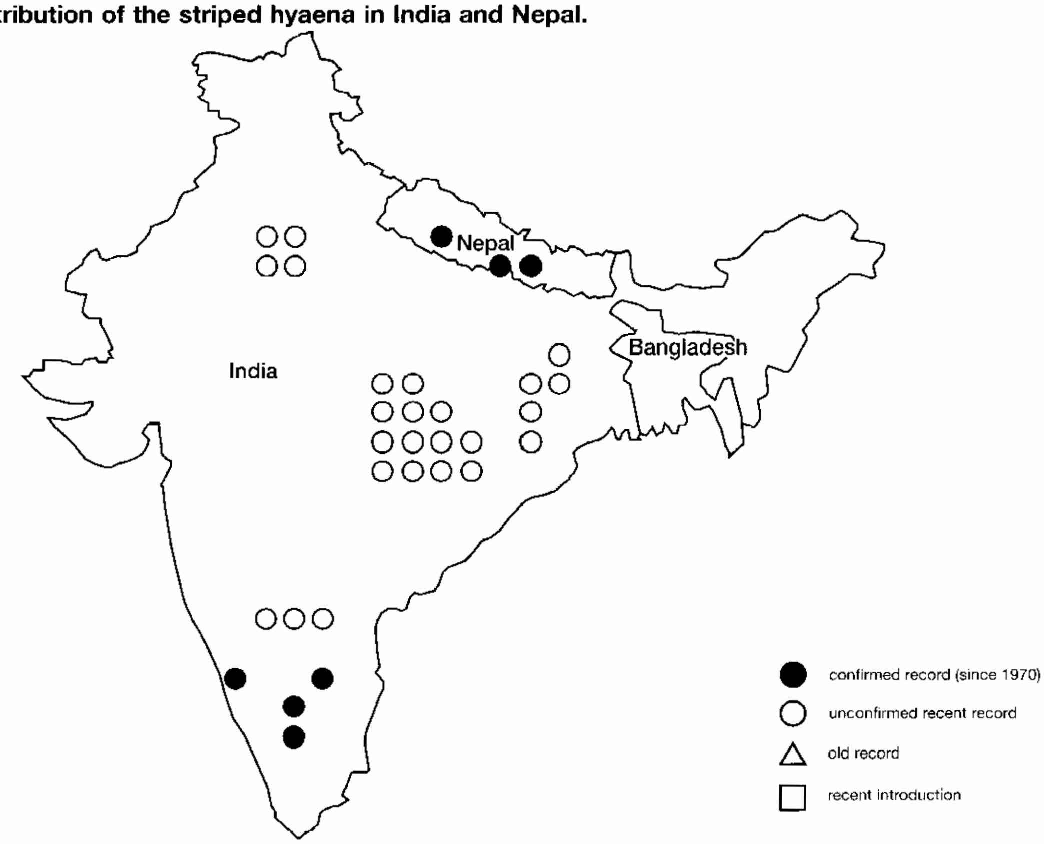


Figure 4.17. Distribution of the striped hyaena in Tadzhikistan, Turkmenistan and Uzbekistan.

Figure 4.18. Distribution of the striped hyaena in India and Nepal.



of the Masai steppe would extend the range into *Brachystegia* ("Miombo") woodland (Anonymous 1972). Recorded in Serengeti National Park, Tarangire National Park, the Ngorongoro Conservation Area and Mkomazi Game Reserve.

Togo. Fig. 4.11. No records.

Tunisia. Fig. 4.12. Historically present in the south and east (Le Berre 1990, Kowalski and Rzebik-Kowalska 1991). No recent records.

Turkey. Fig. 4.15. Historically widespread (Kumerloeve 1967). Now rare in the southeastern and eastern areas of Kurdistan and the areas bordering onto the Caucasus (Harrison and Bates 1991). No recent records.

Turkmenistan. Fig. 4.17. Historically widespread, now patchily distributed. Recent records include the southwest, the shores of the Caspian Sea, western and central Kopetdag State Nature Reserve, the southeastern mountains and parts of the Karakum desert, Badkhyz State Nature Reserve, Maly Balkhan and Kugitang State Nature Reserve (Heptner and Sludskij 1980, Gasperetti *et al.* 1985, Efimenko 1992, Lukarevsky 1995, V.S. Lukarevksy unpublished data).

United Arab Emirates (UAE). Fig. 4.14. Until several decades ago still widespread. No recent records from a survey of mountain chains (Hajar-Shumaylyah; northern Al Hijr al Gharbi; Rus al Jibal, C. and T. Stuart unpublished data). One record from 1984 near Khor Kalba on the Gulf of Oman just inside the UAE (C. and T. Stuart unpublished data) and an unconfirmed recent sighting (Gross 1987).

Uzbekistan. Fig. 4.17. Historically widespread throughout the southern areas in Surkhandarya region. In the past 40 50 years found in the southeast of the country (Heptner and Sludskij 1980) near the lower part of Sherabad river, near Saidabad, Djaririk, Guygerdak, Gaukhana, along the eastern slope of Kugitang ridge, in Termez district near the Amudarya river, in reeds near Sassikkul Lake, in flat sections of Kisirikdara desert, and in mountains of the Sherabad region (E. Mukhina and A. Nuritjanov unpublished data). Current distribution restricted to Surkhan Nature Reserve and nearby Babatag ridge, and along Surkhandarya and Amudarya rivers in Surkhandarya region (Chernogaev *et al.* 1996, E. Mukhina and A. Nuritjanov unpublished data).

Yemen. Fig. 4.14. Historically widespread, still found in many places throughout North and South Yemen (Gasperetti *et al.* 1985, Harrison and Bates 1991).

4.3 Brown hyaena

Historical distribution

Except for a marginal extension into the arid southwestern parts of Angola, it was confined to the South West Arid Zone and the drier parts of the Southern Savannahs in the Southern African Subregion. Its range has shrunk significantly since the end of the 18th century when it was last recorded from Table Bay in the extreme southwest of the continent. At the end of the 19th century it was still regularly found as far south as Malmesbury and Beaufort West (Smithers 1983).

Current distribution

Still widespread in southern Africa (Fig. 4.19).

Angola. Fig. 4.21. Huntley (1974) and Crawford-Cabral and Simões (1990) reported that it has only been recorded from the southwest of the country.

Botswana. Fig. 4.20. Widespread excluding the extreme north (Smithers 1968).

Lesotho. Fig. 4.20. Occurs sparsely in the west of the country (Lynch 1983, Smithers 1986).

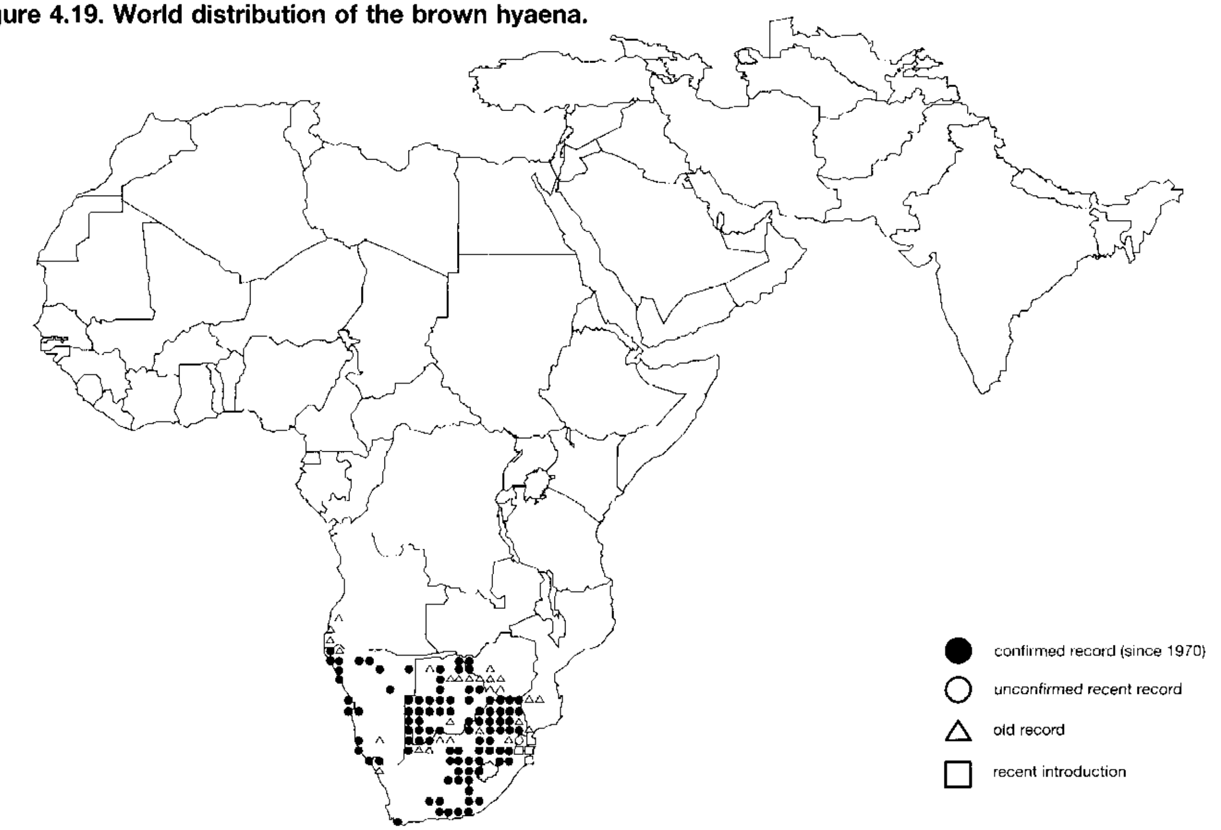
Malawi. Fig. 4.21. Occurrence uncertain, although Hayes (1972) mentioned he had received persistent reports of sightings and Sweeny (1959) stated that he knew of two sight records by experienced naturalists. During the questionnaire survey for the current Action Plan, F. Mkanda (pers. comm.) responded that it has been recorded from the Nkhota-Kota Game Reserve in the centre of the country, but this could not be confirmed. Ansell and Dowsett (1988) maintain that such reports are mistaken and that there is no reason to suppose that the species has ever occurred in this country.

Mozambique. Fig. 4.21. Persistently reported from the Banhine Flats, an arid area in the southwest of the country (Smithers and Lobão Tello 1976, Smithers 1983).

Namibia. Fig. 4.20. Sporadically encountered over most of the country, although seems to be absent from the Caprivi. Today mainly found along most of the coast, in the Etosha National Park, and in Bushmanland in the northeast (P. Stander pers. comm.).

South Africa. Fig. 4.20. (Note: because the information for South Africa was compiled before the new

Figure 4.19. World distribution of the brown hyaena.



constitution was implemented, the old provincial basis is used here).

(a) Cape Province. Extinct in the southwest and southeastern areas of the province, but in 1996 a brown hyaena was recorded from the Gansbaai area near Cape Aghulas (A. Scott pers. comm.). Occurs sporadically in the north, particularly north of the Orange River in the Kalahari Gemsbok National Park and in the Richtersveld in the northwest corner of the province.

(b) Natal. Never common in the province, but recorded irregularly in the drier regions of northwestern Natal. Roberts (1951) mentioned that it was surviving in the game reserves of Zululand, but according to Rowe-Rowe (1992) this distribution was never confirmed. Around 1980 four were introduced into the Hluhluwe-Umfolozi Game Reserve and seven to the Eastern Shores of Zululand, but since 1982 it has only been reported from the area around the Eastern Shores (Rowe-Rowe 1992).

(c) Free State. Historically occurred over the entire province, today very sparsely dispersed over all except the western parts.

(d) Transvaal. Still distributed over most of the province except for the densely populated areas around the big cities in the area known today as Gauteng. Found in many of the smaller game reserves, but absent as a breeding species over the eastern lowveld areas encompassing the Kruger National Park and surrounding private reserves.

Swaziland. Fig. 4.20. Said to occur sparsely in the northeast of the country (Smithers 1986), and also in the extreme west and northwest (Monadjem 1997), but there are no material records.

Zimbabwe. Fig. 4.21. Historical records suggest that it is/was comparatively uncommon in the southwest and northwest of the country (Smithers 1966). Now confined to the western parts of the country especially around West Nicholson.

4.4 Spotted hyaena

Historical distribution

Historically widespread throughout Africa south of the Sahara. Present in all habitats except the most extreme desert conditions, where it is present at densities lower than those of brown hyaenas in the south (Mills 1990), tropical rainforests, and the top of alpine mountains.

Figure 4.20. Distribution of the brown hyaena in Botswana, Lesotho, Namibia, South Africa and Swaziland.

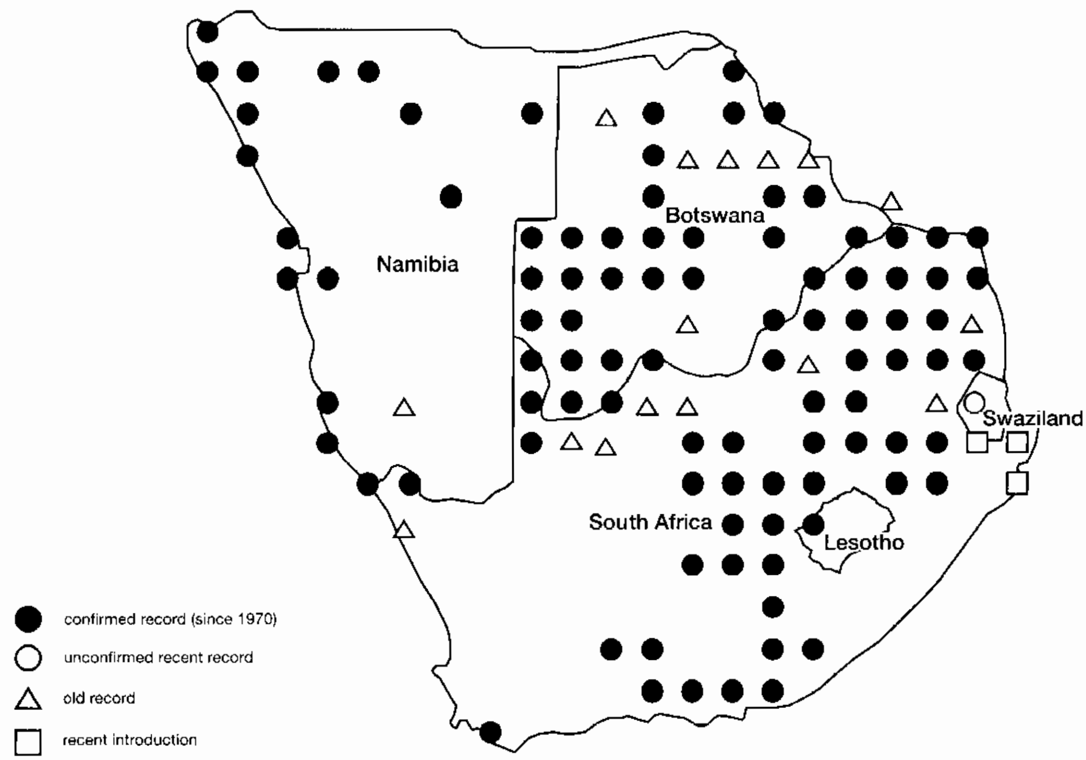
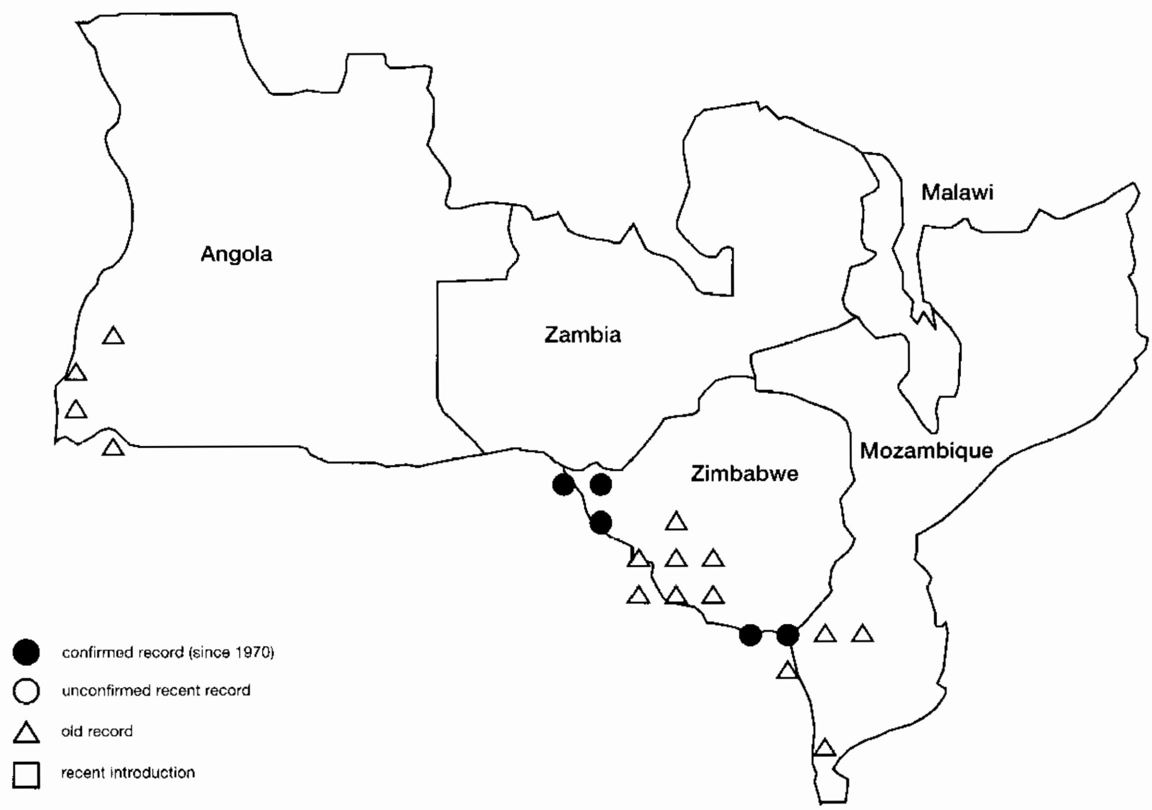


Figure 4.21. Distribution of the brown hyaena in Angola, Mozambique and Zimbabwe.



Current distribution

Distribution now patchy in many places especially in west Africa (Fig. 4.22), with populations concentrated in protected areas and on surrounding land. Continuous distribution over large areas in Ethiopia, Kenya, Tanzania, Botswana, Namibia and the Transvaal Lowveld areas of South Africa. If tolerated by local people, the spotted hyaena adapts to surviving on human-associated carrion and organic rubbish in areas without larger wildlife prey populations. (e.g. in Ethiopia).

Algeria. Fig. 4.29. Historically may have occurred in the Ahaggar and Tassili d'Ajjer but there have been no recent records inside the country (Le Berre 1990, Kowalski and Rzebik-Kowalska 1991). "The presence of stranded individuals in the southernmost regions of Algeria is nevertheless not impossible" (Kowalski and Rzebik-Kowalska 1991).

Angola. Fig. 4.24. Before 1974 widespread across the whole southern belt of Angola, near Kasinga, Kuvelaï, Mupa and Chimporo, and in the west-central zone, including Luanda area and Kassama National Park. One record from the northern border with the Democratic Republic of Congo at the junction of Lunga and Cuilo rivers. No information from east and northeast probably due to lack of observers (Monard 1935, Crawford-Cabral and Simões 1990).

Benin. Fig. 4.28. Recorded in "W" National Park and Pendjani National Park from 1971–81 (Happold 1973, Loevinsohn and Green 1981).

Botswana. Fig. 4.23. Historically widespread throughout the northern and southern parts of the country (Smithers 1968). Currently present in Chobe National Park, Moremi Wildlife Reserve, Central Kalahari Game Reserve, Gemsbok National Park, Nxai Pan, Makgagikgadi Pans Game Reserve, and Tuli Game Reserve.

Burkina Faso. Fig. 4.28. Widespread throughout the country at low densities. Present in Sahel burkinabé, east and southwest Burkina, Suurou, Kassi, and Mouhoun (Volta Noire). Present in Arli National Park, "W" National Park, Pama Reserve, Singou Reserve, Kourtiagou Reserve, Djona Reserve, Atacora Reserve, and Kabore Tambi National Park. Repeated reliable sightings in Koflandé Forest Reserve; small viable population at Nazinga Game Ranch (questionnaire survey).

Burundi. Fig. 4.25. Historically widespread throughout the eastern and western parts of the country. Recent sighting from the border area near the Democratic Republic of Congo.

Cameroon. Fig. 4.27. Historically widespread in the northern savannah zone (Jeannin 1936). Recently recorded from Boubandjida National Park (Happold 1973), Bénoué National Park (Happold 1973), Faro National Park, and Waza National Park. Probably occurs in Kalamaloué National Park. Also present around protected areas and around at least 23 gazetted hunting zones. Possibly occurs in forest reserves (Depierre and Vivien 1992).

Central African Republic. Fig. 4.27. Occurs throughout the northern part of the country at low densities (Table 5.5). Present in Manovo-Gounda-Saint Floris National Park, Gribingui-Bamingui Reserve, Koukourou-Bamingui Reserve, Aouk-Aoukalé Reserve, and Avakaba Presidential Park (questionnaire survey).

Chad. Fig. 4.30. Historical distribution widespread throughout the country, including the Tibesti mountains (Le Berre 1990). Present in Zakouma National Park, Sinianka Minia National Park, and in the areas of Batha, Moyen Chari, Mayo Kebbi, and near N'Djamena (questionnaire survey).

Congo. Fig. 4.27. Recent records from two localities. Present in Odzala National Park and nearby Lekoli-Pandaka Faunal Reserve and M'Boko Hunting Reserve in the northwest of the country (Heckctsweiler 1990, Heckelsweiler *et al.* 1991). Also recorded in Conkouati Hunting Reserve in the southwest of Congo (Heckelsweiler and Mokoko Ikonga 1991, Doumenge 1992).

Côte d'Ivoire. Fig. 4.28. Present in Comoé National Park and adjacent areas, Ouarigué Forest Reserve, and Monts Tingui Forest Reserve (questionnaire survey, K.E. Linsenmair pers. comm.).

Democratic Republic of Congo. Fig. 4.25. Historical and recent records from the south and east in Virunga National Park, Upemba National Park, Kundelungu National Park, Garamba National Park, and areas near Lake Tanganyika and Lake Mobutu (questionnaire survey; Verschuren 1958, 1987, Doumenge 1990).

Djibouti. Fig. 4.26. Historic records indicate presence throughout; no recent records available.

Egypt. Fig. 4.30. Unconfirmed records suggest that the spotted hyaena may exist in Egypt but confirmation of this information was not possible from the questionnaire survey.

Equatorial Guinea. Fig. 4.27. One recent record from Rio Muni (Juste and Castroviejo 1992), otherwise unknown (Fa 1991).

Eritrea. Fig. 4.26. Historical records indicate presence throughout (Yalden *et al.* 1980, 1996); no recent records available.

Ethiopia. Fig. 4.26. Still widespread in rural and even urban populated areas, including Harar (where they are provisioned by the "hyaena men") and the centre of Addis Ababa (Yalden *et al.* 1980, 1996). Present in all protected areas with some degree of protection: Abijatta-Shalla Lakes National Park, Awash National Park, Babille Elephant Sanctuary, Bale Mountains National Park, Gambella National Park, Kuni-Muktar Mountain Nyala Sanctuary, Mago National Park, Nechisar National Park, Omo National Park (Baba *et al.* 1982), Senkelle Swayne's Hartebeest Sanctuary, Simien Mountains National Park, Yabello Sanctuary, and Yangudi-Rassa National Park.

Gabon. Fig. 4.27. No recent records (Wilks 1990); presence in the extreme south near the border with Congo possible.

Gambia. Fig. 4.28. No recent records. The symbols in Fig. 4.28 refer to areas in neighbouring Senegal only.

Ghana. Fig. 4.28. Present in Mole National Park, Kujani Bush Game Reserve, and Volta Game Reserve (Happold 1973).

Guinea. Fig. 4.28. Historic records from the extreme southeast of the country, then belonging to Liberia (Johnston 1905). Unconfirmed recent records from western parts of the country (questionnaire survey).

Guinea-Bissau. Fig. 4.28. Historically widespread throughout the country although rare in dense forests. Still common throughout the country. Faeces can be seen everywhere and 77% of questioned villages in the north and east reported hyaenas coming into the village (Robillard 1989).

Kenya. Fig. 4.25. Historically widespread throughout the country, now virtually extirpated in areas under agriculture and along the entire coast. Rare in populated shore areas along Lake Victoria and in the wider Nairobi area. It has been sighted, however, in the centre of Nairobi City in the early 1990s (A. Spoerry pers. comm.). Still occurs widely outside protected areas. Present in all major protected areas including Masai Mara Game Reserve, Aberdares National Park, Nairobi National Park, Tsavo National Park, Samburu Game Reserve, Marsabit Game Reserve, and Amboseli National Park.

Lesotho. Fig. 4.23. Recent records from neighbouring South Africa suggest that spotted hyaenas may still occur in the west of the country (Lynch 1983).

Liberia. Fig. 4.28. No positive historic or current records. The entire country is contained within the Upper Guinean rainforest zone (Johnston 1905, Kuhn 1965, Anstey 1991) except for one savannah area north of the town of Voinjama, which has not been surveyed and where it may be present.

Malawi. Fig. 4.24. Historically widespread throughout the country, now concentrated in protected areas (Ansell and Dowsett 1988). Largely disappeared from the central highlands of Malawi. Present in all protected areas: Kasungu National Park, Lake Malawi National Park, Majete Game Reserve, Nkhotakota Game Reserve, Mwabi Game Reserve, Vwaza Marsh Game Reserve, Nyika National Park, Lengwe National Park, Liwonde National Park (Table 5.5), and Zomba Plateau Forest Reserve.

Mali. Fig. 4.29. Historically widespread throughout the southern half, also occurred in the Adrar des Iforas in the North (Le Berre 1990). Recent records from Boucle du Baoulé National Park in the west (Happold 1973) and possibly west of the Macina swamps in the centre of the country. Does not occur in the Adrar des Iforas anymore (Sidiyène and Tranier 1990).

Mauritania. Fig. 4.29. Historically widespread throughout the southernmost quarter of the country. Recent records only from the extreme southeast near Nema (questionnaire survey).

Mozambique. Fig. 4.24. Historical distribution widespread throughout the country (Smithers and Lobão Tello 1976). Still present in a number of protected areas, including Gorongoza National Park, Niassa Game Reserve, Gilé Game Reserve, Manomeu Game Reserve, Zriave National Park, Banhine National Park, and Maputo Elephant Reserve (questionnaire survey).

Namibia. Fig. 4.23. Historically widespread throughout the country except the Namib coast (Shortridge 1934, Coetzee 1969). Does not occur in densely populated areas in Ovamboland and along the Namib coast. Widespread in Damaraland, Kawango, Bushmanland, Hereroland, Caprivi, and Kaokoland. Present in Waterberg Plateau Game Park, Mahango Game Park, Kaudum Game Park, Etosha National Park, Mudumu National Park, Mamili National Park, Western Caprivi Game Park, Skeleton Coast National Park, Namib/Naukluft National Park, Fish River Canyon, and Huus Mountain Protected Area.

Niger. Fig. 4.29. Historically widespread throughout the southern half of the country, including the Aïr National Nature Reserve (Le Berre 1990). It is now mostly restricted to the "W" National Park and surrounding areas in the extreme southwest.

Nigeria. Fig. 4.27. Historically widespread throughout the northern and central parts of the country (Rosevear 1953). Recent records from Kainji Lake National Park (Borgu Game Reserve), Yankari National Park (Happold 1973), Gashaka Gumti National Park and adjacent farmland around both Yankari and Gashaka (questionnaires). Possibly in Chad Basin National Park and along the Cameroon border (Green and Amance 1987, Happold 1987).

Rwanda. Fig. 4.25. Historically widespread. Recent records include Akagera National Park, Mutara Hunting Reserve, Masango (near Gitarama), Bicumbi (near Kigali), and Munghuye (near Butare). Possibly present in the Virunga mountains in the northwest of the country, as spotted hyaenas have been recently recorded on side of the Democratic Republic of Congo.

Senegal. Fig. 4.28. Historically widespread throughout the southern half of the country. Currently present in the Tambacounda region (59,602km^2) in Niokolo-Koba National Park (Happold 1973) plus surrounding buffer zones. Recent records also from Basse-Casamance National Park (Ossouye) and Sine-Saloum, around Kaolack (questionnaire survey).

Sierra Leone. Fig. 4.28. Historically thought to occur throughout the northern half of the country. Distribution is now very reduced. Is mostly present in Outamba-Kilimi National Park, as well as possibly outside the National Park (Phillipson undated).

Somalia. Fig. 4.26. Historically widespread throughout the country (Drake-Brockman 1910, Azzaroli and Simonetta 1966). Few recent records.

South Africa. Fig. 4.23. (Note: because the information for South Africa was compiled before the new constitution was implemented, the old provincial basis is used here).

(a) Cape Province. Historically widespread throughout the area (Stuart 1981). Recent distribution restricted to Kalahari Gemsbok National Park, elsewhere only recorded in neighbouring Mier area in the last 10 years. Sightings of hyaenas outside the Kalahari Gemsbok National Park considered to be those of transitory animals (Stuart 1981).

(b) Transvaal. Historically widespread throughout the area. Occurs in the Kruger National Park and surrounding private nature reserves, and vagrants in Langjan Nature Reserve, Messina Nature Reserve, Hans Merensky Nature Reserve, and Vhembe Nature

Figure 4.22. World distribution of the spotted hyaena.

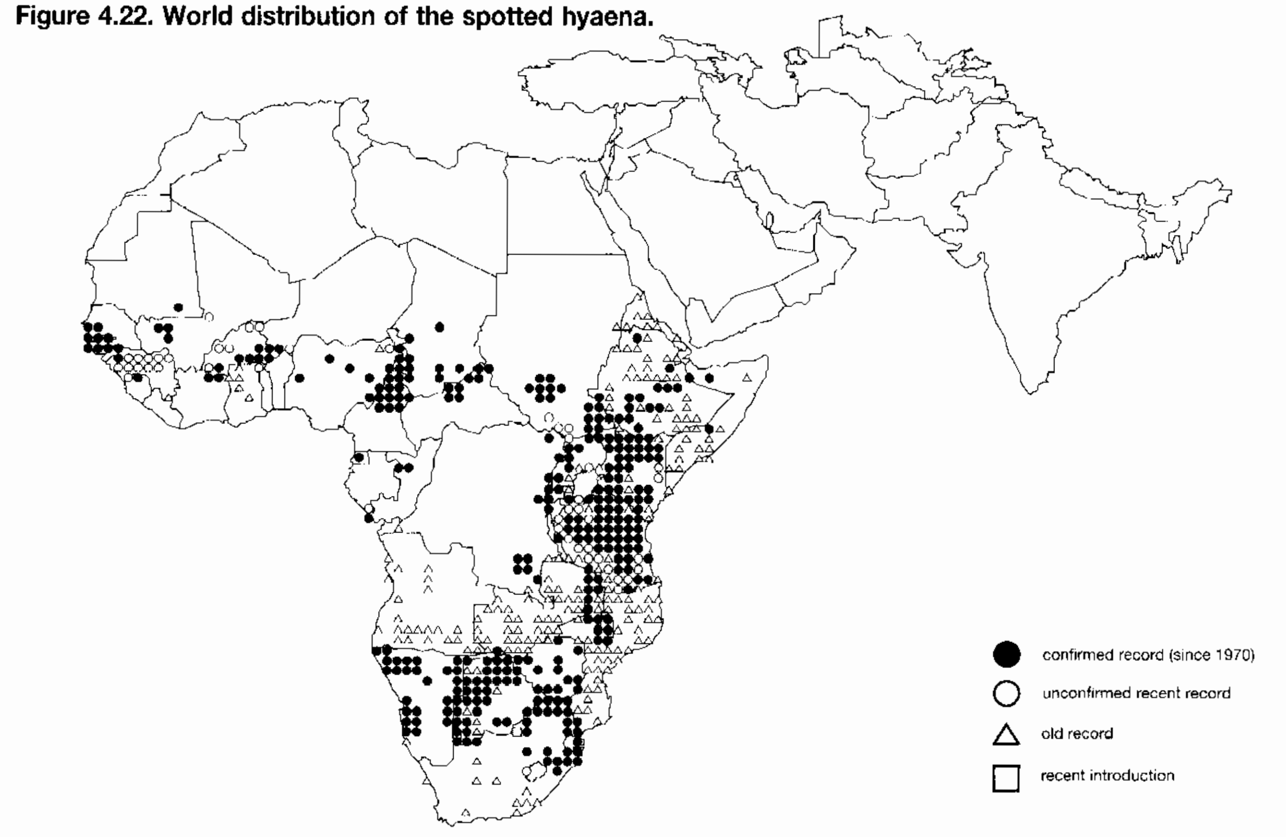


Figure 4.23. Distribution of the spotted hyaena in Botswana, Lesotho, Namibia, South Africa and Swaziland.

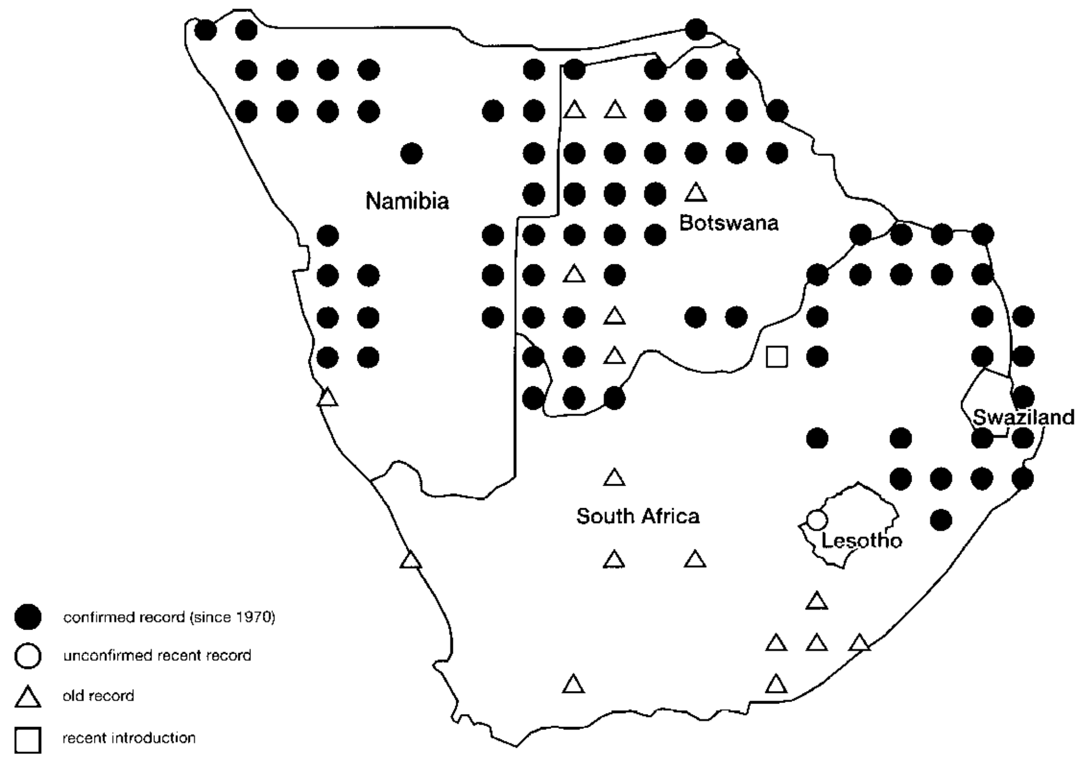


Figure 4.24. Distribution of the spotted hyaena in Angola, Malawi, Mozambique, Zambia and Zimbabwe.

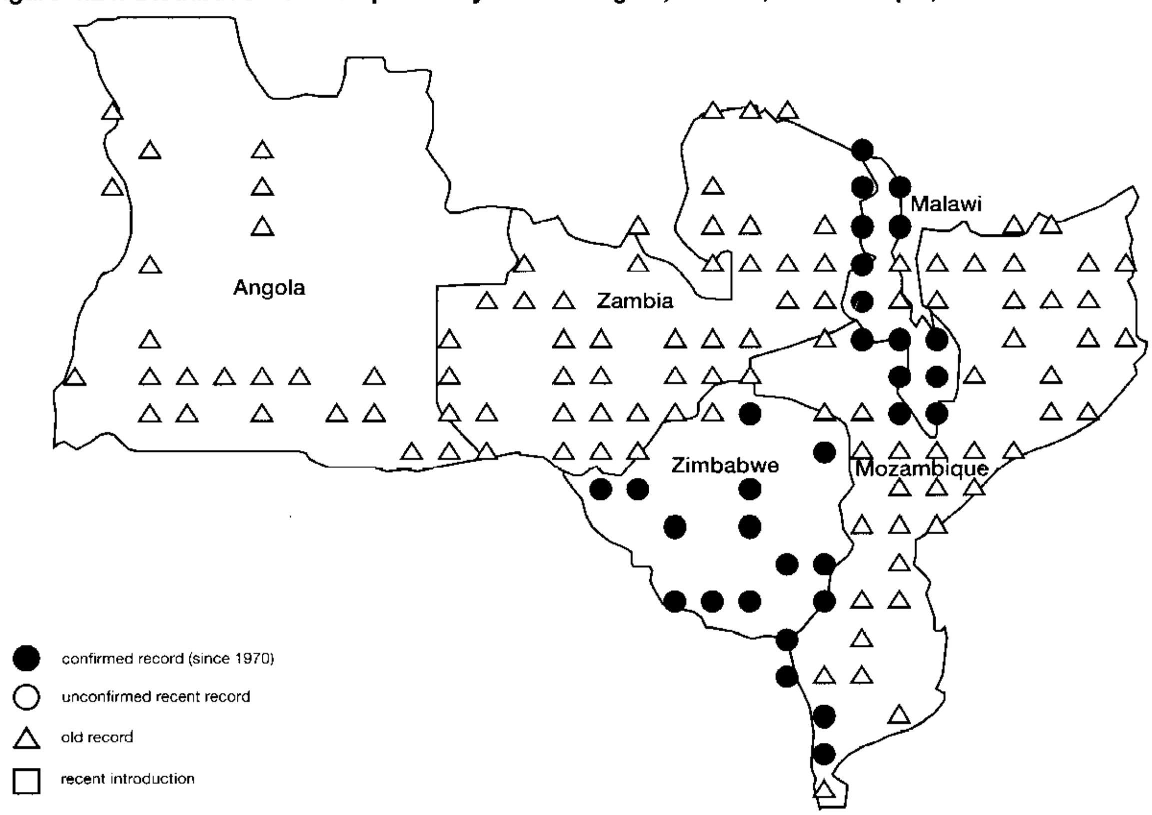


Figure 4.25. Distribution of the spotted hyaena in Burundi, Democratic Republic of Congo, Kenya, Rwanda, Tanzania and Uganda.

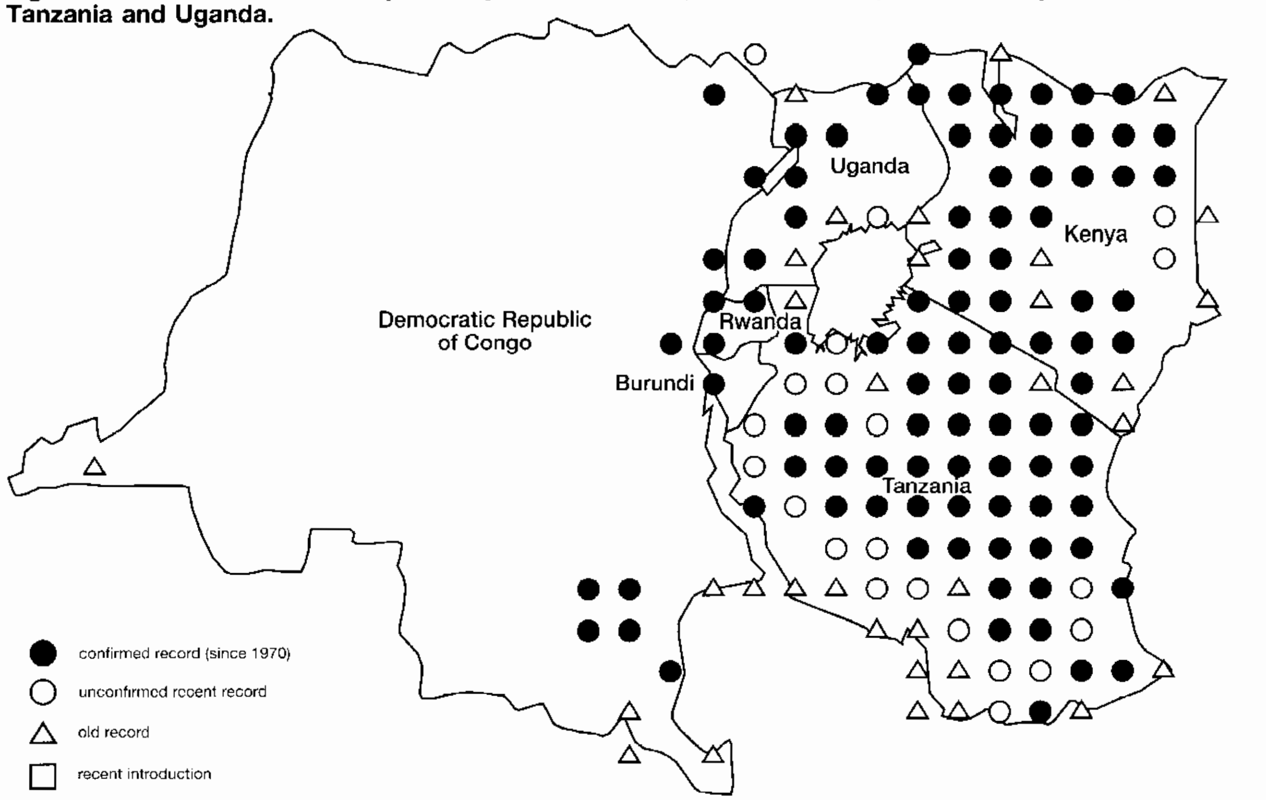


Figure 4.26. Distribution of the spotted hyaena in Djibouti, Eritrea, Ethiopia and Somalia.

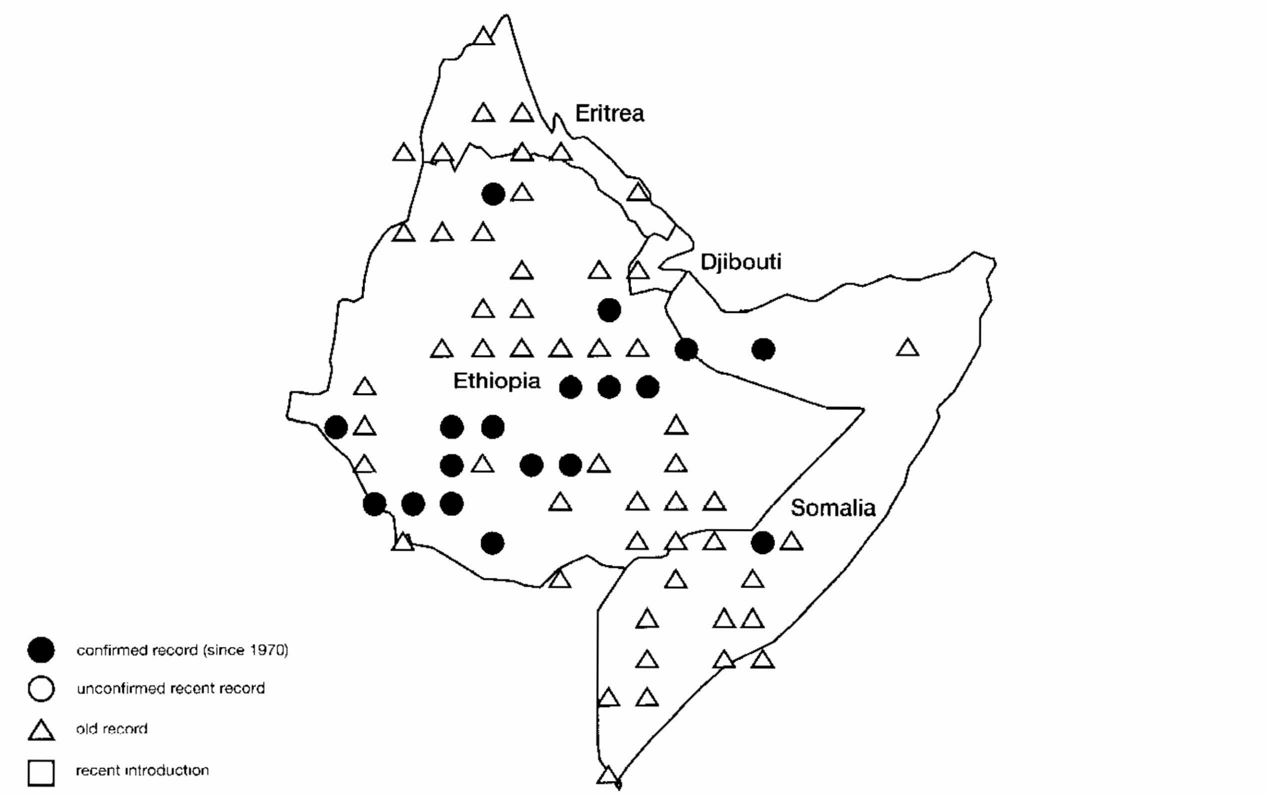


Figure 4.27. Distribution of the spotted hyaena in Cameroon, Central African Republic, Congo, Equitorial Guinea, Gabon and Nigeria.

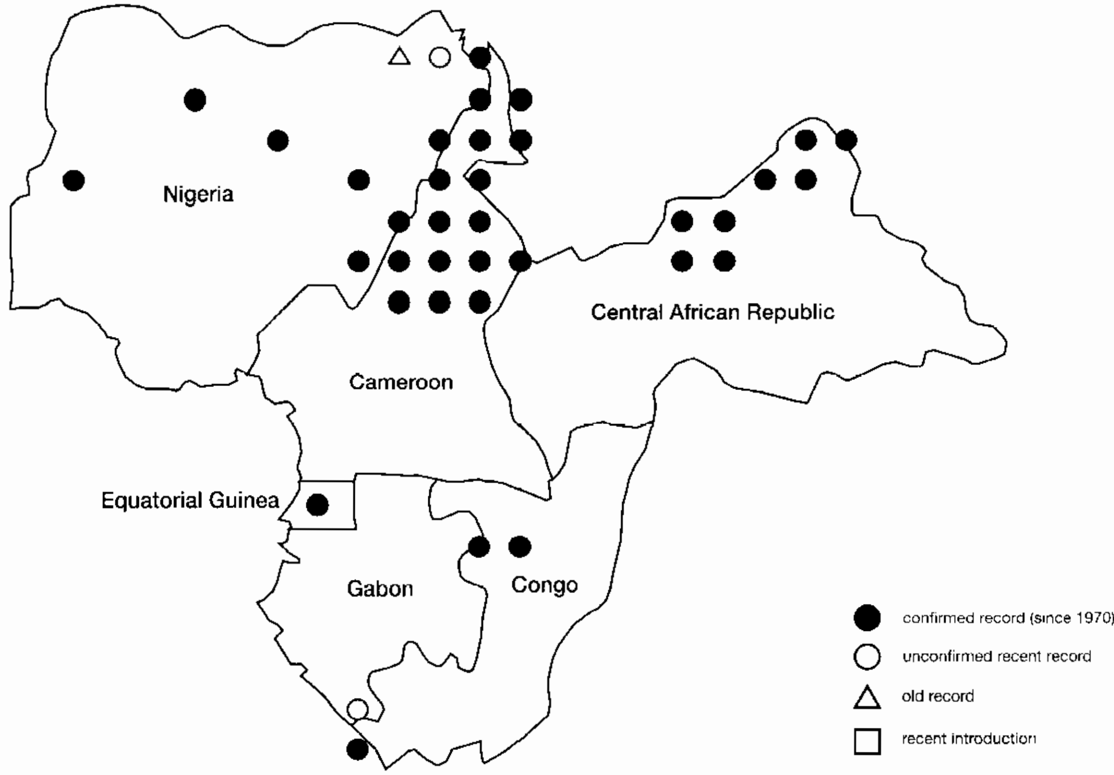


Figure 4.28. Distribution of the spotted hyaena in Benin, Burkina Faso, Cote d'Ivoire, Gambia, Ghana, Guinea, Guinea-Bissau, Senegal, Sierra Leone and Togo.

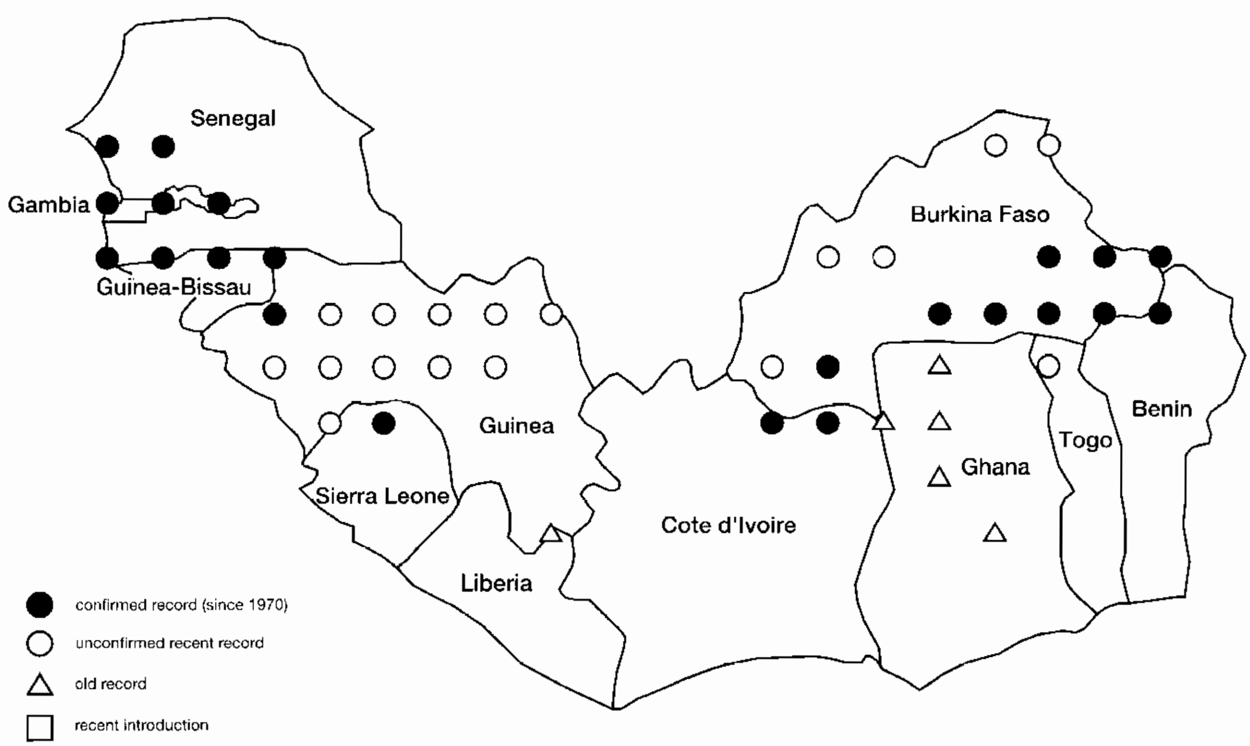


Figure 4.29. Distribution of the spotted hyaena in Mali, Mauritania and Niger.

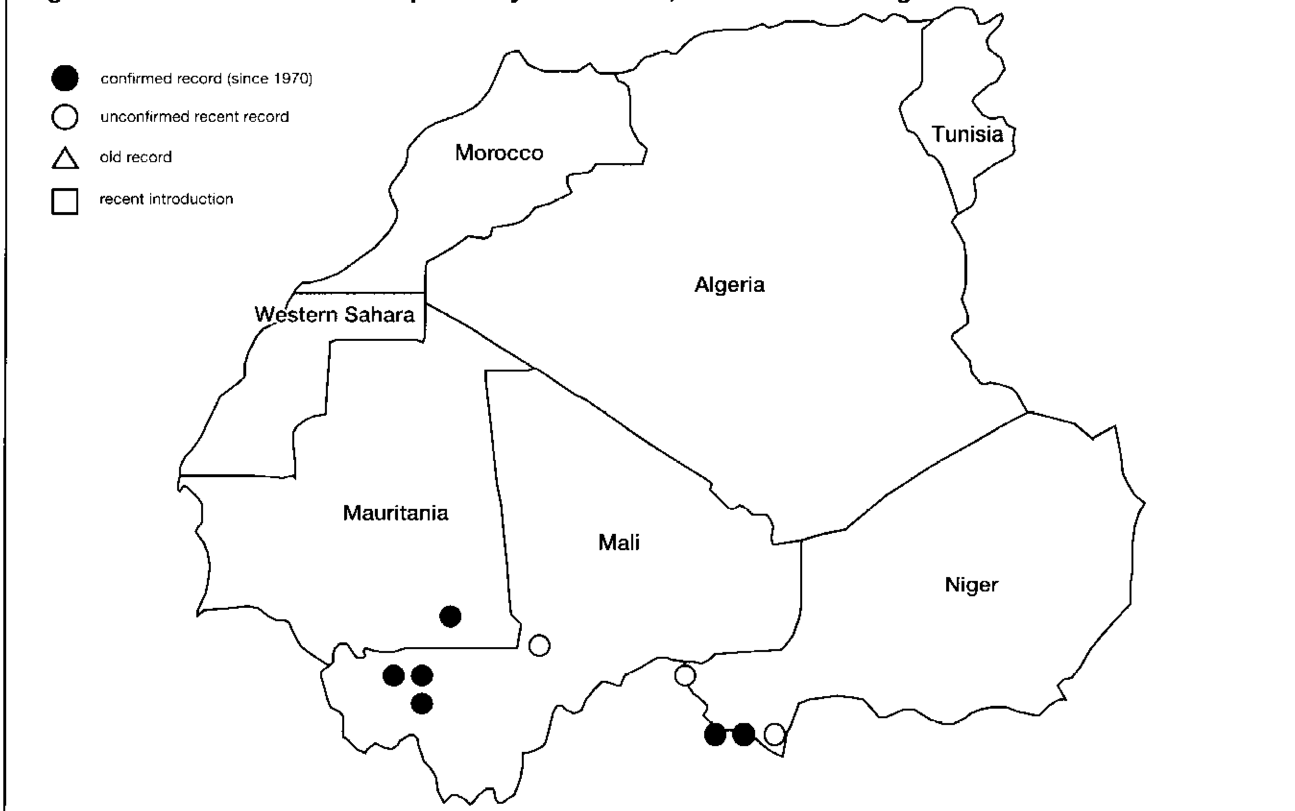
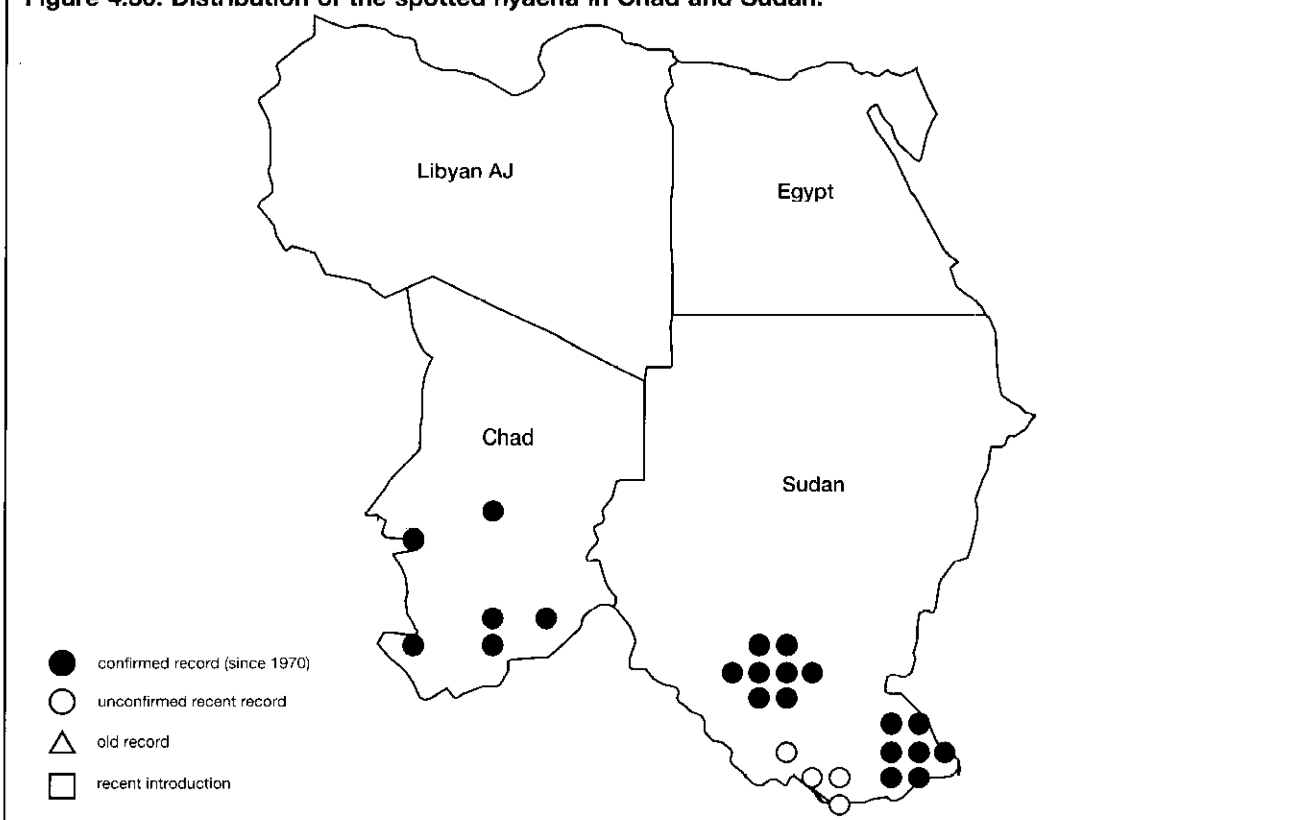


Figure 4.30. Distribution of the spotted hyaena in Chad and Sudan.



Reserve. Recently introduced to Madikwe Game Reserve.

(c) Natal. Historically widespread along the coast and in the north and northeast, and towards the interior along major river catchment areas. Recent distribution concentrated in Hluhluwe-Umfolozi Park, Mkuzi Game Reserve, the eastern shore of St Lucia, Itala, Sodwana State Forest, St Lucia Game Reserve, Weenen Nature Reserve, and Phinda Game Reserve. Also present outside reserves.

(d) Free State. Historically present, now extinct except for a few vagrants.

Sudan. Fig. 4.30. Historically widespread within the Sahel zone in Southern Sudan. Used to occur in Jebel Marra forest reserves where it is now apparently rare. Casual observations (C. Trout pers. comm.) in southern Sudan provide confirmed records in the following areas for the early 1990s: (1) An area of ca. 40,000km^2 in southeastern Sudan, including Boma Plateau and Boma National Park, Pibor River, areas east of the White Nile towards the Ethiopian border, and the southern and eastern edges of flood-plains utilised by white-eared kob during their annual migration. (2) An area of ca. 35,000km^2 northwest outside the papyrus (Sudd), north of Lake Yirol, east of Lake Maleit, and south of the Bahr el Gazal River in traditional Dinka country. This area still has resident herbivores, some water, and access to food of human origin. (3) May occur in southwestern areas including Southern National Park and in areas adjacent to the Garamba National Park in the Democratic Republic of Congo on the Sudanese border, although there are no confirmed recent records from here.

Swaziland. Fig. 4.23. Historically widespread. Small groups reported to still survive and breed in Mlawula Nature Reserve and Hlane National Park in the northeast of the country (Monadjem 1997).

Tanzania. Fig. 4.25. Historically widespread throughout the country. Still widespread in low densities outside protected areas. Occurs in most national parks (Serengeti, Kilimanjaro, Arusha, Tarangire, Lake Manyara, Mikumi, Ruaha), most Game Reserves (Selous, Rungwa/Kizigo, Moyowosi, Maswa, Ikorongo, Grumeti, Mkomazi, Burigi, Biharamulo, Ugalla River), and the Ngorongoro Conservation Area. Occurrence doubtful in Uzungwa Mountains National Park and Mahale Mountains National Park, absent from Gombe National Park.

Togo. Fig. 4.28. Present in Kerau National Park and Fazao-Malfacana National Park (Happold 1973). No recent records.

Uganda. Fig. 4.25. Historically widespread everywhere. Now rarely occurs outside protected areas, probably due to human population pressure and persecution. Present in Queen Elizabeth National Park, Murchison Falls National Park, Lake Mburo National Park, Kidepo Valley National Park, and most of the Game Reserves.

Zambia. Fig. 4.24. Historically widespread throughout the country (Ansell 1960). Still occurs outside protected areas and in most protected areas including the Luangwa Valley.

Zimbabwe. Fig. 4.24. Historically widespread throughout the country. Still present on communal lands, commercial farms, state land, and in the following conservation areas: Hwange National Park, Deka Safari Area, conservation areas in Zambezi Valley, Gonarezhou National Park, Malapati Safari Area, Victoria Falls Matetsi Safari Area, Chizarira National Park, Chirisa Safari Area, Matusadona National Park, Chete Safari Area, Doma Safari Area, Umfurudzi Safari Area, Tuli Safari Area, and Matopos National Park (Anonymous 1991, Bowler 1991). Absent from Hartley Safari Area, Nyanga National Park, Chipinge Safari Area, Chimanimani National Park, Kyle Recreational Park, Mushandike Sanctuary, McIlwaine Recreational Park, Ngezi Recreational Park, and Sibilobilo Safari Area (Anonymous 1991, Bowler 1991).

Chapter 5

Population Size, Threats and Conservation Status of Hyaenas

Heribert Hofer and Gus Mills

This chapter deals with three aspects of the conservation biology of hyaenas. Firstly, we make tentative estimates of total population size for most range countries. Then we discuss the relationship between people and each species in their respective range countries with emphasis on attitudes and activities that may pose a threat. Thirdly, we make an assessment of the conservation status of each species in each range country.

We asked each respondent of the Action Plan questionnaire survey to assess total population size in that respondent's country, according to the following categories: below 10 individuals, between 10 and 100, between 100 and 1,000, or greater than 1,000. In addition, we compiled all estimates of population density or absolute population size we could find from published and unpublished studies for all species. These estimates are described in the text and are also summarised for the striped hyaena in Table 5.1 and for the spotted hyaena in Table 5.5.

From the questionnaire survey and published and unpublished studies we made estimates of the total population size for each range country for the striped, brown, and spotted hyaena. We did not do this for the aardwolf because respondents were reluctant to give even broad estimates of numbers or density, as this species has only been studied in a very small area of its total distribution range. For those species which we do provide estimates we recognise that these are tentative, that the information on which they are based varies tremendously in quality and quantity and are often based on guesswork, and that they may grossly over- or underestimate actual population size. Nevertheless, we believe that these estimates are useful in that they provide an approximate order of magnitude of the likely population sizes. In time, with more information of higher quality, we will be able to revise these estimates and our current status assessments. The results are summarised for the striped hyaena in Table 5.2, the brown hyaena in Table 5.4, and the spotted hyaena in Table 5.6.

For each species we summarise the main threats facing it in an introductory section and discuss historical and current country-specific threats in greater detail in the country accounts. This includes descriptions of the ways in which hyaenas have been hunted, exploited, and utilised for food, magical or medicinal purposes in the past and present. Utilisation methods are summarised for the striped hyaena in Table 5.3 and for the spotted hyaena in Table 5.7. Additional information on sources of mortality and

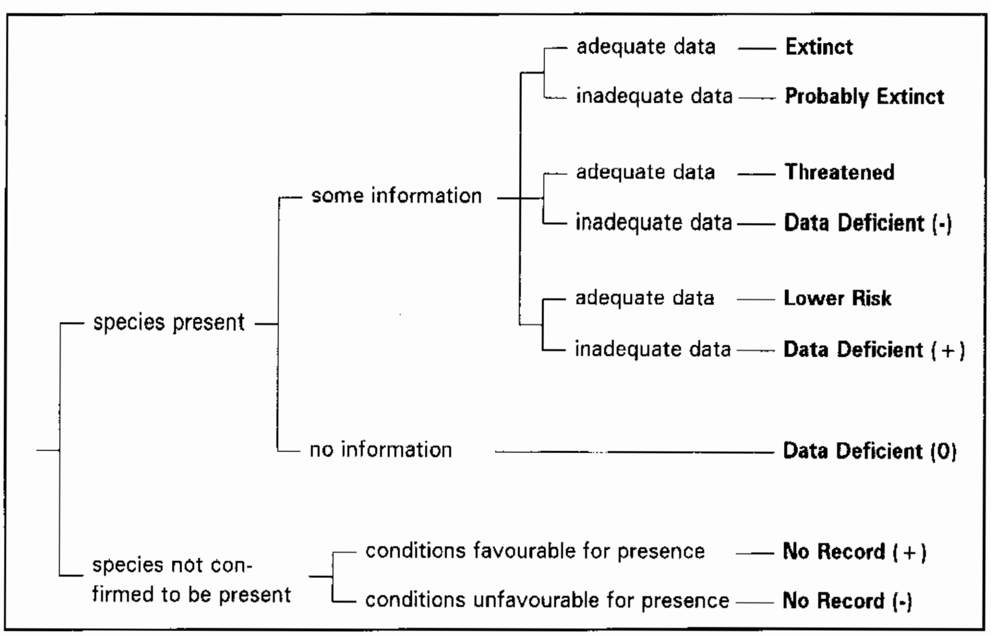


Figure 5.1. The structure of the status categories used in the present status survey (see Box 5.2).

Box 5.1. Definition of Red List Categories as used in this Status Survey.

Extinct. There is no reasonable doubt that the last individual of the species has died in that country.

Probably extinct. There is no doubt that the species did occur in the country, but no indication of its presence in the last 20 years was obtained in the literature and questionnaire surveys.

Threatened. The species is facing a risk of severe reduction which in the medium term could lead to non-viability in that country. Our information is inadequate to be able to distinguish between the IUCN Red List Categories of Critically Endangered, Endangered, and Vulnerable.

Data Deficient (-). Incomplete information suggests that the status of the species in that country is threatened as defined above.

Lower risk. The species does not satisfy the criteria for being classed as threatened under the prevailing conditions in that country. This is equivalent to the IUCN Red List Category of Lower Risk.

Data Deficient (+). Incomplete information suggests that the species does not satisfy the criteria for being classed as threatened under the prevailing conditions in that country.

Data Deficient (0). The species is definitely known to still occur in the country, but no information on its distribution and conservation status was obtained in the literature and questionnaire surveys.

No Record (+). The species could occur in the country because it is known to occur close by and suitable habitat apparently exists, but no records could be found in the literature and questionnaire surveys.

No Record (-). The species is unlikely to occur in the country, either because suitable habitat apparently does not exist, or because it is at some distance from the currently known edge of the range, although in the literature and questionnaire surveys the possibility of its occurrence was noted.

peoples' attitudes can be found in the sections on mortality for each species in Chapter 3, as well as in Chapter 10.

We have also attempted an assessment of the conservation status of each species in each country. Except for a few countries, information is insufficient to provide a country by country assessment based on the 1994 IUCN Red List categories (reprinted in Appendix 6); therefore we have used the Red List categories as the basis for a simplified list of categories (Fig 5.1, Box 5.1). This simplified list includes **Extinct** (representing the IUCN Red List categories *Extinct* and *Extinct in the Wild*), **Threatened** (representing *Critically Endangered, Endangered*, and *Vulnerable*), and **Lower Risk** (representing *Lower Risk-conservation dependent*, *Lower Risk-near threatened*, and *Lower Risk-least concern*). We have used these categories when the species was known to occur in a country and there was enough information on its status available (Fig 5.1). If we had reason to suspect that a species should belong to one of these three categories but felt that the data were inadequate for a firm classification, we assessed the status as **Probably Extinct**, **Data Deficient (-)**, and **Data Deficient (+)**, respectively. When there was no information but the species was definitely known to occur or have occurred in a country, the status was classified as **Data Deficient (0)**, equivalent to *Data Deficient* in the IUCN categories (Appendix 6). We added two categories for cases when there was no confirmed record for a country but we suspected that a particular hyaena species might occur there (**No Record (+)**), or that its occurrence was unlikely even though it had been suggested in the past (**No Record (-)**) (Fig 5.1, Box 5.1).

This system permits a comparison of countries as well as between species in each country. Summary statistics and an interpretation of these assessments are provided in Chapter 11.

5.1 Aardwolf

Introduction

Although the aardwolf may be harvested as a food source and purposefully or accidentally killed in predator control programmes, these mortalities appear to be of little significance in areas with well established populations. The greatest threat to the aardwolf is from spraying poisons on swarms of locusts. These events could significantly affect populations and could even lead to local extinctions, particularly if repeat sprayings occurred within four years of each other.

Although there is little information from most northern range states, we describe the overall status of the aardwolf currently as **Lower Risk: Least Concern** (IUCN 1996, Appendix 6).

Aardwolf: country accounts

Angola. *Data Deficient (+)*. Given its diet and unobtrusive behaviour, it is unlikely to have been affected by recent military conflicts.

Botswana. *Lower Risk*. Status believed to be satisfactory and is a protected species. It may occasionally be killed, either being mistaken for jackals or for food, but does not appear to suffer from human persecution.

Djibouti. *No Record (+).*

Egypt. *Data Deficient (0).*

Eritrea. *Data Deficient (0).*

Ethiopia. *Data Deficient (0).*

Kenya. *Data Deficient (+).*

Lesotho. *No Record (+).*

Mozambique. *Data Deficient (0).* Given its diet and unobtrusive behaviour, it is unlikely to have been affected by the recent military conflicts. Marginal presence (Smithers and Lobão Tello 1976).

Namibia. *Lower Risk.* Although it is a protected species, it is hunted for food in some communal areas and is occasionally killed accidentally during predator control operations. Nevertheless, the population appears to be stable.

Somalia. *Data Deficient (0).*

South Africa. The status of the aardwolf is given as rare in the South African Red Data Book (Smithers 1986). We assess its overall status as *Lower Risk*, although in all provinces aardwolves are occasionally killed because they are mistakenly believed to kill livestock, or are accidentally killed during predator control programmes. (Note: because the information for South Africa was compiled before the new constitution was implemented, the old provincial basis is used here).

(a) Cape Province. *Lower Risk.* In some areas it is also killed for food. Protected throughout the province.
(b) Natal. *Data Deficient (+).* It is protected only inside reserves. Legislation granting protection outside reserves is being considered.
(c) Free State. *Lower Risk.* It does not enjoy any special protection.
(d) Transvaal. *Lower Risk.* Enjoys second highest protection category.

Sudan. *Data Deficient (0).*

Swaziland. *Data Deficient (0).*

Tanzania. *Lower Risk.*

Uganda. *Data Deficient (0).*

Zambia. *Data Deficient (0).*

Zimbabwe. *Lower Risk.*

5.2 Striped hyaena

Introduction

The assessment of the current status and population trends of the striped hyaena is complicated by a number of problems. Because it is nocturnal, solitary, and occurs at low densities often in rugged country (Table 5.1) sightings are infrequent and surveys difficult to carry out. Moreover, in areas where the range of the striped hyaena overlaps with that of the spotted hyaena and the aardwolf, few people acknowledge or recognise a difference between the three species. As a result, records are likely to be lumped under a generic hyaena and may be unreliable.

With these caveats in mind, the results of the questionnaire survey and an evaluation of published information suggest that the striped hyaena is already extinct in many localities and that populations are generally declining throughout its range. The major reasons for this decline are decreasing natural and domestic sources of carrion due to declines in the populations of other large carnivores (wolf, cheetah, leopard, lion, tiger) and their prey, and changes in livestock practices. Moreover, the low densities (Table 5.1) and associated large home ranges

Table 5.1. Population densities of striped hyaenas.

Country	Locality	Year	Population size	Area (km^2)	Density (per km^2)	Trend	Source
Burkina Faso	Nazinga Game Ranch	1991	<20	940	<0.02	stable	GW Frame pers. comm.
Israel	Negev Desert	1980s	1*	60.9*	>0.016§	-	van Aarde *et al.* 1988
Tadzhikistan	Tigrovaya balka Reserve	1970s	4–6*	460*	0.009–0.01	?	Heptner & Sludskij 1980
Tanzania	Serengeti National Park	1960s	2*	44*–72*	>0.01–0.02§	-	Kruuk 1976
Turkmenistan	West Kopeth-Dag Reserve	1980s	70	15,000	0.005	?	V. Lukarevsky, pers. comm.

* indicates clan size and home range size of individually known, usually radio-collared animals, rather than population size
§ population density higher than indicated figure as individuals had overlapping home ranges rather than exclusive territories

are likely to increase the chances of fragmentation of populations into small, non-viable units. This must be considered a key problem for the future. The striped hyaena evokes many superstitious fears because of reputed and documented cases of injuries to humans sleeping outside, snatching and killing of children, and grave robbery. In addition, it is widely exploited as an aphrodisiac, utilised for traditional healing (Table 5.3), and killed because of suspected or real damage inflicted on agricultural produce and livestock (Table 3.1). The striped hyaena has been widely hunted through poisoning, baiting traps, pits, or with the help of dogs. A tentative estimate of the total worldwide population size is 5,000 to 14,000 individuals (Table 5.2).

Table 5.2. Tentative estimate of total world population size of free-ranging striped hyaenas.

Country	Estimate	Minimum estimate	Maximum estimate	Guess
Afghanistan	-			50
Algeria	<100	50	100	
Burkina Faso	100–1,000	100	1,000	
Cameroon	100–1,000	100	1,000	
Caucasus (Armenia, Azerbaidjan, Georgia)	<150–200	100	200	
Chad	-			50
Egypt	>1,000	1,000	2,000	
Ethiopia, Djibouti, Eritrea	-			100
India	>1,000	1,000	3,000	
Iran	-			50
Iraq	100–1,000	100	1,000	
Israel	100–170	100	170	
Jordan	-			50
Kenya	>1,000	1,000	2,000	
Kuwait	0	0	0	
Lebanon	-			50
Libya	-			50
Mali	-			50
Mauritania	-			50
Morocco	<100–500	50	500	
Nepal	<100	10	50	
Niger	100–500	100	500	
Nigeria	-			50
Oman	100–1,000	100	1,000	
Pakistan	-			100
Saudi Arabia	<100–1,000	50	200	
Senegal	<100	50	100	
Somalia	-			50
Sudan	-			100
Syria	-			50
Tadzhikistan	-			100
Tanzania	-			100
Tunisia	-			50
Turkey	-			50
Turkmenistan	100–500	100	500	
United Arab Emirates	0	0	0	
Uzbekistan	<100	25	100	
Western Sahara	-			50
Yemen	-			50
Sum		4,035	13,420	1,250
Total (estimates plus guess)		5,285	14,670	

Table 5.3. Utilisation of striped hyaenas according to questionnaire survey and literature.

Country	Body parts	Utilisation	Reference
Afghanistan	several parts of the body	serves as amulet/aphrodisiac	Naumann & Nogge 1973
Egypt	whiskers and eyeballs	used as protection from the evil eye	Prater 1948, Osborn & Helmy 1980
Egypt	heart	preserved for courage	Prater 1948, Osborn & Helmy 1980
India	tongue	reduce tumors	Prater 1948
India	body fat	cures rheumatism	Prater 1948
Iraq	prepuce	safeguards immunity from danger while travelling	Hatt 1959
Iraq	other parts of the body	used for traditional medicine	questionnaire
Iraq	external female genitalia	cure sexual impotence in men	questionnaire
North Africa	whole body	hyaenas were semi-domesticated and husbanded for consumption for at least 3000 years since the days of Ancient Egypt; still practised in the 20th century by Arabian Bedouins, Sinai Bedouins, Palestinians and Touaregs	Ronnefeld 1969, Osborn & Helmy 1980, Boessneck 1981
North Africa	hairs	used as talisman	Rieger 1979a
North Africa	brain	aphrodisiac	Rieger 1979a, Osborn & Helmy 1980
Turkmenistan	long, narrow stripe of abdominal skin that includes female genitals	used as talisman	Heptner & Sludskij 1980
Turkmenistan	tail	assumed to have magic powers	Heptner & Sludskij 1980
Turkmenistan	male sex organs	aphrodisiac	questionnaires

The upper estimate of the global population size of the striped hyaena exceeds 10,000 individuals. However, fragmentation of the world population into many subpopulations is suspected even though the actual degree of fragmentation is unknown. In addition, a degree of habitat loss and population decline is taking place at an unknown rate, and the minimum population estimate is less than 10,000 individuals. This suggests that a classification of **Lower Risk: least concern** is now inappropriate. We therefore suggest that the status be changed to **Lower Risk: near threatened.**

Striped hyaena: country accounts

Afghanistan. *Data Deficient (-).* Striped hyaenas are caught for organised fights with domestic dogs for entertainment (Naumann and Nogge 1973). Approximately 25 striped hyaenas were reportedly caught for this purpose every year in the 1960s (Kullman 1965, Hassinger 1973). It is also utilised for traditional medicine (Table 5.3).

Algeria. *Threatened.* Decreasing population with less than 100 individuals. At present, hyaenas are still killed by a minority of hunters in the North in the Kabyl zone, the Fôret des Bibans, and in West Sidibelabbes. Other reasons given for population decline are forest fires and disturbance of den sites. Hunting is limited and there is no bounty. The species has been protected by décret no. 83-509 since 20 August 1983 and is fully protected in all conservation areas.

Armenia and Azerbaidjan. *Threatened.* Probably fewer than 50–100 individuals in each country (Arabuli 1970, Heptner and Sludskij 1980). A major decline over the past 100 years has been caused by fur trapping and persecution, as striped hyaenas are held responsible for the disappearance of unattended small children. Other sources of decline are considered to be habitat destruction, a reduction in ungulate and large carnivore populations and changes in stock keeping of livestock (Heptner and Sludskij 1980).

Benin. *No Record (+).* Marginal presence is likely in the "W" National Park at the border with Burkina Faso and Niger.

Burkina Faso. *Data Deficient (+).* Current population is low but apparently stable, with between 100 and 1000 individuals throughout the country. At Nazinga Game Ranch there is an estimated stable population of less than 20 hyaenas (Table 5.1). There is a fixed hunting season outside conservation areas. Fully protected inside national parks and other conservation areas. Often poisoned and trapped if domestic stock are attacked.

Burundi. *No Record (-)*.

Cameroon. *Data Deficient (-)*. Population estimated to number between 100 and 1000 individuals. No legal protection, no specific attention.

Central African Republic. *No Record (+)*. Might occur in the northern savannah areas.

Chad. *Data Deficient (-)*.

Congo. *No Record (-)*.

Côte d'Ivoire. *No Record (-)*.

Democratic Republic of Congo. *No Record (-)*.

Djibouti. *No Record (+)*.

Egypt. *Data Deficient (+)*. Population estimated to exceed 1000 individuals but declining due to persecution, reduced availability of carrion (e.g. camels along former caravan highways), and hunting for utilisation (Table 5.3). Exterminated from a number of oases by poisoning (Osborn and Helmy 1980). No legal protection, viewed as a pest.

Eritrea. *Data Deficient (0)*.

Ethiopia. *Lower Risk*. Specially protected under Schedule 5 of the Wildlife Conservation Amendment Regulations (1974). However, may be hunted under special permit for EtBirr 40 (equivalent to US$20) for science, education or zoology. General attitude is one of benign neglect.

Gabon. *No Record (-)*.

Georgia. *Threatened*. Total population probably less than 50 100 individuals (Arabuli 1970, Heptner and Sludskij 1980, J. Badridze, pers. comm.). Sources of decline over the past 100 years are considered to be fur trapping, habitat destruction, a reduction in ungulate and large carnivore populations, and changes in stock keeping of livestock (Heptner and Sludskij 1980). Listed in the Red Data Books of Georgia and the former USSR (1984) as threatened with extinction.

Ghana. *No Record (+)*.

Guinea. *No Record (+)*. No confirmed records but questionnaires indicate that the species is known to local people.

India. *Data Deficient (+)*. Population probably numbers more than a 1000 individuals but is declining in many places due to persecution and hunting for utilisation (Table 5.3). Ecological factors may also be contributing to the decline, including diminishing food stocks and competition with leopards over shelter (Heptner and Sludskij 1980). No bounty. Hunting is prohibited under the Wildlife (Protection) Act 1972, schedule III, but this is only enforced inside conservation areas.

Iran. *Data Deficient (0)*. Protected by law (Rieger 1981).

Iraq. *Threatened*. Population is decreasing and estimated to number between 100 and 1000 individuals. Wildlife laws regulate hunting of game animals. No bounty. Various parts utilised for traditional medicine (Table 5.3).

Israel. *Threatened*. Population numbers around 150. No major changes since Ilani (1979) estimated the total population to be approximately 100–170 individuals (Nissim 1985, 1986). The striped hyaena has returned to the densely populated coastal plain where it had been exterminated by strychnine poisoning between 1918–1948. Current nature reserves are small and unlikely to ensure the continued existence of viable populations. This may not be such an important problem, however, since the nature reserves contain feeding stations for vultures which are also used by striped hyaenas (Macdonald 1978, Bouskila 1983, Table 5.1). Moreover, the species can live alongside humans. The high number of road accidents, which kill 15 25 every year, are the most serious factor threatening the population. Completely protected by law.

Jordan. *Threatened*. Traditionally considered a threat to human life. Persistent persecution is responsible for a marked population decline (Al Younis 1993).

Kenya. *Lower Risk*. Population currently more than 1000 individuals, however, this is likely to decrease as habitat destruction is accelerating. Shooting, spearing or poisoning is prohibited, but there is no effective protection because officially hyaenas are viewed with contempt, indifference or as a pest.

Kuwait. *Probably extinct*.

Lebanon. *Data Deficient (-)*.

Libya. *Data Deficient (+)*.

Mali. *Data Deficient (-)*.

Mauritania. *Data Deficient (-)*.

Morocco. *Threatened.* Population has declined drastically; remaining individuals have withdrawn into southern mountainous regions. The total population is assumed to number no more than 400 500 individuals and possibly now fewer than 100 individuals (Cuzin 1996). Protected by law since 1955 (Panousse 1957, Aulagnier and Thevenot 1986).

Morocco-Western Sahara. *Data Deficient (-).*

Nepal. *Data Deficient (0).* Recent sightings suggest a small population present and a range extension. The species is not considered a priority by the authorities.

Niger. *Threatened.* Millington and Tiega (1990, 1991) estimate there to be less than 500 individuals for the entire country. Population decline caused primarily by eradication or poisoning, which are apparently still officially sanctioned (see also section on spotted hyaena below), and indirectly through habitat destruction by overgrazing and agricultural encroachment in conservation areas.

Nigeria. *Threatened.* Seldom seen, and assumed to be very rare, as the population numbers fewer than 100 individuals (Happold 1987).

Oman. *Threatened.* Population assumed to be decreasing, as in the past five years there have been fewer sightings and road kills than in the previous 15 years. Estimated to number between 100 and 1000 individuals. No legal protection and no bounty, but government considers them a useful scavenger and encourages people not to destroy carnivores without very good reason (questionnaire survey).

Pakistan. *Data Deficient (0).* Used to be hunted with dogs in Dera Ismail Khan (Roberts 1977).

Qatar. *Probably extinct.*

Rwanda. *No Record (-).*

Saudi Arabia. *Threatened.* Wildlife has been decimated since the 1920s, and the current population is still declining, and estimated to be around 100 individuals. It is still the object of much local superstitious belief, and is generally loathed and severely persecuted (Gasperetti *et al.* 1985, Seddon 1996). In much of its former desert range it was exterminated because it was easily chased by motor vehicles and run over, run to death, or shot. Traffic accidents on the rise. No bounty but no legal protection either except for specially designated areas (Seddon 1996).

Senegal. *Threatened.* Population estimated to number fewer than 100 individuals.

Somalia. *Data Deficient (0).*

Sudan. *Data Deficient (0).*

Syria. *Data Deficient (-).*

Tadzhikistan. *Threatened.* Already rare in the 1930s–1950s, the population declined further throughout the 1960s and 1970s. In the early 1970s total population size was estimated to be around 20 individuals (Isakov *et al.* 1988). In the 1940s approximately 5 12 individuals were shot every year. This number declined, and the last animal recorded as shot was killed in the 1960s (Isakov *et al.* 1988). The Red Data Book of Tadzhikistan lists the striped hyaena as Endangered (Isakov *et al.* 1988). In the Tigrovaya balka Reserve hyaenas still present at low densities (Table 5.1). Hunting is forbidden. The species has been legally protected since 1968 (Isakov *et al.* 1988).

Tanzania. *Data Deficient (+).* In the Serengeti current population density probably lower than the density estimated in the 1960s (Table 5.1). No information available from other parts of the country. Official attitude one of benign neglect. Road kills on national roads (H. Hofer unpublished data) constitute the main source of recorded mortality, but these records may be biased. In theory can be hunted in reserves but is usually not a target species.

Togo. *No Record (-).*

Tunisia. *Data Deficient (-).*

Turkey. *Data Deficient (-).* May be hunted throughout the year (Kumerloeve 1970).

Turkmenistan. *Threatened.* Population has apparently declined for several decades (Gorelov 1973, Heptner and Sludskij 1980) but still estimated to number between 100 and 1000 individuals in Kopeth-Dag and Badhyz (Table 5.1, Gorelov 1973, Efimenko 1992). Occasionally hunted with domestic hunting dogs and killed for utilisation (Table 5.3). Cases of child kidnapping reported until 1948 and grave robbing suspected in some cases when burials where not properly covered over. In protected areas population dynamics seem to be related to the abundance of ungulate populations and wolf densities (Lukarevsky 1988). A major component of the diet are scavenged carcasses killed by wolves (Heptner and Sludskij 1980). Listed in the Red Book of the former USSR (1984) and the Red Book of Turkmenistan (Lukarevsky 1995).

Uganda. *No Record (-).*

United Arab Emirates. *Probably extinct.*

Uzbekistan. *Threatened*. Populations have apparently declined for several decades (Heptner and Sludskij 1980) to the point of comprising only a few individuals (Chernogaev *et al.* 1996). Past population declines mostly due to habitat destruction (cultivation) and persecution based on the popular belief that the species steals children and livestock. Child kidnapping has not been documented and today the species is generally tolerated. As recently as 1996, several hyaenas have been live-trapped for zoos. There is no bounty and hunting prohibited. Included in the Red Data Book of Uzbekistan (1983) as a rare species.

Yemen. *Data Deficient (0)*.

5.3 Brown hyaena

Introduction

Because of its secretive nature and nocturnal habits the brown hyaena, like the striped hyaena, is not easy to encounter and is often overlooked, even in stock farming areas. However, poisoning, trapping and hunting have had a detrimental effect on populations and are a threat to the species in some areas. Intolerance and ignorance by commercial stock farmers in Namibia, South Africa and Zimbabwe have led to the killing of many non-harmful individuals. Although used in traditional medicine and rituals, it is not nearly as sought after in this regard as the spotted hyaena. It also has very little demand as a trophy.

Because it is often overlooked, numbers and distribution records may in fact underestimate its distribution and population size. Given this proviso, the results of the questionnaire survey and an evaluation of published information suggest that a tentative estimate of the total worldwide population size is at a minimum of 5,000 to 8,000 individuals (Table 5.4).

There are several large conservation areas within the brown hyaena's distribution range with viable populations: the Namib-Naukluft, Skeleton Coast and Etosha National Parks in Namibia, the Kalahari Gemsbok and Gemsbok National Parks in South Africa; and Botswana, and the Central Kalahari Game Reserve in Botswana. Furthermore, the species adapts easily to many human activities. As long as these large conservation areas are maintained and a rational approach to the management of brown hyaenas in other areas can be maintained and developed, the future survival of the species can be viewed with optimism. Outside of conservation areas good habitat for brown hyaenas exists on agricultural land, particularly in areas unsuitable for small stock production. In these areas brown hyaena conservation should be promoted through education campaigns on brown hyaena ecology and through supportive management by conservation authorities, such as by helping to remove problem individuals.

In the South African Red Data Book the status of the brown hyaena is given as rare (Smithers 1986). The global population size is estimated to be below 10,000 individuals, and because of this small size and deliberate and incidental persecution, we maintain that it is now inappropriate to classify it as **Lower Risk: least concern** (IUCN 1996). We therefore recommend that the status of the brown hyaenas be changed to **Lower Risk: near threatened**.

Table 5.4. Tentative estimate of total world population size of free ranging brown hyaenas.

Country	Estimate	Minimum estimate	Maximum estimate	Guess
Angola				100
Botswana	3,900	3,500	4,500	
Lesotho				20
Mozambique	100			100
Namibia	500–1,000	500	1,000	
South Africa				
Cape Province	<500	250	500	
Natal	<100	25	100	
Free State	<100	25	100	
Transvaal	1,000	500	1,500	
Zimbabwe	<100	50	100	
Sum		4,850	7,800	220
Total (Estimates plus guess)		5,070	8,020	

Brown hyaena: country accounts

Angola. *Data Deficient (0)*. Eight protected areas occur in the South West Arid region of Angola. However, the recent military conflicts have caused much environmental damage to the area and the present status of wildlife is unknown (Feiler 1990).

Botswana. *Lower Risk*. From Mills (1990) it has been calculated that there are about 400 brown hyaenas in the Gemsbok National Park. An extrapolation of these figures to the Central Kalahari Game Reserve, which at a minimum has a similar density to the Gemsbok National Park (Owens and Owens 1984), indicates there are 1,500 animals in the area. Because much of southern, central and northeastern Botswana is sparsely inhabited and provides ideal brown hyaena habitat, there must be at least as many brown hyaenas in this region as in the two conservation areas combined. It is listed as a protected game animal and may therefore not be hunted. However, even though it is not recorded as a problem animal and rarely takes domestic stock (except occasionally goats) it is shot, poisoned and trapped and is often viewed in the same light as the spotted hyaena as a problem animal.

Lesotho. *Data Deficient (-)*. Less than 100.

Malawi. *No Record (-)*. Occurrence uncertain (see Chapter 4 Distribution). Probably outside its distribution range.

Mozambique. *Data Deficient (+)*. Status uncertain (Smithers and Lab Tello 1976), but may be endangered due to habitat destruction, poaching and the war situation. Said to maim cattle and to be trapped by local people to protect their cattle.

Namibia. *Lower Risk*. Population probably stable or declining. Strictly protected in all national parks and game reserves, but not outside these areas. Treated with suspicion by farmers who are ignorant of its feeding habits. Rarely hunted as a trophy. Probably between 500 1000 animals.

South Africa. Overall country status assessed as *Lower Risk*. (Note: because the information for South Africa was compiled before the new constitution was implemented, the old provincial basis is used here).

(a) Cape Province. *Threatened*. Classified as a Protected Wild Animal, which means that it can only be destroyed if causing damage to stock. Conservation authorities will attempt to remove problem animals and translocate them to other areas. Mills (1990) calculated that there were approximately 175 in the Kalahari Gemsbok National Park. Probably less than 500 in the province.

(b) Natal. *Threatened*. Population numbers less than 100.

(c) Free State. *Threatened*. Population numbers less than 100 in the province. Protected in the nature reserves in the province, but these are too small to contain them and they frequently leave reserves and cause stock losses. Regarded as a problem animal in the Nature Conservation Ordinance of the Orange Free State, which is predominantly a sheep farming region. Tolerated in wheat and cattle ranching areas, but hated in sheep farming areas where it is shot, trapped and poisoned. Hunted by a government sponsored predator control hunting club. An average of two per year (Range zero to nine, total 39) were killed by the hunting club between 1971 and 1991.

(d) Transvaal. *Lower Risk*. Population numbers about 1,000 animals in the province. Classified as Protected Wild Animal and seen by conservation authorities as an asset. Normally quite well tolerated by farmers, although it is shot, trapped, and poisoned where livestock damage occurs.

Swaziland. *No Record (+)*.

Zimbabwe. *Data Deficient (-)*. Limited distribution, probably less than 100. Not protected by law. Largely tolerated in game and cattle ranching areas, but sometimes killed in spotted hyaena control operations. Occurs in Hwange National Park.

5.4 Spotted hyaena

Introduction

Viable populations still exist in a number of countries. The largest known populations occur in the Serengeti ecosystem, Tanzania (7,200 7,700), the Kruger National Park, South Africa (1,300–3,900), and the Masai Mara Game Reserve, Kenya (ca 500- 1,000). In addition, various conservation areas in Zimbabwe each have several hundred individuals. Other areas which support large, but unsurveyed populations include the Selous Game Reserve, Tanzania and the Okavango, Botswana. Population densities vary more than 500-fold: estimates and censuses indicate densities between 0.003 and 1.7 individuals per km^2 (Table 5.5).

The results of the questionnaire survey, systematic censuses, and an evaluation of published information allow a tentative estimate of the total world population of spotted hyaenas. This estimate is likely to suffer from a variety of biases and flaws. In countries where the spotted hyaena is sympatric with either the striped or the brown hyaena, any estimates other than systematic censuses may reflect generic hyaena numbers rather than those of the spotted hyaena alone, thus exaggerating the number of spotted hyaenas. Also, very little information is available from most range countries. This is mainly because wildlife

Table 5.5. Spotted hyaena population densities and population trends (CA Conservation Area, CU Conservation Unit, ICA Intensive Conservation Area, GR Game Reserve, NP National Park, NR Nature Reserve).

(a) Density estimates based on systematic censuses

Country	Locality	Year	Population size	Area (km^2)	Density (per km^2)	Trend	Source
Botswana	Savuti, Chobe NP	1986–88	43*	>100*	<0.4	?	Cooper 1989
Kenya	Aberdare NP	1986–87	94	70	1.3	?	Sillero-Zubiri & Gottelli 1992b
Kenya	Masai Mara GR	1992	45*	70*	0.6	stable	Holekamp *et al.* 1992
Namibia	Etosha pan	1979–86	68	1,430	0.05	?	Gasaway *et al.* 1991
Namibia	Namib along Kuiseb	1977–79	18	3,080	0.006	?	Tilson *et al.* 1980, Tilson & Henschel 1986
South Africa	Hluhluwe GR	1975–77	9*	13*	0.5	?	Whateley & Brooks 1978
South Africa	Umfolozi GR	1979–81	14*	39*	0.4	?	Whateley 1981
South Africa	Kruger NP	1984	1,269–3,886	19,220	0.07–0.2	?	Mills 1985b
South Africa	Mavumbye,Kruger NP	1982–84	11*	130*	0.08	?	Henschel & Skinner 1987
South Africa	Timbavati NR	1975	11*	>25*	< 0.4	?	Bearder 1977
South Africa	Kalahari Gemsbok NP	1972–80	80	10,000	0.008	?	Mills 1990
Tanzania	central Serengeti	1987–92	45*	56*	0.8	declining	Hofer & East 1993a
Tanzania	Serengeti "source" population§	1986	5,214	8,100	0.6	declining	Hofer & East 1995a
Tanzania	Ngorongoro Crater	1966–68	378	220	1.7	?	Kruuk 1972a
Tanzania	Selous Game Reserve	1994		2,600	0.32	?	Creel & Creel 1996
Zimbabwe	Hwange NP	1991	-	-	>0.17–0.18#	?	Bowler 1991
Zimbabwe	Zambezi NP	1991	-	-	>0.13#	?	Bowler 1991
Zimbabwe	Matetsi Safari Area	1991	-	-	>0.03–0.25#	?	Bowler 1991
Zimbabwe	Matetsi CA Area	1991	-	-	>0.04#	?	Bowler 1991
Zimbabwe	Gwaai Valley ICA	1991	-	-	>0.04#	?	Bowler 1991
Zimbabwe	Lemco Ranch	1991	-	-	>0.1#	?	Bowler 1991
Zimbabwe	Gonarezhou NP south	1991	-	-	>0.22#	?	Bowler 1991
Zimbabwe	Gonarezhou NP north	1991	-	-	>0.05#	?	Bowler 1991

(b) Other density estimates

Country	Locality	Year	Population size	Area (km^2)	Density (per km^2)	Trend	Source
Burkina Faso	Nazinga Game Ranch	1991	20–100	940	0.02–0.1	stable	G.W. Frame (pers. comm.)
Central African Republic	Northern part	1980–88	100–1000	35,000	0.003–0.03	stable?	A.A. Green (pers. comm.)
Guinea-Bissau	Dulombi Reserve	1990	-	213.3 km of transects	0.8 faeces/ 10 km	?	Paris 1991
	Comoé NP	1978	100	11,500	0.009	?	Kronberg-Bericht 1979
Kenya	Nairobi NP	1968–72	<10	114	<0.09	increasing	Rudnai 1979
Kenya	Nairobi NP	1976	>30	114	>0.26	?	Rudnai 1979
Kenya	Kitengela CU	1974–75	>40	568	>0.07	?	Rudnai 1979
Malawi	Liwonde NP	?	50	540	0.09	?	R. Bhima (pers. comm.)
Namibia	half of Namibia	1972/82/92	2,000–3000	400,000	0.005–0.0075		E. Joubert (pers. comm.)
South Africa	Mkuzi GR		40	250	0.2		Rowe-Rowe 1992

* indicates clan size and territory size of study animals; density estimates based on clan size divided by territory size
§ the segment of the total Serengeti hyaena population that commutes to or lives on the calving grounds of the large migratory herds of wildebeest, zebra and Thomson's gazelles on the short-grass plains
\# density estimate using playback calls

has never been censused over large portions of its range including many protected areas. This is complicated by the fact that hyaena populations may be small, and individuals are shy and nocturnal and therefore unlikely to be encountered. With these limitations in mind, a tentative estimate puts the total world population of spotted hyaenas at 27,000 to 47,000 animals (Table 5.6).

The spotted hyaena has, and still is, being widely shot, poisoned, trapped, and snared, even inside some protected areas. Persecution most often occurs in farming areas after confirmed or assumed damage to livestock, or as a preventative measure to protect livestock. However, it may also take place "for fun" and as "target practice" (Namibia, Kenya), and out of fear of the animal (west Africa, details in country accounts below). Persecution appears to be the prime source of population decline, which appears to be more pronounced outside protected areas than inside. Most populations in protected areas in southern Africa are considered to be stable, whereas many populations in eastern and western Africa, even in protected areas, are considered to be declining, mostly due to incidental snaring and poisoning. Although sport hunting is permitted in several countries after purchasing a sport

Table 5.6. Tentative estimate of total world population size of free-ranging spotted hyaenas.

Country	Current status	Min. estimate	Max. estimate	Min. Guess	Max. Guess
Angola	?			0	100
Benin	<100	50	100		
Botswana	>1,000	1,000	2,000		
Burkina Faso	100–1,000	100	1,000		
Burundi	?			0	100
Cameroon	100–1,000	100	1,000		
Central African Republic	100–1,000	100	1,000		
Chad	?			50	100
Congo	?			50	100
Democratic Republic of Congo	?			50	100
Djibouti	?			0	50
Equatorial Guinea	?			0	50
Eritrea	?			0	50
Ethiopia	>1,000	1,000	2,000		
Gabon	?			0	0
Ghana	?			0	0
Guinea	?			0	50
Guinea-Bissau	?	100	1,000		
Kenya	several thousand	2,000	4,000		
Liberia	0	0	0		
Malawi	100–1,000	100	1,000		
Mali	?			50	100
Mauritania	?			50	100
Mozambique	?			100	1000
Namibia	2,000–3,000	2,000	3,000		
Niger	<50	20	50		
Nigeria	100	100	100		
Rwanda	?			50	100
Senegal	100–1,000	100	1,000		
Sierra Leone	?			50	100
Somalia	?			0	50
South Africa: Cape	80–100	80	100		
South Africa: Transvaal	50–100	50	100		
South Africa: Kruger NP	1,300–3,900	1,300	3,900		
South Africa: Natal	250–1,000	250	1,000		
Sudan	?			2,000	2,000
Tanzania: Serengeti	7,200–7,700	7,200	7,700		
Tanzania: elsewhere	3,000–4,500	3,000	4,500		
Uganda	<1,000	100	1,000		
Zambia	>1,000	1,000	2,000		
Zimbabwe	5600	5,600	5,600		
Sum		25,350	44,050	2,450	4,150
Total (Estimates+Guess)		27,800	48,200		

Table 5.7. Hunting of spotted hyaenas for utilisation purposes as reported in the questionnaire survey.

Country	Object	Purpose
Burkina Faso	tail	medicine/magic
Cameroon	whole animal	food
Côte d'Ivoire	whole animal	harvested for bushmeat and medicines
Malawi	genitalia, nose tips, tails	hunted for traditional medicine
Mozambique	various parts, particularly paws	used by traditional healers
Senegal	whole animal	some hunted for food
Tanzania	noses, genitals	for traditional medicine

hunting licence, the numbers killed by sport hunters are small as they are not considered an attractive species. It is also killed for food or medicine (Table 5.7). Destruction of habitat operates mostly indirectly; habitat loss and degradation and overgrazing by domestic stock reduce the habitat available to populations of wildlife that are suitable prey for the spotted hyaena.

Official attitudes towards the spotted hyaena vary widely from positive attitudes of active protection, through benign neglect, to negative ones of considering the species vermin. Legal classification varies from "vermin" (Ethiopia) to fully protected in conservation areas. Thus, while it is fully protected in the Serengeti National Park in Tanzania, the spotted hyaena may be legally shot by sport hunters in the adjacent Maswa Game Reserve. According to the questionnaire survey, in most countries regulations and wildlife laws are only enforced as far as financial, logistical and manpower constraints allow them to be (often in an inadequate way). Bounty systems do not operate any more in eastern or southern Africa, although there are still countries where farmers may kill hyaenas at their discretion. A bounty is apparently still offered in Cameroon. There is no information on the presence or absence of bounty systems available from a number of Sahel countries in west Africa.

Although the total world population size of the spotted hyaena is well above 10,000 individuals, several subpopulations exceed 1000 individuals and its range well exceeds 20,000km^2, the rapid decline of populations outside conservation areas due to persecution and habitat loss makes the species increasingly dependent on the continued existence of protected areas. We therefore agree with the latest classification of the spotted hyaena as **Lower Risk: conservation dependent** (IUCN 1996).

Spotted hyaena: country accounts

Algeria. *Extinct* (Le Berre 1990).

Angola. *Data Deficient (-).* It is still present but it is uncertain to what extent the civil war has affected it. During colonial times poisoned by strychnine (Monard 1935).

Benin. *Threatened.* Population declining, probably fewer than 100 individuals. Numbers are depleted because of persecution and declining prey populations. Considered a natural part of the wildlife community and of slight value for tourism. Still poisoned and trapped if domestic stock is attacked, otherwise tolerated. No bounty.

Botswana. *Lower Risk.* Stable population (more than 1000 animals) in protected areas, unknown elsewhere. Legally protected by Fauna Conservation Acts of 1982 and 1987 where it is listed as a "game" animal. Requires a single game licence to be hunted. Considered to be a pest by most officials and treated as such, but no bounty. Now primarily shot. Poisoning has declined compared with previous levels. Control measures involving poisoning or shooting have largely removed it from settled areas (Smithers 1968).

Burkina Faso. *Data Deficient (-).* Possibly stable, 100 1000 individuals. Numbers are depleted because of hunting (Table 5.7), poaching, and declining prey populations. Widespread throughout the country at low densities. Small viable population at Nazinga Game Ranch (Table 5.5). In principle protected in national parks and fauna reserves but can be hunted elsewhere during a fixed hunting season. Considered a common species and natural part of the wildlife community. Perceived as small "vermin" with little touristic value. Bounty system terminated in the 1960s. Shot, poisoned and snared more often during colonial times than now. Still poisoned and trapped if domestic stock is attacked, but otherwise tolerated.

Burundi. *Threatened.* Probably on verge of extinction.

Cameroon. *Threatened.* Size or trend of population unknown, possibly between 100 and 1000 animals. Available habitat is limited to northern savannah region which is gradually being degraded due to desertification and human encroachment. Likely to follow the general trend of declining wildlife populations. Protected in national parks. Shot if there are "problems" around villages or huts of nomadic herdsmen, and hunted for utilisation (Table 5.7). On occasion shot by professional or tourist hunters as spotted hyaenas are considered competitors, especially if the hunting expedition proved unlucky (no trophies). Apparently a bounty is still being offered.

Central African Republic. *Data Deficient (+)*. Unknown but probably stable population of 100–1000 animals. Occurs throughout the northern part of the country at a low density (Table 5.5). Level of legal protection unknown, attitude generally neutral or tolerant. No bounty.

Chad. *Data Deficient (0)*. Still present.

Congo. *Data Deficient (-)*. Completely protected (Hecketsweiler 1990).

Côte d'Ivoire. *Data Deficient (-)*. Between 100–1000 animals. Density in Comoé National Park low (Table 5.5) and likely to be affected by incidental snaring because of increased meat poaching in recent years (K.E. Linsenmair, pers. comm.). Outside conservation areas frequently shot and trapped (Table 5.7).

Democratic Republic of Congo. *Data Deficient (-)*.

Djibouti. *Data Deficient (0)*.

Egypt. *No Record (-)*.

Equatorial Guinea. *Data Deficient (-)*. One recent record (Juste and Castroviejo 1992) suggests a small population in marginal habitat.

Eritrea. *Data Deficient (0)*.

Ethiopia. *Lower Risk*. Stable population with more than 1000 individuals. Of immeasurable value in cleaning up rural and urban populated areas, including the centre of Addis Ababa. The hyaena men of Harar provision spotted hyaenas. Considered vermin by 1974 law but there is no bounty. May be hunted without licence by any person outside national parks and other protected areas for a fee of five Ethiopian Birr (US$ 2.50). Official attitude is one of benign neglect and tolerance due to lack of resources to follow up reports of livestock damage. Have been reported to attack humans, mostly shepherds asleep in the fields, and to enter huts and drag out children (von Rosen 1953). Outside Harar it is tolerated as long as it does not kill stock, in which case it is shot or hunted with traditional weapons.

Gabon. *No Record (+)*. It is likely that the small population in neighbouring Congo extends into the extreme south of Gabon.

Gambia. *No Record (-)*.

Ghana. *Data Deficient (0)*.

Guinea. *Data Deficient (-)*.

Guinea-Bissau. *Lower Risk*. Population of unknown size, probably declining mainly due to persecution. Still relatively common in some protected areas (Table 5.5). 77% of questioned villages in the north and east reported hyaenas coming into the village and causing livestock damage (Robillard 1989). Persecution (shooting and snaring by shepherds) increases in areas where wild ungulates have declined and attacks on domestic stock have become more frequent (Paris 1991). Previously considered useful as a "cleaner of the wild" but now people feel threatened by the spotted hyaena, as it has been held responsible for the kidnapping of unsupervised children (Paris 1991). Currently protected by law but a status change to "vermin" is under consideration, which would open the possibility of legal hunting (Limoges 1989).

Kenya. *Lower Risk*. Status distinctly different for protected and unprotected areas: Lower Risk in protected areas, Threatened elsewhere. Probably several thousand individuals in several populations. Almost certainly declining throughout the country due to persecution, mainly through poisoning, but also shooting, snaring and trapping. Extirpated along the coast and in many agricultural areas, and rare in populated shore areas along Lake Victoria and in the wider Nairobi area. Still occurs outside protected areas but rapidly declining. Shooting, spearing or poisoning not permitted but there is no effective protection because hyaenas are viewed with contempt, indifference or as a pest. Could easily be extirpated in more heavily populated Masailand, where poisoning with anti-arachnid cattle poison dip is increasing (Holekamp *et al.* 1993). Heavily persecuted in the few areas still ranched by Europeans. Sometimes tolerated by pastoralists unless they kill livestock, but occasionally killed "for fun" and reportedly for "target practice".

Lesotho. *Extinct*.

Liberia. *No Record (+)*.

Malawi. *Data Deficient (-)*. Population may number 100 1000 individuals and occur at reasonable densities (Table 5.5). Human population growth, habitat destruction, and reduction of prey and other large predators have caused the spotted hyaena to largely disappear from the central highlands. Protected by the wildlife protection act. Considered an asset inside protected areas and as a pest and menace by many elsewhere. No bounty. Not tolerated by local people and mostly shot or poisoned when straying into villages, as it is assumed to cause problems with domestic stock. May also be hunted (Table 5.7). Killing of more than 16 people near Mbuje was reported for the period from 1955 to 1958 during the hot season, when people often slept outside their houses on their verandas (Balestra 1962).

Mali. *Threatened*.

Mauritania. *Threatened*. Still present in the Adrar (Le Berre 1990).

Mozambique. *Data Deficient (+)*. Protected by law but also utilised (Table 5.7). Recorded as very common in the Gorongoza National Park and on the increase in the Save Valley in the 1970s (Smithers and Lobão Tello 1976). It is unclear what effect the civil war might have had on the population.

Namibia. *Lower Risk*. Status depends on protection status of an area: at Lower Risk in protected areas, Threatened elsewhere. Population numbers 2000–3000 individuals (Table 5.5). Stable in Etosha (and probably other protected areas), increasing in Damaraland, but declining in the rest of the country except for parts of Bushmanland. Viable populations in Etosha, Khaudom, Bushmanland, Hereroland, Waterberg, and Namib-Naukluft. In Caprivi reported to number less than 50 individuals (questionnaire survey), and in Namib Naukluft National Park less than 100 individuals. Protected in all state conservation areas (Ordinance no. 4 of 1975) despite pressure from the Namibian Agricultural Union, but not protected elsewhere. Considered an asset in conservation areas and a problem animal in communal and commercial farming areas. Can be killed after reported as "vermin," but farmers are under no obligation to report if they have killed a spotted hyaena. No bounty. Persecution is frequent as neither commercial nor communal farmers are prepared to accept any stock losses except for a very few conservation-minded farmers. In communal areas it is normally poisoned, in commercial areas shot, poisoned or trapped, and gin traps are freely circulated. In Caprivi it is widely poisoned, as are lion.

Niger. *Threatened*. Probably less than 50 individuals (Millington and Tiega 1991) in a population declining due to drought and desertification, eradication and poisoning. Hunting banned since 1972. The situation regarding poisoning is unclear: Some sources state that poisoning is prohibited and that official departments attempt to make people aware of the environmental problems associated with poisoning. However, others consider systematic, strychnine poisoning of golden jackal and spotted and striped hyaenas as still officially sanctioned (Millington and Tiega 1991). Not tolerated. No bounty.

Nigeria. *Threatened*. On the verge to extinction. Decline of prey populations, persecution due to attacks on domestic stock, and increased farming and agricultural activity are considered to be the main reasons for its decline. Small, declining population of less than 100 individuals in Kainji Lake National Park (Borgu Game Reserve), Yankari National Park, Gashaka-Gumti National Park, and adjacent farmland around both Yankari and Gashaka. In Yankari it is rare inside park and more common on the park fringe; in Gashaka widespread and frequent but uncommon in upland and montane grassland where cattle are abundant and in lowland savannah (Green and Amance 1987, Happold 1987). A bounty was offered by local administrators, for many years resulting in "near extinction" (Rosevear 1974, Happold 1987). This practice is now terminated. No legal protection.

Rwanda. *Threatened*. Still present. The destruction of much of Rwanda's conservation areas and its wildlife as a consequence of recent political events makes it unlikely that many individuals survive even in conservation areas (Wolanski 1996).

Senegal. *Data Deficient (+)*. Population size 100–1000. Protected when inside national parks. Considered useful as "cleaner of the wild", not considered "vermin." No bounty. Not tolerated outside the national parks. Some hunted for food (Table 5.7).

Sierra Leone. *Threatened*. Population size and dynamics unknown. Officially not regarded as a pest any more. During colonial times, the Veterinary Department carried out large-scale poisoning in response to complaints by Fulani cattle owners that their calves were constantly stolen (Rosevear 1974). No bounty.

Somalia. *Data Deficient (0)*. In the 19th century known to hunt sheep and goats during daytime, and reported to enter huts and seize little children or old women (Drake-Brockman 1910).

South Africa. Overall assessed as *Lower Risk*. (Note: because the information for South Africa was compiled before the new constitution was implemented, the old provincial basis is used here).

(a) Cape Province. *Threatened*. Stable, viable population in Kalahari Gemsbok National Park (Table 5.5). Protected by National Park Act no. 57 from 1976. Ruthless persecution (hunting and poisoning) made it a rare species by the beginning of the century (Sclater 1900) and has caused it to become more endangered in the Cape Province than the brown hyaena (Stuart 1981, Stuart *et al.* 1985).

(b) Natal. *Threatened* outside Hluhluwe-Umfolozi. Between 100 and 1000 individuals: in Hluhluwe-Umfolozi approximately 200 individuals and in Mkuzi 40 individuals (Table 5.5). Populations in the reserves have been increasing for the past 25 years. Protected in all game reserves and nature reserves. Trapped or shot only where they kill livestock (e.g. subsistence farmers affected near Hluhluwe-Umfolozi Game Reserve).

(c) Free State. *Threatened*. Practically extinct except for a few vagrants. Formerly, local people are said to believe that witches use hyaenas to ride on their back during the night while pursuing their business (Wolhuter undated).

(d) Transvaal. *Threatened* outside the Kruger ecosystem. Population numbering less than 100 individuals outside the Kruger National Park and surrounding private reserves. Not protected. Seen as an asset in a conservation sense, although official departments assist in "damage control." No bounty and not tolerated. Farmers shoot, poison or trap hyaenas.

Sudan. *Data Deficient (+)*. Casual observations of sightings, kills, and vocalisations suggest that the spotted hyaena occurs at a density of at least 0.025 0.03 individuals per km^2 in areas one and two described in Chapter 4 (Distribution); i.e. at least 1000 individuals each in the areas around the Boma plateau and in the area south of the Bahr el Gazal River. From the latter area there are reports that the spotted hyaena is responsible for attacking people in areas with frequent famines and a high density of displaced people where temporary hospitals provide insufficient protection to some of the patients (C. Trout, pers. comm.).

Swaziland. *Data Deficient (-)*.

Tanzania. *Lower Risk*. Population in excess of 10,000 individuals (in Serengeti alone more than 7,000: Hofer and East 1995a, see Table 5.5) but declining in many places including protected areas, due to unselective snaring. Population expansion in Selous at the end of 1980s suspected due to availability of large numbers of poached elephant carcasses. Protected in conservation areas except for sport hunting in game reserves. Some sport hunting licences are sold every year. Official attitude is neutral, and considered a slight asset for photo-tourism. Still utilised in many parts of the country if a carcass becomes available from incidental snaring or poisoning (Table 5.7).

Detailed studies of the effect of incidental killing of hyaenas by snares set for other species show that snaring is now the most important mortality factor for hyaenas in the Serengeti. Snare mortality has reversed a potential population increase of more than 4% to a population decline in excess of 2% (see section on spotted hyaena mortality in Chapter 3). In Selous, incidental killings in snares set by meat poachers is common in less patrolled areas, as well as accidental poisoning around poacher camps from poisoned food intended for game scouts (questionnaire survey). Outside protected areas populations are declining due to persecution (see Mchitika 1996).

Photo 5.1. Incidental snaring is presently the most important mortality factor for spotted hyaenas in the Serengeti.

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Togo. *Data Deficient (-)*.

Uganda. *Data Deficient (+)*. Population of unknown size or dynamics, less than 1000 individuals. Now rarely occurs outside protected areas, probably due to human population pressure and persecution, typically poisoning. Protected through regulations for protected areas and by-laws. Attitude positive, tolerated. No bounty.

Zambia. *Data Deficient (+)*. More than 1000 individuals in most protected areas in Zambia. Apparently increasing in the Luangwa Valley and declining in other areas. Outside protected areas present in low densities, and persecuted in areas that are more densely populated by people. Little or no interest, but tolerated.

Zimbabwe. *Lower Risk*. Approximately 3,350 individuals in national parks, safari areas, sanctuaries and other conservation areas, 1,150 individuals in communal areas, 800 on commercial farms, and 300 on state land, giving an estimated total of 5,600 individuals for the country (Anonymous 1991). Population has declined due to persecution particularly on commercial farmland, as it is considered a real threat to livestock and of limited value for game-viewing (Bowler 1991). Legally not protected and considered a problem animal in the 8th Schedule of the Parks and Wildlife Act (Bowler 1991).

5.5 Summary

Table 5.8 summarises the status of each species in each country. This permits a comparison of countries as well as between species in each country. Summary statistics and an interpretation of these assessments are provided in Chapter 11.

Table 5.8. Red list categories for the four hyaena species in range countries (definitions of categories in Box 5.1).				
Country	**Aardwolf**	**Striped hyaena**	**Brown hyaena**	**Spotted hyaena**
Afghanistan	-	Data Deficient (-)	-	-
Algeria	-	Threatened	-	Extinct
Angola	Data Deficient (+)	-	Data Deficient (0)	Data Deficient (-)
Armenia	-	Threatened	-	-
Azerbaidjan	-	Threatened	-	-
Benin	-	No Record (+)	-	Threatened
Botswana	Lower risk	-	Lower risk	Lower risk
Burkina Faso	-	Data Deficient (+)	-	Data Deficient (-)
Burundi	-	No Record (-)	-	Threatened
Cameroon	-	Data Deficient (-)	-	Threatened
Central African Republic	-	No Record (+)	-	Data Deficient (+)
Chad	-	Data Deficient (-)	-	Data Deficient (0)
Congo	-	No Record (-)	-	Data Deficient (-)
Côte d'Ivoire	-	No Record (-)	-	Data Deficient (-)
Democratic Republic of Congo	-	No Record (-)	-	Data Deficient (-)
Djibouti	No Record (+)	No Record (+)	-	Data Deficient (0)
Egypt	Data Deficient (0)	Data Deficient (+)	-	No Record (-)
Equatorial Guinea	-	-	-	Data Deficient (-)
Eritrea	Data Deficient (0)	Data Deficient (0)	-	Data Deficient (0)
Ethiopia	Data Deficient (0)	Lower risk	-	Lower risk
Gabon	-	No Record (-)	-	No Record (+)
Gambia	-	-	-	No Record (-)
Georgia	-	Threatened	-	-
Ghana	-	No Record (+)	-	Data Deficient (0)
Guinea	-	No Record (+)	-	Data Deficient (-)
Guinea-Bissau	-	-	-	Lower Risk
India	-	Data Deficient (+)	-	-
Iran	-	Data Deficient (0)	-	-
Iraq	-	Threatened	-	-
Israel	-	Threatened	-	-
Jordan	-	Threatened	-	-
Kenya	Data Deficient (+)	Lower risk	-	Lower risk
Kuwait	-	Probably extinct	-	-
Lebanon	-	Data Deficient (-)	-	-
Lesotho	No Record (+)	-	Data Deficient (-)	Extinct
Liberia	-	-	-	No Record (+)
Libya	-	Data Deficient (+)	-	-
Malawi	-	-	No Record (-)	Data Deficien t(-)
Mali	-	Data Deficient (-)	-	Threatened
Mauretania	-	Data Deficient (-)	-	Threatened
Morocco	-	Threatened	-	-
Morocco-Western Sahara	-	Data Deficient (-)	-	-
Mozambique	Data Deficient (0)	-	Data Deficient (+)	Data Deficient (+)
Namibia	Lower risk	-	Lower risk	Lower risk
Nepal	-	Data Deficient (0)	-	-
Niger	-	Threatened	-	Threatened
Nigeria	-	Threatened	-	Threatened
Oman	-	Threatened	-	-
Pakistan	-	Data Deficient (0)	-	-
Qatar	-	Probably Extinct	-	-
Rwanda	-	No Record (-)	-	Threatened
Saudi Arabia	-	Threatened	-	-
Senegal	-	Threatened	-	Data Deficient (+)
Sierra Leone	-	-	-	Threatened
Somalia	Data Deficient (0)	Data Deficient (0)	-	Data Deficient (0)
South Africa	Lower risk	-	Lower risk	Lower risk
Sudan	Data Deficient (0)	Data Deficient (0)	-	Data Deficient (+)
Swaziland	Data Deficient (0)	-	No Record (+)	Data Deficient (-)
Syria	-	Data Deficient (-)	-	-
Tadzhikistan	-	Threatened	-	-
Tanzania	Lower risk	Data Deficient (+)	-	Lower risk
Togo	-	No Record (-)	-	Data Deficient (-)
Tunisia	-	Data Deficien t(-)	-	-
Turkey	-	Data Deficient (-)	-	-
Turkmenistan	-	Threatened	-	-
Uganda	Data Deficient (0)	No Record (-)	-	Data Deficient (+)
UAE	-	Probably Extinct	-	-
Uzbekhistan	-	Threatened	-	-
Yemen	-	Data Deficient (0)	-	-
Zambia	Data Deficient (0)	-	-	Data Deficient (+)
Zimbabwe	Lower risk	-	Data Deficient (-)	Lower risk

Chapter 6

Role and Management of Hyaenas in Protected Areas

Hans Kruuk

6.1 Introduction

Hyaenas may be appreciated from several different viewpoints when present in national parks or nature reserves. For instance, their presence can be seen as:

1. An attraction for tourists
2. A representation of species in need of conservation in their own right
3. Part of the mechanism whereby prey populations are kept in balance with their resources
4. Species which are 'useful' because they 'clean up' the environment by eating carrion
5. A pest which causes damage to important prey species or neighbouring livestock (by predation), or to populations of other carnivores (by competition)
6. An important subject for scientific research

Spotted hyaenas may be viewed under any of these headings, and in some of the larger national parks they will come under all. Striped and brown hyaenas, as well as aardwolves, are less important as predators, under (3) or (5), although sometimes they may either cause some damage to small livestock (Ilani 1975, Mills 1990), or they may be accused of such crimes because of confusion with other carnivores (e.g. aardwolves, Shortridge 1934, Maberley 1963).

For any of the reasons given above, management plans for protected areas will have to take the presence of hyaenids into account. Hyaenas are important elements in many ecosystems. When considering the management of protected areas, the effects of hyaenas on other species raise many issues. Therefore, in this section I will discuss some of the interactions between hyaenas and other animals.

6.2 Interactions with prey species

In terms of numbers and biomass, spotted hyaenas are the only species of hyaenid which may occur in sufficient abundance to play a major role in the population dynamics of dominant herbivorous prey species. However, at least in theory, all hyaenids could affect less abundant prey species, or the establishment of new species in areas. Kruuk (1972a) suggested that spotted hyaenas in the Ngorongoro Crater, Tanzania, had a substantial effect on population composition of their main prey, the wildebeest: hyaena predation was high, it was the main cause of mortality, and wildebeest died at younger age, with a faster turn-over in the population, than in the neighbouring Serengeti. It was likely that herbivore numbers in the Ngorongoro Crater were limited by food supply, and that hyaena predation was the mechanism whereby wildebeest surplus numbers were adjusted downwards to a level the vegetation could sustain.

Such a predator-prey relationship could occur in a situation where ungulates are more or less resident, or non-migratory. However, in migratory populations such as in the Serengeti, predators periodically have to make a substantial effort to 'commute' between their dens and the main food supply (Kruuk 1972a, Hofer and East 1993a). This may be the reason why predator numbers in the Serengeti are relatively low compared with prey biomass, and consequently the effects of predation are small (Kruuk 1972a, Hilborn and Sinclair 1979). Similarly, the effects of spotted hyaena predation on the migratory Kalahari wildebeest are low. However, it has been argued that spotted hyaenas could affect numbers of a more resident species of the Kalahari, such as the gemsbok (Mills 1990). Henschel and Tilson (1988) found that spotted hyaenas did not limit prey populations in the Namib desert. Gasaway *et al.* (1991) concluded that spotted hyaenas did not contribute substantially to the population regulation of zebra and springbok in Etosha; their impact on populations was less than that of lions. Sillero-Zubiri and Gottelli (1992a) suggested that in the dense forests of the Kenyan Aberdares spotted hyaenas did not depress numbers of ungulates.

Caro (1994) and Laurenson (1995) demonstrated that spotted hyaenas kill some cheetah cubs, but the effect of this on the cheetah population was unclear.

The above studies suggest that in some situations where spotted hyaenas feed on a resident prey population, such as one would also find in a fenced area, the predators could have substantial effects on ungulate numbers and fluctuations therein. However, obvious population effects are often absent since the numerical relationships between predator and prey populations are also likely to be dependent on the presence of alternative prey and other predators, amongst other factors. The response of spotted hyaena populations and their choice of prey to the presence

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Photo 6.1. Spotted hyaenas killing an adult gemsbok in the southern Kalahari. The relationship between spotted hyaenas and their prey is important in the management of both.

of migratory ungulates varies in different areas and is still poorly understood (Kruuk 1972a, Fryxell *et al.* 1988, Mills 1990, Hofer and East 1995a).

A general conclusion for the spotted hyaena is that this species has the potential to play an important role in population regulation of ungulates, but whether this potential is realised in any given area depends on many factors. At this stage we cannot extrapolate from our experience with spotted hyaenas from one area to another. Thus, before conclusions can be drawn about the role of hyaenas in any particular area under conservation management, the animals have to be studied in some detail.

The brown hyaena has not been found to have any demonstrable effect on prey species (Mills 1990, Maddock 1993). Although little is known about the feeding ecology of striped hyaenas (Kruuk 1976), it is likely that their presence also has little effect on prey populations. Aardwolves, highly specialised predators of a few species of termite (*Trinervitermes* spp., and less often a few *Hodotermes*; Kruuk and Sands 1972; Richardson 1987a), are more likely to be themselves food-limited by above-ground availability of their prey than to be exercising any major effects on any species of prey.

The above comments are based on observations of populations of predators and prey which currently live sympatrically. It should be kept in mind that, at least hypothetically: a) any of the hyaenid species may have caused previous extinctions of prey species, and b) new arrivals of potential prey species, whether introduced artificially or naturally, could be affected much more than prey populations already present. This underscores the need for caution and for close study of predation in ecosystems before implementing changes in management practices.

6.3 Effects of prey on hyaenids

There has been a considerable amount of research on the consequences of variation in prey populations for various carnivores. In hyaenids, such consequences may extend to diet, foraging behaviour and success (Kruuk 1972a, Tilson *et al.* 1980, Mills 1990, Cooper 1990, Henschel and Skinner 1990a, Hofer and East 1993b, Holekamp *et al.* 1997); population density, composition and social dynamics (Kruuk 1972a, Mills 1990, Holekamp *et al.* 1993); reproduction (Holekamp *et al.* 1996) and parental behaviour (Hofer and East 1993c); and spatial and social organisation (Kruuk 1972a, Mills 1990, Hofer and East 1993a,b,&c, 1995a, Richardson 1985).

As an example, in the Serengeti, increased numbers of the main ungulate prey of spotted hyaenas in the 1970s and 1980s coincided with increased numbers of the predators themselves (Hofer and East 1993a, 1995a). It was also argued that differences in spotted hyaena population composition between the Ngorongoro Crater and the Serengeti were due to differences in prey availability. The Ngorongoro hyaena population was much denser and had a faster turn-over rate and adults died at younger ages (Kruuk 1970). These characteristics of the Ngorongoro population were related to the greater density and non-migratory nature of prey compared with the Serengeti. Because prey was non-migratory there was closer competition for food between individual hyaenas in the Ngorongoro. Food competition was an important direct cause of hyaena mortality in the Crater (Kruuk 1972a).

In the southern Kalahari brown hyaena numbers were considerably higher in areas with, and during times of, greater food density (Mills 1990). Similarly, numbers of aardwolves appear to be dependent on *Trinervitermes* spp.

termite numbers. Their territory sizes are related to the dispersion of *Trinervitermes* mounds, of which there are about 3000 per territory (Richardson 1985). Hyaenid numbers are also affected by other factors about which we know little. For instance, striped hyaenas, normally rare in the Serengeti, may suddenly show up simultaneously in different parts of the region, where they reproduce and stay for one or more years, and then disappear again (Kruuk 1976). In another example, aardwolves are absent from large parts of Africa even though their termite prey is abundant in these same areas (Smithers 1983).

6.4 Competition with other carnivores

The spotted hyaena often takes kills from most other large carnivores by chasing off the predators before they are satiated (Kruuk 1972a, Mills 1990). Striped and brown hyaenas also do this, but much more rarely (Kruuk 1976, Mills 1990). Consequently, competition between spotted hyaenas and species of special concern such as cheetah, wild dog or leopard should be taken into account when managing protected areas. Of these, wild dogs may be the most strongly affected by hyaenas, although it has not been demonstrated that direct, aggressive competition is a significant factor in any population (i.e. that it affects numbers).

To investigate whether competition between different species of hyaenas and between hyaenas and other carnivores plays an important role in ecosystems, one has to study: a) direct interactions, b) the degree of overlap in diet, and c) whether resources common to the different predators are in short supply. Such data are rarely available. There are many observations of hyaenas displacing other species from a kill or vice versa, but it is much more difficult to demonstrate that this has a significant effect on predator populations.

In the case of brown hyaenas, Mills (1990) argued that they did not have any significant effects on other sympatric carnivores in the Kalahari. According to Mills, they derived some benefits from others' kills (lion, leopard, cheetah, caracal), but usually consumed carcasses only after the original predator was more or less satiated. Elsewhere in South Africa a considerable part of their diet was probably derived from kills made by caracal (Maddock 1993). Brown hyaenas were attacked and even killed by other carnivores, especially lions (Eloff 1973, Owens and Owens 1978, Apps 1982, Mills 1990), but also by spotted hyaenas (Mills 1990). Several other scavenging species (jackals, spotted hyaenas, vultures) consumed carcasses before brown hyaenas could get at them.

Striped hyaenas similarly derive a substantial proportion of their diet by scavenging from other carnivores, including spotted hyaenas (Kruuk 1976) and may lose some of their food to other scavengers. As in the case of brown hyaenas, they are unlikely to affect the food supply of others.

Competition between spotted hyaenas and other carnivores is more complicated than with other hyaena species. In the Serengeti and Ngorongoro, spotted hyaenas would scavenge from lion, cheetah, leopard, wild dog, jackal, and even vultures. With the exception of cheetah and leopard, each of those species was also seen scavenging from the hyaenas (Kruuk 1972a). Some of the scavenging consisted of remains being eaten after the hunter had abandoned the carcass, while on other occasions the 'owner' was displaced before being satiated. Especially in the case of lions, fierce battles between packs of spotted hyaenas and prides may occur over food. On balance, however, "... hyaenas clearly profit from the presence of leopards,

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Photo 6.2. Spotted hyaenas interacting with a lioness, their greatest competitor.

cheetahs, wild dogs and man. Relations with lions, jackals and vultures are more ambiguous, and hyaenas probably more often provide food than take it" (Kruuk 1972a). This general picture is confirmed for this same area by studies of the various other carnivore species involved (Schaller 1972a, Kühme 1965, Estes and Goddard 1967). In the Kalahari, Mills (1990) concluded that "... only lions and cheetahs have an effect on spotted hyaenas, largely to the hyaenas' advantage [and] spotted hyaenas negatively affect all the large carnivores in some way ...". However, Packer *et al.* (1990) argued that hyaenas have no measurable effect on the feeding of lion prides in the Serengeti. Cooper (1991) suggested that spotted hyaenas can significantly reduce the food intake of lion groups in which there are no adult males.

Competition between the various species of hyaenas may also be important, and on occasion it is difficult to separate this from predation. Spotted hyaenas chase striped hyaenas and brown hyaenas (Kruuk 1976, Mills 1990), and brown hyaenas chase aardwolves (Mills 1990). At kill sites, spotted hyaenas are clearly the dominant species, allowing brown and striped hyaenas access to scraps, but at times also chasing them off their food. Mills (1990) argued that in the Kalahari there is a negative association between the brown and spotted species, the brown being suppressed by the spotted. It is likely in areas further north that striped hyaenas are similarly suppressed by the spotted. It is important to note in terms of competition that the habitats of the three species differ to some extent. Spotted hyaenas occupy areas with a higher productivity of ungulate prey and at least some fresh water present, whereas striped and brown hyaenas are able to survive in more desert-like surroundings.

Because their habitats differ in many regions, there is no evidence of competition between the various hyaena species. Only experimental transplants would demonstrate whether the absence of brown and striped hyaenas from many of the high-productivity areas is due to competition from their spotted relatives, or to some other cause. In Kruger National Park the brown hyaena disappeared after the establishment of boreholes about 25 years ago, which led to an increase in resident ungulate herds and numbers of spotted hyaenas (M.G.L. Mills, pers. comm.).

6.5 Some management options

A number of general points should be made in regard to the conservation management of hyaenid species in protected areas.

1. Of all hyaena species, the spotted hyaena is most in need of attention in protected areas (see Appendix 1). This is because (a) it is least able to survive in areas outside protected zones (either agricultural, or in desert or semi-desert; Mills 1990); (b) it is most likely to cause problems in its interactions with prey species and with other carnivores; (c) once a spotted hyaena social group (clan) has disappeared it is difficult to repopulate the area (in other words, the size of the minimum viable population is large), as experience shows from Nairobi (Foster and Coe 1968) and Kruger National Parks (Mills 1985b, Henschel 1986). Because of its dependence on protected areas of high productivity, it is arguable that the spotted hyaena is the species presently most likely to become extinct.
2. Because of the importance of spotted hyaena populations in protected areas, threats of disease (especially rabies) should be closely monitored, and if necessary, immunisation should be considered seriously (Macdonald 1980a, Mills 1990). Similarly, threats from poachers (snaring, trapping, shooting) should be taken seriously, and all possible action should be considered to stop such killing (Hofer *et al.* 1993, 1996).
3. Since most predator populations appear to be food-limited, the maintenance of viable prey populations is a primary requirement for the conservation of all hyaena species.
4. Since spotted hyaenas appear to be somewhat dependent on water, the provision of water-holes, dams, wind-mills etc. in protected areas is likely to favour their presence (it also increases some prey populations). This may negatively affect other hyaena species (e.g. brown hyaenas in the Kalahari), and some of the prey species of the spotted hyaena (e.g. gemsbok; Mills 1990).
5. To promote populations of aardwolves, populations of their main food *Trinervitermes* spp. can be encouraged in grassland areas through frequent burning and allowing heavy grazing (Coaton 1948, Hartwig 1955, Kruuk and Sands 1972).
6. There is a general need to bring the scientific interest and ecological role of hyaenas to the attention of decision-makers and the public. Scientists should play an important role in this (Chapter 10).
7. Before interfering in any interaction between populations of hyaenas and their prey, a detailed local study should be carried out to establish likely consequences. Studies of hyaenas have shown that predator-prey relationships can be completely different in neighbouring areas, even if only a short distance apart (Kruuk 1972a).
8. When considering the introduction of a 'new' species in a protected area, it is important to address the possibility that hyaenas (and other carnivores) might exterminate the introduced population.
9. Much more information and research is needed about the effects of hyaenids on prey populations and vice versa.

Chapter 7

Hyaenas Living Close to People: Predator Control, Attacks on People and Translocations

Gus Mills

7.1 Introduction

This chapter examines the management of hyaenas outside conservation areas, in other words in areas where hyaenas live close to people and do not enjoy the same degree of protection as in areas with conservation status. Central to this subject are the related topics of predation on livestock and predator control. Not surprisingly, the relationship between carnivores and people is also given special attention in both the IUCN Canid (Ginsberg and Macdonald 1990) and Felid (Nowell and Jackson 1996) Action Plans, and some of the ideas and suggestions incorporated in these two documents are reiterated here.

As the most active predator amongst hyaenas, the spotted hyaena is most often implicated in stock losses. Both the brown and striped hyaena have also been inculpated, and at times may actually be involved. The aardwolf has also been implicated as a predator of lambs, but it is exclusively an insect eater (Koehler and Richardson 1990).

A frequently suggested solution to predator problems has been the translocation of culprits to other areas where they may not come into contact with livestock. There are several important practical aspects to this strategy that need to be addressed before this option is chosen. They are discussed below.

7.2 Predator control

General principles

In the commercial farming regions of South Africa, Namibia and Zimbabwe, the spotted hyaena has been all but extirpated due to intensive predator eradication campaigns over the last 50 years or more (Smithers 1983). In some other agricultural areas of Africa the spotted hyaena has managed to survive, although poisoning and other forms of control are carried out and may at times be catastrophic (Holekamp and Smale 1992). The brown hyaena has also been heavily persecuted in commercial farming areas, although because of its shy and retiring habits it is often difficult to locate. Furthermore, there does seem to have been a change of opinion in this species' favour by some farmers over the last two decades. The striped hyaena too has been subject to eradication or decimation campaigns in some areas of its range (details see Chapter 5).

There is no doubt that hyaenas and other predators kill livestock and may on occasion cause extensive damage. Predator control is an essential management practice in stock farming areas. However, the aim should be to seek methods to reduce predator damage, rather than to increase predator mortality (Giles 1978, Andelt 1987). When it is deemed absolutely necessary to reduce hyaena numbers in a particular area, there are good and bad ways to do this. Shooting of particular individuals is probably the best way, while the generalised use of poisons is the worst as this method is unselective.

Few studies have measured the impact of hyaena predation on livestock. Before implementing control efforts, proper cost-benefit analyses should be conducted to determine the effect of predation losses and the estimated costs of control operations. The cost of control should not exceed losses through predation. Bowland, Mills and Lawson (1994) pointed out that the economic impact of predation comprises both direct and indirect costs. Direct costs include not only the loss of the animals, but also veterinary care for injured stock, replacement of breeding stock and reduced profits. Indirect costs are those incurred through predator control practices, such as the acquisition of firearms and ammunition, measures taken to protect stock from attacks, such as the building of protective enclosures, and the cost of labour and time.

Mills (1990) suggested that it is difficult to reconcile the conservation of spotted hyaenas with commercial stock farming. In less developed agricultural areas and on game ranches where spotted hyaenas still survive, the management emphasis should be on damage control. The future of the spotted hyaena, however, lies mainly inside rather than outside large conservation areas (see chapters 5 and 6, and Appendix 1).

In the case of the brown hyaena, suitable habitat has been identified on agricultural land in parts of South Africa (Skinner 1976) and Botswana (Smithers 1971). There is an adequate supply of food from dead domestic animals, human refuse, and wild animals. In addition, their major carnivore competitors, especially the spotted hyaena, are usually absent. Certain areas of South Africa have been designated as suitable only for extensive cattle production.

Stuart, Macdonald and Mills (1985) recommended that these areas also be designated as brown hyaena conservation areas. Here a major effort should be made for the rational management of the brown hyaena. The magnitude of loss of domestic livestock to brown hyaena predation should be established, although it is likely to be negligible. Where necessary, attempts should be made to find economically efficient control methods, with an emphasis on non-lethal or selectively lethal methods as suggested by Sterner and Shumaker (1978) and Wade (1978). The same applies to the striped hyaena over much of its range.

The aardwolf is exclusively an insect eater (Koehler and Richardson 1990) and there is no justifiable case for control of this species.

Several management possibilities need to be tested which might help to minimise the effects of hyaena predation, particularly on domestic livestock. These include synchronising births of livestock, protecting herds at night in enclosures or erecting portable battery-powered electrical fences around herds at night, increased vigilance by shepherds at night during the breeding season, the use of guard dogs, frightening devices such as strobe lights and sirens, and taste aversion conditioning (Andelt 1987, Mills 1991). In addition, research is needed on how farmers can obtain maximum ecological benefits from hyaenas, for example, how best to deal with carcasses of domestic animals that die from disease, how to use hyaenas on their farms for ecotourism and so forth. Once effective measures have been developed they need to be properly implemented through education and training campaigns.

Case studies of hyaenas in farming areas

1. Over large areas in southern Zimbabwe commercial cattle ranching is giving way to game ranching, or the two are being combined. Fences between and within ranches are being removed and conservancies are being formed through the amalgamation of several ranches.

Predation on cattle by large carnivores, in particular spotted hyaenas, has been significantly reduced on certain ranches through the implementation of a specific method of herding cattle (K. Drummond pers. comm.). With this method, a "mob" of 40 same-aged cows are kept together from the age of weaning and allocated to a herdsman. During the day the cattle are allowed to graze where they choose, accompanied by the herdsman, but at night he brings them back to a central area. At this central area there is a simple wire enclosure, or "kraal", plus the herdsman's tent. The calves are placed in the "kraal" and the cows sleep around it. The herdsman's tent is placed close to the "kraal" and his fire is made on the opposite side. If he hears any disturbance during the night he is able to chase the predator away. After about six weeks the kraal is moved to another area.

This system has several additional benefits: it cuts down on stock theft, reduces fence maintenance costs, and better utilises available forage since the cattle are free to move where they want to. The major drawback is that the cattle have fewer hours per day to feed, thus affecting their weight gain. There are also additional costs in the form of extra wages to a herdsman. However, this system also provides employment to local communities.

2. In the area surrounding the Hluhluwe/Umfolozi Game Reserve in Kwazulu/Natal, South Africa, the loss of domestic stock to spotted hyaena predation gave rise to considerable animosity by the local communities towards the Natal Parks Board (Harvey 1992). Because the hyaenas originated from the reserve, the feeling prevailed among the local communities that hyaena predation was the Natal Parks Board's problem. For this reason efforts to encourage the people to build suitable "kraals" in which to place their animals at night did not meet with much success.

A number of problem hyaenas were killed by the Natal Parks Board in an attempt to improve its credibility with the communities. In addition, experiments with electrifying the fence enclosing the reserve proved very successful, as the number of hyaenas leaving the reserve in a 19km test strip dropped from 1.2 per night before electrification to 0.3 per night after electrification (Harvey 1992). Harvey (1992) also recommended implementing neighbour relation programmes such as educational, extension, public relations and community development projects. Apart from the obvious importance of educating people, this might also encourage them to be more proactive in combating predators.

3. Holekamp and Smale (1992) reported that the growing human population around Kenya's Masai Mara National Reserve increased the conflict between carnivores and sympatric pastoralists. Most serious was their report that large-scale poisoning was increasing around the edges of the reserve. A single incident of this practice in June 1991 was reported to have killed at least 14 hyaenas.

4. The best example of a survey on predators and their effect on livestock in Africa comes from Kruuk (1980) in Marsabit District, Kenya. The following illustrates the approach that should be taken when dealing with this problem, but is all too rarely done.

The economically important predators were found to be spotted hyaenas, lions and black-backed jackals. Striped hyaenas, cheetahs and wild dogs were also present, but they were not found to be important stock predators, either because of low numbers (wild dogs and cheetahs), or because of their generally non-predatory habits (striped hyaenas).

Spotted hyaenas were found to take some cattle, but more frequently sheep and goats, all of which were usually young animals. Most livestock were killed by predators while grazing during the day; only spotted hyaenas killed more often at night. Ninety per cent of all kills were made outside the protection of livestock holding areas (bomas), which were successful in preventing stock from roaming at night as well as in keeping out predators. The construction of the boma was found to be important, the most solidly built ones being the most effective. In most predation incidents, Kruuk found that negligence of the herdsmen played an important role. The loss of stock could be prevented by increased vigilance during grazing, by preventing animals from straying, and by returning herds to the manyattas in daylight.

He also identified three general areas of improvement in the protection against predators where government or international organisations could play a role:

a. Because repeated boma building was having an impact on the environment and local resources, he suggested conducting experiments with other less ecologically damaging methods of livestock fencing. Wire-fencing, dry-stone walling, bamboo-fencing and makuti-fencing were some of the alternative methods promoted for investigation.
b. For the same reason, it was suggested that the use of sprays against ticks be promoted since ticks were an important cause of abandoning bomas.
c. It was also found that predation was less common in manyattas or villages with dogs than those without them. Accordingly, it was suggested that extension and education methods should be developed to teach people about the use of dogs, that trials should be conducted with different breeds of dogs, and that research should be started on the occurrence of rabies amongst dogs and in wildlife. The effectiveness of anti-rabies measures should also be investigated. In light of recent findings with regard to canine distemper amongst domestic dogs around the Masai Mara National Reserve, Kenya (Alexander and Appel 1994) this disease should also be carefully monitored.

Compensation payment for livestock losses

The question of paying compensation for livestock losses as a way of encouraging land owners or local communities to tolerate the presence of predators needs to be carefully considered. It may be an effective tool when properly instituted and not abused.

Oli (1991, cited by Nowell and Jackson 1996) discussed a compensation scheme for the snow leopard in Nepal. This can be used as a guideline for a generalised compensation scheme. The aim of such a scheme is to make local communities more likely to cooperate with nature conservation authorities and laws protecting carnivores. To achieve this, the scheme should meet the following criteria:

1. It is the management approach most acceptable to the community.
2. It involves a direct financial incentive to livestock owners.
3. It involves an endowment fund, with the interest used to pay compensation, so that it is sustainable.
4. A management committee is established that includes representatives from local communities as well as regional or national conservation authorities. Local representatives are numerically dominant, so both local people and "outside" conservation authorities on the committee will be held jointly responsible for perceived shortcomings and successes of the scheme, and outside conservation authorities will not solely blamed for any perceived shortcomings.
5. The management committee serves as a link between conservation authorities and local people, and therefore aids implementation of other conservation measures.

It should also be borne in mind that compensation schemes may have drawbacks and these must be weighed against the advantages before a scheme is implemented. The drawbacks mentioned by Oli in the snow leopard proposal were:

1. Livestock losses from any cause may have to be compensated because it is impossible to go to the site and determine the actual cause of death on all occasions.
2. False claims could be difficult to detect, and compensation of such would set a bad precedent.
3. It is possible that local people will accept compensation and continue to kill the predators secretly, and it might be difficult to determine that this was happening.
4. Management committee members might use their position to gain political advantage, leading to a general loss of faith in the compensation scheme.
5. If the committee failed to function efficiently and impartially, it would reflect badly on the conservation authority.

Another important consideration is that compensation schemes are expensive and many of the countries with hyaenas are poor, so the establishment of a suitable fund may be problematic unless the money can be raised from an international conservation agency. Also, the compensation paid must be lower than the market value of the animals killed, otherwise the system will lay itself open to abuse. This, however, will not be satisfactory to the farmers unless they can derive additional benefits from the hyaenas, perhaps through ecotourism. In South Africa it is also possible to insure particularly valuable animals against predation.

7.3 Hyaena attacks on people

Hyaenas will eat humans and traditionally many African tribes put corpses out in the bush for spotted hyaenas to dispose of (Kruuk 1975a, Chapters 5 and 10). In the Middle East the striped hyaena is loathed as a grave robber (Chapter 5). Both these species have also been recorded to take live humans, the best documented case being from the Mlanje region of Malawi where spotted hyaenas were recorded to kill 27 people over a five year period (Balestra 1962). Most of the victims were people sleeping outside at night, usually children, although recently a woman was dragged from a tent in Kenya (S. Simborg *in litt*, Anonymous 1995, Peterzell 1995).

7.4 Translocation

Instead of killing carnivores in areas where they are regarded a nuisance, they have on occasion been caught and relocated to conservation areas. Most of these relocated animals have been released into the new area with little or no attempt being made to monitor their post-release behaviour. Both the brown and spotted hyaenas have been translocated in South Africa, but no published information on the results of these translocations are available at present. Observations on the post-release behaviour of spotted hyaenas in some areas are presently being conducted (M. Hofmeyer pers. com).

The only documented study of the post-release behaviour of a large African carnivore is that of Hamilton (1981) with leopards in Kenya. It was concluded that the translocation was not sufficiently successful to justify its continuation as a rational conservation and management policy.

Mills (1991) concluded that the translocation of large carnivores is a complicated management practice. Animals released into areas where their species already exists will have to compete with the established residents in the area to the detriment of one of these groups. Those that are released in areas where the species has been exterminated will have to face the same pressures as their conspecifics before them did. A translocation should only be attempted if a species is extinct in an area, the causes of its extinction are known and controlled in the new area, and conditions to support a viable population are available. With social carnivores like spotted hyaenas the question of mixing animals from different groups further complicates the problem. Studies of dispersal and social behaviour of spotted hyaenas (Mills 1990, Holekamp *et al.* 1993) suggest that unless matrilineal subgroups of adult females can be translocated together, the effort is likely to fail. Females are clearly uncomfortable moving to a new home range unless they have female kin to ease the transition.

Whenever a translocation operation is carried out, adequate follow-up observations are essential to assess the success of the exercise. Only when an adequate number of studies have been carried out will we be in a position to judge if and when these high profile conservation measures should be embarked upon.

Another important consideration with regard to translocations is the question of genetics. It is important to determine the level of genetic differences between surviving populations before mixing animals from different populations because of the possible deleterious long-term genetic consequences of such a strategy (Ashley *et al.* 1990). Before this information is available a conservative policy with regard to mixing populations is recommended.

Chapter 8

Survey and Census Techniques for Hyaenas

Gus Mills

8.1 Introduction

It is important to be able to assess the status and distribution of animals and to monitor population trends, especially in the case of rare or endangered species. However, as is the case with most carnivores, this is extremely difficult to do with hyaenas. They are nocturnal and often live at low densities, so that ground and air transect methods, routinely used on large herbivores, are not usually appropriate. Accordingly, some special techniques have been developed, or established methods modified to accommodate particular situations. In this chapter the methods that have been used to census and survey hyaenas are reviewed and evaluated. In addition, some suggestions are made for other methods which might prove useful in determining at least order of magnitude measurements of hyaena distribution and abundance.

In general the census methods discussed here have not been tested for bias and accuracy. This means that the results from these types of census must be interpreted with great care. Each method has its drawbacks, is based on a number of assumptions and needs to be calibrated. Ideally, several independent surveys of a population should be carried out in order to arrive at an accurate and precise figure.

8.2 Questionnaire surveys

Questionnaire surveys have been used as a first step in documenting the status and distribution of a species. (As an example, the hyaena questionnaire survey used for this action plan is given in Appendix 5). In Zimbabwe, Bowler (1991) successfully used a carefully constructed questionnaire survey to asses large predator damage to livestock. Questionnaires are advantageous because they reach a large number of people, may cover a large area (e.g., several continents), and are relatively inexpensive. However, the amount and quality of information that is accumulated is limited and inadequate. This in itself can be used to identify problem areas and to initiate more detailed studies.

8.3 Extrapolation

Population densities have been calculated for a range of species, including hyaenas, by extrapolating observations of home range and group size from known or radio collared individuals made during studies not primarily concerned with monitoring population trends (Whately and Brooks 1978, Tilson and Henschel 1986, Richardson 1985, Mills 1990, Chapter 5). Although such observations may lead to accurate measurements of numbers and densities, they are not conducive to census and monitoring studies as they are expensive and time consuming to carry out.

8.4 Line transects

A daytime line transect survey was used to census spotted hyaenas on the short grass plains of the Serengeti during the time of year when the wildebeest migration was concentrated there (Anonymous 1977). The high density of hyaenas on the plains at this time and the extreme openness and flatness of the habitat combine to make this area one of the few places in the world where it is possible to get reasonable data on hyaena population densities by this method.

The method has been modified by Hofer and East (1995a) in an attempt to give a more accurate estimate of the number of spotted hyaenas on the Serengeti plains while taking into account the unusual commuting system of the spotted hyaenas in this area. This modification requires detailed knowledge of some of the animals. A first series of transects is driven during the wet season when the migratory herbivores are present inside the censusing area and many of the hyaenas foraging inside the area are commuters that originate from clans which maintain territories outside the censusing area. In addition, both the proportions p_W (wet season) and p_D (dry season) of commuting clan members from a territory is calculated by tallying known individuals seen at the den of a clan from which all members are known. A second line transect survey is conducted during the dry season when the migratory prey, and therefore the commuting hyaenas, are off the plains and the only hyaenas present originate from territories inside the censusing area.

By applying a simple formula (see Hofer and East 1995a) using data from the two transect surveys and the den surveys, an estimate of the total hyaena population size is obtained:

$$N = (p_D \times N_W - p_W \times N_D)/[p_D \times (1 - p_W)],$$

where N_W and N_D are the census estimates from the wet and dry seasons and p_W and p_D are the proportion of clan members commuting during the wet and dry season, respectively.

The value of this technique is that it gives an estimate of the population even though it is not known from how far the commuting animals have travelled. Simply conducting the transect surveys in the wet and dry seasons gives high (wet season) and low (dry season) figures with no indication of the proportion of animals that are resident on the plains. This method makes the assumption that for a given season in all clans a similar proportion of clan members commute.

In another method, Spong (1995) based a population estimation on the short grass plains of the Serengeti on the number of active dens, rather than on the number of hyaenas observed. The dens were located by driving transects during the dry season (i.e. when the migratory prey were absent). Short-term observations at the dens established which ones were shared by the same clan and which belonged to separate groups. From these data estimates of the number of territories and their approximate sizes were made, and the population size was estimated using a mean clan size calculated from more intensive observations on a sample of the clans in the area.

8.5 Lincoln index

The Lincoln index is a widely applied and most useful method for estimating animal abundance (Seber 1982). It is a mark-recapture method which relies on a number of underlying assumptions. The most important assumptions are that marked and unmarked animals have the same probability of being caught (resighted) in the second sample, and that the population is closed, with no recruitment and mortality during sampling. Several workers have made use of a modified Lincoln index for censusing spotted hyaenas in different habitats.

Kruuk (1972a) calculated the number of spotted hyaenas in the Ngorongoro Crater, Tanzania by marking a sample of animals with ear notches. He then established the proportion of marked hyaenas in each clan range during nine visits to the crater over three years, and compared this with the number of marked hyaenas assumed to be present at that time (i.e. after discounting marked hyaenas that had either died or emigrated). A less elaborate method was applied, whereby merely the proportion of marked to unmarked hyaenas seen during an observation period was noted, regardless of the place of marking and resighting. Interestingly, a similar estimate of total population size to the one derived by the more detailed method was obtained (Kruuk 1972a).

In the Serengeti, where the hyaenas move over a much larger area, and where they do not mix randomly, the area was arbitrarily split into a number of smaller regions and a modified Lincoln index was calculated. The population was assessed as the sum of the populations in the smaller regions (Kruuk 1972a). As has been mentioned, line transect methods have also been used to census this population.

Sillero-Zubiri and Gottelli (1992b) used a Lincoln index approach to study the population of spotted hyaenas in the equatorial mountain forests of Aberdare National Park, Kenya. Because resighting opportunities were so few in the dense vegetation they used amplified tape recordings to attract hyaenas to bait sites. Using sightings of known, ear-notched hyaenas, population size was estimated over a four month study period.

Although this method has heretofore only been used on the spotted hyaena, it could be used on the other species as well. The problem is that the other species generally live at lower densities than spotted hyaenas, hence the effort involved in obtaining resightings of marked animals is likely to be high. For example, resightings of aardwolves are unlikely to be frequent enough to make this method a viable one. Moreover, aardwolves are not known to respond to any type of sound. Brown hyaenas can be attracted by the sound of the distress call of a small prey animal such as a springhare and it is likely that a similar call will attract striped hyaenas as well.

Provided that the assumptions pertaining to the Lincoln index can be met, this is a useful method for censusing spotted hyaenas, and with innovative thinking can be used in a variety of situations. In order to conform to the assumption that the population is closed, the time period for the follow up observations of marked and unmarked animals should be kept to a minimum.

Most users of the Lincoln index have only produced a population estimate, without calculating a variance. This makes it difficult to compare census estimates. A list of available variance estimates is provided in Seber (1982) and whenever possible should be given.

8.6 The use of sound

Spotted hyaenas have been surveyed by the use of sound over large areas of northern Kenya (Kruuk 1980) and over the entire 20,000km^2 Kruger National Park (Mills 1985b, Mills and Juritz in prep). The method has also been used in combination with mark-resighting observations (Kruuk 1972a). In the Kruger National Park an amplified, six minute long tape recording of sounds known to attract spotted hyaenas (i.e. the bleating of a blue wildebeest calf, spotted hyaenas mobbing lions, an inter-clan fight, and hyaenas squabbling over a kill) was played twice at 173 calling stations, with a break of about 5 min between each play-back. All hyaenas attracted to the calling site within 30 minutes of the commencement of the play-back were counted. Calling stations were situated more than 10km apart.

Experiments determined that hyaenas were attracted to the sound from a maximum distance of 3.5km, taking a mean of 21 minutes to appear, and that they responded in groups; i.e. if one responded, all of them did. Within a 3.5km radius of the calling station, the response was independent of distance and was estimated to be 0.55, with the 95% confidence intervals being 0.25 0.60. This information can be combined with the census counts from a given habitat to form a probability model which can then be used to estimate the expected number of hyaenas per unit area. The model also adjusts for non-response and offers the possibility of comparisons between years and between habitats (Mills and Juritz in prep).

A limitation of this method is that spotted hyaenas quickly become habituated to the tape so that the repeatability of the technique is severely limited. Surveys should probably not be repeated in the same area more than twice per year. A possible way to overcome this problem is to offer some kind of reward in terms of food to the animals.

The possibility of using sound to attract brown and striped hyaenas also exists, but because of their solitary habits and generally low densities this method is only likely to produce satisfactory results with intensive sampling, or where the species occur in unusually high densities.

8.7 Identification of individuals

It is possible to identify individuals by using physical characteristics such as pelage patterns and nicks in ears (Holekamp and Smale 1990, Hofer and East 1993a). If these individuals can be photographed or sketched, a reference collection may be built up of animals in a particular area and in this way an idea of the population numbers may be obtained. This method works best on high profile, diurnal species like the wild dog (Maddock and Mills 199) and cheetah (Bowland and Mills in prep) in national parks or game reserves that receive many tourists and have a good network of roads.

It is feasible to photograph animals for individual identification by means of automatic cameras with built-in flashes attached to tread-plates and hidden two-way switches. However, attempts to do so with leopards have met with little success (Smith 1977, Stuart and Stuart 1991) and similar problems are likely to be encountered with hyaenas.

8.8 Tracks, signs, and vocalisations

In India tiger numbers have been estimated by identifying pug marks, by measuring pug mark size or recognising peculiarities or deformities (Panwar 1979). However, the validity of this method has been questioned, as it is often extremely difficult to differentiate between the pug marks of different individuals (Schaller 1967).

Recently, Smallwood and Fitzhugh (1993) developed a technique for identifying individual mountain lions by their tracks. This involves taking measurements from acetate tracings and applying multiple-group discriminant analysis. These authors (Smallwood and Fitzhugh 1995) also describe a technique for detecting population trends of mountain lions in California by counting track sets in randomly selected quadrats. In addition, they maintain that their technique permits estimates of population size and demography after individuals are identified by their tracks, and after linear density on roads is calibrated from spatial density at intensive study sites. It might also be possible to measure spatio-temporal associations with competing species.

Stander (in press) has also shown the validity of track counts for measuring population densities of large carnivores. In Namibia, he compared results from spoor counts with those from radio tracking studies. In this study the track density of leopards, lions and wild dogs showed a strong linear correlation with true density. The success of this study was dependent on the skills of the local San trackers, who proved they were able to differentiate between individual leopards.

A less ambitious application of this technique might be to conduct an initial survey by merely driving along a transect and counting the number of tracks crossing it. Of course this technique is only possible on suitably sandy or soft substrates; dust roads are often ideal. Where brown and spotted hyaenas are sympatric, and, to a lesser extent, striped and spotted hyaenas, care must be taken in differentiating the spoors of the two species.

The prominent white scats left by hyaenas are another potentially useful sign for documenting relative densities, or at least presence of hyaenas. Again the similarities in the scats of brown and spotted hyaenas on the one hand and spotted and striped on the other, demand that considerable caution be applied when assigning the species to the scats. This is complicated by the fact that the scats of other large carnivores, in particular feral dogs, may be also confused with those of hyaenas. The major difference is that bone fragments in hyaena scats are normally smaller and smoother than those in the scats of dogs, because of the more efficient digestive system of hyaenas. Additional information such as tracks or pastings (Mills 1990) should be used if possible to confirm identification. If hyaenas are suspected in an area it might be possible to verify this by putting out a bait for them to feed on.

Vocalisations of spotted hyaenas, in particular the long-distance whoop call, may also be used to at least establish the presence of spotted hyaenas in poorly known areas, or to give an index of relative changes in density over time in a particular area. Taking this method further, M.L. East and H. Hofer (in prep) recorded the rate of whooping sequences at stationary listening stations in a study area. By comparing these with the known rate of whooping in an adjacent better known area an approximate estimate of density in the less well studied area was made.

8.9 Conclusions

Clearly, establishing the status and trends in populations of hyaenas is a difficult process. However, through innovative thinking it may be possible to overcome many of these challenges. (Table 8.1). Each situation should be assessed individually. The method employed will depend on the objectives, the species concerned, the area and habitat, and the amount of money and time available. Quite simple techniques can yield useful information.

At this stage it is important to identify areas where hyaenid surveys are required and to prioritise these. Then the required surveys need to be implemented in order to document the status of hyaenas in the priority areas. Ideally this should be a prerequisite to identifying the most important conservation research and management programs for the Hyaenidae family.

Table 8.1. Methods which may be used to survey and census hyaenas.

Method	Aardwolf	Striped hyaena	Brown hyaena	Spotted hyaena
Questionnaire	Yes*	Yes*	Yes*	Yes*
Extrapolation	Yes*	Yes	Yes*	Yes*
Transect	No	No	No	Yes*
Lincoln Index	Yes	Yes	Yes	Yes*
Sound	No	No	No	Yes*
Individual ID	Yes*	Yes	Yes	Yes*
Tracks and signs	Yes	Yes	Yes	Yes

* Has been used.

Chapter 9

Hyaenids in Captivity and Captive Breeding: Aims and Objectives

Alan H. Shoemaker, Jack M. Grisham, Laurence G. Frank, Susan M. Jenks, Ingo Rieger and Charles A. Brady

9.1 Introduction

Historically, all four hyaena species have been commonly kept in captivity, but often not kept well. Linnaeus described the striped hyaena in 1758, probably basing his description on specimens kept in European menageries. In all too many cases, zoos obtained them as an afterthought to their collection plan (if they had a plan); using them to fill empty cages until something "better" came along. Later, in subsequent planning processes, many zoos allocated larger and better facilities to taxa considered more charismatic by the public and/or staff. As a result of this haphazard approach to hyaena husbandry, hyaenids have been sporadically propagated and too often been relegated to inferior exhibits. As a result, they are now facing "extinction" in many of the world's captive collections.

9.2 Captive trends

Within any collection of captive animals, hyaenas compete for limited cage space with other similarily-sized carnivores. While the exact identity of these competitors varies between institutions, large canids are their most serious competitors. In some institutions, they also compete for exhibit space with medium or large felids, or ursids.

In addition to overt competition, zoos now realise that many large carnivores, including hyaenas, have historically been housed in substandard exhibits. Because these older exhibits were inadequate for many species to demonstrate various aspects of their social and reproductive needs, numerous zoos are now replacing them with better ones that are larger and allow their inhabitants to demonstrate more complete repertoires of natural behaviour. Part of this process, however, includes an overall reduction in the number of exhibits, and hence, a reduction in the number of species being maintained by zoos. As a by-product of this change, hyaenids are losing out to large felids and canids.

From a husbandry point of view, hyaenas are easily kept. Disease problems are minimal and it is not uncommon for captive hyaenas to reach 15 20 years of age. However, propagation in zoos has been limited, and because some owners have experienced problems in placing captive born young, many pairs have been separated or females implanted with birth control devices to prevent further breeding. Compatibility has also been a problem with some pairs, especially when introduced as adults. As a result, many compatible pairs were developed from litter mates and severe inbreeding has been observed in some captive collections (I. Rieger, unpublished data). Also, many individuals, especially spotted hyaenas, have never been closely examined to confirm their genders. As a result, some non-breeding "pairs" have later turned out to be same-sexed specimens.

9.3 ISIS data

Data contained within the International Species Information System (ISIS) give some idea of how hyaenids have fared as a captive, yet unmanaged group of species. ISIS is a computerised data bank containing present and historical inventory information on captive animals held by zoos and other collections which participate in the program. It is housed at the Minnesota Zoological Garden, Apple Valley, MN, USA. For practical purposes, ISIS members include most zoos in North America, as well as a large and continually growing number of zoos and other types of collections in Europe, Australia, and other regions.

To place the situation pertaining to hyaenas in zoos in perspective, ISIS reporting zoos in North America reported holding over 280 lions on 31 December 1995 and ISIS reporting zoos in Europe reported an additional 245 animals.

Aardwolf

Because of its nocturnal habits and poorly understood husbandry requirements, the aardwolf has only sporadically been kept in captivity. This has changed over the past decade and at the end of 1991, 10 zoos reported keeping 39 aardwolves. All are probably derived from the population in southern Africa. Of these, 33 were reported to be captive born and five wild born. There were eight young born in 1991.

Since 1991, this species' population has increased despite no significant change in the number of holding institutions. As a result, ISIS reported 54 aardwolves in 15 zoos by June 1993. This population further reported six captive births, but infant mortality has been high.

Striped hyaena

The striped hyaena has fared little better. During 1991, only 43 animals were reported in 17 zoos. One captive born pair were identified as *Hyaena h. hyaena* and another as *Hyaena h. syriaca*; the rest are not identified by subspecies. Included within this population are 34 animals said to have captive born origins, two that were taken from the wild, and seven of unknown ancestry, a trend suggesting a lack of availability from the wild or a lack of interest in obtaining additional specimens. Thirteen captive births were reported during 1991.

Over the next 30 months, the population reported to ISIS by 20 zoos grew to 62, but this increase could also be caused by a growing participation in the ISIS database by zoos throughout the world. Regardless, the origins of captive striped hyaenas have changed little, with 73% reported being born in captivity and only 7% known to have been captured in the wild. Births declined from 1991 to 1993 from 13 to only 6 despite an apparent increase in the captive population. On 30 June 1996 22 zoos reported holding a total of 64 striped hyaenas.

Brown hyaena

The brown hyaena has fared worst of all. Although the population presently in captivity would appear unchanged over time, data from the international studbook shows a steady decline in animals held captive outside their natural range (Shoemaker 1983). This trend is generally attributed to exhibit problems stemming from the species' nocturnal nature, problems arising from compatibility, and a lack of reproduction. At the end of 1992, 37 individuals were present in 13 collections, but six of these holders were in South Africa or Zimbabwe where stock is obtained from the wild. Moreover, only one zoo outside Africa has reported successfully breeding the species in recent years, and the hand-reared history of this single young suggests it will probably not have any long-term impact on the conservation of the species as a whole. The remaining animals were composed primarily of post-reproductive animals, and were often maintained as single individuals (Shoemaker 1983).

At the end of 1996, there were 10 brown hyaenas at the De Wildt Cheetah Breeding Centre in South Africa, but there have been no births for over five years.

Spotted hyaena

At the end of 1991, 21 zoos participating in ISIS reported data on 55 living spotted hyaenas worldwide. Of these, 36 were born in captivity, nine were born in the wild, and ten were of unknown origin. Admittedly these figures do not include all known animals held in captivity. For example, the large and very successful colony at the University of California at Berkeley has an additional 40 animals that were not reported to ISIS. Regardless, these data do demonstrate a general lack of interest in the species by the several hundred zoos participating in the program. Moreover, these 55 zoo-held animals only produced eight offspring during 1991 (almost certainly not all of which survived). During 1991, four animals were added to the captive population from the wild.

Between 1991 1993, this trend changed little. While ISIS usage expanded over the next 30 months as additional zoos outside North America joined the program, the number of spotted hyaenas reported to be maintained by zoos only increased by two. Moreover, the 24 zoos possessing the animals reported only two births. Were it not for the breeding successes experienced by the Berkeley collection, the captive population would appear unsustainable. In June 1996, 27 zoos reported holding 72 animals.

9.4 Extant programs

Even considering that there are only four species in the Hyaenidae, the present level of regional and international captive management programs is low in comparison to other carnivore families. Only the brown hyaena has pedigree data available in the form of an international studbook (Shoemaker 1983). However, due to continuing problems in propagation, this program has contributed little to the species' overall conservation and was discontinued in 1993. Regionally, an aardwolf studbook exists for captive individuals maintained in North America (Lyon 1994) and a similar studbook for spotted and striped hyaenas maintained in that region is being prepared. Overall, hyaenas are included with the American Zoo and Aquarium Association's (AZA) Canid and Hyaena Taxon Advisory Group (TAG) because of the similarity of husbandry needs for both families.

Management programs in other regions appear to be lacking. The European captive breeding program for the conservation of endangered species (EEP) has no management plans for hyaenas. In the United Kingdom, a Canid and Hyaena TAG exists but no hyaenids are presently targeted for management. In Australia and New Zealand, hyaenas have low priority, with zoos retaining hyaenas for exhibit purposes only. No other management plans are present in Europe, Indian, Japan or India. In

Africa no management plans in the African Preservation Program are in place in any zoos for any hyaenid species and none are planned.

9.5 North American cage space allocation

In North America, a Carnivore Space Survey for AZA zoos was compiled by Mellen *et al.* (1993) that included data on present and future cage spaces allocated for hyaenids by AZA zoos in North America. Although similar studies are not known for zoos in other regions, the general lack of management programs outside North America suggests that the situation in those regions is similar. The survey results are given in Tables 9.1 and 9.2.

Table 9.1. Allocation of current and future cage space to hyaenid species in American Zoo and Aquarium Association (AZA) zoos (Mellen *et al.* 1992).

	Current cage space	Future cage space
Generic Hyaena	0	6
Aardwolf	10	6
Striped Hyaena	7	11
Brown Hyaena	0	0
Spotted Hyaena	11	10
Total	**28**	**33**

Table 9.2. Allocation of present and future cage space to hyaenids in American Zoo and Aquarium Association (AZA) zoos (Mellen *et al.* 1992).

	Cages	Adults	Juveniles
Current population	28	48	1
Current capacity	-	42	30
Future capacity	33	63	54

Based on these results and considerations of age, founder representation and behavioural issues, the AZA Canid and Hyaena TAG developed a Conservation Assessment and Management Plan (CAMP) and recommended that existing hyaena and aardwolf spaces be divided between aardwolves and spotted hyaenas (Anonymous 1992). New founders for the aardwolf are needed. The TAG also recommended that brown hyaenas and striped hyaenas should be phased out of AZA zoos and other collections in North America through natural attrition.

9.6 Objectives for international captive breeding efforts

In developing status categories for international captive programs, the Canid and Hyaena TAG applied proposals based on the Mace and Lande (1990) criteria to hyaenids in order to assess the degree of threat to the various taxa. This system defines three categories of threat:

1. Critical: 50% probability of extinction within 5 years or two generations, whichever is longer.
2. Endangered: 20% probability of extinction within 20 years or ten generations, whichever is longer.
3. Vulnerable: 10% probability of extinction within 100 years.

On the basis of these criteria, the CAMP (section 9.5) concluded that the four species of hyaenids are much less threatened than some other large carnivores. None of the four hyaenid species were considered Critical or Endangered; the brown hyaena was considered Vulnerable and the other three were considered safe. (These status categories preceded the revised status criteria and assessments given in chapter 5). The subspecies of the striped hyaena from northwest Africa, *Hyaena hyaena barbara*, is considered Endangered under the U.S. Fish and Wildlife Service's Endangered Species Act and given the status of Critical.

While the captive status of Hyaenids in all regions of the world is apparently similar to the situation in North America, the collective recommendations of the CAMP for future captive programs of zoos in all regions are different from the recommendations for AZA zoos. They are influenced by the present and future availability of cage spaces, the availability of new founders both now and in the future, and the hope that additional zoos in range countries will become more involved in *ex situ* conservation of hyaenids. Furthermore, captive populations are now being treated as integral parts of metapopulations that are managed by conservation strategies and Action Plans. In this spirit, the canid, hyaena and aardwolf CAMP applied a system of categories for captive propagation to develop a conservation scheme for hyaenids. These categories are defined in Table 9.3.

According to ISIS, there are approximately 145 living hyaenas and 40 aardwolves within participating zoos worldwide. If, as some believe, 25% of the world's captive wildlife within the world's 1100 zoos is entered into ISIS, then there is a conservative possibility of 300 spaces for hyaenas, and 100 spaces for the aardwolf in zoos worldwide, even when competition with large canids is taken into consideration.

As a result, the CAMP's recommendations for captive management of hyaenid species worldwide are that the brown hyaena should be managed as a Nucleus I species, and that the other three species should be managed as Nucleus II species. The North African subspecies of the striped hyaena should be managed as a 90/100 1 species if founders become available, and preferably by zoos within this taxon's natural range.

Table 9.3. Categories of captive propagation used by the canid, hyaena and aardwolf Conservation Assessment and Management Plan (Anonymous 1992) for the development of a captive conservation scheme for hyaenids.

Captive Recommendation	Level of captive program
90/100 I	Population sufficient to preserve a minimum of 90% of the average heterozygosity of the wild gene pool for 100 years developed in 1–5 years.
90/100 II	Population sufficient to preserve a minimum of 90% of the average heterozygosity of the wild gene pool for 100 years developed in 5–10 years.
Nuc I	A captive nucleus (25–100 individuals) to always represent a minimum of 98% of the wild gene pool. This type of program will require periodic, but in most cases modest, immigration/importation of individuals from the wild population to maintain this high level of genetic diversity.
Nuc II	A captive nucleus (25–100 individuals) should be maintained in captivity. These taxa may not be of conservation concern, but may already be present in captivity or otherwise known or poorly monitored, so in some cases, they are included pending review of population estimates or further survey work. For species already present in captivity, the captive nucleus should be managed as well as possible.
Eliminate	A captive nucleus should not be maintained in captivity. These taxa are not of conservation concern and are plentiful in the wild. The present captive population should be managed to extinction. (For some North American and Palaearctic species, decisions to eliminate from captive collections are less conservative. These populations are closely monitored and in the event of a decline can be rapidly brought into captivity).
No rec	Establishment of a captive program is not recommended.

Chapter 10

Cultural and Public Attitudes: Improving the Relationship between Humans and Hyaenas

Marion L. East and Heribert Hofer

One of the aims of this Action Plan is to promote a better understanding of the four existing hyaena species. Our survey of cultural and public attitudes towards hyaenas in this chapter suggests that this will be a major task, given the ingrained prejudices that exist in many cultures towards hyaenas, particularly the spotted hyaena. All hyaena species are probably tainted to some degree by the prejudices suffered by spotted hyaenas, thus any improvement in attitudes towards spotted hyaenas will probably benefit all hyaena species.

First a summary of cultural attitudes as revealed by the information from the Action Plan questionnaires and our general literature survey is presented. Then current public attitudes amongst five important target groups are considered, that have the potential to either enhance or diminish the chances of successful conservation of hyaenas. Finally, some ideas are discussed for the implementation of a public campaign for the conservation of hyaenas.

10.1 Cultural significance of hyaenas: many cultures, many views

Hyaenas are important animals in many cultures. They are viewed with contempt and fear and frequently associated with witchcraft, as their body parts are used as ingredients in traditional medicinal treatments (Tables 5.3 and 5.7). They are thought to influence people's spirits, snatch children, rob graves, and steal livestock. This section summarises some of the historical and present beliefs about hyaenas as described in the Action Plan questionnaire survey and the literature.

Striped hyaena

The striped hyaena evokes many superstitious fears because of reputed and documented cases of injuries to adults sleeping outside, snatching and killing of children and grave robbery. Most cultures consider the striped hyaena to be a predator of livestock. In addition, it is widely exploited as an aphrodisiac and utilised for traditional healing (Table 5.3).

In Armenia, Azerbaidjan and Uzbekistan, the striped hyaena was held responsible for the disappearance of unattended small children.

Throughout the Arabian peninsula and northern Africa it is loathed as a grave robber. Amongst Arabs in Israel, it is considered a demonic creature. A widely believed story says that if you meet a hyaena it rises up on its hindlegs and puts its forelegs on your shoulders. Then it breathes into your face and so hypnotises you. You then have to follow it into its den where it sucks out your brain. The spell can only be broken if somebody meets you while following the hyaena, makes a cut in your skin and spills some drops of your blood. Another belief considers that the flesh of the right side of a striped hyaena has healing properties against many illnesses but the left side is poisonous (H. Mendelssohn, pers. comm.).

Photo 10.1. A striped hyaena strung up on a road sign in Saudi Arabia.

C. Naumann

In Jordan, the striped hyaena was traditionally considered a threat to human life, as man is supposed to be the favourite food of the striped hyaena, and hence "the more hyaenas a man can kill, the stronger and braver he is seen to be" (Al Younis 1993). In northeast Jordan, graves were cemented over to avoid disturbance by striped hyaenas, and nomads constructed cairns of stones to protect the dead (Harrison and Bates 1991).

The striped hyaena is still the object of much local superstitious belief in Saudi Arabia. It is generally loathed as a grave robber and is severely persecuted by baiting, tracking and trapping as evidenced by many reports of dead hyaenas hanging in trees and on sign posts (Gasperetti *et al.* 1985, Seddon 1996).

In India attitudes towards hyaenas vary widely between regions. In some areas it is persecuted by vandals who locate and destroy dens in open habitats, in others it is ignored, and in yet others villagers are known to gather in the evening and watch hyaenas leave their caves at dusk. The animal is often treated as "untouchable" (i.e. left alone) due to its scavenging habits.

In Afghanistan striped hyaenas are caught for organised fights between domestic dogs and hyaenas for entertainment (Naumann and Nogge 1973). Hyaenas are reputedly caught by a naked man who crawls into the den murmuring prayers. This drives the animal to the back of the den where it is tied down with little resistance (Kullman 1965, Naumann and Nogge 1973). In the 1960s, approximately 25 striped hyaenas were caught every year by hunters who overpowered the hyaenas inside their caves. (Kullman 1965, Hassinger 1973).

Brown hyaena

Although used in traditional medicine and rituals, the brown hyaena is not nearly as sought after in this regard as the spotted hyaena.

Spotted hyaena

The spotted hyaena evokes fear and contempt in many cultures because it plays an important role in witchcraft. For instance, in Tanzania some witchdoctors collect spotted hyaena cubs from communal dens and raise them in pens to enhance the witchdoctors' status. The witchdoctors are said to ride on the back of spotted hyaenas to their secret ceremonial gatherings at night. Although there have been documented cases of injuries caused by spotted hyaenas to adults sleeping outside, the reaction of local people to such events is muted and notably different from the reaction of other cultures toward striped hyaenas. We know of no case where spotted hyaenas have been persecuted in such cases, and until recently (see below) there have been no reports of snatching or killing of children or of grave robbery, as is the case with the striped hyaena.

In the Mtwara region of Tanzania people believe that if a child is born at night while a hyaena is crying that child will most likely become a thief. In the same area, hyaena faeces are believed to enable a child to walk at an early age; it is therefore not uncommon to see children wearing pieces of clothes with hyaena faeces wrapped in them (Mchitika 1996).

In several cultures in East Africa it is considered "fun" to taunt and kill spotted hyaenas in traps or during "target practice" (questionnaires, personal observations). All cultures consider the spotted hyaena an important predator of livestock. In some areas it is utilised for traditional healing (Table 5.7).

In Ethiopia, the hyaena men of Harar are famous for provisioning spotted hyaenas, a case worthy of detailed documentation, as here a local culture cherishes hyaenas and has made them a tourist attraction. In other areas of Ethiopia the spotted hyaena is tolerated as long as it does not kill stock. If it does kill livestock, it is shot or hunted with traditional weapons.

In Guinea-Bissau, the spotted hyaena was previously considered useful as a "cleaner of the wild", but now people feel threatened by it as it has been blamed for the kidnapping of unsupervised children (Paris 1991). In the region around Mansoa some men are said to be transformed into spotted hyaenas at night; when they are discovered they are killed but do not recover their human origin (Robillard 1989).

In Kenya, attacks on humans are considered rare; since the 1960s medical assistance by the Flying Doctors was requested for approximately two dozen confirmed cases (A. Spoerry, pers. comm.). The areas in which attacks occur are mostly inhabited by nomadic people with light or temporary housing and where the local people do not bury human corpses but traditionally leave them in the open to be consumed by hyaenas. According to traditional belief amongst Masai and other tribes, something was wrong with a person during his/her lifetime if hyaenas do not consume the corpse. Hence to ensure the consumption of the corpse and to avoid social disgrace, corpses are often covered with fat and blood from a slaughtered ox to make it more attractive for scavengers. The usual assumption (Peterzell 1995) that an attacking hyaena must be rabid has apparently not been confirmed in any case (A. Spoerry, pers. comm.).

In Malawi, the spotted hyaena is considered a pest and menace and not tolerated by local people outside conservation areas.

10.2 Public attitudes

Five target groups are considered because their activities have the potential to influence the conservation of hyaenas in a positive or negative way. Information on the attitudes of these groups was derived from several sources; specific studies of target groups, the Action Plan questionnaire, and a preliminary questionnaire survey in Tanzania to assess current attitudes towards hyaenas and knowledge of the behaviour and ecology of spotted hyaenas. Neither of the questionnaire surveys fulfil all of the requirements for scientific surveys, as no effort was made to target a representative sample. The results should therefore be treated with caution. However, in the absence of any scientific surveys the information gathered by these preliminary exercises may be of some value.

Official attitudes

According to the Action Plan questionnaire survey, official attitudes towards hyaenas vary widely between countries. There is often a discrepancy between the legal classification of a species and the attitude displayed towards it by the activity of officials. This may be an advantage or a disadvantage for the conservation of a species. For instance, the legal classification of the spotted hyaena as "vermin" in Ethiopia is not being followed up by officials due to a combination of lack of funds and benign neglect. On the other hand, shooting, spearing or poisoning of hyaenas is prohibited in Kenya but there is no effective protection because hyaenas are viewed with contempt, indifference, or as a pest by certain officials.

Because it is frequently not recognised as a separate species, or its presence in a country is unknown to most people, the aardwolf is usually ignored. The general official attitude towards the striped hyaena is one of neutrality or neglect. Exceptions where the striped hyaena is considered an asset include Turkmenistan, Oman, where it is considered a useful scavenger, and Israel, where it is protected and tolerated at feeding stations run for vultures.

The official attitude towards the brown hyaena in South Africa varies between provinces. In the Free State, a predominantly sheep farming region, it is regarded as a problem animal and hunted by a government sponsored predator control hunting club. In what constituted the Transvaal, however, the brown hyaena is classified as a Protected Wild Animal and seen by conservation authorities as an asset. In Botswana, the brown hyaena is often viewed like the spotted hyaena as a problem animal, even though it is not recorded as a problem animal and rarely takes domestic stock, except occasionally goats.

Official attitudes towards the spotted hyaena vary widely from positive attitudes of benign neglect to negative ones of considering the spotted hyaena vermin. Legal classification varies from "vermin" (Ethiopia) to fully protected; legal protection is often restricted to conservation areas. The predominant attitude is exemplified in Botswana where it is privately considered by most officials to be a pest and treated as such, although the official attitude is one of neutrality. The spotted hyaena is sometimes considered an asset when it lives inside protected areas, but is a problem animal elsewhere. This attitude can be found in Malawi, Namibia and some provinces (in the sense of the old administrative boundaries) of South Africa. In Senegal, the spotted hyaena is not considered useful as "cleaner of the wild" and not considered "vermin." Similar neutral or positive views prevail in Uganda and Tanzania.

A survey of 73 future senior conservation administrators undergoing training shed some light on these results. Students at the Mweka College of African Wildlife Management, Tanzania, chiefly originate from English-speaking African countries. Students often have several years of practical experience working in national parks or other types of conservation areas within their home countries prior to their training course at Mweka. The survey undertaken by us revealed that most students had a good knowledge of the ecology of the spotted hyaena but the behaviour of this species was poorly understood. More than half of the students thought that the primary role of the spotted hyaena was to clean up the ecosystem, and a quarter also added that it regulates herbivore numbers. Most students' understanding of behaviour was based on a combination of observation and logic. For example, most students thought that spotted hyaenas laugh when they are happy because hyaenas laugh when they are feeding, and any hyaena that is feeding must be happy. Although the majority of students were aware that there are several species of hyaenas, most could only name the spotted hyaena. Surprisingly, only a small number of students (two of eight) from Botswana knew of the existence of the brown hyaena. All students expressed an interest in hyaenas and a wish to understand more about their behaviour. Many also were well versed about the role of the spotted hyaena in witchcraft in their home countries.

Local people

According to the Action Plan questionnaire survey, neutral or negative attitudes to the various hyaena species dominate amongst people living in close contact with hyaenas. It is uncommon for local people to tolerate any hyaena species, even if "problem" animals are killed.

Tolerance, or the absence of it, is difficult to evaluate for the aardwolf because most locals do not know of it (see above and below, and Box 10.1). The striped hyaena is tolerated in Algeria, Burkina Faso, Ethiopia, Kenya (by pastoralists), some parts of India, and Israel. The brown hyaena is usually tolerated in its range countries unless it is suspected to kill livestock. The spotted hyaena is tolerated in Burkina Faso, Cameroon, Central African Republic, Ethiopia, Côte d'Ivoire, Kenya (by pastoralists), Mozambique, Tanzania, and Uganda.

Box 10.1. Names tell a story – a lack of species-specific names tells the wrong story.

Brown hyaena and aardwolf are often given the same name as the spotted hyaena in indigenous languages in areas where two or more species coexist. For instance, in the languages Dioula, Fulbe, Kiswahili, Malinké, Moore, Ngambaye, Ouolof, and Peuhl, the striped and spotted hyaena have identical names (compare Boxes 3.2 and 3.4). In other languages, other hyaena species may be called a "small spotted hyaena," and hence adults of this species can potentially be confused with young of the spotted hyaena. An example are the Kiswahili words for spotted hyaena (fisi, "hyaena") and aardwolf (fisi ndogo, "little hyaena").

There has been no systematic effort to assess whether such linguistic ambiguities influence people's perception of and attitudes towards a species. Are differences in the behaviour and ecology of each species recognised, especially behaviours and activities likely to bring a predator into conflict with humans? The spotted hyaena is often the most common hyaena species, and its body size and communal hunting behaviour makes it more likely to be responsible for the majority of attacks by hyaenas on livestock in a particular area. Other hyaena species have often been erroneously held responsible for attacks on livestock or other conflict-prone activities when the most likely culprit was a spotted hyaena or a large cat or canid. It is therefore quite likely that the reputations of striped hyaena, brown hyaena and aardwolf have suffered from people's perception of the spotted hyaena.

If several species have the same name in an indigenous language, people's perception of these species is likely to be dominated by the most conspicuous behaviour of any of the species involved. When people's perceptions direct people's actions, other hyaena species may be killed or controlled when in fact they are not responsible; creating a conservation problem where there should be none. Conservation research that identifies linguistic ambiguities and conservation education that is sensitive to such ambiguities would therefore be useful for any successful implementation of conservation efforts.

Linguistic ambiguities also occur when each species does have a separate name in a language but these names are not being used. For conservation efforts, at least two contexts are important. The first is the description of current and historic geographic distribution of a species from recent records and the older literature, especially articles and books written by hunters. The second is the incidence, distribution and impact of pathogens from case reports or serological surveys in the veterinary literature. In both contexts, sources often refer to a generic "hyaena", but do not specify the species (see Mebatsion *et al.* 1992, Edelsten 1995, Thesiger 1996), or species identification may be unreliable, as pointed out by several sources in the questionnaire survey.

The preliminary survey of a dozen primary schools near the Serengeti, Tanzania, revealed that knowledge of spotted hyaena behaviour and ecology among primary school children and their teachers was limited. Most pupils and teachers had observed spotted hyaenas around their villages, perceived hyaenas to be stupid, funny or cunning, and quoted African fables that reinforced these ideas. No child knew of the existence of the aardwolf or the striped hyaena in Tanzania, even though both species occur in the Serengeti. Nothing was known about the social behaviour of any hyaena species. Children were most interested to learn the age at which a hyaena dies and the number of offspring that a female can rear in a lifetime. All children were keen to learn more about hyaenas. Teachers enquired whether there are male and female hyaenas, as most were aware that the female spotted hyaena has a pseudo-penis.

A common misconception among teachers was that the spotted hyaena has a "fire" in its stomach. This opinion is derived from the fact that the spotted hyaena is known to produce white faeces, which the teachers considered to be like ash left after a fire. Both teachers and children could imitate many vocalisations of spotted hyaenas, but few knew the function of these calls. All were very interested to learn about these vocalisations and tape recordings were effective as a teaching aid. Wildlife videos about hyaenas were also helpful to demonstrate the hunting abilities of spotted hyaenas.

Farmers and hunters

Evidence from the Action Plan questionnaire survey and two studies (Bowler 1991, Harvey 1992) illustrate that a key issue for farmers across Africa and Asia is the loss of livestock due to predation by hyaenas. Farmers assume that the predators that feed on a carcass are the ones that made the kill, and they sometimes mistakenly assign responsibility for livestock losses to predators that are incapable of killing such livestock.

In small stock farming areas in South Africa, a few farmers still believe that the aardwolf kills their stock and persecute it for this reason. Intolerance and ignorance by commercial stock farmers in Namibia, South Africa and Zimbabwe have led to the killing of many non-harmful brown hyaena individuals. In Namibia, the brown hyaena is treated with suspicion by farmers who are ignorant of its feeding habits. In the Free State in South Africa, the brown hyaena is tolerated in wheat and cattle ranching areas but not in sheep farming areas, whereas in Transvaal the brown hyaena is normally tolerated by farmers.

In Zimbabwe, the brown hyaena is largely tolerated in game and cattle ranching areas. In Namibia, the Namibian Agricultural Union has in the past demanded that the spotted hyaena be officially declared a "problem" animal. It is treated as such and is not tolerated in communal and commercial farming areas, and is frequently killed (if it has been reported as vermin).

The Hluhluwe/Umfolozi Park, a small game reserve (960km^2) in Natal, South Africa, is surrounded by a densely populated area and local communities dominated by subsistence farmers. This situation epitomises several aspects of the problems facing attempts to conserve large predators; dense rural populations, small conservation areas, and animals that break out from conservation areas and cause damage to local communities (Chapter 7). A survey of local communities living near the Hluhluwe Umfolozi Park suggested that:

1. Predation of domestic livestock by spotted hyaenas from the Game Reserve was the key issue of concern to local communities.
2. The communities felt that the Natal Parks Board was "in charge" of wild animals and thus the Board, rather than the communities, was responsible for doing something about "problem" animals (Harvey 1992). Because of this view, attempts to encourage farmers to improve the protection of their livestock at night were met with limited success (Harvey 1992).

Bowler (1991) conducted a large scale survey of attitudes of mixed commercial cattle and wildlife ranchers in Zimbabwe. Of 187 farmers sent questionnaires, 75% replied. In wildlife ranching the farmer's income is primarily dependent on the sales value of safari trophies by hunting clients, or the satisfaction of photo-safari clients. Potential conflicts between farmers and predators arise because:

1. Any predation of domestic livestock by hyaenas would be considered an avoidable loss by the farmer.
2. By taking herbivores, predators reduce the number of safari trophies available to hunting clients.

Of the farmers that replied, 79% operated a mixture of cattle and wildlife production systems. In general, 45% thought that predators were an asset whereas 38% considered them to be a problem. However, of the 35% of respondents that had a view on the spotted hyaena, 45% considered them an asset and 55% a problem. Killing cattle was considered to be the key problem (51% of "problem" responses). Hunting was viewed as the chief asset (40% of "asset" responses), followed by photo-tourism and the recognition that predators are an essential part of the ecosystem (20% each). The spotted hyaena was most frequently named to prey on cattle, but there was no indication that the spotted hyaena, or any of the other large predators, preferred cattle over wildlife. The average stock loss (domestic stock and wildlife combined) perceived by ranchers to be acceptable was 7.4% of the stock per year. This survey indicated that wildlife ranchers were unlikely to tolerate predators for aesthetic reasons alone and that whenever hyaenas occurred in moderate densities on ranchland they were likely to come into conflict with the ranchers (Bowler 1991).

Tourists and tour guides

Bowler (1991) also surveyed the attitudes of photo tourists taken to conservation areas by Zimbabwean safari operators. This questionnaire survey had a low return rate of 7.4%. The survey was used to derive an index of tourist appeal for each of 26 large mammal species, principally herbivores and large carnivores. Tourists were asked to rate each species on a scale from 1 (not interested in viewing the species) to 5 (desperate to see the species). The average score across questionnaires was used to rank species in order of attractivity.

The top three were leopard (score of 4.9), cheetah (4.8) and lion (4.8); the brown hyaena (4.0) ranked eleventh and the spotted hyaena (3.9) ranked twelth, behind the African wild dog at rank ten. Herbivores that were more important to tourists than the two hyaena species included black rhino, elephant, white rhino, giraffe, sable antelope, and hippo, whereas buffalo and birds in general ranked equally high as the spotted hyaena.

Bowler (1991) also asked the tourists whether they had seen the species in question. Of respondents who scored the spotted hyaena in the two top categories (4 or 5), 29% had seen a spotted hyaena, whereas only 16% of respondents who scored the species in the three lower categories had seen one. However, this difference was not statistically significant. Observing a spotted hyaena in the wild obviously did not change the attitude of the average tourist dramatically, but this result suggests that there is scope for improving the hyaena's image. Bowler interpreted these results to indicate that hyaenas suffered from a bad public image. In this context, it would be interesting to know to what extent the views of tourists were influenced by their prior knowledge of hyaenas and how tourist opinions would be influenced by the knowledge and opinions of tour drivers.

In order to explore this issue further, we conducted a preliminary survey to determine hyaena knowledge of tour drivers and tourists that visit the Serengeti. The knowledge of hyaenas among tour guides was highly variable. A minority had a comprehensive knowledge including an understanding of the commuting system of Serengeti hyaenas, but most knew little about the spotted hyaena. Tour guides generally thought their clients were interested in hyaenas, but this interest was thought to vary according to client nationalities. Tourist interest in hyaenas was greatest at kills. The spotted hyaena was thought by most tour drivers to be good for the Serengeti because it was a "cleaner of the wild" and did not run from vehicles, allowing the clients to take good pictures. Most tour guides were aware of the presence of the striped hyaena in the Serengeti but none knew of the aardwolf.

The tourists that were surveyed are not representative, as they were college students from the USA who visited the Serengeti as part of a study tour. The majority of them were well informed about the behaviour and ecology of the spotted hyaena in the Serengeti ecosystem. Most knew that it is an efficient predator, but still thought that the primary role of the spotted hyaena in the Serengeti ecosystem is to be a "sanitation engineer". The most notable gap in student knowledge was information about other hyaena species. Few students knew of the existence of any hyaena species other than the spotted hyaena.

These surveys confirm that hyaenas continue to suffer from a negative public image, partially because most people are unaware of interesting aspects of hyaena ecology and behaviour. However, there are also grounds for optimism, in that appropriate education and encounters with hyaenas in the wild might improve attitudes.

Western media

Articles in the press and television films can have an enormous impact on a large number of people. Unfortunately, even recently, some wildlife film makers have presented incorrect information about hyaenas. For example, in the National Geographic television film called *Eternal Enemies*, the daughter of an alpha female spotted hyaena is depicted as leaving her clan after the death of her mother; a portrayal which contrasts with what is known about the social organisation of the spotted hyaena. There is also a tendency to become anthropomorphic. For example, in the same film, lions and spotted hyaenas are depicted as hating each other.

Other films feed on the combination of ignorance and prejudices that have dominated the views of western people about hyaenas for a long time, as recently documented by Glickman (1995). It is a pity that accurate information on hyaenas is not sought by commercial film makers such as the Walt Disney Studios. In their recent production, *The Lion King*, they have done nothing to rectify the common prejudices towards the spotted hyaena, nor, incidentally, to portray the true nature of lion society.

On the positive side, Hyaena Specialist Group members have been quite active in recent years. Hans Kruuk's (1975) book *Hyaena* and a number of popular articles in various magazines and countries have contributed to portraying a more accurate picture of hyaena behaviour.

Scientifically accurate, yet interesting films on hyaenas are also beginning to be made. An early film of this kind was made by Hugo van Lawick and Jane Goodall in the late 1960s and early 1970s. More recent films are:

1. *The sisterhood*, a film on spotted hyaenas in Botswana filmed by Richard Goss and broadcast for the first time in 1992. This film attempted to illustrate the social organisation of spotted hyaenas and emphasised the consequences of females living in a matrilineal society. An important aspect of this film was the attempt to make the viewer feel positive about hyaenas and show what interesting lives they lead.
2. *Strandwolf*, also by R. Goss, described the life and social organisation of brown hyaenas in the Namib desert, in the ruins of ghost villages, and in the vicinity of Namibian suburbia.
3. *Terminators*, a film on the aardwolf with which Philip Richardson was involved, showed the aardwolf's specialised feeding habits and cuckold monogamous mating system.
4. A recent film from the Serengeti highlighted our discovery of the commuting system of spotted hyaenas in the Serengeti. *The gentle jaws of the Serengeti* (1994) emphasised how maternal care and the social organisation of Serengeti spotted hyaenas depend on the migration of their chief prey.
5. *Tales of the Serengeti: the scavenger's tale* (1995) linked the commuting behaviour of Serengeti hyaenas and the danger posed by poaching to Serengeti wildlife.

Numerous recent films about specific ecosystems (e.g. the Serengeti, the Okavango, the Kalahari etc.) also now frequently include footage about hyaenas. Such footage is becoming more diversified in that it does not just show hyaenas feeding at a kill, but also illustrates some maternal or social behaviour. Furthermore, the commentary is increasingly phrased in a more neutral or even positive way.

10.3 A campaign to modify current attitudes

In spite of some progress, prejudices rather than knowledge about hyaenas still dominate the views of many people. Many common prejudices could be overcome if the behaviour and ecology of hyaenas was more widely appreciated. However, scientific knowledge has by and large failed to filter through to the general public. There is still a need for scientists working on hyaenas to communicate their research findings, not only in scientific journals, but also through popular articles and books, and concerted education campaigns. The media "market" for hyaenas may be smaller than that for the more "glamorous" or appealing carnivores, but the natural history of hyaenas is fascinating and should be publicised. A current problem is the reluctance of publishers to publish books on hyaenas, but the more that is published the easier it will be to continue publishing.

Wildlife articles have the disadvantage that they are primarily read by those already interested in natural history, and thus tend to preach to the converted. Information on hyaenas needs to reach a far broader audience if attitudes are to be changed.

From our experience in trying to promote a better understanding of spotted hyaenas, we have outlined below some approaches we have found useful when developing educational material. Our approach has evolved through contact with school children, college students, tour guides, and tourists to the Serengeti National Park. This approach also developed from the questionnaires we distributed amongst these groups and the feedback we received on preliminary versions of educational material. Those working in different environments, for example with farmers or hunters, may need to adopt a different approach.

Fact sheets

The questionnaires that were used in the Serengeti highlighted the fact that target groups required different kinds of information about hyaenas. To be effective, information leaflets should be tailored for specific target groups, as material designed for museums may not be appropriate for rural schools. With current computer software it is simple and inexpensive to compile information leaflets or fact sheets that can be modified and updated when required. The appeal of such leaflets is enhanced if illustrations are included, particularly when information is directed towards children. The attention of children is easily caught by cartoons and illustrations produced by other children. Information intended to be widely distributed and read must be available in appropriate local languages.

Prior to the production of educational material, research is advisable so that information is presented in an effective manner. Helpful advice may be provided by zoos and museums with active education departments. Discussions with target groups will also generate useful insights. We found the comments of teachers and students very helpful when preparing material on spotted hyaenas for educational institutions in Tanzania. Questionnaires can also be a useful tool to reveal gaps in knowledge that need to be plugged.

Displays and posters

Displays and posters are useful educational material if they are read by many people. The original hyaena specialist group poster "Why Conserve Hyaenas?" was initiated by a former Chair of the Hyaena Specialist Group, John Skinner. It generated much interest in hyaenas among school children and college students in Tanzania and South Africa, many of whom had not seen any species other than the spotted hyaena. There is an urgent need for the production of additional colourful educational posters of this kind.

Research workers should consider producing displays about their research for wildlife lodges and colleges. When producing posters it is important to make them eye-catching (e.g. use large colour photos to illustrate major points) and reduce written sections to informative, but brief statements. Few people have the patience to wade through extensive text.

Television films and videos

Because television and video films have the potential to enchant but also misinform, it is important that this form of communication be carefully developed. It would be useful for the Hyaena Specialist group to compile information leaflets on all hyaena species to guide film makers and others in the media documenting hyaenas. Furthermore, members of the Hyaena Specialist Group must be prepared to give their time and be proactive whenever the opportunity arises for them to contribute to a film in which hyaenas appear.

Chapter 11

Action Plan for Hyaenid Conservation into the 21st Century

Gus Mills and Heribert Hofer

11.1 Introduction

Table 11.1 summarises the knowledge obtained by the Hyaena Specialist Group on the conservation status of the four hyaena species during the production of this Action Plan. The data are extracted from Table 5.8. Much of this evidence is flimsy and contains subjective assessments based on incomplete data procured from countries about which we have no first hand knowledge. Notwithstanding these limitations, the data strongly suggest that of the four species, the striped hyaena is the one in most need of conservation attention. It is also the least well studied of the four species. Although extremely well studied in several areas, the spotted hyaena is also in need of conservation attention in many countries and its future mainly depends on the maintenance of large conservation areas.

In this chapter we list the projects and actions which we believe are priorities for hyaena conservation over the next ten years. In addition, we list current projects. 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 way improve the conservation status of the species involved. Given that no hyaena species is endangered, and that many of the countries inhabited by hyaenas lack scientific and conservation management infrastructure, we have attempted to identify the most needed and practical projects and actions to improve the conservation status of hyaenas, rather than present an all encompassing wish-list of projects, most of which would have little chance of being implemented.

Table 11.1. Number of countries in which each species of hyaenid is gauged to occur at different levels of conservation status.

Conservation status	Aardwolf	Striped hyaena	Brown hyaena	Spotted hyaena
Extinct	0	0	0	2
Probably Extinct	0	3	0	0
Threatened	0	16	0	9
Data Deficient (-)	0	10	2	10
Lower Risk	5	2	3	8
Data Deficient (+)	2	5	1	6
Data Deficient (0)	9	7	1	5
No Record (+)	2	5	1	2
No Record (-)	0	8	1	2
Total	**18**	**56**	**9**	**44**

11.2 Projects and actions involving all species

Database

1 (Project). Establish and maintain a database on the conservation status and state of knowledge of the four hyaena species.

Objectives: To assist implementation of the Hyaena Action Plan by establishing a base from which the Hyaena Specialist Group can collect and distribute conservation related information on hyaenas. This information will be given to potential donors and project executants to improve communication between them, as well as educators and others working towards raising public awareness of the position regarding hyaena conservation.

Implementation details: The centre will serve as a coordinating and information dissemination office. Priority for information will be given to those directly involved with Hyaena Action Plan projects.

Status surveys

2 (Project). Design a data sheet for basic surveys of hyaenids and distribute it as widely as possible to improve knowledge on the distribution and conservation status of each species.

Objective: To improve knowledge on the distribution and status of hyaenas particularly in those countries where the current status is **No Record (+) or Data Deficient** (Table 5.8). Establishing the presence or absence of hyaenids in large (>100 km^2) protected areas with suitable habitat is a priority.

Implementation details: The fact sheet must be simple and easy to use. It should be distributed to people who conduct surveys in areas within the range of one of the four species for other purposes, but who may have an opportunity to record hyaenid presence. It should also be provided to people living in or having experience with a range country or region. In an attempt to ensure that all relevant parties are aware of this project, the chairs of other specialist groups (particularly those responsible for other large African and Asian carnivore groups), the regional IUCN offices in range states, and the office of the Species Survival Commission in Gland, Switzerland, will be provided with data sheets and lists of relevant countries and species and asked to cooperate. The data will be stored in the central database.

3 (Action). Encourage and provide assistance to wildlife researchers and managers to collect data on the population status of hyaenids in all range states, particularly those in which the status of a species is Threatened or Data Deficient (see Table 5.8).

Justification: This will provide the means to make first approximation population estimates from relatively inexpensive and short-term surveys and provide much needed information on the conservation status of hyaenids in several areas.

Education and public relations

4 (Action). Produce a Hyaena Specialist Group Newsletter at least once every two years.

Justification: It is important to keep members of the specialist group and other interested parties abreast of the activities and developments in hyaena conservation. The newsletter will be produced and distributed from the office of the Chair of the Hyaena Specialist Group.

5 (Action). Initiate a campaign through IUCN and other NGOs to establish a policy of limiting or reducing damage to livestock by wild carnivores, by concentrating efforts on improving livestock protection rather than implementing control of predators.

Justification: Many methods are available for reducing predator damage on livestock other than always killing the predators. These need to be tested and tried in different situations. The effective ones need to be promoted and people need to be educated in how to apply them.

6 (Action). Reprint and update the colour poster "Why conserve hyaenas?". Investigate the possibility of translating it into other major range state languages and prioritise these. Circulate it as widely as possible.

Justification: This poster has had widespread appeal and interest and should be distributed far more widely.

7 (Project). Investigate methods for initiating effective education campaigns directed at local people to explain:

1. The ecological role of scavengers in key areas, particularly in the striped hyaena's distribution range.
2. Ways of lessening pastoralist/predator conflicts.
3. Ways to prevent possible attacks of hyaenas on people, including injuries, killings and child snatching.

Objectives: To be able to plan and implement effective campaigns to improve public knowledge and to increase the profile of hyaenas in key areas of their distribution range. This can potentially lead to more sympathetic and objective attitudes towards them by local communities and to the implementation of more enlightened management strategies.

Implementation details: Literature review, questionnaire surveys, interviews. The project must make recommendations and propose strategies for effective education campaigns.

8 (Project). Review the relationship between rural people and hyaenas.

Objectives: To document the role that hyaenas play in the daily lives, traditional medicine and folklore of the people in their distribution range and the importance, cultural significance and attitude of people towards hyaenas. To evaluate the impact of this on hyaena populations.

Implementation details: Extensive literature review, questionnaire surveys, if possible visits to some important areas for first-hand information.

9 (Action). Initiate and support efforts to improve public perceptions of hyaenas.

Justification: The popular image of hyaenas is still largely negative in most societies. The Hyaena Specialist Group must look for opportunities and encourage others to portray an objective and positive image for all four species and to correct negative misconceptions whenever possible. By gaining sympathy and respect the status of hyaenas will improve. This will be reflected in the willingness of people to make contributions to hyaena conservation.

10 (Action). Promote hyaenas as tourist attractions, particularly where this might generate revenue for local communities. To this end investigate the setting up of feeding sites (hyaena restaurants), particularly in urban or semi-urban areas, and encourage people to visit these in order to view hyaenas.

Justification: To increase the value of hyaenas to people so that they may become better disposed towards conserving hyaenas and thereby also improving their own quality of life.

11 (Project). Identify and assess the effects of incentives on hyaena conservation.

Objective: To investigate the role of incentives in shaping the attitudes and behaviours of parties affecting hyaena conservation. Such parties could include policy-makers, park officials, wildlife managers, livestock owners, etc. Incentives could be economic, political, institutional, and cultural. To assess how the removal or addition of incentives could potentially reduce conflicts between humans and hyaenas, which could then facilitate the implementation of conservation measures.

Implementation details: Incentives could be identified and assessed through literature reviews, questionnaire surveys and interviews. Case studies in which incentive measures have effectively promoted hyaena conservation could be collected and analysed. The project should make recommendations on how incentives can further the conservation of the four hyaena species.

11.3 Species projects and actions

Striped hyaena

12 (Action). Change the IUCN global status of the striped hyaena from Lower Risk: Least Concern to Lower Risk: Near Threatened.

Justification: At present, the striped hyaena does not quite fulfil the criteria set for Vulnerable. The upper estimate of global population size exceeds 10,000 individuals. Fragmentation of the world population into many subpopulations is suspected, but the degree of fragmentation is unknown, as are the magnitude and effect of habitat loss and population decline. The following suggest that a classification of Lower Risk: least concern is inappropriate: the undoubted occurrence of habitat loss; systematic and incidental persecution and high susceptibility to persecution directed at similar species; and a minimum population estimate of less than 10,000 individuals.

13 (Project). Assess the potential viability of striped hyaena populations in countries where the species is classified as Threatened and Data Deficient (-).

Countries in which the striped hyaena is classified as Threatened and Data Deficient (-).

Afghanistan, Algeria, Armenia, Azerbaidjan, Cameroon, Chad, Georgia, Iraq, Israel, Jordan, Lebanon, Mali, Mauretania, Morocco, Morocco-Western Sahara, Niger, Nigeria, Oman, Saudi Arabia, Senegal, Syria, Tadzhikistan, Tunisia, Turkey, Turkmenistan, Uzbekistan.

Objective: Identify factors that led to the current status and suggest possibilities of reversing the current trend. Recommend conservation actions that, if implemented, would help to secure the viability of a population.

Implementation details: Assess population size, limiting factors and threats for all major subpopulations in the country. If possible this project should be conducted in collaboration with project 15.

14 (Action). Campaign for increased protection of the striped hyaena throughout its range. Wanton killing of this species should be banned in all countries where it occurs.

Justification: Wanton and needless killing of the striped hyaena is a major cause of declining numbers over most of its range. Exceptions may be considered in cases of proven livestock damage or attacks on humans.

15 (Project). Review the classification of the subspecies of the striped hyaena and the distribution and status of each.

Objectives: To clarify the subspecies of striped hyaena, their status and distribution in order to identify conservation priorities for each subspecies.

Implementation Details: Molecular techniques should be used and material collected from museums, zoos and other sources from as many localities as needed. Questionnaire surveys and data from the central database will be used to document distribution and conservation status. Conservation priorities for the subspecies will be drawn up. If possible this project should be conducted in collaboration with project 13.

16 (Project). Document basic aspects of the population dynamics of the striped hyaena.

Objectives: To obtain data on litter size, cub mortality, recruitment, and adult mortality as a basis for a future Population and Habitat Viability Assessment.

Implementation Details: A suitable study site or sites must be identified for this and the next two projects. These three projects may be combined in order to produce a definitive study on this species in a major habitat. Radio telemetry will be the basic technique utilised.

17 (Project). Investigate the diet and foraging behaviour of the striped hyaena.

Objectives: A detailed assessment of foraging and diet of the striped hyaena, in particular the ratio of killed to scavenged items, and the importance of human-originated carrion in its diet.

Implementation Details: See project 16.

18 (Project). Conduct a behavioural and ecological study of the striped hyaena.

Objectives: A definitive study on the social organisation, home range size, movements, and life history.

Implementation Details: See project 16.

Brown hyaena

19 (Action). The global status of the brown hyaena should be changed from Lower Risk: least concern to Lower Risk: near threatened.

Justification: At present the brown hyaena does not quite fulfil the criteria set for Vulnerable. The global population has not declined by 10% over the past three generations nor is it expected to do so in the next three generations. Its range well exceeds 20,000km^2, but the global population size is estimated to be below 10,000 individuals. Because of the small global population size, incidental persecution, and susceptibility to persecution targeted at other species it is inappropriate to classify it as Lower Risk: least concern.

20 (Project). Survey the status and distribution of the brown hyaena in the urban areas of Gauteng Province in South Africa.

Objective: To establish the presence of the brown hyaena in an urban habitat, as there is evidence of their presence around the city of Johannesburg. To assess the viability of the population and the risks it faces, and to search for ways the brown hyaena can coexist with humans in urban areas.

Implementation details: Survey for tracks and other indirect field signs in likely areas and follow up positive clues with direct observations.

Spotted hyaena

21 (Action). The global status of the spotted hyaena should be changed from Lower Risk: least concern to Lower Risk: conservation dependent.

Justification: At present the spotted hyaena does not fulfil the criteria for Vulnerable. The total world population size is well above 10,000 individuals, several subpopulations exceed 1000 individuals, and its range well exceeds 20,000km^2. However, the rapid decline of populations outside conservation areas due to systematic or incidental persecution and habitat loss makes the species increasingly dependent on the continued existence of protected areas. Without such areas, the conservation status of the spotted hyaena may become Vulnerable.

22 (Project). Assess the potential viability of spotted hyaena populations in countries where the species is Threatened and Data Deficient (-).

Countries in which the spotted hyaena is classified as Threatened and Data Deficient (-).

Angola, Benin, Burkina Faso, Burundi, Cameroon, Congo, Cote d'Ivoire, Democratic Republic of Congo, Equatorial Guinea, Guinea, Malawi, Mali, Mauretania, Niger, Nigeria, Rwanda, Sierra Leone, Swaziland, Togo.

Objective: Identify factors that led to the current status and suggest possibilities of reversing the current trend. Recommend conservation actions that, if implemented, would help to secure the viability of a population.

Implementation details: Assess population size, limiting factors and threats for all major subpopulations in the country.

11.4 Currently running projects

A number of hyaena projects are currently taking place. Even though not all of them are seen as priorities for the conservation of the species by the Hyaena Specialist Group, they are supported by the group because they provide important and interesting information about hyaenas. Those projects marked with an asterisk are considered to be ones that can improve the conservation status of the species and should be given priority. Chapter 3 provides additional descriptions of completed and planned projects for each species.

Striped hyaena

23* (Project). Assessment of the status of the striped hyaena in Georgia and bordering territories and a program for its recovery.

Objective: To set up a recovery program for the striped hyaena, including the establishment of protected areas to safeguard key populations and the reintroduction of individuals if necessary.

Implementation details: Data are being collected on population size and distribution. A detailed study will investigate habitat use, diet and factors affecting population dynamics, including competition with other carnivores, and habitat destruction and other forms of human impact.

Contact: J. Badridze, Noah's Ark Center for the Recovery of Endangered Species, Georgia.

Brown hyaena

24 (Project). Foraging behaviour of brown hyaenas at seal colonies on the Namibian Coast.

Objective: To assess the foraging behaviour and impact of brown hyaenas on seal pups along the Namibian Coast.

Implementation Details: Observations of brown hyaenas foraging at seal colonies at the Namibian Coast, commencing in the second half of 1997.

Contact: Ingrid Wiesel, Department of Zoology, University of Hamburg, Hamburg, Germany.

Spotted hyaena

25* (Project). Behavioural ecology and population dynamics of spotted hyaenas in the Serengeti, Tanzania.

Objectives: To assess social and reproductive behaviour in relation to the ecological framework, the life history and demography of individually known animals, the influence of social status on reproductive success, and the flexibility of maternal behaviour and care on aspects such as cub growth and offspring sex ratios. To identify factors regulating group size, population size and population dynamics. To describe pathogen occurrence and prevalence, and the impact of poaching and other sources of human disturbance on population persistence and demography.

Implementation details: Long-term study with detailed records of the history of individually known members of several clans in two study areas in the Serengeti National Park.

Contact: Marion East and Heribert Hofer, Institute of Zoo Biology and Wildlife Research, D-10315 Berlin, Germany, and Max-Planck-Institute of Behavioural Physiology, D-82319 Seewiesen, Germany.

26* (Project). Behavioural ecology of spotted hyaenas in the Ngorongoro Crater, Tanzania.

Objectives: To assess current population size, number of clans, and clan demography of spotted hyaenas in the Crater. To assess the impact of substantial changes in population size of major prey species on spotted hyaena foraging and demography; a topic previously addressed in Kruuk's studies in the 1960s. To assess the importance of competition and interference by other carnivores, principally lions and jackals. To understand what factors are currently influencing demographic factors such as cub survival, recruitment, adult survival, and birth intervals. To assess the importance of sibling competition and lion predation on cub mortality.

Implementation details: Details of clan size, structure, composition, territory size, and demography are being established by identifying all individuals resident in the Ngorongoro Crater and plotting their movements. Observations at communal dens, hunts and kills will provide data on cub survival, maternal care, prey preferences, and interactions with other carnivores.

Contact: Oliver Höner and Bettina Wachter, Max-Planck-Institute of Behavioral Physiology, D-82319 Seewiesen, Germany.

27* (Project). Long-term ecological monitoring of a hyaena clan in the Masai Mara National Reserve, Kenya.

Objectives: To evaluate long-term patterns of hyaena feeding, space use, dispersal, and reproduction in a clan that has been closely and continuously monitored for several years.

Implementation details: In addition to maintaining accurate long-term records of demography, immigration, and several different reproductive parameters, ecological variables within the study clan's home range are being monitored in order to study interactions between variables in each of these sets. Ecological variables being monitored include rainfall, prey abundance and density, and distribution of other large carnivores within the study area. These data are entered into a GIS database at Michigan State University, where analysis of them is in progress.

Contact: Kay E. Holekamp and Laura Smale, Departments of Zoology and Psychology, Michigan State University, East Lansing, MI 48824, U.S.A.

28 (Project). Behavioral endocrinology of free-living spotted hyaenas.

Objectives: To elucidate hormone-behaviour relationships in free-living hyaenas of known age, social rank and dispersal status.

Implementation details: Subject animals are members of one large hyaena clan in the Masai Mara National Reserve, Kenya. Age, sex, kin relations, and social status are known for all natal animals, and most adult clan members wear radio collars so they can be regularly relocated and observed. All members of this study population are regularly immobilised to draw blood for hormone analysis. In addition, GnRH challenge experiments on selected adults are performed in an attempt to determine how rank effects on reproductive success are mediated physiologically.

Contact: Kay E. Holekamp and Laura Smale, Departments of Zoology and Psychology, Michigan State University, East Lansing, MI 48824, U.S.A.

29 (Project). Behavioural development in the spotted hyaena.

Objectives: To document behavioral changes during ontogeny, to determine when sex differences in behaviour appear, and to evaluate the adaptive significance of behaviours expressed first or uniquely at particular stages in the animal's lifespan.

Implementation details: Subject animals are members of the same clan as in projects 27 and 28. Focal animal data are collected from individual males and females at selected time points throughout ontogenetic development, while concurrently monitoring rank relationships and demography in the clan. These data are entered into a database at Michigan State University, where analyses are currently in progress of behaviour changes observed in all cubs born into the clan since June 1988.

Contact: Kay E. Holekamp and Laura Smale, Departments of Zoology and Psychology, Michigan State University, East Lansing, MI 48824, U.S.A.

30 (Project). The evolution of intelligence in response to social complexity.

Objectives: To examine predictions of a hypothesis suggesting that the evolution of intelligence in mammals has been driven by selection pressures associated with life in a complex social environment; using the spotted hyaena as a model in comparison with social primates.

Implementation details: Subject animals are members of the same clan as in projects 27 29. Using videotaped responses of subjects to playbacks of recorded vocalisations, it will be determined whether hyaenas, like monkeys, can discriminate among conspecific vocalisations based on group membership, kinship, and association patterns. This research will generate two types of useful information: it will (1) elucidate the functions of animal intelligence in the natural habitat, as well as the selection pressures favouring its evolution, and (2) enhance understanding of carnivore social behaviour to facilitate decision-making by wildlife managers and others concerned with biodiversity and conservation of African ecosystems.

Contact: Kay E. Holekamp and Laura Smale, Departments of Zoology and Psychology, Michigan State University, East Lansing, MI 48824, U.S.A.

31 (Project). A multidisciplinary investigation of the proximate mechanisms of female masculinization in the spotted hyaena.

Objectives: The unique biology of this species makes it an interesting model for the study of basic processes of sexual differentiation. Earlier work has described the hormonal and enzymatic processes by which pregnant females produce high levels of androgens. On-going research concentrates on the relative importance of both hormonal and non-hormonal mechanisms of female masculinization and aggressiveness.

Implementation: A breeding colony of 35–40 spotted hyaenas has been set up near the Berkeley campus. Animals are held in large indoor-outdoor enclosures, some of which are fitted with closed circuit video cameras for behavioural observations. Some of the endocrinological research is done by collaborators at other universities. The colony is available to other researchers interested in non-invasive behavioural research.

Contact: Steve Glickman, Department of Psychology, University of California, Berkeley, CA 94720, U.S.A.

32 (Project). The behavioural ecology of the spotted hyaena in a high density population in S.W. Kenya.

Objectives: This project is in its 19th year and seventh generation of spotted hyaenas. It is aligned with projects 27, 28 and 29 and involves the same clan. Long-term data on individual and matrilineal reproductive success have contributed to our understanding of the evolutionary basis of female aggression and masculinization, maternal behaviour, and sibling relations, with an emphasis on the intense sibling aggression that commences at birth.

Implementation: The study clan comprises about 23 adult females, up to 20 adult males, and 30 40 cubs and subadults. Full genealogical information and social history are available for all natal animals born since 1978.

Contact: Laurence Frank, Department of Psychology, University of California, Berkeley, CA 94720, U.S.A.

33* (Project). The Laikipia Large Carnivore Study

Objectives: To collect data for carnivore conservation and management on carnivore-prey interactions on a 400,000 ha privately owned ranch in semi-arid bush country in Kenya. The primary emphasis of the ranch is livestock production, but it has a full complement of wildlife, including all the large carnivores. Local landowners are interested in conserving wildlife, for both economic and aesthetic reasons.

Implementation: A survey of landowners in the district has been completed to synthesise local information on carnivore distribution and abundance, livestock depredation rates and circumstances, livestock husbandry techniques, and the economic impact of large carnivores on the livestock industry. A large scale study of lion and spotted hyaena ecology is planned. All of this information will be incorporated into a long-term management plan.

Contact: Laurence Frank, Department of Psychology, University of California, Berkeley, CA 94720, U.S.A.

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Population and Habitat Viability Analysis for Hyaenas

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Many human activities have altered the natural environment of hyaenas by reducing prey populations and fragmenting or even destroying suitable habitat. The net result of such changes are a reduction in the carrying capacity of a habitat and the isolation of adjacent populations from each other. The chapters on distribution and status indicated that persecution and habitat destruction and fragmentation are important factors contributing to the worldwide decline of all hyaena species. It would therefore be useful to know what happens to a hyaena population when the environment is modified by human actions.

Population and Habitat Viability Analysis (PVHA) is a tool to develop scientifically-based management strategies for small, threatened populations or species (Ellis and Seal 1995). It aims to assess the impact of human-made factors on the viability of populations by simulating their effects in a computer program. This requires the construction of several impact scenarios (habitat change, poisoning, etc.) using appropriate demographic parameters. This means that hypotheses are constructed on how anthropogenic changes affect hyaena population dynamics.

The use of a computer program has a number of advantages: population viability can be predicted for a long time (hundreds of years if required); many scenarios can be explored in which each factor is assumed to operate in isolation or simultaneously with other factors; and results can be obtained quickly. The weakness of a computer program is that the quality of the conclusions that can be drawn from the results ultimately depends on the quality of the data used to run the program. However, as these data come from field observations, computer simulations and field-based observations complement each other in assessing population persistence.

Here we present preliminary results of a joint study that assessed the impact of a variety of human actions on hyaena populations using simulations of population persistence. It was important that the population simulations closely reflected the demographic characteristics and circumstances of actual populations. We therefore chose to investigate the impact of selected human actions on a small aardwolf population with the characteristics of the population studied by P.R.K. Richardson in South Africa, and on low density brown hyaena and spotted hyaena populations resembling those studied by M.G.L. Mills in the southern Kalahari. Although it would be highly valuable to also conduct a PVHA for a striped hyaena population, we considered that the currently available demographic data are insufficient for a PVHA of this species.

A1.1 Factors that may influence hyaena population persistence

Apart from the negative impacts of a reduction in prey populations and habitat fragmentation or destruction, hyaena populations may also be indirectly affected by specific human actions directed at potential prey species, or general anthropogenic changes such as climatic change (global warming). Ultimately, many human-made changes may be usefully expressed as a net change in the carrying capacity of a habitat. We therefore asked how the viability of populations changed if carrying capacity was reduced temporarily (scenario 1: aardwolf) or over longer periods (scenario 1: brown hyaena and spotted hyaena).

A second issue is the increasing isolation of adjacent hyaena populations through fencing, habitat fragmentation or destruction of habitat corridors. We investigated how persistence of populations changed if they were completely isolated (scenario 2).

A third issue is the effect that the persecution of potential prey species may have on the persistence of hyaena populations. We investigated one such scenario where we considered the effect of locust spraying on population persistence in the aardwolf (scenario 3).

A1.1.1 Scenario 1: Reduction in carrying capacity of a habitat

There are many types of systematic environmental degradation. Long-term declines in prey populations due to human intervention can be modelled by reducing the carrying capacity K of the habitat by a certain percentage each year. Small, persistent changes in K may be difficult to measure, yet they could have profound consequences for a population. For instance, a reduction in K by 1% per year over a period of 100 years means that from a value of 700 hyaenas in year one, K would be reduced to 259 individuals by the year 100. If the annual reduction in K was 5% instead of 1%, then the habitat is supposed to sustain only four individuals in year 100! Long-term changes in prey populations and other habitat modifications may be important for the brown and spotted hyaena, and thus populations of these two species were subjected to a variety of reductions in K. In the case of aardwolf populations, changing carrying capacity is more likely to be of an episodic nature and thus we used a different way to explore the effects of such changes (see scenario 3).

It is currently unclear how climate change may modify temperature or rainfall and hence affect prey numbers over the present range of hyaena populations. It could, for instance, imply moderate drought conditions or an increase in the chance of having a severe drought. The consequences of such conditions could be complex and are discussed separately for the aardwolf and the two large hyaena species.

A deterioration in conditions due to drought frequently results in increased food availability for brown and spotted hyaenas, as herbivores weaken and become more vulnerable. Only when a drought reaches very severe proportions will food availability be affected. As ecological conditions improve through increased rainfall, food availability for carnivores might decrease. However, should wet conditions prevail for an extended period this may lead to a build up in large herbivore numbers, which in the Kalahari situation may work in favour of the spotted hyaena. Should the spotted hyaena increase this may have a detrimental effect on the brown hyaena population. Moderate changes in rainfall were therefore simulated as moderate annual environmental variation that may randomly change key demographic parameters. Demographic parameters such as reproductive success and mortality may change in either a positive or detrimental manner within moderate limits (section A1.2). Severe changes in rainfall were considered to effectively decrease K and were included in simulations where K was changed.

Most aardwolves live between the 200–600mm isohyets in dry open grasslands, areas frequently used for cattle and sheep farming. Moderate decreases in rainfall are likely to change stocking from cattle to sheep, but are unlikely to decrease the size of farms. Farms with sheep are likely to increase jackal-proof fencing (which is also aardwolf-proof), but are unlikely to take direct actions against aardwolves. Moderate changes in rainfall were incorporated in the simulations by letting environmental variation change key demographic parameters. Demographic parameters such as reproductive success and mortality may change in a positive or detrimental manner within moderate limits, in a manner similar to the brown and spotted hyaena populations. A serious drought is likely to affect cub survival because adults are unlikely to find sufficient food (P.R.K. Richardson, unpublished data). We simulated such events as "catastrophes." Details about implementing "catastrophes" in the simulations are explained in section A1.2.

Other demographic parameters were held constant when K was reduced. The effects of a change in K on the outcome of the simulations are therefore minimum effects. If changes in K also decreased reproductive success, increased cub mortality, or had a detrimental effect on other demographic parameters, the effects would be even more pronounced.

A1.1.2 Scenario 2: Isolating populations

Habitat fragmentation and actions such as fencing may reduce the frequency of exchange of individuals between adjacent populations. In the southern Kalahari a proposal to fence off the Nossob River between South Africa and Botswana would have effectively isolated the populations of both brown and spotted hyaenas on both sides of the river bed and decreased food availability. Because fencing has been repeatedly advocated as a means of containing conflict between carnivore populations in protected areas and livestock holders in adjacent agricultural land, it seemed instructive to explore the effect of isolating populations for these two species.

A1.1.3 Scenario 3: Persecution of prey populations

If potential prey species are agricultural pests, as in the case of locusts and the aardwolf, persecution of prey species by poisoning or large-scale spraying may have detrimental effects on the persistence of aardwolf populations. From unpublished data by P.R.K. Richardson there is some information on the effect of spraying operations on aardwolf populations. It is possible that the frequency of locust plagues in southern Africa is increasing and that spraying operations will continue at increased frequencies. Locust spraying was therefore incorporated into simulations as a type of "catastrophe", and the effect of spraying intervals on persistence of the aardwolf population was explored.

A1.2 Running the PVHA program

Population viability was projected for 100 years for an aardwolf population in South Africa and for brown and spotted hyaena populations in the southern Kalahari. The data that formed the basis for the simulations were collected by P.R.K. Richardson (unpublished data), Mills (1990) and M.G.L. Mills (unpublished data). Sex ratio at birth was assumed to be equal. Females of all three species were assumed to start breeding at the age of three years. Male aardwolves were assumed to start breeding at the age of three, and male brown and spotted hyaenas at the age of four. Aardwolves were assumed to reach a maximum age of ten, whereas brown and spotted hyaenas were assumed to reach a maximum age of sixteen. Age distributions were taken from empirical data and roughly approximated theoretical stable age distributions. Other quantitative parameters used in the model are listed in Table A1.1.

In all scenarios population viability could be influenced by:

1. Normal, unpredictable environmental variation.
2. Severe events of environmental decline called "catastrophes".
3. Variable reproductive schedules and patterns of immigration (supplementation) from neighbouring populations.

Demographic parameters (litter production, mortality, carrying capacity) could fluctuate randomly due to environmental variation. Environmental variation was any kind of change in the environment which is external to the population and systematically applied to all individuals in that year. The strength of these changes was set to vary randomly from year to year within certain limits determined by the user of the program before the simulation started. Estimates of the effect of environmental variation on mortality were derived from empirical values of the coefficient of variation for age-specific mortalities. These were similar for both males and females in the aardwolf, but twice as high for males compared to the value for female brown and spotted hyaenas. The values did not exceed 20% of average values in the aardwolf and 25% of average values in the brown and spotted hyaenas. There were no data on possible changes in K due to environmental variation, so this was arbitrarily set to 10% in all cases.

It is possible that environmental variation may have effects on reproduction that are correlated with effects on survival. For example, a decline in food availability might decrease both adult survival and the probability of breeding. We assumed, however, that adult hyaenas of any species can usually survive difficult food conditions but may be prevented from breeding, and thus assumed that effects on reproduction were uncorrelated with effects on survival. If there was a

Table A1.1. Parameters for models of aardwolf, brown hyaena and spotted hyaena populations. Entries in bold and with an arrow (→) were varied between simulations to assess the effect of this parameter on population viability.

Parameter	Aardwolf	Brown hyaena	Spotted hyaena
Population	South Africa	Southern Kalahari	Southern Kalahari
Initial population size	25	698	132
Carrying capacity K	30	700	120
% annual change (trend) in K?	No	reduction → **0–5%**	reduction → **0–5%**
Number of years for trend to persist?	-	→ **10–100**	→ **10–100**
Population supplemented from outside?	Yes	→ **Yes or No**	→ **Yes or No**
Types of catastrophes	1:poisoning; 2:drought	none	1: rabies
Expected interval catastrophe 1	every → **8–20 years**	-	every 10 years
Effect on reproduction	unaffected	-	unaffected
Effect on survival	reduced by 36%	-	reduced by 10%
Expected interval catastrophe 2	every → **3–10 years**	-	-
Effect on reproduction	reduced by 39.8%	-	-
Effect on survival	unaffected	-	-
% males in breeding pool	→ **60–90**	15	7.5
Maximum litter size	4	4	2
% females not breeding (litter size 0)	→ **10–40**	42	28.1
% litter size of 1	→ **6–4**	6.44	30.8
% litter size of 2	→ **24–16**	12.89	41.1
% litter size of 3	→ **39–26**	32.22	-
% litter size of 4	→ **21–14**	6.44	-
% annual mortality at age 0-1	25.6	16	21.40
% annual mortality at age 1-2	→ **69.2–54.7**	23.75	7.75
% annual female mortality at age 2-3	→ **44.3–49.6**	27	8.25
% annual male mortality at age 2-3	→ **44.3–49.6**	27	8
% annual male mortality at age 3-4	-	21.5	12.85
% annual adult female mortality	16	16	13.3
% annual adult male mortality	16	16	12.85

correlation between the effects of environmental variation on reproduction and those on survival, then population persistence is likely to be reduced further than the results described. However, an extreme decline in environmental quality, for instance a severe drought, can be more usefully modelled as a "catastrophe". A catastrophe is an extreme form of environmental variation that is assumed to persist for one year and may occur in addition to the "standard" form of environmental variation. "Catastrophes" reduce either survival and/or reproduction by a specified factor for one year. In hyaena populations, known "catastrophes" are events such as poisoning of food species (locust spraying), droughts (aardwolf), and rabies epidemics (spotted hyaena). In the case of the aardwolf, both locust spraying and droughts were allowed to occur independently of each other.

The effects of a reduction in K were modelled in several ways. The importance of the duration of a reduction in K was explored by letting K be reduced by 1% per year over periods of 10, 20, 50 and 100 years. The impact of the strength of the reduction was assessed by setting reductions of K to 1% and 5% annually over a period of 10 years, and to 0.2%, 0.5%, 1% and 2% over a period of 100 years.

There were no data available on the strength of density dependence on breeding success. Rather than using hypothetical values, breeding was assumed to be density independent. This has the advantage that population viability projections are more conservative (more likely to predict population extinction) because density dependence tends to improve population persistence (Ginzburg *et al.* 1990). Possible demographic effects due to the loss of genetic diversity (inbreeding) were not included in the model. Inbreeding is currently considered not an important problem with the aardwolf, brown hyaena, or spotted hyaena because the mating systems of all three species are polygynous, and many populations are still not isolated.

Supplementation describes all processes that introduce animals to the study area, such as immigration from adjacent populations or translocations which may increase in occurrence in the future. In the simulations, supplementation occurred at a low level (one one-year old male and female, one two-year old male and female aardwolf each year; two two-year old male and two two-year old female brown hyaenas each year; one three-year old female and two three-year old male spotted hyaenas every three years). The effect of supplementation, or alternatively, the effect of isolation (lack of supplementation) on population persistence was assessed for the brown and the spotted hyaenas simultaneously with a changing K. Thus, simulations were conducted such that populations experienced a reduction in K as specified above, and were either not supplemented with individuals or were supplemented in the manner detailed above. This also permitted an assessment of the simultaneous effects of decreasing K and isolating populations.

Supplementation was assumed to be an essential feature of aardwolf populations (see below), so changes were modelled in a different way. In the aardwolf, both male and female adolescents disperse and become floaters until they either find an empty territory or die. The proportion of floaters is unknown, but it influences mortality estimates of one-year old and two-year old individuals and the degree to which adjacent populations are supplemented. We considered the effect of varying the proportion of floaters in the adult population by varying the percentage of non-breeding individuals between 10% and 40% and the associated mortality estimates for one-year old and two-year old individuals (Table A1.1).

Harvesting describes all processes that kill animals on top of natural mortality, such as losses incurred because individuals left the study area and were killed by people. In the model it was assumed that if such processes occurred, then their effects are already included in standard mortality estimates because it is usually very difficult to ascertain the precise cause of death.

Population viability projections were calculated for 100 years by simulations using the program VORTEX (Release 5.1, Lacy 1992), a widely used simulation program for Population and Habitat Viability Analyses (Ellis and Seal 1995). The program simulates the fate of small populations by incorporating random (unpredictable) changes in mortality, reproductive success and other demographic parameters. Because of this random component it is important to re-run the program with identical parameter settings many times in order to get an idea of what the typical behaviour of a population would be with these conditions. Each simulation used 1000 repeats (runs), which is a number considered to be more than sufficient to produce stable results (Harris *et al.* 1987).

A1.3 Results

Smaller populations are more likely to go extinct than larger populations (Soulé 1987). When considering the results below one should therefore bear in mind that initial population sizes were very different for the three species (25 for the aardwolf, 132 for the spotted hyaena, and 698 for the brown hyaena), and thus results should not be compared between species.

Results of each simulation run for the three populations of aardwolf, brown hyaena and spotted hyaena were first considered for the most benign situation; i.e. a population that experienced no reduction in K and that was supplemented with individuals from adjacent populations. The first question was whether populations will always persist or whether there was a chance that they could go extinct. The chance of population extinction after 100 years varied between 0.2% and 0.5% for the aardwolf (Table A1.2), and was 0% for the brown and spotted hyaena. Thus, under these conditions both brown and spotted hyaena populations would be likely to persist for at least another 100 years, whereas the aardwolf population would have a small chance of going extinct.

Populations that were supplemented with individuals from adjacent populations might go extinct within the 100 year period but might be re-established by individuals immigrating from adjacent populations. Thus, it is also of interest to ask what is the chance of a population going extinct at least once even if it was re-established later on, and how many years would pass before the first extinction. The chance of going extinct varied for the aardwolf between 26.3% and 31.1% (Table A1.2), and was 0% for the brown hyaena and 14.9% for the spotted hyaena. Time to first extinction varied for the aardwolf between 43.4 and 52.3 years (Table A1.2), and was 48.7 years for the spotted hyaena. Less than 5% of both aardwolf (Table A1.2) and spotted hyaena (4.7%) populations went extinct a second time after a shorter period, between 27.0 and 42.7 years in the aardwolf, and 10.2 years in the spotted hyaena. Final population size after 100 years was lower than the initial population size in all simulations; for the aardwolf this was between 16 and 17 individuals (Table A1.2), in the brown hyaena 668 individuals, and in the spotted hyaena 100 individuals. Final population size as a percentage of initial carrying capacity turned out to be always lower for the spotted hyaena than for the brown hyaena (Fig. A1.4). This may have been a consequence of differences in initial population size, or of demographic differences between species.

Because the proportion of floaters in the aardwolf population is unknown but might affect vital demographic parameters, several simulations were run in which the proportion of floaters (and the associated mortalities for adolescents) was varied between 10% and 40%. The results (top third of Table A1.2) indicated little change in parameters that characterise population persistence. Thus, although the precise value of the proportion of floaters is unknown, the value chosen was unlikely to influence the outcome of those simulations where incidences of droughts or locust spraying were varied (see below).

A1.3.1 Scenario 1: Reducing the carrying capacity of the habitat

How did a reduction in K affect the probability of final population extinction p_E after 100 years? We first considered populations where immigration from adjacent populations was possible. If the period over which K was reduced was fixed at 100 years and the annual reduction of K was between 0.2% and 0.5%, then p_E remained 0 (no population extinction) for both brown and spotted hyaenas. It increased to p_E=0.326 for the brown hyaena and p_E=0.544 for the spotted hyaena at an annual reduction of K of 1%, and to p_E=1 (certain

Table A1.2. The fate of a small aardwolf population of initially 25 individuals in a habitat with a carrying capacity of 30 individuals over a period of 100 years if subjected to different intervals of droughts and locust spraying (*out of 1000 populations per simulation).

% floaters	average interval between locust sprayings (yrs)	average interval between droughts (yrs)	probability of population extinction ± SE	% of populations going extinct at least once*	time to first extinction (yrs)	% of populations going extinct again*	time to re-extinction (yrs)	final population size	population growth rate
10	12	4	0.003±0.002	27.9	47.0±1.7	4.3	37.3±4.0	16.9±0.2	0.070
20	12	4	0.005±0.002	29.2	49.8±1.7	4.7	30.4±3.6	16.8±0.2	0.064
30	12	4	0.002±0.001	31.1	47.5±1.6	4.6	28.6±3.4	16.5±0.2	0.059
40	12	4	0.002±0.001	26.7	49.0±1.8	3.7	31.5±3.4	16.6±0.2	0.057
20	12	3	0.003±0.002	28.8	46.1±1.7	4.2	31.2±3.3	16.3±0.2	0.062
20	12	4	0.005±0.002	29.2	49.8±1.7	4.7	30.4±3.6	16.8±0.2	0.064
20	12	6	0.004±0.002	27.2	43.4±1.8	4.5	31.7±3.0	17.0±0.2	0.067
20	12	8	0.003±0.002	27.6	49.1±1.8	4.9	33.2±3.4	17.3±0.2	0.068
20	12	10	0.005±0.002	30.8	44.9±1.6	4.1	34.9±3.5	17.0±0.2	0.069
20	8	4	0.004±0.002	27.0	48.3±1.7	3.5	34.4±3.8	16.2±0.2	0.057
20	12	4	0.005±0.002	29.2	49.8±1.7	4.7	30.4±3.6	16.8±0.2	0.064
20	16	4	0.004±0.002	26.9	52.3±1.8	4.0	27.0±2.9	17.3±0.2	0.068
20	20	4	0.005±0.002	26.3	46.9±1.8	3.0	42.7±3.5	17.2±0.2	0.070

extinction) at 2% (Fig. A1.1a). If the reduction of K was fixed at 1% annually, p_E remained 0 (no population extinction) for both brown and spotted hyaenas for periods between 10 and 50 years, then increased to p_E=0.326 for the brown hyaena and p_E=0.544 for the spotted hyaena at 100 years (Fig. A1.1b).

A similar picture was obtained for the chance that a population went extinct at least once over the period of 100 years. No matter how the reduction in K was defined, the spotted hyaena population always had a chance of going extinct at least once, and for reductions in K of 1% or higher over a period of 100 years extinction was certain (Fig. A1.2a,b).

In contrast to these results, there was no systematic trend in the average time to first extinction if the period over which K was reduced was fixed (Fig. A1.3a).

Figure A1.1. The probability of final population extinction after 100 years as a function of (a) the annual percent reduction of carrying capacity K over the period of 100 years; (b) the period over which K was reduced by 1% per year.

Circles: brown hyaena population with immigration from adjacent populations; squares: isolated brown hyaena population; triangles: spotted hyaena population with immigration from adjacent populations; inverted triangles: isolated spotted hyaena population.

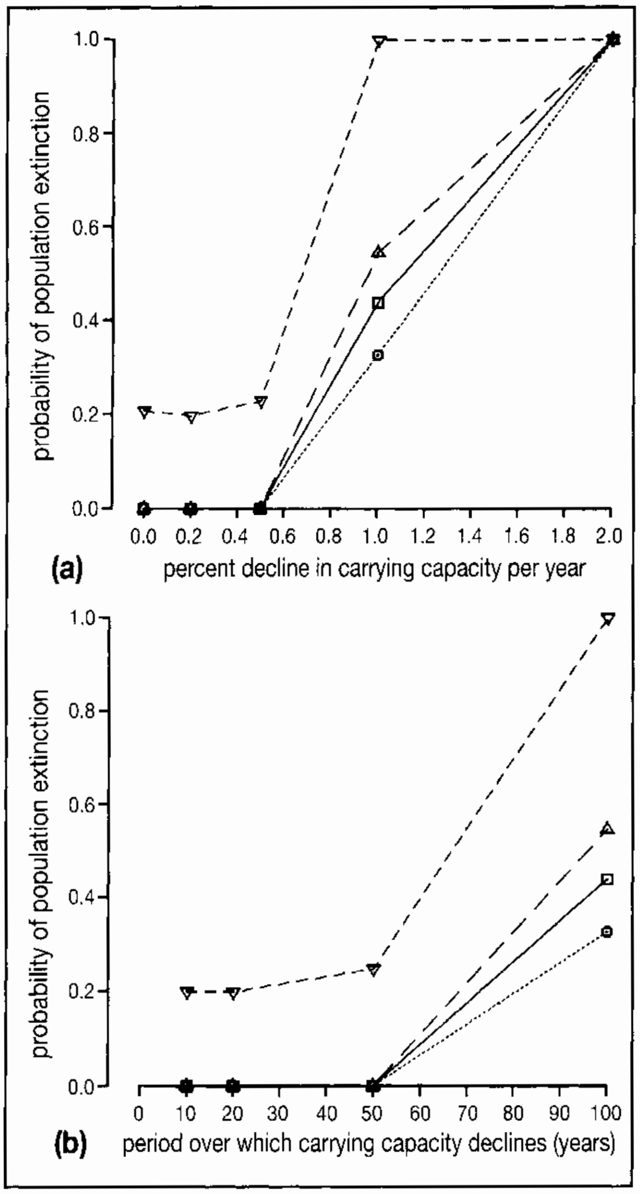
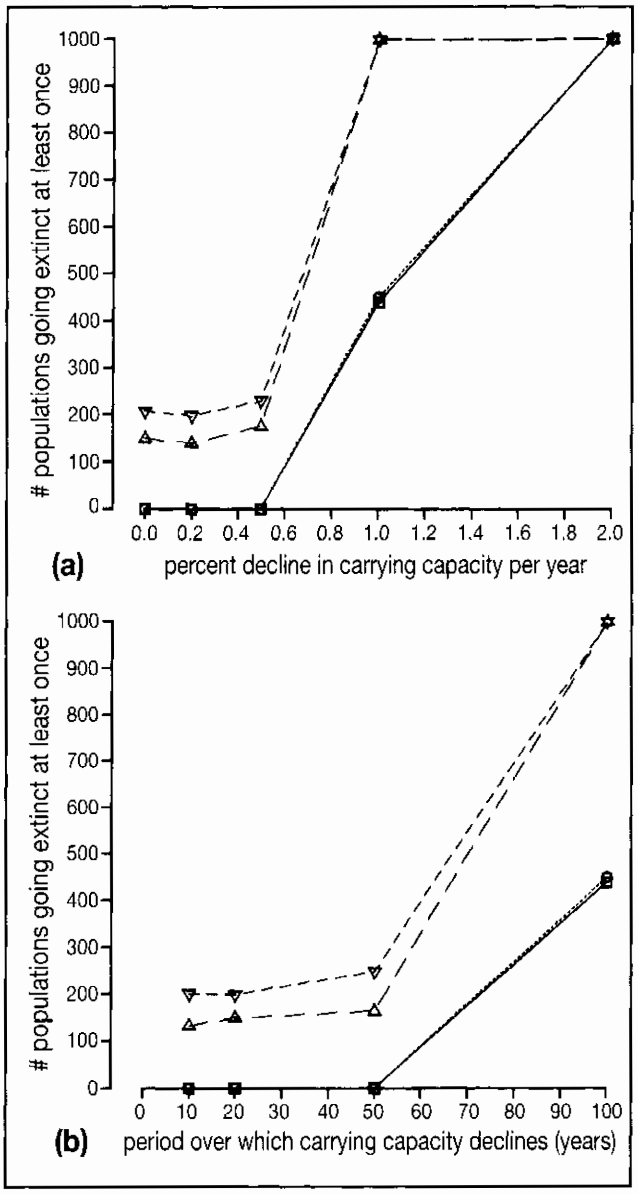


Figure A1.2. The number of populations (out of 1000 populations) going extinct at least once during the period of 100 years as a function of (a) the annual percent reduction of carrying capacity K over the period of 100 years; (b) the period over which K was reduced by 1% per year.

Circles: brown hyaena population with immigration from adjacent populations; squares: isolated brown hyaena population; triangles: spotted hyaena population with immigration from adjacent populations; inverted triangles: isolated spotted hyaena population.



The longest time was recorded for 1% annual reduction in K over a period of 100 years. Shorter periods over which K declined and smaller or steeper reductions in K reduced the time to first extinction (Figs. A1.3a,b).

Final population size showed a steep, linear decline when the amount of annual reduction in K for the fixed period of 100 years was increased (Fig. A1.4a) and/or when the period over which the reduction in K occurred was increased (Fig. A1.4b).

In the case of the brown hyaena when the probability of final extinction was 0, a final population size that comprised approximately 50% of the initial population size was obtained in simulations where: (1) K decreased annually by 5% over 10 years (final size = 331.6 ± 1.1 individuals); (2) K decreased annually by 1% over 50 years

Figure A1.3. The time to first extinction as a function of (a) the annual percent reduction of carrying capacity K over the period of 100 years; (b) the period over which K was reduced by 1% per year.
Circles: brown hyaena population with immigration from adjacent populations; squares: isolated brown hyaena population; triangles: spotted hyaena population with immigration from adjacent populations; inverted triangles: isolated spotted hyaena population.

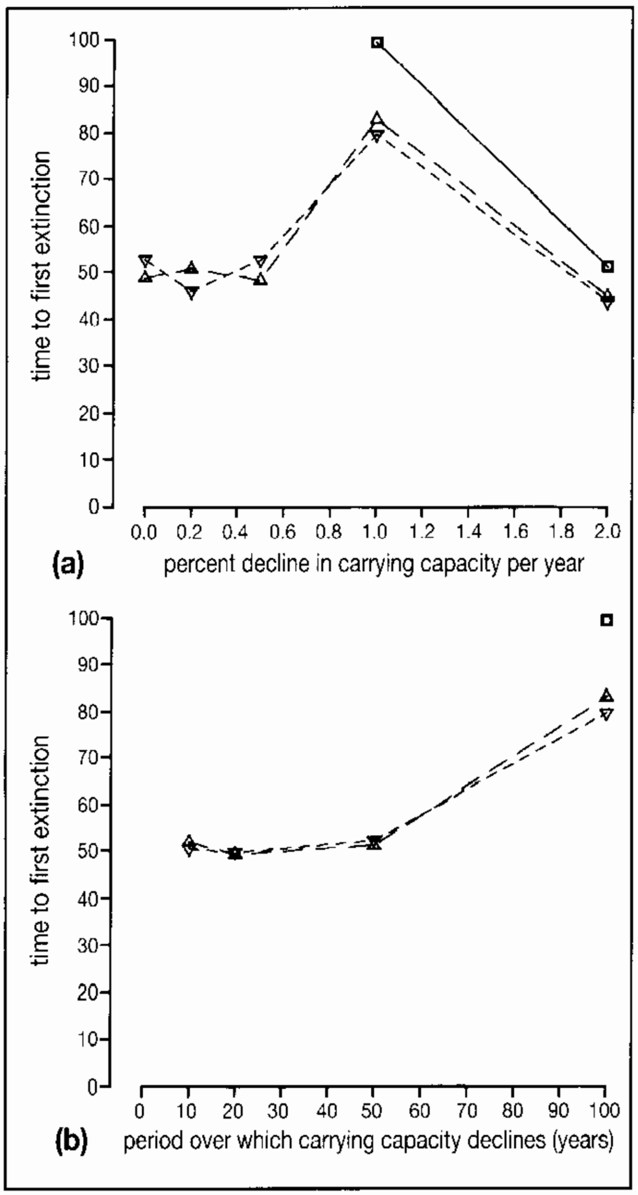
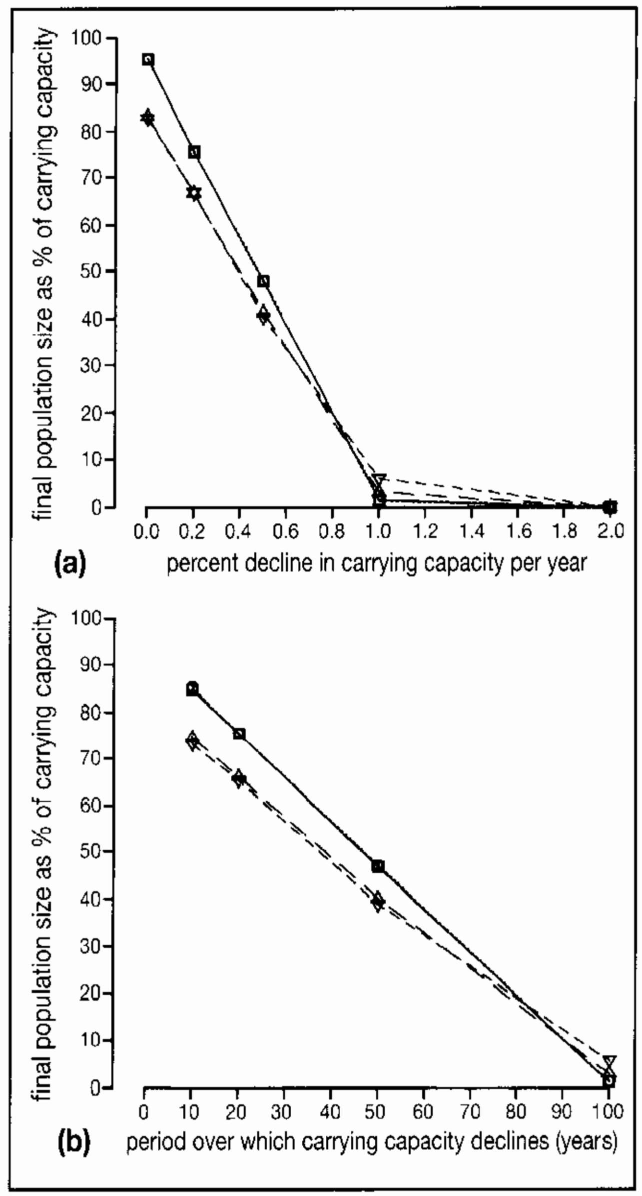


Figure A1.4. Final population size as a function of (a) the annual percent reduction of carrying capacity K over the period of 100 years; (b) the period over which K was reduced by 1% per year.
Circles: brown hyaena population with immigration from adjacent populations; squares: isolated brown hyaena population; triangles: spotted hyaena population with immigration from adjacent populations; inverted triangles: isolated spotted hyaena population.



(final size = 330.1 ± 1.1 individuals); or (3) K decreased annually by 0.5% over 100 years (final size = 335.8 ± 1.0 individuals).

For the aardwolf we assessed changes in K by introducing droughts at different intervals. The minimum drought interval recorded by P.R.K. Richardson was four years. In the simulations, drought intervals varied between three (putative worst case scenario) and ten years. One expectation might have been that the chance of population persistence increased with average intervals between droughts. However, the results in Table A1.2 (middle section) demonstrate no systematic change in either the chance of population extinction or the percentage of populations going extinct at least once. Moreover, there were no systematic trends in any of the other parameters recorded, with the exception of a slight increase in population growth rate and final population size with increasing drought interval (Table A1.2). It appears that population persistence in the aardwolf is minimally affected by the frequency of droughts if droughts occur only for one year at a time.

A1.3.2 Scenario 2: Isolating populations

Isolated populations of both the brown and spotted hyaena repeated the patterns shown by populations where immigration from adjacent populations was possible (Figs. A1.1a,b–A1.4a,b). Isolation reduced population persistence in all parameters measured (Figs. A1.1a,b–A1.4a,b), although this effect varied for the two species. Isolation had a modest negative effect on population persistence in the brown hyaena but a substantial negative effect in the spotted hyaena (Figs. A1.1a,b). In the case of spotted hyaena, isolated populations went extinct with a minimum chance of 20%, whereas isolated brown hyaena populations were guaranteed to persist under some parameter values (p_F=0, Figs. A1.1a,b). A reduction in K of 1% over 100 years resulted in certain extinction of an isolated spotted hyaena population (Fig. A1.1b). The chance that populations went extinct at least once during the period of 100 years was moderately higher in isolated populations of the spotted hyaena (Figs. A1.2a,b) whereas isolation had no such effect on brown hyaena populations (Figs. A1.2a,b). Neither time to first extinction nor final population size were affected by population isolation (Figs. A1.3a,b–A1.4a,b).

One way of looking at the effect of isolating adjacent aardwolf populations is to look at the chance that an aardwolf population goes extinct at least once during the period of 100 years. This is not expected to be exactly the same value as the results of a simulation where the population is isolated from the beginning. This is because immigration during early years may boost population size and thus may sometimes delay extinction (see the case of the spotted hyaena, Fig. A1.3a,b). It is therefore likely to underestimate the chance of population extinction of a truly isolated population, as a comparison of isolated and non-isolated spotted hyaena populations in Fig. A1.2a,b suggests. Nevertheless it provides an initial estimate. This value varied between 26.3% and 31.1%, a value substantially higher than the chance of final population extinction of 0.2 to 0.5% that was obtained through re-establishment of the population by immigration from adjacent populations (Table A1.2).

A1.3.3 Scenario 3: Persecution of prey populations

Average intervals between events of locust spraying operations that may affect aardwolf population persistence were varied from once every eight years to once every 20 years. The results (bottom section Table A1.2) suggest that this interval has little effect on aardwolf population persistence, with the exception of a slight increase in the population growth rate and final population size.

A1.4 Discussion

The results of the simulation of the fate of the three study populations suggest that they are unlikely to go extinct provided they are not isolated (aardwolf) or carrying capacity is held constant (i.e. habitat quality maintained (brown and spotted hyaenas)). An interesting result is the fact that in a variety of conditions the final probability of extinction p_F showed little change, and then suddenly increased (Figs. A1.1a,b). This suggests that there is a threshold below which a gradual worsening of conditions has little effect on the viability of hyaena populations, whereas above that threshold population viability decreases substantially.

Isolation of populations had an impact in all three species studied. In the brown hyaena, the influence of isolation was modest compared to changes in the carrying capacity K. In the spotted hyaena, its influence was substantial although it was exceeded by drastic changes in K. Fencing and other measures that are supposed to separate hyaena populations from livestock in order to minimise potential conflicts between conservation area authorities and local communities (but effectively isolate adjacent hyaena populations) would therefore be expected to reduce population viability. However, this reduction in population viability is exceeded substantially by the effects of changes in K on population viability. The results from the PVHA suggest that allocating areas for conservation and maintaining protected areas in excellent condition are the most efficient way of securing a future for the spotted hyaena.

In the case of a small aardwolf population, isolation increased the chance of population extinction more substantially than changes in the floater population, drought intervals, or the chance of locust spraying operations. This suggests that small aardwolf populations in drier areas predominantly used for sheep farming may be more vulnerable than other aardwolf populations. This is because farmers are more likely to create and maintain jackal-proof (and hence aardwolf-proof) fencing on sheep farms than in the case of other agricultural activities, therefore increasing the possibility of population isolation.

A1.5 Outlook

This population and habitat viability analysis may be fruitfully extended by including an analysis of striped hyaena population persistence and the assessment of the effect of the following factors on population persistence in the aardwolf, brown hyaena and spotted hyaena:

1. Changes in important demographic parameters, including initial population size, breeding success, and cub and adult mortality.
2. The impact of inbreeding on isolated populations.
3. The effect of a systematic reduction in carrying capacity on the aardwolf.
4. The effect of droughts persisting for more than a year on the aardwolf.

Appendix 2

Scientific Names of Vertebrate Species Mentioned in the Text

Aardvark	*Orycteropus afer*
Baboon	*Papio* species
Bat-eared fox	*Otocyon megalotis*
Black-backed jackal	*Canis mesomelas*
Black rhino	*Diceros bicornis*
Blue wildebeest	*Connochaetes taurinus*
Burchell's or plain's zebra	*Equus burchelli*
Bushbuck	*Tragelaphus scriptus*
Cane rat	*Thryonomys* species
Cape buffalo	*Synceros caffer*
Cape fur seal	*Arctocephalus pusillus*
Caracal	*Caracal caracal*
Cheetah	*Acinonyx jubatus*
Colobus monkey	*Colobus* species
Corsac fox	*Vulpes corsac*
Domestic cat	*Felis catus*
Domestic dog	*Canis familiaris*
Eland	*Taurotragus oryx*
Elephant	*Loxodonta africana*
Gemsbok	*Oryx gazella*
Gerenuk	*Litocranius walleri*
Giraffe	*Giraffa camelopardalis*
Golden jackal	*Canis aureus*
Grant's gazelle	*Gazella granti*
Greater kudu	*Taurotragus strepsiceros*
Hippopotamus	*Hippopotamus amphibius*
Hyrax	*Procaviidae* species
Impala	*Aepyceros melampus*
Kob	*Kobus kob*
Kongoni	*Alcephalus busephalus*
Korhaan	*Eupodotis* species
Kori bustard	*Otis kori*
Kulan	*Equus hemionus*
Lechwe	*Kobus leche*
Leopard	*Panthera pardus*
Lesser flamingo	*Phoeniconaias minor*
Lion	*Panthera leo*
Meerkat	*Suricata suricatta*
Mountain lion	*Puma concolor*
Mountain zebra	*Equus zebra*
Pangolin	*Manis temmincki*
Porcupine	*Hystrix africaeaustralis*
Red fox	*Vulpes vulpes*
Reedbuck	*Redunca arundinum*
Roan antelope	*Hippotragus equinus*
Sable antelope	*Hippotragus niger*
Sea otter	*Enhydra lustris*
Snow leopard	*Uncia uncia*
Springbok	*Antidorcas marsupialis*
Springhare	*Pedetes capensis*
Suni	*Neotragus moschatus*
Syke's monkey	*Cercopithecus albogularis*
Thomson's gazelle	*Gazella thomsoni*
Tiger	*Panthera tigris*
Topi	*Damaliscus lunatus*
Vervet monkey	*Cercopithecus aethiops*
Warthog	*Phacochoerus aethiopicus*
Waterbuck	*Kobus ellipsiprymnus*
Water buffalo	*Bubalus arnee*
White rhino	*Ceratotherium simum*
Wild boar	*Sus scrofa*
Wild cat	*Felis silvestris*
Wild dog	*Lycaon pictus*
Wolf	*Canis lupus*

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Appendix 5

The Questionnaire Used in the Hyaena Action Plan Survey

HYAENA CONSERVATION QUESTIONNAIRE

IUCN HYAENA SPECIALIST GROUP

NOTE: 1. Please fill in a separate questionnaire for each species and each country or region.
2. Copies of the final report will be sent to all respondents.

1. Species:

Spotted hyaena   Striped hyaena   Brown hyaena   Aardwolf

2. Country or Region:

3. Date:

4. Reporter:

Name:

Address:

Organisation:

5. Distribution:

Shade in (i) the historic and (ii) the present distribution of the species in the relevant country or region on the maps provided. Also indicate areas where viable populations are known to occur and mark with crosses reliable sightings within the last 10 years outside these last areas.

6. Population

a) Estimated numbers in the wild, in the country or region given in 2 above (Circle where appropriate).

<100   100–1000   >1000

b) Are numbers increasing, decreasing, stable or unknown?

c) Have any population estimates been made?

If yes, in what area?

What was the estimated size of the population?

What was the size of the area?

7. Field Studies:

Has the species been studied in your country?

If yes, by whom?

What aspects are, or have been, studied?

8. Feeding habits:

a) What are the most important food items for the species?

b) Does it cause problems with domestic stock?

If yes how many cases in the country or region per year:

<5 6-10 11-50 >50

c) Which species of domestic animals are killed? Indicate if the species is killed often or only rarely.

Poultry	Sheep	Donkeys
Cats	Goats	Horses
Dogs	Cattle	Camels

9. Attitudes towards these animals:

a) What is your department's attitude, towards this species: For example, is it seen as an asset in any way, or only as a pest? If you do not represent a department what is the government's attitude?

Is a bounty offered for killing it?

b) What is the attitude of the local people? Are these animals:

- Given food?
- Tolerated?
- Hunted for food?
- Shot/poisoned/trapped? (Please provide details)

10. Status:

a) What is the status of the animal in your country?

Satisfactory Threatened Extinct or nearly so

b) If threatened, what are the reasons for this? e.g. habitat destruction, persecution?

11. Conservation measures taken in your country:

a) What legal measures protect this species?

b) To what extent are these laws enforced?

c) Protected areas - does it occur in national parks, reserves etc?

If so, please name:

d) Does it occur outside protected areas?

12. Conservation measures proposed:

Have any specific conservation plans been proposed, or implemented. Does this species require specific attention? If yes, what is required to conserve the population?

13. References:

Please list all relevant published papers and send copies of any that you may have, as well as any non-confidential unpublished reports, project proposals and personal communications.

14. Additional remarks:

Please provide information for which there was insufficient space above, or add any other remarks you wish to make.

Appendix 6

IUCN Red List Categories

Prepared by the IUCN Species Survival Commission
As approved by the 40th Meeting of the IUCN Council, Gland, Switzerland
30 November 1994

I) Introduction

1. The threatened species categories now used in Red Data Books and Red Lists have been in place, with some modification, for almost 30 years. Since their introduction these categories have become widely recognised internationally, and they are now used in a whole range of publications and listings, produced by IUCN as well as by numerous governmental and non-governmental organisations. The Red Data Book categories provide an easily and widely understood method for highlighting those species under higher extinction risk, so as to focus attention on conservation measures designed to protect them.

2. The need to revise the categories has been recognised for some time. In 1984, the SSC held a symposium, 'The Road to Extinction' (Fitter and Fitter 1987), which examined the issues in some detail, and at which a number of options were considered for the revised system. However, no single proposal resulted. The current phase of development began in 1989 with a request from the SSC Steering Committee to develop a new approach that would provide the conservation community with useful information for action planning.

In this document, proposals for new definitions for Red List categories are presented. The general aim of the new system is to provide an explicit, objective framework for the classification of species according to their extinction risk.

The revision has several specific aims:

- to provide a system that can be applied consistently by different people;
- to improve the objectivity by providing those using the criteria with clear guidance on how to evaluate different factors which affect 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. The proposals presented in this document result from a continuing process of drafting, consultation and validation. It was clear that the production of a large number of draft proposals 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 became necessary, a system for version numbering was applied as follows:

Version 1.0: Mace & 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 & 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.

Final Version
This final document, which incorporates changes as a result of comments from IUCN members, was adopted by the IUCN Council in December 1994.

All future taxon lists including categorisations should be based on this version, and not the previous ones.

4. In the rest of this document the proposed system is outlined in several sections. The Preamble presents some basic information about the context and structure of the proposal, and the procedures that are to be followed in applying the definitions to species. This is followed by a section giving definitions of terms used. Finally the definitions are presented, followed by the quantitative criteria used for classification within the threatened categories. It is important for the effective functioning of the new system that all sections are read and understood, and the guidelines followed.

References:

Fitter, R., and M. Fitter, ed. (1987) *The Road to Extinction*. Gland, Switzerland: IUCN.
IUCN. (1993) *Draft IUCN Red List Categories*. Gland, Switzerland: IUCN.
Mace, G. M. *et al.* (1992) "The development of new criteria for listing species on the IUCN Red List." *Species* 19: 16–22.
Mace, G. M., and R. Lande. (1991) "Assessing extinction threats: toward a reevaluation of IUCN threatened species categories." *Conserv. Biol.* 5.2: 148–157.
Mace, G. M. & S. N. Stuart. (1994) "Draft IUCN Red List Categories, Version 2.2". *Species* 21–22: 13–24.

II) Preamble

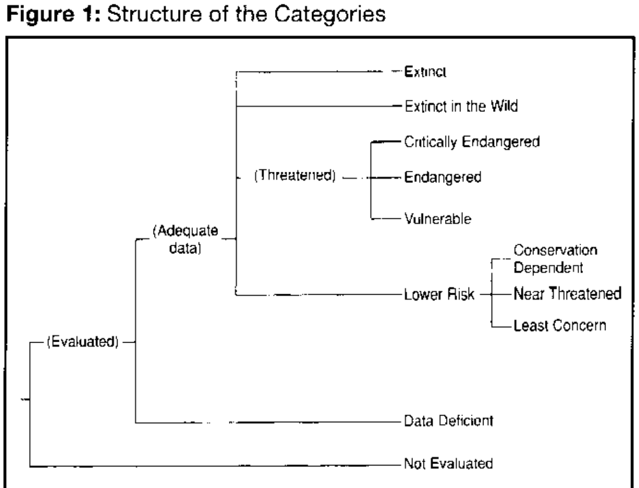
The following points present important information on the use and interpretation of the categories (= Critically Endangered, Endangered, etc.), criteria (= A to E), and sub-criteria (= a,b etc., i,ii etc.):

1. Taxonomic level and scope of the categorisation process
The criteria can be applied to any taxonomic unit at or below the species level. The term 'taxon' in the following notes, definitions and criteria is used for convenience, and may represent species or lower taxonomic levels, including forms that are not yet formally described. There is a 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 11 below. In presenting the results of applying the criteria, the taxonomic unit and area under consideration should be made explicit. The categorisation process should only be applied to wild populations inside their natural range, and to populations resulting from benign introductions (defined in the draft IUCN Guidelines for Re-introductions 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").

2. Nature of the categories
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 species 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 species should be evaluated against all the 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. 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 (other than micro-organisms). 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 which criteria are appropriate for a particular species in advance, each species should be evaluated against all the criteria, and any criterion met should be listed.

Figure 1: Structure of the Categories



4. Derivation of quantitative criteria
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. Some broad consistency between them was sought. However, a given taxon should not be expected to meet all criteria (A–E) in a category; meeting any one criterion is sufficient for listing.

5. 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, species listed in these categories should not be treated as if they were non-threatened, and it may be appropriate (especially for Data Deficient forms) to give them the same degree of protection as threatened taxa, at least until their status can be evaluated.

Extinction is assumed here to be 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 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.

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 to be 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 either the recent past, present or near future can be based on any of a series of related factors, and these factors should be specified.

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 (pathogens, invasive organisms, hybridization).

7. Uncertainty
The criteria should be applied on the basis of the available evidence on taxon numbers, trend and distribution, making due allowance for statistical and other uncertainties. Given that data are rarely available for the whole range or population of a taxon, it may often be appropriate to use the information

that is available to make intelligent inferences about the overall status of the taxon in question. In cases where a wide variation in estimates is found, it is legitimate to apply the precautionary principle and use the estimate (providing it is credible) that leads to listing in the category of highest risk.

Where data are insufficient to assign a category (including Lower Risk), the category of 'Data Deficient' may be assigned. However, it is important to recognise that this category indicates that data are inadequate to determine the degree of threat faced by a taxon, not necessarily that the taxon is poorly known. In cases where there are evident threats to a taxon through, for example, deterioration of its only known habitat, it is important to attempt threatened listing, even though there may be little direct information on the biological status of the taxon itself. The category 'Data Deficient' is not a threatened category, although it indicates a need to obtain more information on a taxon to determine the appropriate listing.

8. 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. In cases where it is only conservation action that prevents the taxon from meeting the threatened criteria, the designation of 'Conservation Dependent' is appropriate. It is important to emphasise here that a taxon require conservation action even if it is not listed as threatened.

9. Documentation

All taxon lists including categorisation resulting from these criteria should state the criteria and sub-criteria that were met. No listing can be accepted as valid unless at least one criterion is given. If more than one criterion or sub-criterion was met, then each should be listed. However, failure to mention a criterion should not necessarily imply that it was not met. Therefore, if a re-evaluation indicates that the documented criterion is no longer met, this should not result in automatic down-listing. Instead, the taxon should be re-evaluated with respect to all criteria to indicate its status. The factors responsible for triggering the criteria, especially where inference and projection are used, should at least be logged by the evaluator, even if they cannot be included in published lists.

10. 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 likelihood of extinction 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 even perhaps the taxonomic distinctiveness of the subject.

11. Use at regional level

The criteria are most appropriately applied to whole taxa at a global scale, rather than to those units defined by regional or national boundaries. Regionally or nationally based threat categories, which are aimed at including taxa that are threatened at regional or national levels (but not necessarily throughout their global ranges), are best used with two key pieces of information: the global status category for the taxon, and the proportion of the global population or range that occurs within the region or nation. However, if applied at regional or national level it must be recognised that a global category of threat may not be the same as a regional or national category for a particular taxon. For example, taxa classified as Vulnerable on the basis of their global declines in numbers or range might be Lower Risk within a particular region where their populations are stable. Conversely, taxa classified as Lower Risk 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. IUCN is still in the process of developing guidelines for the use of national red list categories.

12. Re-evaluation

Evaluation of taxa against the criteria should be carried out at appropriate intervals. This is especially important for taxa listed under Near Threatened, or Conservation Dependent, and for threatened species whose status is known or suspected to be deteriorating.

13. Transfer between categories

There are rules to govern the movement of taxa between categories. These are as follows: (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 Section 9). (C) Transfer from categories of lower to higher risk should be made without delay.

14. 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. Mapping at finer scales reveals more areas in which the taxon is unrecorded. It is impossible to provide any strict but general rules for mapping taxa or habitats; the most appropriate scale will depend on the taxa in question, and the origin and comprehensiveness of the distributional data. However, the thresholds for some criteria (e.g. Critically Endangered) necessitate mapping at a fine scale.

III) Definitions

1. Population

Population is defined as the total number of individuals of the taxon. For functional reasons, primarily owing to differences between life-forms, population numbers are expressed 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

Subpopulations are defined as geographically or otherwise distinct groups in the population between which there is little exchange (typically one successful migrant individual or gamete per year or less).

3. Mature individuals

The number of mature individuals is defined as 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:

- Where the population is characterised by natural fluctuations the minimum number should be used.

- This measure is intended to count individuals capable of reproduction and should therefore exclude individuals that are environmentally, behaviourally or otherwise reproductively suppressed in the wild.

- 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 (e.g. the estimated effective population size).

- 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.

4. Generation
Generation may be measured as the average age of parents in the population. This is greater than the age at first breeding, except in taxa where individuals breed only once.

5. Continuing decline
A continuing decline is a recent, current or projected future decline whose causes are not known or not adequately controlled and so is liable to continue unless remedial measures are taken. Natural fluctuations will not normally count as a continuing decline, but an observed decline should not be considered to be part of a natural fluctuation unless there is evidence for this.

6. Reduction
A reduction (criterion A) is a decline in the number of mature individuals of at least the amount (%) stated over the time period (years) specified, although the decline need not still be continuing. A reduction should not be interpreted as part of a natural fluctuation unless there is good evidence for this. Downward trends that are part of natural fluctuations will not normally count as a reduction.

7. Extreme fluctuations
Extreme fluctuations occur in a number of taxa where 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
Severely fragmented refers to the situation where increased extinction risks to the taxon result from the fact that most individuals within a taxon are found in small and relatively isolated subpopulations. These small subpopulations may go extinct, with a reduced probability of recolonisation.

9. Extent of occurrence
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. 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'). 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).

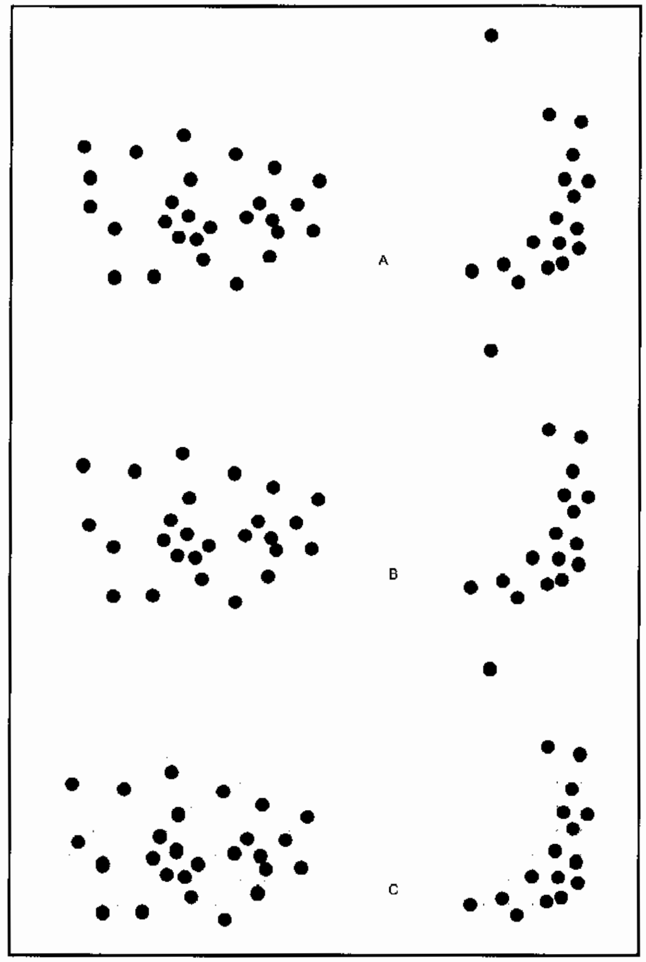


Figure 2: Two examples of the distinction between extent of occurrence and area of occupancy. (a) is the spatial distribution of known, inferred or projected sites of occurrence. (b) shows one possible boundary to the extent of occurrence, which is the measured area within this boundary. (c) shows one measure of area of occupancy which can be measured by the sum of the occupied grid squares.

10. Area of occupancy
Area of occupancy is defined as the area within its 'extent of occurrence' (see definition) 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, for example, contain unsuitable habitats. The area of occupancy is the smallest area essential at any stage to the survival of existing populations of a taxon (e.g. colonial nesting sites, feeding sites for migratory taxa). 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 criteria include values in km^2, and thus to avoid errors in classification, the area of occupancy should be measured on grid squares (or equivalents) which are sufficiently small (see Figure 2).

11. Location
Location defines a geographically or ecologically distinct area in which a single event (e.g. pollution) will soon affect all individuals of the taxon present. A location usually, but not always, contains all or part of a subpopulation of the taxon, and is typically a small proportion of the taxon's total distribution.

12. Quantitative analysis
A quantitative analysis is defined here as the technique of population viability analysis (PVA), or any other quantitative form of analysis, which estimates the extinction probability of a taxon or population based on the known life history and specified management or non-management options. In presenting the results of quantitative analyses the structural equations and the data should be explicit.

IV) The Categories [1]

EXTINCT (EX)
A taxon is Extinct when there is no reasonable doubt that the last individual has died.

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 it is facing an extremely high risk of extinction in the wild in the immediate future, as defined by any of the criteria (A to E) on pages 152-153.

ENDANGERED (EN)
A taxon is Endangered when it is not Critically Endangered but is facing a very high risk of extinction in the wild in the near future, as defined by any of the criteria (A to E) on page 153.

VULNERABLE (VU)
A taxon is Vulnerable when it is not Critically Endangered or Endangered but is facing a high risk of extinction in the wild in the medium-term future, as defined by any of the criteria (A to D) on pages 153 and 154.

LOWER RISK (LR)
A taxon is Lower Risk when it has been evaluated, does not satisfy the criteria for any of the categories Critically Endangered, Endangered or Vulnerable. Taxa included in the Lower Risk category can be separated into three subcategories:

1. **Conservation Dependent (cd)**. Taxa which are the focus of a continuing taxon-specific or habitat-specific conservation programme targeted towards the taxon in question, the cessation of which would result in the taxon qualifying for one of the threatened categories above within a period of five years.

2. **Near Threatened (nt)**. Taxa which do not qualify for Conservation Dependent, but which are close to qualifying for Vulnerable.

3. **Least Concern (lc)**. Taxa which do not qualify for Conservation Dependent or Near Threatened.

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 is lacking. Data Deficient is therefore not a category of threat or Lower Risk. 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 threatened status. If the range of a taxon is suspected to be relatively circumscribed, if 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 assessed against the criteria.

V) The Criteria for Critically Endangered, Endangered and Vulnerable

CRITICALLY ENDANGERED (CR)
A taxon is Critically Endangered when it is facing an extremely high risk of extinction in the wild in the immediate future, as defined by any of the following criteria (A to E):

A) Population reduction in the form of either of the following:

 1) An observed, estimated, inferred or suspected reduction of at least 80% over the last 10 years or three generations, whichever is the longer, based on (and specifying) any of the following:
  a) direct observation
  b) an index of abundance appropriate for 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) A reduction of at least 80%, projected or suspected to be met within the next 10 years or three generations, whichever is the longer, based on (and specifying) any of (b), (c), (d) or (e) above.

B) Extent of occurrence estimated to be less than $100km^2$ or area of occupancy estimated to be less than $10km^2$, and estimates indicating any two of the following:
 1) Severely fragmented or known to exist at only a single location.

 2) Continuing decline, observed, inferred or projected, in any of the following:
  a) extent of occurrence
  b) area of occupancy
  c) area, extent and/or quality of habitat
  d) number of locations or subpopulations
  e) number of mature individuals.

 3) Extreme fluctuations in any of the following:
  a) extent of occurrence
  b) area of occupancy
  c) number of locations or subpopulations
  d) number of mature individuals.

C) Population estimated to number less than 250 mature individuals and either:

1) An estimated continuing decline of at least 25% within three years or one generation, whichever is longer or

2) A continuing decline, observed, projected, or inferred, in numbers of mature individuals and population structure in the form of either:
   a) severely fragmented (i.e. no subpopulation estimated to contain more than 50 mature individuals)
   b) all individuals are in a single subpopulation.

D) Population estimated to number less 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.

ENDANGERED (EN)
A taxon is Endangered when it is not Critically Endangered but is facing a very high risk of extinction in the wild in the near future, as defined by any of the following criteria (A to E):

A) Population reduction in the form of either of the following:

1) An observed, estimated, inferred or suspected reduction of at least 50% over the last 10 years or three generations, whichever is the longer, based on (and specifying) any of the following:
   a) direct observation
   b) an index of abundance appropriate for 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) A reduction of at least 50%, projected or suspected to be met within the next 10 years or three generations, whichever is the longer, based on (and specifying) any of (b), (c), (d), or (e) above.

B) Extent of occurrence estimated to be less than 5000km^2 or area of occupancy estimated to be less than 500km^2, and estimates indicating any two of the following:

1) Severely fragmented or known to exist at no more than five locations.

2) Continuing decline, inferred, observed or projected, in any of the following:
   a) extent of occurrence
   b) area of occupancy
   c) area, extent and/or quality of habitat
   d) number of locations or subpopulations
   e) number of mature individuals.

3) Extreme fluctuations in any of the following:
   a) extent of occurrence
   b) area of occupancy
   c) number of locations or subpopulations
   d) number of mature individuals.

C) Population estimated to number less than 2500 mature individuals and either:

1) An estimated continuing decline of at least 20% within five years or two generations, whichever is longer, or

2) A continuing decline, observed, projected, or inferred, in numbers of mature individuals and population structure in the form of either:
   a) severely fragmented (i.e. no subpopulation estimated to contain more than 250 mature individuals)
   b) all individuals are in a single subpopulation.

D) Population estimated to number less 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.

VULNERABLE (VU)
A taxon is Vulnerable when it is not Critically Endangered or Endangered but is facing a high risk of extinction in the wild in the medium-term future, as defined by any of the following criteria (A to E):

A) Population reduction in the form of either of the following:

1) An observed, estimated, inferred or suspected reduction of at least 20% over the last 10 years or three generations, whichever is the longer, based on (and specifying) any of the following:
   a) direct observation
   b) an index of abundance appropriate for 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) A reduction of at least 20%, projected or suspected to be met within the next ten years or three generations, whichever is the longer, based on (and specifying) any of (b), (c), (d) or (e) above.

B) Extent of occurrence estimated to be less than 20,000km^2 or area of occupancy estimated to be less than 2000km^2, and estimates indicating any two of the following:

1) Severely fragmented or known to exist at no more than ten locations.

2) Continuing decline, inferred, observed or projected, in any of the following:
   a) extent of occurrence
   b) area of occupancy
   c) area, extent and/or quality of habitat
   d) number of locations or subpopulations
   e) number of mature individuals

3) Extreme fluctuations in any of the following:
   a) extent of occurrence
   b) area of occupancy
   c) number of locations or subpopulations
   d) number of mature individuals

C) Population estimated to number less 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, or

2) A continuing decline, observed, projected, or inferred, in numbers of mature individuals and population structure in the form of either:
   a) severely fragmented (i.e. no subpopulation estimated to contain more than 1000 mature individuals)
   b) all individuals are in a single subpopulation

D) Population very small or restricted in the form of either of the following:

1) Population estimated to number less than 1000 mature individuals.

2) Population is characterised by an acute restriction in its area of occupancy (typically less than $100km^2$) or in the number of locations (typically less than five). Such a taxon would thus be prone to the effects of human activities (or stochastic events whose impact is increased by human activities) within a very short period of time in an unforeseeable future, and is thus capable of becoming Critically Endangered or even Extinct in a very short period.

E) Quantitative analysis showing the probability of extinction in the wild is at least 10% within 100 years.

Note: copies of the IUCN Red List Categories booklet, are available on request from IUCN (address on back cover of this Action Plan)

[1] Note: As in previous IUCN categories, the abbreviation of each category (in parenthesis) follows the English denominations when translated into other languages.

IUCN/SSC Action Plans for the Conservation of Biological Diversity

Action Plan for African Primate Conservation: 1986-1990. Compiled by J.F. Oates and the IUCN/SSC Primate Specialist Group, 1986, 41 pp. (Out of print.)

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Dolphins, Porpoises and Whales. An Action Plan for the Conservation of Biological Diversity: 1988-1992. Second Edition. Compiled by W.F. Perrin and the IUCN/SSC Cetacean Specialist Group, 1989, 27 pp. (Out of print).

The Kouprey. An Action Plan for its Conservation. Compiled by J.R. MacKinnon, S.N. Stuart and the 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. Riffei, H. van Rompaey and the IUCN/SSC Mustelid and Viverrid Specialist Group, 1989, 99 pp. (Out of Print.)

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Asian Rhinos. An Action Plan for their Conservation. Compiled by Mohd Khan bin Momin Khan and the 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.

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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 and the 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 together with the IUCN/SSC Cetacean Specialist Group, 1994, 91 pp.

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Asian Rhinos. Status Survey and Conservation Action Plan (Second edition). Edited by Thomas J. Foose and Nico van Strien and the IUCN/SSC Asian Rhino Specialist Group, 1997, 112 pp.

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Crocodiles. Status Survey and Conservation Action Plan, 2nd Edition. Compiled by J. Perran Ross and the IUCN/SSC Crocodile Specialist Group, 1998, 96 pp.

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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 organizations. 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.

The SSC's mission is to conserve biological diversity by developing and executing programs to save, restore and wisely manage species and their habitats. A volunteer network comprised of nearly 7,000 scientists, field researchers, government officials and conservation leaders from 188 countries, 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 organizations.

The IUCN/SSC Action Plan series assesses 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 nature resource managers, conservationists and government officials around the world.

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