reintroduction in the western United States. Continued threats include competition with humans for livestock, especially in developing countries, exaggerated concern by the public concerning the threat and danger of wolves, and fragmentation of habitat, with resulting areas becoming too small for populations with long-term viability.

Commercial use Sustainable utilisation of fur in Canada, Alaska, and the former Soviet Union and Mongolia.

Occurrence in protected areas Occurs in many protected areas across its range.

Protection status CITES – Appendix II, except populations from Bhutan, India, Nepal and Pakistan, which are listed on Appendix I. See individual countries listed above.

Current legal protection Variable, from complete protection, well enforced, to concerted efforts to control some populations. See individual areas above.

Conservation measures taken Protected in various national parks and reserves in Canada and the United States. Extensive legal protection in many European countries; however, enforcement is variable and often non-existent. See individual areas above. Recently reintroduced to Yellowstone National Park, Idaho, and Arizona.

Occurrence in captivity

Lives and breeds well in captivity and is common in many zoological gardens.

Current or planned research projects

Several projects underway in Europe, India, Canada and the United States. See http://www.wolf.org

Gaps in knowledge

One of the most important questions still remaining about wolves involves the nature of their interaction with prey populations. The conditions under which wolves limit, regulate, or control their population is still open and important (Mech and Boitani 2003). Of more academic interest are questions involving wolf genetics, scent-marking behaviour, pseudopregnancy, and diseases (Mech 1995a).

Core literature

Boitani 1995; Carbyn *et al.* 1995; Harrington and Paquet 1982; Mech 1970, 1974; Mech *et al.* 1998; Mech and Boitani 2003; Nowak 1995. A list of about 2,000 references is available at http://www.wolf.org

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5.3 Red fox *Vulpes vulpes* Linnaeus, 1758 Least Concern (2004)

D.W. Macdonald and J.C. Reynolds

Other names

English: silver fox, cross fox; Albanian: dhelpra; Croatian: lisica; Czech: liška obecná; Danish: ræv; Dutch: vos; Estonian: rebane; Faeroese: revur; Finnish: kettu; French: renard roux; German: rotfuchs; Hungarian: vörös róka; Irish: sionnach, madra rua; Italian: volpe rossa, volpe comune; Latvian: lapsa; Lithuanian: rudoji lapë; Luxembourgish: fuuss; Maltese: volpi; Norwegian: rev, rødrev; Polish: lis; Portuguese: raposa; Romanian: vulpe; Russian: Красная дисица; Slovakian: líška hrdzavá; Slovenian: lisica; Spanish: zorro rojo; Swedish: räv; Turkish: tilki.

Taxonomy

Vulpes vulpes Linnaeus, 1758. Syst. Nat., 10th ed., 1:40. Type locality: "Europa, Asia, Africa, antrafodiens" restricted by Thomas (1911), to "Sweden (Uppsala)".

The North American red fox, *Vulpes fulva*, previously has been considered a separate species (as have some other putative subspecies), but is now considered conspecific with the Palaearctic *V. vulpes* (Nowak 1991). Many subspecies were described (see below) on the basis of regional variation, but these have doubtful ecological significance as evidenced by successful introductions and re-introductions around the world.

Chromosome number: The red fox has a diploid number of 34 chromosomes and 3–5 microsomes (Rausch and Rausch 1979).

Description

A medium-sized canid, and the largest fox in the genus Vulpes (Table 5.3.1). Muzzle slender and pointed with white on upper lip. Ears large, pointed, erect and blackbacked. Pelage is reddish-brown but may vary from brown to russet red to yellowish grey. Three main colour morphs: red, silver (black with variable amount of frosting due to silver tips on guard hairs) and cross (greyish brown with long black guard hairs down back and across shoulders) (Banfield 1987; Johnson and Hersteinsson 1993). Some individuals have dark grey-black under throat and belly and the underfur of females during the breeding season may appear pink-tinged. Throat and/or chest may have white markings. Legs long and slender. Lower legs black, may be splashed with white. Tail long, thick and bushy, sometimes with white tip. Enormous geographical variation in size. Adult head and body length may range from 455-900mm, tail length from 300-555mm and body weight from 3–14kg with males generally being larger than females (Nowak 1991). The species is substantially smaller in the

Table 5.3.1. Body measurements for the red fox.					
	Several studies	Ontario, Canada	Canberra, Australia	Kent, UK	Hokkaido, Japan
	from Cavallini (1995)	(Voigt 1987)	(McIntosh 1963)	(Hatting 1956)	(Zhan <i>et al.</i> 1991)
Total length male Total length female		1,026mm n=37 973mm n=34	1,048mm n=84 1,002mm n=60	1,064mm n=9 1,022mm n=10	
HB male HB female	660mm (590–720) n=11 (studies) 630mm (550–680) n=11				
T male	400mm (360–440) n=11				
T female	370mm (280–490) n=11				
WT male	6.3kg (4.4–7.6) n=20	4.1kg (n=37)	6.3kg (n=84)	6.7kg (n=33)	8.7kg (n=20)
WT female	5.3kg (3.6–6.5) n=20	3.4kg (n=37)	5.5kg (n=60)	5.5kg (n=29)	6.1kg (n=25)



Adult male red fox. United Kingdom.

Middle East deserts (Macdonald *et al.* 1999) than in Europe. Smaller also in North America (Voigt 1987). Skull measurements of specimens from northern Algeria are also much smaller than central European populations (Kowalski and Rzebik-Kowalska 1991). Dental formula 3/3-1/1-3/4-3/3=42.

Red foxes from North America are comparatively light, rather long for their mass, and with a high sexual dimorphism. British foxes are heavier but relatively short. European foxes are closer to the general average among populations. Additionally, body mass and length are positively related to latitude (i.e., follow Bergmann's Rule), but this is a smaller effect than that related to geographical origin.

Subspecies Larivière and Pasitschniak-Arts (1996) recognised 44 subspecies, although many are doubtful:

- V. v. abietorum (Stuart Lake, British Columbia, Canada)
- *V. v. aegyptiaca* (Egypt)
- V. v. alascensis (Andreafski, Alaska, USA)

- *V. v. alpherakyi* (Geok Tepe, Araisk, Kazakhstan)
- *V. v. anatolica* (Smyrna, western Asia Minor, Turkey)
- *V. v. arabica* (Muscat, Oman)
- V. v. atlantica (Atlas Mountains, Mitiya, Algeria)
- V. v. bangsi (L'Anse au Loup, Strait of Belle Isle, Labrador, Canada)
- V. v. barbara (Barbary Coast, north-western Africa)
- *V. v. beringiana* (shore of Bering Strait, north-eastern Siberia)
- V. v. cascadensis (Cascade Mountains, Skamania County, Washington, USA)
- *V. v. caucasica* (near Vladikawkaz, Caucasus, Russia)
- *V. v. crucigera* (Thuringia, Germany)
- V. v. daurica (Kharangoi, 45km west of Troizkosavsk, Siberia)
- *V. v. deletrix* (Bay St-George, Newfoundland, Canada)
- V. v. dolichocrania (Sidemi, southern Ussuri, SE Siberia)
- V. v. flavescens (northern Iran)
- *V. v. fulva* (Virginia, USA)
- V. v. griffithii (Kandahar, Afghanistan)

- V. v. harrimani (Kodiak Island, Alaska, USA)
- *V. v. hole* (near Amoy, Fukien, S. China)
- *V. v. ichnusae* (Sarrabus, Sardinia, Italy)
- *V. v. induta* (Cape Pyla, Cyprus)
- V. v. jakutensis (Taiga, south of Yakutsk, E. Siberia)
- *V. v. japonica* (Japan)
- *V. v. karagan* (Kirghiz Steppes, Khirghizia, Russia)
- V. v. kenaiensis (Kenai Peninsula, Alaska, USA)
- *V. v. kurdistanica* (Gelsk Valley, NE Turkey)
- *V. v. macroura* (Wasatch Mountains, near Great Salt Lake, Utah, USA)
- *V. v. montana* (Himalaya)
- *V. v. necator* (Whitney Meadow, near Mt Whitney, Tulare County, California, USA)
- V. v. ochroxantha (Aksai, Semirechyia, E Russian Turkestan, Kirgizia)
- V. v. palaestina (Ramleh, near Jaffa, Occupied Palestinian Territory)
- V. v. peculiosa (Korea)
- V. v. pusilla (Salt Range, Punjab, Pakistan)
- V. v. regalis (Elk River, Sherburne County, Minnesota, USA)
- V. v. rubricosa (Digby, Nova Scotia, Canada)
- V. v. schrencki (Sakhalin, Russia)
- V. v. silacea (near Silos, Burgos, Spain)
- V. v. splendidissima (north and central Kurile Islands, Russia)
- V. v. strepensis (steppes near Kherson, Russia)
- V. v. tobolica (Obdorsk, Tobolsk, Siberia)
- V. v. tschiliensis (Peiping, Chihli, NE China)
- V. v. vulpes (Sweden)

Similar species Arctic fox (*Alopex lagopus*): A white morph superficially resembles white red foxes (some of which are albino) but they are up to 25% smaller, with muzzle shorter and ears shorter and rounder. Similarly,

"silver" (actually black) or "cross" red foxes might be confused with blue morph of Arctic foxes.

Grey wolf (*Canis lupus*), and golden jackal (*Canis aureus*), are larger, have longer legs and relatively shorter tail. Confusion of pelts with those of smaller species more likely, due to clinal variation in body size and coloration between the largest red foxes (probably those in Scotland), and the smallest (perhaps in remote Saudi Arabia).

Great potential for confusion between red fox pelts and all the small Old World foxes (e.g., Tibetan fox, *V. ferrilata*, and corsac, *V. corsac*), the prairie foxes of North America (*V. macrotis* and *V. velox*), and some South American foxes.

A mutant of the red fox found in the wild, the so-called "Samson fox", lacks guard hairs.

Current distribution

Distributed across the entire northern hemisphere from the Arctic Circle to North Africa, Central America, and the Asiatic steppes, the red fox has the widest geographical range of any member of the order Carnivora (covering nearly 70 million km²) (Figure 5.3.1). Not found in Iceland, the Arctic islands, some parts of Siberia, or in extreme deserts. European subspecies introduced into eastern United States and Canada in 17th century, subsequently mixed with local subspecies. The species was also introduced to Australia in 1800s. Elsewhere introduced to the Falkland Islands (Malvinas) and to the Isle of Man (UK), although it may subsequently have disappeared there.

Range countries Afghanistan, Albania, Algeria, Andorra, Armenia, Australia, Austria, Azerbaijan, Bahrain, Bangladesh, Belarus, Belgium, Bolivia, Bosnia and Herzegovina, Bulgaria, Cambodia (?), Canada, Channel Islands, China, Croatia, Cyprus, Czech Republic, Denmark, Egypt, Estonia, Faeroe Islands, Falkland



Islands (Malvinas), Finland, France, Georgia, Germany, Gibraltar (?), Greece, French Guiana, Guyana, Hungary, India, Iran, Iraq, Ireland, Israel, Italy, Japan, Jordan, Kazakhstan, Kyrgyzstan, Korea (North and South), Kuwait, Laos PDR (?), Latvia, Lebanon, Libya, Liechtenstein, Lithuania, Luxembourg, Macedonia, Malta (?), Moldova, Monaco (?), Mongolia, Morocco, Myanmar, Nepal (?), Netherlands, Norway, Oman, Pakistan, Occupied Palestinian Territory, Poland, Portugal, Qatar, Romania, Russian Federation, San Marino, Saudi Arabia, Slovakia, Slovenia, Spain, Sudan, Suriname, Sweden, Switzerland, Syria, Tajikistan, Tunisia, Turkey, Turkmenistan, Ukraine, United Arab Emirates, United Kingdom, United States of America, Uzbekistan, Vietnam (?), Yemen, Yugoslavia (Lloyd 1980, Macdonald and Barrett 1993, Larivière and Pasitschniak-Arts 1996).

Relative abundance

Red fox density is highly variable. In the UK, density varies between one fox per 40km² in Scotland and 1.17/km² in Wales, but can be as high as 30 foxes per km² in some urban areas where food is superabundant (Harris 1977, Macdonald and Newdick 1982, Harris and Rayner 1986). Social group density is one family per km² in farmland, but may vary between 0.2–5 families per km² in the suburbs and as few as a single family per 10km² in barren uplands (Macdonald 1981, Lindsay and Macdonald 1986).

Fox density in mountainous rural areas of Switzerland is 3 foxes per km² (Meia 1994). In northern boreal forests and Arctic tundra, they occur at densities of $0.1/km^2$, and in southern Ontario, Canada at $1/km^2$ (Voigt 1987). The average social group density in the Swiss mountains is 0.37 family per km² (Weber *et al.* 1999).

Estimated populations/relative abundance and population trends The pre-breeding British fox population totals an estimated 240,000 (195,000 in England, 22,000 in Wales; Harris *et al.* 1995). Mean number of foxes killed per unit area by gamekeepers has increased steadily since the early 1960s in 10/10 regional subdivisions of Britain, but it is not clear to what extent this reflects an increase in fox abundance. Although an increase in fox numbers following successful rabies control by vaccination was widely reported in Europe (e.g., fox bag in Germany has risen from 250,000 in 1982–1983 to 600,000 in 2000–2001), no direct measures of population density have been taken.

Habitat

Red foxes have been recorded in habitats as diverse as tundra, desert and forest, as well as in city centres (including London, Paris, Stockholm, etc.). Natural habitat is dry, mixed landscape, with abundant "edge" of scrub and woodland. They are also abundant on moorlands, mountains (even above the treeline, known to cross alpine passes), deserts, sand dunes and farmland from sea level to 4,500m a.s.l. In the UK, they generally prefer mosaic patchworks of scrub, woodland and farmland. Red foxes flourish particularly well in urban areas. They are most common in residential suburbs consisting of privately owned, low-density housing and are less common where industry, commerce or council rented housing predominates (Harris and Smith 1987). In many habitats, foxes appear to be closely associated with man, even thriving in intensive agricultural areas.

Food and foraging behaviour

Food Red foxes are adaptable and opportunistic omnivores, with a diet ranging from invertebrates (e.g., earthworms and beetles) to mammals and birds (including game birds), and fruit. They also scavenge in rural areas (e.g., in Europe and Canada on deer and sheep carcasses which may be the major food source in upland areas in winter), and in urban areas (on bird tables, compost heaps and refuse). As predators, foxes typically kill birds and mammals up to about 3.5kg (equivalent to an adult brown hare). They require about 500g food per day, caching food that is in excess to their requirements and having a highly developed memory for location of hoards (Macdonald 1976, 1977a).

Foraging behaviour Foraging is mainly nocturnal and crepuscular, although more diurnal where they are undisturbed. They are independent and thus generally solitary foragers, although individuals may forage in close proximity where resources are clumped. Accounts of cooperative hunting, for example of young ungulates have not been studied systematically (Macdonald 1980a).

Damage to livestock or game Foxes are considered a major predator of ground-nesting colonial birds such as terns (many species of which are of conservation concern), and their effect on harvestable game-bird populations can be significant. They also predate hand-reared and released game-birds. Lambs may be taken locally but losses caused by foxes are typically only a small percentage (<2%) of all lambs born (Macdonald *et al.* 2000).

Adaptations

Paradoxically, it is probably the red fox's generalist conformation and lack of specialist adaptations that makes it the widely successful species that it is. The weakest element in this general formula, exploited by man and other predators, is the period of vulnerability of the young at the breeding den.

The red fox has great endurance and can gallop for several kilometres if pursued, they are able to run at speeds of up to 48km/h, jump fences two metres high and swim well (Haltenorth and Roth 1968). Red foxes can locate sounds to within one degree at 700–3,000Hz, though less accurately at higher frequencies. They are adapted to pounce on their prey with great precision, manipulating take-off angle to adjust length of jump and force of landing. They have relatively longer hind legs than other members of the dog family thereby increasing their propulsive force.

Dense, but short, fur covers approximately one-third of the body's surface area, particularly the face, dorsal part of head, nose, ears, lower legs and paws, and likely functions as a major heat exchange surface for thermoregulation (Klir and Heath 1992). The nose is used for evaporative cooling and probably forms part of a brain cooling mechanism as described in domestic dogs (Klir and Heath 1992). The physiology of their senses and their physical size and agility mean foxes are particularly well suited to preying on small rodents.

Red foxes can dig their own dens or may enlarge the burrows of other species, such as rabbits (*Oryctolagus cuniculus*), marmots (*Marmota* spp.), European badgers (*Meles meles*), or even other foxes. Dens normally are dug into banks, tree root systems, rocky crevices and even under buildings.

Social behaviour

The basic social unit is a pair, but groups with up to six members (usually one adult male and 2–5, probably related, vixens) may share a territory, depending on habitat. Range size is habitat dependent and can cover from less than 0.40km² (e.g., urban foxes in Oxford, UK), to as much as >40km²(>30km² in Arctic), depending on habitat (reviewed by Voigt and Macdonald 1984). One fox in the deserts of Oman had a range spanning 50km² (Lindsay and Macdonald 1986). There are reports of overlapping home ranges in some (but not all) urban (e.g., Harris 1979) and rural environments (Meia and Weber 1996) and drifting territories in other urban settings (Doncaster and Macdonald 1991).

Red foxes communicate with facial expressions, vocalisations and scent marking. Scent marking involves urine and facees (urine marking is sometimes confined to dominant females within a group), anal sac secretions, violet or supracaudal gland (more active in males during breeding season) as well as glands around lips, in the angle of the jaw and between pads of the feet. Some 28 different categories of vocalisation have been described, and are used to communicate over long distances and at close quarters. Individuals have characteristically different voices.

Mating behaviour is highly variable, and may include monogamous pairs, a single male with two breeding vixens that may or may not share a communal den, to a single breeding female with several non-breeding female helpers. There is always only one breeding male in the group although additional matings do occur outside the group. Territorial male red foxes make frequent excursions beyond their territories during the mating season, during which itinerant males also make incursions into territories (Macdonald 1987).

Juveniles may disperse between six and 12 months of age, mostly between October and January. All or most males disperse but the proportion of each sex dispersing varies between habitats and may depend on extent of mortality (e.g., due to rabies or control). Males typically disperse further than females (e.g., males 13.7km, females 2.3km in Welsh hills; Lloyd 1980; Trewhella *et al.* 1988). Dispersal distance correlates positively with home range size (Macdonald and Bacon 1982). In the UK, distances are generally less than 5km to more than 50km, but distances up to 394km have been recorded in the USA (Ables 1975) to 250km in Sweden (Englund 1970).

Reproduction and denning behaviour

Males are seasonally fecund. Mating occurs between December and February (June to October in Australia); the onset of breeding is correlated with day length and so starts earlier at more southerly latitudes. Females are receptive over a period of three days. Following a gestation period of 49–55 days, births occur from March to May. Birth weight is around 100g. Underground dens are needed to shelter cubs while they are very young. Lactation lasts for four weeks, and the cubs are fully weaned at 6-8 weeks. Sexual maturity is reached at 9-10 months. The proportion of breeding females in the group, and litter size (3-12 young per litter, usually 4–5 in Europe, 6–8 in Ontario; Voigt and Macdonald 1984), varies with food availability. Fox populations that are dense relative to food resources are generally less productive than those that are less dense. A single litter per year is the norm.

In high-density red fox populations where interactions with the dominant vixen are high, subordinate females do not usually breed, although they may breed successfully in low-density populations (in the UK, usually only one or two females in a group breed) (Macdonald 1980b, 1987). Both parents, and sometimes other females in the group, care for the young (Macdonald 1979b). The male provides food to the lactating female which is generally confined to the den prior to weaning. Weaned food is provided for the cubs by both parents. Non-breeding females may also feed, groom and tend the cubs and have been known to adopt them if orphaned (Macdonald 1979b). If two females breed within a group, they may share a den and litters may be communally suckled.

There is socially-mediated suppression of reproduction amongst females, with lowest productivity tending to occur where fox density is high or food supply poor. Where food is not limited, social status itself can suppress reproduction, with only the dominant female breeding. Behavioural mechanisms by which this occurs include harassment of subordinates, infanticide and cannibalism of subordinate vixens' cubs, and possibly the dominant male courting only the dominant females (Macdonald 1977b, 1980). A hormonal mechanism whereby stress leads to lowered productivity through foetal reabsorption has also been identified (Hartley *et al.* 1994). Consistent with this mechanism, Heydon and Reynolds (2000) found that in populations where productivity was low, reproductive performance was suppressed consistently at all stages of pregnancy, from conception to birth.

Competition

Red foxes compete with Arctic foxes where the two species occur sympatrically in the Eurasian tundra. Red foxes are larger and generally out-compete Arctic foxes (and has been known to kill both adults and young), but are limited to the north of their range, partly by the cold and partly by limited resources. Although both species are well adapted to cold conditions, adaptations of Arctic foxes are superior: 70% Arctic fox pelage is underfur, *cf.* 20% in red foxes; the lower critical temperature for Arctic fox *c.* -40°C, *cf. c.* -13°C for red fox). Larger red foxes also have greater energy requirements and reach a point (as productivity decreases in the north) where they cannot maintain a large enough home range to provide sufficient prey (Hersteinsson and Macdonald 1982). See also *Alopex lagopus* account.

Grey wolves and red foxes were originally sympatric throughout their shared range, but there is little dietary overlap between the two, and they may or may not use different habitats. Similar diets between covotes (Canis latrans) and red foxes lead to interference competition. In this case, the larger covote tends to be distributed wherever there are sufficient food resources and no other limiting factors, while red foxes occupy adjacent areas with lower amounts of food resources. Red fox numbers tend to be greater where coyotes are absent and foxes do not rear cubs where coyotes are active (Voigt and Earle 1983). Ratio of coyotes to foxes is lower where wolves are present than where wolves are absent in the USA (Peterson 1995). Diets are also similar between red and gray foxes (Urocyon cinereoargenteus), which are similar in size. In this case, exploitative competition for food is likely and habitat partitioning common. There is some evidence that gray foxes, despite being smaller, dominate red foxes in parts of eastern North America (Follmann 1973, Tuller and Berchielle 1982). Red foxes also kill kit foxes (Vulpes macrotis) (Ralls and White 1995). Red foxes kill stone martens (Martes foina) in areas where they feed on similar resources (Weber et al. 2002). European badgers will charge and displace foxes at feeding sites (D. Macdonald pers. obs.).

Mortality and pathogens

Natural sources of mortality Red fox life-history patterns are typified by high juvenile and subordinate adult mortality and lower adult mortality. Although demography can differ markedly between populations, roughly 75% of foxes die in their first year, and thereafter mortality is approximately 50% in each adult year.

Red foxes have few natural predators, although golden eagles (*Aquila chrysaetos*) may kill both cubs and adults, and badgers and domestic dogs may kill cubs. Red foxes are a regular prey of the Eurasian lynx (*Lynx lynx*) in the Swiss Jura Mountains (Jobin *et al.* 2000). In addition, coyotes and wolves have both been recorded killing adults and cubs (Voigt and Earle 1983; Pacquet 1992).

Persecution In the UK, people (through secondary poisoning, shooting and other methods of attempted control) are typically the major cause of fox mortality, which is especially high amongst dispersers. Foxes are widely culled as pests. In the UK, for instance, culling is widespread, though highly variable among regions in methods, intensity and impact (Heydon and Reynolds 2000). Shooting is the principal method. Controversially, foxes are also hunted with dogs in the UK, France, Belgium, Portugal, Italy, Germany, Switzerland, Australia, the USA and Canada. Mounted fox hunts, together with upland foot and gun packs, probably are responsible for the deaths of about 21,500-25,000 foxes annually in the UK, which at this national level is about 4% of total mortality (Macdonald et al. 2000). Reliable estimates of numbers dying through other individual causes not available (for example, the extent of both deliberate and secondary poisoning is largely unknown).

Hunter bags in other countries are: Germany 600,000 (2000–2001); Austria 58,000 (2000–2001); Sweden 58,000 (1999–2000); Finland 56,000 (2000–2001); Denmark 50,000 (1976–1977); Switzerland 34,832 (2001); Norway 17,000 (2000–2001); Saskatchewan (Canada) 2,000 (2000–2001); Nova Scotia (Canada) 491 (2000–2001); New Mexico (USA) 69 (1999–2000).

Hunting and trapping for fur Worldwide trade of wildcaught foxes in 1985–1986 was 1,543,995 pelts. In the USA, red fox made up 45% of trade in wild-caught pelts worth \$50 million in 1983. Most red foxes are killed for a variety of reasons, of which their value as fur is only one.

Road kills Where road-traffic is a dominant feature in modern landscapes, many red foxes are killed by vehicles. Juvenile and dispersing (mostly juvenile male) foxes are thought to be particularly susceptible. The impact of this mortality on population dynamics is not clear, and in both urban and rural environments, red fox populations exist alongside heavy road traffic. Fox density among three regions of England and Wales matched variation in culling pressure but did not match variation in road traffic density (Heydon *et al.* 2000).

Pathogens and parasites Populations are locally and periodically reduced by rabies epizootics (mortality rates

estimated at 60-80% by simulation models; Voigt et al. 1985), although recovery appears to be swift (e.g., Western Europe, USA; Wandeler et al. 1974). Red foxes are a widespread reservoir of rabies, especially in central Europe, south-eastern Canada and north-eastern USA (Chomel 1993). Oral vaccines have been successfully used in some European countries (Kappeler et al. 1988) but there are still areas where rabies control has failed (Funk et al. 2001). Oral vaccination is regarded by the World Health Organization and European Union as an ongoing experiment. The red fox is host to a wide range of parasites including at least 58 species of helminths in Europe alone (Wolfe et al. 2001; Simpson 2002). One of the most serious of the parasites infecting foxes is the skin-dwelling mite (Sarcoptes scabei var. vulpes) which causes sarcoptic mange. This disease is locally and temporally prevalent. It appeared in Finland in 1967 and spread to Norway and Sweden in the 1970s and 1980s, where it reduced the red fox population by over 70% (Holt and Berg 1990; Lindström 1992). Since then it has spread across most of Europe including England, where it wiped out over 90% of the fox population in Bristol, UK in the early 1990s (Macdonald et al. 1997) and south-west to Spain (Gortazar et al. 1998) and New York (Tullar et al. 1974). Several other diseases are also recorded, including canine distemper, parvovirus, toxoplasmosis, bovine tuberculosis, and paratuberculosis but these do not appear to be major determinants of fox density (Little et al. 1982; Voigt 1987; Beard et al. 1999).

Longevity Foxes can live up to nine years in the wild, although only an estimated one in 10,000 will do so. Foxes in agricultural Europe generally live less than three years.

Historical perspective

Red foxes are widely represented in folklore. They have been hunted since the 4th century B.C. Fox hunting with dogs has been a notable part of European culture since at least the 11th century and was spread world-wide by British colonists. Red foxes are an increasingly important component of fur harvest taken from North America. As with most other furbearers, 20th century sales numerically far exceeded those in any previous century (Obbard *et al.* 1987). In 1992–1993, red fox fur was the third most important wild-caught furbearer in North America, in terms of commercial value (Sheiff and Baker 1987). Numbers sold, and therefore presumably harvests, fluctuate heavily with demand, although in settled regions culls are also related to pest status.

Conservation status

Threats Habitat degradation, loss, fragmentation; exploitation, direct and indirect persecution; government policies. Other threats: Local, national, or international socio-economic and political factors. Increasing human population and thus increasing development. Red foxes' versatility and eclectic diet are likely to ensure their persistence despite changes in landscape and prey base. Culling may be able to reduce numbers well below carrying capacity in large regions (Heydon and Reynolds 2000), but no known situations exist where this currently threatens species persistence on any geographical scale. There are currently bounties on subspecies V. v. pusilla (desert foxes) in Pakistan to protect game birds such as Houbara bustards (*Chlamydotis undulata* macqueenii), with a high hunting value.

Commercial use The number of foxes raised for fur (although much reduced since the 1900s) exceeds that of any other species, except possibly mink (*Mustela vison*) (Obbard 1987). Types farmed are particularly colour variants ("white", "silver" and "cross") that are rare in the wild.

Worldwide trade in ranched red fox pelts (mainly "silver" pelts from Finland) was 700,000 in 1988–1989 (excluding internal consumption in the USSR). Active fur trade in Britain in 1970s was negligible.

Occurrence in protected areas Present in most temperate-subarctic conservation areas with the exception of some inaccessible islands in the Old World and South America.

Protection status Widely regarded as a pest and unprotected. CITES – not listed.

V. v. necator in the Sierra Nevada, California, USA, is rare, possibly declining (Nowak 1991). The subspecies *griffithi, montana* and *pusilla* (*=leucopus*) are listed as CITES – Appendix III (India).

Current legal protection Most countries and/or states where trapping or hunting occurs have regulated closed versus open seasons and restrictions on methods of capture. In the European Union, Canada, and the Russian Federation, trapping methods are regulated under an agreement on international trapping standards between these countries which was signed in 1997. Other countries are signatories to ISO/DIS 10990-5.2 animal (mammal) traps which specifies standards for trap testing.

Conservation measures taken In Europe and North America, hunting traditions and/or legislation impose closed seasons on fox hunting. In the UK and a few other European countries, derogation from these provisions allows breeding season culling for pest-control purposes. Here, traditional hunting ethics encouraging restrained "use" may be at odds with harder hitting pest-control ambitions. This apparent conflict between different interest groups is particularly evident in the UK, where fox control patterns are highly regionally variable (Macdonald *et al.* 2003). In some regions, principal lowland areas where

classical mounted hunting operates, limited economic analyses suggest that the principal motive for these communal fox hunts is as a sport – the number killed is small compared with the cost of the hunting. In these regions, most anthropogenic mortality is by individual farmers shooting foxes. The mounted communal hunts do exhibit restraint – hunting takes place for a limited season, and for a prescribed number of days per week. Elsewhere, in upland regions, communal hunting by foot with guns and dogs may make economic sense, depending on the number of lambs lost to foxes (data on this is poor), and also on the current value of lost lambs. This type of fox hunting may also be perceived as a sport by its participants.

An individual deciding whether or not to control foxes, and by what means, has a complex set of factors to consider, including other interest groups, practicality and economics. For some farmers, there is evidence that a decision to control foxes may be economically perverse. Macdonald *et al.* (2003) modelled the interactions between foxes, rabbits, and rabbit-induced crop damage. For some farmers at least, a decision to kill a fox may, in some circumstances, cost that farmer a significant amount of crop loss to the rabbits that the fox and its descendants would have killed.

Occurrence in captivity

In addition to fur farms, red foxes are widely kept in small wildlife parks and zoos, but there appears to be no systematic data on their breeding success. Being extremely shy they are often poor exhibits.

Current or planned research projects

Controlling red foxes may be necessary where rare species, or threatened populations, are under threat, e.g., nest predation by foxes, has completely prevented recruitment to an internationally important sandwich tern colony in a number of consecutive years (Musgrave 1993). Attempting to control predation by lethal means can be problematic, i.e., intensive fox removal has been shown to have only local and short-term effects on predation because of swift replacement by conspecifics (Chesness *et al.* 1968; Reynolds *et al.* 1993). Non-lethal methods might prove useful in managing undesirable behaviour, with some potential shown for learned food aversions for manipulating fox feeding behaviour (Macdonald and Baker 2003).

Core literature

Baker and Harris 2004; Doncaster and Macdonald 1991; Harris and Rayner 1986; Larivière and Pasitschniak-Arts 1996; Lloyd 1980; Macdonald 1977a, 1979b, 1987; Meia 1994.

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5.4 Raccoon dog *Nyctereutes procyonoides* (Gray, 1834) Least Concern (2004)

K. Kauhala and M. Saeki

Other names

Chinese: háo/háo-zi; Croatian: kunopas; Czech: psíik mývalovitý; Danish and Norwegian: mårhund; Dutch: wasbeerhond; Estonian: kährikkoer; Finnish: supikoira; French: chien viverrin; Georgian: entiseburi dzagli; German: marderhund; Hungarian: nyestkutya; Indonesian: tjerpelai; Italian: cane procione; Japanese: tanuki; Korean: nurgoori; Latvian: jenotsuns; Lithuanian: usûrinis ðuo; Polish: jenot; Portuguese: câo-mapache; Romanian: câinele enot; Russian: enotovidnaya sobaka; Slovakian: psík medviedikovitý; Slovenian: rakunasti pes; Spanish: perro mapache; Swedish: mårdhund.

Taxonomy

Canis procyonoides Gray, 1834. Illustr. Indian Zool., 2: pl. 1. Type locality: Unknown; restricted to "vicinity of Canton, China" by Allen (1938).

The raccoon dog lineage diverged from other canids probably as early as 7–10 million years ago (Wayne 1993). Some features of the skull resemble those of South American canids, especially that of the crab-eating fox (*Cerdocyon thous*), but genetic studies have revealed that they are not close relatives (Wayne *et al.* 1997).

It has been suggested that N. p. viverrinus and N. p. albus (collectively called 'tanuki') can be separated as a different species from the other subspecies. Tanuki has fewer chromosomes than other continental subspecies with 2n=38 (Wada *et al.* 1998), while others have 2n=54(Mäkinen 1974; Mäkinen et al. 1986; Ward et al. 1987; Wada et al. 1991). The chromosome number of tanuki has decreased as a result of Robertsonian translocations, which usually happens during speciation. In addition to a number of phenotypic and behavioural differences, preliminary DNA-analyses also suggest that there are considerable differences in gene frequencies between tanuki and N. p. ussuriensis from Finland (K. Kauhala unpubl.), and skull and tooth morphometrics also differ (Kauhala et al. 1998a). In addition, there are differences in the quality of fur and physiology; since the Japanese raccoon dog is adapted to mild marine climate, it has a stomach of small volume, thin fur with poor insulation properties and a poor ability to alter its body energy reserves seasonally (Korhonen et al. 1991).

Description

For *N. p. ussuriensis*: In autumn and winter, the raccoon dog is very fat and has thick fur, giving an expression of a round animal with short and thin legs. The black facial