

CHAPTER 9

Island foxes

The evolution, behavioural ecology, and conservation of island foxes

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A yearling, male Santa Cruz island fox just *Urocyon littoralis santacruzae* prior to dispersal © G. Roemer.

The island fox is (*Urocyon littoralis*) endemic to the California Channel Islands, a continental archipelago located off the coast of the southwestern United States. A descendent of the mainland gray fox (*U. cinereo argenteus*), it is hypothesized that island foxes first colonized the three northern Channel Islands (Santa Cruz, Santa Rosa, and San Miguel) by chance over-water dispersal. Native Americans then transported foxes from these islands to three southern Channel Islands (Santa Catalina, San Clemente, and San Nicolas). Each island fox population is

currently recognized as a distinct subspecies, and both the hypothesized colonization scheme and the current taxonomic classification are supported by morphological and genetic evidence.

An insular existence has had a profound influence on the evolution, ecology, and genetic structure of island foxes. A dwarf form of the gray fox, island foxes are the smallest canid in North America. Compared to mainland canids of similar size, island foxes have shorter dispersal distances (mean = 1.39 km, SD = 1.26, range = 0.16–3.58 km, $n = 8$),

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a smaller average home range size (mean annual home range = 0.55 km^2 , $SD = 0.2$, $n = 14$) and higher population densities ($2.4\text{--}15.9 \text{ foxes/km}^2$). Although they are distributed as socially monogamous pairs, island foxes are not completely monogamous. Extra-pair fertilizations (EPFs) accounted for 25% of all offspring whose parents were determined through paternity analysis. This relatively high rate of EPFs may be related to high population density and the proximity of suitable partners other than social mates. Finally, the genetic gradient among fox populations appears steeper than mainland populations suggesting that smaller dispersal distances on islands result in increased population structure.

An insular existence coupled with small population size may have also increased the vulnerability of the island fox to extinction. Over the past decade, five of the six subspecies have declined and two are extinct in the wild. Factors contributing to these declines include predation by golden eagles (*Aquila chrysaetos*), the introduction of canine distemper virus and predator control efforts aimed at controlling foxes to protect an endangered bird. A multifaceted conservation strategy that includes the live-capture and removal of golden eagles, the vaccination of foxes against canine distemper virus, the eradication of feral herbivores and the captive propagation of island foxes is currently underway to avert the impending extinction of this endemic canid.

Introduction

The bow sliced through the calm waters of the bay and then quietly slid to a stop on the gently sloping beach. Limú was glad the journey was half over. The crossing from Santa Cruz Island to this sheltered bay at the west end of Santa Catalina Island had been rough. The swells were half as tall as his *tamal* was long, and more than once he had felt they would lose their cargo. Their safety was critical to the success of his trading effort. He was sure they would fetch a handsome price, perhaps a few steatite bowls, soapstone cookware coveted by all the tribes of the Channel Islands, or maybe several sea otter pelts. Yes, indeed, he was sure these gentle creatures with their beautiful cinnamon, white and grey coats, their large hazel eyes, and their inquisitive and playful

nature would bring a handsome price. Limú, of the Chumash Indians of Santa Cruz Island was about to introduce an animal that the Gabrielino Indians of Santa Catalina Island had never seen. The Gabrielino were about to meet the island fox.

Although fictional, this scene may well depict how island foxes colonized the southern most Channel Islands, a continental archipelago located off the coast of southern California, USA (Fig. 9.1). Archaeological, ethnographic, morphological, and genetic evidence support the contention that foxes were brought to the southern Channel Islands (Santa Catalina, San Clemente, and San Nicolas) by Native Americans between 2,200 and 5,200 YBP (Collins 1991a,b, 1993; Wayne *et al.* 1991b; Vellanoweth 1998). Native Americans of the Channel Islands harvested foxes to make arrow-quivers, capes, and head-dresses from their pelts, they ceremonially buried foxes, conducted an Island Fox Dance and most likely kept foxes as pets or semi-domesticates (Collins 1991b). Island foxes played a prominent role in the

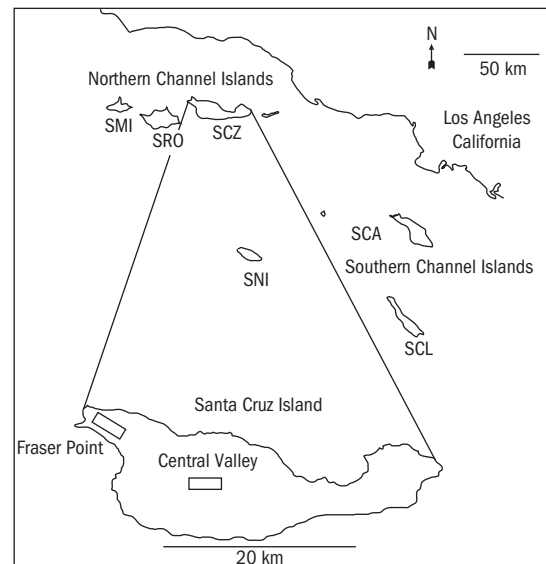


Figure 9.1 Island foxes occur on the six largest California Channel Islands. The three northern islands are Santa Cruz (SCZ), Santa Rosa (SRO), and San Miguel (SMI), and the three southern islands are Santa Catalina (SCA), San Clemente (SCL), and San Nicolas (SNI). The enlargement of Santa Cruz Island shows the relative placement and size of two trapping grids, Fraser Point and Central Valley, which were used to capture island foxes.

spiritual and personal lives of these island Americans. Fossil evidence dates the arrival of foxes to the northern Channel Islands (Santa Cruz, Santa Rosa, and San Miguel) much earlier, from 10,400 to 16,000 YBP (Orr 1968). Their actual colonization probably occurred between 18,000 and 40,000 years ago, when these northern islands were joined into one large island known as 'Santarosae' (Collins 1982, 1993; Johnson 1983). At its closest, Santarosae was a mere 6 km from the North American continent, having reached its maximum size 18,000–24,000 YBP. It is hypothesized that sometime during this period, mainland gray foxes, the progenitor of the island fox, colonized Santarosae by chance over-water dispersal, by either swimming or by rafting on floating debris (Collins 1982, 1993). As glaciers retreated and sea levels rose, Santarosae was subdivided into separate islands. Santa Cruz Island was formed first, some 11,500 YBP. Sea levels continued to rise separating the remaining land mass once again, approximately 9,500 YBP, to form Santa Rosa and San Miguel Islands. Native Americans then colonized the Channel Islands 9,000–10,000 YBP, and after establishment of an extensive trade route, transported foxes to the southern islands.

The island syndrome

In general, insular populations differ from their mainland counterparts in aspects of form, genetics, demography, and behaviour. They may be dwarfed or gigantic, they typically have lower levels of genetic diversity, occur at higher densities, have decreased dispersal tendencies, and reduced aggression (Stamps and Buechner 1985; Adler and Levins 1994; Burness *et al.* 2001). Island foxes are no exception. A dwarf form of the mainland gray fox, island foxes are the smallest North American canid, varying in body mass from 1.4 to 2.5 kg, roughly two-thirds the size of a mainland grey fox (Moore and Collins 1995; Roemer *et al.* in press). Further, each insular population differs in body mass and morphology (Collins 1982, 1993; Wayne *et al.* 1991; Roemer *et al.* in press). For example, Santa Catalina has the largest island foxes (*U. littoralis catalinae*), San Clemente's foxes (*U. littoralis clementae*) have the smallest craniums and San Miguel foxes (*U. littoralis littoralis*) have the shortest tails, owing to a reduction in the number of caudal vertebrae

(Collins 1982; Moore and Collins 1995). Morphology is so distinctive that each fox population can be distinguished from the other solely on osteological traits. Using 29 cranial and mandibular characters measured from 2,207 island and gray fox specimens, Collins (1982, 1993) correctly classified 91% of all island fox specimens to their island of origin.

Insularity has also had a profound influence on genetic diversity and the phylogeography of the island fox. Founder events, genetic drift, and selection have played significant roles reducing phenotypic and genetic variation, and creating six genetically distinct populations. Island foxes contain about 35% of the genetic variation observed in mainland grey foxes, and the fox population on San Nicolas Island is one of the most genetically invariant wild populations known (Table 9.1). Genotype profiles generated from hypervariable minisatellite and microsatellite DNA were identical for all foxes assayed from San Nicolas (Gilbert *et al.* 1990; Goldstein *et al.* 1999). Of the five

Table 9.1 Genetic diversity at 19 microsatellite loci in the island fox and a mainland California population of gray fox

Population	<i>n</i>	Alleles/ %		He	HW-He
		locus	Polymorphic		
San Miguel	17.8 (0.8)	1.7 (0.2)	47.4	0.106 (0.045)	0.155 (0.048)
Santa Rosa	25.4 (0.9)	2.5 (0.4)	57.9	0.198 (0.056)	0.274 (0.065)
Santa Cruz	22.4 (1.1)	2.3 (0.3)	57.9	0.209 (0.047)	0.284 (0.058)
San Nicolas	26.4 (0.9)	1.0 (0.0)	0	0 (0.0)	0 (0.0)
San Clemente	24.9 (1.1)	2.1 (0.3)	52.6	0.228 (0.061)	0.248 (0.064)
Santa Catalina	25.4 (1.1)	2.5 (0.2)	89.5	0.341 (0.046)	0.405 (0.043)
Grey fox	11.9 (0.6)	6.3 (0.5)	94.7	0.700 (0.045)	0.752 (0.047)

Note: The San Nicolas island fox population is genetically invariant at all loci. *n*: mean sample size per locus (\pm SD); Alleles/locus: mean number of alleles per locus; % Polymorphic: the percentage of loci that had two or more alleles; He: direct count of heterozygosity and HW-He: heterozygosity assuming Hardy-Weinberg equilibrium in allele frequencies.

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mitochondrial DNA (mtDNA) haplotypes found in island foxes, none is shared with a nearby mainland sample of gray foxes and all island fox populations share a unique restriction enzyme site, a synapomorphy that clusters the six populations into a single monophyletic clade (Wayne *et al.* 1991). Each island fox population contains population-specific restriction-fragment profiles (Gilbert *et al.* 1990). Genotypes generated from 19 microsatellite loci were used to correctly classify 181 out of 183 island/gray fox samples to their population of origin (Goldstein *et al.* 1999). The three northern island populations and the three southern island populations consistently cluster into two groups, and the Santa Rosa and San Miguel fox populations are more closely related than either is to Santa Cruz (Gilbert *et al.* 1990; Wayne *et al.* 1991; Goldstein *et al.* 1999). This phylogeographic structure supports the view that colonization followed by vicariant events created the northern island fox populations and that human-assisted dispersal aided the colonization of the southern islands. These morphological and genetic differences also clearly justify the taxonomic classification of the island fox as a separate species (Wilson and Reeder 1993) and support the individual subspecific classifications of the six island fox populations (Hall 1981; Moore and Collins 1995).

Higher densities are predicted to be characteristic of island vertebrates (Adler and Levins 1994) and island foxes have some of the highest population densities of any canid. On Santa Cruz, densities from 7 to 8.1 foxes/km² have been recorded (Laughrin 1977; Roemer *et al.* 1994) and on San Clemente densities at three sites varied from 4.8 to 8 foxes/km² over a 10-year period (Roemer *et al.* 1994; Garcelon 1999; Roemer 1999). On San Miguel and San Nicolas Islands, the two smallest islands that harbour foxes, densities have varied from near zero to 16 foxes/km² (Coonan *et al.* 2000; Roemer 2000). Densities of mainland gray fox populations are typically much lower, averaging 1.2 to 2.1 foxes/km² across a range of studies (Fritzell and Haroldson 1982). Some variation in apparent density between species may arise from methodology. For example, on Santa Cruz Island, the density of island foxes in 1993 determined with a capture–recapture approach was 7.0 foxes/km² whereas density for the same population determined via home range size was approximately 35% lower or 4.5 foxes/km².

Regardless of methodology, densities of island foxes are high compared to mainland foxes and are

probably a result of the small home ranges of island foxes. In mixed habitat on Santa Cruz Island, fox home ranges averaged between 0.25 and 0.33 km² ($n = 12$) (Crooks and Van Vuren 1996) and in coastal grassland seasonal home range size varied from 0.15 to 0.87 km² ($n = 42$), with a mean annual home range size of 0.55 km² ($n = 14$) (Fig. 9.2(a)—Roemer *et al.* 2001b). On San Clemente Island, home ranges are larger (mean = 0.77 km², $n = 11$) perhaps due to the lower productivity of this more southerly island (Thompson *et al.* 1998). On San Miguel, average home range size of five yearlings was 2.26 km² (range = 1.72–2.91 km²) during a period of low density (T. Coonan personal communication) and on Santa Cruz fox home ranges expanded (range = 16–266%, $n = 5$) as territorial neighbours were killed by golden eagles, suggesting that density of foxes and the spatial distribution of neighbours may influence territory size (Roemer 1999; Roemer *et al.* 2001b). The small home range size observed in island foxes is related to their more insectivorous diet and to the high resource density common to insular ecosystems (Macdonald 1983; Stamps and Buechner 1985; Roemer *et al.* 2001b).

Insular species are predicted to have reduced aggression and a reduction in territoriality because of the increased costs of territory maintenance at high population densities (Stamps and Buechner 1985). These predictions stem from the difference in ecological conditions between insular and mainland systems. Insular systems typically have higher resource densities and lower levels of interspecific competition owing to a depauperate fauna. These conditions cause higher densities of both territory holders and non-territorial floaters. An increase in the number of floaters leads to increased defence costs for territory holders and ultimately to a reduction in territorial behaviour. This reduction in territoriality may be manifested as: (1) reduced territory size; (2) increased territory overlap; (3) acceptance of subordinates within the territory; and (4) reduced intraspecific aggression (Stamps and Buechner 1985). Contrary to these predictions, island foxes are distributed as socially monogamous pairs that defend discrete territories (Crooks and Van Vuren 1996; Roemer *et al.* 2001b). On Santa Cruz Island, home ranges of mated pairs overlapped (mean = 85%, SD = 0.05%) significantly more than those of neighbours (mean = 11%, SD = 0.13%) (Fig. 9.2(a)—Roemer *et al.* 2001b).

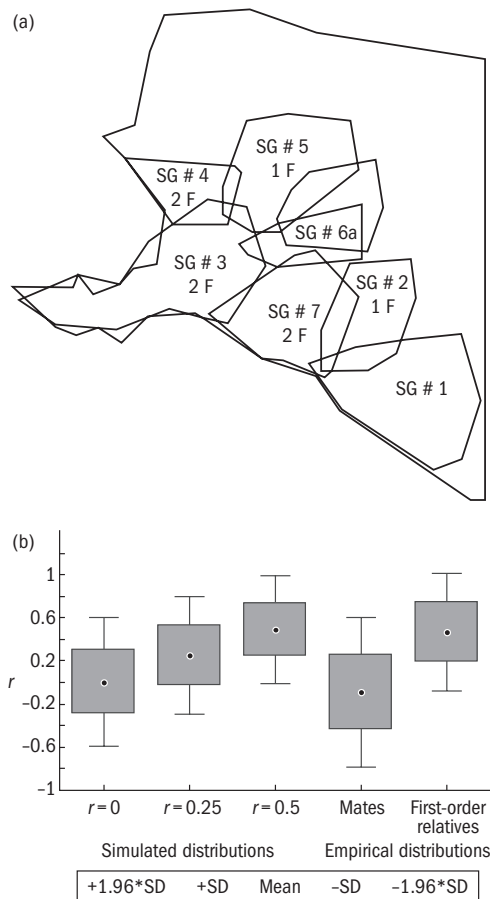


Figure 9.2 (a) The distribution of male, island fox territories at Fraser Point, Santa Cruz Island from April to August 1994. The letter and number (e.g. 1F) represent the number and sex of pups born in that season. (b) Empirical distributions (mean \pm 1 SD and 1.96 SD) of the coefficient of relatedness (r) for first-order relatives and for mated pairs of island foxes. Social relationships among the foxes were determined from observations of spatial distribution or by paternity analysis using microsatellite loci. Simulated distributions of r for first-order relatives ($r = 0.5$), for distantly related relatives ($r = 0.25$), and for unrelated individuals ($r = 0$) are shown for comparison. (Modified from Roemer *et al.* 2001b).

Island foxes might also be predicted to be monogamous given their territorial nature and the general trend towards monogamy in the Canidae that increases with decreasing body size (Geffen *et al.* 1996; but see Sillero-Zubiri *et al.* 1996a). However, EPFs are not uncommon in island foxes, 4 (25%) of

16 pups whose parents were identified through paternity analysis were a result of EPFs (Roemer *et al.* 2001b). Three of the four EPFs were by the two largest male foxes in the study and bite wounds were observed on males only during the breeding season (Roemer 1999). These observations suggest that male-male competition for mates may be intense. Further, nearly all pairings occurred between unrelated male and female foxes, suggesting that foxes avoid inbreeding and practice mate choice (Fig. 9.2(b)—Roemer *et al.* 2001b).

Like other canids, island foxes display a relatively high degree of bi-parental care. Dependent young accompany parents on forays and have been observed foraging with their parents for insects in grassland, and for striped-shore crabs (*Pachygrapsus crassipes*) in intertidal habitats (G. Roemer personal observation). Additionally, both parents have been observed transferring artificially provided food to dependent pups, and vertebrate prey have been found outside of traps containing captured pups (Garcelon *et al.* 1999). It is also not uncommon for full-grown young to remain within their natal range into their second year, or for offspring to associate with their parents after gaining independence (Roemer 1999). Although helping by independent young may occur, it has not been observed. The average number of adult-sized foxes occupying a single territory on Santa Cruz Island was 3.38 (SD = 1.12, $n = 13$) (Roemer *et al.* 2001b).

Finally, because of small size and a finite border, dispersal opportunities on small islands are more limited than on the mainland. This reduction in dispersal distance is predicted to increase the viscosity of gene flow, creating greater population substructure compared with mainland populations (Roemer *et al.* 2001b). Similar to insular rodent populations (Sullivan 1977; Tamarin 1977), island foxes disperse less frequently and over shorter distances than mainland canids of similar size. On Santa Cruz, five juveniles (three males and two females) dispersed to areas within the study site (mean = 0.99 km, SD = 0.61) and one male dispersed 3.58 km from the study site. Thus, only one (17%) of six juvenile island foxes successfully dispersed from its natal area, moving a distance greater than two average home range diameters (average home range diameter = 0.84 km) (Roemer *et al.* 2001b). Tullar and Berchielli (1982, cf. Fritzell 1987) found that 63% of juvenile female and 73% of

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juvenile male gray foxes left their natal area. Dispersal distances of male and female island foxes were limited compared with those of mainland fox species. Eight island foxes on Santa Cruz, including six juveniles and two young adults that were probably subordinate offspring, dispersed an average of 1.39 km (SD = 1.26) with the longest dispersal distance recorded being less than 4 km. In Alabama, Nicholson *et al.* (1985) recorded a mean dispersal distance of 15 km (SD = 9.5) for three male gray foxes. The kit fox, only slightly larger than the island fox, has an average dispersal distance of 11.1 km ($n = 47$, range 1.7–31.5) (O'Farrell 1984). The longest recorded dispersal distance for a gray fox is 84 km (Sheldon 1953) and for the kit fox is 64 km (O'Neal 1985). The maximum beeline distance over which an island fox could disperse is 38 km, the total length of Santa Cruz Island. In addition, significant genetic subdivision was observed on Santa Cruz between two sampling sites separated by only 13 km, suggesting restricted gene flow ($Nm = 1.6$ – 2.5 —Roemer *et al.* 2001b). Similar values of Nm are found between populations of mainland canids separated by several hundred kilometres (Mercure *et al.* 1993; Roy *et al.* 1994b).

Historic demography and the decline of the island fox

Prior to Laughrin's (1977, 1980) work in the early and mid-1970s, there had been no systematic attempts to quantify the abundance of island foxes. Laughrin (1977, 1980) estimated the density of foxes on all six islands by live trapping along road transects. Most populations were at moderately high density (1.2–4.3 foxes/km²), except for San Nicolas (0.1–2.7 foxes/km²) and Santa Catalina (0–0.8 foxes/km²) that were at relatively lower densities (Laughrin 1980). Santa Catalina had apparently been at a low density throughout the 1970s whereas the San Nicolas population had declined between 1971 and 1977. Although feral cats were known competitors and suspected as a potential agent involved in the declines, the causes of the low numbers on Santa Catalina, or of the apparent decline on San Nicolas were unknown (Laughrin 1980).

In the 1980s, Kovach and Dow (1981, 1985) employed the first use of trapping grids to estimate island fox population density and size. Using a series of 12 small, trapping grids (30 traps), they trapped approximately 37% of San Nicolas Island. In 1981, density estimates varied from zero to 6.9 foxes/km² with an estimated population size of 110 foxes (Kovach and Dow 1981). In 1985, the estimate of population size increased to 520 foxes (Kovach and Dow 1985). These data implied that the fox population on San Nicolas had recovered from apparently low numbers in the 1970s.

A capture–recapture design incorporating large trapping grids (48–80 traps—see Fig. 9.1) has been used on San Clemente (1988–97 and 1999–2002), Santa Catalina (1989 and 1990), Santa Cruz (1993–99), San Miguel (1993–99), and San Nicolas Islands (2000–02) (Roemer *et al.* 1994, 2001a, 2002; Garcelon 1999; Roemer 1999, 2000; Coonan *et al.* 2000). Between the late 1980s and early 1990s, data from the capture–recapture studies coupled with anecdotal observations by island residents suggested that island fox populations on all the Channel Islands were at relatively high density. Depending on grid (habitat) and island, densities varied from 2.4 to 15.9 foxes/km² (Roemer *et al.* 1994; Coonan *et al.* 2000; Coonan 2003). Estimates of population size varied from approximately 350 adult foxes on San Miguel, the smallest island, to greater than 1300 adult foxes on Santa Cruz, the largest island (Roemer *et al.* 1994, 2001a). It was estimated that there were approximately 6400 adult foxes distributed among the six island populations (Roemer *et al.* 1994).

In the mid- to late-1990s, fox populations on the three northern islands underwent drastic population declines (Roemer 1999; Coonan *et al.* 2000; Roemer *et al.* 2001a). By 1998, mean fox density on San Miguel and Santa Cruz Islands had dropped to 0.8 (± 1.0) foxes/km², capture success had decreased six-fold, from 25.7% (1993) to 4.3% (1998), and population size on both islands had plummeted. Only 15 adults were known to be alive on San Miguel in 1999 with an estimated 133 foxes remaining on Santa Cruz. The San Miguel and Santa Cruz fox populations were estimated to have a 50% probability of persistence within the next decade (Roemer *et al.* 2001a). Capture success in 1998 on nearby Santa Rosa Island was also low (4.8%) suggesting that fox

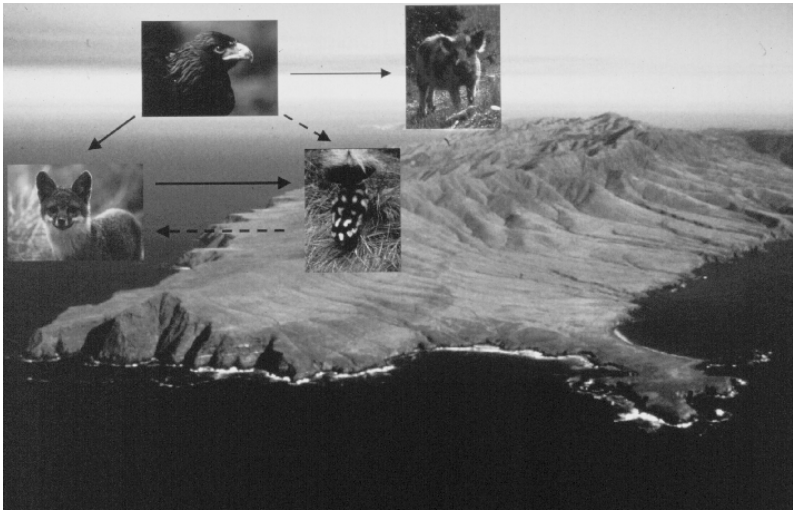


Figure 9.3 The introduction of feral pigs to Santa Cruz represented an abundant food source that enabled golden eagles to colonize the island. Golden eagles preyed on pigs, foxes and skunks, but predation pressure was greatest on the unwary fox. As foxes were driven to extinction, skunks were released from fox competition, and their numbers increased © G. Roemer.

populations had declined on all three northern Channel Islands. These data showed that the three subspecies on the northern Channel Islands were critically endangered and in need of immediate conservation action (Mace and Lande 1991; Coonan 2003; Roemer *et al.* 2001a, 2002).

Disease was initially suspected as a contributory agent, but further investigation proved that the most important proximate driver of the fox population declines was the presence of an exotic species, the feral pig (*Sus scrofa*) (Roemer *et al.* 2000a, 2001a, 2002). Pigs, by acting as an abundant food, enabled mainland golden eagles to colonize the northern Channel Islands and through hyperpredation caused the decline in the fox populations. Hyperpredation is a form of apparent competition whereby an introduced prey, well adapted to high predation pressure, indirectly facilitates the extinction of an indigenous prey by enabling a shared predator to increase in population size (Holt 1977; Courchamp *et al.* 1999). Pigs, by producing large numbers of piglets, sustained the eagle population and because of their high fecundity could cope with the increased levels of predation. In addition, as piglets mature, they eventually escape predation by growing beyond the size range that eagles typically prey upon (Roemer *et al.* 2002). Foxes, on the other hand, are small, active during the day, and produce relatively few young each year. Thus, predation by eagles had

an asymmetrical effect on the more vulnerable fox, driving the fox populations toward extinction (Fig. 9.3).

The presence of pigs had further ramifications causing a wholesale reorganization of the island food web. Historically, island foxes were the largest terrestrial carnivores and were competitively dominant to the island spotted skunk (*Spilogale gracilis amphiala*) (Crooks and Van Vuren 1996; Roemer *et al.* 2002). Three to four times larger than an average skunk, a fox consumes nearly three times as much insects and small rodents. Prior to the arrival of eagles, capture success of foxes (28.3%, SD = 8.7%) was 35 times higher than that of skunks (0.8%, SD = 1.0%) on Santa Cruz Island (Roemer *et al.* 2002b). However, once fox populations declined, skunks were released from competition with foxes and subsequently increased. By 1999, skunk capture success had increased 17-fold to 13.9% (SD = 8.5%), and fox capture success had dropped to an all-time low of 4.3% (SD = 1.9%). These community-level dynamics were predicted by a mechanistic model parameterized with independent data sets, which also confirmed that pigs were the indirect driver of this food web transformation (Fig. 9.4). In this case, the presence of an exotic prey indirectly caused apparent competition to replace resource competition as the primary biotic force structuring this carnivore community (Roemer *et al.* 2002b).

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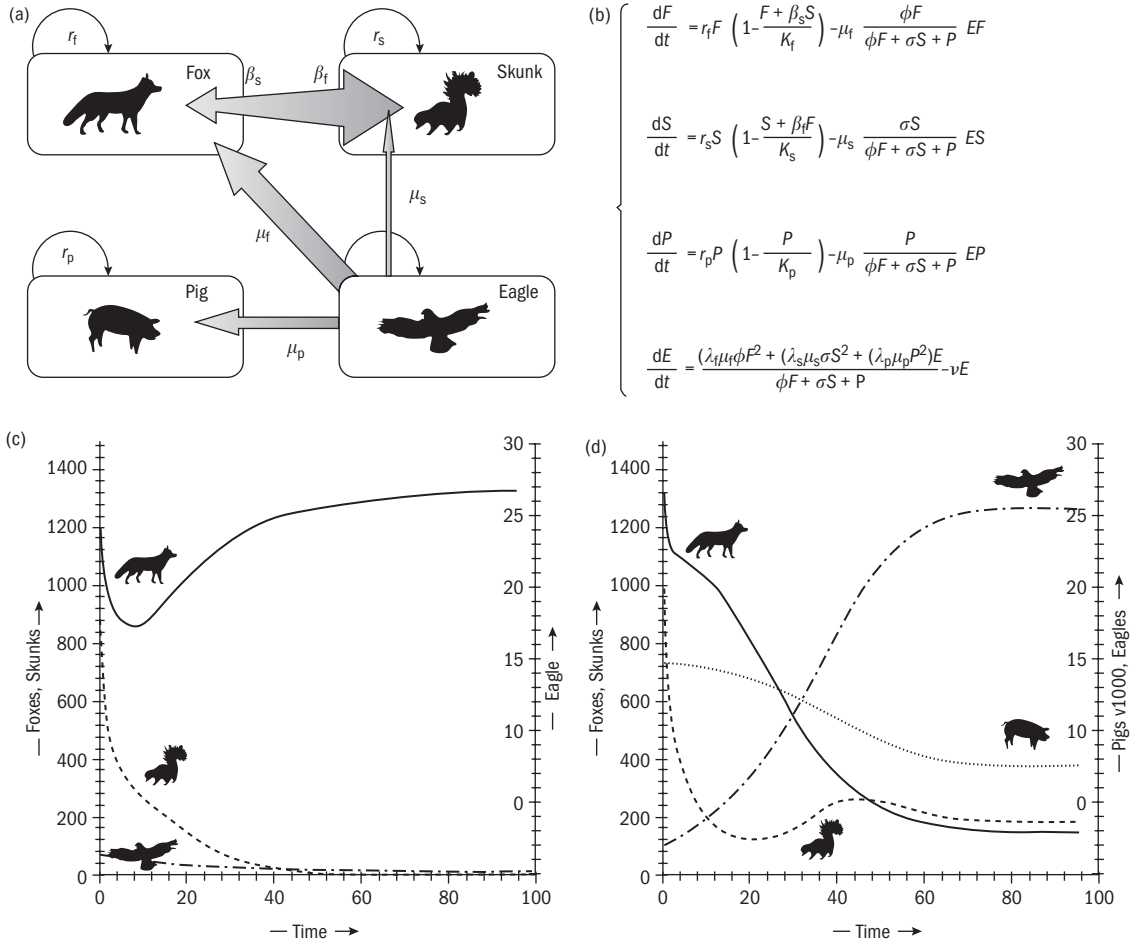


Figure 9.4 (a) Schematic representation, (b) corresponding set of equations, and (c-d) demographic relationships among island foxes, island spotted skunks, feral pigs, and golden eagles on Santa Cruz Island. (c) Without pigs, eagles are unable to colonize the island because of insufficient food. Foxes out-compete skunks and are the dominant terrestrial predator. (d) With pigs, eagles colonize the island and through hyperpredation drive the foxes toward extirpation. The decline in foxes releases skunks from fox competition. (From Roemer *et al.* 2002.)

Although pigs were unequivocally linked to the decline in foxes on the northern islands, it was further hypothesized that the ultimate cause of this interaction was a result of historic, human-induced perturbations to the islands, to the mainland, and to the surrounding marine environments (Roemer *et al.* 2001a). European agricultural practices together with overgrazing by introduced herbivores reduced vegetative cover and probably increased the vulnerability of foxes to a diurnal, avian predator. Environmental

degradation of the marine environment then led to the extirpation of the bald eagle (*Haliaeetus leucocephalus*) from the Channel Islands by 1960 (Kiff 1980). Bald eagles are primarily piscivorous, forage over marine habitats, and are not a significant predator of the island fox. However, bald eagles are territorial, aggressive towards conspecifics and other raptors, and may have competed with golden eagles for nest sites (Roemer *et al.* 2001a). The extirpation of the bald eagle probably paved the way for

colonization of the islands by golden eagles. Finally, increased urbanization along the southern California coast reduced golden eagle habitat possibly displacing them to new hunting grounds on the islands. This series of complex interactions may have ultimately allowed golden eagles to colonize the islands and drive island foxes toward extinction.

As the declines on the northern islands were in full swing, another catastrophe occurred when canine distemper virus was introduced to Santa Catalina Island between late 1998 and to mid-1999 (Timm *et al.* 2000). This epizootic caused an estimated 95% reduction in the fox population on the eastern 87% of Catalina Island (Timm *et al.* 2000). Luckily a suspected barrier to fox dispersal, and hence to the spread of the disease, was in place on the western end of the island in the form of the town of Two Harbors. The fox population on the remaining 13% of the island west of Two Harbors appeared to be unaffected with 49 individual foxes being captured in 137 trap nights (36% capture success) (Timm *et al.* 2000). Domestic dogs are hypothesized to have introduced the virus but the actual agent is unknown.

The fox population on San Clemente Island was thought to be in gradual decline since the early 1990s, with an estimated 20% chance of extinction in the next 100 years (Garcelon 1999; Roemer 1999; Roemer *et al.* 2001a). However, recent demographic modelling suggests that the population may be declining at a much higher rate (Roemer *et al.* 2000b). Deterministic estimates of intrinsic growth rate ($\lambda = 0.956$) imply a 4.4% decline in annual population size, or a decline of nearly 50% from 1988 ($N = 850$ foxes) to 2002 ($N = 457$ foxes).

This decline may have been exacerbated by an interesting endangered species conflict that is occurring on San Clemente Island (Roemer and Wayne 2003). Over the past decade, a monumental effort has been undertaken to prevent the extinction of the critically endangered San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*—Juola *et al.* 1997; USDA 1998). Erroneously classified as a separate subspecies in the 1930s (Miller 1931) based on a flawed method of systematic classification (Collister and Wicklum 1996), the San Clemente loggerhead shrike also has equivocal genetic distinction (Mundy *et al.* 1997a,b). As part of efforts to bring this 'subspecies' back from the brink of extinction, predator control

measures have been instituted that include lethal removal, permanent removal to zoological institutions, and temporary containment of island foxes, an identified nest predator (Garcelon 1996; Cooper *et al.* 2001). Ten to thirty per cent of the fox population is placed in temporary confinement each year and/or repeatedly trapped on consecutive nights during the reproductive season (Cooper *et al.* 2001). Pregnant and lactating females are contained resulting in pups being born in captivity as well as dependent pups in the wild probably dying because of removal or confinement of their mother (Cooper *et al.* 2001). For example, in 1999, 49 foxes were held temporarily in small pens (~ 0.55 m²) during the fox reproductive season. Of the foxes held captive, 20 females were suspected of having dependent pups still in the wild (Cooper *et al.* 2001). Adult female San Clemente island foxes wean an average of 1.25 (SE = 0.015) pups per reproductive event (Roemer 1999). Thus, an estimated 25 pups would be expected to have starved to death as a result of confinement of their mothers. The impact of these measures on the fox population has not been critically evaluated. Within the last decade, four island fox populations have experienced dramatic population declines and a fifth population is in significant decline. Only the San Nicolas fox population, the most genetically invariant population of all, is currently at high density (Roemer 2000).

Conservation of the island fox

Channel Islands National Park (CINP) has established several recovery actions to prevent the extinction of the northern Channel Island fox populations (Coonan 2001). In 1998, CINP established an Island Fox Conservation Working Group, a team of experts whose expertise was used to guide recovery actions on the northern Channel Islands (Coonan 2003). Following the recommendation of the Working Group, CINP contracted the Santa Cruz Predatory Bird Research Group to begin live-capture and removal of golden eagles. From November 1999 to June 2002, a total of 22 golden eagles, 20 adult or subadult golden eagles and 2 chicks, were live-captured and removed from Santa Cruz Island (Coonan 2003; B. Latta personal communication). In 1999, an island fox captive-breeding facility was

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Figure 9.5 An inquisitive Santa Cruz island fox (*Urocyon littoralis santacruzae*). This picture was taken by the author at a distance of ~3 m © G. Roemer.

established on San Miguel and a second facility was added on Santa Rosa in 2000. In June 2002, there were 28 foxes in captivity on San Miguel and 45 on Santa Rosa. Recently, each of these facilities has been divided into two separate facilities to safeguard against disease. Genetic information is being used to establish mated pairs (Gray *et al.* 2001) and the health of the captive populations is being monitored by veterinary examination and disease and parasite surveys (L. Munson and M. Willet personal communication). Releases are being planned for Santa Rosa Island in 2003, and demographic modelling is being used to guide future recovery efforts (Roemer *et al.* 2000b; Coonan 2003).

Monitoring of the Santa Cruz fox population is continuing (Fig. 9.5). The most recent estimate of the number of foxes on Santa Cruz is below 100. Eighty-two foxes were captured in an island-wide trapping effort, with six additional deaths of foxes owing to predation by golden eagles occurring in 2000–01 (Dennis *et al.* 2001). In cooperation with The Nature Conservancy, CINP has established a third captive

breeding facility on Santa Cruz. Following recommended actions from the Island Fox Conservation Working Group, a total of 12 bald eagles have been released on Santa Cruz Island with another 12 birds planned for release over the next 4 years (60 bald eagles total) (Vallopi *et al.* 2000; Coonan 2002, 2003). A feral pig eradication effort is being planned and should be underway by 2003 (Coonan 2001).

The Institute for Wildlife Studies (IWS), funded by the Catalina Island Conservancy, has initiated a wild fox vaccination programme against the canine distemper virus on Santa Catalina, and is continuing monitoring efforts. It has also established a captive breeding facility (Timm *et al.* 2000). Unfortunately, during the construction of the captive facility, a decision was made to bring pregnant foxes into captivity in late spring 2001. Females gave birth in the facility and 12 of 18 pups subsequently died, owing to apparent stress-related abandonment by the females (Timm 2001). Currently there are 11 pairs of foxes in the facility that are adjusting well and captive reared foxes have been released in late 2001 (J. Floberg personal communication).

On San Clemente, the IWS, funded by the US Navy and in compliance with actions enforced by the US Fish and Wildlife Service, is continuing containment efforts of the island fox to protect the endangered San Clemente loggerhead shrike (Cooper *et al.* 2001). The fox population is declining. In 2000, monitoring of the San Nicolas island fox population was resumed (Roemer 2000) and is being continued by the IWS (G. Smith personal communication).

In response to the declines in fox populations, the IWS along with the Center for Biological Diversity petitioned the US Fish and Wildlife Service to list the three northern island fox populations and the Santa Catalina island fox population as endangered. Curiously, both the San Clemente and San Nicolas island fox populations, the only populations managed jointly by the US Navy and IWS, were excluded from this petition. The four populations are now being considered for listing as endangered under the Endangered Species Act in a proposed rule by the US Fish and Wildlife Service (USDI 2001).

The IUCN—Canid Specialist Group has undertaken an independent assessment of the status of the island fox (Roemer *et al.* in press). Using the IUCN Red List categories (IUCN 2001), the subspecies on

San Miguel and Santa Rosa Islands, *U. littoralis littoralis* and *U. littoralis santarosae*, are recommended listed as Extinct in the Wild. The subspecies on Santa Cruz and Santa Catalina Islands, *U. littoralis santacruzae* and *U. littoralis catalinae*, are recommended listed as Critically Endangered and the subspecies on San Clemente Island, *U. littoralis clementae*, is recommended listed as Endangered. The subspecies on San Nicolas Island, *U. littoralis dickeyi*, is recommended listed as Vulnerable (Roemer *et al.* in press). Further, it has been recommended that the entire species, not just four of the six subspecies, receive protection under the Endangered Species Act (Roemer 1999). The objective guidelines provided by the IUCN and used by Roemer *et al.* (in press) support this view.

Island foxes are located on islands that are managed by public or private resource agencies that are governed by state and federal laws that mandate the

preservation of wildlife. Given that the island fox is unique in terms of its biological, scientific, and cultural qualities, the protection of this critically endangered canid is clearly a high priority.

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