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Urocyon littoralis.

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Urocyon littoralis (Baird, 1858)

Island Fox

Vulpes littoralis Baird, 1858:143. Type locality San Miguel Island, Santa Barbara County, California.
Urocyon littoralis: Merriam, 1888:135. First use of current name combination.
Urocyon catalinae Merriam, 1903:74. Type locality Catalina Island, Los Angeles County, California.
Urocyon clementae 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. clementae 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 *U. cinereoargenteus* (Collins, 1982). The coloration is similar to that of *U. cinereoargenteus*, except the tones are duller and the pattern is less sharply marked due to a diffusion of black on individual hairs (Grinnell et al., 1937). Cranial characters that differentiate island foxes from gray foxes include: smaller size, approximately 83% as large (Collins, 1982); nasal bones that are wider relative to their lengths; lack of bifurcation along the anterior base of the malar; lyre-shaped temporal ridges that are less developed and more widely separated; and a more convex roof to the cranium between the temporal ridges (Fig. 2; Grinnell et al., 1937). Other skeletal traits that distinguish *U. littoralis* from *U. cinereoargenteus* include: more massive postcranial bones that have more accentuated muscle scars and tuberosities; a shorter sacrum relative to its width; a stouter fibula; a relatively longer ilium; longer lateral metapodials; a heavier and relatively longer baculum; and legs that are considerably shorter in proportion to overall body size (Hildebrand, 1952*b*, 1954).

GENERAL CHARACTERS. 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 (Fritzell 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).

Island foxes show marked differences in size between males and females. Of 28 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. clementae* (*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 (608–825), 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), 183 (157–210), 245.9 (195–280), 253 (214–300); length of hind foot, 110.6 (103–118), 109.9 (105–115), 115.3 (103–124), 111.1 (102–120), 102.3 (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 (93.4–104.9), 97.7 (93.2–101.9), 99.1 (92.2–102.9); zygomatic breadth, 58.6 (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 (54.0–59.7); 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 (25.3–28.8), 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 (37.9–41.4), 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 (40.3–45.0), 43.0 (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. clementae* (*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), 686 (625–760), 745.8 (665–807), 659.1 (628–692), 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 (104–115), 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–

FIG. 1. Photograph of an adult island fox *Urocyon littoralis* from San Miguel Island, Santa Barbara Co., California. Photograph by P. W. Collins.

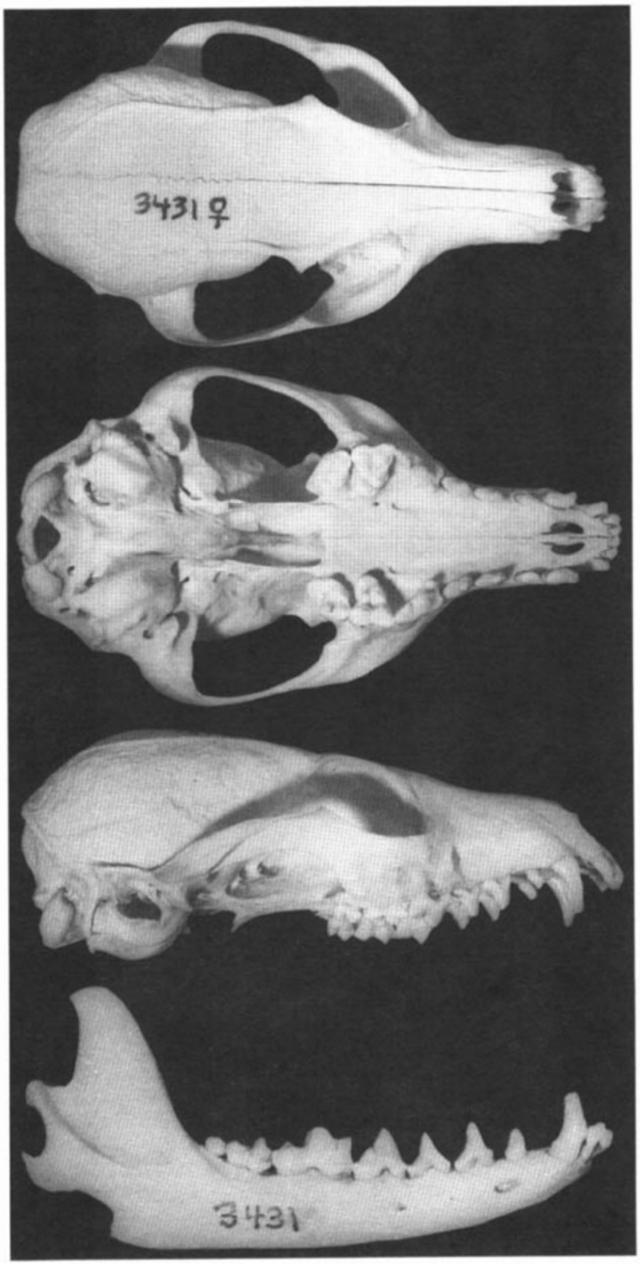

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Urocyon littoralis dickeyi* (female, Santa Barbara Museum of Natural History, No. 3431, San Nicolas Island, near Building 265 on Owen Rd., Ventura Co., California). Condylobasal length is 98.9 mm. Photographs by H. Uhles.

67), 70.6 (67–74); condylobasal length of cranium, 99.8 (93.0–103.9), 93.2 (89.1–98.7), 95.6 (91.9–101.2), 98.7 (95.0–102.2), 95.1 (89.8–98.9), 96.1 (88.6–100.8); zygomatic breadth, 57.3 (52.8–61.4), 54.7 (52.7–57.7), 54.7 (51.1–57.4), 56.6 (55.2–58.0), 55.2 (51.6–57.0), 55.1 (51.1–57.5); interorbital width, 30.5 (27.4–33.0), 28.6 (27.4–29.8), 28.8 (27.0–31.0), 32.3 (30.9–34.2), 30.8 (27.9–33.2), 31.7 (27.5–34.1); postorbital width, 27.2 (25.0–28.4), 26.3 (25.4–27.0), 26.5 (25.5–27.7), 27.2 (25.7–28.6), 27.3 (25.8–29.1), 27.0 (25.0–28.5); breadth of cranium, 40.8 (39.8–42.2), 38.9 (37.7–39.7), 39.3 (38.0–40.8), 40.5 (39.4–41.6), 39.7 (37.6–41.2), 40.4 (39.0–42.0); length of maxillary toothrow, 43.5 (41.3–45.5), 41.5 (38.5–44.1), 41.5 (39.4–43.8), 42.1 (40.9–44.2), 41.8 (39.8–43.7), 42.0 (39.8–43.8; Collins, 1982). Range of body mass, in g, for adult males ($n = 21$) is 1,200–2,700 and 1,070–2,722 for females ($n = 20$; Collins, 1982; Grinnell et al., 1937). The largest island foxes occur on Santa Catalina Island and the smallest occur on Santa Cruz Island (Collins, 1982).

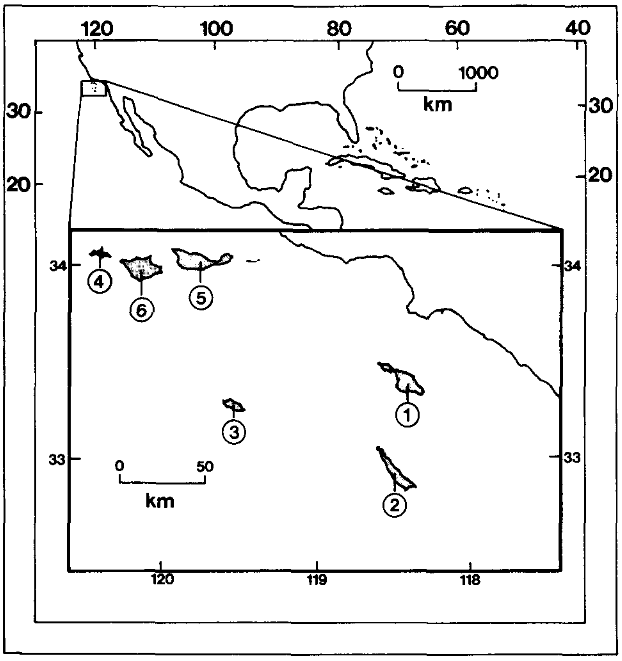

FIG. 3. Distribution of *Urocyon littoralis* in California (Hall, 1981): 1, *U. l. catalinae*; 2, *U. l. clementae*; 3, *U. l. dickeyi*; 4, *U. l. littoralis*; 5, *U. l. santacruzae*; 6, *U. l. santarosae*.

DISTRIBUTION. Island foxes inhabit the six largest islands off the coast of southern California. In the Northern Channel Island complex, they are found on San Miguel, Santa Rosa, and Santa Cruz Islands, while in the Southern Channel Islands they occur on San Nicolas, Santa Catalina, and San Clemente Islands (Fig. 3). 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, 1991*a*, 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, 1991*a*, 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 occurence of island foxes in the archaeological record, coupled with comparison of island fox cranial material from archaeological samples with present day samples, suggests that Native Americans were responsible for introducing island foxes from the Northern Channel Islands to the Southern Channel Islands possibly to serve as a source of pelts, as pets or semidomesticates, or to be used in rituals and religious ceremonies (Collins, 1982, 1983, 1991*a*, 1991*b*).

The origin of island foxes on San Clemente Island is unclear. Europeans were once believed to be responsible for introducing foxes to this island in the late 1880s (Grinnell et al., 1937). However, evidence found in unpublished 19th century letters (Johnson, 1975) and skeletal remains from archaeological sites (Collins, 1982, 1991*a*) suggest that island foxes had been on San Clemente and the other Southern Channel Islands for an extended period of time prior to the arrival of Europeans.

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 Tecolote geologic formation, which dates from 10,400 to 16,000 years of age (Orr, 1968). Analysis of cranial characters demonstrates that this specimen is virtually indistinguishable in size and shape from present-day female foxes on San Miguel and Santa Rosa Islands (Collins, 1982, 1991*a*, 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 3,880–800 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, 1991*a*).

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 obscures an elongated tail gland similar to that described for the gray fox (Hildebrand, 1952*a*).

Prior to their first molt, juveniles are woolly in appearance with only a few, fine, long overhairs projecting beyond a thick-dark underfur. The entire upper surface of the tail is black. The ears and the top of the head are overlaid with extensive patches of long, fine hairs. Areas that are buffy 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 (Fritzell, 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 basisphenoid-basioccipital and basisphenoid-presphenoid sutures open and evident. Young adults are characterized by having all sutures on the base of the skull closed and completely obliterated, having no v-shaped gap between the presphenoid and vomer bones, and having an elongated area of exposed dentine between the metaconule and protocone of the first upper molar. Adults exhibit extensive wear on M1 with conules worn close to the depth of interconule space and with a broad band of exposed dentine between the metaconule and protocone. Old adults show excessive wear on M1 with all of the conules worn down to or below the gum and with most of the molar 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 nasals, 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 coarsely surfaced, with a narrow deep base, a deep urethral grove 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 ($n = 31$) had an average of 21–22 caudal vertebrae (Collins, 1982).

Island foxes have tapetal reflection 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 the claw marks usually are evident (Fritzell, 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 tracks 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).

ONTOGENY 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 when first found. Parturition usually occurs from the end of April through early May (Laughrin, 1977).

Island foxes will 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, log, stump, or shrub (Laughrin, 1973). Sites known to be used as dens include brush piles, small caves, rock crevices, manmade structures, log piles, hollowed limbs, stumps of large trees, and hollows under dense brush (Blake, 1887; Laughrin, 1977). If no suitable den site is found, then island foxes will dig a simple tunnel. Dens protect the young from predators and adverse weather and only are used by adults when the young are very small. Dens generally are abandoned by mid-summer when the young begin to forage with their parents. 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 finer (Laughrin, 1977). It is not until the end of August or early September, when the winter pelage develops, that young-of-the-year begin to approximate 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; Laughrin, 1977). Young begin 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 the natal home range in late September, but young remain in their natal areas until at least December (Fausett, 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 cactus scrub, island chaparral, southern coastal oak woodland, island woodland, southern riparian woodland, Bishop and Torrey pine 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 conducted. Island fox densities recorded using line transect data were 0.31/km^2 for *U. l. catalinae*, 4.2/km^2 for *U. l. clementae*, 1.2/km^2 for *U. l. dickeyi*, 2.7/km^2 for *U. l. littoralis*, 7.9/km^2 for *U. l. santacruzae*, and 4.2/km^2 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 San Clemente) 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 San Clemente 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/km^2 in woodland habitat and 2.4/km^2 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 (Laughrin, 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 9.8/km^2. From 1971 to 1977 island fox densities on San Nicolas Island ranged from 2.7 to 0.12/km^2, 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).

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 islands (Laughrin, 1977). Free-ranging island foxes live an average of 4–6 years, based on wear patterns on M1 (Collins, 1982). The longevity record for captive island foxes is at least 8 years (Laughrin, 1973, 1977).

Collision with vehicles may constitute an important source of mortality for island foxes on San Clemente, San Catalina, and San Nicolas, which have extensive road systems and relatively heavy traffic (Laughrin, 1977). Twenty eight percent of the dead island foxes carcasses found on Santa Cruz Island died as a result of collisions with vehicles. Other sources of mortality reported for island foxes include disease, parasites, predation, and accidents (Laughrin, 1977). The only known predator of island foxes, except for humans, is the red-tailed hawk (*Buteo jamaicensis*), which preys upon young island foxes. Other possible predators of island foxes include domestic dogs (*Canis domesticus*); common ravens (*Corvus corax*); golden eagles (*Aquila chrysaetos*); and, in the past, bald eagles (*Haliaeetus leucocephalus*; Laughrin, 1973, 1977).

Feral cats are the principal competitors of *U. littoralis* on San Clemente and Santa Catalina Islands (Laughrin, 1973). On San Nicolas Island, where feral cats reach densities of 4 cats per km^2, island foxes were excluded from suitable habitat via spatial and food resource competition (S. D. Kovach and R. J. Dow, in litt.). On Santa Rosa and Santa Cruz Islands, where *U. littoralis* is sympatric with the western spotted skunk (*Spilogale gracilis*), competition for similar food resources probably occurs (Laughrin, 1973). Island foxes may also compete with rodents and birds for insects, fruits, seeds, and carrion (Laughrin, 1973).

The home ranges of island foxes vary in size according to the sex of the animal and the season (Fausett, 1982; Laughrin, 1977). Male island foxes have larger home ranges during the autumn and winter than during the spring and summer (Fausett, 1982; Laughrin, 1977). The winter home range of a male island fox on Santa Cruz Island was estimated to be 41.2 ha and its summer home range was 20.4 ha. The winter home ranges of neighboring female island foxes on Santa Cruz Island overlap slightly whereas the ranges of males overlap extensively with other males and with two or three females. During spring and summer the home range of an adult male is contained within the range of one female. Females occupy approximately the same home range throughout the year (Fausett, 1982).

Daily movements are confined to an island fox's established home range. On Santa Cruz Island the mean distance moved along a line transect was 0.14 km. The greatest distance traveled, 2.7 km, was covered by a 5-year-old male island fox that was radio collared on Santa Cruz Island. Other five- and six-year-old island foxes on Santa Cruz Island travelled 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-fig, *Carpobrotus aequilaterus* (Collins, 1980).

Plant material eaten by island foxes is composed almost exclusively of fruits of *Arctostaphylos*, *Atriplex*, *Carpobrotus*, *Comarostaphylis*, *Ficus*, *Heteromeles*, *Mesembryanthemum*, *Opuntia*, *Prunus*, *Rhamnus*, *Rhus*, *Rosa*, *Schinus*, *Solanum*, and *Vaccinium* (Collins, 1980; Laughrin, 1977). Fruits of *Arctostaphylos*, *Heteromeles*, *Comarostaphylis*, *Opuntia*, *Prunus*, and *Mesembryanthemum* are the most frequently eaten plants (Laughrin, 1973, 1977). The importance of fruit in the diet of island foxes is related to a 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 autumn (Laughrin, 1977). On San Miguel Island, fruits of sea-figs (*Carpobrotus aequilaterus*) comprised 88% of the volume of feces during the summer and occurred in 71–96% of all spring, summer, and autumn feces. The only other significant plant materials found in San Miguel Island fox feces were boluses 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 the 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 Haroldson, 1982; Laughrin, 1977). Mammals, especially deer mice (*Peromyscus maniculatus*), comprise the largest vertebrate portion of the diets of island foxes on Santa Cruz Island where they have been found in 4–13% of the feces examined (Laughrin, 1977). Deer mice comprise 53% of the volume of winter feces (Collins, 1980). Other potential rodent prey includes *Spermophilus beecheyi*, *Reithrodontomys megalotis*, *Microtus californicus*, *Rattus rattus*, and *Mus musculus* (Laughrin, 1973; von Bloeker, 1967). Reptiles and amphibians do not constitute a significant proportion of the overall diet of island foxes (Collins, 1980). The Pacific chorus frog (*Pseudacris regilla*) is the only amphibian that island foxes are known to eat (Laughrin, 1977). Although it has been suggested that island foxes may eat all species of reptiles that are found on the islands (Laughrin, 1977), only three species of lizards (*Xantusia riversiana*, *Sceloporus occidentalis*, and *Elgaria multicarinata*) have been found in fecal samples (Collins, 1980; S. D. Kovach and R. J. Dow, 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 3–6.2% of the samples from throughout the year on Santa Cruz Island (Laughrin, 1977). Twelve species of birds have been reported from island fox feces, 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 (*Stenopelmatus* sp.), the most important insect prey of island foxes, has been recorded throughout the year in feces. 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 Curculionidae) were identified in feces collected in the spring from San Clemente Island (Doyen, 1974). The most common were *Trigonoscuta* sp. (Curculionidae), june beetles (Scarabaeidae), and two tenebrionids (*Coelus remotus* and *Eusattus robustus*). Island foxes appear to avoid beetles that possess defensive quinonoid secretions such as *Eleodes laticollis* (Doyen, 1974). Land snails (*Helminthoglypta* sp.) are the only molluscs 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 seroprevalence to six canid diseases (Garcelon et al., 1992). Foxes from each island tested positive for antibodies against canine parvo virus (64%), while there were island-specific exposures to canine herpes (4.1%), canine adenovirus (64.4%), canine corona virus (7.2%), toxoplasmosis (10.8%) and *Leptospira interogans* serovar *interohaemorrhagiae* (2.1%). No antibodies for rabies, canine distemper virus, or *L. i.* serovar *canicola* were found (Garcelon et al., 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. rugosus* on Santa Rosa and Santa Cruz Island foxes (Bennett, 1987; Bennett et al., 1989; Lane et al., 1982). Several species of fleas that normally infest deer mice (*Peromyscus maniculatus*) 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 mephitidis*, 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, 1987). Endoparasites reported for island foxes include the cestode *Mesocestoides 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, thin pelage, mange, ergotism, deformities of the forelimbs (S. D. Kovach and R. J. Dow, in litt.), torn ears, grass seeds and cactus spines under the eyelids, cactus spines embedded under the skin, cloudy or opaque corneas, eyelids sealed with dried mucous, and missing, broken or severely worn teeth (Grinnell et al., 1937; Laughrin, 1977). Ten percent of island foxes ≥5 years of age on Santa Cruz Island had opaque-white corneas (Laughrin, 1977). Although it has been suggested that blindness and eye disease in foxes on Santa Cruz Island may have resulted from cactus spines becoming embedded in their eyes (Grinnell et al., 1937), the opaque-white corneas are probably associated with increasing age (Laughrin, 1977). Ear deformities found in adult island foxes are caused by damage associated with increasing age, ear biting between sexes, and injury to the ear when ear tags tear out (Laughrin, 1977).

Wire mesh live traps of several sizes (20 by 20 by 46 cm, 24 by 24 by 66 cm, 15 by 15 by 36 cm, and 15 by 15 by 61 cm) are used to capture island foxes (Fausett, 1982; Laughrin, 1977). Traps should be covered with burlap to protect animals from exposure and any odorous canned cat food can be used to bait the traps. Ear tagging is the most commonly used method of marking captured foxes. Island foxes can usually be handled without the use of drugs (Laughrin, 1977).

BEHAVIOR. Island foxes are known for their docile nature and general lack of fear of humans (Blake, 1887; Grinnell et al., 1937; Laughrin, 1977). Island foxes can be easily tamed and have been known to tug on the blankets of people sleeping on the ground and to approach within a meter of a person to retrieve scraps of meat and fish (Blake, 1887). The docile behavior and diurnal habits exhibited by island foxes probably result from an absence of large predators and freedom from human harassment (Laughrin, 1977).

Island foxes use auditory, visual, and olfactory signals to communicate with one another (Laughrin, 1977). They can commonly be heard barking at night (Blake, 1887; Grinnell et al., 1937). Island fox barks have been described as resembling the sound produced by turning the handle of a well-filled coffee mill half-way around, sharply and suddenly (Blake, 1887), or like the barks produced by a rat terrier (Grinnell et al., 1937). They also bark and growl when handled (Laughrin, 1977) and produce hisses (Blake, 1887) and short sharp growls during intraspecific aggression (Fausett, 1982). All types of vocalizations are used by both sexes to establish dominance between individuals during intraspecific encounters (Fausett, 1982; Laughrin, 1977). Behavior and visual expressions associated with submissive and aggressive interactions between island foxes are indistinguishable from those described for the gray fox (Fox, 1970; Laughrin, 1977). Submissive expressions for island foxes include head lowered with horizontally extended neck, ears flattened and turned down to sides, licking, nibbling, whining, and looking away. Aggressive expressions include growls, barks, head high and neck arched, direct stare, and ears flattened and turned back (Laughrin, 1977). Intraspecific fighting is often accompanied by growling, barking, tail and ear biting, chasing, scuffling, and hip slamming (Fausett, 1982; Laughrin, 1977). When first approached by a human, captured island foxes show aggressive expressions but after the animal is grasped its behavior changes to one of submission. Mutual grooming occurs between paired adults and occasionally between an adult and a juvenile (Laughrin, 1977).

Olfactory cues from urine and feces deposition are used as another form of intraspecific communication. Island foxes deposit urine and feces along trails and road edges on protruding, prominent objects such as rocks, sticks, cow manure, fox feces, grass clumps, and small bushes (Laughrin, 1977). 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; 51% of the feces found on Santa Cruz Island occurred 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 (Fausett, 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 (Fausett, 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 84.4% 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., 1991*b*). 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., 1991*b*). Island foxes from San Nicolas, San Miguel, and San Clemente islands have only one genotype for mitochondrial DNA (Wayne et al., 1991*b*). Unique genotypes for mitochondrial DNA are also found in populations on San Nicolas and Santa Catalina islands (Gilbert et al., 1990; Wayne et al., 1991*b*).

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., 1991*a*). Allozyme heterozygosity of island foxes is lower (0.000–0.055) than for mainland gray foxes (0.097; Wayne et al., 1991*a*, 1991*b*). 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 one allele with a frequency of ≥0.910 (Wayne et al., 1991*a*, 1991*b*). 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., 1991*a*).

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 (Corbet and Hill, 1980; Grinnell et al., 1937; Hall, 1981; Jones et al., 1986, 1992; Wayne et al., 1991*a*; 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., 1991*a*, 1991*b*).

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