**Urocyon littoralis** (Baird, 1858)

Island Fox

_Vulpes littoralis_ Baird, 1858:143. Type locality San Miguel Island, Santa Barbara County, California.

_Urocyon littoralis_ Merriam, 1898:135. First use of current name combination.

_Urocyon catalinae_ Merriam, 1903:74. Type locality Catalina Island, Los Angeles County, California.

_Urocyon elementeae_ Merriam, 1903:75. Type locality San Clemente Island, Los Angeles County, California.

**CONTEXT AND CONTENT.** Order Carnivora, Family Canidae, Subfamily Caninae. The genus _Urocyon_ contains 2 species: _U. cinereoargenteus_ and _U. littoralis_ (Wilson and Reeder, 1993). Six subspecies of _Urocyon littoralis_ currently are recognized (Hall, 1981):

_U. l. catalinae_ Merriam, 1903:74, see above.

_U. l. elementeae_ Merriam, 1903:75, see above.

_U. l. dickeyi_ Grinnell and Linsdale, 1930:154. Type locality San Nicolas Island, Ventura County, California.

_U. l. littoralis_ Baird, 1858:143, see above.

_U. l. santacruzae_ Merriam, 1903:75. Type locality Santa Cruz Island, Santa Barbara County, California.

_U. l. santarosae_ Grinnell and Linsdale, 1930:154. Type locality “Santa Rosa Island, Santa Barbara County, California.”

**DIAGNOSIS.** _Urocyon littoralis_ (Fig. 1) is similar to _U. cinereoargenteus_ of the adjacent mainland, but can be distinguished by its smaller size (Grinnell et al., 1937) and somewhat darker overall coloration (Collins, 1982). Most linear measurements of island foxes average 25% less than those of the gray fox. The tail is conspicuously short, being 34% as long as the body and with a length of about 244 mm, as compared with 383 mm for _Vulpes litteralis_ (Baird, 1858). The dorsal surface of the ears is grizzled like the back, changing to a shorter sacrum relative to its width; a stouter fibula; a relatively longer ilium; longer lateral metapodials; a heavier and relatively more convex roof to the cranium between the temporal ridges (Fig. 1) is similar to _U. cinereoargenteus_. Cranial characters that differentiate island foxes from mainland foxes average 25% less than those of the gray fox. The tail is shorter than the top of the head (Grinnell et al., 1937). The lower one-half of the face and part of the throat are pure white. The tail has a well-defined narrow black stripe along the dorsal surface, is hoary on the sides, and is rusty underneath (Baird, 1858; Grinnell et al., 1937).

Island foxes show marked differences in size between males and females. Of 26 cranial and 5 external measurements, significant secondary sexual variation was found, with males being larger than females in 26 cranial measurements and all five of the external measurements (Collins, 1982, 1993). Means (and ranges) of external and cranial measurements, in mm, for adult males for _U. l. catalinae_ (n = 21), _U. l. elementeae_ (n = 23), _U. l. dickeyi_ (n = 45), _U. l. littoralis_ (n = 20), _U. l. santacruzae_ (n = 64), and _U. l. santarosae_ (n = 28), respectively are: total length, 754.8 (700-812), 732.6 (665-775), 761.5 (606-825), 686.6 (645-725), 701.9 (610-749), 733.6 (658-775); length of tail vertebrae, 281.4 (235-316), 262.9 (230-295), 280 (140-322), 185 (157-210), 245.9 (195-280), 253 (214-300); length of hind foot, 110.6 (103-118), 109.9 (105-115), 115.3 (110-124), 111.1 (102-120), 103.3 (92-115), 114.1 (105-120); length of the ear from crown, 67.1 (61-71), 67.5 (61-72), 68.7 (60-73), 65.7 (57-72), 64 (54-72), 70.2 (65-75); condylobasal length of cranium, 101.9 (94.7-106.4), 97.6 (92.9-102.9), 99.5 (92.3-104.3), 100.6 (98.4-104.9), 97.7 (93.2-101.9), 99.1 (92.2-102.9); zygomatic breadth, 54.8 (53.7-62.1), 56.7 (53.7-59.7), 56.8 (53.6-59.8), 58 (55.1-60.5), 56.7 (54.5-59.8), 56.6 (54-59.7); interorbital width, 30.6 (27.5-33.3), 29.6 (27.8-31.8), 30.1 (27.9-33.0), 32.7 (31.1-34.3), 31.3 (28.2-34.2), 32.4 (28.4-35.0); postorbital width, 26.9 (24.4-28.5), 26.4 (24.9-28.1), 26.7 (25.2-28.2), 27.2 (25.3-28.6), 27.3 (25.3-29.2), 27.1 (25.0-29.3); breadth of cranium, 41.0 (39.2-42.3), 39.7 (37.6-41.7), 40.0 (38.7-41.4), 41.7 (40.6-43.0), 40.1 (38.0-42.2), 40.7 (39.7-42.6); length of maxillary toothrow, 44.0 (41.0-46.3), 43.2 (41.3-45.3), 43.0 (40.6-45.0), 41.0 (41.6-45.0), 42.8 (40.3-44.6), 43.6 (40.8-45.8). Means (and ranges) of external and cranial measurements, in mm, for adult females for _U. l. catalinae_ (n = 16), _U. l. elementeae_ (n = 16), _U. l. dickeyi_ (n = 59), _U. l. littoralis_ (n = 17), _U. l. santacruzae_ (n = 64), and _U. l. santarosae_ (n = 31), respectively are: total length, 754.8 (700-787), 788.6 (725-760), 745.8 (665-807), 674.9 (585-787), 708.1 (630-757); length of tail vertebrae, 270.1 (242-294), 238.1 (200-285), 277.7 (192-309), 175.6 (148-206), 223.6 (154-246), 243.6 (185-277); length of hind foot, 109.1 (104-118), 102.4 (92-114), 112.8 (92-120), 110.1 (95-117), 99.2 (87-113), 111.4 (100-115); length of the ear from crown, 66.1 (60-70), 63.1 (59-67), 67.4 (59-72), 64.2 (60-72), 63.0 (58-60).}

**GENERAL CHARACTERISTICS.** In general, the dorsal coloration is mixed grayish-white and black. As with _Urocyon cinereoargenteus_, the grizzled color along the back and sides is as result of individual guard hairs being banded by white, gray, and black (Frittsell and Haroldson, 1982). The base of the ears and sides of the neck and limbs are cinnamon-rufous in color (Grinnell et al., 1937). The venter is dull white with intermediate areas of pale rusty. The dorsal surface of the ears is grizzled like the back, changing to light cinnamon-rufous on the base and sides (Baird, 1858). The entire chin, borders of the lips, and area between the eyes and the nose are black. The sides of the snout are gray and slightly darker than the top of the head (Grinnell et al., 1937). The lower one-half of the face and part of the throat are pure white. The tail has a well-defined narrow black stripe along the dorsal surface, is hoary on the sides, and is rusty underneath (Baird, 1858; Grinnell et al., 1937).
Islands inhabited by *U. littoralis* are located 30 (Santa Cruz Island) to 98 km (San Nicolas Island) from the adjacent mainland and are separated from each other by water barriers that are five to >40 km wide (Philbrick, 1967).

Two hypotheses have been proposed to describe the origin of island foxes. An early hypothesis suggests that the island fox represents a relict form of a smaller continental race that was once more widespread (Remington, 1971; Stock, 1943; von Bloeker, 1967). The absence of any small-sized gray fox fossils on the mainland tends to refute this hypothesis (Collins, 1982). A second hypothesis states that, during the mid-to-late Pleistocene, large gray foxes from the mainland colonized one of the northern islands (probably Santa Rosa), where unique selective pressures during an initial period of isolation resulted in a reduction in body size and in the evolution of genetic differences (Collins, 1983, 1991a, 1993; George and Wayne, 1991; Johnson, 1983; Wenner and Johnson, 1980).

Subsequent sea level changes during the Pleistocene helped to disperse island foxes to the remaining Northern Channel Islands (Johnson, 1983). An analysis of genetic variability in island fox populations suggests that all island foxes are descended from one colonization event (George and Wayne, 1991). One or more gray foxes from the mainland most likely reached one of the northern islands by chance overwater dispersal, probably by rafting on floating debris. Fossil evidence shows that foxes were present on these islands prior to the arrival of Native Americans 9-10,000 years ago (Collins, 1991a, 1993) and evolutionary trees constructed from genetic data indicate that the northern islands were the first islands colonized (George and Wayne, 1991). There is no geological evidence that land bridges between the islands and mainland existed during the Pleistocene, when the foxes are believed to have first reached the islands (Johnson, 1983). Thus, foxes could not have reached the islands by means of a land bridge (Wenner and Johnson, 1980). There is no evidence that *U. cinereoargenteus* (the probable ancestor of *U. littoralis*) is capable of swimming a distance of 6 km, the shortest distance between the northern islands and the mainland during the Pleistocene (Johnson, 1978). An analysis of the occurrence of island foxes in the archaeological record, coupled with comparison of island fox cranial material from archaeological samples with pres-
FOSSIL RECORD. *Urocyon littoralis* is known from only one early Holocene fossil site. An island fox skull was found on Santa Rosa Island in the Upper Tepolote geologic formation, which dates from 10,400 to 16,000 years of age (Orr, 1986). Analysis of cranial characters demonstrates that this specimen is virtually indistinguishable from present-day foxes on San Miguel and Santa Rosa Islands (Collins, 1982, 1991a, 1993).

Bones of island foxes have been found in 27 archaeological sites on the Channel Islands. Skeletal remains of island foxes have been found throughout Native American occupation on Santa Cruz and Santa Rosa Islands but do not occur on the Southern Channel Islands until 3,800-3,000 years ago on Santa Catalina Island, 3,400 years ago on San Clemente Island, and 2,200 years ago on San Nicolas Island (Collins, 1982, 1991a).

FORM AND FUNCTION. *Urocyon littoralis* molts once per year from August to early November. The guard hairs are most prominent along the middle of the back and are 35-38 mm long, while the soft underfur is 16-25 mm long. These long hairs are the last to be molted. The late spring and summer pelage of adult foxes on San Miguel and San Nicolas Islands shows signs of fading and looks burned, with all of the black parts of the hair turned to a reddish brown and the ends of the guard hairs curled at their tips. This condition results from exposure to salt air and sun (Grinnell et al., 1937). There is a concealed mane of stiff bristly hairs along the top of the tail (Baird, 1858), which obliterates an elongated tail gland similar to that described for the gray fox (Hildebrand, 1952a).

Prior to their first molt, juveniles are woolly in appearance with only a few, fine, long hair shafts projecting beyond a thick dark underfur. The entire upper surface of the tail is black. The ears and the top of the head are brown with extensive patches of long, fine hairs that are bristly or rufous in adults tend to be duller and paler in color on juveniles, except for the ears, which are darker (Grinnell et al., 1937).

The dental formula is: i 3/3, c 1/1, p 4/4, m 2/3, total 42 (Fittrell, 1987). Except for normal dental attrition and wear, no abnormal dental formulas (supernumerary molars) have been found (Collins, 1982). Island foxes can be grouped into age categories by examining the wear pattern of the first upper molar and cranial suture closures (Collins, 1982, 1993). Juveniles and subadults are characterized by having no exposed dentine and little wear on the conules of the first upper molar, and by having the basiphoniod-basophysiod and basiphoniod-phalangeal sutures open and evident. Young adults are characterized by having all sutures on the base of the tooth completely obliterated, having no v-shaped gap between the praeconid and vomer bones, and having an elongated area of exposed dentine between the metacone and protocone of the first upper molar. Adults exhibit extensive wear on M1 with conules worn down to or below the gum and with most of the oval surface composed of exposed dentine (Collins, 1982). It is difficult to determine the age of island foxes beyond 5 years of age because the molar tooth used for aging is either missing or worn to the gum level (Laughrin, 1977).

Nasal bone morphology varies geographically, with three of the island populations (San Nicolas, San Clemente, and San Miguel Islands) exhibiting high frequencies of occurrence for only one nasal shape. Island foxes from San Nicolas and San Clemente Islands can usually be identified based solely on the shape and projection of the posterior margins of the nasal, but island foxes on the other islands cannot. Bregmatic bones are found more frequently in island foxes than in mainland gray foxes, with the highest frequency, 17.1%, occurring on San Nicolas Island (Collins, 1982).

The baculum of the island fox is morphologically similar to that of *U. cinereoargenteus*. The long, straight baculum is Y-shaped in cross section and curved, with a deep base, a deep urethral groove that nearly encloses the urethra, a long high dorsal crest, small lateral crests, and a slender probelike apex (Hildebrand, 1954).

The decrease in the length of the tail in island foxes is due to a reduction in the number of caudal vertebrae. The average number of caudal vertebrae in 47 island foxes ranged from 15 (San Miguel Island) to 22 (San Nicolas Island), but gray foxes (43-51) had an average of 21-22 caudal vertebrae (Collins, 1982).

Island foxes have tapetal reflexion and dichromatic color vision identical to that recorded for the gray fox and domestic dog. Island foxes have two cone pigments with peak sensitivities of 555 nm and 430-435 nm respectively (Jacobs et al., 1993).

Tracks made by island foxes are similar to those of house cats and gray foxes, except claw marks usually are evident (Fittrell, 1987; Grinnell et al., 1937). The hind foot is about 38 mm long and 29 mm wide. The tracks of the front foot are considerably larger than those of the hind foot. The distance between tracks is 18-23 cm with the track of the hind foot often overlapping with the track of the front foot (Grinnell et al., 1937).

ONTOGEOGENY AND REPRODUCTION. Pair formation and courtship generally occur from January through March with most breeding occurring in late February and early March. Pairs are most often seen from mid-January through April and infrequently from September through December. The length of the gestation period is estimated to range from 50 to 53 days based on the reproductive condition of captured females and estimated ages of young foxes when first found. Parturition usually occurs from the end of April through early May (Laughrin, 1977).

Island foxes mate at the end of their first year (Laughrin, 1977). Thirty-one percent of the females collected in February 1928 from Santa Cruz Island were pregnant (H. H. Sheldon, in litt.). About 79% of female foxes ≥1 year of age on San Nicolas Island had litters in 1980 (S. D. Kovach and R. J. Dow, in litt.). On Santa Cruz Island, only a small percentage of the 6-year-old or older females were in breeding condition (Laughrin, 1977). Island foxes give birth to their young in dens, which are usually not excavated by the foxes. Rather they use any readily available sheltered site. Dens usually are simple structures located at the end of a short tunnel or in a depression under a rock, stump, or shrub (Laughrin, 1977). Sites known to be used as dens include brush piles, small caves, rock crevices, manmade structures, logs, hollowed limbs, stumps of large trees, and hollows under dense brush (Blake, 1887; Laughlin, 1977). If no suitable den site is found, then island foxes dig a simple tunnel. Dens protect the young from predators and adverse weather and only are used by adults when in the breeding season. Some dens are reused in successive years, while others are used only once (Laughrin, 1977).

Litter size ranges from one to five, but usually averages two or three. Based on counts of young at 24 dens, the mean litter size was 2.17 on Santa Cruz Island, with a sex ratio of 1:1. Over a period of 5 years, a captive pair of foxes produced litters ranging from one to five (Laughrin, 1977). The number of embryos recovered from 11 Santa Cruz Island foxes ranged from two to four with a mean of 2.27 (H. H. Sheldon, in litt.).

There have been no direct observations of parturition for *U. littoralis*, but it is believed that young of island foxes are born blind and helpless. One young, estimated to be 19 days old, had closed eyes and was covered with short, gray hair. In the middle of June (38 days of age) the eyes had opened and the young fox weighed 167 g. By the second week of July, this fox began to acquire longer hairs of adult color, and toward the end of July, it resembled an adult in overall color pattern, although the pelage was somewhat silvery. This cat was not until the end of August or early September, when the winter pelage develops, that young-of-the-year begin to approach adults in size and pelage.

Young emerge from the den at about 3-4 weeks of age with the majority being seen during the first week of June (Laughrin, 1977). By 2 months of age, young are spending most of the day outside of the den (Fausett, 1982; Laughlin, 1977). Young begin the day by playing with their mother for at least 2 hours and the cubs then nurse for 20-30 minutes. Both parents are usually present during the day, although the young are sometimes found alone, but they do not leave the den. The mother will attempt to retrieve her young when they are outside the den and bring them back to the nest. Young foxes are not capable of killing their own food until they are about 5 months old. Juveniles are independent of their parents by the end of their first year.
to forage with their parents in mid- to late June and will remain with their parents throughout the summer (Laughrin, 1977). Parents disperse away from thenatal home range in late September, but young remain in their natal areas until at least December (Faussett, 1982; Laughrin, 1977).

**ECOLOGY.** Island foxes occur in all natural habitats on the islands included within their range (Laughrin, 1977, 1980). The majority of habitats found on the islands are similar in structure and plant species composition to those of the adjacent mainland. Island habitats include valley and foothill grasslands, southern coastal dune, coastal bluff, coastal sage and maritime cañon, island chaparral, southern coastal oak woodland, island woodland, southern riparian woodland, Bishop and Toreadora forests, and coastal marsh (Philbrick and Haller, 1977). The native vegetation on most islands has been modified by exotic animals, especially goats, sheep, pigs, cattle, and rabbits (Laughrin, 1973). The larger islands have water available throughout the year from springs and a few small streams (Laughrin, 1973).

Densities vary depending upon the island, habitat, and year in which the trapping was being conducted. Island fox densities recorded using line transect data were 0.31/km² for *U. l. catalinana*, 4.27/km² for *U. l. elementalis*, 1.2/km² for *U. l. dicycus*, 2.7/km² for *U. l. littoralis*, 7.9/km² for *U. l. santacruzae*, and 4.2/km² for *U. l. santarosae* (Laughrin, 1980). These densities for island foxes are generally higher than fox populations on the mainland. Island fox populations are less dense and more evenly distributed on islands with low topographic relief, reduced habitat diversity, and limited woody vegetation (Laughrin, 1977). The four largest islands (Santa Cruz, Santa Rosa, Santa Catalina, and Santa Catalina Is.) have varied topography and the greatest diversity of vegetation (Philbrick and Haller, 1977). Woodland habitats support higher densities because these habitats have greater food availability (Laughrin, 1977, 1980).

Santa Cruz and Santa Catalina Islands have extensive areas of woodland vegetation whereas Santa Rosa and Santa Contreras Islands have restricted woodlands that make up only a small percentage of the overall plant cover (Laughrin, 1977). On Santa Rosa Island, densities were 5.8/km² in woodland habitat and 2.4/km² in grassland habitat. On Santa Cruz Island, the probability of encountering an island fox was 0.63 in woodland habitats and 0.37 in open grasslands (Laughrin, 1977).

Recent studies suggest that island fox populations are relatively stable; however, anecdotal observations suggest that population size has fluctuated widely during recorded history (Laughrin, 1980). The reason for these population fluctuations is presently unknown (Laughlin, 1973). During a 5-year trapping study in a chaparral woodland habitat on Santa Cruz Island, the island fox population ranged from 5.9 to 8.5 km². From 1971 to 1977 island fox densities on San Nicolas Island ranged from 2.7 to 0.12/km², respectively. The low abundance of island foxes on Santa Catalina Island and the limited geographical distribution of all the island populations led the California Fish and Game Commission, in 1971, to classify *Urocyon littoralis* as rare (Laughrin, 1980). These densities for island foxes are

There is a higher proportion of older animals (4–6 years of age) in island fox populations than in populations of mainland gray foxes, which may suggest that island fox populations are subject to lower mortality and turnover rates (Laughrin, 1977, 1980). The mean juvenile to adult ratio for island foxes is 0.26 for all of the island foxes sampled (Laughrin, 1977). Fruits of *Arctostaphylos*, *Heteromeles*, *Mesembryanthemum*, *Opuntia*, *Prunus*, *Rhamnus*, *Rhus*, *Solanum*, *Vaccinium*, *Carpobrotus*, and *Comarostaphylis* are the most frequently eaten plants (Laughrin, 1977, 1980). The importance of fruit in the diet of island foxes is dependent upon the plant's fruiting season. For example, island foxes on Santa Cruz Island utilize fruits from Heteromeles (41% by volume) in the winter and early spring, *Arctostaphylos* (54%) in the summer, and *Comarostaphylis* (29%) in the winter (Laughrin, 1977). On San Miguel Island, fruits of sea-figs (*Carpobrotus aequale*) comprised 88% of the volume of the diet of island foxes during the summer and comprised 71–96% of all spring, summer, and autumn foxes. The only other significant plant materials found in San Miguel Island fox feces were bokhees of grass. Grass was found in only 4% of the summer fecal samples but was present in 32–42% of samples during the remainder of the year (Collins, 1980).

Island foxes have limited vertebrate prey, because the vertebrate fauna of Channel Islands is depauperate (Wenner and Johnson, 1980). Compared to the gray fox, island foxes show a reduced dependence on vertebrate prey (Fritzell, 1987; Fritzell and Homer, 1982; Laughrin, 1977). Mammals, especially deer mice (*Peromyscus maniculatus*), comprise the largest vertebrate portion of the diet of island foxes on Santa Cruz Island where they have been recorded exclusive of fruits in 4–13% of the summer and 10% of the winter home range of a male island fox on Santa Cruz Island. Other five- and six-year-old island foxes on Santa Cruz Island traveled 1.9–2.4 km. No significant differences in distances moved have been found between sexes or age classes (Laughrin, 1977).

Island foxes eat a wide variety of plant and animal remains (Collins, 1980; Laughrin, 1973, 1977). They forage opportunistically on any food items encountered within their home range and generally do not move great distances to feed on abundant yet localized food resources. Principal foods eaten include mice, ground nesting birds, arthropods, and fruits. As with other canids, island fox diets vary according to seasonal availability of foods and island sampled (Laughrin, 1977). For example, San Miguel Island lacks arborescent fruiting shrubs; hence animals rely more on the fruits of sea-figs (*Carpobrotus aequale*).

Plant material eaten by island foxes is composed almost exclusively of fruits of *Arctostaphylos*, *Atiplex*, *Carpobrotus*, *Comarostaphylis*, *Ficus*, *Heteromeles*, *Mesembryanthemum*, *Opuntia*, *Prunus*, *Rhamnus*, *Rhus*, *Solanum*, *Vaccinium*, *Carpobrotus*, and *Comarostaphylis* (Collins, 1980; Laughrin, 1977). Fruits of *Arctostaphylos*, *Heteromeles*, *Comarostaphylis*, *Opuntia*, *Prunus*, and *Mesembryanthemum* are the most frequently eaten plants (Laughrin, 1977, 1980). The importance of fruit in the diet of island foxes is dependent upon the plant's fruiting season. For example, island foxes on Santa Cruz Island utilize fruits from Heteromeles (41% by volume) in the winter and early spring, *Arctostaphylos* (54%) in the summer, and *Comarostaphylis* (29%) in the winter (Laughrin, 1977). On San Miguel Island, fruits of sea-figs (*Carpobrotus aequale*) comprised 88% of the volume of the diet of island foxes during the summer and comprised 71–96% of all spring, summer, and autumn foxes. The only other significant plant materials found in San Miguel Island fox feces were bokhees of grass. Grass was found in only 4% of the summer fecal samples but was present in 32–42% of samples during the remainder of the year (Collins, 1980).

Island foxes have limited vertebrate prey, because the vertebrate fauna of Channel Islands is depauperate (Wenner and Johnson, 1980). Compared to the gray fox, island foxes show a reduced dependence on vertebrate prey (Fritzell, 1987; Fritzell and Homer, 1982; Laughrin, 1977). Mammals, especially deer mice (*Peromyscus maniculatus*), comprise the largest vertebrate portion of the diet of island foxes on Santa Cruz Island where they have been recorded exclusive of fruits in 4–13% of the summer and 10% of the winter home range of a male island fox on Santa Cruz Island. Other five- and six-year-old island foxes on Santa Cruz Island traveled 1.9–2.4 km. No significant differences in distances moved have been found between sexes or age classes (Laughrin, 1977).

Island foxes eat a wide variety of plant and animal remains (Collins, 1980; Laughrin, 1973, 1977). They forage opportunistically on any food items encountered within their home range and generally do not move great distances to feed on abundant yet localized food resources. Principal foods eaten include mice, ground nesting birds, arthropods, and fruits. As with other canids, island fox diets vary according to seasonal availability of foods and island sampled (Laughrin, 1977). For example, San Miguel Island lacks arborescent fruiting shrubs; hence animals rely more on the fruits of sea-figs (*Carpobrotus aequale*).

Plant material eaten by island foxes is composed almost exclusively of fruits of *Arctostaphylos*, *Atiplexes*, *Carpobrotus*, *Comarostaphylis*, *Ficus*, *Heteromeles*, *Mesembryanthemum*, *Opuntia*, *Prunus*, *Rhamnus*, *Rhus*, *Solanum*, and *Vaccinium* (Collins, 1980; Laughrin, 1977). Fruits of *Arctostaphylos*, *Heteromeles*, *Comarostaphylis*, *Opuntia*, *Prunus*, and *Mesembryanthemum* are the most frequently eaten plants (Laughrin, 1977, 1980). The importance of fruit in the diet of island foxes is dependent upon the plant's fruiting season. For example, island foxes on Santa Cruz Island utilize fruits from Heteromeles (41% by volume) in the winter and early spring, *Arctostaphylos* (54%) in the summer, and *Comarostaphylis* (29%) in the winter (Laughrin, 1977). On San Miguel Island, fruits of sea-figs (*Carpobrotus aequale*) comprised 88% of the volume of the diet of island foxes during the summer and comprised 71–96% of all spring, summer, and autumn foxes. The only other significant plant materials found in San Miguel Island fox feces were bokhees of grass. Grass was found in only 4% of the summer fecal samples but was present in 32–42% of samples during the remainder of the year (Collins, 1980).
in litt.). Reptile scales were found in 6 of 208 fecal samples from San Miguel Island (Collins, 1980). Ground nesting birds were found in 22% of fecal samples collected in the spring from San Miguel Island (Collins, 1980) and in 3–5.2% of the samples from throughout the year on Santa Cruz Island (Laughrin, 1977). Twelve species of birds have been reported from island foxes, with horned lark (Eremophila alpestris), western meadowlark (Sturnella neglecta: Collins; 1980; Laughrin, 1977), and chukar (Alectoris chukar; S. D. Kovach and R. J. Dow, in litt.) being the most common. Human refuse areas and carrion, especially carcasses of pigs, sheep, cattle, and marine mammals, provide supplemental food sources for island foxes, especially during seasons of the year when alternate foods are scarce (Laughrin, 1973, 1977).

Insects, particularly Orthopterans, are an important food for island foxes (Laughrin, 1977). The Jerusalem cricket (Stenopelma sp.), the most important insect prey of island foxes, has been recorded throughout the year in foxes. During the summer and autumn, grasshoppers become increasingly important in diets of island foxes. Although beetles (Coleoptera) and Lepidopteran larvae do not constitute a significant proportion of the overall diet of island foxes, they tend to be most abundant in fox feces during the spring and autumn (Collins; 1980; Laughrin, 1977). Nine species of beetles from three families (Tenebrionidae, Scarabaeidae, and Carabidae) were identified in feces collected in the spring from San Clemente Island (Doyen, 1974). The most common were Trigonomus sp. (Curculionidae), jane beetles (Scarabaeidae), and cutworms (Coelus rematus and Eusattus robustus). Island foxes appear to avoid beetles that possess defensive quinonoid secretions such as Eusattus laticollis (Doyen, 1974). Land snails (Helminthoglypta sp.) are the only mollusks known to be eaten by island foxes (Laughrin, 1977).

Six island foxes on Santa Cruz Island tested positive for antibodies against San Miguel Sea Lion Virus sero type 5 and one animal had antibodies for San Miguel Sea Lion Virus sero type 2. These foxes probably became infected by scavenging on beaches occupied by pinnipeds (Prato et al., 1977). Serum samples from 100 Santa Cruz Island foxes tested negative for canine distemper, leptospirosis, and rabies (Laughrin, 1977). However, recent tests on serum collected from 194 island foxes throughout their range detected serovar I. pacificus (4.1%), canine adenovirus (64.4%), canine corona virus (7.2%), toxoplasmosis (10.8%) and Leptospira interrogans serovar inter­haemorrhagiae (2.1%). No antibodies for rabies, canine distemper virus, and feline coronavirus were detected (Laughrin, 1992).

Ectoparasites reported from island foxes include fleas, ticks, and lice. The most common ticks found on island foxes include Ixodes pacificus on San Miguel, Santa Rosa, Santa Cruz, and Santa Catalina Island foxes, and I. ruginosus on Santa Rosa and Santa Cruz Island foxes (Bennett, 1987; Bennett et al., 1989; Lam et al., 1982). Several species of fleas that have been found on raccoons (Procyon cancrivorus) have also been observed on island foxes. Except for San Nicolas Island, the typical flea found on island foxes is P. simulans (P. W. Collins, in litt.). Neotrichodectes mephitiditus, the striped skunk louse, is common and has been found on island foxes from San Miguel, Santa Cruz, and Santa Catalina Islands (Emerson and Price, 1957). Endoparasites reported for island foxes include the cestode Mesocestodes corti (Voge, 1955) and unidentified nematodes found in fresh feces (Laughrin, 1977).

Other anomalies that have been observed in island fox populations include: shortened or broken tails, small pelage, mange, er­gots, deformities of the forelimbs (S. D. Kovach and R. J. Dow, in litt.), torn ears, grass seeds and cactus spines under the eyelids, clouded or opaque corneas (Laughrin, 1977). Animal studies have shown that the activity patterns of island foxes vary seasonally in response to changes in ambient air temperature. During the summer, foxes show very little activity during the middle of the day but are most active during the early morning and evening. During the winter, the reverse is true with little activity occurring during the middle of the day but are most active during the early morning and evening. Although there is no pattern to the frequency of marking, some individuals have been observed stopping as often as every 6–9 m to deposit one or two drops of urine. The feces of island foxes are generally deposited in groups of two or more with a mean of 54 droppings per sample recorded from 31 samples (Laughrin, 1977).

Compared to the gray fox, island foxes exhibit more daytime activity with peaks occurring during periods of low light intensity such as at sunset and sunrise (Laughrin, 1973, 1977). Radiotelemetry studies have shown that the activity patterns of island foxes vary seasonally in response to changes in ambient air temperature. During the summer, foxes show very little activity during the middle of the day but are most active during the early morning and evening. During the winter, the reverse is true with little activity occurring from 2200 to 0500 h and most of the foraging occurring during the day (Faussett, 1982). On Santa Cruz Island, midday activity of foxes decreases during the spring, while in the summer and autumn foxes are active during the midday when the air temperature remains below 22°C. No significant differences have been observed in the length of activity periods of males and females, or between females with and without young (Faussett, 1982). Island foxes are agile tree climbers (Laughrin, 1973).

GENETICS. An analysis of mitochondrial and nuclear DNA restriction fragments from the six island populations showed that genetic variability among islands was greater than that within a single island population (Gilbert et al., 1990). The average percent difference (APD) in the restriction fragments present among all the islands ranged from 43.8 to 84.5% while the APD among individuals from the same island ranged from 0.0 (San Nicolas Island) to 25.3%
(Santa Catalina Island) compared with 52.9% among mainland gray foxes (Gilbert et al., 1990; Wayne et al., 1991b). The lack of variability in restriction fragment profiles for island foxes on San Nicolas Island could be a result of extensive inbreeding or bottlenecking associated with low population density on this island (George and Wayne, 1991; Gilbert et al., 1990). Foxes on four of the islands (San Clemente, San Miguel, San Nicolas, and Santa Cruz) can be distinguished by the presence of hypervariable DNA restriction fragments unique to their respective islands (Gilbert et al., 1990; Wayne et al., 1991b). Island foxes from San Nicolas, San Miguel, and San Clemente islands have only one genotype for mitochondrial DNA (Wayne et al., 1991b). Unique genotypes for mitochondrial DNA are also found for populations on San Nicolas and Santa Catalina islands (Gilbert et al., 1990; Wayne et al., 1991b).

Nei's allozyme genetic distance between island foxes and mainland foxes averages 0.115, which is as large as that observed for discrete canid species (Wayne et al., 1991a). Allozyme heterozygosity of island foxes is lower (0.000-0.055) than for mainland gray foxes (0.097; Wayne et al., 1991a, 1991b). Island foxes from San Nicolas and Santa Catalina islands have no detectable allozyme variation while foxes from San Miguel and San Clemente islands have relatively low levels of allozyme variation, varying in 2 of the 7 loci that show variation with each of these 2 loci having only one allele with a frequency of ≥0.910 (Wayne et al., 1991a, 1991b). Island foxes have a karyotype with a diploid number of 66, composed of 62 acrocentric chromosomes, a submetacentric pair and typical mammalian sex chromosomes; this karyotype is identical to that found in U. cinereoargenteus (Wayne et al., 1991a).

REMARKS. Vernacular names that have been used for U. littoralis include island fox, coast fox, short-tailed fox, island gray fox, channel island fox, channel islands gray fox, California channel island fox, and insular gray fox (Corbett and Hill, 1980; Grinnell et al., 1937; Hall, 1981; Jones et al., 1986, 1992; Wayne et al., 1991a; Williams, 1979).

Although some researchers feel that the island fox is a subspecies of U. cinereoargenteus (Van Gelder, 1978), multivariate morphometric analysis and genetic studies support full specific status for U. littoralis (Collins, 1993; George and Wayne, 1991; Gilbert et al., 1990; Wayne et al., 1991a, 1991b).

LITERATURE CITED

BAIRD, S. F. 1857 [1858]. Mammals. In Reports of explorations and surveys for a railroad route from the Mississippi River to the Pacific Ocean. Beverly Tucker, Printer, Washington, D.C., Report 3:1-757 + pp. 143-145.

BENNERT, S. G. 1987. Medically important and other ectoparasitic Acarines on vertebrates from Santa Catalina Island, California. Bulletin of the Society of Vector Ecologists, 12:534-538.

BENNERT, S. G., J. P. WEBR, JR., AND P. W. COLLINS. 1989. Ixodes roguesi, Bishop (Acari: Ixodidae): description of larvae from Santa Rosa Island, California. Bulletin of the Society of Vector Ecologists, 14:262-265.

BLAKE, E. W., JR. 1887. The coast fox. West American Scientist, 3:49-52.

COLLINS, P. W. 1980. Food habits of the island fox (Urocyon littoralis littoralis) on San Miguel Island, California. Pp. 152-164, in Proceedings of the Second Conference on Scientific Research in the National Parks, 25-30 November, San Francisco, California, Volume 12. United States Department of the Interior, National Park Service, Washington, D.C. NTIS:PB81-100133, 410 pp.

. 1982. Origin and differentiation of the island fox: a study of evolution in insular populations. M. A. thesis, The University of California, Santa Barbara, 303 pp.

. 1983. The origin of island foxes. Santa Barbara Museum of Natural History Museum Bulletin, 59:1-2.

. 1991a. Interaction between island foxes (Urocyon littoralis) and Indians on islands off the coast of Southern California: I. morphologic and archaeological evidence of human assisted dispersal. Journal of Ethnobiology, 11:51-81.

. 1991b. Interaction between island foxes (Urocyon littoralis) and Native Americans on islands off the coast of Southern California: II. ethographic, archaeological, and historical evidence. Journal of Ethnobiology, 11:205-229.

. 1993. Taxonomic and biogeographic relationships of the island fox (Urocyon littoralis) and gray fox (Urocyon cinereoargenteus) from western North America. Pp. 351-390, in Proceedings of the third Channel Islands symposium: recent advances in California Islands research (F. C. Hochberg, ed.). Santa Barbara Museum of Natural History, Santa Barbara, California, 661 pp.

CORBIN, G. B., AND J. E. HILL. 1989. A world list of mammalian species. Cornell University Press, Ithaca, New York, 226 pp.

DOVEN, J. T. 1974. Differential predation of darkling ground beetles (Coleoptera: Tenebrionidae) by the channel island fox. The Pan-Pacific Entomologist, 50:86-87.

EMERSON, K. C., AND R. D. PRICE. 1987. New records of chewing lice (Mallophaga: Trichodectidae) found on North American wild foxes north of Mexico. Journal of the Kansas Entomological Society, 60:332-333.

FAUSETT, L. S. 1982. Activity and movement patterns of the island fox, Urocyon littoralis. Baird 1857 (Carnivora: Canidae). Ph.D. diss., The University of California, Los Angeles, 132 pp.

FOX, M. W. 1970. A comparative study of the development of facial expressions in canids: wolf, coyote and foxes. Behaviour, 36:49-73.

FRIETZELL, E. K. 1987. Gray fox and island gray fox. Pp. 408-420, in Wild furbearer management and conservation in North America (M. Novak, J. A. Baker, M. E. Oblard, and D. Malloch, eds.). Ontario Trappers Association and Ontario Ministry of Natural Resources, Ontario, Canada, 1130 pp.

FRIETZELL, E. K., AND J. K. HARDISON. 1982. Urocyon cinereoargenteus. Mammalian Species, 189:1-8.

GARCÉLON, D. K., R. K. WAYNE, AND B. J. GONZALEZ. 1992. A serologic survey of the island fox (Urocyon littoralis) on the Channel Islands, California. Journal of Wildlife Diseases, 28:223-229.

GEORGE, S. B., AND R. K. WAYNE. 1991. Island foxes. A model for conservation genetics. Terra, 30:18-23.

GILBERT, D. A., N. LEHMAN, S. J. O'BRIEN, AND R. K. WAYNE. 1990. Genetic fingerprinting reflects population differentiation in the California Channel Island fox. Nature, 344:764-767.

GRINNELL, J., AND J. M. LINDSAL. 1937. Two new foxes from the southern California Islands. Proceedings of the Biological Society of Washington, 43:153-156.

GRINNELL, J. S. DIXON, AND J. M. LINDSAL. 1937. Fur-bearing mammals of California: their natural history, systematic status, and relations to man. University of California Press, Berkeley, 2:452-471.

HALL, E. R. 1981. The mammals of North America, Second ed. John Wiley & Sons, New York, 1:600 + 90.

HILDEBRAND, M. 1952a. The integument in Canidae. Journal of Mammalogy, 33:419-428.

. 1952b. An analysis of body proportions in the Canidae. American Journal of Anatomy, 90:217-256.

. 1954. Comparative morphology of the body skeleton in recent Canidae. University of California Publications in Zoology, 52:399-470.

JACOBS, G. H., J. F. DEEGAN, II, M. A. CROCHNALE, AND J. A. FENWICK. 1993. Photopigments of dogs and foxes and their implications for canid vision. Visual Neuroscience, 10:173-180.

JOHNSON, D. L. 1975. New evidence on the origin of the fox, Urocyon littoralis clementae, and feral goats on San Clemente Island, California. Journal of Mammalogy, 56:925-928.

. 1978. The origin of island mammoths and the Quaternary land bridge history of the Northern Channel Islands, California. Quaternary Research, 10:204-225.

. 1983. The California continental borderline: land-bridges, watergaps and biotic dispersals. Pp. 481-527, in Quaternary coastlines and marine archaeology: towards the prehistory of land bridges and continental shelves (P. M. Masters and N. C. Fleming, eds.). Academic Press, London, 641 pp.

JONES, J. K., JR., H. H. GENOWAYS, R. S. HOFFMANN, D. W. RICE, AND C. JONES. 1986. Revised checklist of North American mammals north of Mexico, 1986. Occasional Papers Museum Texas Tech University, 107:1-22.

JONES, J. K., JR., R. S. HOFFMANN, D. W. RICE, J. E. BAKER, AND M. D. ENGSTROM. 1992. Revised checklist of North American mammals north of Mexico, 1991. Occasional Papers Museum Texas Tech University, 146:1-23.

LANE, R. S., S. E. MILLER, AND P. W. COLLINS. 1982. Ticks...
(Acari: Argasidae and Ixodidae) from the California Channel Islands. Pan-Pacific Entomologist, 58:96-104.

Laughlin, L. L. 1973. The island fox. Environment Southwest, 458:6-9.

. 1977. The island fox: a field study of its behavior and ecology. Ph.D. dissert., The University of California, Santa Barbara, 83 pp.

. 1980. Populations and status of the island fox. Pp. 745-749, in The California islands: proceedings of a multidisciplinary symposium (D. M. Power, ed.). Santa Barbara Museum of Natural History, Santa Barbara, California, 787 pp.

Merriam, C. H. 1888. Description of a new fox from southern California. Proceedings of the Biological Society of Washington, 4:135-138.

. 1903. Eight new mammals from the United States. Proceedings of the Biological Society of Washington, 16:73-78.

Orr, P. C. 1968. Prehistory of Santa Rosa Island. Santa Barbara Museum of Natural History, Santa Barbara, California, 253 pp.

Philbrick, R. N. (ed.). 1967. Proceedings of the symposium on the biology of the California islands. Santa Barbara Botanic Garden, Santa Barbara, California, 363 pp.

Philbrick, R. N., and J. R. Haller. 1977. The Southern California Islands. Pp. 893-906, in Terrestrial vegetation of California (M. G. Barbour and J. Major, eds.). John Wiley & Sons, New York, 1,002 pp.

Prato, C. M., T. G. Akers, and A. W. Smith. 1977. Calicivirus antibodies in wild fox populations. Journal of Wildlife Diseases, 13:448-450.

Remington, C. L. 1971. Natural history and evolutionary genetics on the California channel islands. Discovery, 7:3-18.

Stock, C. 1943. Foxes and elephants of the channel islands. New discoveries on the channel islands. Los Angeles County Museum Quarterly, 3:6-9.

Van Gelder, R. C. 1978. A review of canid classification. American Museum Novitates, 2646:1-10.

Voge, M. 1955. A list of Cestode parasites from California mammals. The American Midland Naturalist, 54:413-417.

Von Bloeker, J. C., Jr. 1967. The land mammals of the Southern California Islands. Pp. 245-265, in Proceedings of the symposium on the biology of the California Islands (R. N. Philbrick, ed.). Santa Barbara Botanic Garden, Santa Barbara, California, 363 pp.

Wayne, R. K., S. B. George, D. Gilbert, and P. W. Collins. 1991a. The channel island fox (Urocyon littoralis) as a model of genetic change in small populations. Pp. 639-649, in The unity of evolutionary biology: proceedings of the fourth international congress of systematic and evolutionary biology. Volume II. (E. C. Dudley, ed.). Dioscorides Press, Portland, Oregon, 1048 pp.

Wayne, R. K., S. B. George, D. Gilbert, P. W. Collins, S. D. Kovach, D. Girman, and N. Lehman. 1991b. A morphologic and genetic study of the island fox, Urocyon littoralis. Evolution, 45:1849-1868.

Wenner, A. M., and D. L. Johnson. 1980. Land vertebrates on the California Channel Islands: sweepstakes or bridges? Pp. 497-530, in The California Islands: proceedings of a multidisciplinary symposium (D. M. Power, ed.). Santa Barbara Museum of Natural History, Santa Barbara, California, 787 pp.

Williams, D. F. 1979. Checklist of California mammals. Annuals of Carnegie Museum, 48:425-433.

Wilson, D. E., and D. M. Reeder (eds.). 1993. Mammal species of the world: a taxonomic and geographic reference. Second ed. Smithsonian Institute, Washington, 1,206 pp.

Editors of this account were Elaine Anderson, Guy N. Cameron, Alicia V. Linzey, and Karl Koopman. Managing editor was Joseph F. Merritt.

C. M. Moore, Department of Zoology and Wildlife Science, Auburn University, Alabama 36849-5414; P. W. Collins, Santa Barbara Museum of Natural History, 2559 Puesta Del Sol, Santa Barbara, California 93105 (Present Address of CMM: P. O. Box 84, Camp Hill, Alabama 36850).