CURRENT STATUS OF THE SANTA CRUZ ISLAND FOX (*UROCYON LITTORALIS SANTACRUZAE*)

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Abstract—Santa Cruz Island fox (*Urocyon littoralis santacruzae*) populations declined precipitously in the last decade. To assist fox recovery, removal of predatory golden eagles (*Aquila chrysaetos*) and feral pigs (*Sus scrofa*) is underway. We report on the current status of the fox based on trapping and radiotelemetry over six seasons (summer: May–October, winter: November–April) beginning winter 2000. We captured 173 foxes 590 times in 6,766 trap nights and radiocollared 58 foxes. Most estimates of abundance were approximately steady throughout the study period, including minimum number known alive (approx. 70–80 foxes) and mark-recapture estimates of abundance (approx. 105–128 according to the best model), although trap success declined sharply (83% in the Central Valley). Trap success varied spatially, with relatively more foxes captured in the Central Valley than elsewhere. Annual non-pup survival tended to increase in summer and winter 2002 relative to the previous year based on telemetry data (80% vs. 59%, $P = 0.17$). Annual pup survival averaged 62% throughout the study, but substantial uncertainty accompanied this estimate. The ratio of pups to non-pups captured in summer averaged 0.45. Similarly, birth rate estimates based on lactation rates and numbers of pups weaned was 0.34 for yearlings and 0.45 for adults. Although we could not detect spatial differences in reproduction, foxes in the Central Valley were heavier than foxes elsewhere, and age distributions showed relatively more pups there, both suggestive of higher reproductive rates. Current vital rates yielded a simple deterministic growth rate estimate of $\lambda = 1.00$, consistent with a stabilizing population. Although many demographic parameters had considerable uncertainty due to small sample sizes inherent to rare populations, most results supported the conclusion that the population is small but approximately stable, survival is steady or increasing, and the Central Valley is providing the highest quality habitat.

Keywords: abundance, demography, island fox, reproduction, Santa Cruz Island, survival

INTRODUCTION

Island foxes (*Urocyon littoralis*) are endemic to the Channel Islands, occurring only on the six largest islands. Each island supports a unique subspecies (Gilbert et al. 1990, Wayne et al. 1991), and the three subspecies inhabiting the northern Channel Islands have declined dramatically in the last decade (Roemer et al. 2001a, Coonan 2003). On Santa Cruz Island, foxes numbered over 1300 in the early 1990s, but only about 130 remained by 1999 (Roemer et al. 2001b). Concurrently, San Miguel and Santa Rosa Island populations dropped to fewer than 30 foxes, and all individuals (except one on San Miguel Island) were removed from the wild and placed in captive breeding pens (Roemer et al. 2001a, Coonan 2003). A captive breeding program was also established on Santa Cruz Island. Listed as a threatened species by the State of California and critically endangered by the IUCN, the fox is one of the most imperiled carnivores in North America.

As the largest of the islands, Santa Cruz Island has historically held the largest fox populations, and at the time of this study was the only northern island with a wild population. The Santa Cruz Island fox (*U. littoralis santacruzae*) is threatened by golden eagles (*Aguila chrysaetos*), which may be maintained at high levels by feral pigs (*Sus scofa*), an exotic prey species introduced in the 1850s (Roemer et al. 2001b). Golden eagle sightings were historically rare on Santa Cruz Island but rose in the 1990s, perhaps spurred by loss of mainland habitat (Roemer et al. 2002). The extirpation of piscivorous territorial bald eagles (*Haliaeetus leucocephalus*) resulting from organochloride contamination may have further facilitated the colonization of the island by golden eagles (Roemer et al. 2001a, Coonan 2003). Hyperpredation on island foxes by golden eagles appears to have decreased fox survival rates by nearly 80% between 1993 and 1995 (Roemer et al. 2001a). Also, feral pigs have converted many native shrublands to grasslands (Van Vuren and Coblentz 1987), reducing cover available to foxes and potentially increasing their vulnerability to eagles. Major ecosystem restoration is currently being initiated on Santa Cruz Island, including final removal of predatory golden eagles and feral pigs.

We report on the current status of the Santa Cruz Island fox based on trapping and telemetry from winter 2000 through summer 2003. Our objectives were to assess abundance and population vital rates through time, across space, and by age. Because of the relatively small sample sizes and important management implications inherent to data on small populations, we compare demographic parameters derived using a variety of methods.

MATERIALS AND METHODS

Study Area and Seasons

Santa Cruz Island (34º0'N, 119º45'W, 250 km^2), located 40 km south of Santa Barbara, has rugged mountainous terrain, including two east-west oriented ranges reaching 750 m, which bracket a broad Central Valley. For spatial analyses, we divided the island into six zones (Fig. 1a) defined by topographic features, each of which contains a variety of vegetation types. In general, the West End (56 km^2) is characterized by rolling grasslands, riparian zones, and a pine forest. The North Ridge (54 km^2) is traversed by steep-sided canyons with barren slopes dropping to riparian bottoms, while numerous broader canyons with rich riparian vegetation cut across the South Side (46 km^2). The Central Valley (32 km^2) contains a mosaic of chaparral, coastal sage scrub, grasslands, eucalyptus and oak stands, and some human settlements. Both the Isthmus (39 km^2) and the East End (23 km^2) contain rolling grasslands and steeper barren slopes, with a large stand of fennel (*Foeniculum vulgare*) found in the former.

The island experiences a maritime Mediterranean climate with periodic cool winter rains typically beginning in November and a hot dry summer beginning in May. For temporal analyses, we divided the year into two seasons, beginning with summer (May–October) followed by winter (November–April). These seasons roughly correspond to biological seasons for foxes because pups are born in late April and May (Laughrin 1977), while parents leave the natal range and pups begin to disperse from October through December (Laughrin 1977, Fausett 1993).

Trapping

Trapping, conducted by the Institute for Wildlife Studies, occurred from December 2000 through October 2003, excluding the parturition season (April–May). Foxes were captured in 23- x

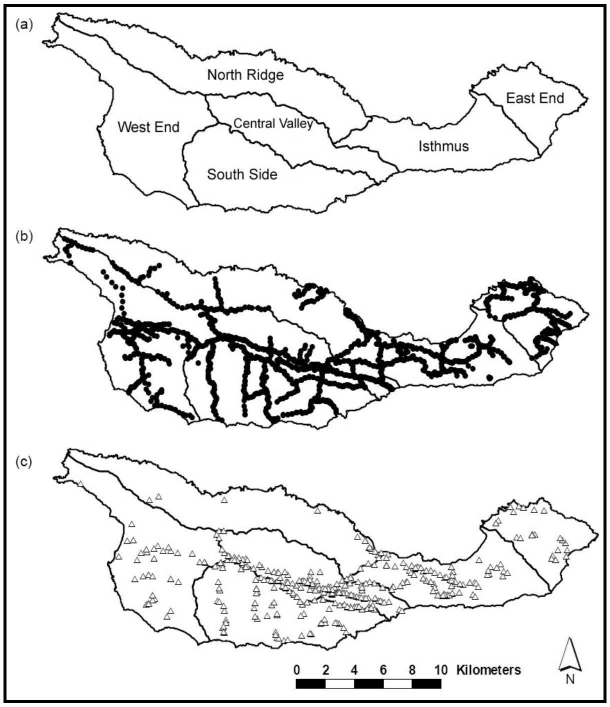

Figure 1. (a) Zones of Santa Cruz Island defined by topographic features, (b) trap locations, and (c) capture locations for Santa Cruz Island foxes.

23- x 68-cm Tomahawk box traps baited with wet and dry cat food and loganberry paste. Traps were arranged in traplines situated along roadways, drainages, ridges, and other topographic features that allowed easier access for field crews and provided potential movement paths for foxes (Laughrin 1977; Fig. 1b). Traplines averaged 12 traps (range 2–49, mode 15) with ~250 m spacing. Trapping was conducted to estimate distribution and abundance of foxes, to radiocollar foxes for survival and movement analyses, and to transfer individuals to captive breeding pens, and these multiple goals influenced location and timing of effort. Extensive island-wide trapping was conducted in the early part of the study (summer–winter 2001). After this period, trapping was halted in areas that appeared to have few or no foxes.

All captured foxes received a passive integrated transponder (PIT) tag (Biomark Inc. Boise, ID), and some foxes were radiocollared for survival analysis (see below). For each fox, field crews recorded sex, reproductive condition, weight, and age based on tooth wear patterns (modified from Wood 1958, Collins 1993). Age classes roughly corresponded to the following age ranges: 0: 0–8 months, 1: 9–24 months, 2: 25–36 months, 3: 37–48 months, 4: >48 months (Collins 1993, Crooks 1994, D. Garcelon unpubl. data). Age class 0 foxes typically show tooth wear characteristic of age class 1 near the end of their first calendar year. To adjust age classes to numerical age for the first two age classes, we re-categorized all age class 1 foxes caught January through April to age class 0 if we had evidence that this was the pup's first winter (i.e., captures as age class 0 the previous summer or as age class 1 the subsequent summer). All age-specific analyses divided foxes into three age classes: pups (revised age class 0), yearlings (revised age class 1), and adults (age class ≥2).

Abundance and Distribution

We calculated several measures of abundance, including trap success, minimum number of foxes known alive (MNKA), mark-recapture abundance, and density-extrapolated abundance. We calculated trap success as the number of captures per trapnight, making point estimates for each trapline each time it was run (i.e., each trap session, typically three days), and censoring traps closed due to disturbance or non-target captures (i.e., unavailable traps). We performed an ANOVA (PROC GLM; SAS Institute Inc. 2000) to investigate differences in the trap success among island zones using Tukey's HSD for post-hoc pairwise comparisons. To evaluate whether trap success changed through time, we assessed the slope of the regression line between trap success and time (seasons numbered chronologically) using regression (PROC REG). Because temporal changes in trap success could be affected by the areas trapped each season, we divided the island into areas of high and low trap success and included area as a dummy variable in our regression model.

We counted the MNKA for each season by incorporating individuals known to be alive in the wild at some point during the interval based on radiotelemetry and trapping data. Thus, we included foxes captured and removed from the wild to captive breeding pens during the interval, but excluded foxes produced in captivity and those residing in captivity throughout the interval.

We analyzed mark-recapture data to estimate island-wide abundance using the Cormack-Jolly-Seber model in program MARK (White 1997). We considered each of the six seasons as a potential encounter and any capture during that season a positive encounter. Most locations experienced some retrapping each season. We censored areas only trapped in one season (the coast of the North Ridge and the western part of the West End). Thus, population estimates exclude these areas. Because we collapsed extensive trapping effort into each of our encounter periods and each had variable trap effort, we performed this analysis to evaluate general trends in abundance. Population sizes for each season were estimated by dividing the number of individuals captured by the estimated recapture rate. We selected the best model (constant vs. time-varying survival and recapture rates) based on Akaike Information Criterion values adjusted for sample size. We tested for goodness-of-fit by performing chi-squared tests to assess the effects of marking on survival and recapture rates using program RELEASE, run from within MARK, and by comparing the model deviance to the mean deviance from 500-bootstrapped samples (Cooch and White 2002).

To produce another estimate of population size, we estimated density as the mean number of individual foxes captured per trap, after censoring unavailable traps, for each trapline divided by the mean home range size (0.505 km^2; Roemer et al. 2001c) as an estimate of effective trap area. We then calculated the mean density for each island zone, multiplied by the zone area, and summed zone populations. Because this method does not adjust for capture rate, this estimator is conservative. We estimated 95% confidence intervals by summing the lower and upper 95% confidence intervals for each zone. Because lower confidence limits were truncated at 0, confidence intervals may be asymmetrical.

We censored traplines with fewer than 10 traps or <175 m spacing, typically targeted at capturing specific individuals, from estimates of trap success, mark-recapture abundance, and density, which assume standardized effort and equal probability of capture. We included them in calculations of minimum numbers known alive, which accounts for individuals by all means possible.

Survival

We fitted foxes with radiocollars equipped with mortality signals for survival analyses, maintaining a sample of 20–30 individuals distributed across age classes and sexes. We checked each collar for a mortality signal at least once per week. If a collar entered mortality mode, field crews located the collar to confirm the mortality and searched for evidence of the cause of death, including signs of golden eagle predation (talon holes, degloved limbs, damaged bones, and/or feathers and whitewash at the carcass; Hockett 1989, Roemer et al. 2001b). All carcasses were necropsied (University of California, Wild Carnivore Pathology Laboratory), and both necropsies and field observations were used to determine cause of death.

For adults and yearlings, we estimated survival from radiotelemetry data using an extension of the Kaplan-Meier estimator for staggered entry designs (Pollock et al. 1989), based on a declining step function in which the at-risk population changes monthly with losses from death and censoring (battery failure, transfer to captive breeding) and gains from addition of new collars. We compared survival among ages, years, and areas with high and low fox abundance using log-rank tests (Pollock et al. 1989). Pups were only monitored during part of each year, beginning when they attained a large enough size for collaring, generally after mid-September, and ending when they became yearlings in May. Thus, we calculated pup survival based on binomial probabilities rather than the Kaplan-Meier estimator. We also estimated survival from trapping data using program MARK as described above.

Reproduction and Condition

Because we did not trap during the parturition season and did not disturb radiocollared females at natal dens, we used two indirect measures to estimate birth rate, defined as the number of female pups produced per female non-pup per year. First, after testing for equal sex ratios (binomial test, PROC FREQ), which are expected for this species (Laughrin 1977, Crooks 1994), we estimated birth rate as the number of pups captured per non-pup in summer following the birth pulse. Because Roemer et al. (2001a) found that this estimator was biased by pup undercounts on San Clemente Island, we examined pup detection rates as the proportion of yearlings caught in summer 2002 not caught as pups in summer 2001 and compared it to similar detection rates for yearlings and adults (Roemer et al. 2001a).

We also estimated birth rate as the product of the mean number of pups weaned per litter, the proportion of females breeding, and the proportion of female pups per litter. Mean number of pups weaned was determined by assigning to the same litter pups caught in traps in close proximity to each other (i.e., within the mean home range radius of 400 m, Roemer et al. 2001c) during the same trap session (≤ 5 days) during summer. The proportion of females breeding was estimated as the proportion of non-pup females captured from June through August showing signs of lactation. We used log-likelihood ratio G-tests (PROC FREQ) for all comparisons of proportions.

Because we lacked extensive spatial data on reproduction, we assessed fox body mass as an index of condition that may be correlated with breeding success. We compared body mass in areas of high and low fox abundance using an ANOVA (PROC GLM) and also examined season, sex, age and their interactions. For all analyses of reproduction, we only analyzed data from complete years (i.e., 2001 and 2002).

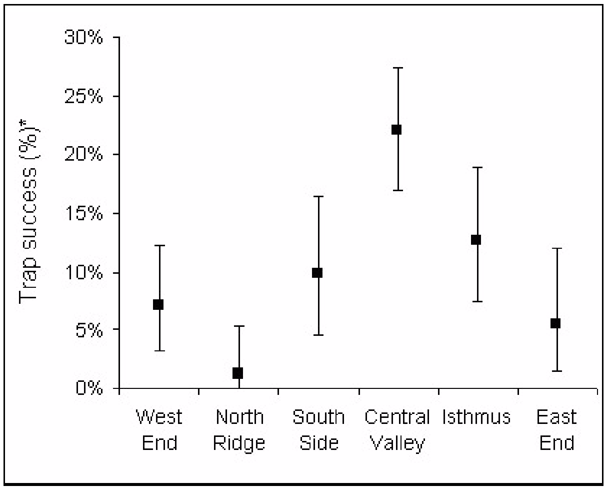

Figure 2. Trap success (± 95% CI) for Santa Cruz Island foxes by island zone. Trap success was arcsine-square-root transformed for ANOVA, and back transformed least square means are shown. Back transformation yields different values than mean untransformed values (see Table 1) and asymmetric error bars.

Population Characteristics

We assessed the age distributions of captured foxes and compared them across areas of high and low abundance. To assist in evaluation of trends in abundance and population health, we calculated a simple deterministic growth rate using a stage-structured Lefkovitch matrix model with current estimates of survival and reproductive rate for pups, yearlings and adults, where different.

RESULTS

Abundance and Distribution

We trapped from December 2000 through October 2003, logging 6,766 trap nights with 1,931 trap nights censored due to closures. We captured 173 individual foxes (89 males, 84 females) a total of 590 times (313 males, 277 females; Fig. 1c).

Trap success differed among zones (ANOVA $P < 0.001$), with trap success in the Central Valley exceeding all other zones ($P \leq 0.002$) except Isthmus ($P = 0.210$) and South Side ($P = 0.059$; Fig. 2). Isthmus rates exceeded those of the North Ridge ($P = 0.015$; Fig. 2), but trap success did not differ between any other zones ($P > 0.110$). For all other spatial analyses, we compared the Central Valley to all other zones combined. We were unable to include winter 2002 in any analyses of abundance except MNKA because only one uncensored trapline was run in the Central Valley and only two in all other zones.

Both area (Central Valley zone or not, $B = 0.426$, $P < 0.001$) and area × season number ($B = -0.060$, $P = 0.007$) were significant predictors of trap success in a model that included season number ($B = -0.011$, $P = 0.444$), explaining one-third of the variation in trap success (adjusted $R^2 = 0.333$, model $P < 0.001$; Fig. 3). Thus, season number predicted trap success only in the Central Valley; trap success decreased over time there and equaled that of other zones by the end of the study period (Fig. 3), as indicated by the strong negative interaction.

Minimum numbers known alive ranged from 59–80 after the first season of trapping (Table 1, Fig. 4). MNKA included 18 foxes captured and removed from the wild to captive breeding pens during the study period, but excluded foxes produced in captivity.

The mark-recapture model receiving the most statistical support held both survival and recapture rates constant through time (Phi [.] P[.], QAIC 250.1; Table 1, Fig. 4). A model in which both survival and recapture rates varied by season (Phi [t] P[t]) was also supported (QAIC 252.8; Table 1, Fig. 4). The former model suggests that populations remained approximately constant through time

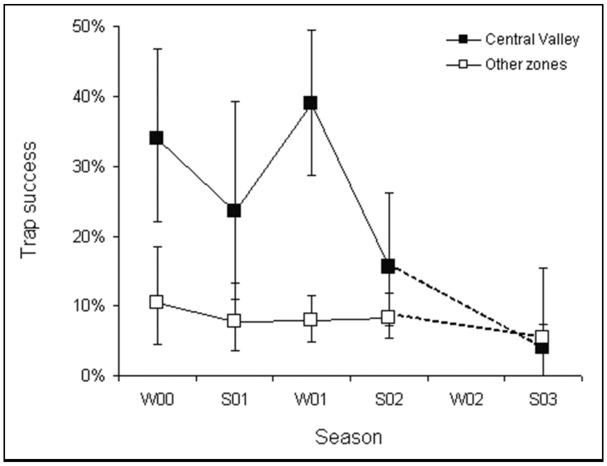

Figure 3. Changes in trap success (±95% CI) for Santa Cruz Island foxes by area (Central Valley zone or not) and season (winter 2000 through summer 2003, winter: Nov.– Apr., summer: May – Oct.). Trap success was arcsine-square-root transformed for regression, and back transformed values are shown. Back transformation yields different values than mean untransformed values (see Table 1) and asymmetric error bars.

Table 1. Estimates of abundance (± 95% CI) of the Santa Cruz Island fox population from winter (November – April) 2000 (W00) through summer (May – October) 2003 (S03). Trap success data include both 95% CI and sample sizes (number of traplines) after censoring (see text). Too few traps were set to allow abundance estimates in winter 2002.

	W 2000	S 2001	W 2001	S 2002	W 2002	S 2003
New captures	33	53	27	26	3	32
Recaptures	0	8	29	36	17	33
Known alive - trapping	0	13	16	7	25	0
Known alive - telemetry	0	6	7	2	14	14
MNKA - season	33	80	79	71	59	79
Trap nights	425	1122	901	1667	274	2377
Mark-recapture N (model: Phi[.] P[.])	-	115 (89 – 161)	107 (83 –149)	128 (99 – 179)	-	105 (81 – 146)
Mark-recapture N (model: Phi[t] P[t])	-	187 (110 – 370)	125 (98 –193)	79 (67 – 113)	-	-
Density-based N	61 (29 – 93)	63 (36 – 89)	70 (14 – 124)	47 (23 – 72)	-	30 (13 – 47)
Trap success (%) – Central Valley	34.4 (23.0 – 45.7) 5	25.0 (10.0 – 39.9) 6	39.2 (29.6 – 48.9) 6	18.5 (10.0 – 27.1) 9	-	6.0 (0 – 12.7) 4
Trap success (%) – Other zones	10.7 (5.8 – 15.5) 3	11.4 (5.8 – 17.1) 18	9.4 (6.4 – 12.3) 15	9.5 (6.5 – 12.6) 12	-	5.8 (3.9 – 7.6) 10

with numbers of foxes between 105 and 128. The latter indicates a drop from 187 in summer 2001 to about 80 in summer 2002. Marking did not appear to influence survival and recapture rates ($P > 0.194$).

Density-based estimates increased from 61 in winter 2000 to 70 in the middle of the study, then dropped to 30 by summer 2003 (Table 1, Fig. 4). Density-based estimates were lower than the minimum number known alive for all but the first season. The Central Valley was trapped in all seasons for which we derived a density-based estimate; for other zones not trapped in particular seasons, we used the average density of all zones trapped, excluding the Central Valley.

Survival

A total of 58 wild-born foxes was radiocollared (31 males, 27 females) and monitored for survival from 19 December 2000 through 31 October 2003, averaging 23 at any one time. Of these, 18 died. We attributed 12 mortalities to possible or probable golden eagle predation (67%), and three more incomplete carcasses may have been golden eagles kills. Cause of death was not golden eagle predation for only three foxes (17%).

We monitored a total of 15 wild-born pups; six in 2000, three in 2001, two in 2002, and four in 2003. All of these pups survived their entire first year, although most were monitored for only four to five months before becoming yearlings. In addition, three captive-born pups were collared and released in winter 2002, and two of these were killed by golden eagles within 16 days. Combining wild and captive-born pups, we estimated an annual pup survival of 62.0% (95% CI: 22.2–91.9) based on two fox deaths in 1,527 monitored fox-days.

Annual survival of adults and yearlings appeared to increase during the study period (Fig. 5a), rising from 58.8% (42.6–74.9) in 2001 to 80.0% (63.9–96.1) in 2002, but the difference was not significant ($P = 0.115$). Overall, adult and yearling survival during the study was 74.3% (65.2–81.7). Survival rates did not differ between adults and yearlings ($P = 0.956$; Fig. 5b). Survival in the Central Valley, where fox abundance was highest, was similar to survival elsewhere (annual survival 79.1 vs. 72.3%, $P = 0.447$; Fig. 5c).

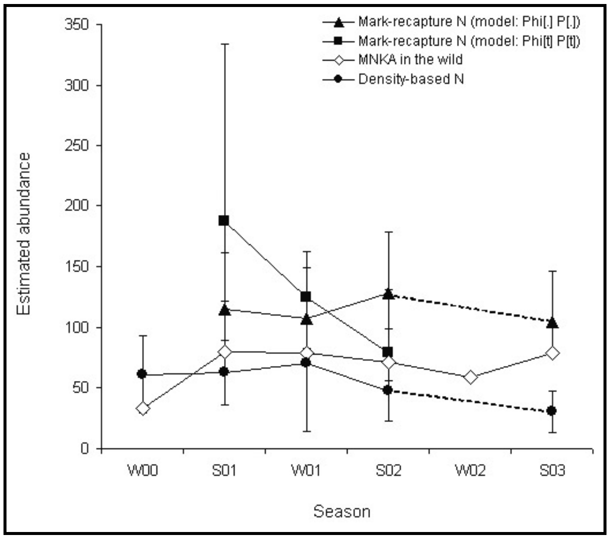

Figure 4. Estimates of abundance (±95% CI) for the Santa Cruz Island fox from winter 2000 through summer 2003. Mark-recapture N estimates are based on the two models with the most statistical support: the best model, Phi (.) P (.), holds both survival (Phi) and recapture rates (P) constant through time, and model Phi (t) Phi (t) is an alternate model in which both survival and recapture rates vary by season.

The annual survival rate for all ages based on trapping data was 63.9% (45.1–78.4) assuming a model with constant survival. By comparison, annual survival for all ages based on telemetry data averaged 76.4% (68.0–83.4).

Reproduction and Condition

Birth rate, estimated as the number of pups captured per non-pup in summer, averaged 0.45 (0.32–0.63, *n* = 123) and did not differ between 2001 and 2002 (*P* = 0.471). Sex ratios did not differ from unity for pups or non-pups (*P* > 0.547, *n* = 139). The proportion of individuals captured in 2002 not captured in 2001 did not differ between age classes (pups = 0.15, yearlings = 0.26, adults = 0.06, *P* ≥ 0.224, suggesting that pups were not undercounted.

The estimated number of pups weaned per litter averaged 1.68 (1.20–2.16, *n* = 22 litters) and did not differ between years (Mann-Whitney test, *P* = 0.191). All pups assigned to the same litter were captured in the same traps except for three. The proportion of yearlings (40.0%, 19.1–64.0%, *n* = 15) showing signs of lactation in summer (June–August) tended to be lower than the proportion of adults (53.8%, 28.7–77.6%, *n* = 13) but the difference was not significant (*P* = 0.428). A

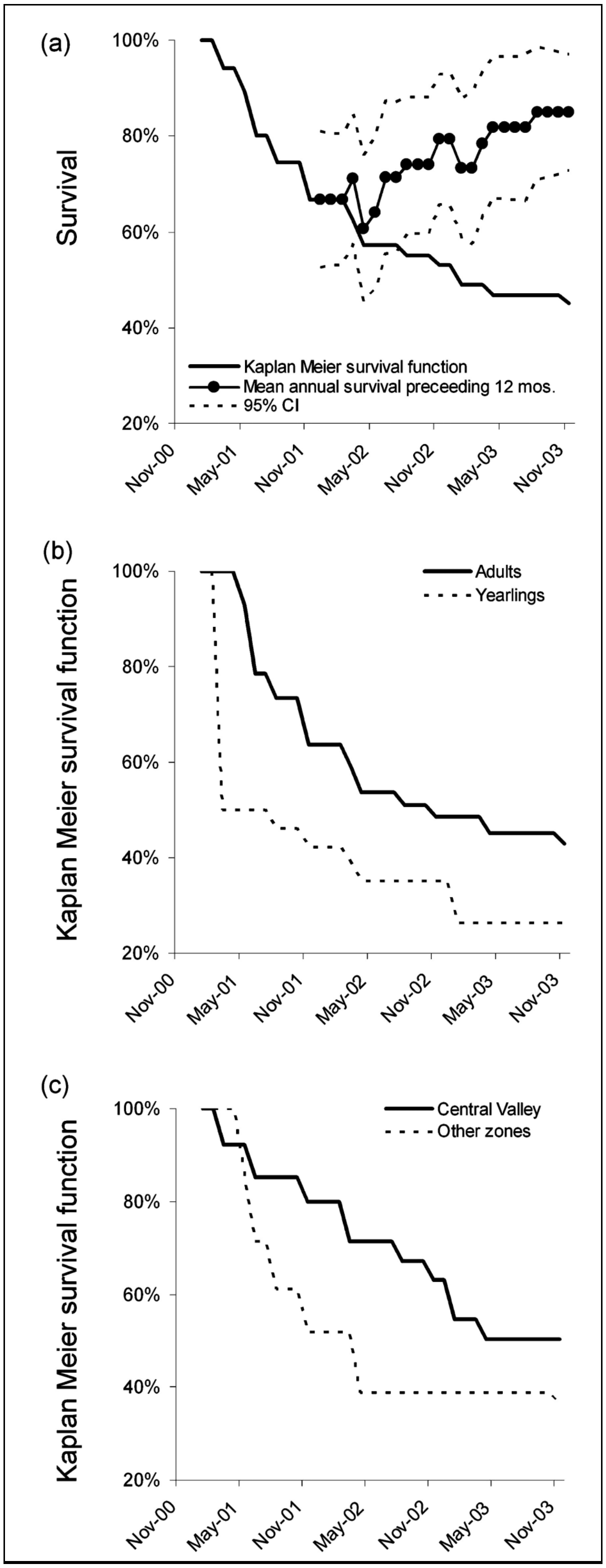

Figure 5. Survival of radio-collared Santa Cruz Island foxes: (a) Kaplan-Meier survival function and mean annual survival (±95% CI) for the preceding 12 months for all areas for adults and yearlings, (b) survival functions of adults vs. yearlings, and (c) survival functions by area.

second estimate of birth rate based on these lactation rates and numbers of pups weaned was 0.34 (0.12–0.69) for yearlings and 0.45 (0.17–0.84) for adults.

Foxes in the Central Valley were significantly heavier than those in other zones (Table 2, Fig. 6). Body mass was also greater for male foxes, for foxes in winter, and for yearlings and adults relative to pups. There were significant area × age, age × season, and age × season × sex interactions, in part because body masses differed between areas primarily for younger foxes, because pups had disproportionately lower mass in summer and because pregnant females increased mean female mass in winter.

Population Characteristics

Age distributions were skewed toward pups and yearlings, except areas outside the Central Valley in 2002 (Fig. 7). The Central Valley had relatively more pups and fewer non-pups than other zones ($P = 0.023$, no difference between years, $P > 0.747$; Fig. 7).

Using current estimates of vital rates in a stage-structured Lefkovitch matrix model (Table 3) yielded a simple deterministic growth rate estimate of $\lambda = 1.00$. Despite overlapping confidence intervals in vital rates between pups and non-pups, we used a two-stage matrix because previous demographic analyses documented differences between these age classes (Roemer et al. 2001b).

Table 2. ANOVA comparing body mass of the Santa Cruz Island fox by area (Central Valley–other zones; Fig. 1), age (pup–yearling–adult), season (winter–summer), and sex.

Source	df	F	*P*
Area	1	16.62	<0.0001
Age	2	72.05	<0.0001
Season	1	34.22	<0.0001
Sex	1	16.56	<0.0001
Area × age	2	4.40	0.013
Area × season	1	1.37	0.243
Area × sex	1	2.05	0.154
Age × season	2	28.79	<0.0001
Age × sex	2	1.40	0.248
Season × sex	1	0.14	0.705
Area × age × season	2	1.43	0.242
Area × age × sex	2	0.76	0.471
Area × season × sex	1	0.61	0.434
Age × season × sex	2	4.28	0.015
Area × age × season × sex	2	1.67	0.190

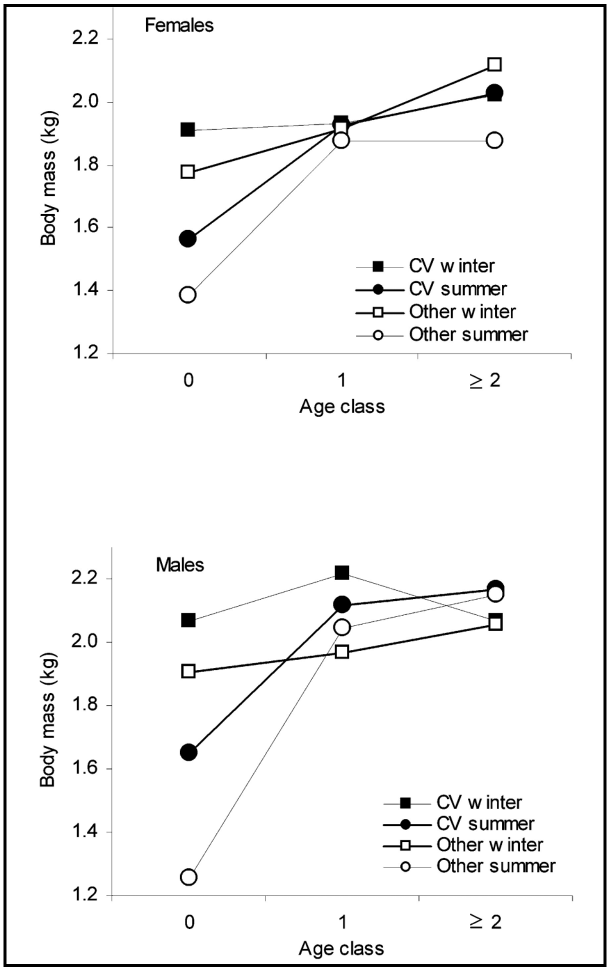

Figure 6. Body mass of captured Santa Cruz Island foxes by sex, area (Central Valley vs. other zones), season, and age.

DISCUSSION

The population of foxes on Santa Cruz Island appears to have slowed its steep decline of the 1990s. Most measures of abundance appeared to stabilize during the study period. Minimum numbers known alive were approximately steady, varying between 71 and 80 individuals for all seasons in which trap effort exceeded 900 (Table 1, Fig. 4). MNKA for winters 2000 and 2002 are likely biased low due to reduced trapping effort (Table 1). Mark-recapture estimates also held approximately steady according to the best statistical model used for estimation (Table 1, Fig.

Figure 7. Age distributions of captured Santa Cruz Island foxes by area (Central Valley vs. other zones), and year (2001 vs. 2002).

4). Trap success, however, is typically highly correlated with population size in island foxes (Roemer et al. 2002), and it declined by over 80% in the Central Valley in three years. Trap success may be influenced by changes in trappability, which can be affected by factors such as availability of prey and other food resources. Density-derived estimates of abundance dropped by about half in three years, but this estimator, which does not correct for changes in trappability, was frequently below the MNKA, and thus performed poorly. Consistent with estimates of abundance showing a stabilizing population, the deterministic growth rate estimate of 1.00 based on vital rates for the same time period indicates a stable population. This estimate of λ, however, fails to incorporate stochastic variation in vital rates, which would produce a lower observed growth rate.

Annual survival of adult and yearling foxes appeared to be steady or increasing based on radiotelemetry data, rising from 59% in summer and winter 2001 to 80% the following year. These survival rates represent a dramatic increase over rates observed in the 1990s, in which annual survival dropped to 33% (21% over 17 months; Roemer et al. 2001b), and are comparable to rates reported prior to the decline (45% for pups, 92% for yearlings, and 69% for adults; Roemer et al. 2001). The annual survival estimate for radiocollared pups (62%) should be interpreted with caution due to small samples sizes and subsequent wide confidence intervals and to the nature of the sample itself. The two pups dying during the study were released from captive-breeding pens, and they may have been more naïve than wild pups and therefore more susceptible to predation. Captive-bred foxes are necessarily inexperienced both at exploration and with the release area. On the other hand, the survival of wild born pups, which was 100%, is likely biased high because most pups were collared in December and January, and pups may experience significant mortalities in summer and fall. Age distributions were more skewed toward pups and yearlings than those reported for the island for 1973–1976 (Laughrin 1980) and 1998 (Crooks et al. 2001), a difference that can result from decreased survival rates (Moore and Collins 1995).

The increase in annual non-pup survival to 80% was recorded during a period of intensive golden eagle removal from November 1999 through June 2003 during which time 27 eagles were captured (Coonan et al. 2005). Despite these efforts, however, two active nests and five to eight eagles remained each year, and we attributed at

Table 3. Stage-structured Lefkovitch matrix for the Santa Cruz Island fox. Stage-specific fertilities (F) appear in row 1 and were calculated as the birth rate (b) for the stage × the annual survival rate (S) for the preceding year. Stage-specific survival rates appear in the second group. Both birth rate and survival estimates were based on this study. Growth rate (λ) = 1.00.

$F_{yearling} = b_{yearling} \times S_{pup}$	$F_{adult} = b_{adult} \times S_{adult}$
S_{pup}	S_{adult}
0.208 = 0.336 × 0.620	0.336 = 0.452 × 0.743
0.620	0.743

least 67% of fox mortalities observed in this study to eagle predation. Population viability analyses (Coonan 2003; Miller et al. 2003) indicate that on Santa Cruz Island a non-pup survival of 78% is needed for a stable or growing population if pup survival is 60% (close to our estimate of 62%). Despite a likely increase in non-pup survival on the island, vital rates appear too low to translate into an increasing population. Impending pig eradication is intended to remove the primary prey supporting breeding eagles on the islands. If eagle populations are eliminated through this effort, fox survival and abundance should increase in the long term, but the loss of eagle prey may increase predation on foxes in the short term (Courchamp et al. 2003).

Our two independent estimates of birth rate were similar; 0.45 overall based on the ratio of pups captured per non-pup and 0.34 for yearlings and 0.45 for adults based on estimates of lactation rates and numbers of pups weaned per litter. Both birth rate estimates were somewhat low relative to estimates from 1993 and 1994 prior to the current fox decline when rates were 0.42 for yearlings, 0.54 for young adults and 0.69 for older adults (Roemer et al. 2001a). We captured ≤85% of the known pups, which could have led to an underestimate of the number of pups weaned. Our estimated number of pups weaned (1.68) is, however, comparable to other estimates for Santa Cruz Island: 1.53 (weaned pups; Miller et al. 2003), 2.17 (*n* = 24 dens; Laughrin 1977), and ≤2.27 (mean embryo count, *n* = 10 females; Moore and Collins 1995), and similar to estimates for other islands of 1.8 (weaned pups on Santa Catalina Island, *n* = 14 dens; D. Fritcher pers. comm.). Our lactation rates (40.0% of yearlings, 53.8% of adults) were somewhat low relative to the proportion of females weaning pups on Santa Cruz Island in previous studies (38.6% of yearlings, 61.3% of adults; Miller et al. 2003). True lactation can be difficult to distinguish in the field and pseudolactation may occur in island foxes as in other canids (Asa and Valdespino 1998).

The Central Valley appeared to be superior habitat for foxes. We found abundance indices (i.e., trap success) to be generally higher in the Central Valley than elsewhere (Figs. 2 and 3), and although abundance may not indicate quality (Van Horne 1983, Pulliam 1988), our evidence indicates that vital rates in the Central Valley are likely equal to or higher than rates in other areas. Survival was similar in different areas (Fig. 5), but the higher body mass of younger foxes in the Central Valley (Fig. 6) suggests individuals there are in better condition, which may increase reproductive rates. Age distributions revealed disproportionately high numbers of pups in the Central Valley. This difference could be produced by higher birth rates and pup survival or by lower non-pup survival in the Central Valley relative to other zones. Our survival data do not support the latter possibility, and our body mass data may support the former. The large number of yearlings outside the Central Valley may represent immigration of pups produced in the Central Valley. The Central Valley supports a rich mosaic of habitats, ample cover, and a diverse prey base for the island fox, consisting of a variety of plant and animal dietary items, and such conditions may contribute to higher birth and growth rates.

Overall, our data indicate that the Santa Cruz Island fox decline has slowed and populations are stabilizing, that survival is steady or increasing, and that the Central Valley provides the best habitat on the island. Due to the small sample sizes inherent to monitoring small populations, substantial uncertainty accompanies many of our individual estimates of abundance and vital rates. Nonetheless, the demographic parameters we calculated using different methods produced similar results and supported similar conclusions, decreasing overall uncertainty. These data can help guide management of the Santa Cruz Island fox and can serve as a baseline against which to compare the health of the population during and after eagle and feral pig removal.

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