

# Wild Furbearer Management and Conservation in North America



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CHAPTER 30: ISLAND FOX



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## ACKNOWLEDGEMENTS

We thank the numerous entities and individuals that helped with the success of this project, including chapter authors and reviewers, financial supporters, in-kind supporters, and all others that contributed. We also thank Milan Novak, James A. Baker, Martyn E. Obbard, and Bruce Malloch, editors of the 1987 book by the same title. Their achievement set the bar very high.

This project was financially supported by Alberta Conservation Association, Alberta Trappers Association, Association of Fish and Wildlife Agencies, Colorado Trappers and Predator Hunters Association, Fur Takers of America, Government of Saskatchewan Ministry of Environment Fish and Wildlife Development Fund, Illinois Department of Natural Resources (State Furbearer Fund Grant Program), Iowa Trappers Association, National Wildlife Control Operators Association, North Carolina Trappers Association, U.S. Fish and Wildlife Service, Vermont Trappers Association, Wildlife Ecology Institute, Wisconsin Department of Natural Resources, Wisconsin Trappers Association, and Fred Fouse. We thank you for your financial support.

We are grateful for the in-kind support provided by Alan Sinner (Alan Sinner Photography; numerous wildlife images), and Jay Villemarette and Josh Villemarette (Skulls Unlimited International; images of skulls for each furbearing species). We also thank Tom Walker (illustrations of each furbearing species); Jamie McFadden (Wildlife Ecology Institute; construction and revision of distribution maps for each furbearing species based on available information and input from chapter authors); James Baker and Pierre Canac-Marquis (Fur Institute of Canada; furbearer harvest data from Canada); and Jeff Bowman, Martyn Obbard (Emeritus), and Peter Carter (Ontario Ministry of Natural Resources and Forestry) for providing background information and assistance associated with the 1987 book of the same title.

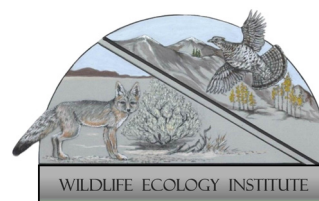


This project was funded by a Multistate Conservation Grant F19AP00097, a program funded from the Wildlife and Sport Fish Restoration Program, and jointly managed by the U.S. Fish and Wildlife Service and the Association of Fish and Wildlife Agencies.



STATE FURBEARER FUND

This project has received educational grant funding support from the Illinois Department of Natural Resources - State Furbearer Fund. The Furbearer Fund provides grants to appropriate not-for-profit organizations, governmental entities, educational institutions, and corporations to benefit furbearing mammals and improve furbearer hunting and trapping opportunities.



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## CHAPTER 30: ISLAND FOX

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*Citation:*

Coonan, T. J. 2024. Island fox. Pages 30.1–30.15 in T. L. Hiller, R. D. Applegate, R. D. Bluett, S. N. Frey, E. M. Gese, and J. F. Organ, editors. Wild furbearer management and conservation in North America. Wildlife Ecology Institute, Helena, Montana, USA. <https://doi.org/10.59438/NPJA5305>

First edition published 2024  
by Wildlife Ecology Institute  
PO Box 4725, Helena, Montana 59604-4725, USA  
web page: [www.wildlifeecology.org](http://www.wildlifeecology.org)

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Chapter 30: Island Fox

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<https://doi.org/10.59438/NPJA5305>

Published 12 June 2024.

Front cover image of an island fox (*Urocyon littoralis*) courtesy of National Park Service, USA.

Color species illustration by Tom Walker, Hardin, Iowa, USA.

Typesetting by Tim L. Hiller, Wildlife Ecology Institute, Helena, Montana, USA.



# 30

## ISLAND FOX

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Island foxes (*Urocyon littoralis*) are one of the smallest and most geographically restricted of the canid species, occurring only on the 6 largest of the 8 Channel Islands in California, USA. Each of the 6 islands is occupied by a distinct subspecies: San Clemente Island fox (*Urocyon littoralis clementae*), San Miguel Island fox (*Urocyon littoralis littoralis*), San Nicholas Island fox (*Urocyon littoralis dickeyi*), Santa Catalina Island fox (*Urocyon littoralis catalinae*), Santa Cruz Island fox (*Urocyon littoralis santacruzae*), and Santa Rosa Island fox (*Urocyon littoralis santarosae*).

Island foxes are a diminutive relative of the gray fox (*Urocyon cinereoargenteus*) in mainland North America, from which they evolved <10,000 years ago, and exist in small populations of 300–3,000 individuals. Their insular evolution renders them vulnerable to diseases and parasites, and also to predation by novel predators. During the 1990s, island foxes declined to near extinction on the northern Channel Islands due to predation by golden eagles (*Aquila chrysaetos*) and on Santa Catalina Island due to canine distemper virus (CDV). Island foxes on 4 islands were listed as endangered under the U.S. Endangered Species Act (ESA) in 2004, and became the subjects of intense recovery actions, including captive breeding and reintroduction efforts, capture and relocation of golden eagles, and vaccination against CDV and rabies. Endangered subspecies of island foxes subsequently recovered and were either delisted or downlisted in 2016, marking the quickest recovery of a mammal in the history of the ESA. Still vulnerable to disease, predation, and the effects of climate change, populations of island foxes currently continue to be intensively monitored to assess cause-specific mortality and population trends.

### DESCRIPTION

Island foxes are 12–17% (females) and 14–18% (males) smaller than gray foxes (Collins 1982). A thorough physical description of the species was provided in Moore and Collins (1995). The island fox is similar in appearance to the gray fox (see Prange and Fritzell 2025 [Chapter 29]), with mixed grayish-white and black dorsal coloration and generally dull white on the ventral side (Fig. 30.1). The sides of the neck and limbs, as well as the base of the ears, are cinnamon-

rufous. The tail is somewhat short, with a black dorsal stripe and rust coloration underneath. Males are somewhat larger than females. During 2007–2014, body weight of adult males on San Miguel Island ranged from 2.2 to 2.6 kg (4.9–5.7 lb), whereas weights of adult females ranged from 1.9 to 2.4 kg (4.2–5.3 lb; Coonan et al. 2015). The dental formula for island foxes is  $I = 3/3$ ,  $C = 1/1$ ,  $P = 4/4$ ,  $M = 2/3$ , for a total of 42 teeth (Fig. 30.2).

Foxes from different islands were first recognized as different taxa by Merriam (1903), and the current designation as 6 subspecies of *Urocyon littoralis* was proposed by Grinnell et al. (1937), and is supported by more recent genetic and morphometric research (Gilbert et al. 1990, Collins 1993, Wayne et al. 1991, Goldstein et al. 1999). The 6 subspecies differ in body size, nasal shape and projection, and the number of vertebrae in the tail (Collins 1982). Tails of island foxes on San Miguel Island are shortest, with 15 caudal vertebrae compared to 19 caudal vertebrae for foxes on San Clemente, Santa Cruz, and Santa Rosa islands; 21 vertebrae for foxes on Santa Catalina Island; and 22 vertebrae for foxes on San Nicolas Island.



Fig. 30.1. Coloration of island foxes (*Urocyon littoralis*) is mixed grayish-white and black (dorsal), dull white (ventral), and cinnamon-rufous (base of ears, sides of neck and limbs). Image courtesy of T. Coonan, National Park Service, USA.



Fig. 30.2. Skull characteristics of the island fox (*Urocyon littoralis*), Channel Islands, California, USA. Image courtesy of Skulls Unlimited International, USA.

Cranial measurements alone can be used to identify the subspecies (Collins 1982, 1993). Foxes on Santa Cruz Island are smallest, whereas foxes on San Miguel and Santa Catalina islands are largest. Isolation, small population size, and the relatively low number of elapsed generations since founding contribute to the low morphological and genetic variability in the island fox compared to that in the gray fox (Wayne et al. 1991). Similarly, there is less phenetic variation in island foxes on the smaller islands (i.e., San Miguel and San Nicolas) than on the larger islands.

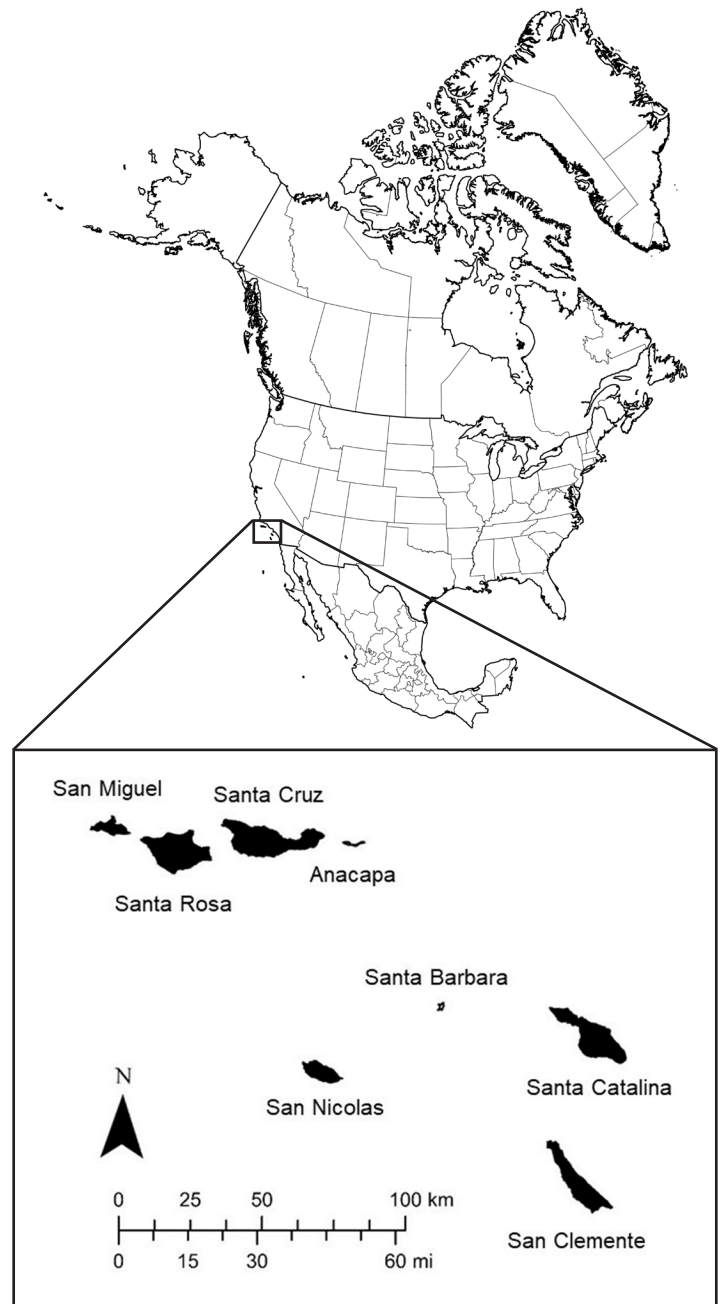


Fig. 30.3. Estimated current geographic distribution of island foxes (*Urocyon littoralis*) is the 6 largest of 8 Channel Islands, California, USA. Based on information modified from U.S. Geological Survey (2018).

## DISTRIBUTION

Island foxes occur only on the 6 largest of the 8 Channel Islands in California, with a different subspecies recognized on each island (Moore and Collins 1995; Fig. 30.3). Their current and historical geographic distributions are identical, and they are not known to have occurred anywhere else. Islands on which foxes occur are small, and range in size from 38 km<sup>2</sup> (15 mi<sup>2</sup>; San Miguel Island) to 250 km<sup>2</sup> (97 mi<sup>2</sup>; Santa Cruz Island).

Island foxes have a relatively short evolutionary history, and may have evolved as recently as 6,000–10,000 years ago (Rick et al. 2009, Hofman et al. 2015). Following their relatively recent arrival to the Channel Islands, island foxes rapidly differentiated into the 6 currently recognized subspecies, one on each island where the species occurs (Rick et al. 2009, Coonan et al. 2010, Hofman et al. 2015, Funk et al. 2016). The fossil record for island foxes is scant, comprising only 4 localities on the islands. Recent accelerator-mass spectrometry and radiocarbon dating indicate that no known bones of island foxes are older than 6,500 years (Rick et al. 2009). Humans colonized the northern Channel Islands  $\geq 13,000$  years ago, and the recent dates of fossil bones of island foxes suggest that foxes may have been introduced to the northern islands by Indigenous peoples between about 7,000 and 10,000 years ago (Rick et al. 2009). Foxes had previously been thought to colonize the islands at the end of the Pleistocene, before the arrival of humans, by opportunistic overwater dispersal of gray foxes from mainland North America (Wayne et al. 1991). The more recent dates of fossils of island foxes make that less probable. Island foxes were likely introduced to the 3 southern islands of San Clemente, San Nicolas, and Santa Catalina by the Chumash and Tongva peoples (summarized in Coonan et al. 2010). Recent genetic studies support a colonization 7,000–10,000 years ago, and rapid divergence into the 6 subspecies that are currently recognized (Hofman et al. 2015, Funk et al. 2016).

## LIFE HISTORY

### Reproduction

Breeding behavior of island foxes (summarized in Coonan et al. 2010) is now well-established, based on recent studies of both captive and wild foxes. The onset of pair formation occurs during late winter, with physical mating occurring in late February and early March. Parturition occurs in late April or early May, and 5–6 weeks later, pups emerge from the den. The male, separated from the female and pups until birth, provides food to them at the den, and forages with the family group throughout the first summer of the pups. Pups are weaned by mid-summer and family groups forage together, with pups still highly dependent on adults for food. There is evidence for this from annual population monitoring of island foxes, which documented adults leaving deer mice (*Peromyscus maniculatus*) near pups captured in box traps (Garcelon et al. 1999). By fall, juveniles are similar in size to adults, forage on their own, and may either disperse or remain in some portion of their natal territory (Roemer et al. 2001a).

Research on captive island foxes has elucidated some factors which influence their reproduction (Asa 2010, Coonan et al. 2010). Across all islands and population densities, as well as in captivity, the mean number of pups weaned in a litter is about 2.0. First-year females can reproduce, though not as successfully as older females (Roemer et al. 2001a, Coonan et al. 2005). Data from all populations of island foxes indicate that population growth increases as population density decreases (Bakker et al. 2009), and conversely, reproductive effort (as represented by number of pups weaned in a litter) declined on San Miguel and Santa Rosa islands as populations increased during recovery (Coonan et al. 2015).

Island foxes are monestrous, but unlike other canids, they display induced estrus and induced ovulation (Asa et al. 2007, Asa 2010). Hormone profiles (estrogen and progesterone) in captive females indicated that the presence of a male was required to induce estrus, perhaps an adaptation for the less social and somewhat secretive behaviors of island foxes. Video monitoring in captive-breeding facilities revealed substantial aggression in mated pairs, sometimes to the point of injury, and mortality of pups occurred due to unknown factors. Possible causes included pre-term abortion, full-term stillbirth, or neonatal death, which could have been due to parental neglect or infanticide. A bout of mastitis was also a source of mortality for pups in captivity (Asa 2010).

### Mortality

The substantial population decline of 4 subspecies of the island fox during the 1990s led to extensive research which identified causes of mortality for their populations on all 6 islands (Coonan et al. 2010). The most important causes to date have been predation by golden eagles on the northern Channel Islands (Roemer et al. 2001a, Coonan et al. 2005), and CDV on Santa Catalina Island (Timm et al. 2009, Munson 2010). In both cases, populations of island foxes declined nearly to extinction and became the subject of extensive, and successful, population-recovery efforts (Coonan et al. 2010). Both sources of mortality were the direct or indirect result of anthropogenic influences. Impacts of golden eagles on island foxes were a case of hyperpredation, in which golden eagles, which had not bred on the Channel Islands prior to the 1990s, successfully colonized the islands due to the presence of a non-native ungulate prey base (feral pigs [*Sus scrofa*] on Santa Cruz Island, mule deer [*Odocoileus hemionus*] on Santa Rosa Island; Roemer et al. 2001a, 2002; Coonan et al. 2010). CDV was introduced to Santa Catalina Island by northern raccoons (*Procyon lotor*) that were accidentally transported from the mainland, and the virus spread rapidly throughout the population of island foxes during 1999–2000 (Coonan et al. 2010, Munson 2010).

Comprehensive population monitoring of island foxes began during the 1990s, and provided information about other causes of mortality (Table 30.1). The more important of these include ceruminous gland carcinomas (ear tumors) on Santa Catalina Island (Munson 2010, Moriarty et al. 2015, Vickers et al. 2015), vehicle strikes on those southern islands with paved roads (Munson 2010), and emaciation related to drought and parasites on San Miguel Island (Coonan et al. 2005, Munson 2010, Coonan et al. 2015).

## ECOLOGY

### Habitat

The generalist nature of the island fox and its relatively few natural predators allow the species to utilize all land-cover types on the islands, which include chaparral, coastal scrub, exotic grass and fennel monocultures, riparian areas, sand dunes, sandy beaches, and woodlands (Laughrin 1977, Moore and Collins 1995, Roemer et al. 2001a, Drake et al. 2015, Page et al. 2021). Island foxes may exhibit less selectivity in habitat at their typically high population densities (see below), and more selectivity at low

Table 30.1. Primary sources of mortality for island foxes (*Urocyon littoralis*), and the islands for which each source has been documented, Channel Islands, California, USA.

Mortality source	Island(s)	Source
Amyloidosis	San Clemente	Munson 2010
Canine distemper virus	Santa Catalina	Timm et al. 2009, Coonan et al. 2010, Munson 2010
Ceruminous gland carcinoma (ear tumor)	Santa Catalina	Munson 2010, Moriarty et al. 2015, Vickers et al. 2015
Emaciation	San Miguel	Coonan et al. 2015
Intraspecific aggression	All islands	Munson 2010
Parasites		
Acanthocephalans	San Miguel	Coonan et al. 2015
<i>Angiocaulus</i>	San Miguel	Coonan et al. 2005, Munson 2010
<i>Spirocerca</i>	San Miguel, San Nicolas, Santa Rosa, Santa Cruz	Coonan et al. 2005, Munson 2010
<i>Uncinaria</i>	San Miguel	Coonan et al. 2005, Munson 2010
Pneumoconiosis (black lung)	San Clemente	Munson 2010, Maestas et al. 2017
Poisoning via rodenticide	San Clemente	Munson 2010, Maestas et al. 2017
Predation via golden eagles ( <i>Aquila chrysaetos</i> )	San Miguel, Santa Cruz, Santa Rosa	Roemer et al. 2001a, Coonan et al. 2005, Coonan et al. 2010
Vehicle strikes	San Clemente, San Nicolas	Munson 2010

population densities (Drake et al. 2015). Roemer (1999) found that island foxes on Santa Cruz Island were most abundant in woodland and shrub communities, and also that foxes avoided exotic annual grasslands, possibly due to the high density of low-growing vegetation (Roemer and Wayne 2003). On Santa Rosa Island, in a low-density population during recovery, male foxes selected for valley bottoms overall and for bare areas and grasslands at night (Drake et al. 2015).

### Population Density and Dynamics

Population densities and dynamics of island foxes have been studied extensively since the 1990s and through the period of population decline and recovery, resulting in a good understanding of their populations (summarized in Coonan et al. 2010). Application of standardized mark-capture methodology across all islands since the 1990s yielded comparable estimates of population abundance and density. Typical population densities for the species are in the range of 4–15 adults/km<sup>2</sup> (10–39/mi<sup>2</sup>). Under certain conditions, island foxes can exist at relatively high population densities (e.g., >20 adult foxes/km<sup>2</sup> [52/mi<sup>2</sup>]; Roemer et al. 1994, Bakker et al. 2009). These population densities, which are among the highest recorded for any canid species, are due to the limited spatial extent on the islands; relative abundance of resources; broad, omnivorous diet of the species; presence of few competitors; and relatively few sources of mortality expected to have population-level effects (Coonan et al. 2010).

Although population densities can be high for island foxes, the limited spatial extent of each island results in overall low population sizes, which range from several hundred individuals on the smaller islands (San Miguel and San Nicolas) to about 2,500 individuals on the larger islands (Santa Catalina, Santa Cruz, and Santa Rosa; Roemer et al. 1994, Bakker et al. 2009, Coonan et al. 2010, Coonan et al. 2014, King et al. 2014). The inherently low population sizes contribute to the vulnerability of their populations to stochastic extinction processes.

Population monitoring, which began in the late 1980s and continued through the period of population decline, led to a greater understanding of population dynamics and formed the basis for a comprehensive demographic modeling effort for island foxes (Bakker et al. 2009). The population viability analysis (PVA) revealed several drivers of population dynamics for this species, the most important of which was climate. The increase in annual precipitation due to periodic El-Niño events (El Niño-Southern Oscillation) promotes plant growth and higher populations of deer mice on the islands (Schwemm 2008). Bakker et al. (2009) found that precipitation associated with El Niño had delayed, positive effects, presumably through increased availability of resources, but also a negative effect on survival of pups on the northern islands, perhaps due to more inclement winter weather.

Bakker et al. (2009) also detected density-dependent effects. All populations of island foxes showed slower rates of population growth at higher population densities, but the effects differed by size of island. At low population densities, rates of population growth were higher on smaller islands, suggesting an Allee effect (Holsinger 2000) on the larger islands (i.e., foxes experience difficulty finding potential mates at low population densities on larger islands). Density-dependent effects are apparent from population monitoring as well. Reproductive effort on San Miguel Island, as estimated by the ratio of pups to adult females, was high at low population densities as the population began to recover, then declined as population density increased (Coonan et al. 2015).

Recent demographic research on the subspecies on San Nicolas Island, which had exhibited a stable, or perhaps declining, population, provided additional information about the roles of both climate and population density on population dynamics (Bakker et al. 2021). Reproduction of island foxes was found to depend on both previous level of precipitation (a positive effect) and previous population density (a negative effect). High levels of reproduction (number of pups/adult) was only observed in years following a relatively high amount of precipitation and lower population

density. Drought also directly affected survival, but only for older (i.e.,  $\geq 4$  yr) foxes; foxes 6 months to 3 years old had very high rates of survival. There was evidence of portfolio effects: foxes in different parts of the island and in different land-cover types had higher productivity (i.e., larger litters, higher population densities) in different years. This asynchrony buffers the overall population of the island during drought years, and probably holds for foxes on the largest and most florally diverse islands (Santa Catalina, Santa Cruz, and Santa Rosa).

Evidence from island fox monitoring program conducted by the National Park Service for San Miguel and Santa Rosa islands supports this understanding of population drivers for the island fox (Coonan et al. 2014, 2015; Dillon et al. 2021; T. Coonan, National Park Service [NPS], unpublished data). Foxes on both of these islands were absent from the wild during the captive-breeding period, which began during 1999–2000. Releases from captivity commenced during 2003–2004, and populations on both islands increased through a period which included 2 droughts (2007–2009, 2012–2016). The droughts had a greater effect on the population on San Miguel Island, which had increased rapidly to levels approaching, if not exceeding, ecological carrying capacity. Reproductive effort of island foxes on San Miguel Island decreased during both droughts, and survival decreased during the second drought. Body weights of foxes decreased, and there were more incidences of emaciation. These effects were not observed on the adjacent and larger Santa Rosa Island, where the population steadily increased over time, at lower overall population densities, and perhaps buffered by portfolio effects.

Since the 1990s, population dynamics of the island fox have been characterized by predation and disease-caused decline, followed by population increase due to effective recovery actions (Coonan et al. 2010, 2014, 2015; King et al. 2014). Population dynamics prior to the 1990s are generally unknown, or at least unquantified, but populations may have fluctuated markedly in their short history (Coonan et al. 2010). Anecdotal accounts incorrectly reported that island foxes were absent from Santa Cruz Island in 1940, and scarce on San Miguel Island during the 1930s following drought, scabies, and overgrazing by domestic sheep (*Ovis aries*). The population of foxes on San Nicolas Island are believed to have declined to <20 individuals during the 1970s (Kovach and Dow 1985), a decline supported by genetic evidence (Aguilar et al. 2004). Some of this apparent population fluctuation may have been due to periodic outbreak of CDV, or a related morbillivirus circulating in the populations (Clifford et al. 2006, Munson 2010).

## Space Use and Movements

Island foxes typically exist at high population densities, have high tolerance of conspecifics, and show low dispersal rates and no long-range immigration. Due to these aspects of their insular evolutions, as well as their small stature, island foxes have some of the smallest home-range sizes of any canid (Table 30.2). Estimated home-range sizes ranged from 0.5 to 2.0 km<sup>2</sup> (0.2–0.8 mi<sup>2</sup>; Crooks and Van Vuren 1996, Roemer et al. 2001a, Powers 2009, Sanchez 2012), except during a period of low population density for the recovering population on Santa Rosa Island, when home-range sizes of males were >3.0 km<sup>2</sup> (1.2 mi<sup>2</sup>; Drake et al. 2015).

Island foxes, unlike most other mammalian carnivores, are partially diurnal (Garcelon et al. 1991, Crooks 1994, Roemer 1999, Swarts et al. 2009), due to their evolution primarily in the absence of diurnal predators. There is some evidence that predation from golden eagles during the 1990s caused island foxes to temporally shift to somewhat more nocturnal patterns of activity (Swarts et al. 2009), although this shift did not reduce their risk of extinction (Hudgens and Garcelon 2011).

## Diseases and Parasites

As canids with a short, insular evolutionary history, island foxes have relatively little exposure to diseases and parasites from mainland North America, are pathogenically naïve, and are therefore vulnerable to pathogens introduced from the mainland. Indeed, CDV caused a substantial population decline of island foxes on Santa Catalina Island during 1999–2000 (Timm et al. 2009, Munson 2010), and disease is now considered the primary threat to recovered populations (U.S. Fish and Wildlife Service [USFWS] 2016), so much so that all subspecies of the island fox are vaccinated against CDV and rabies, and epidemic-response plans have been developed for each population (Coonan et al. 2014, King et al. 2014).

The substantial population declines of island foxes during the 1990s resulted in focused attention on the potential role of disease and parasites in these declines, and prompted a species-wide survey of pathogens, utilizing both necropsies of fox carcasses and serosurveys of blood samples collected from foxes during annual population-monitoring efforts (Clifford et al. 2006, Munson 2010). Results showed that island foxes had been exposed to a variety of pathogens, at least one (CDV) of which was an important cause of mortality on Santa Catalina Island (see Mortality section; Table 30.3). The fact that island foxes

Table 30.2. Estimates of home-range sizes for island foxes (*Urocyon littoralis*), Channel Islands, California, USA. MCP = minimum convex polygon.

Island	Year(s)	<i>n</i>	Home-range size (km <sup>2</sup> )	Estimation method	Source
San Clemente	2006–2007	29	0.75 (0.29 mi <sup>2</sup> )	95% Isopleth	Resnick 2012
	2010–2011	40	0.42 (0.16 mi <sup>2</sup> )	95% MCP	Sanchez 2012
San Nicolas	2005–2006	14	1.81 (0.70 mi <sup>2</sup> )	95% MCP	Powers 2009
Santa Catalina	2007–2008	17	1.05 (0.41 mi <sup>2</sup> )	95% MCP	King et al. 2014
Santa Cruz	1992	12	0.34 (0.13 mi <sup>2</sup> )	95% MCP	Crooks and Van Vuren 1996 Roemer et al. 2001a
	1993–1994	14	0.55 (0.21 mi <sup>2</sup> )	100% MCP	
Santa Rosa	2009–2010	11 <sup>a</sup>	3.39 (1.31 mi <sup>2</sup> )	95% MCP	Drake et al. 2015

<sup>a</sup>Males only.

Table 30.3. Distribution of primary pathogens associated with populations of island foxes (*Urocyon littoralis*), Channel Islands, California, USA. Based on information from Clifford et al. (2006), Namekata et al. (2009), and Munson (2010).

Pathogen	Island					
	San Clemente	San Miguel	Santa Catalina	Santa Cruz	Santa Rosa	San Nicolas
<i>Bartonella</i> spp.	X	X	X	X	X	X
Canine adenovirus	X	X		X	X	X
Canine coronavirus			X			
Canine distemper virus	X		X	X	X	X
Canine herpesvirus	X			X		
Canine parvovirus	X	X	X	X	X	X
<i>Leptospira</i> spp.	X		X	X	X	
<i>Toxoplasma gondii</i>	X		X	X	X	

showed seroprevalence to other diseases that are apparently not pathogenic suggests that island foxes themselves are hosts and the pathogens are endemic (Munson 2010). Alternatively, the clear pathogenicity of CDV in island foxes indicates that foxes have not evolved with that pathogen, or at least not with the strain that caused recent population declines. That pathogenic strain was likely introduced by northern raccoons to Santa Catalina Island. There is some evidence that a distemper-like morbillivirus circulates in populations of island foxes, without the presence of other hosts (Clifford et al. 2006).

Island foxes co-exist with few other carnivore species, which are nonetheless potential hosts of pathogens. Island spotted skunks (*Spilogale gracilis amphiala*) inhabit Santa Cruz and Santa Rosa islands. Santa Catalina Island has a sizable population of humans, and is the only island with domestic dogs and cats. Domestic cats were recently removed from San Nicolas Island (Campbell et al. 2011). Indigenous peoples introduced domestic dogs to the islands sometime after settlement, as early as 13,000 years ago (Rick et al. 2008), and thus domestic dogs may have been an early source of some pathogens for island foxes (Munson 2010). Dogs were also used on the islands during the ranching period.

The notable absence of rabies in populations of the island fox suggests that island foxes have never been exposed to it, and that rabies could result in high levels of mortality if introduced to the islands. Because of this, and the difficulty in modelling disease spread in their populations (Sanchez and Hudgens 2019), a portion of all of the populations of island foxes are vaccinated against rabies, and CDV, on an annual basis (Coonan et al. 2014, King et al. 2014).

As with viruses and protozoans, island foxes on different islands harbor different ectoparasites and endoparasites (Munson 2010, Harris et al. 2013). Several parasites have been identified as contributing to the mortality of island foxes, including *Angiocaulus*, *Uncinaria*, and *Spirocerca* (see Mortality section). Additionally, ear mites have been associated with ceruminous gland tumors on island foxes on Santa Catalina Island (Moriarty et al. 2015, Vickers et al. 2015). Further, the presence of mites on individual foxes has been associated with an altered microbial biome and *Staphylococcus* infection, suggesting that bacterial infections also contribute to inflammation and ceruminous gland tumors in Catalina foxes (DeCandia et al. 2019).

Amyloidosis, the deposition of protein deposits or plaques in organs, occurs at high levels in island foxes, particularly on San Clemente Island (Munson 2010, Gaffney et al. 2016). It is associated with high levels of serum amyloid A, and predisposing conditions include inflammation and chronic disease. Amyloidosis was more common in captive versus wild island foxes (Gaffney et al. 2016).

## FOOD HABITS

Food habits, similar to habitat use and activity patterns, of island foxes reflect the strong influence of its island environment: small geographic area, low diversity of vertebrates, and abundant food resources. Island foxes are omnivorous, similar to other members of the genus *Urocyon*, and their diet includes both plant and animal material (Moore and Collins 1995). The relative proportion of individual items of plant and animal materials in diets of the island fox changes throughout the year, according to abundance, and likely changes somewhat annually, due to climatic variation in availability of food resources from El Niño-Southern Oscillation cycles. Cypher et al. (2014a) conducted an extensive year-long, species-wide study of the diets of island foxes and found substantial variation among foxes on different islands; similarity among foxes on individual islands ranged from 20% to 70%. The variation reflects the difference in microclimates between the southern and northern islands, and the diversity in size of islands, topography, and vegetation communities. For example, toyon (*Heteromeles arbutifolia*) was the most common food item on the large and diverse Santa Catalina Island. Conversely, trees do not occur on the smaller San Miguel Island, where insects and deer mice were more common in diets of island foxes. Seasonally, deer mice may be more important during winter and spring, when foxes require high-energy food resources for reproduction (Coonan et al. 2010). Insects (e.g., beetles, crickets) are consumed when available, such as during emergence events (Roemer 1999).

Despite the diverse diet of island foxes and the general abundance of resources on the islands, recent information indicates that their energetic needs are not always met, especially during drought and when populations are dense (Coonan et al. 2015). An extended drought during 2012–2014 resulted in emaciation being an important source of mortality on San Miguel Island, where recovered populations were at high density. Body weights and index values for body condition of island foxes also declined during drought.

## BEHAVIOR

The social structure of island foxes is characterized by mated pairs that generally remain together until 1 member dies, although there is some extra-pair fertilization that occurs at territorial boundaries (Roemer 1999). Mated pairs occupy and maintain year-round territories, and there is little territorial overlap with adjacent pairs (Roemer et al. 2001*b*). Data from proximity dataloggers (Ralls et al. 2013) showed that contact rates between pair members was highest during February, when mating occurred, but also that paired females spent time with other males during estrus. Asynchronous estrus among females facilitated extra-pair copulations.

## GENETICS

Because island foxes exist at small population sizes and have evolved in an island setting over a relatively short time, their genetics has been of great interest and management concern. Extensive research on genetics began during the 1990s, utilizing protein electrophoresis, mitochondrial DNA, and microsatellites, and documented that island foxes have low or undetectable levels of genetic variation, some of the lowest levels recorded for any vertebrate species (Gilbert et al. 1990, Wayne et al. 1991, Goldstein et al. 1999). The low genetic variability is likely due to founder effects and frequent bottleneck events in their small and fluctuating populations. The low genetic variability of the subspecies on San Nicolas Island, which had apparently declined to <20 individuals during the 1970s (Kovach and Dow 1985), was especially notable. Foxes on San Nicolas Island had almost no variation at any of the markers studied. Subsequent research showed foxes on San Nicolas Island had significant genetic variation at the major histocompatibility genes, despite being monomorphic at 10 microsatellite genes; modeling confirmed a bottleneck event consistent with the population decline observed during the 1970s (Aguilar et al. 2004).

More recent studies have used genomic methods, which include whole genomes or numerous loci, to confirm the recent evolution, rapid divergence, and history of bottlenecks of this species. Island foxes apparently colonized the northern Channel Islands between 7,000 and 9,000 years ago, and then were transported to the southern islands (Hofman et al. 2015). Genetic and morphological divergence of their populations (the currently recognized 6 subspecies) occurred rapidly, in <2,000 years. Although there has been a history of bottlenecks, island foxes had multiple mitochondrial haplotypes. A separate genomic analysis of single nucleotide polymorphisms loci confirmed the extremely low genetic variation for the species, and identified genetic drift as the primary driver of genetic divergence among the subspecies, and between the species and the gray fox (Funk et al. 2016). The results were consistent with earlier concerns about the population on San Nicolas Island, and other small populations of island foxes, whereby their lack of genetic variation and small effective population sizes make them vulnerable to fixation of deleterious alleles, decreased fitness, and reduced adaptive potential.

The population declines of the 1990s exacerbated genetic concerns about the island fox. The small number of foxes left on the islands and subsequently brought into captivity (15 individuals from each of San Miguel and Santa Rosa islands) raised concerns about the small numbers of founders and possible effects of inbreeding (Coonan et al. 2010). Captive populations were therefore managed to preserve the genetic diversity remaining after the substantial (>90–95%) population declines. Genetic research determined relatedness of captive foxes, allowing pedigree charts to be constructed, and pairings were made to minimize relatedness between potential mates. A population-management plan for island foxes, or studbook, was created by the Association of Zoos and Aquariums to facilitate decisions about pairing, retention, and release into the wild.

The actual number of founders that bred in captivity on San Miguel and Santa Rosa islands was low (8 and 12 individuals, respectively), but comparable to other captive-breeding programs (Coonan et al. 2010). Captive foxes bred prolifically, leading to recovered populations of 500 to >1,000 in the wild (Coonan et al. 2014), and as of 2020, there had been no apparent negative effects of inbreeding in captive or wild populations. Although island foxes may have evolved to tolerate inbreeding (Wayne et al. 1991), concern remains regarding the genetic vulnerability of their populations, which exist at low abundance and have low genetic variability (Funk et al. 2016).

## MANAGEMENT AND CONSERVATION

### Sexing and Aging Techniques

Island foxes are aged according to tooth eruption and wear patterns on the first upper molar (Wood 1958, Roemer et al. 1994, Roemer 1999, Coonan et al. 2005, Hudgens et al. 2008, Hudgens and Garcelon 2010, Coonan et al. 2015). Foxes are assigned to discrete age classes: pups (age class 0), young adults (age class 1: ca. 7 mo–2 yr), adults (age class 2: ca. 2–4 yr), mature adults (age class 3: ca. 3–6 yr), and old adults (age class 4: >4 yr). Many studies have utilized known-age individuals (i.e., individuals captured as pups and permanently marked). Evaluation of tooth wear in known-age individuals has shown that there is substantial overlap among the age categories for tooth wear (Hudgens et al. 2008, Hudgens and Garcelon 2010).

### Population Monitoring and Survey Techniques

Population monitoring of island foxes has been ongoing since the 1980s, and has become standardized, a distinct advantage for conservation efforts. During the 1980s, NPS selected island foxes as an important element to monitor on San Miguel Island, as part of its long-term ecological-monitoring program for Channel Islands National Park (Fellers et al. 1988, Davis et al. 1994). NPS subsequently implemented monitoring methods that had been developed for island foxes on Santa Cruz Island (Roemer et al. 1994, Coonan et al. 1998). This standardized, grid-based method for population monitoring ultimately enabled estimation of population density and island-wide population size across

the distribution of the species. Initial efforts used arrays of large numbers (>40) of traps spaced 250 m (820 ft) apart and set for 6 consecutive nights. Population size and density were estimated using mark-recapture methods (White et al. 1982).

These methods detected the predation-caused population declines on the northern islands (Roemer et al. 2001b, Coonan et al. 2005) and precipitated the recovery actions implemented during the 1990s. Data derived from these methods formed the basis for a species-wide PVA for the species (Bakker et al. 2009), and the development of recovery criteria for endangered populations (Bakker and Doak 2009). For the latter, probabilities of extinction were estimated for combinations of population size and annual rates of mortality, with isoclines representing various levels of extinction risk for island foxes on each island. Three-year averages of population size and annual rates of mortality, both for adults, were derived from current monitoring efforts, and were then assessed to determine if those values would result in an acceptable level of extinction risk (identified by Bakker and Doak [2009] as  $\leq 5\%$  over 50 years; Fig. 30.4).

Refining these methods was a task identified by the Island Fox Recovery Team, and population-monitoring methods were subsequently improved to utilize advances in analysis (Rubin et al. 2007, Hudgens et al. 2015). An important change was a general shift from a small number of large grids to multiple smaller grids (i.e., mini-grids or ladder grids, so named for their ladder-like,  $2 \times 6$  configuration of traps; Fig. 30.5). For the larger grids, island-wide population density had been extrapolated from local grid densities, which used mark-recapture methods and estimates of

effective trapping area. The use of these methods with transect-shaped units results in difficulty yielding precise estimates of population density due to edge effects; therefore, the shift to smaller, multiple grids was used with spatially explicit capture-recapture methods, such as those in Program DENSITY to estimate population density at the island scale (Efford et al. 2004). These methods use animal movement and detection patterns (as opposed to estimates of effective trapping area), and model animal captures as a joint function of population density, detection and spatial scale (movement), parameters. The multiple smaller grids provided better spatial coverage of the island, and better representation of land-cover types. Recommended configurations for trapping arrays were developed for each island, based on characteristics of each island, including area, topography, and relative ease of access. Protocols were selected for each island considering trade-offs among access, effort, and precision of estimates, as indicated by coefficient of variation of parameters.

Estimating annual rates of mortality of adults has been critical for monitoring both population decline and population recovery, and is prescribed for all populations of island foxes as part of annual population-monitoring efforts (Roemer et al. 2001b; Coonan et al. 2005, 2010, 2014, 2015; Rubin et al. 2007, Bakker and Doak 2009, King et al. 2014). Estimates of annual rates of survival for island foxes are derived from aerial- or ground-based monitoring of radio-marked foxes with collars equipped with mortality sensors. Necropsies of fresh carcasses have resulted in identification of causes of mortality (Munson 2010), and estimates of annual rates of survival based on known-fate models.

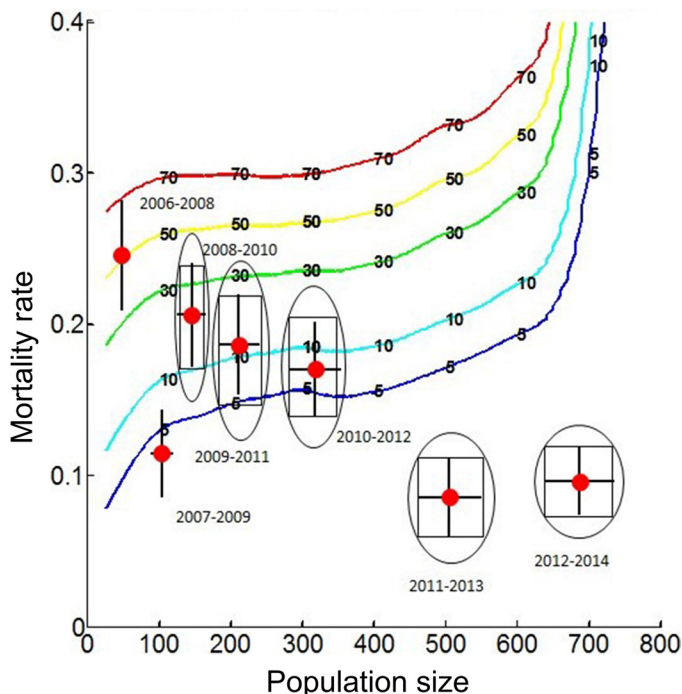


Fig. 30.4. Extinction risk for island foxes (*Urocyon littoralis santarosae*) on Santa Rosa Island, California, USA. Mortality rate population size are based on 3-year averages for adults during 2006–2014 (Coonan et al. 2015).

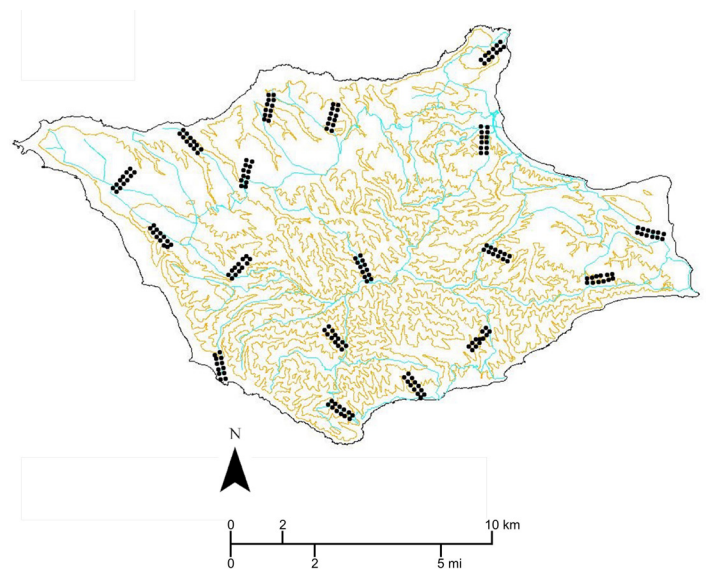


Fig. 30.5. Location of minigrids, or ladder grids, for estimating population density of island foxes (*Urocyon littoralis*) on Santa Rosa Island, California, USA (Coonan et al. 2015).

## Harvest

Island foxes have not been historically nor are currently harvested.

## Damage Management

Island foxes do not cause any economically substantial damage, although their docile behavior and rapid acclimation to humans can result in individual foxes becoming a nuisance in campgrounds and residential areas. Management actions to address this have focused on modifying behavior of humans, rather than management of foxes. Fox-proof garbage containers have been installed on Santa Catalina Island, and NPS installed fox-proof food lockers on Santa Cruz Island to prevent island foxes from raiding food stores of campers (Coonan et al. 2010, 2015; King et al. 2014).

The only instance of island foxes being managed to mitigate damage occurred on San Clemente Island, where they (as well as domestic cats) were identified as important predators of nests of the endangered San Clemente shrike (*Lanius ludovicianus mearnsi*). Management actions implemented by the U.S. Navy included lethal removal of island foxes, which was controversial (Roemer and Wayne 2003). As a result, the program of lethal removal of foxes, in which 15 island foxes were killed, shifted to a program of live capture and removal of island foxes, and use of electrical-shock collars to prevent foxes from approaching nests (Cooper et al. 2005). The program of live removal of foxes resulted in 14 individuals being relocated to zoo facilities on the mainland in 1999 (Coonan et al. 2010).

## Capture and Handling

Island foxes are relatively easy to handle compared to other carnivore species. Island foxes are successfully captured in box-type traps (as opposed to snares or padded-jaw foothold traps), and can be handled without chemical immobilization due to their relatively docile nature, not unlike other species of foxes (Roemer et al. 1994, Coonan et al. 2010; e.g., Peek et al. 2024 [Chapter 34]; Fig. 30.6). Traps are typically covered with burlap, baited with dry cat food and an olfactory lure, and fitted with a polyethylene tube to minimize tooth damage via chewing.

## Marking

For population monitoring, island foxes have been permanently marked with ear-tags and passive integrated transponder (PIT) tags. More intensive research has been accomplished with very high frequency (VHF) collars, and more recently with global positioning system (GPS) and proximity logger collars. Grid-based population monitoring during the 1990s initially utilized plastic ear tags (Roemer et al. 1994, Coonan et al. 2005), which caused occasional but minor damage to ears and occasional loss of tags. The availability of PIT tags obviated those problems, and so PIT tags are currently used for permanent marking of island foxes (Coonan et al. 2010, 2014, 2015; King et al. 2014). PIT tags are inserted subcutaneously between the shoulder blades.

VHF collars affixed with mortality sensors have been used on island foxes to collect data on causes and rates of mortality since the 1990s (Roemer 1999; Roemer et al. 2001a; Coonan et al. 2005, 2014;

King et al. 2014). As of 2024, all 6 subspecies of the island fox were being monitored annually for cause-specific mortality through the use of VHF collars affixed with mortality sensors, aerial- and ground-based telemetry, and necropsies of carcasses. A sample of  $\geq 40$  radiomarked foxes, none of which are vaccinated so that diseases can be detected, are maintained on each island.

VHF collars have also been used to evaluate habitat use and other ecological aspects of island foxes (Crooks and Van Vuren 1995, 1996; Roemer 1999; Roemer et al. 2001b). More recent studies on island foxes have used GPS collars to investigate island-level habitat selection and space use (Cypher et al. 2014b, Drake et al. 2015). Proximity dataloggers were used on San Clemente and San Miguel islands to infer social relationships among foxes (Ralls et al. 2013). Cypher et al. (2014a) reviewed the performance of GPS collars and proximity loggers in island fox studies, and provided recommendations for their use.

## Conservation

Island foxes have been the subject of much conservation concern since the population declines of the 1990s, resulting in federal listing of several subspecies, development of recovery actions and a recovery plan, implementation of recovery actions, and eventual population recovery and federal delisting or downlisting of subspecies. An organized and cooperative conservation effort preceded and succeeded the recovery process. One result is consensus, clear guidance, and standardization of monitoring populations and threats, which may continue into the foreseeable future given the inherently small populations and vulnerability of this species.



Fig. 30.6. As with several other species of foxes, island foxes (*Urocyon littoralis*) can be handled without chemical immobilization for radio-collaring and basic collection of data. Image courtesy of National Park Service, USA.

All 6 subspecies of the island fox were listed as threatened by the State of California in 1987 (California Department of Fish and Game 1987). In 2004, 4 of the 6 subspecies were federally listed as endangered by USFWS under the federal ESA (USFWS 2004). The northern subspecies (populations on San Miguel, Santa Rosa, and Santa Cruz islands) were federally listed due to population declines caused by predation from golden eagles. Island foxes on Santa Catalina Island were federally listed because of a population decline likely due to CDV. The species is currently listed as Near Threatened on the Red List of the International Union for Conservation of Nature (Coonan et al. 2013).

Although 4 subspecies were federally listed as endangered in 2004, concern about populations of island foxes prompted development and implementation of recovery actions prior to 2004. Discovery of predation-caused population declines on San Miguel and Santa Cruz islands prompted NPS to convene a team of experts in 1999 to assess the situation and recommend population-recovery actions. That team continued meeting annually and became the Island Fox Conservation Working Group, a cooperative conservation effort comprising landowners; representatives from management agencies, universities, zoos, and nonprofit organizations; and subject-matter experts as needed (Coonan et al. 2010). In its >25-year existence, the team has provided expertise and recommendations to land-management agencies for recovery actions, was assumed into an official recovery team by USFWS, and contributed substantially to the recovery plan for the island fox, especially technical portions, published in 2012 (USFWS 2012).

Implementation of recovery actions began in 1999 with captive breeding of island foxes, capture and removal of golden eagles, and development of a vaccine against CDV (Coonan et al. 2010). Captive breeding occurred on San Miguel, Santa Catalina, Santa Cruz, and Santa Rosa islands. Although very few foxes remained in the wild as a source for captive breeding (15 each on San Miguel and Santa Rosa islands), foxes bred successfully in captivity. Releases to the wild began in 2003, reintroduced foxes successfully bred and survived, and all captive-breeding efforts concluded, and facilities closed, by 2008. More than 250 island foxes were released to the wild from captivity.

Removal of golden eagles began in 1999 with their capture by bow-net trapping (Coonan et al. 2010). Most of the  $\geq 40$  eagles relocated from the Channel Islands were captured via bow-net, although some eaglets were hand-captured at nests, and the last adult pair was removed via net-gun capture near their nest in 2006. All captured eagles were released in northeastern California, and the first 12 eagles captured were also monitored via satellite telemetry, which confirmed that none returned to the Channel Islands, nor to southern California in general.

The removal of golden eagles increased rates of survival for island foxes released to the wild, and populations of all 4 endangered subspecies subsequently increased in abundance. By 2014, the population size of adults ranged from >500 foxes on San Miguel Island to 1,000–2,000 foxes on Santa Catalina, Santa Cruz, and Santa Rosa islands. All 4 federally listed subspecies met the criteria for delisting, which had been developed through the species-

wide PVA (Bakker and Doak 2009, Bakker et al. 2009). Those criteria required each listed subspecies to have  $\leq 5\%$  probability of extinction in the next 50 years, based on estimates of population size and rates of adult mortality, and to have threat-mitigation plans in place. Subsequently, in 2016, USFWS delisted the 3 northern subspecies and downlisted the subspecies on Santa Catalina Island from endangered to threatened (USFWS 2016). The subspecies on Santa Catalina Island was downlisted, rather than delisted, because of the continued threat of disease transmission from domestic dogs and cats to island foxes on that island.

One of the most valuable outcomes of the 20-year cooperative conservation effort for island foxes was development, refinement, and consensus on population goals, conservation measures and methods, and annual monitoring for the species. Recovery goals were developed through population viability management (PVM; Bakker and Doak 2009) in which simulation of alternative management actions, based on monitoring, was incorporated into PVA to inform goal setting and allow for adaptive management. The recovery criteria for federally listed island foxes were developed directly during the PVM effort, which also included modeling the level of annual effort necessary to accurately monitor populations and avoid substantial population losses in the future.

Although federally listed subspecies of the island fox were biologically recovered by 2016, USFWS required management agencies to commit to annual monitoring, and to mitigation of threats detected by monitoring, before delisting could occur. For example, prior to delisting, NPS signed a conservation agreement with USFWS (USFWS and NPS 2015), and NPS committed to: 1) implement long-term monitoring of population status and trend, in order to annually estimate the risk of extinction, using the methods developed by Bakker and Doak (2009); 2) continue to collect carcasses of radio-marked foxes, monitoring for mortality via predation at an interval frequently enough to detect a predation rate from golden eagles of 5% over 3 years for each subspecies as per Bakker et al. (2009), in order to reduce the potential for future substantial declines in population abundance due to predation; 3) continue CDV and rabies vaccinations of a portion of each population of island foxes annually to reduce the potential for future substantial declines in population abundance due to disease outbreaks; and 4) in the event that monitoring detects rates of mortality due to disease or predation which exceed predetermined thresholds, implement the appropriate response prescribed in the epidemic-response plan or eagle-management plan.

To fulfill the conditions outlined above, epidemic-response plans (e.g., Hudgens et al. 2013) were developed for each Channel Island, and simulation of detecting and preventing the spread of rabies and CDV (Sanchez and Hudgens 2020) indicated optimal frequency and intensity of sentinel monitoring that would reduce the time to disease detection and minimize percentage of the population infected. A golden eagle management strategy was developed for the northern islands (NPS 2016). The federal-delisting effort established the primacy and importance of annual monitoring for population trend and cause-specific mortality, and the land-management agencies will be implementing such into the foreseeable future.

The recently documented impacts (decreased reproduction, increased mortality) of drought on the population on San Miguel Island underscore the vulnerability of their populations, particularly the smaller populations on San Miguel and San Nicolas islands, to climate change, as periods of drought are expected to increase in frequency and intensity in the future (Diffenbaugh et al. 2015). Although island foxes may not be a conservation-reliant species in the sense that their persistence requires continual management (Scott et al. 2005), their inherently small population sizes and vulnerability to sources of mortality that can have population-level effects, such as disease and predation, as well as to the yet unknown effects of climate change, underscore the need for annual monitoring, perhaps in perpetuity.

### Research Needs

The substantial declines in population abundance during the 1990s prompted a flurry of research aimed at identifying and mitigating the causes of the decline, and developing and refining recovery actions. Investigations included reproductive biology and the problem of low rates of survival for pups in captivity (Asa 2010, Ralls et al. 2013), disease and parasites (Clifford et al. 2006, Munson 2010, Harris et al. 2013, Sanchez and Hudgens 2019), ecology and resource utilization (Cypher et al. 2014a,b; Drake et al. 2015), influence of predation on activity patterns (Swarts et al. 2009, Hudgens and Garcelon 2011), genetics (Aguilar et al. 2004, Hofman et al. 2015, Funk et al. 2016), and population viability and recovery goals (Bakker and Doak 2009, Bakker et al. 2009).

Research needs have also been identified annually by the Island Fox Conservation Working Group. Annual meeting reports include summaries of subgroup work, such as the veterinary group and the wild-population group, on conservation and management issues associated with island foxes, including the need for future research. Recent meetings of the group (Coonan 2014, 2015) have identified several research needs as described below.

#### *Acanthocephalan on San Miguel Island*

A novel acanthocephalan parasite has been recorded during necropsies of island foxes on San Miguel Island since 2012. The parasite, recently identified as *Pachysentis canicola*, causes peritonitis and perforation of the intestine and is associated with emaciation. Parasitic loads and prevalence of acanthocephalans can be quite high in infected individuals. Research is required to identify the host of the parasite, to determine whether it is native or introduced, to determine its impact on foxes at both the individual and population level, and to investigate whether treatment is warranted and feasible.

#### *Vaccine Trials*

Island foxes have been vaccinated against CDV since 2000, with a Canary Pox virus recombinant vaccine (Purevax Ferret Distemper Vaccine, Merial Limited, Duluth, Georgia, USA). Field trials and vaccination have shown that the vaccine poses no harm to island foxes, and produces an antibody response. However, it remains

unclear whether the vaccine provides protection from the virus. Thus, a vaccine-challenge study is needed, in which island foxes, or a closely related species (e.g., gray foxes), are challenged with exposure to the virus after vaccination.

#### *Potential Inbreeding in Island Foxes*

Although there are no clinical or morphological signs of inbreeding in island foxes, recent genetic research indicates substantial loss of genetic diversity as well as low effective population size in island foxes, particularly those on San Nicolas Island. This could lead to inbreeding depression, the inability to adapt to climate change, or other changes. Therefore, a study is required to investigate possible inbreeding depression by assessing genetics and fitness in individual foxes.

### ACKNOWLEDGMENTS

This chapter benefited greatly from review by David Garcelon and Brian Hudgens of the Institute for Wildlife Studies, and from review and assistance provided by Brian Cypher of California State University, Stanislaus Endangered Species Recovery Program. Thanks also to Deana Clifford of the California Department of Fish and Wildlife, Wildlife Health Lab, for pointing me in this direction and giving me encouragement, and to Tim Hiller for insightful review and patience.

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