

DECLINE OF AN ISLAND FOX SUBSPECIES TO NEAR EXTINCTION

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ABSTRACT—We documented a catastrophic decline in the island fox (*Urocyon littoralis littoralis*) population on San Miguel Island from 1994 to 1999, and used radiotelemetry to investigate mortality causes in the latter part of the decline. Annual population monitoring via capture-mark-recapture techniques revealed that densities of adult foxes declined up to 100% on 3 trapping grids monitored during the study period. The estimated population size on San Miguel declined from 450 adults in 1994 to less than 20 in 1999. Apparent survival of all age classes declined over the study. A radiotelemetry-based survival study conducted in 1998 and 1999 revealed high winter mortality, most likely due to golden eagle (*Aquila chrysaetos*) predation. Necropsy of 7 carcasses during the study period confirmed raptor predation for 5 carcasses. Three carcasses were infested with a pathogenic parasite, *Angiocolus gubernaculatus*, not found in island fox populations on San Nicolas, San Clemente, Santa Catalina, Santa Cruz, or Santa Rosa Islands, and 2 carcasses had *Uncinaria stenocephala* and colonic granulomas from *Spirocerca* infection. Because pup production was low and reproductive effort limited in young females, the island fox population on San Miguel is unlikely to recover without significant intervention. In 1999, 14 island foxes were brought into captivity, and only 1 was known to exist in the wild on San Miguel Island.

RESUMEN—Documentamos una declinación catastrófica en la población del zorro *Urocyon littoralis littoralis* en la Isla de San Miguel entre 1994 y 1999, y usamos radioteleetría para investigar las causas de la mortalidad en la última parte de la declinación. El muestreo anual de la población por medio de técnicas captura-recaptura indicó que la densidad de los zorros adultos declinó hasta un 100% en tres cuadrantes durante el periodo de estudio. El tamaño poblacional estimado en San Miguel declinó de 450 adultos en 1994 a menos de 20 en 1999. La supervivencia aparente de todas clases de edad declinó durante este periodo. Un estudio de supervivencia conducido en 1998 y 1999 por medio de radioteleetría reveló alta mortalidad durante el invierno, debida probablemente a la depredación por la águila real (*Aquila chrysaetos*). Análisis postmortem de 7 carcasas durante el estudio confirmó la depredación por aves de presa en 5 carcasas. Tres carcasas fueron infestadas con un parásito patogénico, *Angiocolus gubernaculatus*, que no se encuentra en las poblaciones de zorros en las islas de San Nicolás, San Clemente, Santa Catalina, Santa Cruz o Santa Rosa, y 2 carcasas tuvieron *Uncinaria stenocephala* y granulomas en el colon de la infección *Spirocerca*. Porque la producción de cachorros fue baja y la capacidad reproductiva limitada en las zorras jóvenes, la población del zorro en San Miguel probablemente no se recupere sin intervención importante. En 1999, 14 zorros fueron apresados para cautiverio, y se sabe de 1 solo zorro que seguía viviendo libre en la isla de San Miguel.

A diminutive relative of the mainland gray fox (*Urocyon cinereoargenteus*), the island fox (*U. littoralis*) is distributed as 6 subspecies on the 6 largest of the 8 California Channel Islands (Moore and Collins, 1995). Island foxes have historically existed at low population sizes,

ranging from several hundred to several thousand (Roemer et al., 1994). The species was listed as threatened by the state of California due to its small population size on several islands (California Department of Fish and Game, 1987), and 4 of the 6 subspecies, in-

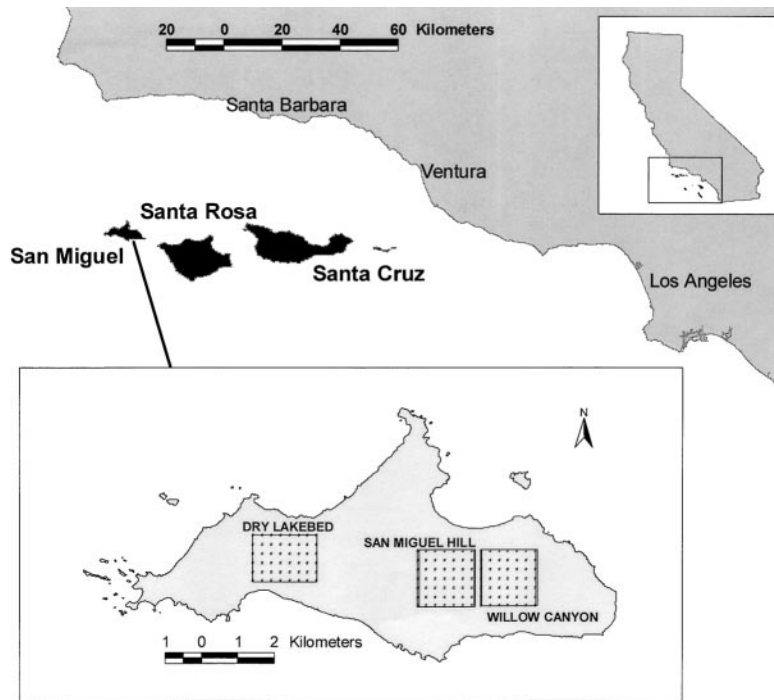


FIG. 1—Location of island fox trapping grids on San Miguel Island, California. Island foxes occurred on San Miguel, Santa Rosa, and Santa Cruz islands, as well as on San Nicolas, San Clemente, and Santa Catalina islands (not shown).

cluding the San Miguel subspecies, were federally listed as endangered in 2004 (United States Fish and Wildlife Service, 2004).

For small populations, extinction risk is increased by small initial population size and demographic and environmental stochasticity (Lande, 1993, 1998). Small, isolated carnivore populations are vulnerable to extinction via catastrophic sources of mortality as well (White et al., 2000), and the importance of quantifying factors affecting extinction risk is paramount for such populations (Vucetich and Creel, 1999).

From 1993 to 1999, we conducted annual population monitoring of island foxes (*Urocyon littoralis littoralis*) on San Miguel Island, as part of a long-term ecological monitoring program at Channel Islands National Park. By 1999, island fox populations on the 3 northern Channel Islands (San Miguel, Santa Rosa, and Santa Cruz islands) had declined to the point where extinction of 2 subspecies was likely within a matter of years, with the most parsimonious explanation for the decline being predation by

golden eagles (*Aquila chrysaetos*) (Roemer, 1999). In this paper, we demonstrate the demographic vulnerability of a small population of insular carnivores by reporting on the scope of the catastrophic decline and the limited reproductive success of island foxes at low densities. The vulnerability is underscored by the considerable incidence of parasitism in the San Miguel Island foxes and a high level of predation, and subsequent low survivorship, in the final year of the decline. We summarize 7 y of population monitoring data from San Miguel Island and report results from a 12-mo radio-telemetry study that investigated mortality factors. The results of this study are relevant to the development of efficacious recovery actions for the diminished island fox population.

METHODS—We studied the island fox population on San Miguel Island, the smallest (38.7 km²) and westernmost of the northern Channel Islands (Fig. 1). San Miguel Island was recovering from a period of severe overgrazing and erosion caused by historic sheep ranching (Hochberg et al., 1979; Coonan et al., 2002).

Grasslands, including introduced annuals such as *Avena* and *Bromus* (Hochberg et al., 1979), as well as native bunchgrasses (*Nasella pulchra*), covered most of the island, and coyote brush (*Baccharis pilularis*) invaded some grassland areas. The dominant shrub community was *Isocoma* scrub, characterized by coast goldenbush (*Isocoma menziesii*), San Miguel Island locoweed (*Astragalus miguelensis*), and California saltbush (*Atriplex californica*). Silver lupine (*Lupinus al-bifrons*), giant coreopsis (*Coreopsis gigantea*), and introduced iceplant (*Mesembryanthemum crystallinum* and *M. nodiflorum*) occurred in coastal areas.

To determine island fox density, population size, and trends, we used a standardized capture–recapture protocol developed specifically for island foxes and used by Roemer et al. (1994) on other sites in the Channel Islands. We monitored island foxes annually from 1993 to 1998 on 2 trapping grids (Willow Canyon and San Miguel Hill), and from 1994 to 1998 on a third grid (Dry Lakebed) (Fig. 1). The Willow Canyon and San Miguel Hill grids each had 49 traps arrayed in a 7×7 grid, and the third (6×8) grid contained 48 traps. Distance between traps on all grids was 250 m. Annual trapping was conducted July through September with live traps ($23 \times 23 \times 66$ cm, Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with dry cat food and a fruit scent (Knob Mountain Raw Fur Co., Berwick, Pennsylvania). Captured foxes were protected from the elements by careful placement of traps and by a burlap cover on each trap. A polyethylene tube chew-bar was wired inside each trap. Each grid was trapped for 6 consecutive d, and traps were checked once during every 24-h period.

Upon first capture, foxes were weighed (± 25 g), and we recorded sex, age, reproductive condition, and injuries. Foxes were aged according to tooth eruption and wear patterns on the first upper molar (Wood, 1958) and were assigned to discrete age classes: pups (Age Class 0), young adults (Age Class 1: ca. 7 mo to 2 y), adults (Age Class 2: ca. 2 to 3 y), mature adults (Age Class 3: ca. 3 to 4 y) and old adults (Age Class 4: >4 y). At first, we marked individuals with colored ear tags (Rototag, Dalton Supplies, Australia) inserted in the pinna, with passive integrated transponder (PIT) tags (Biomark, Seattle, Washington) inserted subcutaneously between and just anterior to the scapulae or with both. During the course of the study, we shifted from ear tags to PIT tags because the latter had a lower loss rate, produced fewer injuries, and were less conspicuous. Females were identified as having lactated if milk was expressed from their teats, or if the fur around their teats was sparse and had been stained rust-colored by milk (Egoscue, 1975).

Annual adult population size for 1993 through 1998 was estimated for each grid using closed population models with program CAPTURE (White et

al., 1982; Roemer et al., 1994). Because the models in CAPTURE do not work well with small population sizes, we estimated the population size on the Dry Lakebed with Chapman's modification of the Lincoln-Peterson estimator (Lancia et al., 1996) in 1996. We captured too few adults to estimate population sizes for the Dry Lakebed grid in 1997 and 1998, and for the San Miguel Hill grid in 1998.

We estimated adult density because it is a more conservative indicator of population change than total density, which includes variability due to annual differences in pup survival. Naïve (or crude) density is calculated as $D = N/A$, where N is the estimate of population size and A is the area of the trapping grid. Although closed population models assume that populations are isolated both demographically and geographically, they do not account for "edge effect," or incomplete geographic closure. Therefore, we used the estimates of mean maximum distance moved provided by CAPTURE to estimate the effective trap area $A(W)$, where W is the boundary strip around the grid (Wilson and Anderson, 1985). We multiplied average annual densities by island area to estimate population size on the island for 1993 to 1998.

Densities on the Dry Lakebed grid in 1997 and 1998, and on the San Miguel Hill grid in 1998, were not estimated because we failed to capture adults. The island-wide population in 1999 was estimated using Chapman's modification of the Lincoln-Peterson estimator, applied to sightings of marked and unmarked foxes from 17 remote, automated camera stations operated variously from March to September 1999. Over this period, we accumulated a large sample using the cumulative sample estimator approach for sampling with replacement (Jaeger et al., 1991). In November 1998, we began radiocollaring island foxes to determine mortality sources (see below). The radiocollars were visible in the remote camera images, and the radiocollared foxes were thus a marked sample of the population. Because the number of marked foxes varied during the sampling period due to staggered entry into the radiotelemetry study, we used the mean number of marked animals for the estimator.

Because foxes are territorial and fundamentally monogamous (Crooks and Van Vuren, 1996; Roemer et al., 2001), we estimated pup productivity for 34 females in reproductive condition by assigning captured pups to females based on trap locations. We used program MARK (White and Burnham, 1999) to annually estimate apparent survival (the probability of recapturing an animal between encounter sessions) of adults and pups. Apparent survival does not account for emigration and might underestimate true survival (the probability of surviving between encounter sessions). Appropriate models were selected based on Akaike's Information

TABLE 1—Population and density estimates for island foxes (*Urocyon littoralis littoralis*) captured on 3 trapping grids, San Miguel Island, California, 1993 through 1998.

Grid/year	Popula- tion esti- mate			Model ^a	A(W) km ²	Density of foxes/km ²		95% CI
	Number of adults	mate	SE			SE		
Willow Canyon								
1993	26	28	3	M(bh)	3.59	7.8	0.8	6.2–9.4
1994	27	34	7	M(bh)	3.45	9.9	2.1	5.7–14.0
1995	28	34	4	M(h)	3.09	11.0	1.4	8.4–13.7
1996	13	17	4	M(h)	3.26	5.2	1.1	3.0–7.4
1997	10	12	3	M(h)	4.61	2.6	0.7	1.3–3.0
1998	4	5	2	M(o)	5.70	0.9 ^b		
San Miguel Hill								
1993	27	27	0	M(bh)	3.38	8.0	0.1	7.9–8.1
1994	27	27	0	M(bh)	3.34	8.1	0.1	7.8–8.4
1995	21	23	3	M(h)	3.40	6.8	1.0	4.9–8.6
1996	6	8	2	M(h)	4.67	1.7	0.4	1.0–2.5
1997	8	16	5	M(h)	5.70	2.8	0.9	1.0–4.6
1998	1							
Dry Lakebed								
1994	53	54	2	M(bh)	3.41	15.9	0.5	14.9–16.8
1995	14	21	5	M(h)	3.58	5.9	1.4	3.2–8.6
1996	2	2	2	na	na	0.9	na	na
1997	0							
1998	0							

^a Refers to model used by program CAPTURE (White et al., 1982) to estimate population. M(o) = null model; M(h) = heterogeneous capture probability model; M(bh) = combination of behavior model and heterogeneous capture probability model. na = number of captures was too small to use CAPTURE; Chapman's modifier of the Lincoln-Peterson estimator (Lancia et al., 1996) was used instead.

^b With only 1 recapture, SE and CI could not be estimated.

Criterion value and likelihood ratio tests among competing models. With this ranking procedure, we tested survival models that included year and sex as variables for both adults and pups, and we identified the most parsimonious model as the one with the lowest Akaike's Information Criterion value.

To identify causes of mortality, we equipped 15 foxes with 50-g radiocollars with mortality sensors (Advanced Telemetry Systems, Isanti, Minnesota) from November 1998 to November 1999. Radiocolled foxes were monitored daily from time of capture until the mortality signal was detected, or until the animals were removed for captive breeding. Survival was estimated using the nonparametric Kaplan-Meier procedure with staggered entry (Pollock et al., 1989). Staff recorded the presence of raptors, and feathers found at fox kill sites were identified to species at the National Fish and Wildlife Forensics Laboratory, Ashland, Oregon.

Necropsies of fox carcasses were performed at the Veterinary Medical Teaching Hospital, University of California, Davis. Samples of all available organs were fixed in 10% buffered formalin, processed rou-

tinely for histopathology, and examined by a pathologist (LM). Parasites collected at necropsy were identified by light microscopy. Fecal samples were analyzed by sedimentation, floatation, and Baermann techniques, and all ova and larva identified. Blood smears were air-dried and stained with Diff-Quik stain (Baxter Scientific Products, McGaw Park, Illinois) and examined by light microscopy for microfilaria and hemoparasites.

We evaluated differences in parameters among years with analysis of variance (ANOVA), chi-square analysis, or, for count data, nonparametric Kruskal-Wallis tests (SYSTAT 7.0, SPSS Inc., Chicago, Illinois). Significance levels were set at 0.05 for all tests.

RESULTS—We captured 300 individuals a total of 919 times. Overall, density on each grid declined (Table 1) and island-wide estimates of adults fell from near 450 in 1994 to fewer than 20 in 1999 (Fig. 2). During the remote camera study in 1999, we recorded 231 images of foxes, of which 93 were marked. Because the av-

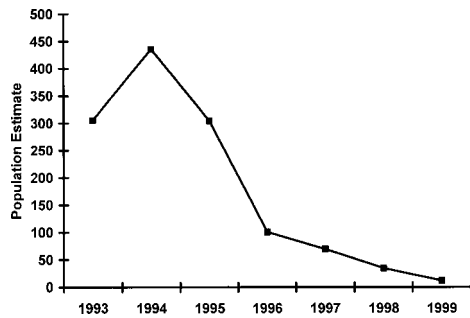


FIG. 2—Island-wide population estimates for adult island foxes, San Miguel Island, 1993 through 1999. Reproduced, with revision, from Coonan et al. (2002), with permission from the Santa Barbara Museum of Natural History.

erage number of marked animals in the field at any one time was 5.5, the population estimate for 1999 was 14 foxes. This estimate was corroborated by capture efforts for a captive breeding program in 1999. From May to December 1999, National Park Service staff captured 14 island foxes on San Miguel Island, with only 1 radiocollared fox known to remain on the island.

The most parsimonious model for survival of both adults and pups included time (year) as a factor, but not sex. Apparent annual survival of adults declined from near 1.00 in 1993–1994 to approximately 0.30 for the remainder of the study (Fig. 3). Pup survival was lower than adult survival in all years, and fell to 0 from 1997 to 1998 (Fig. 3).

Overall, the proportion of juvenile and adult females that bred, as indicated by signs of lactation, was 42.8% (54/126). The proportion of breeding females was independent of year ($\chi^2 = 7.297$, $df = 4$, $P = 0.199$), but age class was associated with the proportion of females that bred ($\chi^2 = 21.502$, $df = 3$, $P < 0.001$). Only 19% of young adult females bred, whereas 60% of all other adult females bred.

The number of pups on each grid generally decreased over the study period (Fig. 4). Numbers of pups per reproductive female ranged from 1 to 4, and the mean pup production of 2.0 ($n = 34$, $SE = 0.9$) did not differ by age class (Kruskal-Wallis test statistic = 3.539, $P = 0.316$). Mean pups per reproductive female differed by year (Kruskal-Wallis test statistic = 11.769, $P = 0.019$) but did not decline over time.

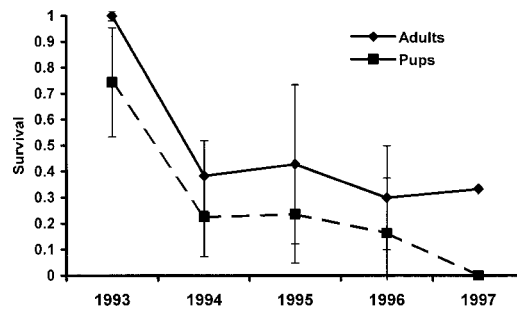


FIG. 3—Annual estimates of apparent survival, with 95% confidence intervals, for adult and pup island foxes on San Miguel Island, 1993 through 1997. Survival estimates were generated from program MARK (White and Burnham, 1997). Reproduced, with revision, from Coonan et al. (2002), with permission from the Santa Barbara Museum of Natural History.

Of the 15 radiocollared foxes, 8 were females and all but 3 were yearlings. Over the study period, 7 of the collared foxes died, including 6 yearlings, and 7 were brought into captivity. The Kaplan-Meier survivorship estimate for the 12-mo period was 0.120 ($SE = 0.063$). Five of the 7 carcasses had been fed upon extensively and eviscerated by the time of carcass retrieval, and in 2 of the 5, predation was determined to be antemortem because of hemorrhages associated with the wounds. The absence of visceral organs and advanced post-mortem decomposition prevented us from determining whether disease was a mortality factor.

The condition of all 5 scavenged carcasses

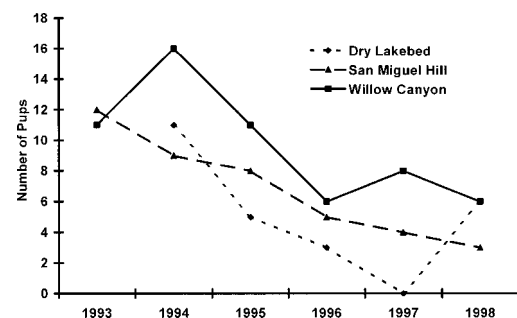


FIG. 4—Total number of island fox pups captured on each of 3 trapping grids, San Miguel Island, 1993 through 1998. Reproduced, with revision, from Coonan et al. (2002), with permission from the Santa Barbara Museum of Natural History.

suggested predation by a large raptor, such as a golden eagle (e.g., degloving of skin on limbs), and feathers found at 2 of the sites were identified as golden eagle feathers (P. Trail, United States Fish and Wildlife Service, pers. comm.). Furthermore, despite continual researcher presence on the study site for daily monitoring of telemetered foxes, golden eagles were observed only during the time of suspected eagle predation.

The 2 dead foxes with intact carcasses were emaciated and extensively parasitized by *Uncinaria stenocephala* and *Angiocaulus gubernaculatum* (S. Patton, University of Tennessee, pers. comm.; W. Boyce, University of California, Davis, pers. comm.). *Angiocaulus* is a pathogenic nematode not found in foxes on Santa Rosa, Santa Cruz, Santa Catalina, San Clemente, and San Nicolas islands (Faulkner et al., 2001; L. Munson, University of California, Davis, unpubl. data; S. Patton, University of Tennessee, unpubl. data). The foxes also had colonic granulomas from *Spirocerca* and small intestinal *Mesocostoides*. One fox died from aspiration pneumonia secondary to obstruction of the esophagus and stomach by a large trichobezoar (a dense mass of undigested fur), and showed extensive chronic pulmonary damage from nematode larval granulomas (presumed *Angiocaulus*). The other fox died from head and leg traumas and agonal aspiration pneumonia, most likely due to a fall from a cliff. This fox also had lesions of acute stress (lymphocytolysis), chronic debility (mycotic glossitis and emaciation), and evidence of trauma to the brain.

DISCUSSION—Over a short period of time, the island fox population on San Miguel Island declined to a level (15 animals) at which population persistence is problematic, if not unlikely. Although other populations of island foxes have fluctuated over time, the range of the decline on San Miguel Island was greater than that reported for other populations. Within-grid adult density on San Miguel Island varied from 8.0 to 15.9 foxes/km², whereas densities varied approximately 2 to 3 foxes/km² on 4 grids over a 6-year period on San Clemente Island, and approximately 6 foxes/km² on 1 grid over a 2-year period on Santa Catalina Island (Roemer et al., 1994). The decline on San Miguel Island occurred at the

same time as a documented decline on Santa Cruz Island and an apparent decline on Santa Rosa Island (Roemer et al., 2001). Over the study period, trap success (number of fox captures per number of trap nights × 100) on San Miguel Island fell from 40% in 1994 to less than 2% in 1999.

Predation by golden eagles seemed to be the primary mortality factor for radiocollared foxes. Golden eagle predation also was identified as the primary mortality factor for island foxes on Santa Cruz Island, and has likely caused the population declines on all 3 northern islands (Roemer et al., 2001). Red-tailed hawks (*Buteo jamaicensis*) breed on San Miguel Island and are known to prey upon juvenile island foxes on other islands (Laughrin, 1977), but golden eagles are the only known predator of adult island foxes (Roemer, 1999).

Golden eagles never bred historically on the northern Channel Islands, but the first sightings were recorded on Santa Cruz Island in the mid 1980s, at which time expanding mainland eagle populations began producing sufficient young to colonize the islands (B. Latta, University of California, Santa Cruz, pers. comm.). Golden eagles currently breeding and roosting on Santa Cruz Island are supported by feral pigs (Roemer et al., 2002).

The apparently strong influence of predation on a canid population is not without precedent. Predation is an important mortality factor for other fox populations (Ralls and White, 1995; Sovada et al., 1998; Olson and Lindzey, 2002), and golden eagles prey on canids in other areas of their range (Watson, 1997; Ellis et al., 1999). Island foxes on the northern Channel Islands might be especially vulnerable to raptors because they are more diurnal than other canids (Laughrin, 1977; Crooks and Van Vuren, 1995), and because historic sheep grazing has converted island shrub to alien annual grasslands (Hochberg et al., 1979), which offer less cover from aerial predators. Other possible sources of mortality include poor nutrition due to decreased prey availability, parasites, and viral diseases.

Declines in prey availability can drive population dynamics of other fox species, both those tied to a single prey source (MacPherson, 1969; Zabel and Taggart, 1989; White and Ralls, 1993) and those that are generalist predators (Root and Payne, 1985). The island

fox is a generalist omnivore, and prey selection changes seasonally according to availability (Moore and Collins, 1995). We studied island foxes during a period of wet winters, and prey availability probably did not decline over the period (T. Coonan, National Park Service, unpubl. data). Deer mice (*Peromyscus maniculatus*), which are an important food item for San Miguel Island foxes (Collins and Laughrin, 1979), increased over the study period (Coonan et al., 2002) from 400 mice/ha to as many as 1,000 mice/ha in 1999.

Recorded weights of island foxes captured during annual summer monitoring did not decline over time (T. Coonan, National Park Service, unpubl. data), further indication that nutrition was probably not a factor in the decline. Moreover, there was no association between body weight and death for 16 radiocollared foxes on Santa Cruz Island (Roemer, 1999), and the 14 island foxes brought into captivity on San Miguel Island in 1999 were all in good physical condition (T. Coonan, National Park Service, unpubl. data). Four of 7 carcasses recovered during telemetry were emaciated, but emaciation might be due more to parasites than to inadequate nutrition.

The poor body condition and heavy parasitism of 2 carcasses recovered during this period of low population density and abundant food sources suggests that parasites affected individual health. *Angiocaulus* infection in 2 of the predated foxes might have predisposed them to predation. The intravascular and pulmonary nematode, *Angiocaulus*, found in the San Miguel population is not normally found in canids (Faulkner et al., 2001). The tissue damage from the larvae of *Angiocaulus*, as well as from the infestations by *Spirocerca*, might have caused debility and contributed to the 2 deaths. Moreover, the extensive infestation of *U. stenocephala* in the 2 foxes might have contributed to their poor health. *Uncinaria stenocephala* can occasionally cause emaciation, weakness, hypoproteinemia, and coma in canids (Soulsby, 1982). However, it is usually non-pathogenic (Georgi and Georgi, 1991) and does not seem to impact the health of captive island foxes (S. Patton, University of Tennessee, pers. comm.).

Although other effects of *Angiocaulus* infections are unknown at this time, the extensive damage to the lungs of 1 fox is typical of an

aberrant host-parasite relationship. It is not known why San Miguel foxes, but not other island foxes, are infested with *Angiocaulus*. Superinfections with *Angiocaulus* might have occurred if the intermediate hosts (snails or slugs) were more plentiful or became the preferred food source during climatic changes. *Uncinaria* superinfections also could occur if contaminated dens were reused for kit rearing. Of the 28 adult foxes currently in captivity, 12 are infected with *Angiocaulus* and all are infected with *Uncinaria* (S. Patton, University of Tennessee, unpubl. data). These foxes are under observation for clinical signs, and a panel of experts currently is investigating effects of parasites on individual fox health and possible mitigating measures.

High seroprevalence to heartworm (*Dirofilaria immitis*) antigen has been found in island fox populations on the northern Channel Islands, but no adult *Dirofilaria* or microfilaria were found in 3 necropsied San Miguel Island foxes, and dirofilariasis cannot account for massive declines across all age classes (Roemer et al., 2000). Furthermore, no *Dirofilaria* has been found in >150 island foxes necropsied to date from other islands (L. Munson, University of California, Davis, unpubl. data).

Although viral diseases, such as canine distemper virus, can be important mortality factors (Nicholson and Hill, 1984), necropsy of island foxes in this study did not reveal any evidence of viral disease. However, viral disease cannot be ruled out as a mortality factor during the decline, because fox carcasses or tissue samples were not available during the initial phase of the decline.

Implications for Recovery—The flat reproductive rate displayed by island foxes throughout the study period has implications for captive breeding as a recovery action. Generally, fox populations respond to changes in prey availability by increasing the proportion of breeding females or the number of pups produced (White and Ralls, 1993). Although vertebrate food availability (deer mice) increased over the study period (Coonan et al., 2002), pup production on San Miguel was low and did not increase as the population declined. The proportion of females that bred did not increase, and breeding success for young adult females remained low throughout the study. During the same time period, the average number of

pups per reproductive female was lower for island foxes on Santa Cruz Island (1.73) and San Clemente Island (0.35), than in this study (2.00) (Roemer, 1999). On Santa Cruz Island, island fox fertility decreased over time, most likely due to a reduction in mate availability or disruption of pair bonds following death of 1 member of a pair (Roemer, 1999). The lack of response to low fox density and high prey availability of the population on San Miguel suggests that recovery on San Miguel Island will be slow, if reproductive success cannot be increased.

Alternatively, predation by golden eagles might have prevented the San Miguel Island fox population from increasing reproductive effort and success as densities declined. Predation could have affected reproduction if adult males were killed during the period when males provision the female and young (Garcelon et al., 1999), if pregnant females or females with young were killed, or if young were killed prior to our annual trapping sessions.

The demographic consequences of small population size (Lande, 1988) indicate that the extremely small number of adults on San Miguel Island decreases the probability of this population persisting over time. If island fox populations on the northern Channel Islands are to recover to viable levels, sources of mortality need to be minimized, and fox populations need to increase. The National Park Service began implementing recovery actions for island foxes on the northern Channel Islands in 1999. These actions included captive breeding of island foxes on San Miguel and Santa Rosa islands, and relocation of golden eagles from the northern Channel Islands to distant locations on the mainland.

Thirty-seven golden eagles were removed from 1999 to 2004, and as many as 8 eagles remained as of August 2004 (B. Latta, Santa Cruz Predatory Bird Research Group, unpubl. data). The remaining eagles still are visiting significant predation upon island foxes on Santa Cruz Island (D. Garcelon, Institute for Wildlife Studies, unpubl. data). Even a handful of eagles can cause or maintain a substantial fox decline (Roemer et al., 2002). However, if eagles are successfully removed, the high annual survivorship in the first year of this study (Fig.

3) suggests there would be few other sources of mortality for a recovering population.

Because of the critically low final wild population size (15 adults) and low reproductive success, even at low densities, removal of golden eagles alone does not guarantee recovery of the San Miguel Island fox population to a viable level. Captive breeding is required to maximize reproductive potential of island foxes, minimize mortality factors, and increase the population to the point where it is self-sustaining. Persistence of San Miguel Island foxes now hinges on an unprecedented removal program for golden eagles and on a captive breeding program for a species that has never before been bred in captivity, and for which there are a small number of founders.

The study was funded by the National Park Service, Channel Islands National Park; Canon USA Inc. (through its Expedition into the Parks program); the Institute for Wildlife Studies; and the Wildlife Health Center, University of California at Davis. Some results of this study were presented by Coonan et al. (2002) in a non-refereed symposium proceedings, and are reproduced here with permission from the Santa Barbara Museum of Natural History. Assistance in fieldwork was provided by G. Austin, H. David, J. Goldzman, J. Howarth, K. Rutz, and M. Willett. K. Rutz conducted the telemetry fieldwork. We thank W. Boyce, C. Faulkner, and S. Patton for identification of parasites, E. Buckles and M. Willett for assistance with necropsies, and P. Trail for identification of raptor feathers. The Spanish translation of the abstract was provided by T. S. Coonan. The manuscript was improved considerably by the critique of 2 anonymous reviewers.

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Submitted 30 August 2002. Accepted 15 July 2004.
Associate Editor was Cheri A. Jones.