1 · *Introduction*

To the hiker it was a subtle change to the landscape, but nearly overwhelming in its implications. On the trail were small fox tracks, simple footprints made casually as the animal walked, probably quickly but not necessarily in a hurry. Animals often use human trails to conserve energy while traveling, so the observation of the prints was not in itself surprising. It was the simple existence of the tracks that made the hiker stop, look around, and smile inwardly at the thought; island foxes were again roaming the wilderness of San Miguel Island.

Island foxes are a unique species of small carnivore that live only on the Channel Islands located off the coast of Southern California in the United States of America. The California Channel Islands consist of eight islands, four in the northern group and four in the southern group. Of the eight, three in the north – Santa Cruz, Santa Rosa, and San Miguel – and three in the south – San Nicolas, San Clemente, and Santa Catalina – support populations of island foxes, and on each island a unique subspecies has evolved:

- San Miguel Island fox: *Urocyon littoralis littoralis*;
- Santa Rosa Island fox: *Urocyon littoralis santarosae*;
- Santa Cruz Island fox: *Urocyon littoralis santacruzae*;
- San Nicolas Island fox: *Urocyon littoralis dickeyi*;
- Santa Catalina Island fox: *Urocyon littoralis catalinae*;
- San Clemente Island fox: *Urocyon littoralis clementae*.

San Miguel and Santa Rosa Islands are managed by the National Park Service (NPS), Santa Cruz is co-managed by the National Park Service and The Nature Conservancy, Santa Catalina is managed by the Catalina Island Conservancy, and San Nicolas and San Clemente are managed by the US Navy (Fig. 1.1).

As recently as 1990, populations of island foxes were considered stable. Fox populations on each island were naturally small and varied in relation to island size, but reproduction and survival were high, and observed

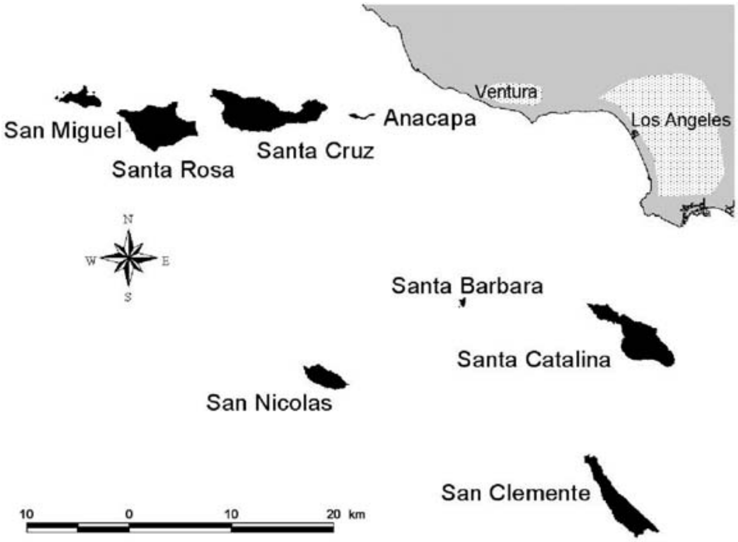

Figure 1.1 The eight California Channel Islands. A separate island fox subspecies occurs on each of the six largest islands (thus, on every island but Anacapa and Santa Barbara).

densities greater than for almost any other North American carnivore. Management efforts were limited to annual population monitoring, and research was directed at basic ecological and biological questions such as food habits, reproductive behavior and social structure. The insular habitats that support island foxes were assumed to be nearly as protected from human impacts as is possible on Earth today.

Then, within a second of evolutionary time, the status of four of the six island fox populations went from stable to perilous. Annual survival rates dropped from over 80% to less than 40%, and managers and scientists struggled to determine the causes of fox deaths at the same time as they worked to protect those remaining. Population declines were so rapid that within four years of the initial observations of downward trends there were 15 remaining wild foxes on each of the two smaller islands, and on the larger islands the wild populations had declined to 10–20% of historic levels.

A combination of directed research, focused management, and the collaborative efforts of many people determined that there were two primary but unrelated factors causing island fox mortalities: predation by non-native golden eagles on Santa Cruz, Santa Rosa, and San Miguel

Islands, and canine distemper virus on Santa Catalina Island. Although ecologically unrelated, both impacts were the result of human activities, which brought novel threats to historically isolated populations. The obstacles to rapid implementation of emergency recovery actions included lack of funding, gaps in the knowledge of island fox biology and the nature of the threats, and the fact that the species was not officially recognized as Endangered. The future of all four populations depended on the coincident success of two primary recovery strategies.

First, the remaining foxes had to be protected from disease and predation and the populations grown. Captive breeding programs for endangered mammals generally require years to develop, and under the best of circumstances are biologically challenging and expensive. Island fox managers had to facilitate breeding quickly before the remaining adults were unable to breed, while addressing a myriad of genetic and disease issues that required a separate captive program on each island. Second, the population-level threats had to be eliminated; unless fox populations were ultimately free from predation and disease, even the most successful captive breeding program would not produce enough animals to support self-sustaining wild populations.

In response, managers and scientists embarked on three unprecedented efforts. Island foxes had never been vaccinated against any disease, and on Santa Catalina veterinarians worked for two years to test and ultimately administer a canine distemper vaccine that now protects all island fox populations. On the northern islands a golden eagle removal program was established to relocate all of the eagles from the islands. This effort proved to be immensely challenging and at times controversial, but ultimately over 40 birds were trapped and removed. Finally, discouraging future golden eagle utilization of the islands required a reversal of the ecological changes that had led to golden eagle colonization. The separate tasks of feral pig (prey) removal and bald eagle (competitor) reintroduction were undertaken to tip the ecological balance in favor of long-term persistence of island fox populations and resilient island ecosystems.

Cumulatively these efforts were successful, and island foxes are now recovered or close to recovery on all of the Channel Islands. Feral pigs are gone and reintroduced bald eagles have started breeding, and vaccination and monitoring programs will hopefully protect island foxes from future disease outbreaks. Island fox recovery efforts included large-scale ecosystem manipulation, animal translocations, captive breeding and disease prevention, and required the expertise and commitment of hundreds of professionals and volunteers over nearly a decade.

The purpose of this book is threefold. The island fox is a unique and fascinating creature, and we present here the first comprehensive description of the evolution, biology, genetics, behavior, and ecology of this species. The presentation of this information poses some challenges, as much of what is now known about island fox biology was attained as a direct result of recovery efforts. Specifically, we present the chapters on disease and reproductive biology after the chapters that describe applied recovery actions because most of this information was gained through the research efforts of L. Munson and C. Asa and their colleagues in response to specific recovery needs. Second, we summarize the chronology of the population declines and the resulting recovery actions, including initial research efforts, the contribution of long-term monitoring, and the veterinary, husbandry, and education efforts, all of which were critical to success in island fox recovery.

Finally, we place the story of island foxes into a larger conservation context and attempt to answer several questions: How did a species that lives only on protected islands come to be in danger of imminent extinction? What combination of factors most facilitated island fox recovery? And what has been learned from the island fox experience that can assist in future ecosystem recovery efforts, preserve the unique ecosystems of the California Channel Islands, and prevent future extinctions? Cumulatively we hope this book will help define the daunting challenges of conserving biodiversity in an increasingly interconnected world, and the importance and urgency of protecting remaining species and natural systems.

As the hiker walked on there were more tracks, but eventually the evidence of the fox's presence disappeared from the trail. At some point it had moved off to the grasslands or down into the canyon, or was perhaps resting under a nearby shrub. But wherever it was, the hiker knew, was exactly where it was supposed to be.

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2 · *Evolution and genetics*

The island fox is a recently and rapidly evolved species that is smaller than its mainland ancestor, the gray fox (*Urocyon cinereoargenteus*). Examination of the evolution and current genetic status of island foxes illustrates the vagaries of dispersal to islands, the influences on evolution in island settings, and the challenges of conservation for small, genetically depauperate populations. Although the fossil history is scant, the archeological record indicates a species with a close relationship to Native Americans who transported foxes to the southern islands and may be responsible for their introduction to all the Channel Islands. Extensive morphologic and genetic studies – in conjunction with the islands' geologic history (sea level rise and island separation) – have established a pattern of island colonization and the genetic and physical basis for description of the six island fox subspecies. Island fox populations have relatively little genetic variability, due to naturally small population sizes and historic fluctuations that have resulted in population bottlenecks. The precarious genetic status of island foxes has consequences for both the management of captive populations and long-term population viability.

2.1 Description

The island fox (Fig. 2.1) was first described as *Vulpes littoralis* by Spencer F. Baird in 1857 from the type locality on San Miguel Island (Baird 1857). Baird was the assistant secretary of the Smithsonian Institution, and examined zoological specimens brought back by the US Army's topographical engineers who had been tasked with surveying a route for a transcontinental railroad. Baird's report also included descriptions of specimens collected from San Miguel Island and other Pacific localities by a Lieutenant William P. Trowbridge, who was conducting tidal observations at San Miguel Island in January 1856 for the US Coast and Geodetic Survey. Baird was the first of many to compare the size of the diminutive island fox to a house cat. His description (Baird 1857, p. 143)

Figure 2.1 Island fox, San Miguel Island, 1994. Courtesy of National Park Service.

noted both the tame behavior of island foxes and their morphological similarity to the gray fox, and correctly suggested that the short tail was due to one missing vertebra:

This very curious fox, the smallest of all the North American species, was brought by Lieut. Trowbridge from the island of San Miguel, on the coast of California, where quite a number of specimens were seen. It is stated by Lieut. Trowbridge to be very tame, scarcely taking the trouble to get out of the way, and when escaped from a trap, returning directly to the same place. His men found no difficulty in outrunning these foxes in a fair race, although it is possible, that owing to their unusual tameness, their full powers were not exerted.

The species is a miniature of the common gray fox of the United States, and so closely like it in external appearance as to induce the belief of it possibly being a local race. Gray foxes from the main land of California, are, however, of full size, and there are some differences of importance in the skull and teeth. As is well known, also, many species of foxes of different regions resemble each other so closely that it is very difficult to separate them – more closely, indeed, than the present fox and the common gray species.

The *Vulpes littoralis* is scarcely more than half the size of the common gray fox, in length and height, in fact, exceeded by some common house cats. The body, however, is considerably stouter than the house cat. The limbs are short, slender and weak. The tail in the specimen before me is very short, not more than one-third the length of the head and body. It has probably lost some of the terminal vertebra at an early age, although the tip is now covered with hair. Two living specimens in captivity are said by Lieut. Trowbridge to possess this same brevity of tail.

Foxes from different islands were first recognized as separate taxa by Merriam (1903), who reclassified the island fox into the genus *Urocyon* and described foxes from Santa Catalina and San Clemente Islands as separate species (*Urocyon catalinae* and *Urocyon clementae*), while recognizing Santa Cruz foxes as a subspecies (*santacruzae*) of *Urocyon littoralis*. The species' current designation as six subspecies of *Urocyon littoralis* was proposed by Grinnell *et al.* (1937) and has been corroborated by recent genetic and morphometric work (Gilbert *et al.* 1990, Wayne *et al.* 1991b, Collins 1993, Goldstein *et al.* 1999).

Morphologically, the six subspecies differ in such features as body size, nasal shape and projection, and the number of tail vertebrae, and the subspecies can be correctly identified based solely on cranial characters and measurements (Collins 1982, 1993). Santa Catalina foxes are the largest, followed by San Miguel foxes, and the smallest are found on Santa Cruz. The tails of San Miguel foxes are considerably shorter than those of the other subspecies, averaging 15 caudal vertebrae compared to 19 to 22 for the other islands (Collins 1982). However, due to isolation, small population size, and the relatively low number of elapsed generations since founding, island foxes display less morphological and genetic variability than mainland gray foxes (Wayne *et al.* 1991b).

2.2 Dwarfism and the island syndrome

Island fox evolution illustrates both the phenomenon of dwarfism, wherein island species are sometimes smaller than the mainland progenitor from which they originated, as well as the 'island syndrome', general changes in various life history characteristics due to selection pressures unique to island environments (Foster 1964, Van Valen 1973). Compared to the mainland gray fox, male island foxes are on average 14–18% and females 12–17% smaller (Collins 1982). Although selection for small body size in island foxes was originally thought to have resulted from the predominance of smaller-sized foods (insects, seeds, fruits, berries, and deer mice) on the islands (Collins 1982), it is more likely that resource limitations on islands select for small body size (Lawlor 1982). Resource limitation and competitive release may explain changes

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in body size among insular mammals (Lomolino 1985, Demetrius 2000), although it is possible that such changes are simply random (Meiri *et al.* 2004).

One of the most spectacular cases of island dwarfism also occurred on the Channel Islands. The dwarf or pygmy mammoth (*Mammuthus exilis*; Roth 1993, Agenbroad 2002, Agenbroad *et al.* 2005) was one-third the size of its mainland ancestor, the Columbian mammoth (*M. columbi*), and occurred on the Channel Islands during the Pleistocene, from about 47,000 years before present (BP) to about 13,000 BP. Conversely, a trend toward gigantism in insular rodents is illustrated by the extinct giant island deer mouse (*Peromyscus nesodytes*) and giant vole (*Microtus miguelensis*) of the Channel Islands (Guthrie 1993). Gigantism in island rodents may be due to reduced seed-size variability, which selects for larger body size among generalist seed predators in the more homogenous environments of the islands (Foster 1964, Lawlor 1982).

2.3 Evolution of the island fox

Although the scant fossil history of island foxes places them only as far back as the early Holocene epoch (12,000 years ago to present; Rick *et al.* 2009), island fox evolution is marked by the rapid differentiation from its mainland ancestor into the six subspecies recognized today. Despite the sparse fossil record, evidence from the archeological record, geologic history, and genetic studies provide evidence of the pattern and rate of colonization. However, significant questions remain regarding the exact mechanism of the initial arrival of gray foxes on the islands, and the means by which foxes later dispersed to all of the Channel Islands.

2.3.1 Colonization of the islands

Only four fossil localities (three on San Miguel and one on Santa Rosa) are known to contain samples of fox bones (see Rick *et al.* 2009). An island fox fossil was reported by Orr (1968, as reported in Moore and Collins 1995) from a stratified Pleistocene locality in the Upper Tecolote Formation on Santa Rosa Island. Based on dates Orr obtained from radiocarbon (^{14}C) dating of associated materials, the specimen was originally estimated to be between 12,000 and 18,000 years old. This date range for the earliest appearance of the fully dwarfed island fox species was used in several reconstructions of the fox's evolutionary history (Gilbert *et al.* 1990, Wayne *et al.* 1991a, 1991b, Goldstein *et al.* 1999), all of which assume colonization of the islands by foxes around 16,000 BP. However, recent accelerator-mass spectrometry (AMS) dating of the original specimen put its date at about 1,400 BP, and subsequent ^{14}C dating of three additional island fox bones collected from the surface of possible Pleistocene fossil localities on San Miguel Island suggest that none are older than about 6,500 BP (Rick *et al.* 2009). Because humans colonized the northern Channel Islands at least 13,000 years ago, Rick *et al.* (2009) suggest that the new dates for island foxes may indicate that Native Americans introduced foxes to the northern islands, possibly between about 7,000 and 10,000 BP. The difference in dates for colonization of the islands, although small, has enormous ramifications for the likely method of dispersal of gray foxes to the islands.

Until recently, fox colonization of the islands was assumed to have occurred by chance overwater dispersal, whereby one or more gray foxes arrived on the northern islands via rafting on floating debris (Collins 1982, 1993, Wayne *et al.* 1991b). Current distances between the mainland and the northern islands range from 20–90 km, but sea levels were as much as 100–125 m lower during the last glacial maximum of the Ice Age (~20,000 BP). During this time the northern islands, which were never connected to the mainland, coalesced into a larger island now referred to as Santarosae (Fig. 2.2), which was separated from the mainland by as little as 6–10 km (Wenner and Johnson 1980). A likely source for vegetation debris upon which gray foxes could have floated to the islands are two large rivers, the Ventura and the Santa Clara, which flow into the Pacific Ocean from the western transverse mountain ranges of Southern California. During periodic El Niño-driven winter storms, debris from the rivers can wash far out to sea, occasionally ending up on the north-facing shorelines of the northern Channel Islands (Inman and Jenkins 1999).

However, the lack of fossil evidence of island foxes on the islands prior to the arrival of humans suggests that foxes could have been intentionally introduced to the northern islands by Native Americans (Rick *et al.* 2009). Native American ancestors of the historic Chumash and Tongva (Gabrielino) peoples arrived on the northern islands by 13,000 BP (Table 2.1). Exploiting the rich marine environments, the early island inhabitants engaged in shellfish harvesting, kelp-bed fishing, and hunting marine mammals (Johnson *et al.* 2002, Erlandson *et al.* 2005). Early peoples introduced domestic dogs (*Canis familaris*) to the islands, and it is possible that they introduced foxes from the mainland to the islands as well (Rick *et al.* 2009). Still, the presence of only small-sized

Table 2.1 *Timeline of events in evolutionary history of island foxes.*

Epoch	Years BP[a]	Event
Pleistocene	> 20,000	Existence of superisland Santarosae
	16,000	Possible arrival of foxes from mainland, by natural dispersal (rafting)
	15,000	
	14,000	
	13,000	Arrival of humans on the Channel Islands
	12,000	Separation of Santa Cruz from superisland
Holocene	11,000	
	10,000	Separation of San Miguel from Santa Rosa
	9,000	
	8,000	
	7,000	
	6,000	Earliest fossil remains of island foxes (San Miguel); Earliest archeological remains of island foxes on the southern Channel Islands

[a] BP = before present

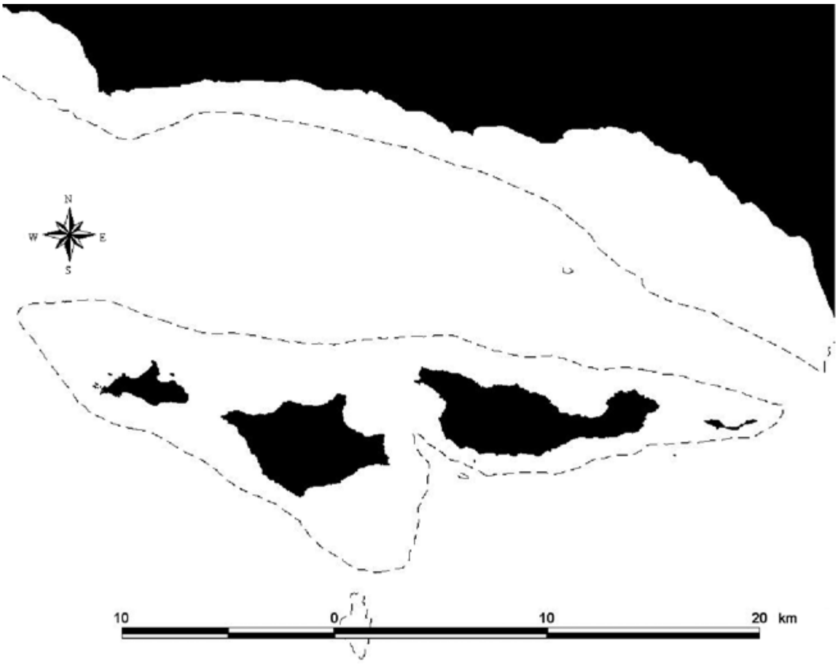

Figure 2.2 Current sea level and shorelines (in black), compared with those in the late Pleistocene, when the current northern Channel Islands were coalesced into a superisland, Santarosae.