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FACTORS CONTRIBUTING TO SUCCESS OF ISLAND FOX REINTRODUCTIONS ON SAN MIGUEL AND SANTA ROSA ISLANDS, CALIFORNIA

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Abstract—Documented success in the reintroduction of endangered canids is rare. Here, we report on the success of reintroductions for San Miguel Island foxes (*Urocyon littoralis littoralis*) and Santa Rosa Island foxes (*U. l. santarosae*), each of which had been extirpated in the wild by 2000, when the remaining 15 individuals of each subspecies were brought into captivity. From 2003 to 2007, 123 foxes were released to the wild, and were monitored to determine sources of mortality and to estimate annual survival, pup production, and population size. Annual survival increased to 90% on both islands by 2007, and high reproductive success resulted in wild populations of at least 62 on Santa Rosa and 105 on San Miguel. Several factors contributed to reintroduction success. First, survival of island foxes is very high in the absence of predation, and mortality due to predation had been substantially reduced on both islands by removal of most golden eagles (*Aquila chrysaetos*). Second, foxes were released into low-density habitats, which facilitated high reproductive success and rapid population growth. Finally, release plans included contingencies to address potential predation impacts, and post-release monitoring allowed management decisions to be supported by comparison of wild and captive fox demographic parameters.

INTRODUCTION

Although reintroduction of extirpated species to formerly occupied range is intuitively appealing as a recovery action, the overall success of reintroductions has not been high (Armstrong and Seddon 2007). This is especially true for endangered canids, which have an extremely low reintroduction success rate (Ginsberg 1994; Boitani et al. 2004). In particular, captive-raised carnivores have lower post-release survival than translocates (Jule et al. 2008). Canid reintroductions have been hampered by a number of obstacles, including low survival of captive-born individuals (African wild dogs [*Lycaon pictus*]; Gusset et al. 2008), behavioral variation among captive-raised individuals (swift foxes [*Vulpes velox*]; Bremner-Harrison et al. 2004), hybridization with other species (red wolves [*Canis rufus*]; Kelly et al. 2004), and conflict with and persecution by humans (Mexican wolves [*Canis lupus baileyi*]; Paquet et al. 2001; Povilitis et al. 2006). A handful of canid reintroduction programs have reported success, and these include gray wolves (*C. l. nubilis*) in the Northern Rockies and greater Yellowstone area (Sime and Bangs 2007), and swift foxes in Canada (Carbyn et al. 1994) and Montana (Ausband and Foresman 2007). Here we argue that the reintroduction of island foxes (*Urocyon littoralis*) from captivity to San Miguel and Santa Rosa islands is also a successful canid reintroduction, and we discuss factors responsible for the apparent success.

Island foxes are endemic to the California Channel Islands, and the six largest of the eight islands each support a unique subspecies of fox (Grinnell et al. 1937). Island foxes on San Miguel (*U. l. littoralis*) and Santa Rosa (*U. l. santarosae*) declined catastrophically in the mid-1990s due to predation by golden eagles (*Aquila chrysaetos*; Roemer et al. 2001a; Coonan et al. 2005b). By 2000 the Santa Rosa and San Miguel fox subspecies had each declined to 15 individuals (Coonan et al. 2005a), leaving captive breeding and reintroduction as the only option for recovery of these two island fox subspecies. Captive facilities were established by the National Park Service (NPS) on both islands, and the remaining foxes were removed from the wild and brought in to these facilities. Precipitous island fox declines also occurred on Santa Cruz (Roemer et al. 2001a) and Santa Catalina islands (Timm et al. 2002), and captive breeding programs were established on Santa Catalina Island by Santa Catalina Island Conservancy and Institute for Wildlife Studies, and on Santa Cruz Island by The Nature Conservancy and NPS. Fortunately, foxes were never extirpated from the wild on those islands, and translocations and reintroductions occurred with existing wild populations of at least 100 on Santa Catalina and 65 on Santa Cruz Island. In contrast, when reintroductions began on Santa Rosa and San Miguel, foxes had been absent from the wild for several years, and the captive populations had grown from the original 15 foxes to above 50 individuals on each island.

Because the San Miguel and Santa Rosa island fox subspecies, along with those on Santa Cruz and Santa Catalina, were listed as endangered in 2004 by the U.S. Fish and Wildlife Service (USFWS), the ultimate measure of reintroduction success might be the achievement of recovery criteria and the delisting of those taxa. However, such definitions, which as yet do not exist for island foxes, incorporate administrative as well as biological recovery milestones. A more purely biological definition of canid reintroduction success was recently proposed (Boitani et al. 2004), under which reintroduction success is characterized by a) breeding by the first wild-born generation; b) a 3-year breeding population in which recruitment exceeds adult death rate; and c) establishment of a self-sustaining population. We herein present the results of island fox releases from 2003 to 2007 on San Miguel and Santa Rosa islands, and assess the success of those reintroductions in light of these definitions.

MATERIALS AND METHODS

Study Area

San Miguel and Santa Rosa islands are respectively the smallest (38.7 km^2) and second-largest (216.0 km^2) of the six California islands where island foxes occur. Both islands are managed by the NPS, although San Miguel is owned by the U.S. Navy. San Miguel is primarily a gently sloping plateau with long, sandy beaches along the coastline. The island is fully exposed to the prevailing northwesterly wind and is recovering from a period of severe overgrazing and erosion caused by historic sheep ranching (Hochberg et al. 1979). Grasslands cover much of the island, and include both native bunchgrasses (*Nasella pulchra*) and introduced annuals such as *Avena* spp. and *Bromus* spp. Some grassland areas have been colonized by shrubs such as coyote brush (*Baccharis pilularis*), and thick stands of giant coreopsis (*Coreopsis gigantea*) intermix with grasses in many areas. The dominant shrub community is *Isocoma* scrub, characterized by low-growing plants up to 1 m high. No trees occur on San Miguel Island.

The larger size, higher elevations, more varied topography, and unique land-use history of Santa Rosa result in vegetation associations not found on San Miguel. Santa Rosa is instead characterized by a central highland dissected by drainages; a relatively gentle marine terrace occurs north of the highland, whereas steep, deeply incised drainages comprise much of the south portion of the island. Nonnative annual grasslands cover about two-thirds of the island, although native perennial grasses are increasing in distribution. Common scrub communities include coastal sage (*Artemisia californica*) and baccharis (*Baccharis pilularis)* scrub. Island chaparral, characterized by *Arctostaphylos* spp. and *Adenostoma fasciculatum,* is found on the slopes of the central highland and at South Point, and less than 1% of Santa Rosa is covered by woodlands. As on San Miguel, the vegetation on Santa Rosa Island is recovering from the impacts of a history of grazing. A sheep ranching operation in the latter half of the nineteenth century gave way to cattle grazing, which occurred from the early twentieth century until 1998. Non-native mule deer (*Odocoileus hemionus*) and elk (*Cervus elephas*) were also brought to the island early in the last century for hunting, and currently exist at population levels of 400–1000 each.

All of the Channel Islands are subject to a Mediterranean climate regime characterized by cool, wet winters and warm, dry summers. On Santa Cruz Island, where there is a 102-yr record, average precipitation is 50 cm/year (Bakker et al. 2009), but with significant annual variation due in part to the El Niño/Southern Oscillation phenomenon. Some annual precipitation occurs in the form of fog drip, particularly on San Miguel Island.

Release Methods

Between 2003 and 2007, foxes were released to the wild during the fall (October–December). By this time the young of the year have grown to adult size and begin dispersing from their natal areas (Moore and Collins 1995). Conditions under which foxes were kept in captivity have been previously described (Coonan et al. 2005a). Foxes were released as groups of unmated animals, as pairs of potential mates, as pairs that had previously been housed together in captivity for up to one year, and as family groups (siblings or parent-sibling groups). Animals released as potential mates were housed together for 7–14 days prior to release.

Foxes were released at sites that had no or little fox use, as indicated by radiotelemetry of collared foxes, and were known to have been utilized by foxes prior to the establishment of the captive breeding programs. Releases occurred in the late afternoon in areas providing substantial vegetative cover. Foxes were released using a modified hard-release methodology, meaning that foxes were not acclimated to their release areas in temporary pens prior to release, but were released directly from crates. Foxes were supplementally fed after release to ease their transition to the wild, to enhance initial survival, and to encourage released animals to stay in or near their release sites (Kleiman 1996). Remote feeding stations were placed near the release sites, and were subsequently moved in some cases dependent upon the actions of individual animals. Feeding stations were supplied daily with dog kibble for the first month, and then three times a week for the next two weeks.

Prior to release each fox was outfitted with a 38-g radio-collar (M1930, Advanced Telemetry Systems, Inc., Isanti, MN; or MI-2, Holohil Systems Ltd., Ontario, Canada) fixed with a mortality sensor to allow for tracking, mortality monitoring, and potential recovery of animals from the field if necessary. Radio-collars were also affixed to a portion of the wild-born foxes captured during fall trapping (see below) in years subsequent to initial release of foxes into the wild, in order to track survival and mortality causes for the recovering populations. The ultimate goal was to maintain at least 40 active radio-collars on each island, because that was the number required to detect mortality rates of 0.025 with 95% confidence (Doak 2007). Thus, on San Miguel the number of collared animals was 84 (61 released foxes and 23 wild-born) and 82 on Santa Rosa (62 released foxes and 30 wild-born).

Each released fox was tracked on a daily basis for the first month after release, three times per week during the second month, and then at least once per week for the remainder of the year following release. If a mortality signal was detected, the carcass was recovered as soon as possible and sent to the Veterinary Medical Teaching Hospital, University of California–Davis for necropsy. Foxes were determined to have died from golden eagle mortality if they possessed any of the following characteristics: evisceration, degloving of limbs, talon marks, or presence of eagle feathers and whitewash (uric acid) at the carcass site (Roemer et al. 2001a; Coonan et al. 2005b). In 2003 and 2004 foxes were trapped one month after release to check general body condition and weight. If a trapped fox had lost > 20% of its release weight, it was returned to captivity until it had gained back enough weight to be re-released.

Locations of radio-collared foxes were determined by triangulation or by visual confirmation. Coordinates of each visually confirmed location were recorded with a geographic positioning system (GPS) device (Garmin International, Inc., Olathe, KS), as were locations from which triangulated bearings were obtained. A minimum of three bearings was used to determine locations by triangulation using program LOCATE II (Pacer Computing, Truro, NS, Canada). Likely den sites were identified when the locations of radio-collared females became consistent over a 2-week time period in one location during early to mid-April, and remote camera stations were then set up near these sites in early summer (when pups emerge from dens) to record the number of pups weaned from each litter. Each camera station included a box trap (23 X 23 X 66 cm, Tomahawk Live Trap Co., Tomahawk, WI), wired open and baited with dog kibble. A digital camera (Digital Scout, Penn's Woods Products, Inc., Export, PA) recorded fox activity in or near the trap when triggered by a passive infrared detector. Assignment of adult pair members to each camera site was determined by overlap of their female ranges with those of males, direct observation of males and females traveling together, and visual identification of individuals at camera stations.

Wild fox populations were monitored annually from October through January via transect trapping (both islands) and small grids (San Miguel only). Box traps were baited with dry and wet cat food and a fruit scent (Knob Mountain Raw Fur Co., Berwick, PA), and a polyethylene tube chew bar was wired inside each trap to reduce incidence of tooth damage. Upon first capture, animals were weighed in the trap, and then removed and handled without anesthesia to collect data on sex, reproductive status, age class, and general physical condition (e.g., condition of coat, presence of ectoparasites, injuries). Captured foxes that had not been released or captured previously were marked with passive integrated transponder (PIT) tags (Biomark, Boise, ID) inserted subcutaneously between and just anterior to the scapulae.

Data Analyses

Annual survival of radio-collared foxes was estimated with the non-parametric Kaplan-Meier procedure. This analysis derives cumulative survival in a time period based on the cumulative mortalities and the staggered entry of foxes into the sample as they were released to the wild, and of wild-born foxes as they were radio-collared (Pollock et al. 1989). For each island, survival was thus estimated for a pooled sample comprising both adults and juveniles, and released and wild-born individuals. We determined the minimum number of foxes known to be alive (MNKA) annually on San Miguel and Santa Rosa Island via transect trapping (both islands) and small grids (San Miguel only), in concert with data from radiotelemetry. Other population estimation methods, such as estimation of density from grids, are appropriate at medium to higher fox population levels (Roemer et al. 1994) and although we began such density estimation on San Miguel in 2006, those data are not included here because we do not have comparable data from Santa Rosa. The MNKA was estimated as the sum of the number of individuals caught during fall trapping and the number of radio-collared individuals not caught during trapping but known to be alive via regular telemetry monitoring. We estimated λ, the annual rate of population growth, included the captive facilities, and subsequent interactions between captive and wild foxes resulted using the equation $\lambda = \frac{MNKA'_{t+1}}{MNKA_t}$, where $MNKA'_{t+1}$ is the *MNKA* for year *t*+1 minus the number of foxes released in year *t*+1. Results from annual trapping were used to estimate reproductive success as the ratio of pups to the number of adult (>1 yr old) females. We compared reproductive effort to islandwide population size, including those data from the period of decline (1993–1998; Coonan et al. 2005b), to assess the relationship between density dependence and reproductive effort.

For the 123 foxes released from 2003–2007 on Santa Rosa and San Miguel islands, we also used logistic regression (SYSTAT 10, SPSS Inc., Chicago, IL) to determine if fate of released foxes (dead or alive) was affected by island, age of fox at release, or sex.

RESULTS

From 2003 to 2007, 123 island foxes were released to the wild on San Miguel (n = 61) and Santa Rosa (n = 62) islands (Fig. 1). Releases began a year earlier (2003) on Santa Rosa than on San Miguel (2004), because the captive population on Santa Rosa reached the target captive population size (40 foxes or 20 pairs) sooner on that island (Coonan et al. 2005a). Of the seven foxes released in 2003 on Santa Rosa, five were captured and returned to captivity because their home range

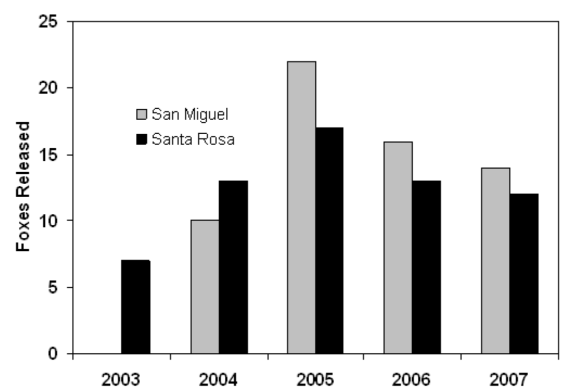

Figure 1. Number of island foxes released annually on San Miguel Island (total = 62) and Santa Rosa Island (total = 62), 2003–2007.

Table 1. Annual minimum number of foxes known to be alive (MNKA) on San Miguel and Santa Rosa islands, calculated as the sum of the number of foxes trapped and the number of additional foxes known to be alive via radiotelemetry, and annual rate of population growth (λ).

	Trap nights	No. trapped	On air[a]	MNKA	Adjusted MNKA[b]	λ
San Miguel						
2004		--	10	10		
2005	252	23	17	40	18	1.8
2006	458	72	8	80	64	1.6
2007	471	83	22	105	91	1.1
Santa Rosa						
2003		--	7	7		
2004	513	15	--	15		
2005	309	20	12	32	15	1.0
2006	887	38	2	40	27	0.8
2007	681	49	13	62	50	1.3

[a] Number of additional foxes known to be alive via radiotelemetry.

[b] Annual MNKA – number of foxes released that year.

in injuries to four individuals. The fifth animal was returned to captivity due to unacceptable weight loss and then was re-released within two weeks.

The minimum number known to be alive (MNKA) increased on both islands, and by 2007 was greater than 100 on San Miguel and greater than 60 on Santa Rosa (Table 1). The annual rate of population growth (λ) on the two islands ranged from 0.8 to 1.8, and averaged 1.2.

Annual survival ranged from 34 to 93% on Santa Rosa, where 33 radio-collared foxes died, and 84 to 100% on San Miguel, where 12 radio-collared foxes died (Fig. 2). Golden eagle predation was the most common mortality cause, accounting for 13 of the 45 mortalities (Fig. 3). No mortalities due to predation occurred in the final year of the study period, by which time 44 eagles had been removed from the northern Channel Islands, with only 1 possibly remaining (Table 2; Latta et al. 2005; Institute for Wildlife Studies 2006). Santa Rosa foxes also incurred mortalities in 2006 due to various factors not related to predation (intestinal intussusception, cholecystisis with septicemia, aggression-caused wounds, and entrapment in irrigation pipes; Coonan et al. 2007).

Results of logistic regression analysis indicated that island ($t = 3.166$, $p = 0.002$) and age at release ($t = -2.703$, $p = 0.007$) affected survival of released foxes, whereas sex ($t = 0.784$, $p = 0.433$) did not. Foxes released on San Miguel were 1.9 times as likely to survive as foxes released on Santa Rosa. Younger released foxes were more likely to survive than older foxes; odds of surviving declined by 20% with each additional year of age. Of the 39 released foxes that died during the study period, over half (20) died within three months of release, a period which coincided with the highest golden eagle activity (winter-spring).

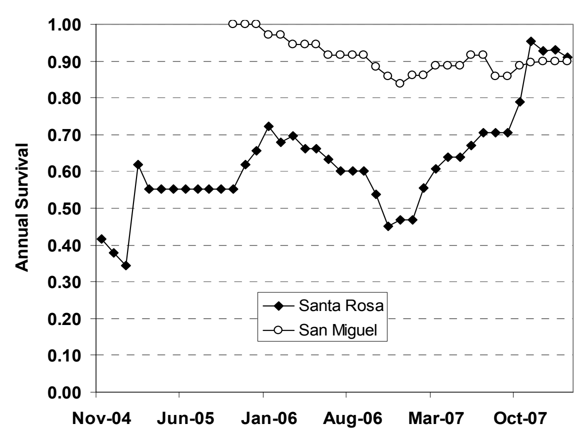

Figure 2. Annual survival of released and wild island foxes on San Miguel and Santa Rosa Islands, 2003–2007. Each point represents annual survival for the previous 12 months.

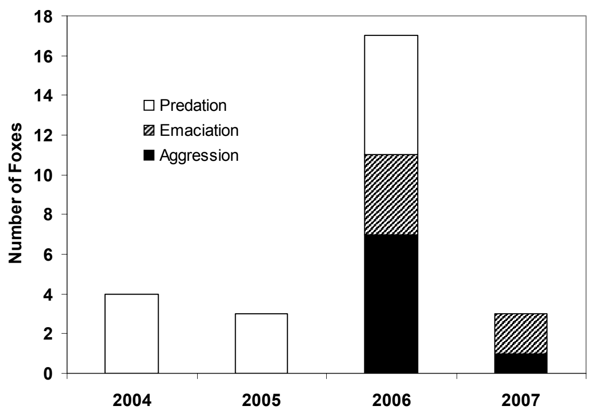

Figure 3. Mortality causes for radio-collared island foxes on San Miguel and Santa Rosa Islands, 2003–2007.

Released and wild-born foxes produced at least 119 pups, including 74 on San Miguel and 45 on Santa Rosa, as indicated by the number of pups trapped during annual population monitoring (Table 3). Remote camera monitoring of selected pairs in 2005 and 2006 revealed that 74% of monitored pairs produced pups (Table 4). Reproductive success was higher on San Miguel (94%) than on Santa Rosa (50%). Camera data indicated that eight of nine released females on San Miguel bred in the wild after release, whereas only three of eight did so on Santa Rosa.

Foxes in the wild reproduced at a fairly young age (Table 4). All of the females released on San Miguel in the fall of 2004 were juveniles, and all produced litters the following spring. In subsequent years at least 10 juveniles born to released foxes also bred and produced litters at the end of their first year. Reproduction by the first generation of wild-born individuals occurred on both islands. Seven successful breeding pairs from both islands included at least one individual born the previous spring; and for two successful pairs on San Miguel, both the male and the female were born in the wild the previous spring. The reproductive success by juvenile foxes, both released and wild-born, stands in contrast to that recorded on San Miguel prior to the decline, when only 19% of juvenile females bred successfully (Coonan et al. 2005b).

The average number of pups produced by monitored pairs was greater on Santa Rosa ($\bar{x} = 2.9$, $n = 7$) than on San Miguel ($\bar{x} = 2.2$, $n = 16$), though this difference was influenced by the occurrence of one very unusual five-pup litter on Santa Rosa in 2005. The ratio of pups to adult females from annual trapping data varied from 0.4 to 2.5 (Table 3). On San Miguel Island productivity was inversely correlated with islandwide population size (Fig. 4), suggesting a density-dependent birth rate.

DISCUSSION

In 2001 island foxes were absent from the wild on San Miguel and Santa Rosa. By 2007, within three to four years after initial releases to the wild, island fox populations on San Miguel and Santa Rosa islands could be characterized as established, recovering populations, due to high survival, high reproductive success, and subsequent high annual rate of growth. The apparent success of the reintroductions is corroborated by application of the reintroduction success standards proposed by Boitani et al. (2004). First, breeding by the first wild-born generation, as evidenced by remote camera observations, occurred quickly on both islands. Some foxes released from captivity bred in the first spring following fall releases, particularly on San Miguel, and many pups produced by released foxes also bred at the end of their first year.

Table 2. Number of golden eagles removed from the northern Channel Islands, and estimated number of golden eagles remaining, after annual capture efforts in 2000–2007.

	Eagles removed	Eagles remaining
2000	13	10
2001	6	8
2002	3	14
2003	9	13
2004	7	11
2005	3	3
2006	3	2
2007	0	1
Total	44	

Data are from Latta et al. 2005; Institute for Wildlife Studies 2006; and D. Garcelon, Institute for Wildlife Studies, unpublished data.

Table 3. Wild pups captured during annual trapping efforts, and ratio of pups to adult females trapped, on San Miguel and Santa Rosa islands, 2005–2007.

	San Miguel		Santa Rosa	
	Pups	Pups/ adult female	Pups	Pups/ adult female
2004	--	--	2	0.4
2005	10	2.5	9	1.0
2006	37	2.5	21	2.1
2007	27	1.4	13	0.76
Total	74		45	

Second, recruitment exceeded adult death rate on both islands over a three-year period, as reflected in average lambda.

The third reintroduction success factor of Boitani et al. (2004) is the establishment of a self-sustaining population, a condition best evaluated with demographic modeling. Recent demographic modeling (Bakker and Doak 2009; Bakker et al. 2009) suggests that at the present 90% survivorship, a sustained population size of as few as 150 yields acceptable extinction risk. As of 2008 the San Miguel population had met this demographic goal and at current levels of recruitment and survivorship, the Santa Rosa population may reach this demographic target within several years (T. Coonan, unpublished data).

Population growth rates were higher on San Miguel, due to both higher survival and higher reproductive success. Santa Rosa foxes suffered higher predation due to the continued presence of golden eagles, which bred on Santa Rosa but never on San Miguel (Latta et al. 2005). The lower reproductive success on Santa Rosa may be attributed to the Allee effect (difficulty in finding mates at low densities). Recent demographic modeling found evidence for Allee effects in island fox population dynamics (Bakker et al. 2009). Santa Rosa's larger size may have made it more difficult for released foxes to find mates. Foxes traveled farther from release sites on Santa Rosa than on San Miguel (T. Coonan, unpublished data).

The success of these initial releases of island foxes to the wild on San Miguel and Santa Rosa islands bodes well for eventual recovery of those two subspecies, and we identify five factors common to both islands that have contributed to this success: 1) mitigation of the primary mortality factor; 2) release location and habitat quality; 3) high reproduction at low densities; 4) comprehensive monitoring of released animals; and 5) a flexible adaptive management strategy. We discuss each of these factors below.

Reduced Predation

The primary reason for the recovery of island fox populations was the early detection and mitigation of eagle predation, the primary cause of fox mortality. Eagle removal eliminated this catastrophic mortality factor, increased fox survivorship, and allowed reintroduction to succeed. By 2007, virtually all the golden eagles present at the beginning of the decline had been removed from the islands or had left of their own accord (Latta et al. 2005; Institute for Wildlife Studies 2006). From 1999 to 2004 a total of 31 adult golden eagles were removed from Santa Cruz and Santa Rosa islands, with a corresponding increase in wild fox survival on Santa Cruz from 61% to >80% (Coonan et al. 2005a) as well as the increase in survival on Santa Rosa, documented in this study. During the study, golden eagle presence and breeding supported by an alien prey base were the substantial differences between Santa Rosa and San Miguel. For species naïve to diurnal predators (Roemer et al. 2001b), the presence of even a few golden eagles tips the balance toward decline (Bakker et al. 2009). On San Miguel, in the absence of eagles, natural productivity was extremely high, and annual survival was over 90% (Fig. 2).

Minimizing eagle impacts on foxes in the long run may ultimately depend on removing the factors that attract and support them there. Golden eagle presence on the islands was facilitated by an alien prey base—feral pigs on Santa Cruz Island and mule deer on Santa Rosa Island (Collins and Latta 2006). By 2008 significant progress had been made toward changing the ecological conditions that allowed golden eagles to persist on the northern Channel Islands. The eradication of feral pigs on Santa Cruz Island is complete (Morrison et al. 2007), but mule deer will remain on Santa Rosa Island until their scheduled removal in 2011. As long as this food source persists on the island it could continue to draw golden eagles from the mainland. Golden

Table 4. Breeding success of radio-collared wild fox pairs on San Miguel (SMI) and Santa Rosa (SRI) islands, 2005–2006, as determined by remote cameras.

Island	Year	Pair#	Female	Born	Age	Male	Born	Age	Pups
SMI	2005	M0501	F302	Captive	1	M203	Captive	3	2
SMI	2005	M0502	F301	Captive	1	M201	Captive	4	2
SMI	2005	M0503	F303	Captive	1	M206	Captive	2	4
SMI	2005	M0504	F304	Captive	1	M205	Captive	1	2
SMI	2006	M0601	F301	Captive	2	M201	Captive	5	1
SMI	2006	M0602	F302	Captive	2	M203	Captive	4	1
SMI	2006	M0603	F304	Captive	2	M205	Captive	2	3
SMI	2006	M0604	F303	Captive	2	M206	Captive	3	1
SMI	2006	M0605	F305	Captive	3	M202	Captive	4	2
SMI	2006	M0606	F308	Captive	4	M209	Captive	3	0
SMI	2006	M0607	F313	Captive	2	M214	Captive	4	2
SMI	2006	M0608	F306	Captive	3	M223	Wild	1	2
SMI	2006	M0609	F309	Captive	1	M210	Captive	1	4
SMI	2006	M0610	F311	Wild	1	M208	Captive	1	1
SMI	2006	M0611	F310	Wild	1	M207	Captive	3	4
SMI	2006	M0612	F316	Wild	1	M222	Wild	1	2
SMI	2006	M0613	F315	Wild	1	M218	Wild	1	2
SRI	2005	R0501	F118	Wild	1	M09	Captive	1	3
SRI	2005	R0502	F106	Wild*	6	M05	Captive	3	2
SRI	2005	R0503	F111	Captive	4	M06	Captive	3	0
SRI	2005	R0504	F104	Captive	2	M08	Captive	2	3
SRI	2006	R0601	F104	Captive	3	M08	Captive	3	5
SRI	2006	R0602	F118	Wild	2	M09	Captive	2	4
SRI	2006	R0603	F103	Captive	4	M02	Captive	5	1
SRI	2006	R0604	F111	Captive	5	M06	Captive	4	0
SRI	2006	R0605	F125	Captive	3	M12	Captive	5	0
SRI	2006	R0606	F107	Captive	3	M20	Wild	1	0
SRI	2006	R0607	F109	Captive	4	M18	Captive	6	0
SRI	2006	R0608	F126	Captive	5	M14	Wild	1	0
SRI	2006	R0609	F129	Wild	1	M19	Captive	1	2
SRI	2006	R0610	F121	Wild	1	M10	Captive	1	0

*1 of 15 foxes brought into captivity in 2000, successful founder.

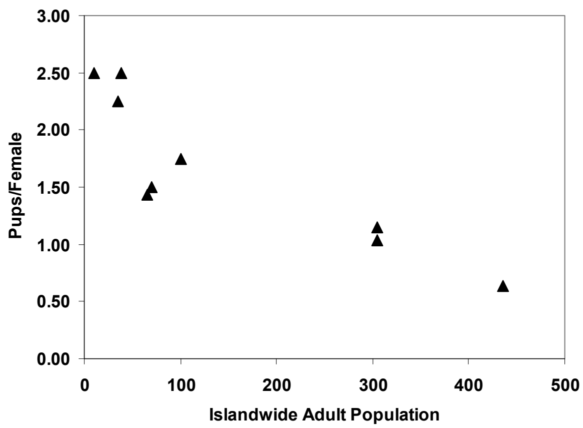

Figure 4. Island fox reproductive effort (pups/adult female) and islandwide population size, San Miguel Island, 1993–2007.

eagles may be discouraged from remaining long on the islands due to the islands' recovering population of bald eagles (*Haliaeetus leucocephalus*), which were reintroduced to the northern Channel Islands from 2002 to 2006. Bald eagles compete with golden eagles for territories, and do not prey as heavily on island foxes (Buehler 2000; Collins et al. 2005; Collins and Latta 2006). As of 2008, more than 30 young bald eagles inhabited the islands, and two bald eagle pairs fledged young from nests on Santa Cruz Island in 2006, representing the first successful nesting attempts by bald eagles on the islands in over 50 years (D. Garcelon, Institute for Wildlife Studies, unpublished data).

Habitat Quality

Foxes were released into the core of their historic range (Wolf et al. 1996), habitat that is likely of similar or better quality than when foxes were extirpated. On San Miguel Island, for example, sheep grazing during the last century resulted in extreme reductions in vegetative cover. Since the removal of sheep from the island in 1968, native vegetation communities have increased in distribution, expanding into areas that were previously denuded and covered with sand (Hochberg et al. 1979). This condition provides fox habitat that is likely better now than at any other time in the last 50–100 years, and food resources for foxes (including insects, rodents, and fruits [Moore and Collins 1995]) that are likely more plentiful. Similarly, the removal of cattle from Santa Rosa Island in 1998 likely resulted in increased cover and overall habitat quality for both foxes and small vertebrate prey. Deer mice (*Peromyscus maniculatus*), a primary food for foxes (Moore and Collins 1995), have reached higher densities on San Miguel since foxes have been absent (NPS unpublished data), a condition that is likely mimicked on Santa Rosa Island. Moreover, the entire range of each subspecies is completely protected as a National Park, and there has been no net loss of habitat area on either island since foxes have been in captivity. Reduction in core habitat size and/or quality, prey availability, and threats from humans have been identified as primary reasons for previous failures of rare species reintroductions (Fischer and Lindenmayer 2000; Woodroffe and Ginsberg 2000; Moehrenschlager and Macdonald 2003; Van Zant and Wooten 2003; Steury and Murray 2004), but none are a factor for released foxes on San Miguel and Santa Rosa islands. Conversely, the ability of the habitat at this point to provide substantial resources appears to be excellent, resulting in rapid population increase and high survival. For example, on San Miguel Island, the number of foxes in the wild in 2007 was 105, approximately one quarter of the total population estimated to exist on the island prior to the decline (Roemer et al. 1994).

Absence of Competition and High Reproductive Success at Low Densities

The first groups of foxes were released into areas with no conspecifics and were consequently unconstrained in home range establishment. This may be the reason that reproductive success was extremely high not only for released foxes but for their offspring. The reproductive success by juvenile foxes, both released and wild-born, stands in contrast to that recorded on San Miguel prior to the decline, when only 19% of juvenile females bred successfully (Coonan et al. 2005b). Young, inexperienced females may have been able to breed successfully in the wild following release because fox densities were low enough to preclude limitation by lack of territory availability (Roemer et al. 2001b), yet individuals still had access to potential mates because multiple individuals were released at each release site.

Cumulative data from San Miguel populations at all densities from 1993–2007 (10–400/island), show that reproductive success is inversely density dependent. Given suitable habitat, access to potential mates, and minimal sources of mortality, at low densities the population exhibited extremely rapid growth. As the recovering populations approach carrying capacity, available territories will become scarce, and reproductive success may decline to levels similar to those seen in the early 1990s, at high densities. Nevertheless, the high reproductive success of released and wild foxes at low densities is responsible for quick re-establishment of fox populations. While it is possible that Allee effects (Angulo et al. 2007; Bakker et al. 2009) explain differences between reproductive success on San Miguel and that on Santa Rosa, the overall ability of island foxes to reproduce well at low and medium densities obviates the need for a long-term reintroduction program. In effect, the foxes are recovering themselves.

Monitoring

Comprehensive monitoring of released foxes and wild populations has allowed quick assessment of predation rates, fox survival, and recruitment in the wild, all critical metrics for evaluating the success of releases (Sarrazin and Barbault 1996). All released foxes were radio-collared, as were the majority of the pups born in the wild, and by the end of the study period there were over 80 radio-collared foxes on the two islands. Mortality checks were conducted several times per week, thus providing critical information on predation events and general locations of eagles, and remote camera monitoring and annual trapping proved excellent tools for assessing wild reproductive success. Understanding these dynamics of the recovering wild populations allowed NPS to make informed management decisions regarding the captive breeding and release program, as described below.

Adaptive Management

A recovery approach that includes adaptive management has contributed greatly to the success of the program to date. The formal island fox recovery team established by USFWS was known as the Recovery Coordination Group (RCG) and included individuals from the land management agencies (such as NPS), the USFWS, and non-agency scientists. Management recommendations and requests for information from this group were transmitted through the USFWS to the land-management agencies. For example, by 2003 and 2004 the Santa Rosa and San Miguel captive populations had reached the target sizes at which releases to the wild could be considered, but the prospect of releasing foxes in the presence of golden eagles was controversial (Roemer et al. 2002; Courchamp et al. 2003; Coonan et al. 2004; Roemer and Donlan 2004). The RCG was generally cautious regarding this approach, but the USFWS recommended that releases might be conducted with pre-determined mortality thresholds that, if reached, would require that foxes be returned to captivity. In the spring of 2005, the pre-determined recapture trigger (five predation-caused mortalities) was reached on Santa Rosa Island, but recapture efforts at that time would potentially have separated whelping females from their pups. Accordingly, the USFWS recommended against recapture efforts. Eagle-caused mortalities subsequently ended, and four litters were born in the wild to females that otherwise might have been returned to captivity. The flexibility of such an adaptive approach is critical for a recovery program where management actions are based largely on the results of ongoing monitoring of the released species as well as the behavior of another species, both being factors that can vary considerably within a short period of time.

Decision to Close Captive Breeding

Although the San Miguel captive breeding program produced 53 pups from 1999 to 2006, no pups were produced in 2007 (Coonan and Dennis 2007; T. Coonan, National Park Service, unpublished data). Moreover, from 2005 to 2007 the number of pups produced in the wild was over four times that produced in captivity, and was specifically greater for juvenile females and first-year pairings compared to that in captivity. The lack of breeding by juvenile females in captivity might have been due to social suppression, since mated pairs held in captivity are separated from adjacent pairs by distances of only 3–50 m (C. Asa, St. Louis Zoo, unpublished data). In contrast, the unconstrained mate choice that occurs in the wild likely leads to many more successful pairings than can be “arranged” in captivity. Freedom of movement also allows wild females to avoid injuries due to male aggression during the breeding season, an occurrence that became increasingly common in the captive populations. The additional problem of neonatal mortality surfaced in the latter years of the captive breeding program. In 2007, comparison of ultrasound results with the number of pups eventually whelped showed that females lost 7 of 14 pups observed on ultrasound on San Miguel and 14 of 21 observed on Santa Rosa (Clifford and Vickers 2007). Some neonatal loss comprised late-term abortion, which is rare in canids, and underlying causes may have included bacterial infection due to reduced maternal immune response, perhaps mediated through stress (C. Asa, St. Louis Zoo, unpublished data). These captive reproductive problems were never resolved.

Given the apparent difference in productivity, by 2007, maintaining foxes in captivity, as opposed to allowing them to reproduce in the wild, was no longer a sound investment strategy for island fox recovery, at least on San Miguel Island. Accordingly, in 2007 all the remaining captive foxes (save two very old females) were released on San Miguel and the facility was closed. In fall 2008 the Santa Rosa captive breeding program was also closed, and all remaining foxes (except for two considered unreleasable) were released to the wild. As on San Miguel, the reproductive rate in the wild had greatly exceeded that in captivity. Ceasing captive breeding marked the achievement of one practical measure of reintroduction success, in addition to the biological milestones presented in this paper.

By 2008, the MNKA for Santa Rosa was 122 foxes, and the population estimate for the San Miguel subspecies, derived from mark-resight efforts on four small grids, was 172 adults, with an additional 100 pups (Coonan 2009). This put the San Miguel subspecies at biological recovery, as determined by comparison to population modeling-derived recovery criteria (Bakker and Doak 2009), and represented an eightfold increase in the Santa Rosa subspecies since its nadir in 2000. Less than 10 years after the remaining 15 individuals from each subspecies had been removed from the wild for captive breeding, both subspecies were recovered or recovering, fully in the wild. Compared to other canid species, there were fewer impediments to recovery for the island fox. They reproduced adequately in captivity and spectacularly in the wild following release, perhaps due to their relatively simple mating system compared to wolves and African wild dogs. No economic development or commercial activity such as ranching was hampered by their recovery; their entire range was managed by conservation organizations; and most importantly, the primary mortality factor was effectively mitigated. Island fox recovery was perhaps most similar to that of reintroduced swift foxes in Montana (Ausband and Foresman 2007), where mortality from predation was overcome by high reproductive success to produce increasing populations. The calculated risk of island fox releases had paid off: though eagle predation had not been completely mitigated when releases began in 2003, high reproduction by released foxes and the resulting quick establishment of wild populations justified that calculated risk.

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