

Central and North America (Nearctic)

4.1 Coyote

***Canis latrans* Say, 1823**
Least Concern (2004)

E.M. Gese and M. Bekoff

Other names

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

Taxonomy

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

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

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

Description

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

Table 4.1.1 Body measurements for the coyote.

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



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

David Shackleton

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

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

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

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

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

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



Figure 4.1.1. Current distribution of the coyote.

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Distribution

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

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

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

Relative abundance

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

Coyote densities in different geographic areas and seasons (Table 4.1.2) vary from 0.01–0.09 coyotes/km² in the winter in the Yukon (O'Donoghue *et al.* 1997) to 0.9

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

km² in the fall and 2.3/km² during the summer (post-whelping) in Texas (Knowlton 1972; Andelt 1985).

Estimated populations/relative abundance and population trends

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

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

Habitat

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

Food and foraging behaviour

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

Foraging behaviour Studies on the predatory behaviour of coyotes show that age of the coyote, wind, habitat, and snow conditions all influence their ability to capture small mammals (Bekoff and Wells 1986; Gese *et al.* 1996a). Coyotes hunt small mammals alone, even when pack size is large (Gese *et al.* 1996a). When preying on native ungulates, cooperation among pack members may facilitate the capture of prey, but is not essential. Environmental factors are important to the success of an attack on adult ungulates. Presence of the alpha pair is important in determining the success of the attack, and younger animals generally do not participate. The number of coyotes is not as important as who is involved in the attack (Gese and Grothe 1995). Also,

the ability of the ungulate to escape into water, defensive abilities of the individual and cohorts, and nutritional state of the individual under attack, contribute to the outcome (Gese and Grothe 1995). In areas with an ungulate prey base in winter, resource partitioning and competition for a carcass may be intense, even among members of the same pack (Gese *et al.* 1996b). When coyotes prey on sheep, they generally attack by biting the throat and suffocating the animal. Defensive behaviours by sheep sometimes can deter coyotes from continuing their attack.

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

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

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

Adaptations

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

Social behaviour

Coyotes are considered less social than wolves (but see Gese *et al.* 1996b, c). The basic social unit is the adult, heterosexual

pair, referred to as the alpha pair. Coyotes form heterosexual pair bonds that may persist for several years, but not necessarily for life. Coyotes may maintain pair bonds and whelp or sire pups up to 10–12 years of age. Associate animals may remain in the pack and possibly inherit or displace members of the breeding pair and become alphas themselves. Associates participate in territorial maintenance and pup rearing, but not to the extent of the alpha pair. Other coyotes exist outside of the resident packs as transient or nomadic individuals. Transients travel alone over larger areas and do not breed, but will move into territories when vacancies occur.

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

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

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

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

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

Reproduction and denning behaviour

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

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

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

The pups are born blind and helpless in the den. Birth weight is 240–275g; length of the body from tip of head to base of tail is about 160mm (Gier 1968). Eyes open at about 14 days and pups emerge from the den at about

three weeks. The young are cared for by the parents and other associates, usually siblings from a previous year (Bekoff and Wells 1986). Pups are weaned at about 5–7 weeks of age and reach adult weight by about nine months.

Competition

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

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

Mortality and pathogens

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

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

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

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

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

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

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

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

Historical perspective

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

Conservation status

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

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

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

Protection status CITES – not listed.

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

Conservation measures taken None at present.

Occurrence in captivity

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

Current or planned research projects

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

Gaps in knowledge

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

influencing prey selection; communication; adaptations in urban and rural environments; and interactions with threatened species.

Core literature

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

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

4.2 Red wolf

Canis rufus Audubon and Bachman, 1851 Critically Endangered – CR: D (2004)

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

Other names

None.

Taxonomy

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

In recent history the taxonomic status of the red wolf has been widely debated. Mech (1970) suggested red wolves may be fertile hybrid offspring from grey wolf (*Canis lupus*) and coyote (*C. latrans*) interbreeding. Wayne and Jenks (1991) and Roy *et al.* (1994b, 1996) supported this

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

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

Description

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



Male red wolf, age unknown.

Art Beyer

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

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

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

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

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

Distribution

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

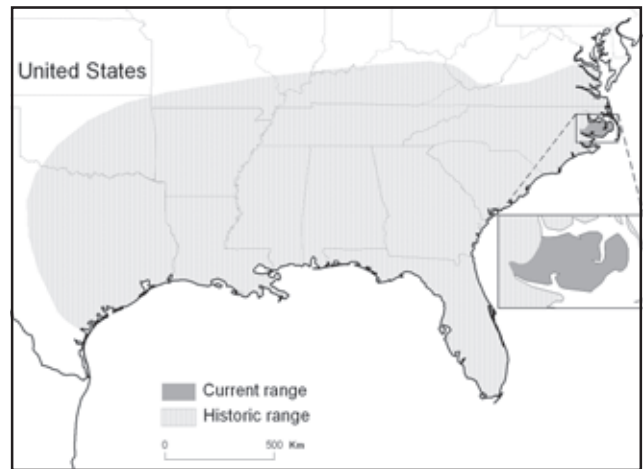


Figure 4.2.1. Current distribution of the red wolf.

but even greater extension of historic range into Algonquin Provincial Park in southern Ontario, Canada.

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

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

Relative abundance

Extinct in the Wild by 1980, the red wolf was reintroduced by the United States Fish and Wildlife Service (USFWS) in 1987 into eastern North Carolina. The red wolf is now common within the reintroduction area of roughly 6,000km² (Table 4.2.2). However, the species' abundance outside the reintroduction area is unknown.

Estimated populations/relative abundance and population trends

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

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

Habitat

Very little is known about red wolf habitat because the species' range was severely reduced by the time scientific

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

Food and foraging behaviour

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

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

Damage to livestock or game Historically, the red wolf was believed to be a killer of livestock and a threat to local game populations, despite lack of data to support such a belief. As of September 2002, the reintroduced population in north-eastern North Carolina has been responsible for only three depredations since 1987 (USFWS unpubl.).

Adaptations

Red wolves are well adapted to the hot, humid climate of the south-eastern United States. Their relatively large ears allow for efficient dissipation of body heat, and they moult once a year, which results in them replacing their relatively thick, heat-retaining, cold-season pelage with a thin and coarse warm-season pelage. Such a moult pattern ensures that red wolves are not only able to tolerate the warm humid conditions that predominate in the south-eastern United States, but also the wide range of annual climatic conditions that characterise the region in general. A potential specific adaptation appears to be the ability of the red wolf to survive heartworm infestation. All the adult wild red wolves tested for heartworm in the restored population in North Carolina test positive for heartworm; yet, unlike in domestic dogs and other canids, it is not known to be a significant cause of mortality. More general adaptations include the tolerance of the red wolf's metabolic system to the feast/famine lifestyle that results from the species' predatory habits.

Social behaviour

Like grey wolves, red wolves normally live in extended family units or packs (Phillips and Henry 1992; Phillips *et al.* 2003). Packs typically include a dominant, breeding pair and offspring from previous years. Dispersal of offspring typically occurs before individuals reach two years of age (Phillips *et al.* 2003). Group size in the reintroduced population typically ranges from a single breeding pair to 12 individuals (Phillips *et al.* 2003; USFWS unpubl.). Red wolves are territorial and, like other canids, appear to scent mark boundaries to exclude non-group members from a given territory (Phillips *et al.* 2003; USFWS unpubl.). Home range size varies from 46–226km², with variation due to habitat type (Phillips *et al.* 2003).

Reproduction and denning behaviour

Red wolves typically reach sexual maturity by 22 months of age, though breeding at 10 months of age may occur (Phillips *et al.* 2003). Mating usually occurs between February and March, with gestation lasting 61–63 days (Phillips *et al.* 2003). Peak whelping dates occur from mid-April to mid-May producing litters of 1–10 pups (USFWS unpubl.). In a given year, there is typically one litter per pack produced by the dominant pair. Two females breeding within a pack is suspected but has not yet been proven. During the denning season, pregnant females may establish several dens. Some dens are shallow surface depressions located in dense vegetation for shelter at locations where the water table is high, while other dens are deep burrows often in wind rows between agricultural fields or in canal banks; dens have also been found in the hollowed out bases of large trees (Phillips *et al.* 2003; USFWS unpubl.). Pups are often moved from one den to another before abandoning the den altogether, and den attendance by

male and female yearlings and adult pack members is common (USFWS unpubl.).

Competition

The degree of competition for prey and habitat between red wolves, coyotes and red wolf × coyote hybrids, is uncertain. Studies to determine this are currently underway (see Current or planned research projects below). In contrast, competition for mates between red wolves and coyotes or red wolf × coyote hybrids appears to be significant (Kelly *et al.* 1999) (see Conservation status: Threats below). Red wolves may also compete, to a lesser degree, with black bears (*Ursus americanus*). The destruction of red wolf dens by black bears has been observed, although it is unknown if these dens had already been abandoned (USFWS unpubl.). Conversely, wolves have also been observed killing young bears (USFWS unpubl.).

Mortality and pathogens

Natural sources of mortality Natural mortality accounts for approximately 21% of known mortality. There are no known major predators of red wolves, although intraspecific aggression accounts for approximately 6% of known red wolf mortalities (USFWS unpubl.).

Persecution Human-induced mortality in red wolves is significant in the reintroduced population and more substantial than natural causes of mortality. It accounts for approximately 17% of known red wolf deaths (primarily from gunshot, traps, and poison) (USFWS unpubl.). Direct persecution by humans was a key factor in the eradication of red wolves from much of the south-eastern United States.

Hunting and trapping for fur There are currently no legal hunting or trapping for fur programmes for red wolves in the United States. Wolves purported to be red wolf-like wolves *Canis lupus lycaon* (see Taxonomy section above) are trapped for fur in Canada when they migrate out of Algonquin Provincial Park.

Road kills In the reintroduced population, road kills are the most common mortality factor accounting for 18% of known red wolf deaths (USFWS unpubl.). However, a proportionately higher number of deaths from vehicle strikes occurred earlier in the reintroduction efforts when captive wolves were released, suggesting that a tolerance in those wolves to human activities predisposed them to spend more time on or near roads (Phillips *et al.* 2003; USFWS unpubl.).

Pathogens and parasites Heartworms (*Dirofilaria immitis*), hookworms (*Ancylostoma caninum*), and sarcoptic mange (*Sarcoptes scabiei*) have been considered important sources of mortality in red wolves (USFWS

1990). In the reintroduced population in North Carolina, both heartworms and hookworms occur, but, neither appear to be a significant source of mortality (Phillips and Scheck 1991; USFWS unpubl.). Mortalities related to demodectic mange and moderate to heavy tick infestations from American dog ticks (*Dermacentor variabilis*), lone star ticks (*Amblyomma americanum*), and black-legged ticks (*Ixodes scapularis*) have also occurred in the reintroduced population but, likewise, do not appear to be significant mortality factors (USFWS unpubl.). Tick paralysis of a red wolf has been documented in North Carolina (Beyer and Grossman 1997).

Longevity Appears to be similar to other wild canids in North America. In the absence of human-induced mortality, red wolves have been documented to have lived in the wild as long as 13 years (USFWS unpubl.).

Historical perspective

Although red wolves ranged throughout the south-eastern United States before European settlement, by 1980 they were considered Extinct in the Wild (McCarley and Carley 1979; USFWS 1990). There are no known traditional uses of red wolves by Native Americans or early settlers. Rather, it is likely that red wolves were viewed by early settlers as an impediment to progress and as pests that were best destroyed. Demise of the species has largely been attributed to human persecution and destruction of habitat that led to reduced densities and increased interbreeding with coyotes (USFWS 1990). These factors were largely responsible for the eradication of the species, with the exception of those individuals found occupying marginal habitats in Louisiana and Texas in the 1970s. In these habitats, red wolves frequently suffered heavy parasite infestation (Goldman 1944; Nowak 1972, 1979; Carley 1975).

The plight of the species was recognised in the early 1960s (McCarley 1962), and the red wolf was listed as endangered in 1967 under United States legislation that preceded the Endangered Species Act (ESA) of 1973. A recovery programme was initiated after passage of the ESA in 1973. It was during the early 1970s that the USFWS determined recovery of the species could only be achieved through captive breeding and reintroductions (see Conservation measures taken below) (USFWS 1990).

Conservation status

Threats Hybridisation with coyotes or red wolf × coyote hybrids is the primary threat to the species' persistence in the wild (Kelly *et al.* 1999). While hybridisation with coyotes was a factor in the red wolf's initial demise in the wild, it was not detected as a problem in north-eastern North Carolina until approximately 1992 (Phillips *et al.* 1995). Indeed, north-eastern North Carolina was determined to be ideal for red wolf reintroductions because

of a purported absence of coyotes (Parker 1986). However, during the 1990s, the coyote population apparently became well established in the area (P. Sumner pers. comm.; USFWS unpubl.).

It has been estimated that the red wolf population in North Carolina can sustain only one hybrid litter out of every 59 litters (1.7%) to maintain 90% of its genetic diversity for the next 100 years (Kelly *et al.* 1999). However, prior to learning of this acceptable introgression rate, the introgression rate noted in the reintroduced population was minimally 15% (Kelly *et al.* 1999) or approximately 900% more than the population can sustain to maintain 90% of its genetic diversity for 100 years. If such levels of hybridisation continued beyond 1999, non-hybridised red wolves could disappear within 12–24 years (3–6 generations). An adaptive management plan designed to test whether hybridisation can be reduced to acceptable levels was initiated in 1999 (Kelly 2000) (see Current or planned research projects below). Initial results from this plan suggest that the intensive management specified in the plan may be effective in reducing introgression rates to acceptable levels (B. Fazio pers. comm.).

In the absence of hybridisation, recovery of the red wolf and subsequent removal of the species from the U.S. Endangered Species List is deemed possible. It is noteworthy that similar hybridisation has been observed in the population of suspected red wolf-type wolves in Algonquin Provincial Park, Ontario, Canada (see Taxonomy above). If these wolves are ultimately shown to be red wolf-type wolves, this will enhance the conservation status of the species and nearly triple the known number of red wolf-type wolves surviving in the wild.

As noted above (see Mortality), human-induced mortality (vehicles and gunshot) can be significant. However, the threat this mortality represents to the population is unclear. Most vehicle deaths occurred early in the reintroduction and were likely due to naive animals. Nonetheless, the overall impact of these mortality factors will depend on the proportion of the losses attributable to the breeding segment of the population (effective population (N_e) and what proportion of the overall population is lost due to these human factors (both N and N_e).

Commercial use None.

Occurrence in protected areas The only free-ranging population of red wolves exists in north-eastern North Carolina in an area comprised of 60% private land and 40% public land. This area contains three national wildlife refuges (Alligator River NWR, Pocosin Lakes NWR, and Mattamuskeet NWR) which provide important protection to the wolves. Red wolves or a very closely related taxon may also occupy Algonquin Provincial Park, Ontario, Canada (see Taxonomy above).

Protection status CITES – not listed.

Current legal protection The red wolf is listed as ‘endangered’ under the U.S. Endangered Species Act (ESA) (United States Public Law No. 93-205; United States Code Title 16 Section 1531 *et seq.*). The reintroduced animals and their progeny in north-eastern North Carolina are considered members of an experimental non-essential population. This designation was promulgated under Section 10(j) of the ESA and permits the USFWS to manage the population and promote recovery in a manner that is respectful of the needs and concerns of local citizens (Parker and Phillips 1991). Hunting of red wolves is prohibited by the ESA. To date, federal protection of the red wolf has been adequate to successfully reintroduce and promote recovery of the species in North Carolina.

Conservation measures taken A very active recovery programme for the red wolf has been in existence since the mid-1970s (Phillips *et al.* 2003; USFWS 1990), with some measures from as early as the mid-1960s (USFWS unpubl.). By 1976, a captive breeding programme was established using 17 red wolves captured in Texas and Louisiana (Carley 1975; USFWS 1990). Of these, 14 became the founders of the current captive breeding programme. In 1977, the first pups were born in the captive programme, and by 1985, the captive population had grown to 65 individuals in six zoological facilities (Parker 1986).

With the species reasonably secure in captivity, the USFWS began reintroducing red wolves at the Alligator River National Wildlife Refuge in north-eastern North Carolina in 1987. As of September 2002, 102 red wolves have been released with a minimum of 281 descendants produced in the wild since 1987. As of September 2002, there is a minimum population of 66 wild red wolves in north-eastern North Carolina, with a total wild population believed to be at least 100 individuals. Likewise, at this same time, there is a minimum population of 17 hybrid canids present in north-eastern North Carolina. The 17 known hybrids are sterilised and radio-collared (USFWS unpubl.).

During 1991 a second reintroduction project was initiated at the Great Smoky Mountains National Park, Tennessee (Lucash *et al.* 1999). Thirty-seven red wolves were released from 1992 to 1998. Of these, 26 either died or were recaptured after straying onto private lands outside the Park (Henry 1998). Moreover, only five of the 32 pups known to have been born in the wild survived but were removed from the wild during their first year (USFWS unpubl.). Biologists suspect that disease, predation, malnutrition, and parasites contributed to the high rate of pup mortality (USFWS unpubl.). Primarily because of the poor survival of wild-born offspring, the USFWS terminated the Tennessee restoration effort in 1998 (Henry 1998).

Occurrence in captivity

As of September 2002, there are approximately 175 red wolves in captivity at 33 facilities throughout the United States and Canada (USFWS unpubl.). The purpose of the captive population is to safeguard the genetic integrity of the species and to provide animals for reintroduction. In addition, there are propagation projects on two small islands off the South Atlantic and Gulf Coasts of the U.S. which, through reintroduction of known breeding individuals and capture of their offspring, provide wild-born pups for release into mainland reintroduction projects (USFWS 1990).

Current or planned research projects

In an effort to understand and manage red wolf hybridisation with coyotes and red wolf x coyote hybrids, the USFWS is implementing a Red Wolf Adaptive Management Plan (RWAMP) (Kelly 2000). The plan, which employs an aggressive science-based approach to determine if hybridisation can be managed, was developed after consultation with numerous wolf biologists and geneticists and first implemented in 1999 (Kelly *et al.* 1999; Kelly 2000). The goal of the plan is to assess whether hybridisation can be managed such that it is reduced to an acceptably low level (see Conservation status: Threats above). As of September 2002, the initial results from the RWAMP indicate that this seems to be the case. If these initial results hold, the next questions that need to be addressed for the conservation of the red wolf in the wild will be: (1) what is the long-term feasibility of sustaining the intensive management of the RWAMP?; and (2) will introgression rates remain at an acceptable level in the absence of the current intensive management? As part of the RWAMP, several research projects are underway:

L. Waits and J. Adams (University of Idaho, USA) are using non-invasive genetic techniques to monitor presence and distribution of canids in the reintroduction area, and are working to improve genetic identification techniques.

The USFWS is examining whether red wolves and coyotes compete with each other for space or share space and partition resources, and is testing the use of captive-reared pups fostered into the wild red wolf population to enhance genetic diversity.

P. Hedrick and R. Frederickson (Arizona State University, USA) are conducting sensitivity analyses of a deterministic genetic introgression model.

D. Murray (Trent University, Canada) is developing a survival-based spatial model of wolf-coyote interactions.

M. Stoskopf and K. Beck (North Carolina State University, USA) are studying the use of GPS collars to monitor wolf movements, the social behaviour of red wolves and coyotes, and the epidemiology of coyote introgression into the wild red wolf population.

K. Goodrowe (Point Defiance Zoo and Aquarium, Washington, USA) is conducting extensive research regarding various aspects of the red wolf reproductive cycle.

D. Rabon (University of Guelph, Canada) is studying the roles of olfactory cues and behaviour in red wolf reproduction.

Core literature

Kelly 2000; Kelly *et al.* 1999; Nowak 1979, 2002; Paradiso and Nowak 1972; Phillips. *et al.* 1995, 2003; Riley and McBride 1972; USFWS 1990.

Reviewers: David Mech, Richard Reading, Buddy Fazio.

Editors: Claudio Sillero-Zubiri, Deborah Randall, Michael Hoffmann.

4.3 Gray fox *Urocyon cinereoargenteus* (Schreber, 1775) Least Concern (2004)

T.K. Fuller and B.L. Cypher

Other names

English: tree fox; **Spanish:** zorro, zorro gris, zorra gris (Mexico), zorro plateado, gato de monte (southern Mexico), gato cervan (Honduras).

Taxonomy

Canis cinereoargenteus Schreber, 1775. Die Säugethiere, 2(13):pl. 92[1775]; text: 3(21):361[1776]. Type locality: “eastern North America” (“Sein Vaterland ist Carolina und die Wärmeren Gegenden von Nordamerica, vielleicht auch Surinam”).

Gray foxes traditionally were considered to be distinct from other foxes. Clutton-Brock *et al.* (1976) and Van Gelder (1978) proposed reclassifying gray foxes as *Vulpes*. However, Geffen *et al.* (1992e) determined that gray foxes represent an evolutionary lineage that is sufficiently distinct from vulpine foxes to warrant recognition as a separate genus.

A molecular phylogenetic analysis of the Canidae showed that there are four monophyletic clades (*Canis* group, *Vulpes* group, South American foxes and the bush dog/maned wolf clade) and three distantly related basal taxa, one of which is the gray fox (*U. cinereoargenteus*; Wayne *et al.* 1997). The gray fox often clusters with two other ancient lineages, the raccoon dog (*Nyctereutes procyonoides*) and the bat-eared fox (*Otocyon megalotis*) but the exact relationship among these taxa is unclear. The early origination of these lineages has resulted in significant sequence divergence that may have masked unique sequence similarities (i.e., synapomorphies) that would have resulted

from common ancestry (Wayne *et al.* 1997). Despite the unclear affinities, *Urocyon* is currently considered a basal genus within the Canidae and has only two surviving members, the gray and island fox (*Urocyon littoralis*).

Chromosome number is $2n=66$ (Fritzell and Haroldson 1982).

Description

The gray fox is medium sized with a stocky body, moderately short legs and medium-sized ears (Table 4.3.1). The coat is grizzled grey on the back and sides with a dark longitudinal stripe on top of a black-tipped tail, dark and white markings on its face, and a conspicuous cinnamon-rusty colour on its neck, sides and limbs. There is also white on its ears, throat, chest, belly and hind limbs, while the undercoat is mostly buff and grey. The tail is thick and bushy, and the fur is coarse-appearing. The dental formula is $3/3-1/1-4/4-2/3=42$. The posterior ventral border of the dentary has a prominent notch or “step”, and on the cranium, the temporal ridges are separated anteriorly but connect posteriorly to form a distinctive “U” shape (Hall 1981).

Total length male	981mm (900–1,100) n=24
Total length female	924mm (825–982) n=20
T male	385mm (333–443) n=24
T female	357mm (280–407) n=20
HF male	137mm (100–150) n=24
HF female	130mm (115–140) n=20
E male	79mm (60–89) n=24
E female	77mm (55–101) n=20
WT male	4.0kg (3.4–5.5) n=18
WT female	3.3kg (2.0–3.9) n=16

Adult gray fox, sex unknown. Fresno, California, USA, 2003.



Karen Brown

Subspecies Up to 16 subspecies are recognised (Fritzell and Haroldson 1982):

- *U. c. borealis* (New England)
- *U. c. californicus* (southern California)
- *U. c. cinereoargenteus* (eastern United States)
- *U. c. costaricensis* (Costa Rica)
- *U. c. floridanus* (Gulf states)
- *U. c. fraterculus* (Yucatan)
- *U. c. furvus* (Panama)
- *U. c. guatemalae* (southernmost Mexico south to Nicaragua)
- *U. c. madrensis* (southern Sonora, south-west Chihuahua, and north-west Durango)
- *U. c. nigrirostris* (south-west Mexico)
- *U. c. ocythous* (Central Plains states)
- *U. c. orinomus* (southern Mexico, Isthmus of Tehuantepec)
- *U. c. peninsularis* (Baja California)
- *U. c. scottii* (south-western United States and northern Mexico)
- *U. c. townsendi* (California and Oregon)
- *U. c. venezuelae* (Colombia and Venezuela)

Similar species Island fox (*Urocyon littoralis*): very similar in appearance to the gray fox, but tends to be somewhat darker and is 25–50% smaller (Crooks 1994; Moore and Collins 1995); confined to the Channel Islands off the southern coast of California, and considered to be descended from mainland gray foxes (Collins 1982; Wayne *et al.* 1991; Moore and Collins 1995).

Current distribution

The gray fox is widespread in forest, woodland, brushland, shrubland, and rocky habitats in temperate and tropical regions of North America, and in northernmost montane regions of South America.

Historical distribution In North America, the historical northernmost distribution of the gray fox probably was somewhat further south than its current northern limit (Fritzell and Haroldson 1982). Also, the range of the species probably did not extend significantly into the Great Plains because of the lack of brushy cover. Habitat modifications, such as fire suppression and tree planting, have facilitated occupation of this biome (Fritzell 1987). The species also was formerly found on Martha’s Vineyard, a small offshore island in the state of Massachusetts (Waters 1964). In Central America, gray foxes were much more widespread before the conversion of forested land into pastures and urban areas (de la Rosa and Nocke 2000).

Current distribution The gray fox ranges from the southern edge of central and eastern Canada, and Oregon, Nevada, Utah, and Colorado in the United States south to

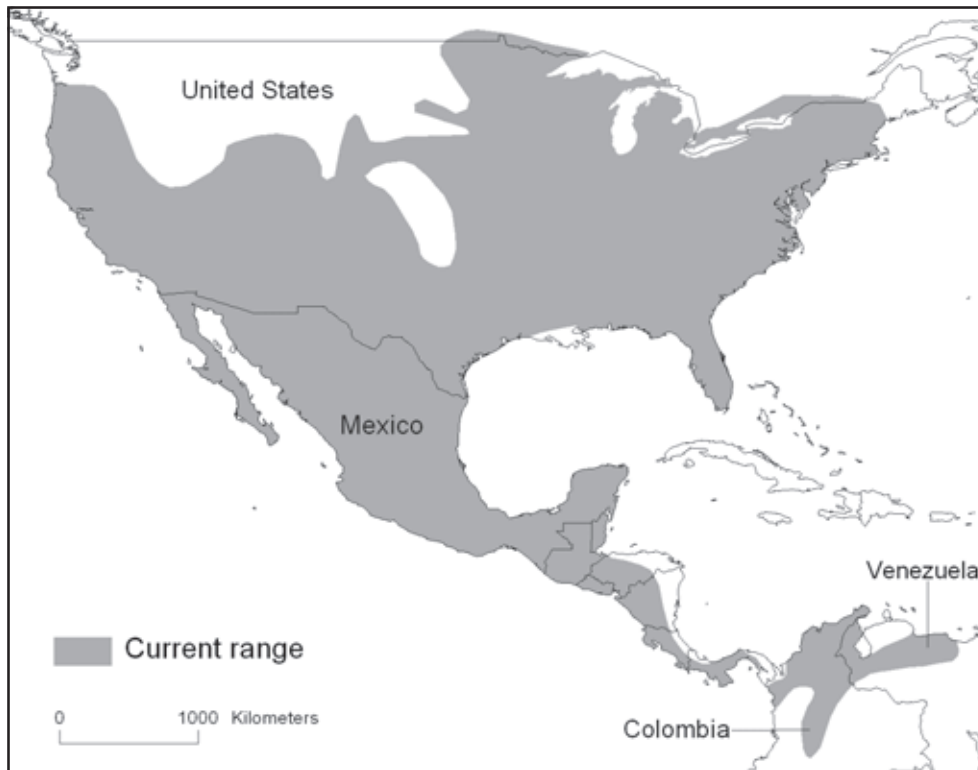


Figure 4.3.1. Current distribution of the gray fox.

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northern Venezuela and Colombia; and from the Pacific coast of the United States to the Atlantic and Caribbean oceans. The species is not found in the northern Rocky Mountains of the United States, or in the Caribbean watersheds of Honduras, Nicaragua, Costa Rica, and western Panama (Figure 4.3.1).

Range countries Belize, Canada, Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, United States of America, Venezuela (Hall 1981; Fritzell 1987; Eisenberg 1989; de la Rosa and Nocke 2000).

Relative abundance

The gray fox is common in occupied habitat, but appears to be restricted to locally dense habitats where it is not excluded by sympatric coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) (Farias 2000b).

Estimated populations/relative abundance and population trends No estimates of total gray fox abundance have been attempted. Reported densities range from 0.4/km² in California (Grinnell *et al.* 1937) to 1.5/km² in Florida (Lord 1961). There is no good evidence that gray fox numbers are increasing or decreasing in any part of their range.

Habitat

In eastern North America, the gray fox is most closely associated with deciduous/southern pine forests

interspersed with some old fields and scrubby woodlands (Hall 1981). In western North America, it is commonly found in mixed agricultural/woodland/chaparral/riparian landscapes, and shrub habitats. The species occupies forested areas and thick brush habitats in Central America, and forested montane habitats in South America (Eisenberg 1989). Gray foxes occur in semi-arid areas of the south-western U.S. and northern Mexico where cover is sufficient. They appear to do well on the margins of some urban areas (Harrison 1997).

Food and foraging behaviour

Food Gray foxes have been identified as the most omnivorous of all North American fox species (Fritzell and Haroldson 1982). They consume primarily rabbits (*Sylvilagus* spp.) and rodents during cold winter months, then greatly diversify their diets in spring and summer to include insects, particularly Orthoptera (e.g., grasshoppers), birds, natural fruits and nuts, and sometimes carrion. Fruit and nut consumption often increases in the autumn as availability of these foods increases (Fritzell and Haroldson 1982).

Foraging behaviour Gray foxes are more active at night than during the day. They also increase their home ranges during late autumn and winter, possibly in response to changes in food resource availability and distribution. Male foxes also may increase their ranges during spring, probably in response to increased food requirements of more sedentary females and newborn pups (Follman 1973;

Nicholson *et al.* 1985). No information has been reported on specific hunting behaviour of gray foxes.

Damage to livestock or game Although historically considered a potentially significant predator of small game and poultry, gray foxes currently are not considered an important threat to game populations or livestock (Fritzell and Haroldson 1982).

Adaptations

With relatively short legs, a greater ability to rotate the radius on the ulna compared to other canids, and a relatively greater ability to abduct the hind limb, gray foxes are notable tree climbers (Feeney 1999). They can climb branchless, vertical trunks to heights of 18m, as well as jump vertically from branch to branch.

Social behaviour

Monogamy with occasional polygyny is probably most typical in gray foxes (Trapp and Hallberg 1975), but few quantitative data are available, and it is not known if breeding pairs remain together during consecutive years. The basic social unit is the mated pair and their offspring of the year (Trapp and Hallberg 1975; Greenberg and Pelton 1994). Offspring typically disperse at 9–10 months of age, and although long distance dispersal (over 80km) has been reported (Sheldon 1953; Sullivan 1956), young foxes may also return to and settle down near their natal ranges (Nicholson *et al.* 1985). Gray foxes exhibit some territoriality, as home ranges of adjacent family groups may overlap, but core areas appear to be used exclusively by a single family (Chamberlain and Leopold 2000). Home range size ranges from 0.8km² (Yearsley and Samuel 1982) to 27.6km² (Nicholson 1982), and size may vary with habitat quality and food availability.

Gray foxes scent mark by depositing urine and faeces in conspicuous locations (Fritzell and Haroldson 1982). They also communicate vocally via growls, alarm barks, screams, and “coos” and “mewing” sounds during greetings (Cohen and Fox 1976). Gray foxes engage in allogrooming with adults grooming juveniles and each other (Fox 1970).

Reproduction and denning behaviour

Gray foxes reach sexual maturity at 10 months of age, although not all females breed in their first year (Wood 1958; Follman 1978). Breeding generally occurs from January to April with gestation lasting about 60 days (Sullivan 1956). Litter size ranges from 1–10 and averages around four pups (Fritzell 1987). Eyes of pups open at about 10–12 days. Pups accompany adults on foraging expeditions at three months and forage independently at four months (Trapp and Hallberg 1975). Females appear to be responsible to provision pups (Nicholson *et al.* 1985), although there is some evidence that males may also

contribute to care of pups (Chamberlain 2002). Juveniles reach adult size and weight at about 210 days (Wood 1958).

During parturition and pup rearing, gray foxes use earthen dens, either dug themselves or modified from burrows of other species. They will also den in wood and brush piles, rock crevices, hollow logs, hollows under shrubs, and under abandoned buildings (Trapp and Hallberg 1975). Gray foxes may even den in hollows of trees up to nine metres above the ground (Davis 1960). In eastern deciduous forests, dens are in brushy or wooded areas where they are less conspicuous than dens of co-occurring red foxes (*Vulpes vulpes*) (Nicholson and Hill 1981). Den use diminishes greatly during non-reproductive seasons when gray foxes typically use dense vegetation for diurnal resting locations.

Competition

Red foxes are sympatric with gray foxes over much of the gray fox range, but competitive interactions between the two species are not well understood. Historically, differences in food and habitat preferences may have reduced competition between the species, but recent deforestation and other anthropogenic disturbances appear to have resulted in increased habitat use overlap (Churcher 1959; Godin 1977). Competition between gray and kit (*Vulpes macrotis*) or swift (*Vulpes velox*) foxes has not been recorded, probably because of differences in habitat preference (wooded and brushy versus shrub-steppe, arid and semi-arid desert and open grasslands, respectively) that precludes interactions between the species. Coyotes, on the other hand, opportunistically kill gray foxes (Wooding 1984; Farias 2000b; B. Cypher unpubl.), and appear to limit gray fox abundance in some areas (but see Neale and Sacks 2001). Gray fox abundance is inversely related to coyote abundance in California (Crooks and Soulé 1999), and gray fox numbers increased following coyote removal in Texas (Henke and Bryant 1999). In southern California, coyotes may limit gray foxes to thicker chaparral cover (Farias 2000b; Fedriani *et al.* 2000). Bobcats also may kill gray foxes (Farias 2000b). Conversely, gray fox populations may limit the number of weasels (*Mustela* spp.) in some areas (Latham 1952; Hensley and Fisher 1975).

Mortality and pathogens

Natural sources of mortality In addition to coyotes and bobcats, golden eagles (*Aquila chrysaetos*) and mountain lions (*Felis concolor*) kill gray foxes (Grinnell *et al.* 1937; Mollhagen *et al.* 1972).

Persecution In the past, gray foxes may have been persecuted because they were deemed predators of domestic livestock or poultry, or hunted as a result of general bounties, but persecution currently is not a significant mortality factor for the species.

Hunting and trapping for fur Trapping of gray foxes is legal throughout much of their range, and is likely to be the most important source of mortality where it occurs and probably can limit their populations locally. Annual harvests of gray foxes were approximately 182,000 in the 1970s and increased to 301,000 in the 1980s (Obbard *et al.* 1987). During 1994 to 1995, more than 80,000 gray foxes were harvested in 40 states (International Association of Fish and Wildlife Agencies unpubl.). In the south-eastern United States, gray foxes are traditionally hunted with hound dogs (Fritzell 1987). There is little evidence that regulated trapping has adversely affected gray fox population numbers.

Road kills Occasionally, gray foxes are hit by vehicles, but this does not appear to be a significant source of mortality. In Alabama, 14% of gray fox deaths were attributed to vehicles (Nicholson and Hill 1984).

Pathogens and parasites Local populations have been reduced as a result of distemper (Nicholson and Hill 1984) and rabies (Steelman *et al.* 2000). In Alabama, 36% of gray fox deaths were attributed to distemper (Nicholson and Hill 1984). Of 157 gray fox carcasses examined in the south-eastern United States, 78% were diagnosed with distemper (Davidson *et al.* 1992). A variety of external and internal parasites have been found among gray foxes including fleas, ticks, lice, chiggers, mites, trematodes, cestodes, nematodes, and acanthocephalans (Fritzell and Haroldson 1982). Gray foxes appear to be highly resistant to infestation by sarcoptic mange mites (Stone *et al.* 1972).

Longevity It is rare for a gray fox to live longer than 4–5 years, although Seton (1929) reported that some individuals could live 14–15 years.

Historical perspective

Humans have probably harvested gray foxes for their fur for as long as the two have been in contact with one another. Gray foxes are trapped for utilitarian and economic reasons (including the perceived elimination of livestock depredation), and also for recreation. However, recent changes in social attitudes towards trapping have resulted in lower participation in the activity and its outright ban in some states (e.g., Arizona, California, Colorado, Florida, Massachusetts, New Jersey) (Armstrong and Rossi 2000).

Conservation status

Threats No major threats, but habitat loss, fragmentation, and degradation, may be particularly problematic in regions where human numbers are increasing rapidly and important habitat is converted for agricultural, industrial, and urban uses.

Commercial use Because of its relatively lower fur quality compared to other species, commercial use of the gray fox

is somewhat limited. However, 90,604 skins were taken in the United States during the 1991 and 1992 season (Linscombe 1994). In Mexico, gray foxes are frequently sold illegally as pets (R. List pers. comm.).

Occurrence in protected areas Gray foxes occur in numerous protected areas throughout their range, such as Big Bend NP, San Joaquin National Wildlife Refuge, Rocky Mountain NP and Everglades and Dry Tortugas NP, and Adirondack NP.

Protection status CITES – not listed.

Current legal protection The gray fox is legally protected as a harvested species in Canada and the United States (Fritzell 1987).

Conservation measures taken No specific measures are currently being implemented, and none appear necessary at this time.

Occurrence in captivity

According to ISIS, there are 74 foxes in captivity, although there may be more in the hands of private collections/individuals who do not report to ISIS. Gray foxes appear to fare well in captivity and commonly are on display at zoos and wildlife farms.

Current or planned research projects

R. Sauvajot (U.S. National Park Service, Thousand Oaks, California) and collaborators at the Santa Monica Mountains National Recreation Area in California recently investigated gray fox ecology, space use, interspecific interactions, and response to human development.

Researchers at the Savannah River Ecology Laboratory (Aiken, South Carolina) are investigating the demographic characteristics of a non-harvested population of gray foxes in South Carolina.

R. List (Instituto de Ecología, National University of Mexico) and colleagues are studying the ecology and demography of a closed gray fox population, in a 1.6km² reserve within central Mexico City, to determine management needs.

M. Gompper (University of Missouri, Columbia) has proposed a genetic and ecological investigation of an island gray fox population on Cozumel, Mexico.

Gaps in knowledge

Because of the relatively high abundance and low economic value of gray foxes, surprisingly little research has been conducted on this species. Basic ecological and demographic information is needed for each of the major habitats occupied by gray foxes. Also, data on the response of gray foxes to human-altered landscapes (e.g., urban environments) are needed. No region-wide or range-wide

population estimate has been produced. Furthermore, extremely little is known about the status and ecology of gray foxes outside of the USA and Canada. The effects of gray foxes on populations of smaller vertebrates, especially in urban and suburban settings without larger predators, may be important.

Core literature

Fritzell 1987; Fritzell and Haroldson 1982; Hall 1981; Harrison 1997; Lord 1961; Trapp and Hallberg 1975.

Reviewers: Gary Roemer, Rurik List. **Editors:** Deborah Randall, Claudio Sillero-Zubiri, Michael Hoffmann.

4.4 Island fox

***Urocyon littoralis* (Baird, 1858)**
Critically Endangered – CR:A2be+3e (2004)

G.W. Roemer, T.J. Coonan, L. Munson and R.K. Wayne

Other names

English: island gray fox, Channel Islands fox, California Channel Island fox.

Taxonomy

Vulpes littoralis Baird, 1858:143. Type locality: San Miguel Island, Santa Barbara County, California, USA [34°02'N, 120°22'W].

Urocyon is currently considered a basal genus within the Canidae and has only two surviving members, the gray fox (*U. cinereoargenteus*) and the island fox (*U. littoralis*) (Wayne *et al.* 1997). The island fox is believed to be a direct descendant of the gray fox, having reached the Channel Islands either by chance over-water dispersal or human-assisted dispersal (Collins 1991a, b). Each island population differs in genetic structure and of the five mtDNA haplotypes found in island foxes, none are shared with a nearby mainland sample of gray foxes. However, all island fox populations share a unique restriction enzyme site, clustering the populations into a single monophyletic clade (Wayne *et al.* 1991b). Population specific restriction-fragment profiles have been identified from minisatellite DNA (Gilbert *et al.* 1990), and multilocus genotypes from hypervariable microsatellite DNA were used to correctly classify 99% of 183 island/gray fox samples to their population of origin (Goldstein *et al.* 1999). The two misclassifications occurred between nearby island populations. These data clearly justify the current classification of island foxes as a separate species (Wozencraft 1993) and the subspecific classifications of the six island populations (Hall 1981; Moore and Collins 1995).

Chromosome number is identical to *U. cinereoargenteus* with 2n=66; 62 acrocentric chromosomes, a submetacentric pair and two sex chromosomes (Wayne *et al.* 1991b).

Description

Island foxes are the smallest North American canid. Males are significantly heavier than females (Moore and Collins 1995) (Table 4.4.1). The head is grey with black patches on the lateral sides of the muzzle in the vicinity of the vibrissae, with black outlining the lips of both jaws. White patches

Table 4.4.1. Body measurements for the Island fox. Measures of adult foxes were taken in 1988 for all subspecies except for San Clemente (R. Wayne unpubl.). Weight for San Clemente foxes was measured in 1988 (D. Garcelon and G. Roemer unpubl.), other measures for San Clemente foxes are from Moore and Collins (1995).

	Northern Channel Islands	Southern Channel Islands
HB male	536mm (470–585) n=44	548mm (513–590) n=28
HB female	528mm (456–578) n=50	538mm (475–634) n=30
T male	213mm (145–255) n=44	272mm (230–310) n=51
T female	202mm (115–265) n=50	248mm (180–295) n=46
HF male	111mm (94–124) n=44	112mm (104–120) n=51
HF female	107mm (95–122) n=50	107mm (92–115) n=46
E male	60mm (53–68) n=44	63mm (55–72) n=51
E female	60mm (54–67) n=50	62mm (59–67) n=46
WT male	2.0kg (1.4–2.5) n=44	2.0kg (1.4–2.5) n=51
WT female	1.8kg (1.5–2.3) n=50	1.8kg (1.3–2.4) n=46

Adult female island fox, San Miguel Island, California, USA, 1994.



Timothy J. Coonan

on the muzzle extend behind the lateral black patches to the cheek and blend into the ventral surface of the neck which is mostly white and bordered by rufous dorsally. Small white patches are present lateral to the nose. Variable degrees of white and rufous colour the chest and extend throughout the belly. The body and tail are mostly grey, with the latter having a conspicuous black stripe on the dorsal surface ending in a black tip. The grey of the body extends partially down the legs giving way to mostly rufous, both in the middle and towards the rear. On both San Clemente and San Nicolas Islands, a brown phase coat colour occurs in which the grey and black of the body are largely replaced with a sandy brown and deeper brown, respectively. It is unclear if the brown phase is a true coat colour morph, a change that occurs with age or possibly a change that occurs because of an interaction with *Opuntia* spines that get imbedded within the pelt (Sheldon 1990). Pelage is relatively short (20–40mm deep) with a single moult resulting in a thin summer coat and a dense winter coat. Eight mammae are present. Dental formula is 3/3-1/1-4/4-2/3=42. Island foxes typically have fewer caudal vertebrae, 15–22 (n=47), than the gray fox, 21–22 (n=31) (Moore and Collins 1995).

Subspecies Six subspecies are currently recognised (Moore and Collins 1995):

Northern Channel Islands

- *U. l. littoralis* (San Miguel Island, 34°02'N, 120°22'W)
- *U. l. santarosae* (Santa Rosa Island, 33°57'N, 120°10'W)
- *U. l. santacruzae* (Santa Cruz Island, 33°57'N, 119°45'W)

Southern Channel Islands

- *U. l. dickeyi* (San Nicolas Island, 33°14'N, 119°30'W)
- *U. l. clementae* (San Clemente Island, 32°52'N, 118°27'W)
- *U. l. catalinae* (Santa Catalina Island, 33°24'N, 118°24'W)

Similar species Gray fox (*Urocyon cinereoargenteus*): coloration very similar with a similar dark longitudinal stripe on top of a black-tipped tail. The gray fox also has dark and white markings on its face, and a conspicuous cinnamon-rusty colour on its neck, sides and limbs. There is also white on the gray fox's ears, throat, chest, belly and hind limbs, while the undercoat is mostly buff and grey. The gray fox is at least 30% larger than the island fox (Fritzell and Haroldson 1982).

Current distribution

The current distribution is thought to be a consequence of waif dispersal to the northern Channel Islands during the late Pleistocene, followed by Native American assisted dispersal to the southern Channel Islands (Collins 1982, 1991a, b, 1993; Wayne *et al.* 1991b; Goldstein *et al.* 1999; see also Historical perspective). The species is now

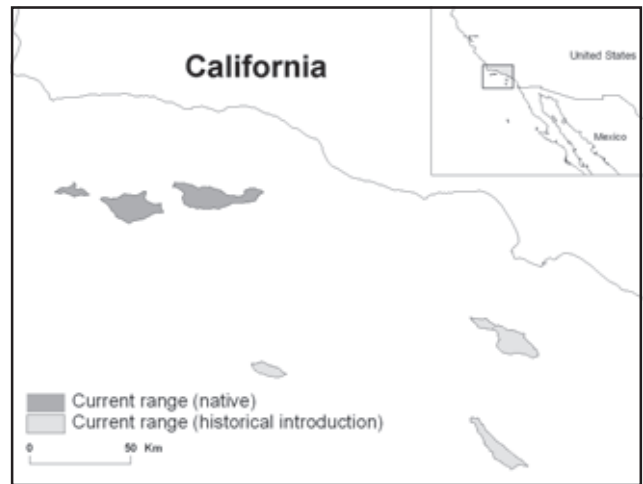


Figure 4.4.1. Current distribution of the island fox.

geographically restricted to the six largest of the eight California Channel Islands located off the coast of southern California, USA (Figure 4.4.1).

Range countries United States (Moore and Collins 1995).

Relative abundance

Island foxes exhibit substantial variability in abundance, both spatially and temporally.

Estimated population size, relative abundance and population trends Total island fox numbers have fallen from approximately 6,000 individuals (Roemer *et al.* 1994)

Figure 4.4.2. Trend in fox population size on San Clemente (SCL), Santa Cruz (SCR) and San Miguel (SMI) Islands.

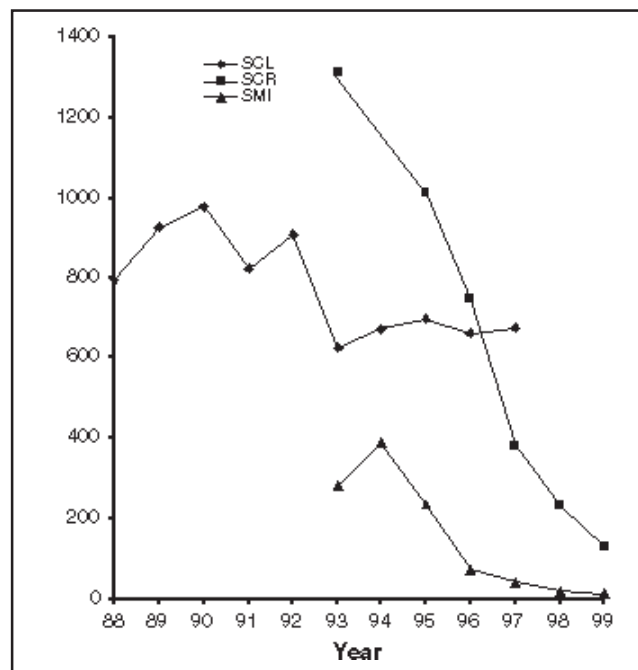


Table 4.4.2. Status of island foxes in the Channel Islands (Trend: S=stable, D=decreasing).

Island	Initial Population ¹	Protected areas		Other areas		Total	
		Population	Trend	Population	Trend	Population	Trend
San Miguel	450	28	D			28	D
Santa Rosa	?	45	D			45	D
Santa Cruz	1,312	17	D	60–80		77–97	D
San Nicolas	520			435–734	S	435–734	S
Santa Catalina	1,342	24		200	D	224	D
San Clemente	825			410	D	410	D

¹ Initial population sizes (N_0) were estimated from data collected in the mid- to late 1980s or early 1990s using a capture-recapture approach (Kovach and Dow 1981; Roemer *et al.* 1994; Garcelon 1999; Roemer 1999; Coonan *et al.* 2000). Current population sizes (N) are the best estimates for 2002 (Garcelon 1999; Roemer 1999; Coonan 2002, 2003; Coonan *et al.* 2000; Timm *et al.* 2000; Roemer and Wayne 2003; G. Smith unpubl.).

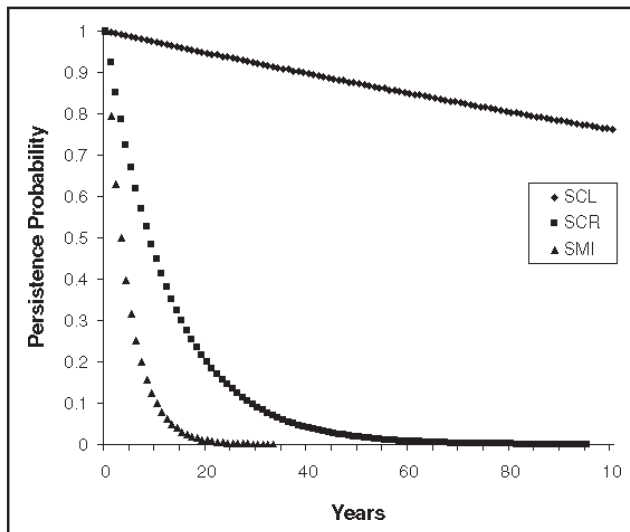


Figure 4.4.3. The probability of population persistence for each of three island fox populations: San Clemente (SCL), Santa Cruz (SCR) and San Miguel (SMI). The estimates of $T_e(n_0)$ used to generate the population persistence probabilities are 381, 5 and 13 years, respectively (G. Roemer *et al.* unpubl.).

to less than 1,500 in 2002 (Table 4.4.2). Four of the six island fox subspecies have experienced precipitous declines in the last four years. Fox populations on both San Miguel and Santa Cruz Islands declined by >90% between 1995 and 2000 (Figure 4.4.2). Similar declines also occurred on Santa Rosa and Santa Catalina Islands (Roemer 1999; Timm *et al.* 2000; Roemer *et al.* 2001a, 2002; Coonan 2003). Only 28 foxes are left on San Miguel and 45 foxes on Santa Rosa, and all are in captivity (Coonan 2002, 2003). The Santa Cruz population has dropped from an estimated 1,312 foxes in 1993 to 133 foxes in 1999 (Roemer 1999; Roemer *et al.* 2001a). Estimates for 2001 suggest that this population may have declined to as low as 60–80 individuals in the wild (Coonan 2002). A captive-breeding facility was initiated on Santa Cruz Island in 2002 when three adult pairs were brought into captivity; one pair had

five pups in the spring (Coonan 2002). The subspecies on all three northern Channel Islands are in imminent danger of extinction (Figure 4.4.3). Fox populations on San Miguel and Santa Cruz Islands have an estimated 50% chance of persistence over the next decade, are in need of immediate conservation action (Roemer 1999; Roemer *et al.* 2001a, 2002; Coonan 2003). On Santa Catalina, island foxes are now rare on the larger eastern portion of the island as a result of a canine distemper outbreak that swept through the population in 1999 (Timm *et al.* 2000). The San Clemente population could be as low as 410 adult foxes, down from a high of 800–900 foxes. The causes of this decline are not yet clear (Garcelon 1999; Roemer 1999); however, it has been suggested that management actions aimed at protecting the threatened San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*) may be a major factor in this decline (Cooper *et al.* 2001; Schmidt *et al.* 2002; Roemer and Wayne 2003). The San Nicolas population appears to be at high density (5.6–16.4 foxes/km²) and currently harbours one of the largest populations (estimate=734 foxes, Roemer *et al.* 2001b). However, this estimate may be positively biased and the actual population size may be closer to 435 foxes (G. Smith pers. comm.).

All of the current estimates of density and population size in island foxes have been conducted using modifications of a capture-recapture approach (Roemer *et al.* 1994). In its simplest application, population size is determined by multiplying average density among sampling sites times island area. Population estimates could be improved by first determining habitat-specific estimates of density and multiplying these densities times the area covered by the specific habitat (Roemer *et al.* 1994), an approach amenable to analysis with geographical information systems. However, density estimates made from aggregating home ranges suggest that the use of capture-recapture data may also overestimate density. For example, fox density estimated at Fraser Point, Santa Cruz Island using the capture-recapture approach was 7.0 foxes/km² (Roemer *et al.* 1994). A simultaneous estimate

of density based on the distribution of home ranges for 14 radio-collared foxes with overlapping home ranges was approximately 31% lower (4.8 foxes/km²) (Roemer 1999). Thus, the size of island fox populations may be lower than current capture-recapture analyses suggest.

Habitat

Island foxes occur in all habitats on the islands including native perennial and exotic European grassland, coastal sage scrub, maritime desert scrub, *Coreopsis* scrub, *Isocoma* scrub, chaparral, oak woodland, pine woodland, riparian, and inland and coastal dune.

Although fox density varies by habitat, there is no clear habitat-specific pattern. When fox populations were dense, foxes could be trapped or observed in almost any of the island habitats, except for those that were highly degraded owing to human disturbance or overgrazing by introduced herbivores. More recently, foxes have become scarce owing to precipitous population declines. On the northern Channel Islands where the declines are principally a consequence of hyperpredation by golden eagles (*Aquila chrysaetos*) (Roemer *et al.* 2001a, 2002), foxes are more numerous in habitats with dense cover, including chaparral and introduced stands of fennel (*Foeniculum vulgare*) (G. Roemer pers. obs.).

Food and foraging behaviour

Food Island foxes are omnivorous and feed on a wide variety of insects, vertebrates, fruits, terrestrial molluscs and even near-shore invertebrates (Laughrin 1973, 1977; Collins 1980; Kovach and Dow 1981; Crooks and van Vuren 1995; Moore and Collins 1995; Roemer *et al.* 2001b). The relative abundance of insects, mammals and plant material in the fox diet has been found to differ by habitat type (Laughrin 1977; Crooks and van Vuren 1995; Roemer *et al.* 2001b), and by island, depending upon availability of food items (Laughrin 1973; Collins and Laughrin 1979). For example, on San Miguel Island where deer mouse (*Peromyscus maniculatus*) densities are high, they form a large proportion of the diet of the island fox (Collins 1980). On Santa Cruz Island, Jerusalem crickets (*Stenopelmatus fuscus*) are a principal prey whereas on San Clemente Island, Jerusalem crickets are absent from the fauna and therefore unavailable. In contrast, the fruits of the coastal prickly pear cactus (*Opuntia littoralis*) are a principal food on San Clemente Island, especially during winter, but the cactus was nearly eradicated from Santa Cruz Island (Goeden *et al.* 1967) and thus comprises only a small portion of the fox diet there. The frequency of bird remains in the scat of island foxes is usually low (3–6%) but on San Miguel Island bird remains were found in 22% of scats (n=208) examined (Laughrin 1977; Collins and Laughrin 1979; Crooks and van Vuren 1995). For an exhaustive list of foods consumed by island foxes and the inter-habitat and inter-island variability see Laughrin

(1973, 1977), Collins and Laughrin (1979) and Moore and Collins (1995).

Foraging behaviour Island foxes primarily forage alone, mostly at night, but they are also active during the day (Laughrin 1977; Fausett 1982; Crooks and van Vuren 1995). Dependent young accompany adults on forays and adult foxes may also forage together on occasion (G. Roemer pers. obs.). Foxes forage by coursing back and forth through suitable habitat patches and then moving, rather directly, through little-used habitats to other suitable habitat patches. Foxes are unable to extract prey as easily from the denser habitat and thus forage in more open habitats where prey availability, but perhaps not abundance, is greater (Roemer and Wayne 2003).

Damage to livestock or game Island foxes are not known to prey on livestock, but the introduced chukar (*Alectoris chukar*), occurs in the diet (Moore and Collins 1995), and it is probable that foxes feed on California quail (*Callipepla californica*), which are found on both Santa Catalina and Santa Cruz Islands.

Adaptations

Island foxes are a dwarf form of the mainland gray fox and this reduction in body size may be a consequence of an insular existence (Collins 1982). Reduced interspecific competition, reduced predation and lack of large prey may have contributed to their smaller body size.

Social behaviour

Island foxes typically exist as socially monogamous pairs that occupy discrete territories (Crooks and van Vuren 1996; Roemer *et al.* 2001b). It is not uncommon for full-grown young to remain within their natal range into their second year or for independent, territory-holding offspring to visit their parents in their former natal range (Roemer *et al.* 2001b).

The home range size of the island fox is one of the smallest recorded for any canid. On Santa Cruz Island, fox home ranges varied by season and habitat type, generally ranging between 0.15 and 0.87km² (Crooks and van Vuren 1996; Roemer *et al.* 2001b). Mean annual home range on Santa Cruz Island was 0.55km² (n=14, Roemer *et al.* 2001b). On San Clemente Island, mean home range size was larger (0.77km², n=11), perhaps due to the lower productivity of this more southerly island (Thompson *et al.* 1998). On Santa Cruz Island, fox home ranges expanded when territorial neighbours were killed by golden eagles, suggesting that density of foxes and the spatial distribution of neighbours may influence territory size (Roemer *et al.* 2001b).

Foxes communicate using visual, auditory and olfactory cues. Both submissive and aggressive behaviours have been observed and are similar to those described for the

gray fox (Laughrin 1977; Fausett 1982; Moore and Collins 1995). Males have been observed chasing other male foxes and have also been observed fighting. Bite wounds were noted in 4 of 1,141 captures of foxes on Santa Cruz Island but were observed only in males and only during the breeding season (Roemer 1999). Foxes demarcate territory boundaries with latrine sites and have been observed urinating as frequently as every 6–9m (Laughrin 1977).

Reproduction and denning behaviour

Foxes breed once a year with parturition usually occurring in early April. Recent research suggests this canid may have induced ovulation (C. Asa pers. comm.), a physiological character that may allow for plasticity in the timing of reproduction. Pups have been born in early February on San Clemente Island and as late as 27 May on Santa Catalina Island (Schmidt *et al.* 2002; Timm *et al.* 2002). Of 35 foxes captured and killed in the month of February 1928 on Santa Cruz Island, 11 (46%) were pregnant (Sheldon 1990). An increase in territory vigilance by males occurs as early as January with actual copulations in captivity typically observed in early March (Coonan and Rutz 2000; Roemer *et al.* 2001b).

Length of gestation is unknown but has been estimated at 50–53 days (Moore and Collins 1995). Litter size varies from one to five but most litters are smaller, from one to three. Of 24 dens located on Santa Cruz Island, average litter size was 2.17 (Laughrin 1977). Average litter size for two captive breeding facilities on the northern islands was 2.6 (n=5, Coonan and Rutz 2000). In 2002, one captive pair on Santa Cruz Island produced a litter of five pups (Coonan 2002). Weaning is complete by mid- to late June and pups reach adult weight and become independent by September (Garcelon *et al.* 1999). Although most foxes are typically monogamous, extra-pair fertilisation has

been recorded. Of 16 pups whose paternity was determined by genetic analysis, 25% were the result of extra-pair fertilisations (Roemer *et al.* 2001b). Dens used include rock piles, dense brush and naturally occurring cavities in the ground or under tree trunks.

Competition

The only known competitors of island foxes are island spotted skunks (*Spilogale gracilis amphiala*) on Santa Cruz and Santa Rosa Islands (von Bloeker 1967; Laughrin 1977; Crooks and van Vuren 1995; Roemer *et al.* 2002) and feral cats on all three southern Channel Islands (Laughrin 1977; Kovach and Dow 1981).

Mortality and pathogens

Natural sources of mortality Hyperpredation by golden eagles has been identified as a primary mortality factor for island foxes on the northern Channel Islands, and is likely responsible for the recent catastrophic population declines of those three subspecies (Roemer 1999; Roemer *et al.* 2001a, 2002.). The presence of an exotic omnivore, the feral pig (*Sus scrofa*), enabled eagles to colonise the islands, increase in population size, and overexploit the fox. Evidence from 28 fox carcasses from Santa Cruz and San Miguel Islands implicated eagles in nearly 90% of the mortalities, and a logistic model of hyperpredation showed that pigs would have been necessary to support a large, resident eagle population (Figure 4.4.4) (Roemer 1999; Roemer *et al.* 2001a, 2002). Further, the prevalence of other potential mortality factors, such as disease and parasites, were found to be incongruent with the pattern of fox population declines (Roemer *et al.* 2000a, 2001a). Red-tailed hawks (*Buteo jamaicensis*) may kill kits (Laughrin 1977). Interspecific aggression is another source of natural mortality.

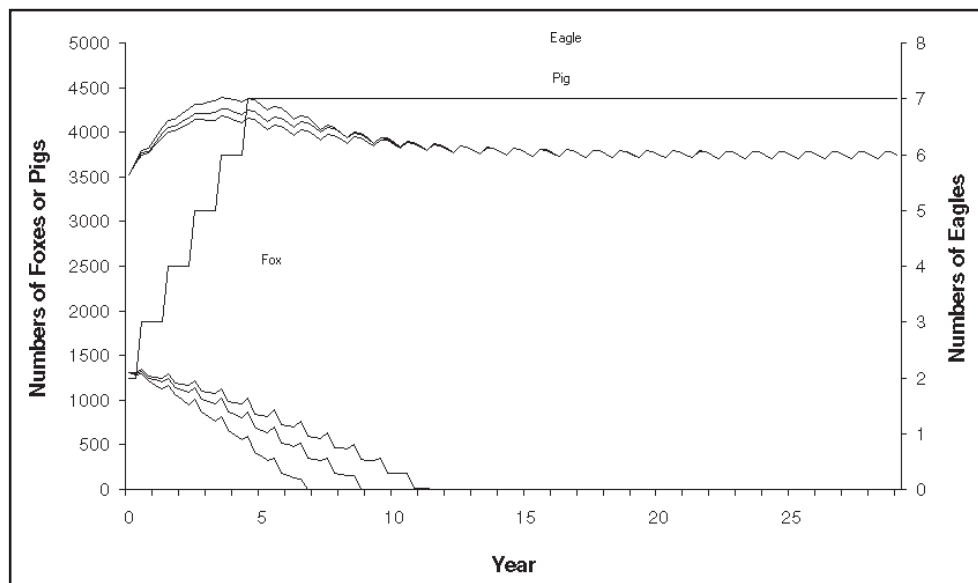


Figure 4.4.4. Trend in the fox, pig and eagle populations on Santa Cruz Island predicted from a logistic model of hyperpredation. Our time unit is a day and we plotted population size every 90 days. The regular peaks in fox population size are due to modelling growth as a single pulse each year. The three trajectories for each of the prey populations are due to differences in predator preference for the prey (pigs: foxes). The preference ratios modelled are 3, 1, and 0.33. Time to extinction for the fox populations given these preferences was 11.5 years, 8.7 years, and 6.7 years, respectively.

Persecution Island foxes are not persecuted except for the predator control programme currently being instituted by the U.S. Navy to protect the San Clemente loggerhead shrike.

Hunting and trapping for fur Island foxes are not currently hunted or trapped for their fur, but may have been historically. Sheldon (1990) took 155 foxes in the winter of 1927–1928 during 20 days of trapping with the intent of selling the pelts. It is not known if a market for fox pelts was established. Native Americans used fox pelts to create ceremonial headdresses, arrow-quivers, capes and blankets (Collins 1991b).

Road kills On San Clemente, Santa Catalina and San Nicolas Islands, trauma from automobiles is a significant source of mortality (Garcelon 1999; G. Smith pers. comm.).

Pathogens and parasites Canine diseases are considered important potential mortality sources for island foxes (Garcelon *et al.* 1992). This is underscored by the epidemic of canine distemper virus (CDV) that decimated the Santa Catalina Island fox population in 1998 to 2000 (Timm *et al.* 2000). CDV was apparently introduced sometime between late 1998 to mid-1999 and has caused an estimated 95% reduction in the fox population on the eastern 87% of Catalina Island. Human settlement on a narrow isthmus likely formed a barrier to fox dispersal and the spread of the disease to the western portion of the island. A total of 148 foxes have been captured in 2000 to 2001 on the western 13% of Santa Catalina Island supporting the contention that foxes there were not exposed to CDV (S. Timm pers. comm.). Antibodies to CDV were recently detected in foxes from San Nicolas Island but the titre levels observed may represent false positives (Coonan 2002; S. Timm pers. comm.).

Exposure to other various canine pathogens has been confirmed but morbidity or mortality has not been substantiated (Timm *et al.* 2000; L. Munson unpubl.). Positive antibody titres have been detected for canine parvovirus, canine adenovirus, canine herpesvirus, canine coronavirus, leptospirosis, toxoplasmosis and for heartworm (*Dirofilaria immitis*) (Garcelon *et al.* 1992; Roemer 1999; Roemer *et al.* 2000a, 2001a; Crooks *et al.* 2001). In addition a number of intestinal pathogens have been identified including *Ancylostoma*, *Toxascaris*, *Mesocostoides*, *Isospora*, *Sarcocystis*, and *Neospora* (Roemer *et al.* 2001a). Island foxes from San Miguel are infested with three pathogenic parasites, *Uncinaria*, *Angiocaulus* and an as yet unidentified spirurid that causes granulomas in the intestinal tract and mesentery (L. Munson unpubl.). These parasitic granulomas are likely the cause of the rectal prolapses that were observed in two wild foxes, one of which later died (G. Roemer pers. obs.) and in two captive foxes that recovered after reinsertion

(K. Rutz pers. comm.). Other sources of mortality include trauma as a result of injury and aspiration pneumonia. A captive fox on Santa Rosa recently died from an aggressive oral cavity cancer (M. Willett and L. Munson unpubl.) and cancer of the ear canal (ceruminous gland carcinomas) has been observed in three foxes from Santa Catalina Island (L. Munson unpubl.).

Foxes on all islands also have thyroid atrophy, hepatic fibrosis and amyloidosis, and recently foxes from San Clemente Island have shown evidence of Quintox poisoning (L. Munson unpubl.), an anti-coagulant rodenticide used to control rodents as part of the San Clemente Loggerhead Shrike Recovery Program (Cooper *et al.* 2001).

Longevity Foxes as old as 10 years of age have been captured on San Miguel Island (Coonan *et al.* 1998).

Historical perspective

Island foxes played a spiritual role in earlier Native American societies on the Channel Islands (Collins 1991b). Native Americans of the Channel Islands harvested foxes to make arrow-quivers, capes and headdresses from their pelts, they ceremonially buried foxes, conducted an Island Fox Dance and most likely kept foxes as pets or semi-domesticates (Collins 1991b). Their current distribution is a direct consequence of historical interaction with humans (Collins 1991a, b; Wayne *et al.* 1991b; Goldstein *et al.* 1999). Fossil evidence dates the arrival of foxes to the northern Channel Islands (Santa Cruz, Santa Rosa and San Miguel) from 10,400–16,000 ybp (years before present) (Orr 1968). Their actual colonisation probably occurred between 18,000 and 40,000 years ago, when these northern islands were joined into one large island known as “Santarosae” (Collins 1982, 1993). At its closest, Santarosae was a mere 6km from the North American continent, having reached its maximum size 18,000–24,000 ybp. It is hypothesised that sometime during this period, mainland gray foxes, the progenitor of the island fox, colonised Santarosae by chance over-water dispersal, by either swimming or by rafting on floating debris (Collins 1982, 1993). As glaciers retreated and sea levels rose, Santarosae was subdivided into separate islands. Santa Cruz Island was formed first, some 11,500 ybp. Sea levels continued to rise separating the remaining land mass once again, approximately 9,500 ybp, to form Santa Rosa and San Miguel Islands. Native Americans then colonised the Channel Islands 9,000–10,000 ybp, and after establishment of an extensive trade route, transported foxes to the southern islands. The southern islands were thought to have been colonised by foxes between 2,200 and 5,200 ybp (Collins 1991a, b, 1993; Wayne *et al.* 1991b; Vellanoweth 1998).

Island foxes also represent a significant scientific resource. Their geographic distribution and resulting isolation has created a set of model populations that has

extended our knowledge regarding the effects of insularity on mammalian social organisation (Roemer *et al.* 2001b), has contributed to an understanding of the molecular evolution of highly variable gene regions (Gilbert *et al.* 1990; Goldstein *et al.* 1999) and their recent decline is a clear example of the potential impact that invasive species can have on insular systems (Roemer *et al.* 2001a, 2002).

Conservation status

Threats The current primary threats to the species include golden eagle predation on the northern Channel Islands (Roemer 1999; Roemer *et al.* 2001a, 2002) and the possible introduction of canine diseases, especially CDV, to all populations (Garcelon *et al.* 1992; Roemer 1999; Timm *et al.* 2000). All populations are small, several critically so, and are threatened by demographic stochasticity and environmental variability. The small populations are especially vulnerable to any catastrophic mortality source, be it predation, canine disease, or environmental extremes (Roemer *et al.* 2000b).

Recently, there has also been a management conflict between island foxes and the San Clemente Island loggerhead shrike (Roemer and Wayne 2003). Island foxes were euthanised on San Clemente Island in 1998 as part of a programme to protect nesting shrikes (Elliot and Popper 1999; Cooper *et al.* 2001). Although euthanasia of foxes has stopped, a number of foxes are now retained in captivity each year, during the nesting and fledging stage of the shrike, and subsequently released back into the environment. The impact to fox reproduction and the potential disruption of the social system are unknown, but may be significant. These actions may have contributed to a 60% decline in the fox population on San Clemente Island (Cooper *et al.* 2001; Schmidt *et al.* 2002; Roemer and Wayne 2003). Considering the precipitous declines in foxes on four of six islands and the continued decline in the San Clemente population, this current management practice needs further scrutiny.

Commercial use There is no commercial use of island foxes.

Occurrence in protected areas The three subspecies on the northern Channel Islands occur within the Channel Islands National Park. Approximately two-thirds of Santa Cruz Island is owned by The Nature Conservancy (TNC), and managed as the Santa Cruz Island Preserve. The Preserve is within the boundaries of the Channel Islands National Park, and the TNC and NPS (National Parks Service), co-manage natural resources together under a cooperative agreement. Approximately 87% of Santa Catalina Island is owned by the Santa Catalina Island Conservancy, a non-profit conservation organisation, and both San Clemente and San Nicolas Islands are owned and managed by the U.S. Navy.

Protection status CITES – not listed.

Current legal protection The species was formerly a category II candidate for federal listing, but is not currently listed by the U.S. Fish and Wildlife Service (USFWS) as ‘threatened’ or ‘endangered’ under the Federal Endangered Species Act. The species is listed by the state of California as a ‘threatened’ species (California Department of Fish and Game 1987). The current legal status has not been sufficient to prevent recent catastrophic population declines. In June 2000, the USFWS was petitioned to list the populations on the three northern Channel Islands and Santa Catalina Island as ‘endangered’ (Suckling and Garcelon 2000). The USFWS recently proposed to list these four subspecies as ‘endangered’ (USDI 2001).

Conservation measures taken Based upon recommendations from an *ad hoc* recovery team, the Island Fox Conservation Working Group, the National Park Service (NPS) began initiating emergency actions in 1999, with the objectives being to remove the primary mortality factor currently affecting island foxes (golden eagle predation), and to recover populations to viable levels via captive breeding. Between November 1999 and June 2002, 22 eagles were removed from Santa Cruz Island and relocated to north-eastern California. In 1999, the NPS established an island fox captive breeding facility on San Miguel Island, added a second facility on Santa Rosa in 2000 and a third on Santa Cruz Island in 2002 (Coonan 2002, 2003; Coonan and Rutz 2000, 2002). Fourteen foxes were originally brought into captivity on San Miguel; current captive population is now 28. There are currently 45 foxes in captivity on Santa Rosa, and 12 adult foxes in the Santa Cruz facility that produced a single litter of five pups (Coonan 2002, 2003).

The NPS has prepared an island fox recovery plan for the northern Channel Islands (Coonan 2001) and an island-wide restoration plan for Santa Cruz Island (USDI 2002). The measures taken thus far on the northern Channel Islands (golden eagle removal and captive breeding) will form the basis for long-term recovery for the subspecies on the northern Channel Islands. In addition, the reintroduction of bald eagles (*Haliaeetus leucocephalus*), the eradication of feral pigs, and the removal of exotic plants have been recommended and are being implemented (Roemer *et al.* 2001a; USDI 2002). Demographic modelling indicates that recovery to viable population levels could take up to a decade (Roemer *et al.* 2000b).

On Santa Catalina Island, The Santa Catalina Island Conservancy has taken a series of measures to mitigate the effects of canine distemper virus on that subspecies. Close to 150 foxes from the west end have been field-vaccinated for CDV, and both translocation and captive breeding

programmes have been established to aid in recolonising the eastern portion of the island (Timm *et al.* 2000, 2002).

Although the Island Fox Conservation Working Group recognised the need for a species-wide recovery plan, there is currently no formal vehicle to accomplish such a planning effort, because the species is not listed under the Federal Endangered Species Act. Nonetheless, the Working Group recognised that the following actions need to be implemented in order to ensure recovery of island fox populations to viable levels (Coonan 2002, 2003):

- Complete removal of golden eagles from northern Channel Islands.
- Implement monitoring/response programme for future golden eagles.
- Remove feral pigs from Santa Cruz Island.
- Reintroduce bald eagles to the northern Channel Islands.
- Eliminate canine distemper as a mortality factor on Santa Catalina Island.
- Vaccinate wild foxes against canine distemper virus, as needed.
- Monitor populations for diseases causing morbidity and mortality through necropsy and faecal and blood testing.
- Enforce no-dog policy on islands, and vaccinate working dogs.
- Educate the public about potential disease transmission from domestic dogs.
- Establish and maintain captive breeding facilities on San Miguel, Santa Rosa, Santa Cruz and Santa Catalina Islands.
- Supplement wild populations with captive-reared foxes.
- Implement annual population monitoring of each subspecies/population.
- Halt management actions to protect the San Clemente loggerhead shrike that are adversely affecting the San Clemente island fox.
- Develop adaptive management programme.

Occurrence in captivity

Island foxes currently are kept in captivity on four islands. The National Park Service's captive breeding programme maintains facilities on San Miguel, Santa Rosa and Santa Cruz Islands, in which there are currently 28, 45 and 17 island foxes, respectively. The Santa Catalina Island Conservancy and the Institute for Wildlife Studies have established a captive breeding facility on that island, and there are currently 12 adult pairs of foxes there (Timm *et al.* 2002). Small numbers (1–4) of San Clemente Island foxes are kept in a total of four zoos on the mainland with a variable number of foxes held in captivity each year on that island (Cooper *et al.* 2001).

Current or planned research projects

M. Gray (UCLA, Los Angeles, California), G.W. Roemer

(New Mexico State University, Las Cruces, New Mexico) and E. Torres (California State University, Los Angeles, California) are currently conducting a genetic analysis of captive island foxes, assessing genetic relatedness to formulate captive breeding strategy and maintain genetic diversity of founders.

A. Aguilar and R.K. Wayne (UCLA, Los Angeles, California) are assessing variation at the major histocompatibility complex (Mhc) in the island fox.

C. Asa (St. Louis Zoo, Saint Louis, Missouri) is studying timing of the reproductive cycle via hormonal analysis of captive island foxes.

D.K. Garcelon (Institute for Wildlife Studies, Arcata, California) conducted transect trapping and radio-telemetry studies in 2001 which will be used to estimate basic population parameters for Santa Cruz Island foxes and determine mortality factors for this subspecies. Ongoing work will include annual population monitoring, and studies on spatial organisation and survival of island foxes on San Clemente Island using capture-recapture and radio-telemetry. This work will also include annual population monitoring on San Nicolas Island, using a grid-based, capture-recapture study for estimating density, survival and recruitment

S. Timm (Institute for Wildlife Studies, Arcata, California) is studying survival of translocated foxes on Santa Catalina Island.

L. Munson and D. Fritcher (University of California, Davis, California) are monitoring disease in the island fox. They aim to determine all diseases and parasites present in island foxes from all populations, both historically through archived frozen carcasses and presently through necropsy of dead foxes.

G.W. Roemer (New Mexico State University, Las Cruces, New Mexico) and P. Miller (IUCN Conservation Breeding Specialist Group) are undertaking a population viability analysis of the island fox with the aim to refine previous analyses of population viability and threat.

Gaps in knowledge

It is known that wild island fox pairs are unrelated and that extra-pair copulations occur (Roemer *et al.* 2001b), but little is known about how island foxes select mates and whether mate choice could play a role in improving the currently low reproduction characterising captive foxes (Coonan and Rutz 2002). Controlled mate-choice experiments are needed.

It has been suggested that intense predation by golden eagles could have altered island fox activity patterns and selected for greater nocturnal activity in those foxes that have survived predation (Roemer *et al.* 2002). The survival of the remaining wild island foxes on Santa Cruz Island is being monitored, but there has been no attempt to document daily activity levels (Dennis *et al.* 2001). The

pattern of daily activity of wild Santa Cruz Island foxes needs to be assessed, and compared to the activity of captive and captive-reared foxes that are released into the wild. If captive-reared foxes are more active during diurnal and crepuscular periods than their wild counterparts, it is probable that captive-reared foxes reintroduced into the wild will suffer higher mortality owing to golden eagle predation.

There has been only a single study that has examined dispersal in island foxes (Roemer *et al.* 2001b) and the number of dispersal events recorded was small (n=8). Additional information on island fox dispersal patterns on different islands and during periods of high and low density are needed.

Core literature

Collins 1991a,b, 1993; Crooks and van Vuren 1996; Laughrin 1977; Moore and Collins 1995; Roemer 1999; Roemer *et al.* 2001a,b, 2002; Roemer and Wayne 2003; Wayne *et al.* 1991b.

Reviewers: Lyndal Laughrin, David K. Garcelon, Paul Collins. **Editors:** Claudio Sillero-Zubiri, Deborah Randall, Michael Hoffmann.

4.5 Kit fox

***Vulpes macrotis* Merriam, 1888**
Least Concern (2004)

R. List and B.L. Cypher

Other names

English: desert fox; **German:** wüstenfuchs; **Spanish:** zorra del desierto, zorra norteña.

Taxonomy

Vulpes macrotis Merriam, 1888. Type locality: “Riverside, Riverside County, California“ [United States, c. 34°00’N, 117°15’E].

The kit fox has been considered conspecific with the swift fox, *V. velox*, based on morphometric similarities and protein-electrophoresis (Clutton-Brock *et al.* 1976; Hall 1981; Dragoo *et al.* 1990). Others have treated *V. macrotis* as a distinct species based on multivariate morphometric data (Stromberg and Boyce 1986) and more recently based on mitochondrial DNA (Mercure *et al.* 1993).

Chromosome number not known.

Description

The kit fox is one of the smallest foxes in the Americas (Table 4.5.1). The most conspicuous characteristic is the large ears. The fur is short, with yellowish to greyish head, back and sides; the shoulders and the outside of the legs are brown-yellow; the belly and the inner side of legs are white-yellowish; the tip of the tail is black. The neck, legs and belly may have buffy highlights. The hair is dense

Table 4.5.1 Body measurements for the kit fox from Janos, Chihuahua, Mexico (List and Jimenez Guzmán in press).

HB male	537mm (485–520) n=7
HB female	501mm (455–535) n=5
T male	308mm (280–340) n=8
T female	289mm (250–305) n=5
E male	82mm (71–95) n=8
E female	80mm (74–95) n=6
WT male	2.29kg (1.7–2.7) n=8
WT female	1.9kg (1.6–2.2) n=6



Adult kit fox, sex unknown, standing at the entrance of its burrow. Janos, Chihuahua, Mexico, 2001.

Rurik List

between the foot-pads. Dental formula: 3/3-1/1-4/4-2/3=42. Mean cranial measurements from 35 specimens of *V. m. mutica* were: condylobasal length 114.4mm; zygomatic breadth 62.1mm; palatal length 57.8mm; interorbital breadth 23.1mm; postorbital breadth 21.4mm (Waithman and Roest 1977).

Subspecies Eight subspecies have been recognised (McGrew 1979). Fewer taxonomic studies have been conducted on kit foxes in Mexico, and therefore the taxonomy of kit foxes in Mexico is less certain.

- *V. m. arsipus* (south-eastern California, southern Arizona, and northern Sonora)
- *V. m. devia* (southern Baja California)
- *V. m. macrotis* (south-western California – extinct)
- *V. m. mutica* (San Joaquin Valley of California)
- *V. m. neomexicana* (New Mexico, western Texas, and north-west Chihuahua)
- *V. m. nevadensis* (Great Basin of the U.S.)
- *V. m. tenuirostris* (northern Baja California)
- *V. m. zinseri* (north central Mexico).

Similar species Swift fox, *Vulpes velox*: Sympatric with the kit fox only in a small contact zone (c. 100km wide); shorter, more rounded ears that are set farther apart on the head, and a shorter tail relative to body length.

Current distribution

The kit fox inhabits the deserts and arid lands of western North America (Figure 4.5.1). In the United States, it occurs from southern California to western Colorado and western Texas, north into southern Oregon and Idaho. In

Mexico, it occurs across the Baja California Peninsula and across northern Sonora and Chihuahua to western Nuevo León, and south into northern Zacatecas (McGrew 1979; Hall 1981).

Range countries Mexico, USA (Hall 1981).

Relative abundance

The species is common to rare. Density fluctuates with annual environmental conditions, which are dependent upon precipitation (Cypher *et al.* 2000). In Utah, density ranged from 0.1–0.8/km² (Egoscue 1956, 1975). In California, density varied from 0.15–0.24/km² over a period of three years on one study site (White *et al.* 1996) and from 0.2–1.7/km² over 15 years on another study site (Cypher *et al.* 2000). Kit fox densities in prairie dog town complexes in Mexico were 0.32–0.8/km² in Chihuahua (List 1997) and 0.1/km² in Coahuila and Nuevo Leon (Cotera 1996).

Estimated populations/relative abundance and population trends

In Mexico, data on which to base a population estimate for kit foxes are only available from two localities with very specific characteristics (presence of prairie dog towns). Therefore, the estimation of a population size for the country or even population trends is not possible with current information. However, because natural habitats occupied by the kit fox are being transformed, it is safe to assume that, overall, populations of the kit fox in Mexico are declining. In the past 10 years, about 40% of prairie dog towns in Coahuila and Nuevo Leon were converted to agriculture (L. Scott and E. Estrada unpubl.).



Figure 4.5.1. Current distribution of the kit fox.

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In the United States, kit fox abundance is unknown. Population trends are assumed to be relatively stable in Texas, New Mexico, Arizona, Utah, and Nevada where harvests for fur continue. Populations in Idaho, Oregon, and the Mojave Desert in California also may be relatively stable due to a lack of significant threats. Populations are potentially increasing in Colorado where foot-hold trapping was recently banned. Populations of the 'endangered' San Joaquin kit fox in the San Joaquin Valley of California are likely still declining due to continuing habitat loss, fragmentation, and degradation (USFWS 1998).

Habitat

The kit fox inhabits arid and semi-arid regions encompassing desert scrub, chaparral, halophytic, and grassland communities (McGrew 1979; O'Farrell 1987). It is found in elevations ranging from 400–1,900m a.s.l., although kit foxes generally avoid rugged terrain with slopes >5% (Warrick and Cypher 1998). Loose textured soils may be preferred for denning. Kit foxes will use agricultural lands, particularly orchards, on a limited basis, and kit foxes also can inhabit urban environments (Morrell 1972).

Food and foraging behaviour

Food Kit foxes primarily consume rodents, leporids, and insects. Primary prey includes kangaroo rats (*Dipodomys* spp.), prairie dogs (*Cynomys* spp.), black-tailed jackrabbits (*Lepus californicus*), and cottontails (*Sylvilagus* spp.). Other items consumed include birds, reptiles, and carrion (Egoscue 1962; Jiménez-Guzmán and López-Soto 1992; White *et al.* 1995; List 2003; Cypher *et al.* 2000). Plant material is rarely consumed, although cactus fruits are occasionally eaten (Egoscue 1956).

Foraging behaviour Kit foxes mostly forage solitarily. They are mainly active by night and occasionally exhibit crepuscular activity (List 1997).

Damage to livestock and game There is no evidence that kit foxes significantly impact game or livestock populations.

Adaptations

Kit foxes are well adapted to a life in warm, arid environments. To dissipate heat while conserving water, they have a large surface area to body mass ratio and large ears which favour non-evaporative heat dissipation and can vary panting rates (Klir and Heath 1992). Predominantly nocturnal activity and diurnal den use also reduce water loss. Kit foxes can obtain all necessary water from their food, but to do so must consume approximately 150% of daily energy requirements (Golightly and Ohmart 1984).

Social behaviour

Kit foxes are primarily monogamous with occasional polygyny (Egoscue 1962). Pairs usually mate for life (Egoscue 1956). Young from previous litters, usually females, may delay dispersal and remain in natal home ranges where they may assist with raising the current litter (List 1997; Koopman *et al.* 2000). Kit foxes are not strongly territorial and home ranges may overlap, although core areas generally are used exclusively by one family group (White and Ralls 1993; Spiegel 1996). Home range size is variable, even within similar vegetation types, and ranges from 2.5km² (Knapp 1978) to 11.6km² (White and Ralls 1993).

Kit foxes sometimes bark at approaching predators or to recall pups, and they sometimes emit a "hacking growl" during intraspecific encounters. Foxes in dens or captivity make a closed-mouth vocalisation during times of anxiety (Egoscue 1962). Scent-marking by kit foxes has not been investigated.

Reproduction and denning behaviour

Kit foxes mate from mid-December to January and give birth from mid-February to mid-March after a gestation of 49–55 days (Egoscue 1956; Zoellick *et al.* 1987). Litter size ranges from 1–7 (mean=4; Cypher *et al.* 2000). Reproductive success is considerably lower for yearling females and varies annually with food availability for all age classes (Spiegel 1996; Cypher *et al.* 2000). Pups emerge from dens at about four weeks, are weaned at about eight weeks, begin foraging with parents at about 3–4 months, and become independent at about 5–6 months (Morrell 1972; R. List unpubl.). Mean dispersal age in California was eight months (Koopman *et al.* 2000).

Kit foxes use dens year round and have multiple dens within their home ranges (White and Ralls 1993; Koopman *et al.* 1998). Although they can excavate their own dens, kit foxes frequently occupy and modify the burrows of other species, particularly prairie dog, kangaroo rats, squirrels (*Spermophilus* spp.) and badgers (*Taxidea taxus*) (Morrell 1972; Jiménez-Guzmán and López-Soto 1992; Cotera 1996; List 1997). Occasionally, they will den in man-made structures (e.g., culverts, pipes), but young are almost always born in earthen dens (Spiegel 1996; Zoellick *et al.* 1997).

Competition

Potential competitors for food and dens include coyotes (*Canis latrans*), bobcats (*Lynx rufus*), red foxes (*Vulpes vulpes*), badgers, skunks (*Mephitis* spp. and *Spilogale* spp.), and feral cats (White *et al.* 1995; Cypher and Spencer 1998; B. Cypher unpubl.). Strategies such as year-round den use, resource partitioning, and habitat partitioning allow kit foxes to mitigate competitive effects and coexist with most of these species. Non-native red foxes are increasing within the range of kit foxes (Lewis *et al.* 1993), and may present

a more significant competitive threat due to greater overlap in resource exploitation patterns and potential for disease transmission. Although coyotes compete with and even kill kit foxes, they also may provide a benefit to kit foxes by limiting the abundance of red foxes (Cypher *et al.* 2001).

Mortality and pathogens

Natural sources of mortality Predation, mainly by coyotes, usually is the main source of mortality for kit foxes and commonly accounts for over 75% of deaths (Ralls and White 1995; Spiegel 1996; Cypher and Spencer 1998). Other predators include bobcats, red foxes, badgers, feral dogs, and large raptors (O'Farrell 1987).

Persecution In Mexico, kit foxes sometimes are shot opportunistically, but they are not actively persecuted. In the USA, large numbers of kit foxes were killed during predator control programmes that targeted other species, particularly coyotes and wolves (*Canis lupus*). However, such programmes have been discontinued or are more species-specific.

Hunting and trapping for fur Kit fox fur has relatively low value, and kit foxes are usually caught incidentally in traps set for other furbearers. About 1,200 were harvested in the United States between 1994 and 1995 (International Association of Fish and Wildlife Agencies unpubl.).

Road kills Vehicles are an important source of mortality and are the primary mortality factor in some areas (Cotera 1996; B. Cypher unpubl.).

Pathogens and parasites Kit foxes frequently carry antibodies to a variety of viral and bacterial diseases indicating exposure. However, disease does not appear to be a significant source of mortality, although rabies could have contributed to a decline in one population of the San Joaquin kit fox (White *et al.* 2000). A variety of ectoparasites (e.g., fleas, ticks, lice) and endoparasites (e.g., cestodes and nematodes) have also been found in kit foxes, but no morbidity or mortality associated with these parasites has been reported.

Longevity Kit foxes on two sites in California were known to reach at least seven years of age (B. Cypher unpubl.).

Historical perspective

Because of their small size and nocturnal habits, kit foxes are relatively inconspicuous. Thus, they are not particularly important for native or modern cultures, and are not well represented in arts and crafts or traditional uses.

Conservation status

Threats The main threat to the long-term survival of the kit fox is habitat conversion, mainly to agriculture but

also to urban and industrial development. In both western and eastern Mexico, prairie dog towns which support important populations of kit foxes are being converted to agricultural fields, and in eastern Mexico the road network is expanding, producing a concomitant increase in the risk of vehicle mortality. In the San Joaquin Valley of California, habitat conversion for agriculture is slowing, but habitat loss, fragmentation, and degradation associated with industrial and urban development are still occurring at a rapid pace.

Commercial use In Mexico, kit foxes are occasionally sold illegally in the pet market. Kit foxes are harvested for fur in some states in the USA, but otherwise are not used commercially.

Occurrence in protected areas

— In Mexico, kit foxes are found in the Biosphere Reserves of El Vizcaino, Mapimi and El Pinacate, in the Area of Special Protection of Cuatro Ciénegas, and are probably found in another eight protected areas throughout their range.

— In the United States, they occur in numerous protected areas throughout their range. The 'endangered' subspecies *V. m. mutica* occurs in the Carrizo Plain National Monument and various other federal, state, and private conservation lands.

Protection status CITES – not listed (considered a subspecies of *V. velox*).

The kit fox is considered 'vulnerable' in Mexico (SEDESOL 1994). In the United States, the San Joaquin kit fox (*V. m. mutica*) is federally classified as 'endangered', and as 'threatened' by the state of California (USFWS 1998). In Oregon, kit foxes are classified as 'endangered'.

Current legal protection Harvests are not permitted in Idaho, Oregon, or California, and the kit fox is a protected furbearer species (i.e., regulated harvests) in Utah, Colorado, Arizona, New Mexico, and Texas.

Conservation measures taken In Mexico, the 'vulnerable' status of the kit fox grants conservation measures for the species, but these are not enforced. In the United States, state and federal protections for kit foxes are being enforced.

Efforts are underway to protect the prairie dog towns of both eastern (Pronatura Noreste) and western Mexico (Institute of Ecology from the National University of Mexico), which are known to be strongholds for the kit fox, but no specific actions focused on the kit fox are being undertaken in Mexico. In the United States, a recovery plan has been completed (USFWS 1998) and is being implemented for the San Joaquin kit fox. Recovery actions include protection of essential habitat, and

demographic and ecological research in both natural and anthropogenically modified landscapes.

Occurrence in captivity

No captive breeding efforts are currently being conducted for kit foxes. Facilities such as the Arizona-Sonora Desert Museum in Tucson, Arizona, California Living Museum in Bakersfield, California, and several zoos keep live kit foxes for display and educational purposes. Also, Humboldt State University in Arcata, California maintains a small number of kit foxes for research and education.

Current or planned research projects

R. List (Institute of Ecology, National University of Mexico) is currently assessing the abundance of kit foxes in the prairie dog towns of north-western Chihuahua to compare the densities to those in 1994 to 1996. He is also planning to map the current distribution in Mexico using GIS.

B. Cypher, D. Williams, and P. Kelly (California State University-Stanislaus, Endangered Species Recovery Program – ESRP) are conducting a number of investigations on the San Joaquin kit fox, including ecology and demography in agricultural lands and urban environments, use of artificial dens, kit fox-red fox interactions, highway impacts, pesticide effects, and restoration of retired agricultural lands.

K. Ralls and colleagues (Smithsonian Institution, Washington D.C., USA), in collaboration with the ESRP, are conducting range-wide genetic analyses for the San Joaquin kit fox and investigating the use of tracker dogs (to find scats) in gathering information on kit fox presence and ecology.

Two working groups of the National Center for Ecological Analysis and Synthesis (University of California, Santa Barbara, USA) are conducting population modelling studies and investigating conservation strategies for the San Joaquin kit fox.

The California State University, San Luis Obispo and the California Army National Guard are investigating the effects of military activities on the San Joaquin kit fox and monitoring kit fox abundance on military lands in California.

R. Harrison (University of New Mexico, Albuquerque) is investigating kit fox ecology in New Mexico.

The U.S. Army is sponsoring an investigation of military effects and kit fox ecology on the Dugway Proving Grounds in Utah.

Gaps in knowledge

In general, demographic and ecological data are needed throughout the range of the kit fox so that population trends and demographic patterns can be assessed. In Mexico, information available on the kit fox is scarce. The most important gaps in our knowledge of the species are

the present distribution of the species and population estimates throughout its range. General biological information is needed from more localities in the Mexican range of the kit fox. In the United States, information is required on the San Joaquin kit fox including assessing the effects of roads and pesticides on kit foxes, investigating dispersal patterns and corridors, determining metapopulation dynamics and conducting viability analyses, developing conservation strategies in anthropogenically altered landscapes, assessing threats from non-native red foxes, and range-wide population monitoring.

Core literature

Cypher *et al.* 2000; Egoscue 1962, 1975; McGrew 1979; O'Farrell 1987; Spiegel 1996.

Reviewers: Mauricio Cotera, Patrick Kelly, Ellen Bean.

Editors: Claudio Sillero-Zubiri, Michael Hoffmann, Deborah Randall.

4.6 Swift fox

***Vulpes velox* (Say, 1823)**

Least Concern (2004)

A. Moehrensclager and M. Sovada

Other names

French: renard véloce; **German:** flinkfuchs; **Indigenous names:** senopah (Blackfoot Tribe, Canada and USA).

Taxonomy

Canis velox Say, 1823. James, Account of an Exped. from Pittsburgh to the Rocky Mtns, 1:487. Type locality: "camp on the river Platte, at the fording place of the Pawnee Indians, twenty-seven miles below the confluence of the North and South, or Paduca Forks."

The swift fox is phenotypically and ecologically similar to the kit fox (*Vulpes macrotis*) and interbreeding occurs between them in a small hybrid zone in west Texas and eastern New Mexico (Rohwer and Kilgore 1973; Mercure *et al.* 1993; Rodrick 1999). Some morphometric comparisons and protein-electrophoresis have suggested that these foxes constitute the same species (Ewer 1973; Clutton-Brock *et al.* 1976; Hall 1981; Dragoo *et al.* 1990; Wozencraft 1993). Conversely, other multivariate morphometric approaches (Stromberg and Boyce 1986), as well as mitochondrial DNA restriction-site and sequence analyses (Mercure *et al.* 1993; Rodrick 1999) have concluded that they are separate species. Swift and kit foxes are most closely related to Arctic foxes (*Alopex lagopus*), and this genetic association is the closest among the *Vulpes*-like canids (Wayne and O'Brien 1987), although Arctic foxes are classified in a different genus.

Description

The swift fox is one of the smallest canids, with an average weight of 2.4kg (Table 4.6.1). The winter pelage is dark greyish across the back and sides extending to yellow-tan across the lower sides, legs, and the ventral surface of the tail. The ventral fur is white with some buff on the chest. In summer, the fur is shorter and more rufous. Swift foxes can be distinguished from other North American canids, except the closely related kit fox, by black patches on each side of the muzzle, a black tail tip, and their small body size. Dental formula: 3/3-1/1-4/4-2/3=42.

Subspecies Stromberg and Boyce (1986) concluded that significant geographic variation exists among swift foxes, but Merriam's (1902) classification of swift foxes into northern (*V. velox hebes*) and southern (*V. v. velox*) subspecies is likely unjustified (Stromberg and Boyce 1986; Mercure *et al.* 1993).

Table 4.6.1 Body measurements for the swift fox from specimens at least nine months old in north-eastern New Mexico (Harrison 2003).

HB male	523mm (500–545) n=11
HB female	503mm (475–540) n=10
T male	286mm (250–340) n=11
T female	278mm (250–302) n=10
HF male	121mm (115–127) n=11
HF female	116mm (109–126) n=10
E male	64mm (59–68) n=10
E female	62mm (57–68) n=10
WT male	2.24kg (2.0–2.5) n=18
WT female	1.97kg (1.6–2.3) n=9

Similar species Kit foxes (*V. macrotis*) have longer, less rounded ears that are set closer to the midline of the skull, a narrower snout, and a proportionately longer tail to their body length than swift foxes.

Distribution

Historical distribution The swift fox is native to short-grass and mixed-grass prairies of the Great Plains in North America (Egoscue 1979). On the northern limit of its range, swift foxes were present in the Canadian provinces of Alberta, Saskatchewan, and Manitoba. The southern species boundary was New Mexico and Texas in the United States. Historical records also exist for areas in Montana, Wyoming, North Dakota, South Dakota, Nebraska, Kansas, Colorado, and Oklahoma. Some historical range descriptions mention swift foxes in Minnesota and Iowa; however, there are no verified records of occurrence in either state (Sovada and Scheick 1999). Iowa has one fossil record and several unconfirmed accounts. Minnesota has no records and no account of any merit.

Current distribution Following swift fox extirpation from Canada by 1938 (Soper 1964), reintroduction releases since 1983 have established a small swift fox population in Alberta, Saskatchewan, and Montana which now constitutes the northern extent of the species' range (Moehrensclager and Moehrensclager 2001) (Figure 4.6.1). The southern periphery of the range is still central New Mexico and north-western Texas, and, in terms of historic distribution, swift foxes are currently not found in Manitoba or North Dakota. Current estimates for the United States suggest that swift foxes are located in 39–



Juvenile swift fox, approximately 2.5 to 3 months old, sex unknown. Near Shirley Basin, Wyoming, USA, 1998.

Travis Olson

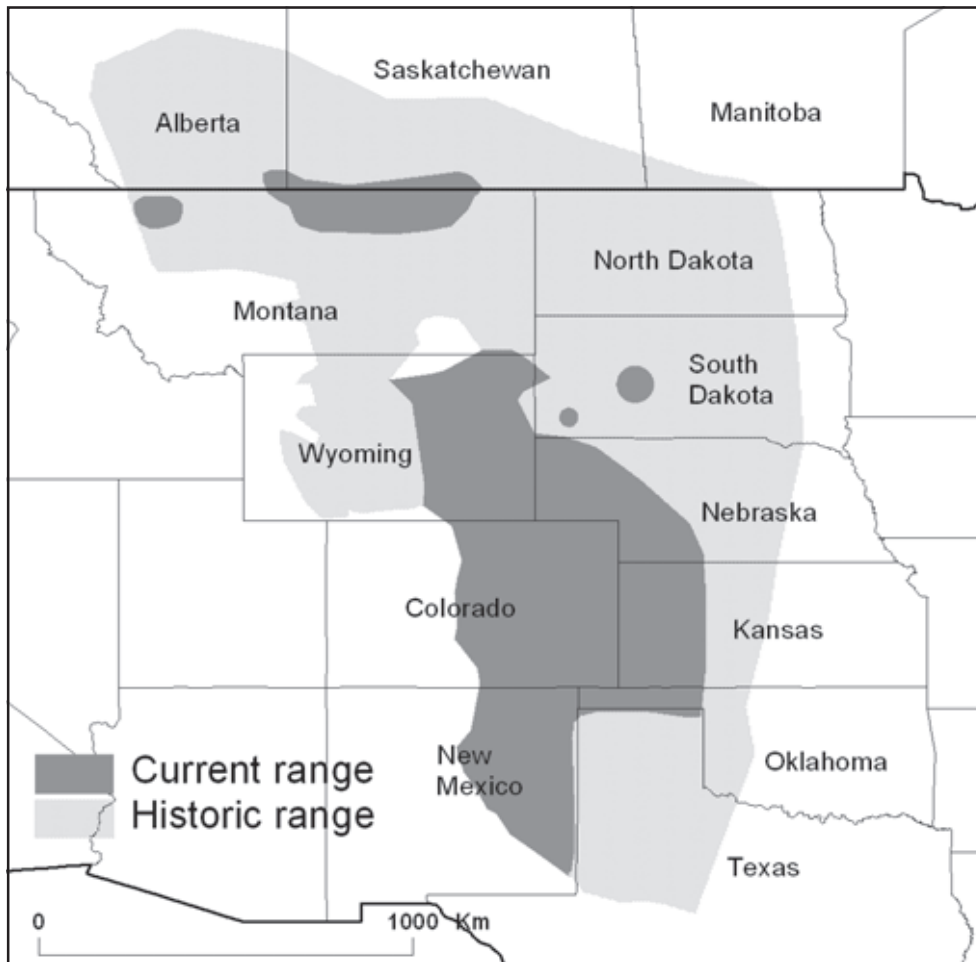


Figure 4.6.1. Current distribution of the swift fox.

42% of their historic range depending on conservative versus liberal estimates of historic range and the time span of records that are considered (Sovada and Scheick 1999). As such, the conservative estimate, based on the relative presence or absence of swift foxes in counties throughout individual states, is that swift foxes are distributed across 505,149km² while the liberal estimate is 607,767km² (Sovada and Scheick 1999). But in much of the distribution populations are fragmented.

Range countries Canada, USA (Sovada and Scheick 1999).

Relative abundance

Historically, the swift fox was considered an abundant predator of the prairies, but their numbers were severely depleted by the late 1880s and early 1900s. In Canada, the last recorded specimen was collected in 1928 (Carbyn 1998) and a single sighting was made in 1938 (Soper 1964). Zumbaugh and Choate (1985) provided evidence that, in Kansas, swift foxes were extremely abundant in the mid-1800s, but became less abundant by the turn of the 20th century. The species was probably extirpated from Kansas

by the 1940s (Black 1937; Cockrum 1952; Hall 1955; Sovada and Scheick 1999). There are similar reports of population declines from other states (see Sovada and Scheick 1999).

Swift fox populations began to recover over portions of their former range beginning in the 1950s (Martin and Sternberg 1955; Glass 1956; Anderson and Nelson 1958; Andersen and Fleharty 1964; Kilgore 1969; Sharps 1977; Egoscue 1979; Hines 1980). In the core of their distribution, in Kansas, Colorado, the Oklahoma panhandle, and New Mexico, populations are considered stable whereas populations in Texas and Wyoming are fragmented and more susceptible to decline. Swift foxes are rare in Nebraska, South Dakota, and Montana, and extirpated from North Dakota (Allardyce and Sovada 2003).

Estimated populations/relative abundance and population trends

Following approximately 50 years of extirpation, a swift fox reintroduction programme was initiated in Canada in 1983. By 1997, 942 foxes had been released, primarily utilising captive breeding but also through the use of translocations (Moehrensclager and Macdonald 2003). Using live trapping, a 1996/1997 census

estimated the Canadian population to consist of 289 individuals in two isolated subpopulations. A second census that re-sampled these sites during the same season in 2000/2001 also expanded the survey area into Montana (Moehrensclager and Moehrensclager 2001; Moehrensclager *et al.* 2004). The results showed that swift fox population size in Canada had increased three-fold since 1996/1997, the total known distribution including Montana spanned at least 17,500km², the combined population size was approximately 877 individuals, and that 98.6% of the population is now wild-born. This population is considerably isolated from the contiguous swift fox range in the United States and needs to be considered separately in terms of population viability.

In the United States, swift fox populations are believed to be stable in Texas, New Mexico, Oklahoma, Colorado, and Kansas. The population in Wyoming is relatively stable but fragmented. Less is known about the population in Nebraska, but there appear to be four disjunct populations of unknown status. In South Dakota, populations are small and fragmented; some are considered stable. Swift foxes are extinct in North Dakota. Reintroductions of swift foxes are being implemented at two sites in South Dakota. The Turner Endangered Species Fund began reintroducing foxes in 2002 in the Bad River Ranch south-west of Pierre. Reintroduction to the Badlands National Park began in 2003. The Defenders of Wildlife are currently supporting (1998–present) a swift fox reintroduction in northern Montana's Blackfeet Reservation.

Habitat

The swift fox is predominately found on short-grass and mixed-grass prairies in gently rolling or level terrain (Kilgore 1969; Hillman and Sharps 1978; Hines 1980). In Kansas, swift foxes have been found to den and forage in fallow cropland fields such as wheat (Jackson and Choate 2000; Sovada *et al.* 2003). Survival rates (and reproductive rates, although sample sizes were small; Sovada *et al.* 2003) between foxes in grassland and cropland sites were not significantly different suggesting that swift foxes may be able to adapt to such habitat in some cases (Sovada *et al.* 1998). Notably, the distribution and density of dens are considered important components of swift fox habitat requirements (Herrero *et al.* 1991), particularly in terms of evading coyote predation or red fox competition (Tannerfeldt *et al.* 2003).

Food and foraging behaviour

Food Swift foxes are opportunistic foragers which feed on a variety of mammals, but also birds, insects, plants, and carrion (Kilgore 1969; Hines 1980; Cameron 1984; Uresk and Sharps 1986; Hines and Case 1991; Zimmerman 1998; Kitchen *et al.* 1999; Moehrensclager 2000; Sovada *et al.* 2001b). Leporids have been reported as a primary prey

item in several studies (Kilgore 1969 [winter]; Cameron 1984; Zumbaugh *et al.* 1985). In South Dakota, mammals accounted for 49% of prey occurrences with prairie dogs (*Cynomys ludovicianus*) as the primary prey item (Uresk and Sharps 1986). Sovada *et al.* (2001b) in Kansas, and Hines and Case (1991) in Nebraska, found that murid rodents were the most frequently occurring prey in swift fox diets. Several studies have reported a high frequency of insects, but insects likely constituted a small portion of biomass (Kilgore 1969). Birds and bird eggs have been identified as a food of swift foxes (Kilgore 1969; Uresk and Sharps 1986; Sovada *et al.* 2001a). Swift fox studies typically have reported a relatively high frequency of plant materials found in samples, but most often in relatively small amounts per sample. However, several studies identified prickly pear cactus fruit, wild plums, and sunflower seeds as a food resource (Kilgore 1969; Hines and Case 1991; Sovada *et al.* 2001b).

Foraging behaviour Swift foxes are mostly solitary hunters, foraging throughout the night. They also exhibit some crepuscular activity and will hunt diurnal species such as birds and ground squirrels during the summer. Caching of food by swift foxes has been observed (Sovada *et al.* 2001b).

Damage to livestock and game There is no evidence that swift foxes significantly impact game or livestock populations.

Adaptations

Swift foxes can run at speeds of up to 60km/hr, which helps to elude predators, and facilitates the hunting of fast prey such as jackrabbits. Predominantly nocturnal activity and diurnal use of dens reduces water loss.

Social behaviour

The typical social group consists of a mated pair with pups. Occasionally, the social group is a trio or group of two males and two or three females, with one breeding female and non-breeding helpers (Kilgore 1969; Covell 1992; Sovada *et al.* 2003; Tannerfeldt *et al.* 2003). Pups remain with the parents until dispersal, which commences in August or September in Oklahoma (Kilgore 1969), September/October in Colorado and Kansas (Covell 1992; Sovada *et al.* 2003) and August in Canada (Pruss 1994). Moehrensclager (2000) reported that only 33% (n=12) of juveniles had left natal home ranges at 9.5 months of age while all recaptured individuals aged 18 months or older had dispersed (n=7).

Published estimates of swift fox home ranges are quite variable and difficult to compare because different techniques and criteria have been used to estimate home-range size (Tannerfeldt *et al.* 2003). Hines and Case (1991) reported an average home range size of 32.3km² (range=

7.7–79.3km²) for seven swift foxes in Nebraska using the minimum convex polygon method, but four animals were followed for fewer than five nights in winter or very early spring. Andersen *et al.* (2003) reported a similar average MCP home-range size of 29.0km² (range=12.8–34.3km²) on the Pinon Canyon Maneuver Site in south-eastern Colorado (1986 to 1987) for five swift foxes with >34 locations over a minimum period of seven months. A slightly smaller estimate (MCP) of average home range, 25.1km² (SE=1.9, range=8.7–43.0km²), was determined for 22 swift foxes with >60 locations in western Kansas (Sovada *et al.* 2003). Zimmerman *et al.* (2003) estimated average MCP home-range size of 10.4km² (range=7.3–16.9km²) for five swift foxes in Montana. Using the 95% adaptive kernel method, Kitchen *et al.* (1999) reported average home-range size of 7.6km² for foxes (with >60 locations per season) on the Pinon Canyon Maneuver Site during 1997 to 1998. In western Kansas, Sovada *et al.* (2003) reported a mean ADK estimate of 19.5km² for 22 foxes (SE=1.4). Pechacek *et al.* (2000) estimated mean 95% ADK home range sizes of 11.7km² and 100% MCP estimates of 7.7km² for 10 swift foxes in south-eastern Wyoming.

Early studies suggested that swift foxes were not territorial (Hines 1980; Cameron 1984), although more recent data have provided evidence of territoriality. Andersen *et al.* (2003) reported nearly total exclusion of an individual swift fox's core activity area to other same-sex individuals. Pechacek *et al.* (2000) and Sovada *et al.* (2003) found areas used by mated pairs had minimal overlap with areas used by adjacent pairs, and core areas were exclusive. In Canada, Moehrenschrager (2000) reported swift fox home ranges overlapped by 77.1% among mates and 21.4% between neighbours.

Avery (1989) described the vocal repertoire of the swift fox from recordings made of captive foxes. He identified eight different vocalisations: courting/territorial call, agonistic chatter, submissive whine, submissive chatter, precopulatory call, growls, excited yip/bark, and social yips.

Reproduction and denning behaviour

Swift foxes are primarily monogamous (Kilgore 1969) although additional females that act as helpers in raising pups are occasionally observed at den sites (Kilgore 1969; Covell 1992; Olson *et al.* 1997; Sovada *et al.* 2003; Tannerfeldt *et al.* 2003). Also, a male has been seen with litters of two different adult females on the same day (Moehrenschrager 2000). Swift foxes are monoestrus and the timing of breeding is dependent upon latitude (Asa and Valdespino 2003). Breeding occurs from December to January in Oklahoma (Kilgore 1969), from January to February in Colorado (Scott-Brown *et al.* 1987; Covell 1992), from February to early March in Nebraska (Hines 1980) and in March among wild and captive Canadian foxes (Pruss 1994; Moehrenschrager 2000). The mean

gestation period is 51 days (Schroeder 1985). Average litter sizes of 2.4–5.7 have been reported based on counts of pups at natal dens (Kilgore 1969; Hillman and Sharps 1978; Covell 1992; Carbyn *et al.* 1994; Schauster *et al.* 2002b; Andersen *et al.* 2003). In Colorado, litter sizes were greater for mated pairs with helpers than for those without (Covell 1992). Pups open their eyes at 10–15 days, emerge from the natal den after approximately one month, and are weaned at 6–7 weeks of age (Kilgore 1969; Hines 1980). Both members of the pair provide for the young and young foxes remain with the adults for 4–6 months (Covell 1992), which is longer than other North American canids.

Swift foxes are among the most burrow-dependent canids and, unlike most others, depend on dens throughout the year (Kilgore 1969; Egoscue 1979; Hines 1980; Tannerfeldt *et al.* 2003). Swift foxes will excavate their own dens and modify the burrows of other species. Dens serve several functions, such as providing escape cover from predators, protection from extreme climate conditions in both summer and winter, and shelter for raising young.

Competition

Predation by and interspecific competition with coyotes (*Canis latrans*) and expansion of red fox (*Vulpes vulpes*) populations may be the two most serious limiting factors to swift fox recolonisation of suitable habitat identified within the species' historic range (Moehrenschrager *et al.* 2004). Coyote killing of swift foxes significantly affected the reintroduction efforts of swift foxes in Canada (Scott-Brown *et al.* 1987; Carbyn *et al.* 1994). Since coyotes frequently do not consume swift foxes, their killing may primarily be a form of interference competition (Sovada *et al.* 1998). Since red foxes and swift foxes have greater dietary overlap than swift foxes and coyotes in sympatric areas of Canada (A. Moehrenschrager unpubl.), the potential for exploitative competition is highest between the two fox species. Moreover, contrasted to coyotes, red foxes tend to be found in higher densities, with smaller home ranges, and they move as individuals rather than as pairs or groups. Therefore, in sympatric populations there is greater chance of red fox-swift fox encounters than coyote-swift fox encounters. Preliminary results from an experimental study examining the swift fox-red fox relationship suggest that red foxes can be a barrier preventing swift fox populations from expanding into unoccupied, but suitable areas (M. A. Sovada unpubl.). In Canada, red fox dens were significantly closer to human habitation than coyote dens while swift fox dens were found at all distances (Moehrenschrager 2000). As coyotes avoid high human activity areas, red foxes may utilise these sites to begin their invasion of swift fox home ranges. While coyotes reduce swift fox numbers through direct, density-dependent killing within the swift fox range, red foxes could potentially exclude swift foxes through a combination of interference and exploitative competition.

Mortality and pathogens

Reported annual mortality rates range from 0.47 to 0.63 (Covell 1992; Sovada *et al.* 1998; Moehrenschrager 2000; Schauster *et al.* 2002b; Andersen *et al.* 2003), and those of translocated foxes have been similar to those of wild residents in Canada (Moehrenschrager and Macdonald 2003).

Natural sources of mortality Coyotes have been identified as the principal cause of swift fox mortality (Covell 1992; Carbyn *et al.* 1994; Sovada *et al.* 1998; Kitchen *et al.* 1999; Moehrenschrager 2000; Andersen *et al.* 2003). Other predators of swift foxes that have been identified include golden eagles (*Aquila chrysaetos*) and American badgers (*Taxidea taxus*) (Carbyn *et al.* 1994; Moehrenschrager 2000; Andersen *et al.* 2003).

Persecution Mortality factors associated with human activities include poisoning, shooting, and trapping (Kilgore 1969; Carbyn *et al.* 1994; Sovada *et al.* 1998).

Hunting and trapping for fur Swift foxes formed an important part of the North American fur trade. Records of the American Fur Company's Upper Missouri Outfit (near the confluence of the Big Sioux and Missouri Rivers) from 1835 to 1838 included 10,427 swift fox pelts compared to 1,051 red fox pelts and 13 gray fox (*Urocyon cinereoargenteus*) pelts received during the same period (Johnson 1969). Alexander Henry's journals noted the take of 117 "kit" foxes from 1800 to 1806 in north-eastern North Dakota with an additional 120 "kit" foxes received from the Hudson's Bay Company at Pembina in 1905–1906 (Reid and Gannon 1928).

Currently, swift foxes are legally protected under State laws in all 10 states and are protected from harvest through laws or regulations in seven of these. Colorado, Montana, North Dakota, and Oklahoma list swift fox as furbearers but the harvest season is closed all year. Nebraska lists swift fox as "endangered," and in South Dakota they are "threatened." Wyoming lists swift fox in their non-game regulations, and only incidental harvest is allowed to provide additional distribution data. States that do provide harvest opportunities, Kansas, New Mexico, and Texas, regulate harvest by season length and monitor harvest numbers annually. Harvest is minimal (e.g., 181 foxes harvested in Kansas in 1994–2001), and largely incidental captures by coyote trappers. In Canada, where swift foxes are federally listed as 'endangered', swift foxes cannot be legally harvested; however, incidental injuries or mortalities occur in traps or snares set for other species (Moehrenschrager 2000).

Road kills Collisions with automobiles are a significant mortality factor for young animals in some landscapes (Sovada *et al.* 1998).

Pathogens and parasites No significant disease outbreaks have been documented in swift fox populations to date; however, Olson (2000) reported deaths of two swift foxes to canine distemper. Swift foxes host a variety of internal and external parasites (Kilgore 1969; Pybus and Williams 2003). Fleas (*Opisocrostos hirsutus* and *Pulex* spp.) are the most common and abundant ectoparasite. Kilgore (1969) suggested that the large numbers of fleas found in swift fox dens might be a reason for the frequent changes in dens used by foxes. Other parasites include hookworms (*Ancylostoma caninum*, *Uncinaria* sp.) and whipworms (*Trichuris vulpis*), as well as miscellaneous protozoans and ectoparasites (Pybus and Williams 2003).

Longevity Captive-born and translocated swift foxes in Canada that were marked at the time of release have been recaptured as late as eight years old, with extremely worn teeth (A. Moehrenschrager unpubl.).

Historical perspective

Swift foxes were of cultural importance to many Plains Indian Nations. The Kit (Swift) Fox Society of the Blackfoot Tribe of south-western Alberta and northern Montana ranked high in status and performed sacred functions. Remains of swift foxes have been found in archaeological sites dating back several thousand years.

Conservation status

Threats Since swift foxes are primarily prairie specialists, ongoing conversion of grassland to cropland threatens to reduce population sizes and further fragment populations. The conversion of native grassland prairies has been implicated as one of the most important factors for the contraction of the swift fox range (Hillman and Sharps 1978). We believe that alteration of the landscape likely influences local and seasonal prey availability, increases risk of predation for swift foxes, and leads to interspecific competition with other predators such as the coyote and red fox. Moreover, an increasing trend towards irrigation of crops from the dry-land farming practices of fallow cropland every other year could exclude swift foxes that have adapted to den and forage successfully under the dryland farming rotational practices. The planting of tall, dense vegetation as a part of the United States Conservation Reserve Program, may also negatively impact swift foxes because they avoid these densely vegetated habitats. In Canada, the oil and gas industry is expanding dramatically and previously isolated prairie areas are now targeted for exploration. Associated road developments will potentially decrease the habitat carrying capacity and increase vehicle-caused swift fox mortalities. Greater urbanisation coupled with coyote control may facilitate red fox expansion, which could lead to the competitive exclusion of swift foxes in established prairie areas. In the United States, the 1972 presidential ban on predator toxicant use (e.g.,

strychnine, compound 1080) on Federal lands may have contributed to swift fox recovery. However, 1080 is currently being legalised in prairie areas of Saskatchewan, Canada, which will likely limit reintroduced swift fox populations. Moreover, landowners that are attempting to protect their livestock from coyote depredation use poisons illegally and swift foxes readily consume such baits (Moehrenschrager 2000).

Commercial use None.

Occurrence in protected areas In Canada, swift foxes are found mainly on unprotected lands, but approximately one-sixth of the population falls within the boundaries of Grasslands National Park. In the United States, there are 24 National Park Service Units (Parks, Monuments, Historic Sites) located in the historic range of swift foxes. Although there are no records of swift foxes in any of these units, 14 have potential for swift fox presence. One unit, Badlands National Park in South Dakota, began a reintroduction in 2003.

Protection status CITES – not listed.

The swift fox has been down-listed from ‘extirpated’ to ‘endangered’ in Canada as a result of the swift fox reintroduction programme.

Current legal protection In the United States, the swift fox was petitioned for listing under the Endangered Species Act. In 2001 the U.S. Fish and Wildlife Service determined listing to be unwarranted.

Conservation measures taken

- In Canada, the National Swift Fox Recovery Team is currently revising its national swift fox recovery strategy, which will be implemented through national and provincial action plans as of 2003. The Canadian federal government has just passed the country’s first ‘Species at Risk Act’, which will provide greater legal protection of swift foxes and promote landowner stewardship programmes facilitating local conservation efforts.
- In the United States, the Swift Fox Conservation Team operates under a Swift Fox Conservation Strategy Plan with identified goals up to the year 2005. The team continues to monitor populations, assess critical habitat conditions, review the potential for reintroductions, and provide research support for ongoing projects.

Occurrence in captivity

In Canada, swift foxes are present in the Calgary Zoo, Cochrane Ecological Institute, Kamloops Wildlife Park, and Saskatoon Zoo. In the United States, swift foxes are represented in the Bismarck Zoo, Bramble Park Zoo,

Houston Zoo, Lee Richardson Zoo, Living Desert, Minnesota Zoo, Philadelphia Zoo, Pueblo Zoo, Sunset Zoo, Tulsa Zoo, and Wild Canid Center. The Fort Worth Zoo has put forward a petition to manage a swift fox Species Survival Plan on behalf of the American Zoo Association. On behalf of the Canid Taxon Advisory Group, the St. Louis Zoo is currently devising recommendations for swift fox space allocations in the North American programme.

Current or planned research projects

M. Sovada (Northern Prairie Wildlife Research Centre, U.S. Geological Survey, Jamestown, North Dakota, USA) is working in the state of Kansas, where she is developing methodology for long-term monitoring of swift foxes on a landscape scale with spatial smoothing. Preliminary assessments have been conducted for western Kansas and the final model will provide the basis for determining future expansion or retraction of swift fox range.

The Swift Fox Conservation Team, M. Sovada (Northern Prairie Wildlife Research Centre, U.S. Geological Survey, Jamestown, North Dakota, USA) and others are examining swift fox habitat requisites at a range-wide scale. They intend to use location and remote-sensing habitat data, multivariate statistical techniques, and GIS to model swift fox habitat range wide.

R. Harrison and Jerry Drago (University of New Mexico, Albuquerque, New Mexico, USA) in conjunction with the New Mexico Department of Game and Fish, are developing a monitoring plan for tracking swift fox relative to population density, range-wide in New Mexico. They are testing scat collection followed by species verification with mitochondrial DNA analysis.

R. Harrison, M.J. Patrick (Pennsylvania State University, Altoona, Pennsylvania, USA) and C. G. Schmitt (New Mexico Department of Game and Fish, Santa Fe, New Mexico, USA) are also identifying and creating voucher specimens of fleas from four fox species in New Mexico (swift, kit, grey, and red foxes).

E. Gese (National Wildlife Research Center, Utah State University, Utah, USA) is continuing a long-term study on swift foxes on the U.S. Army Pinon Canyon Maneuver Site in south-eastern Colorado. Entering the sixth year of this study, over 200 swift foxes have been radio-collared and tracked. Currently, a Ph.D. student is examining the influence of land-use patterns on plant composition and productivity, the small mammal community, and swift fox demographics. An M.Sc. student will be investigating helper behaviour and swift fox pup survival from den emergence to independence.

A. Moehrenschrager (Calgary Zoo and University of Calgary, Calgary, Alberta, Canada), P. Fargey (Grasslands National Park, Parks Canada, Saskatchewan, Canada), and S. Alexander (University of Calgary, Calgary, Alberta, Canada) are developing a predictive GIS habitat suitability

model for the reintroduced Canadian/Montana swift fox population.

A. Moehrenschrager (Calgary Zoo and University of Calgary, Calgary, Alberta, Canada) and C. Strobeck (University of Alberta, Edmonton, Alberta, Canada) are testing gene flow and connectivity in the reintroduced Canada/Montana swift fox population using hair samples collected from 1995 to 2001.

A. Moehrenschrager (Calgary Zoo and University of Calgary, Calgary, Alberta, Canada) and A. Aguirre (Wildlife Trust, Palisades, New York, USA) have tested swift fox serology in Canada and will create a serological profile for all sympatric prairie canids (swift fox, red fox, coyote and domestic dog).

Gaps in knowledge

In Canada and the United States assessments of historical distribution and the identification of critical swift fox habitats for legal protection are hampered by the fact that swift fox habitat use is not well understood. Future studies should assess to what degree swift foxes can utilise differing types of habitats, including habitats considered atypical, such as those dominated by cropland. Information is needed to identify why swift foxes are unable to move into areas of apparently suitable habitat. Identification of barriers, both physical and ecological (e.g., competitive exclusion with other canids), to dispersal would improve the ability to manage and ultimately conserve this species. Future investigations should focus on parameters that might affect the range-wide, long-term viability of the populations.

The primary stochastic factor influencing small canid populations around the world is disease (Woodroffe *et al.* 1997; Laurenson *et al.* 1998; Woodroffe and Ginsberg 1999a), and such risks are enhanced when animals are transferred between populations (Woodford and Rossiter 1994). Although the Canadian population was partly established through translocation, swift fox exposure to canid diseases has not been assessed in Canada. The prevalence of disease exposure in different age classes and regions should be assessed in both countries and the likelihood of disease transfer between swift foxes and sympatric coyotes, red foxes, and domestic dogs should be evaluated. In addition, genetic analyses should be conducted to examine bottlenecks, genetic variability, connectivity, and dispersal distances in Canada and within isolated population fragments of the United States. Finally, data on swift fox demography, disease prevalence, genetics, habitat use, and population trends should be incorporated into population viability models to guide conservation planning on a provincial/state or federal basis.

Core literature

Egoscue 1979; Hines and Case 1991; Jackson and Choate 2000; Kilgore 1969; Kitchen *et al.* 1999; Moehrenschrager 2000; Moehrenschrager and Macdonald 2003; Schauster *et al.* 2002a,b; Sovada and Carbyn 2003; Sovada *et al.* 1998, 2001b, 2003.

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