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Vulpes vulpes.

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Vulpes vulpes (Linnaeus, 1758)
Red Fox

Canis vulpes Linnaeus, 1758:40. Type locality "Sweden."
Canis alopex Linnaeus, 1758:40. Type locality "Sweden."
Canis karagan Erxleben, 1777:566. Type locality "Kirghiz Steppes, Russian Asia" [presumably Khirghizia].
Canis crucigera Bechstein, 1789:250. Type locality "Thuringia, Germany."
Canis barbarus Shaw, 1800:311. Type locality "Barbary, i.e., coast of North-Western Africa."
Canis melanotus Pallas, 1811:44. No type locality given.
Canis aegyptiacus Sonnini, 1816:524. Type locality "Egypt."
Canis fulvus Desmarest, 1820:203. Type locality "Virginia."
Canis niloticus Desmarest, 1820:204. Type locality "Egypt."
Canis nigro-argenteus Nilsson, 1820:91. Type locality "Lofoten Islands, Norway."
Canis melanogaster Bonaparte, 1832:1. Type locality "near Rome, Italy."
Canis anubis Hemprich and Ehrenberg, 1833:2. Type locality "Fayum, Egypt."
Canis vulpecula Hemprich and Ehrenberg, 1833:2. Type locality "Fayum, Egypt."
Canis himalaicus Ogilby, 1837:103. Type locality "Mussooree, Kumaon, [Uttar Pradesh], North-Western India."
Vulpes nepalensis Gray, 1837:578. Type locality "Nepal."
Vulpes hypomelas Wagner, 1841a:405. Type locality "Oberbayern, [=southern Bavaria], Germany."
Vulpes flavescens Gray, 1843:118. Type locality "Northern Persia" [=Iran].
Vulpes macrourus Baird, 1852:309. Type locality "Wasatch Mountains bordering Great Salt Lake, Utah."
Vulpes leucopus Blyth, 1854:729. Type locality "Multan, Punjab," [Pakistan].
Vulpes pusillus Blyth, 1854:729. Type locality "Salt Range, Punjab," [Pakistan].
Vulpes griffithii Blyth, 1854:730. Type locality "Kandahar, Afghanistan."
Vulpes algeriensis Loche, 1858:4. Type locality "wooded parts of Algeria."
Vulpes japonica Gray, 1868:517. Type locality "Japan."
Vulpes hoole Swinhoe, 1870:631. Type locality "near Amoy, Fukien, Southern China."
Vulpes lineiventer Swinhoe, 1870:632. Type locality "near Amoy, Fukien," [China].
Vulpes persicus Blanford, 1875:310. Type locality "Shiraz, Persia," [=Iran].
Vulpes (*sic.*) *pennsylvanicus* Rhoads, 1894:524. No type locality given [presumably Pennsylvania].
Vulpes deletrix Bangs, 1898*a*:36. Type locality "Bay St-George, Newfoundland," [Canada].
Vulpes harrimani Merriam, 1900*a*:14. Type locality "Kodiak Island, Alaska."
Vulpes alascensis Merriam, 1900*b*:668. Type locality "Andreafski, about 70 mi. above delta of Yukon River, Alaska."
Vulpes cascadensis Merriam, 1900*b*:665. Type locality "Trout Lake, south base of Mount Adams, Cascade Mountains, Skamania County, Washington."
Vulpes kenaiensis Merriam, 1900*b*:670. Type locality "Kenai peninsula, Alaska."
Vulpes necator Merriam, 1900*b*:664. Type locality "Whitney Meadow, near Mount Whitney, High Sierra, Tulare County, California."
Vulpes regalis Merriam, 1900*b*:672. Type locality "Elk River, Sherburne County, Minnesota."
Vulpes anadyrensis Allen, 1903:167. Type locality "Marcova, Anadyr Province, Eastern Siberia," [Russia].
Vulpes alpherakyi Satunin, 1906:46. Type locality "Geok Tepe, Araisk, subdistrict of former govt. of Elisabetpol, Russian Turkestan," [Kazakhstan].
Vulpes kurdistanica Satunin, 1906:48–53. Type locality "Gelsk Valley, Kars district, Western Transcaucasia" [probably in extreme North-Eastern Turkey].
Vulpes waddelli Bonhote, 1906:303. Type locality "Kambajong, Tibet," [China].
Vulpes ichnusae Miller, 1907:391. Type locality "Sarrabus, Sardinia," [Italy].
Vulpes indutus Miller, 1907:392. Type locality "Cape Pyla, Cyprus."
Vulpes ladacensis Matschie, 1907:167. Type locality "Ladak," [India].
Vulpes aurantioluteus Matschie, 1907:168. Type locality "Tatsienlu, Szechuan, China."
Vulpes tschiliensis Matschie, 1907:169. Type locality "Peiping, Chihli, North-Eastern China."
Vulpes kamtschadensis Brass, 1911:456. No type locality given, [presumably Kamchatka, Russia].
Vulpes huli Sowerby, 1923:44. Type locality "Manchuria," [China].
Vulpes peculiosa Kishida, 1924*a*:4. Type locality "Korea."
Vulpes dolichocrania Ognev, 1926:232. Type locality "Sidemi, region of southern Ussuri, South-Eastern Siberia," [Primorsk Kray, Russia].
Vulpes kiyomasai Kishida and Mori, 1929:82. Type locality "North-Eastern Korea."

CONTEXT AND CONTENT. Order Carnivora, Family Canidae. The genus *Vulpes* includes 10 species: *V. bengalensis*, *V. cana*, *V. chama*, *V. corsac*, *V. ferrilata*, *V. pallida*, *V. rueppelli*, *V. velox*, *V. vulpes*, and *V. zerda* (Wozencraft, 1993). The North American red fox had been considered a separate species, *V. fulva*, but most authorities now consider it to be conspecific with the Palearctic *V. vulpes* (Nowak, 1991). *V. velox* and *V. macrotis* sometimes are classified as distinct species (Nowak, 1991), but are treated as conspecific by Hall (1981). The subspecies (Banfield, 1987; Ellerman and Morrison-Scott, 1966; Wozencraft, 1993) of *V. vulpes* include:

V. v. abietorum Merriam, 1900*b*:669. Type locality "Stuart Lake, British Columbia, Canada" (*sitkaensis* Brass is a synonym).
V. v. aegyptiaca Sonnini, 1816:524, see above (*niloticus* Desmarest, *anubis* Hemprich and Ehrenberg, *vulpecula* Hemprich and Ehrenberg are synonyms).
V. v. alascensis Merriam, 1900*b*:668, see above.
V. v. alpherakyi Satunin, 1906:46, see above.
V. v. anatolica Thomas, 1920:121. Type locality "Smyrna, Western Asia Minor," [Turkey].
V. v. arabica Thomas, 1902:489. Type locality "Muscat, Arabia," [Oman].
V. v. atlantica Wagner, 1841*b*:31. Type locality "Atlas Mountains, Mitiya, Algeria" (*algeriensis* Loche is a synonym).
V. v. bangsi Merriam, 1900*b*:667. Type locality "L'Anse au Loup, Strait of Belle Isle, Labrador."
V. v. barbara Shaw, 1800:311, see above (*acaab* Cabrera is a synonym).
V. v. beringiana Middendorf, 1875:990. Type locality "shore of Bering Strait, North-Eastern Siberia," [Russia] (*anadyrensis* Allen, *kamtschadensis* Brass are synonyms).
V. v. cascadensis Merriam, 1900*b*:665, see above.
V. v. caucasica Dinnik, 1914:449. Type locality "near town of Vladikawkaz, Caucasus," [North Osetia, Russia].
V. v. crucigera Bechstein, 1789:250, see above (*nigra* Borkhausen,

cinera Bechstein, *lutea* Bechstein, *melanogaster* Bonaparte, *hypomelas* Wagner, *meridionalis* Fitzinger, *toschii* Lehmann, *hellenica* Douma-Petridou and Ondrias, *diluta* Bobrinskii are synonyms).

V. v. daurica Ognev, 1931:331. Type locality "Kharangoi, 45 km. west from town of Troizkosavsk, Siberia," [Russia].

V. v. deletrix Bangs, 1898*a*:36, see above.

V. v. dolichocrania Ognev, 1926:232, see above.

V. v. flavescens Gray, 1843:118, see above (*splendens* Thomas is a synonym).

V. v. fulva Desmarest, 1820:203, see above.

V. v. griffithii Blyth, 1854:730, see above.

V. v. harrimani Merriam, 1900*a*:14, see above.

V. v. hoole Swinhoe, 1870:631, see above (*lineiventer* Swinhoe, *aurantioluteus* Matschie, *eckloni* Jacobi are synonyms).

V. v. ichnusae Miller, 1907:391, see above.

V. v. induta Miller, 1907:392, see above.

V. v. jakutensis Ognev, 1923:116. Type locality "taiga south from town of Yakutsk, Eastern Siberia," [Russia].

V. v. japonica Gray, 1868:517, see above.

V. v. karagan Erxleben, 1777:566, see above (*melanotus* Pallas, *ferganensis* Ognev, *kasachstanica* Tolstova and Lazarev, *tarimensis* Matschie are synonyms).

V. v. kenaiensis Merriam, 1900*b*:670, see above.

V. v. kurdistanica Satunin, 1906:48–53, see above (*alticola* Ognev is a synonym).

V. v. macroura Baird, 1852:309, see above.

V. v. montana Pearson, 1836:313. Type locality "Himalayas" (*himalaicus* Ogilby, *nepalensis* Gray, *waddelli* Bonhote, *ladacensis* Matschie are synonyms).

V. v. necator Merriam, 1900*b*:664, see above.

V. v. ochroxantha Ognev, 1926:225. Type locality "Aksai, Semirechyia, Eastern Russian Turkestan," [Kirgizia].

V. v. palaestina Thomas, 1920:122. Type locality "Ramleh, near Jaffa, Palestine," [Israel].

V. v. peculiosa Kishida, 1924*b*:47, see above (*kiyomasai* is probably a synonym).

V. v. pusilla Blyth, 1854:729, see above (*leucopus* Blyth, *persicus* Blanford are synonyms).

V. v. regalis Merriam, 1900*b*:672, see above.

V. v. rubricosa Bangs, 1898*b*:272. Type locality "Digby, Nova Scotia, Canada" (renaming of *Vulpes vafra* Bangs, preoccupied).

V. v. schrencki Kishida, 1924*b*:47. Type locality "Sakhalin," [Russia].

V. v. silacea Miller, 1907:393. Type locality "near Silos, Burgos, Spain."

V. v. splendidissima Kishida, 1924*b*:47. Type locality "North and Central Kurile Islands."

V. v. stepensis Brauner, 1914:15. Type locality "Steppes near town of Kherson, Russia." (*krimeamontana* Brauner, *crymensis* Brauner are synonyms).

V. v. tobolica Ognev, 1926:227. Type locality "Obdorsk, Government of Tobolsk, Siberia," [Russia].

V. v. tschiliensis Matchie, 1907:169, see above (*huli* Sowerby is a synonym).

V. v. vulpes Linnaeus, 1758:40, see above (*alopex* Linnaeus, *nigroargenteus* Nilsson, *lineatus* Billberg, *nigrocaudatus* Billberg, *variegatus* Billberg, *septentrionalis* Brass are synonyms).

DIAGNOSIS. *Vulpes vulpes* (Fig. 1) is the most common and well-known species in the genus. Its long tail (70% of head and body length) and typical coloration make the red fox instantly recognizable (Voigt, 1987). Coat color ranges from pale yellowish red to deep reddish brown on the upper parts and is white on the underparts. The ears are black-tipped, the lower parts of the legs and feet are black, and the tip of the tail is white (Nowak, 1991; Voigt, 1987).

GENERAL CHARACTERS. *V. vulpes* is a relatively small, slender canid with an elongated muzzle, large pointed ears, and round, bushy tail, usually as long as the head and body (Hall, 1981; Stroganov, 1969). Red foxes have long slender legs, relatively small feet, eyes moderate in size, and elliptical pupils (Banfield, 1987; Jackson, 1961). Three color morphs of the red fox have been identified: red, silver or black, and cross (Johnson and Hersteinsson, 1993).

In the typical red fox, yellow to reddish-brown tones predominate in the upper body; cheeks, chin, throat, and abdomen are white; face and rump are rusty; legs and ear tips are black; and the tail, with a distinctive white tip, is mixed profusely with black (Jackson, 1961). Both the silver and cross morphs are rare, but in some areas may represent approximately 10 and 25% of individuals, respectively (Nowak, 1991). In the silver fox, coat color varies from silver to nearly black with a variable amount of frosting resulting from silver tips on the guard hairs (Banfield, 1987). The cross fox is predominantly grayish-brown, and gets its name from the long black guard hairs that form a line down the back and another across the shoulder (Banfield, 1987).

FIG. 1. Adult *Vulpes vulpes* from Prince Albert National Park, Saskatchewan, Canada. (Photograph by M. Pasitschniak-Arts.)

Vulpes vulpes shows wide individual and geographical variation in size. Length of head and body in adults can range from 455 to 900 mm, tail length from 300 to 555 mm, and body mass from 3 to 14 kg (Nowak, 1991). Males are on average larger than females, but there are no other variations associated with sex (Jackson, 1961). Mean body measurements (mm) of males and females, respectively, and sample sizes (males, females) are Canberra, Australia: total length, 1,046.7, 1,001.7; length of tail, 396.5, 377.5; length of hind foot, 153.3, 146.4; and length of ear, 91.8, 88.2 (n = 84, 60; McIntosh, 1963); Kent, England: total length, 1,064.4, 1,022.5; length of tail, 400.6, 391.5; length of hind foot, 148.9, 140.5; and length of ear, 91.1, 90.0 (n = 9, 10; Hattingh, 1956); Ontario, Canada: total length, 1,026, 973 (n = 37, 34); length of tail, 382, 362 (n = 45, 44); and length of hind foot, 167, 158 (n = 44, 44; Voigt, 1987). Mean adult mass (kg) and sample sizes (males, females) are: Canberra, Australia, 6.3, 5.5 (n = 84, 60; McIntosh 1963); England, 6.7, 5.4 (n = 33, 29; Hattingh, 1956); Ontario, Canada, 4.1, 3.4 (n = 37, 37; Voigt, 1987); and Hokkaido, Japan, 8.7, 6.1 (n = 20, 25; Zhan et al., 1991).

The skull is long and slender (Fig. 2), with a flat interorbital and frontal region, slightly inflated frontal sinuses, and a long and narrow rostrum with a slight depression below the frontal region. Postorbital processes have well-marked fossae on the dorsal side, paroccipital processes are small, and audital bullae are prominent. Two parietal ridges run from the supraorbital processes in front and unite behind to form a single sagittal crest. The palate ends medially in front of the last molar, the canines are long and slender, and the medial incisors show slight lobes (Banfield, 1987; Jackson, 1961; Stroganov, 1969). Skull measurements (mm) of adult males and females, respectively, and sample sizes (males, females) from Minnesota, USA are: total length, 150.2, 142.3; postorbital constriction, 23.0, 23.1; post maxillary length, 25.2, 24.5; mastoidal breadth, 48.4, 47.3; width of rostrum, 21.8, 21.3; zygomatic breadth, 76.7, 75.2; palatal width, 40.4, 39.0; condyle length of premaxillae, 144.0, 137.1; and length of jaw, 84.7, 80.4 (n = 16, 11; Storm et al., 1976).

DISTRIBUTION. *Vulpes vulpes* is the most widely distributed carnivore in the world (Fig. 3; Voigt, 1987). It occurs throughout Europe and the countries of the Commonwealth of Independent States and Russia (formerly USSR), but does not penetrate into the interior of the tundra or the extreme north of Siberia. It is found in Afghanistan, Algeria, Arabia, Asia Minor, China, Indo-China, Cyprus, Egypt, India, Iraq, Japan, Libya, Manchuria, Mongolia, Morocco Palestine, Persia, and Tibet. Red foxes were brought to Aus-

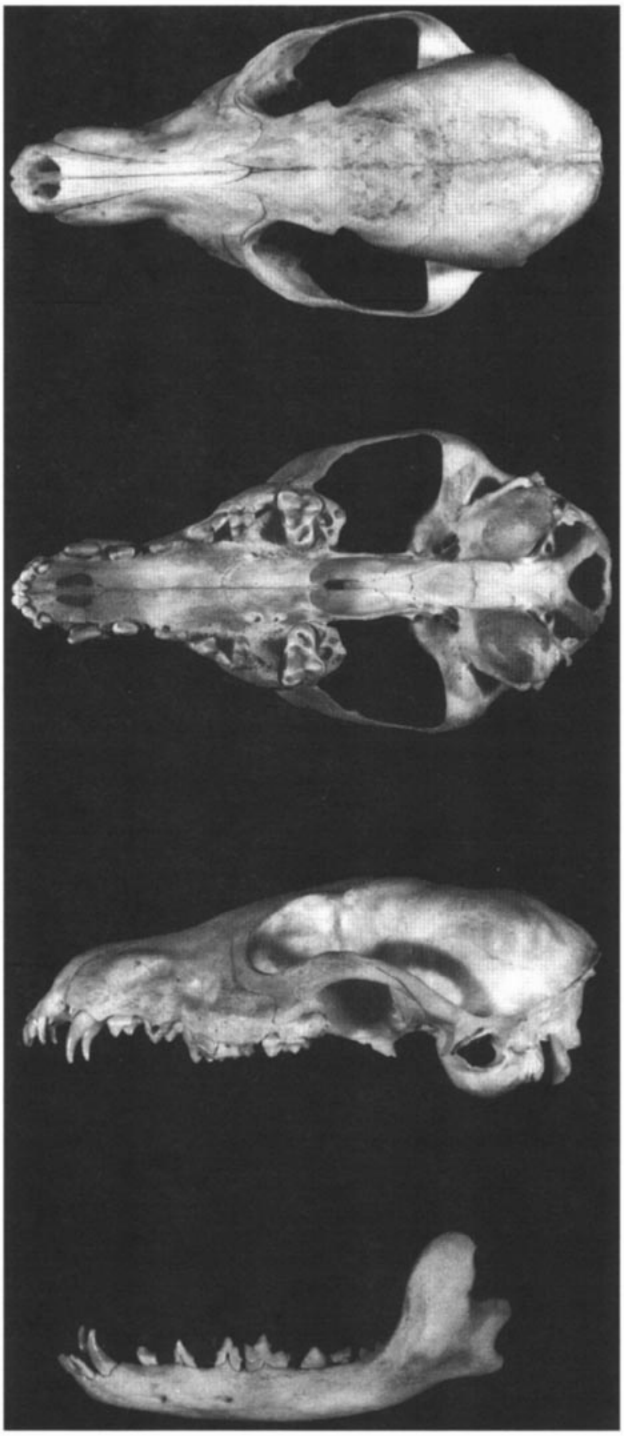

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Vulpes vulpes* from Kermen's Prairie, Saskatchewan (female, University of Saskatchewan, Saskatoon 2472). Greatest length of cranium is 124.2 mm.

tralia in 1868 and have spread over much of the continent (Corbet and Hill, 1980; Ellerman and Morrison-Scott, 1966; Voigt, 1987; Wozencraft, 1993). In North America, *V. vulpes* is found throughout Canada (including Baffin Island, Northwest Territories) and the USA (including Alaska), except in parts of the arctic, the southern Atlantic coastal region, southwestern desert and Pacific coastal region, and areas of the south-central Great Plains (Samuel and Nelson, 1982; Voigt, 1987).

The red fox was apparently native to North America north of 40–45°N, but in aboriginal times was scarce or absent in the middle Eastern USA and in the hardwood forests where the gray fox (*Urocyon cinereoargenteus*) was common (Churcher, 1959; Gilmore, 1946). In colonial times (1650–1750), *V. vulpes* was introduced from England to North America for fox hunting (Gilmore, 1946). This resulted in an increase in numbers of red foxes in areas not previously occupied. Three factors appear to have had the greatest influence on red fox populations in midwestern North America: interspecific canid competition, human impact, and habitat changes (Sargeant, 1982). It has been postulated that the red fox has increased its range in areas where the gray wolf (*Canis lupus*) and red wolf (*C. rufus*) have been extirpated (Sargeant, 1982; Voigt, 1987), as well as in response to human-caused decrease in coyote (*C. latrans*) numbers (Hall, 1981; Sargeant, 1982). In southern areas of North America, this expansion coincided with clearing of forests. In many areas, intense harvest for fur held populations at low levels, but numbers rebounded with reduced harvest pressure, the depression, and World War II (Sargeant, 1982).

FOSSIL RECORD. *Vulpes vulpes* originated in the Old World and probably arose from Villafranchian populations of *V. alopecoides* (Kurtén, 1968; Kurtén and Anderson, 1980). The ancestral form was likely small, judging from the size of the species in the early Toringian, ca. 300 ka. Outside Europe, the history of *V. vulpes* dates back to the earliest 400 ka. Late Pleistocene records are common in both caves and open-air sites (Kurtén, 1968).

Colonization of the New World dates from the Rancholabrean (122–132 ka), and the oldest American fossils of *V. vulpes* have been found in fissure deposits of that age (Conard Fissure, Arkansas; Kurtén, 1968). No record apparently antedates the Sangamonian, except possibly in the far north. The species has been recorded in the Fairbanks District, Alaska, USA, at Medicine Hat, Alberta, Canada, and at Old Crow, Yukon, Canada. The red fox also is present at >25 sites of Wisconsinan age in Arkansas, California, Colorado, Idaho, Missouri, Montana, Nevada, New Mexico, Tennessee, Texas, Virginia, and Wyoming (Kurtén and Anderson, 1980). *V. vulpes* ranged far south in the Wisconsinan, however, evidence suggests that its range shrank towards the north with warmer conditions.

FORM AND FUNCTION. The outer fur of *V. vulpes* is long and silky. The underfur is long and thick, gray at the base and buff towards the tips (Banfield, 1987). The pelt is at its prime (i.e., long and dense guard hairs and dense underfur) beginning in December (Voigt, 1987). In fully prime pelts, the guard hairs are >9 cm and the underfur is approximately 4 cm (Obbard, 1987). In early spring, winter pelage is replaced by summer fur, which is markedly shorter, sparser, and duller than winter fur (Stroganov, 1969). There is no seasonal variation in color. Red foxes undergo one annual molt (Jackson, 1961).

The skeletal structure resembles that of a small, slender dog. The animal is light and agile, with the normal gait being a spritely walk, occasionally breaking into a running trot (Jackson, 1961). The red fox may run at speeds of up to 48 km/h when pursued, may gallop for many kilometers, and is a good swimmer (Jackson, 1961). *V. vulpes* occasionally climbs trees (Sklepkovych, 1994). Senses of sight, hearing, and smell are well developed (Nowak, 1991).

The forefoot and hindfoot have five and four toes, respectively, each with long nonretractile claws (Samuel and Nelson, 1982). The track of *V. vulpes* is similar but generally narrower than that of a small dog, and the imprint of the claw is clearly evident. The footprint is oval and the toepads are smaller than those of the gray fox. In winter, *V. vulpes* has furred footpads (Banfield, 1987).

The dental formula is: i 3/3, c 1/1, p 4/4, m 2/3, total 42 (Hall, 1981). Typical of carnivores, the lower first molar and upper fourth premolar form the meat-shearing carnassial teeth (Voigt, 1987).

In *V. vulpes*, surface areas such as the face, dorsal part of the head, nose, ears, lower legs and paws likely function as major heat exchange surfaces for thermoregulation (Klir and Heath, 1992). Fur on these thermoregulatory surfaces is dense but short throughout the year enabling animals to control heat loss. Peripheral vasodilation and vasoconstriction and increased and reduced blood flow result in higher and lower heat loss, respectively. These thermoregulatory surfaces represent 32.9% of the total surface area in red foxes (Klir and Heath, 1992). The critical ambient temperature for surface regions with short fur is between −20° and −15°C. *V. vulpes* use the nose for evaporative cooling and the nose is probably

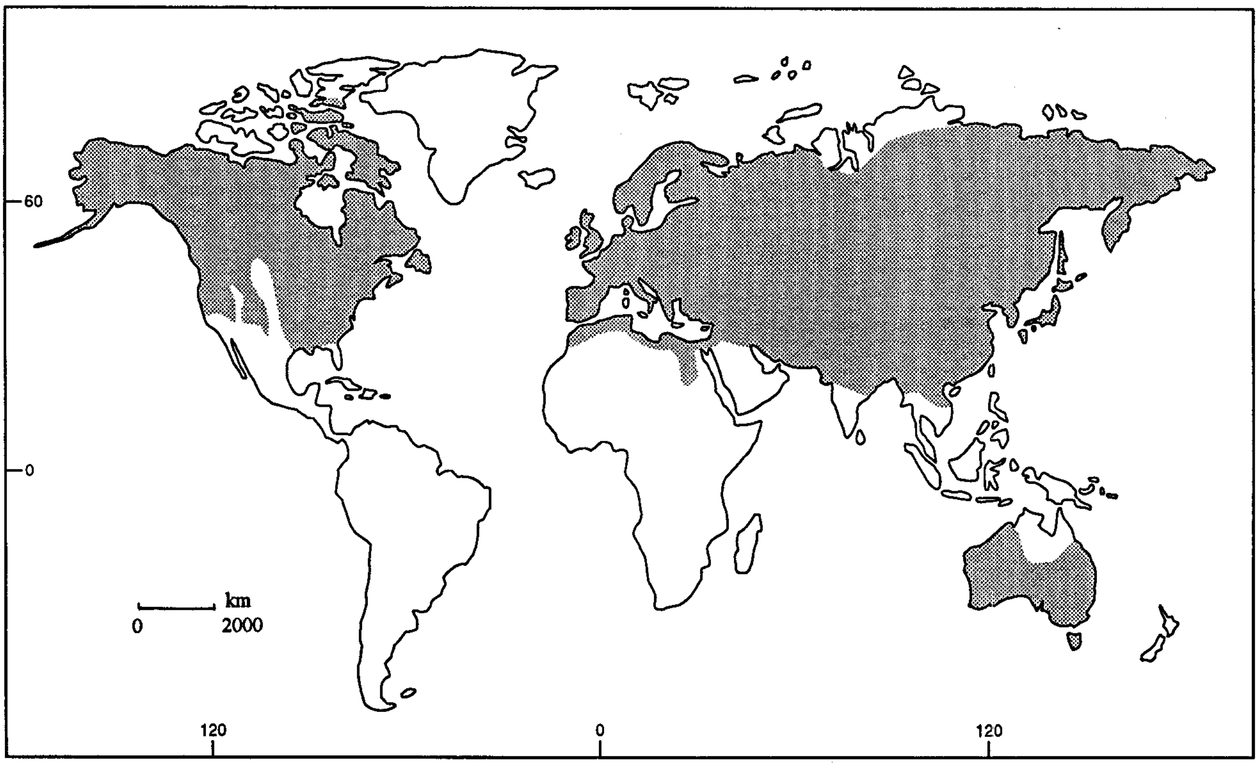

FIG. 3. Distribution of *Vulpes vulpes* (Henry, 1986; Samuel and Nelson, 1982; Voigt, 1987).

a part of the brain cooling mechanism similar to that described in dogs (Klir and Heath, 1992).

Red foxes have a 2-cm-long subcaudal gland on the upper portion of the tail that gives off a "foxy" odor. The function of this gland is not known, but it may be used in individual recognition (Samuel and Nelson, 1982). The long tail is used for balance and for keeping the face warm while sleeping.

Males and females have similar heart rate and body temperature except when sleeping, when females have higher heart rates than males (Kreeger et al., 1989). The hypothesized difference is due to the relationship between size and metabolic rate. Sleeping foxes have a pronounced respiratory sinus arrhythmia of undetermined adaptive significance, which disappears with activity (Kreeger et al., 1989).

ONTOGENY AND REPRODUCTION. *Vulpes vulpes* is seasonally monogamous (Ables 1975). In temperate environments, red foxes breed from December through April, although most matings occur in January and February (Allen, 1984; Macdonald, 1980*a*, Storm et al., 1976). In Australia, breeding occurs between June–October (Ryan, 1976). Female red foxes usually breed during their first autumn (Allen, 1984), but in areas of extreme high density, most yearlings do not produce pups (Harris, 1979). In areas of lower density, 80–90% of yearlings and 95% of older vixens may breed successfully (Voigt and Macdonald, 1984). Food abundance, physiological immaturity, and inhibition related to polygynous associations may inhibit pregnancy (Harris, 1979).

Females are monestrous (McIntosh, 1963; Ryan, 1976), and estrus lasts from 1 to 6 days (Voigt, 1987). Duration of copulation averages 26 minutes, but ranges from 1 to 67 minutes (Pearson and Bassett, 1946). Parturition occurs after a gestation of 52 days (Voigt, 1987).

Mean litter size in red foxes can be determined using counts of *corpora lutea* (Layne and McKeon, 1956), placental scars (Allen, 1983; Harris, 1979), and embryos (Allen, 1983). A proportion of ova may not implant, and 5–8% of fetuses may be resorbed (Layne and McKeon, 1956; Ryan, 1976). Litter size ranges from one to 12; most often three to six offspring are born. Litter size increases with food availability (Goszczynski, 1989*a*) and with age of females (Allen, 1984; Englund, 1970; Harris, 1979; Vos, 1994). Highest fecundity of vixens was reported in Ontario, Canada (placental scars: average = 8.0, maximum = 14; Voigt, 1987). Communal denning (Tullar and Berchielli, 1980; Tullar et al., 1976) may explain the abnormally high number of pups observed occasionally (Holcomb, 1965).

Sex ratio in *V. vulpes* is often unbalanced within a litter (Storm et al., 1976). Coat color of newborn foxes is dark gray, and the inner and distal portions of legs are lighter. The feet are whitish-brown, with creamy-white footpads and toenails (Sargeant et al., 1981; Storm and Ables, 1966). Pelage of young foxes changes from grayish-brown at birth to pale buff at 8–14 days of age, and to red at 9–14 weeks of age (Linhart, 1968; Sargeant et al., 1981). Dorsal and ventral hairs of the newborn pups are ca. 7–10 mm and 3–5 mm, respectively. Eyes are closed at birth, opening at 3 weeks of age (Linhart, 1968; Storm and Ables, 1966). Mean body mass of four newborn females and three males from Illinois, USA, was 105.2 g and 117.8 g, respectively. Average total length, length of tail, length of hind foot, and length of ear of the same litter were 211, 67, 32, and 13 mm, respectively (Storm and Ables, 1966). Pups are able to walk after 3 weeks (Linhart, 1968). Lactation lasts ca. 5 weeks, and weaning occurs gradually (Henry, 1986).

ECOLOGY. Red foxes live in a variety of habitats, ranging from semi-arid deserts to tundra, in farmland and boreal forests. Generally, heterogeneous and fragmented landscapes constitute better fox habitat than homogeneous environments (Lloyd, 1980; Catling and Burt, 1995). Prey availability seems to be the most important factor affecting habitat use (Halpin and Bissonette, 1988; Jones and Theberge, 1982; Phillips and Catling, 1991). In temperate environments, brushy habitats are preferred in winter, whereas mature hardwood stands are avoided, possibly because of greater snow accumulations and lower snow hardness (Halpin and Bissonette, 1988; Theberge and Wedeles, 1989). In the tundra, *Salix* shrub communities are preferred, and open tundra is avoided (Jones and Theberge, 1982). In urban areas, red foxes are more abundant in residential suburbs and less abundant in industrial and commercial areas (Harris and Rayner, 1986).

Captive adults require 2.3 kg of prey per week, while pups aged 5–8 weeks, 9–12 weeks, and pups in the post-denning period (>12 weeks old) require 1.4, 1.9 and 2.5 kg of prey/week, respectively (Sargeant, 1978). The red fox has a varied diet (Scott, 1943). Small ground dwelling mammals, lagomorphs, and sciurids constitute the most important part of the diet (Blumstein and Robertson, 1995; Borkowski, 1994; Lindström, 1994; Lucherini and Crema, 1994; Scott, 1943; Weber and Aubry, 1993). Occasionally, mustelids, raccoons (*Procyon lotor*), opossums (*Didelphis virgianiana*), and muskrats (*Ondatra zibethicus*) are consumed (Borkowski, 1994; Henry, 1986; Jones and Theberge, 1983). In Sweden, roe deer (*Capreolus capreolus*) fawns are killed by foxes (Cederlund and Lindström, 1983). Carrion may be seasonally or locally important (Hewson, 1983), and winter-killed big game animals are readily exploited (Schofield, 1960). In the Northwest Territories, Canada, a red fox was observed feeding on a newborn ringed seal (*Phoca hispida*) that it presumably killed (Andriashek and Spencer, 1989).

Galliformes are the most important group of birds consumed (Sequeira, 1980), whereas passeriformes, columbiformes, anseriformes, and birds of prey are occasionally eaten (Henry, 1986; Kolb and Hewson, 1979; Sargeant et al. 1984). In certain areas, the red fox is an important predator of nesting birds and their eggs (Sargeant et al., 1984; Southern et al., 1985). In North Dakota, predation by red foxes on nesting hens was considered the principal cause of mortality among adult ducks (Sargeant, 1972; Sargeant et al., 1984). Fish, reptiles, insects (Green and Osborne, 1981; Lucherini and Crema, 1994), earthworms (*Lumbricus terrestris*; Macdonald, 1980*b*), fruits (Lovari et al., 1994; Serafini and Lovari, 1993), sunflower (*Helianthus* sp.) seeds (Sargeant et al. 1986), balsam fir (*Abies balsamea*) cones (Sklepkovych, 1994), and garbage (Doncaster et al., 1990) may be locally or seasonally important.

Population estimates have been obtained using standardized traplines (Wood, 1959), track counts (Wood, 1959), questionnaires (Lemke and Thompson, 1960), bounty records (Hewson and Kolb, 1973), rural mail-carrier sightings (Allen and Sargeant, 1975), spring counts of fox litters (Harris, 1981), sightings from school children (Harris, 1981), aerial census of rearing dens (Sargeant et al., 1975), hunting and trapping harvest (Hewson, 1984; Voigt, 1987), and large-scale characterization of fox habitats (Macdonald et al., 1981). Densities vary locally; 0.43 fox/km^2 in Poland (Goszczynski, 1989*a*), 1.0–1.7 fox/km^2 in Spain and Ontario, Canada (Rau et al., 1985; Voigt, 1987), and 2.1–30 foxes/km^2 in the UK (Harris and Rayner, 1986; Insley, 1977; Page, 1981).

Red foxes are highly mobile, often covering daily distances >10 km (Goszczynski, 1989*b*; Voigt, 1987). Home ranges are generally exclusive with nonoverlapping borders (Voigt, 1987; Voigt and Macdonald, 1984). In some areas, home ranges may overlap, although this may be explained by groups of genetically related individuals (Voigt, 1987). Most evidence suggests that home ranges are actively defended and thus should be considered territories (Voigt, 1987). Territories are larger in winter, and smallest during the rearing period (Kolb, 1986), but are maintained throughout the year (Voigt, 1987). In Poland, fox families occupied the same territory during several consecutive winters (Goszczynski, 1989*b*). In Australia and Japan, territories of single males (4.5 km^2 to 6.8 km^2) are larger than that of single females (0.3 ha–5.3 km^2; Phillips and Catling, 1991; Takeuchi and Koganezawa, 1992). In urban environments, and in the UK, home range varies from 42 ha to 4.6 km^2 for males, and is ca. 1.5 km^2 for females (Kolb, 1986). In Maine, annual home range of red foxes varied between 14.7–19.9 km^2 (Harrison et al., 1989; Major and Shepburne, 1987). During the breeding season, recorded home ranges were 5.0–6.5 km^2 in Poland (Goszczynski, 1989*b*), and up to 11.9 km^2 in North Dakota, USA (Sargeant et al., 1987). Mean summer ranges of foxes in a tundra habitat were 16.1 km^2 (Jones and Theberge, 1982).

In the northern hemisphere, dispersal occurs from September to January (Andrews et al., 1973; Storm et al., 1976; Tullar and Berchielli, 1980). Males usually disperse further than females (Allen and Sargeant, 1993; Schantz, 1981; Storm et al., 1976). In the USA, mean dispersal distances of males and females were 31 and 11 km, respectively (Storm et al., 1976). Smaller dispersal distances (for males 7.9 and 2.8 km, for females 3.1 and 1.6 km) characterize urban fox populations (Harris and Trewhella, 1988; Page, 1981). The longest dispersal movement recorded between tagging and recovery locations was 302 km in North Dakota, USA (Allen and Sargeant, 1993). Dispersal distance was negatively correlated with population density in the UK (Trewhella et al., 1988), but not in the USA (Allen and Sargeant, 1993). Within a litter, individuals possessing weak social bonds with other members of the group are most likely to disperse (Harris and White, 1992). Dispersal direction of individuals is similar between sexes (Harris and Trewhella, 1988), and among littermates (Allen and Sargeant, 1993). Cities, highways, lakes, rivers, and railway lines may influence dispersal directions (Allen and Sargeant, 1993; Kolb, 1984; Storm et al., 1976; Trewhella and Harris, 1990).

Red foxes can live up to 8.6 years in the wild (Allen and Sargeant, 1993; Tullar, 1983), although few individuals live to 6 years (Storm et al., 1976). Most foxes harvested in the autumn are <1.5 years old (Allen and Sargeant, 1993). Wolves (*Canis lupus*; Mech, 1970), coyotes (*C. latrans*; Sargeant and Allen, 1989), mountain lions (*Puma concolor*; Currier, 1983), lynx (*Felis lynx*; Stephenson et al. 1991), bobcats (*L. rufus*; Petraborg and Gunvalson, 1962), and domestic dogs (*C. familiaris*; Storm et al., 1976; Tullar and Berchielli, 1982) may occasionally kill adult *V. vulpes*. Most common human-related deaths include trapping, shooting, and roadkills (Allen and Sargeant, 1993; Harris and Smith, 1987; Page, 1981; Storm et al., 1976; Takeuchi and Koganezawa, 1994). The red fox is killed for fur harvest, sport, to protect domestic animals and game, and to prevent the spread of rabies (Obbard, 1987).

In North America, raising red foxes in captivity was an important industry during the early 1900s. Today, the number of foxes raised for fur is greatly reduced but still exceeds that of any other furbearer, except possibly mink (*Mustela vison*; Obbard, 1987). Red fox fur is used in coats, stoles, scarves, and trimmings (Obbard, 1987). Although red foxes have been persecuted extensively by man, only a single native subspecies *V. v. necator* in the Sierra Nevada, California, USA, is rare and possibly declining (Nowak, 1991).

For research, wild red foxes have been captured alive using snares, foot-hold traps, and by capturing individuals in dens (Ables, 1969; Allen and Sargeant, 1993; Storm et al., 1976). They can be immobilized using ketamine/xylazine, ketamine/promazine, ketamine/midazolam, or tiletamine/zolazepam (Kreeger et al., 1990; Travaini and Delibes, 1994). Age usually is determined by counting annular cementum rings in molars and premolars (Allen, 1974; Harris, 1978). Age of pups in days can be determined from hind foot length or from a description of pelage color and body size (Sargeant et al., 1981).

In London, UK, fox harvests did not reduce the number of fox family groups, but reduced mean family group size (Harris and Smith, 1987). In Japan, intensive hunting pressure decreased the survival rate of adult foxes, shortened mean longevity, increased the proportion of juveniles in the population, and affected the sex ratio in favor of females (Yoneda and Maekawa, 1982). Populations may be controlled through trapping, hunting, gassing, poisoning, and immunocontraceptive vaccination (Bradley, 1994; Thompson and Fleming, 1994; Voigt, 1987).

Although red foxes and coyotes can be sympatric, the smaller red fox usually avoids coyotes by locating its territory on the periphery of coyote territories (Sargeant et al., 1987; Voigt and Earle, 1983), or by avoiding habitats heavily used by coyotes (Dekker, 1989). Red foxes are more aggressive than arctic foxes (*Alopex lagopus*; Rudzinski et al., 1982) and will occasionally kill arctic foxes (Bailey, 1992; Frafjord et al., 1989). The presence of red foxes is believed to limit the southern distribution of the arctic fox (Hersteinsson and Macdonald, 1992). Limited information seems to suggest dominance of the gray fox (*Urocyon cinereoargenteus*) over *V. vulpes* (Voigt, 1987).

Vulpes vulpes harbors many internal parasites such as protozoans *Isospora* sp., *Sarcocystis* sp., *Toxoplasma gondii* (Davidson et al., 1992; Quinn et al., 1976; Reed and Turek, 1985), heartworms *Angiostrongylosis vasorum* (Bolt et al., 1992) and *Dirofilaria immitis* (Gortazar et al., 1994), cestodes *Amoebotaenia paradoxa, Diphyllobothrium latum, Dipylidium caninum, Echinococcus multilocularis, Hydatigena taeniaeformis, Mesocestoides litteratus, Taenia crassiceps, T. hydatigena, T. pisiformis, T. polyacantha, T. serialis, T. taeniaformis* (Brochier et al., 1992; Dagmar and Eckert, 1993; Dibble et al., 1983; Wessbecher et al., 1994*a*), nematodes *Ancylostoma caninum, Capillaria aeophila, C. plica, Phylasoptera rara, Pterygodermatites affinis, Toxascaris leonina, Toxocara canis, Trichinella spiralis, Trichuris vulpis, Uncinaria stenocephala* (Ballek et al., 1992; Davidson et al., 1992; Dibble et al., 1983; Steinbach et al., 1994; Wessbecher et al., 1994*b*), and trematodes *Alaria alata, A. arisaemoides, A. americana, Apophallus donicus, Istmiophora melis, Metorchis albidus, Opisthorchis felineus, Paragonimus kellicotti, Pseudamphistomum truncatum* (Carvalho-Varela and Costa Durao, 1977; Davidson et al., 1992; Dibble et al., 1983; Steinbach et al., 1994). Ectoparasites include ringworm (*Microsporum sp.*; Ross and Fairley, 1969), ticks (*Amblyomma americanum*; Smith et al., 1986; *Ixodes persulcatus*, Isogai et al., 1994), *Cediopsylla simplex* (Davidson et al., 1992), and mites *Sarcoptes scabiei*, which cause sarcoptic mange (Lindström et al., 1994; Trainer and Hale, 1969).

Infections from α and β haemolytic streptococci, *Leptospira ictohaemorrhagica* and *L. canicola*, as well as chronic interstitial nephritis were observed in red foxes in France and Ireland (Barrat et al., 1985; Ross and Fairley, 1969). Canine parvovirus, adenovirus, rotavirus (Evans, 1984), herpesvirus and parainfluenza virus were recorded in foxes from South Carolina, USA (Davidson et al., 1992). Canine distemper virus was detected in foxes from Spain (López-Peña et al., 1994), and Lyme disease spirochetes were found in a fox from Japan (Isogai et al., 1994).

Red foxes represent the most widespread reservoir of rabies in the wild (Chomel, 1993). The geographical foci of fox rabies is in central Europe (Anderson et al., 1981), south-eastern Canada and north-eastern USA (Chomel, 1993; Johnston and Beauregard, 1969). Attempts to control rabies outbreaks have included reduction of populations and oral vaccination (Anderson et al., 1981). The latter is particularly effective in Europe (Kihm et al., 1992) and may permit large-scale eradication of the virus (Brochier et al., 1991).

BEHAVIOR. The basic social unit of *Vulpes* is a monogamous pair (Macdonald, 1979). The male provides parental care, and the male-female association lasts until cubs are reared (Macdonald, 1979). Occasionally, females without young may be present within a group, and assist in rearing of young of another female (Macdonald, 1979). Groups with helpers are most commonly reported in European countries (Schantz, 1981, 1984). Inter-group encounters are uncommon, almost always aggressive (White and Harris, 1994), and consist mostly of agonistic behaviors and chases rather than physical contact (Preston, 1975).

Most fox dens are found in sandy soil (Sheldon, 1950), in pastures (Sargeant, 1972), or in agricultural land (Hewson, 1986). Fox dens often have several entrances. The main entrance is usually 40 cm high, and the tunnel can be up to 22.5 m long (Sheldon, 1950).

Red foxes are mostly nocturnal (Ables, 1969; Travaini et al., 1993; Weber et al., 1994) and their activity pattern overlaps with that of their principal prey (Ables, 1969; Lovari et al., 1994). Females may exhibit increased activity during the day while rearing young (Phillips and Catling, 1991). Daytime is spent in regular rest areas (Storm, 1965). Red foxes usually select above-ground rest sites, but may use underground burrows (Meia and Weber, 1993).

Vulpes vulpes uses different hunting strategies for various prey species. Small mammals are located, often by sound, from a "mousing position" (i.e., erect head and extreme alertness; Henry, 1986). An aerial jump, which may exceed 4 m in length, is often used to capture small mammals (Henry, 1986). Prey are pinned to the ground with forepaws, and then bitten. Arboreal prey are captured following a quick, horizontal thrust. Rapid terrestrial prey are caught by stalking followed by quick pursuit (Henry, 1986). On occasion, a red fox may nap near a previously missed prey burrow and wait for the prey to re-emerge (Henry, 1986). Play with live prey is common among both juvenile and adult red foxes (Henry, 1986).

Red foxes cache surplus food for future consumption (Macdonald, 1976). When depredating nests, red foxes will often carry eggs away and cache them (Tinbergen, 1965). Red foxes sometimes cache ducks alive (Sargeant and Eberhardt, 1975).

Red foxes communicate by facial expressions (Fox, 1970), vocalizations (Henry, 1986), and scent marking. Scent marking commonly involves <20 ml of urine, and is usually of short duration (mean = 2.25 sec, *SD* = 0.48, *n* = 40; Henry, 1977). Urine markings apparently serve as dominance displays (Henry, 1977; Macdonald, 1979), social records (Tinbergen, 1965), and as a "no food" signal in the investigation of food remains during scavenging (Henry, 1977). In Poland, frequency of scent marking was 4.41 urine marking and 0.35 scats/km of fox trail (Goszczynski, 1990). The border and the interior of red fox territories were marked with similar intensity, although possibly anal-sac secretions are deposited more frequently along the perimeter (Goszczynski, 1990; White et al., 1989). Vocal communication in *V. vulpes* is limited (Peters and Wozencraft, 1989). Simple vocalizations such as barking and growling can be superimposed to produce more complex sounds (Tembrock, 1963), but their importance is secondary to scent marking in the maintenance of dyadic social bonds (Montgomery, 1974).

GENETICS. The red fox has a diploid number of 34 chromosomes and 3–5 microsomes. The sex chromosomes are comprised of a submetacentric X chromosome and subtelocentric Y chromosome (Rausch and Rausch, 1979).

Adalsteinsson et al. (1987) hypothesize that the loci A (agouti), B (black/chocolate brown pigment) and E (extension of eumelanin vs phaeomelanin) all occur in *V. vulpes*. The dominant allele, A^r, produces the typical red color, with only traces of black at the extremities. The recessive allele, a, in the homozygous condition results in the black color of the silver or black fox. The dominant allele, B, produces black eumelanin pigment, whereas b, in the homozygous condition produces chocolate brown pigment. Genes at the E locus determine the extension of black/chocolate brown eumelanin versus red or tan phaeomelanin. In the homozygous condition, E has no effect on color, and the phenotype is determined by alleles on the A locus. In the heterozygous form, the E^d allele produces the cross fox color (Adalsteinsson et al., 1987). The genetic formulas for the red and silver color morphs are A^rA^rBBEE and aaBBEE, respectively (Adalsteinsson et al., 1987). The genetic formula for the cross fox may be $A^rA^rBBE^dE$ or A^raBBE^dE (Adalsteinsson et al., 1987).

REMARKS. *Vulpes vulpes* means the fox's fox (Henry, 1986) and is sometimes called the colored fox (Churcher, 1959). It has a reputation in history and fables as being sly, wise and cunning, and is widely represented in folklore, fiction, poetry, and literature (e.g., Melnyk, 1978).

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