MSRP Seabird Restoration Program – San Nicolas Island, California

Annual Report on Island Fox Care and Monitoring Provided in Support of the San Nicolas Island Seabird Restoration Program–2012

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Executive Summary

In 2009-2010, the Montrose Settlements Restoration Program, in cooperation with the U.S. Navy, carried out a project to remove feral cats (*Felis catus*) from San Nicolas Island in order to protect seabirds and other native wildlife. The Institute for Wildlife Studies was contracted to evaluate impacts of the leg-hold trapping effort used to capture feral cats on the fox population overall. This report summarizes the findings from evaluation of fox monitoring carried out on 26 - 2 × 6 trapping grids (12 trap) in 2010, and again in 2012, and 3 larger (48-50 trap) long-term monitoring grids trapped annually from 2000-2012. There was reduced apparent adult survivorship in 2009 from the long-term monitoring grids, and lower recapture rates in 2012 of foxes captured in 2010 on mini-grids located in areas intensively trapped for feral cats relative to foxes captured in areas with low intensity or no leg-hold trapping in 2009-2010. There was also a decline in 2009 of the fox population within the area covered by the two westernmost long-term monitoring grids. The third long-term monitoring grid did not show a decline in foxes, nor did the fox population in areas covered by the mini-grids decline from 2010-2012. These results indicate a possible short-term, but not long-term, effect of cat removal activities on the San Nicolas Island fox population. However, other results suggest that the observed decline in the fox population may not be related to cat-trapping. First, leg-hold trapping was more intensive nearest the long-term monitoring grid that did not experience a population decline from 2009-2010 compared to the two grids that did experience a decline. Second, previous analyses have shown that foxes captured in leg-hold traps were no less likely to survive than foxes never captured in leg-hold traps. I evaluated several alternative explanations for the observed declines. Although we did not find any strong evidence in support of the alternative explanations, most of the *post-hoc* analyses conducted had low power since data were not collected for the purpose of evaluating the proposed hypotheses and we could not rule out contributions of environmental factors unrelated to cat trapping. This study did not find evidence that cat removal is likely to have a negative impact on island foxes but does point to the recommendation that future attempts to remove an invasive species should employ more intensive monitoring of native species, such as tracking of radio-collared animals, before, during, and immediately after removal activities.

Introduction

In 2009, the Montrose Settlements Restoration Program (MSRP), in cooperation with the U.S. Navy, initiated a project to protect seabirds and other native wildlife on San Nicolas Island (SNI) through the removal of feral cats (*Felis catus*). Feral cats kill millions of birds and small mammals each year (Warner 1985, ABC 2004), can severely impact island bird populations (Merton 1977, Moors and Atkinson 1984, Dowding and Murphy 2001) and have been responsible for the extinction of at least 33 bird species worldwide (Lever 1985). The removal of feral cats from SNI was initiated to help restore seabird populations, reduce impacts on native species such as the island night lizard (*Xantusia riversiana*) and reduce competition for resources with species such as the island fox (*Urocyon littoralis*) (USFWS 2009).

After release of the draft Environmental Assessment (USFWS 2008), the U.S. Fish and Wildlife Service and the U.S. Navy entered into dialog with The Humane Society of the United States (HSUS) regarding the feral cat removal project, including discussion regarding whether lethal removal would be used as the main removal method. The Institute for Wildlife Studies (IWS) was contracted by MSRP to work with HSUS, in their effort to evaluate if using live-capture box traps would be an effective means of capturing the cats. Results from this investigation found that capture success for feral cats was significantly higher in leg-hold traps compared to box traps, suggesting that feral cats may be wary of entering box traps (Garcelon 2009). Leg-hold traps were adopted as the primary method for conducting the bulk of cat removal due to the much greater efficiency to capture feral cats on SNI The trapping effort began in June 2009 by Island Conservation (IC), the organization contracted to conduct the removal of the feral cats. IWS was contracted to provide support for the project by caring for any foxes that might become injured in traps during the project, and to evaluate impacts of the leg-hold trapping effort on the fox population overall. The majority of the leg-hold trapping component of the feral cat removal project on SNI had been completed by the end of 2009 (Hanson et al. 2010, 2011). During this period, IWS had 116 fox patients admitted to the mobile clinic, of which 79 had conditions associated with having been captured in a leg-hold trap (Garcelon 2011).

IWS was tasked with evaluating the status of the fox population on the island during and after the leg-hold trapping was conducted. These objectives were accomplished through capture-mark-recapture efforts on mini-grids set up in each major habitat type on the island and evaluation of population changes and demographic rates observed on long-term monitoring grids. The primary concern IWS attempted to address was what negative impacts, if any, cat removal had on island fox survival and population size. Because leg-hold trapping took place outside of the breeding season, there was not a concern that cat-removal activities would impact fecundity.

This evaluation addressed the following questions: 1) Did the fox population decline from 2009-2010, potentially signaling a short-term effect of cat removal activities?; 2) Did the fox population decline from 2009-2012, potentially signaling a lasting effect of cat-removal activities?; 3) If there was a fox population decline from 2009-2010, is there any indication of population recovery by 2012?; 4) Was adult survival from 2009-2010 lower than expected based on observed variation in adult survival from 2000-2009, potentially signaling an impact of cat removal activities?; 5) Was adult survival consistently low from 2010-2012 potentially indicative of long-term impacts of cat-removal activities?; and 6) Were areas more intensively trapped for cat removal in 2009-2010 more likely to be associated with reduced fox density or survival than less intensively trapped areas?

If any of these questions were answered in the affirmative, we attempted to determine if reduced survival or population size from 2009-2010 was indeed due to cat-removal activities or to unrelated factors. Analyses were conducted in a spatially explicit way allowing us to compare spatial variation in population decline or decreased survival to spatial variation in leg-hold trapping effort. The potential impacts of density dependence, fox population age structure, disease, and fox health on survival were also examined.

Methods

Estimating Change in Fox Density on the Island

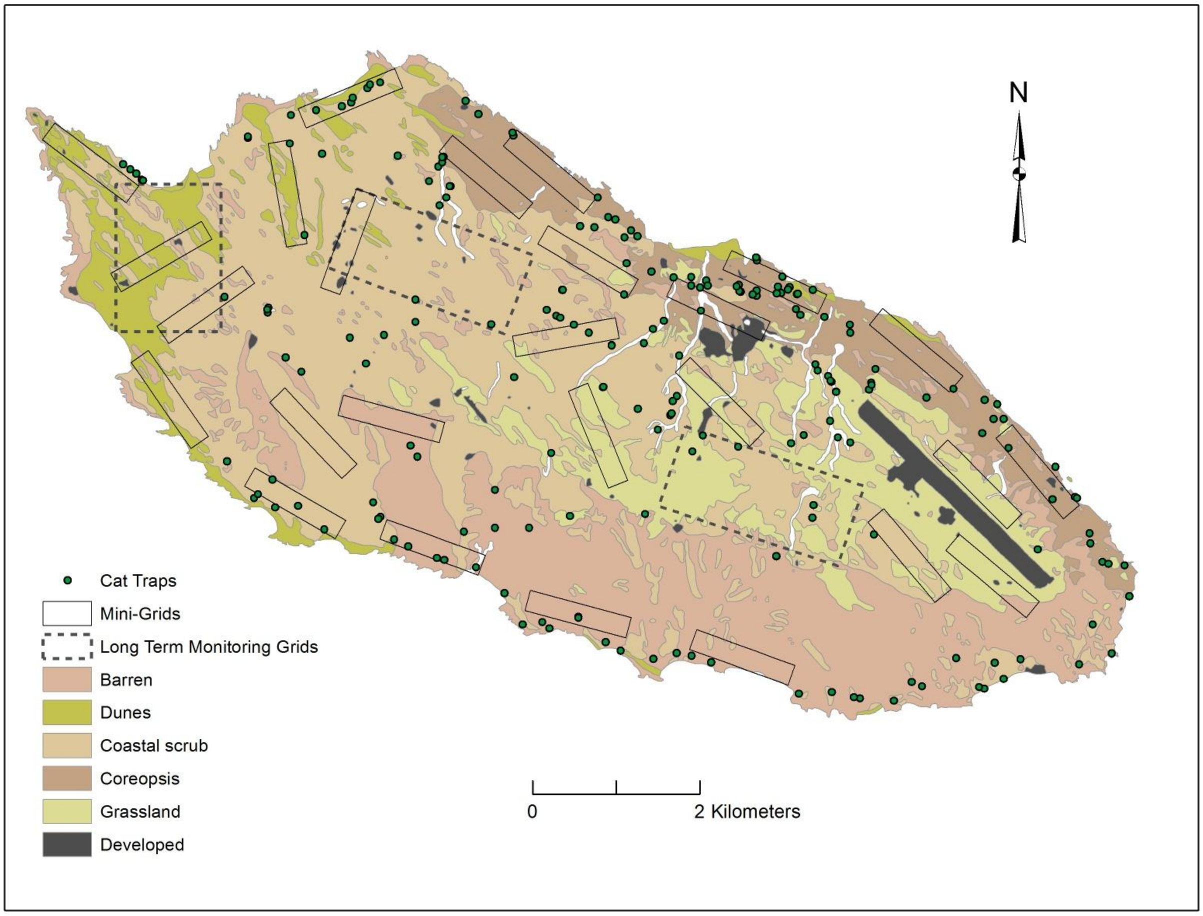
The Navy has monitored foxes on three established trapping grids annually since 2000. This has been the principal means of tracking trends in density, survival and reproduction in the island fox population. These rectangular grids were comprised of 48-50 traps with 250 m spacing between them and were operated for 6 days (Figure 1). In 2009, these grids were trapped concurrently with cat removal activities on San Nicolas Island. Because these grids encompass a relatively small portion of island (18%; Garcelon and Hudgens 2011), and do not include all of the available habitat types present on the island, they cannot be used to detect changes in fox demography on a habitat-specific or a spatially comprehensive basis. In an effort to assess potential changes in fox density across SNI on a habitat-specific basis, we established 26 mini-grids that were configured in a 2 × 6 arrangement with 250 m spacing between traps and operated for four days (Figure 1). This approach follows the recommendations by Spencer et al. (2006) for island fox monitoring, and that used by the National Park Service for monitoring island foxes on San Miguel and Santa Rosa islands (Coonan 2010).

The mini-grids were placed within each of the following habitat types: coreopsis forest, grassland, coastal dune and coastal scrub. Additional grids were placed in what was classified as “Barren” areas, which constituted habitat that was primarily void of vegetation and was dominated by rocky exposed soils. To the degree possible, the grids were oriented such that all of the traps were encompassed within one habitat type, although this was not always possible due to the irregular nature of some habitat patches (Figure 1). To avoid capturing foxes on more than one grid at a time when trapping multiple grids concurrently, trapping was scheduled such that grids directly adjacent to each other we not operated at the same time.

Statistical Analyses

Mini-grids: Data from the mini-grids was assessed to answer three questions: 1) was there an island-wide decline in adult fox population size from 2010-2012; 2) were there habitat-specific declines in adult fox population size from 2010-2012; and 3) was there a relationship between the fox survival (return rate- see below) in 2012 and cat-trapping intensity in 2009-2010?

Figure 1. Map of San Nicolas Island showing locations of mini-grids and long-term monitoring grids relative to habitat types, cat-trapping locations, waterways and areas of major development (Nictown and the airport). Long-term monitoring grids are named in the text, from east to west, Skyline, Tuft's, and Redeye.



In order to look for island-wide population effects of cat removal on foxes, population size was assessed from mark-recapture data using the Cormack-Jolly-Seber (CJS) methods within Program MARK. Analyses assumed a closed-capture robust design (Pollock et al. 1990) with animals grouped by the habitat in which they were initially captured. This had the effect of lumping mini-grids placed within the same habitat. In this analysis, population size for each habitat was derived from the number of individuals captured divided by the annual probability of capturing an animal living in the area covered by any of the grids within that habitat. Capture, recapture, and survival probabilities for both pups and adults were simultaneously estimated. Several models making different assumptions about capture, recapture and survival probabilities were tested (Table 1). Capture and recapture probabilities were either fixed across habitat types and years, fixed by year only but varied across habitat type, fixed by habitat type but allowed to vary by year, or allowed to vary by habitat type and year. Models were tested that either assumed that capture and recapture probabilities were equal (no response to capture) or varied independently, allowing for a trap response. Finally, models were tested that assumed that pup and or adult survival varied across all habitats, was similar in all habitats, or differed in the barrens and dunes but was similar in scrub, grassland and coreopsis dominated habitats. Models were ranked using AICc and parameter estimates and their confidence intervals were calculated using model averaging (Burnham and Anderson 2002).

Table 1. Models tested in mark-recapture analysis to determine habitat-specific fox population indices from mini-grid trapping effort. Models with Delta AICc>2 are considered significantly worse than the top model.

Model Rank	Pup Survival	Adult Survival	Capture (c) Recapture (p)	No. Par.[1]	AICc	Delta AICc	AICc Weight
1	barrens, dunes, coreopsis = grass = scrub	barrens, coreopsis = dunes = grass = scrub	varies by year, habitat; c=p	14	2683.47	0.00	0.54
2	barrens, coreopsis = dunes = grass = scrub	barrens, coreopsis = dunes = grass = scrub	varies by year, habitat; c=p	13	2684.85	1.37	0.27
3	barrens = coreopsis = dunes = grass = scrub	barrens = coreopsis = dunes = grass = scrub	varies by year, habitat; c=p	12	2687.10	3.62	0.09
4	habitat specific	barrens = coreopsis = dunes = grass = scrub	varies by year, habitat; c=p	15	2687.16	3.69	0.09
5	habitat specific	habitat specific	varies by year, habitat; c=p	19	2691.79	8.32	0.01
6	habitat specific	habitat specific	varies by habitat only; c=p	14	2692.60	9.13	0.01
7	habitat specific	habitat specific	varies by year, habitat, age; c=p	29	2692.88	9.41	0.00
8	habitat specific	habitat specific	varies by habitat, age; c=p	19	2696.34	12.87	0.00
9	habitat specific	habitat specific	varies by habitat only; c≠p	19	2697.44	13.97	0.00
10	habitat specific	habitat specific	varies by year, age; c=p	13	2711.75	28.28	0.00
11	habitat specific	habitat specific	varies by year, age; c≠p	17	2715.52	32.05	0.00
12	habitat specific	habitat specific	varies by year, habitat, age; c≠p	49	2722.47	39.00	0.00

1. No. Par.=number of model parameters estimated for the model.

Attempts were made to estimate fox densities on individual grids using spatially explicit mark-recapture methods described by Efford (2004) and implemented in Program DENSITY, but dropped this analysis when estimates could not be generated for several grids. Island-wide population estimates were estimated as the sum of populations within each of the five habitat-types assessed.

Apparent survival from 2010-2012 of both adult and juvenile foxes was lower for animals captured on mini-grids in high cat-trapping intensity areas than animals captured only in low cat-trapping intensity areas was evaluated in order to more explicitly examine cat-trapping effects on local fox densities. Mini-grids with $\geq$ 3 leg hold traps within 250 m were considered to be in “high intensity” trapping areas, and mini-grids with $\leq$ 2 leg hold traps operated within 250 m of the area covered by the grid were considered to be in “low intensity” trapping areas.

Long-term monitoring grids: Mark-recapture data from long-term monitoring grids were used as a complimentary data set to look at patterns of fox population dynamics and survival before, during, and after cat-removal. Analyses specifically determined: 1) was there an island-wide population decline from 2009 to 2010?; 2) was there an island-wide population decline from 2010-2012?; and 3) was fox survival lower in 2009 than expected? For these analyses, data were restricted to adult foxes.

Fox population size was determined using CJS methods within Program MARK assuming a multi-state robust design. In this analysis, population size for each of the three grids (i.e., states) was derived from the number of individuals captured divided by the annual probability of capturing an animal living in the area covered by each grid. Capture and recapture probabilities were simultaneously estimated along with survival and transition probabilities, where transitional probabilities reflect the chance an animal captured on one grid in year *t* disperses to another grid in year *t+1*. Based on previous analyses we assumed that capture and recapture probabilities varied by grid and by year, but that dispersal (transition) probabilities were constant across grids and time (Garcelon and Hudgens 2011). We tested several models of adult survival, allowing survival to vary by grid, by year, by grid and by year (Table 2). In order to explicitly address whether fox survival was impacted during cat-removal, models were also included that assumed survival was constant in all years except 2009. Based on previous analyses, we also included models assuming that survival rates did not differ between Redeye and Tuft’s grids, but were different between those two west-end grids and Skyline grid. As above, parameter estimates used to determine population numbers were calculated using model averaging techniques.

Table 2. Models tested in mark-recapture analysis to determine fox population indices from long-term monitoring grids. Models with Delta AICc>2 are significantly worse than the top model.

Survival Model[1]	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.[2]	Deviance
S RT × 2 class-yrs since marked × 2009 (RT)	16773.08	0	0.999	1	84	16601.6
S RT × 2 class-yrs since marked (RT)	16797.42	24.34	0. 001	0	82	16630.1
S RT × 2 class-yrs since marked	16813.73	40.65	0	0	83	16644.3
S RT × 2 class-yrs since marked X 2009	16824.56	51.47	0	0	85	16651.0
S RT	16839.5	66.41	0	0	79	16678.4
S RT ×year	16912.78	139.70	0	0	95	16718.3
grid ×year	16949.79	176.712	0	0	102	16740.6

1. The term S RT indicates that survival on Redeye and Tuft's grids are constrained to be equal. Equivalent to lumping these grids into a single unit for evaluation, with Skyline being treated separately. Class years are 0-4 years since first captured as an adult, or 5+ years since first captured as an adult. The term × 2009 indicates that survival is assumed to be the same in all years except 2009-2010. The term (RT) indicates that survival on Skyline grid is assumed not to be affected by the preceding variable.
2. No. Par.=number of model parameters estimated for the model.

Because age class 4 foxes are known to have substantially lower survival rates than foxes in age classes 1-3 (Hudgens et al. 2007), survival was assessed using a multi-state robust design in which the fox population was divided into states based on location and age class. For this analysis there were six possible states an animal could transition between: three states for "young adult" foxes (age classes 1-3) corresponding to the three trapping grids, and three states for "old foxes" (age class 4) corresponding to each of the three trapping grids. Separate transition probabilities were estimated for state transition from a young adult to an old adult within the same grid, dispersal among grids while remaining in the same age class, and dispersing among grids in the same year that an animal transitions from young adult to old adult. Transition probabilities of old foxes into young adults were fixed to zero. A similar set of models was tested as in the previous analysis, with additional models included to examine if patterns of survival differed among young adults and old adults (Table 3). Parameter estimates were calculated using model averaging techniques.

Table 3. Models tested in mark-recapture analysis to determine adult fox apparent survival from long-term monitoring grids. Models with Delta AICc>2 are considered significantly worse than the top model.

Model[1]	AICc	Delta AICc	AICc Weights	No. Par.[2]	Deviance
s=AC X S RT X 2009 (RT)	43277.02	0.00	0.83	87	43099.2
s=AC X S RT X 2009	43280.18	3.16	0.17	89	43098.18
s=AC X S RT	43298.58	21.55	0.00	85	43124.93
s=AC X grid	43302.39	25.36	0.00	87	43124.56
s= AC	43319.78	42.76	0.00	83	43150.3
s=AC X S RT X year	43325.47	48.45	0.00	129	43059.01
s=AC X year	43330.48	53.45	0.00	105	43114.89
s=AC X grid X year	43340.92	63.89	0.00	153	43022.95
s= S RT	43392.28	115.26	0.00	83	43222.8
s= grid	43394.32	117.30	0.00	84	43222.76
s=AC X S RT X year	43395.27	118.24	0.00	105	43179.68

1. AC=age class: survival assumed to differ between young and old foxes; S RT= survival constrained to be equal on Redeye and Tuft's grids but vary independently on Skyline grid; X 2009= survival differs in 2009 from other years; (RT)= the preceding variable is applied only to animals from Redeye and Tuft's grids.
2. No. Par.=number of model parameters estimated for the model.

Because there was evidence of a population decline and reduced adult survival potentially caused by cat-trapping, available data from the mini-grid and long-term monitoring trapping grids were analyzed to examine several alternative hypotheses about underlying mechanism/s:

> *H1: Cat trapping increased fox mortality;*
>
> *H2: Cat trapping led to greater fox movement because foxes captured in leg hold traps left areas where they were trapped or foxes held at the fox hospital led to disrupted territorial boundaries;*
>
> *H3: Density dependent survival coupled with unusually high fox densities*;
>
> *H4: A disease epidemic impacted the fox population*;
>
> *H5: Extreme weather such as prolonged drought or an unusually wet and cold winter*.

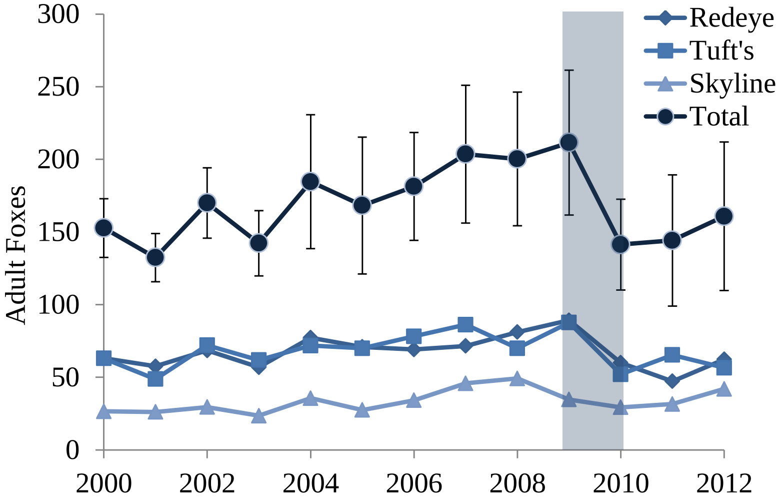
The analyses employed to evaluate each hypothesized mechanism are described in Appendix A.

Results

Population monitoring

The fox population numbers on the long-term monitoring grids were relatively stable from 2000-2009, with about twice as many animals living around the two western grids (Redeye and Tuft's) as around the Skyline grid (Figure 2). The largest observed decline during this period was a 16.3% drop from 2002-2003. In contrast, there was a 33.2% decline over the period of cat removal, from 2009-2010. The decline was primarily driven by reduced fox numbers on the two western grids, which declined 36.7% from 2009-2010, while fox numbers increased on Skyline grid in both years by 11%-13%. Fox numbers on the long-term monitoring grids increased 2% from 2010-2011 and 11.6% from 2011-2012 with a cumulative change of 13.2% from 2010-2012.

Figure 2. Fox population size on San Nicolas Island 2000-2012. Total fox population shows the sum of population estimates on three long-term monitoring grids. Error bars on total population estimate show sum of the upper and lower 95% confidence limits of population estimates on long-term monitoring grid. Shaded area indicates period of cat removal.

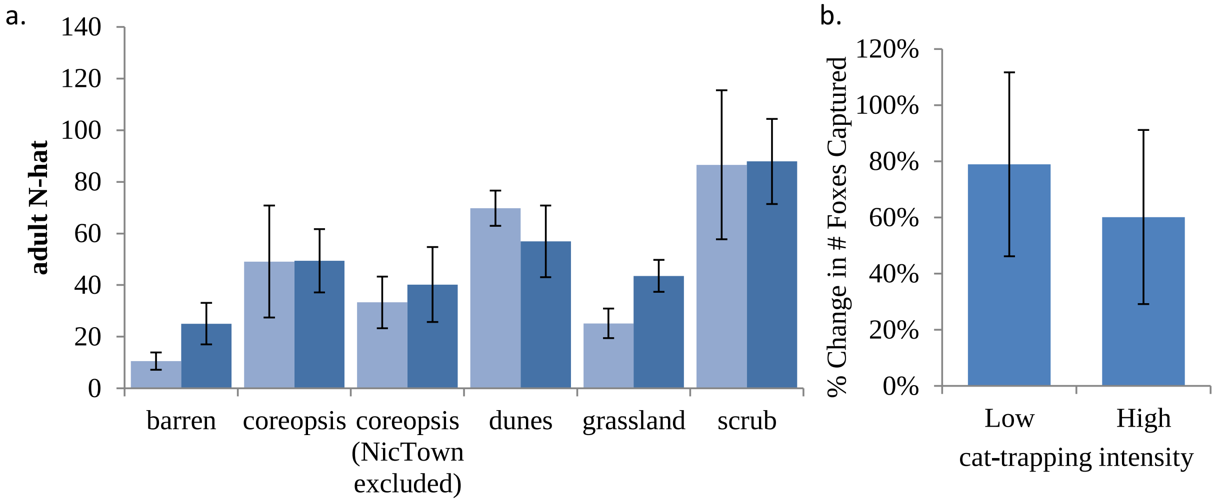


There were 221 adult foxes and 51 fox pups captured on mini-grids in 2012. The adult fox population size estimated from mini-grids increased 10.4% from 2010-2012. There were significant increases in fox numbers in barren and grassland habitats, and non-significant increases (i.e., the difference was not greater than the degree of uncertainty in the population estimates) in coreopsis habitat (excluding the grid located adjacent to of NicTown) and scrub habitats (Figure 3a). There was a non-significant decrease in fox numbers in dunes habitats. There was no relationship between cat-trapping intensity near a mini-grid and the change in the number of foxes captured on the grid between 2010 and 2012 (Figure 3b). More foxes were captured in each mini-grid in 2012 than in 2010 with few exceptions. The same number of foxes was captured on the mini-grid located adjacent to NicTown, and fewer foxes were captured in 2012 on four of the five mini-grids in the stabilized sand dunes.

Apparent Survival

Apparent adult survival rates from 2000-2012 depended on age class, location, and time (Figure 4, Table 3). Over the 13 year span, old adults had lower survival rates than young adults, with an average annual survival near 50% regardless of location. Young adult survival varied by location, with foxes captured on Redeye and Tuft's grid generally surviving better than foxes captured on Skyline grid. Survival of all adults from Redeye and Tuft's dipped significantly from 2009 to 2010, regardless of age class, while survival of Skyline foxes was higher than average over the same period. Young adults from Skyline did, however, experience relatively low survival just prior to cat removal, from 2007 to 2009. Survival in 2010-2011 was near normal for all age classes and locals.

Figure 3. Mini-grid measures of fox population dynamics 2010-2012. a) Habitat-specific population estimates in 2010 (light bars) and 2012 (dark bars). Bars indicate the number of foxes living within the effective trap area of all mini-grids within the habitat indicated. Bars indicate 95% confidence limits. b) Mean (+/- 1 std err) change in the number of foxes captured on mini-grids in low and high intensity cat-trap areas.



Apparent survival of both fox adults and pups captured on mini-grids in 2010 to 2012 was negatively associated with cat-trap intensity (Figure 5, Table 4). Animals captured on mini-grids in highly trapped areas (i.e., 4+ leg hold traps within 250 m) were less than half as likely to survive as animals captured on mini-grids with two or fewer leg hold traps within 250 m.

Testing alternative mechanisms:

H2: Fox movement. There was no evidence that cat trapping lead to increased fox movement. Inter-annual changes in trapping locations did not differ for foxes trapped in 2009 and 2010 compared to previous years, nor was there any indication that foxes were more likely emigrate from or disperse among long-term monitoring grids in 2009 relative to previous years (Figure 6). There also was no difference between high and low cat-trapping intensity areas in the proportion of foxes captured on multiple mini-grids in 2010 or between 2010 and 2012. In 2010, 12.3% (10 of 81) of adult foxes and 21.4% (6 of 28) of juvenile foxes trapped in high intensity cat-trapping areas were captured on multiple grids, compared to 16.7% (12 of 60) of adult and 18.2% (2 of 11) and juvenile foxes captured only in low intensity areas (adults: X^2= 0.58, p=0.447 ; juveniles: X^2= 0.05, p=0.821). Few adult foxes moved between mini-grids between 2010 and 2012 regardless of cat-trapping intensity; 14.3% (3 of 21) of adult foxes trapped in high intensity cat-trapping areas and 10.8% (4 of 37) captured in low intensity areas in 2010 were recaptured only on new mini-grids in 2012 (X^2=0.15 , p=0.696) . Foxes captured as juveniles in 2010 were more likely than adults to exhibit a home-range shift in 2012. As with adults, there was no difference in the proportion of pups captured in 2010 on mini-grids in high or low cat-trap intensity areas that were subsequently only recaptured on different mini-grids in 2012 (% of pups exhibiting a home-range shift: high intensity=21.4%, n=14; low intensity=28.6%, n=7; X^2=0.13 , p=0.717).

Figure 4. Apparent survival by age class of adults captured on a) Redeye or Tuft's grids or b) Skyline grid. Dark lines indicate young adults (tooth wear based age class 1-3), light lines represent old adults (age class 4). Solid lines without points show model-averaged parameter estimates. Dotted lines show 95% confidence limits of model-averaged parameter estimates. Solid lines with points show annual estimates assuming that survival varies annually independent of any other factors.

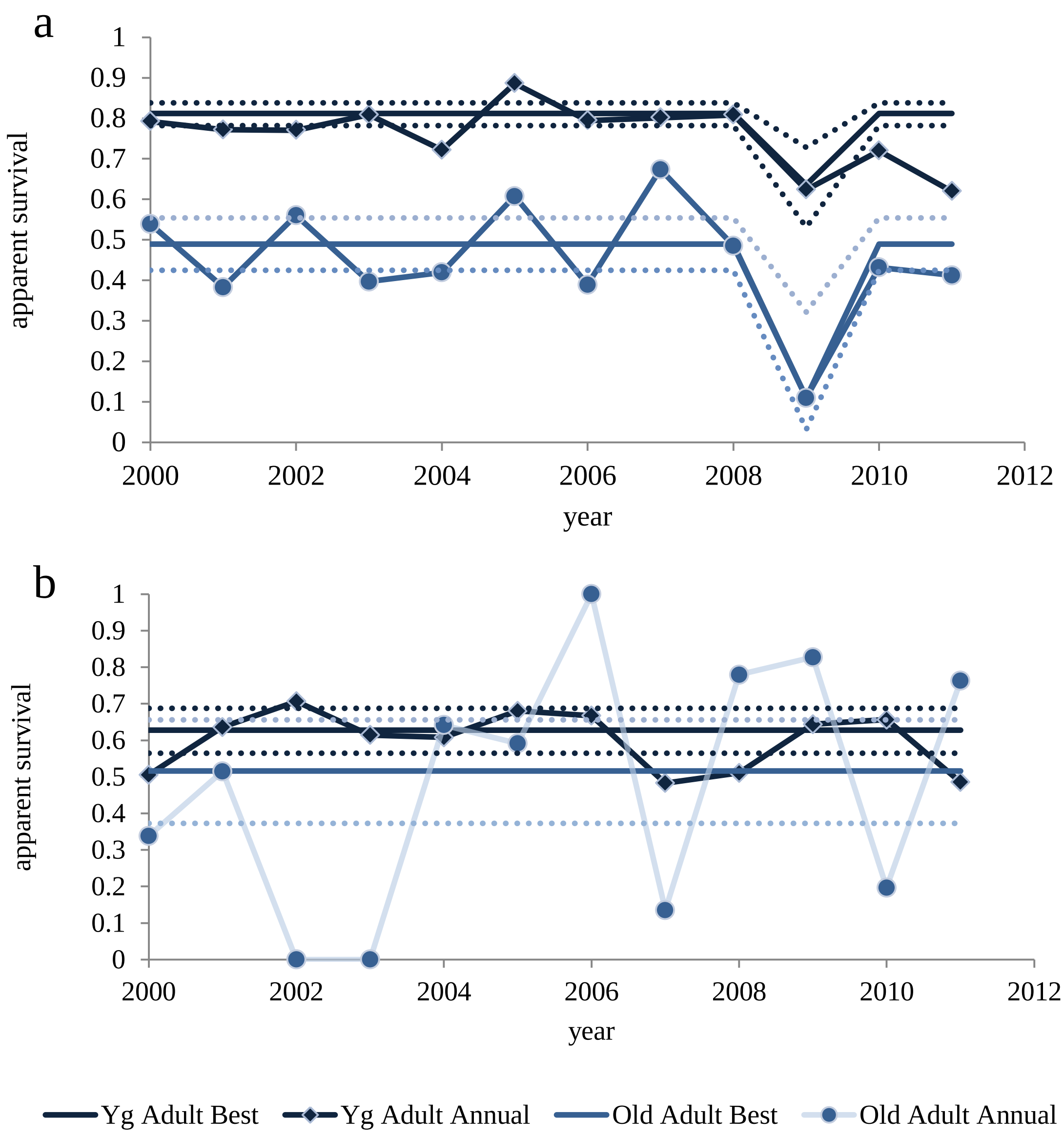


Figure 5. Model averaged apparent survival of foxes captured on mini-grids in low or high intensity cat-trapping areas in 2010. Error bars indicate 95% confidence intervals of estimates.

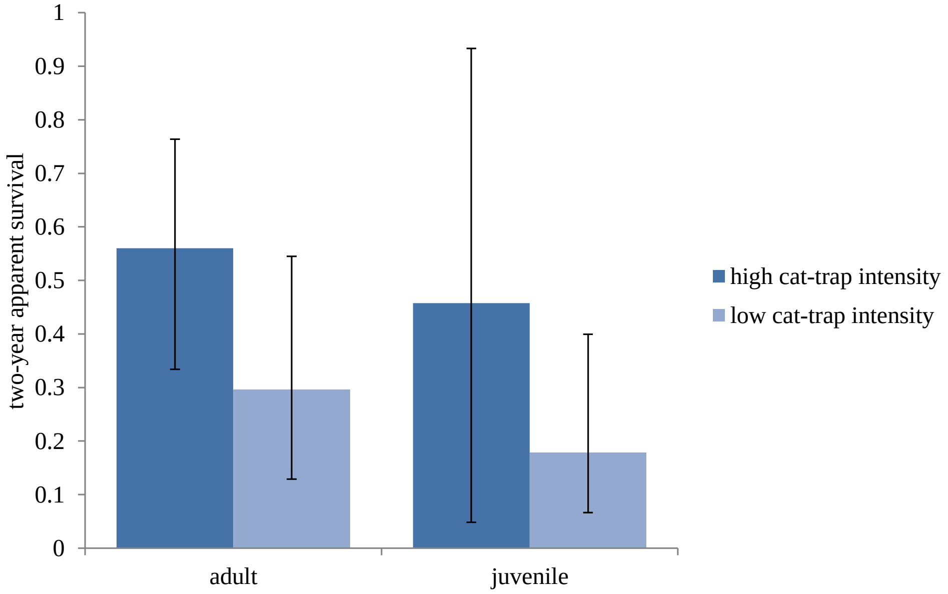
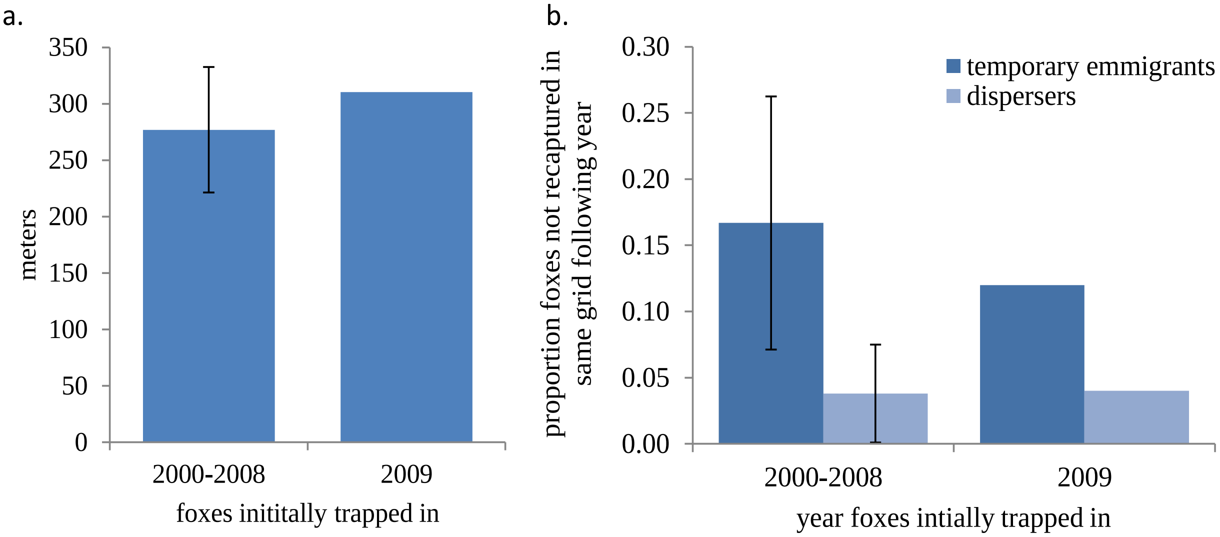


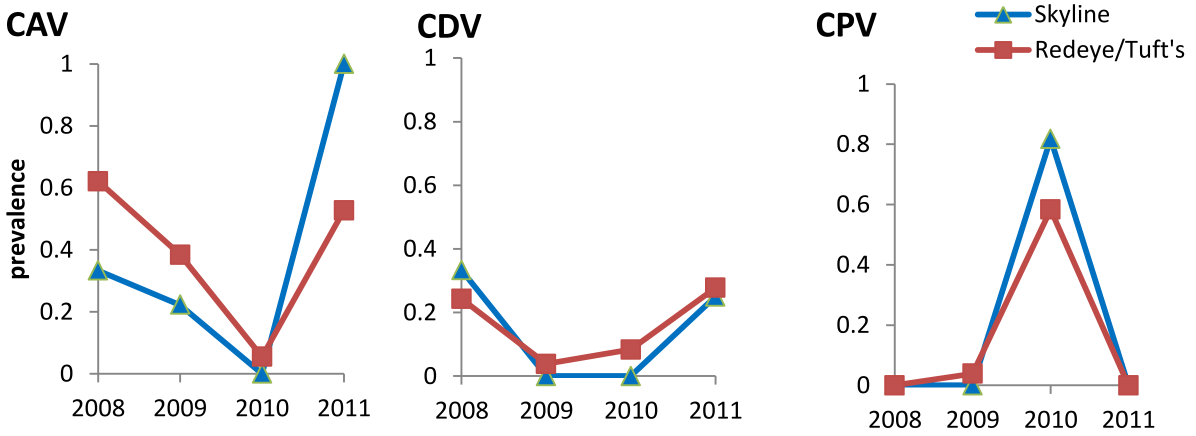
Figure 6. Fox movement inferred from trap locations on long-term monitoring grids. Panels show: a) Distance between central point of trap locations in consecutive years, and b) proportion of foxes that were either temporary emigrants from a grid or dispersed between long-term grids. Temporary emigrants refer to animals captured in a grid in one year, not recaptured the following year, but captured again on the grid two or more years later. Dispersers are animals captured in one year and on a different grid the next year they are captured. Error bars indicate 95% confidence interval for annual means from 2000-2008.



H3: Density dependence. Fox survival on Redeye and Tuft's was poorly correlated to adult fox numbers on the grids (young adults: r=-0.036; p>>0.1 old adults: r=-0.15; p>>0.1). There was a marginally significant negative correlation between adult population size on Skyline and annual survival for young adults (r=-0.48, p<0.1) but not old adults (r=+0.30; p=NA for one-way hypothesis of negative correlation).

H4: Disease. There was no evidence linking monitored pathogens to the observed survival or population declines from 2007-2009 on Skyline grid or 2009-2010 on the two western grids. On Skyline grid, seroprevalence of two pathogens, CAV and CDV, was higher in 2008 than in 2009, but neither pathogen increased in prevalence over the same period on the western grids (Figure 7). Exposure to a third pathogen, CPV, was recorded in <5% of animals at both locations in both 2008 and 2009 (Figure 7).

Figure 7. Prevalence of three pathogens in San Nicolas Island Foxes. Pathogen presence inferred from positive titers of antibodies against each pathogen in blood samples collected during trapping long-term monitoring grids.



H5: Extreme weather: The 2009-2010 winter was cooler and drier than the 2005-2012 (temperature) and 2000-2012 (precipitation) averages, but did not represent a period of extreme weather (Figure 8). While weather may influence adult survival, we did not find evidence that extreme winter weather was a contributing factor to reduced adult survival in 2009-2010.

H6: Fox health. Although fox weight did influence survival probabilities, there was no indication that fox weights were lower in 2009 than other years or that the effect of weight on survival was stronger in 2009. The best statistical model explaining return rates of young adult foxes included effects of fox weight (corrected for sex) and negative density dependence (Table 6). However, even accounting for the combined effects of low fox weights and high fox numbers observed on the western two grids in 2009, adult survival there was lower than expected, with the largest negative difference between observed survival and that predicted by the statistical model.

Figure 8. Winter weather indicators. a) Total winter precipitation (November to the following April) from two nearby coastal weather stations. b) Average daily temperature (dark line, left axis) and proportion of days with mean temperature below 51.9 F (light line, right axis) at San Nicolas Island Airport.

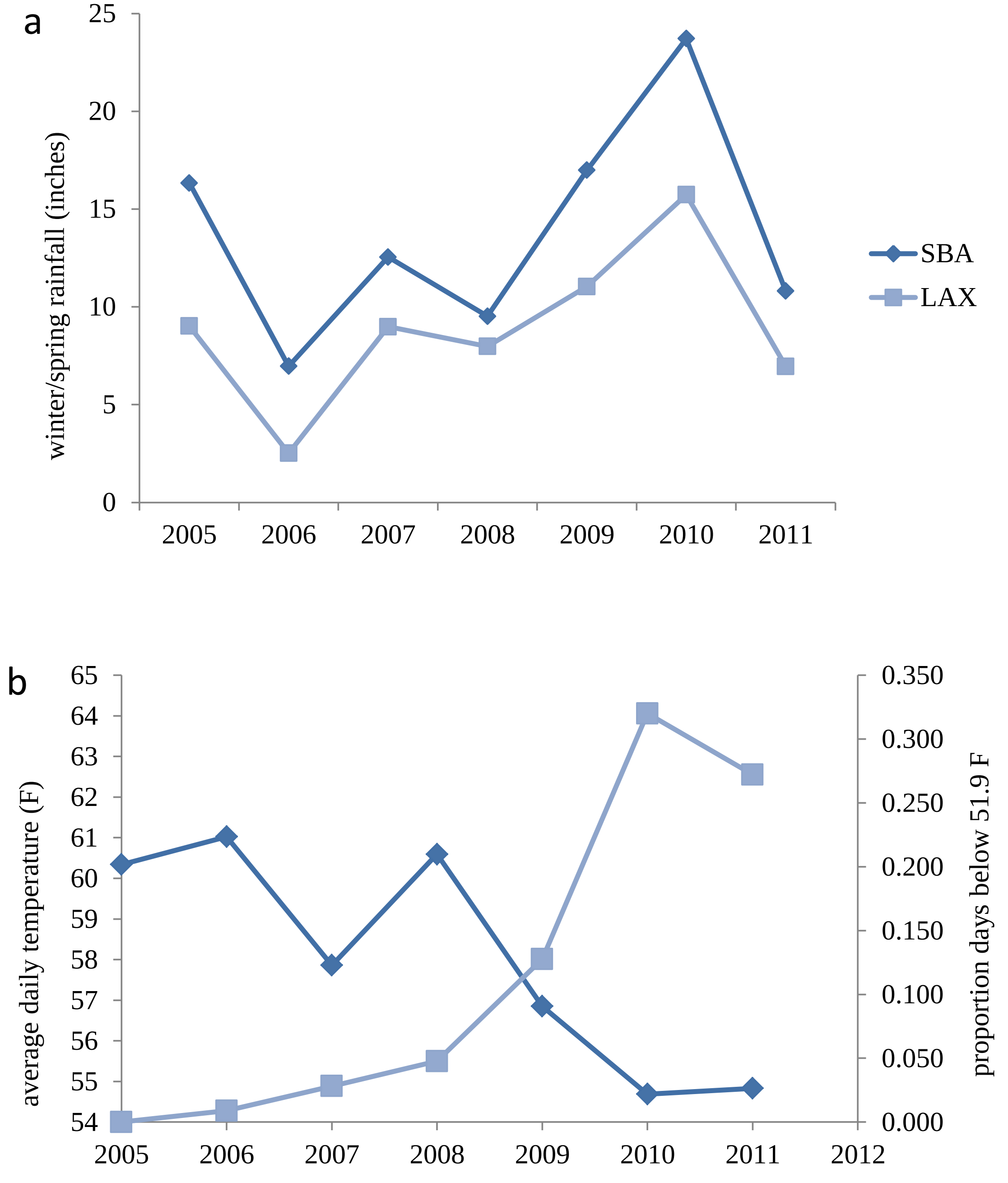


Table 6. Model ranks for fox return rates from 2000 to 2012 for animals captured on long-term monitoring grids accounting for animal weight corrected for sex. Models with Delta AICc>2 are considered significantly worse than the top model.

Model[1]	-ln L	No. Par.[2]	AIC	delta AIC	model likelihood	model weight
weight(sex) *N*(location)	-430.45	4	868.90	0.00	1.00	0.707
location weight (sex) *N*(location)	-430.36	5	870.72	1.82	0.40	0.285
N(location)	-437.22	2	878.44	9.54	0.01	0.006
location *N*(location)	-437.09	3	880.18	11.28	0.00	0.003
location weight (sex)	-498.28	3	1002.56	133.66	0.00	0.000
weight(sex)	-508.55	2	1021.09	152.19	0.00	0.000

1. 1. Terms: weight(sex) indicates that weights were nested within sex, N(location) indicates that population estimates (N) were nested within location. There were two locations: Tuft's + Redeye grids and Skyline grid.
2. No. Par.=number of model parameters estimated for the model.

Discussion

We found circumstantial evidence of a potential short term impact of cat-trapping on island foxes; there was a population decline and low apparent survival observed on long-term monitoring grids from 2009-2010 and lower apparent survival from 2010-2012 on mini-grids in areas with higher cat-trapping intensity. However, because reduced survival on long-term grids was not spatially associated with cat-trapping activity, and trapped foxes were not less likely to survive, it is likely other mechanisms were at play. If there was an impact of cat-trapping on foxes, the population effect was short lived; survival rates returned to normal in the year following cat removal and population estimates from both long-term monitoring grids and mini-grids show no decline from 2010-2012. We tested several potential mechanisms as explanations for the observed low adult survivorship in 2009 and in high intensity cat-trapping areas, but found no evidence supporting a large contribution of those mechanisms.

There are two pieces of evidence suggesting a short-term impact of cat-removal activities on island foxes. First, apparent adult survival was unusually low from 2009-2010, concurrent with cat-removal activities. Moreover, the reduction in adult survival affected both young and old adults. Second, foxes captured in 2010 on mini-grids in high intensity cat-trapping area were less likely to be recaptured in 2012.

Other evidence, however, indicates that cat-trapping did not directly affect fox survival. Individual foxes captured in leg-hold traps were no less likely to be captured in subsequent years than foxes not captured in leg-hold traps, indicating that being captured in leg-hold traps did not increase mortality risk (Garcelon 2010). On a broader scale, reduced adult survival on long-term monitoring grids was observed for foxes captured in the western two grids, but not Skyline grid. Cat trapping efforts, in contrast, were greater on Skyline grid and nearby barrens. There were few leg-hold traps near Redeye grid, though there was a concentration of traps near the eastern edge of Tuft's grid (Figure 1). In a similar vein, habitat specific population estimates indicated increased populations from 2010 to 2012 in the habitats with the most leg-hold traps- barrens, coreopsis groves, and grasslands- while the population decreased from 2010-2012 in the dunes, where few leg-hold traps were placed.

We explored several alternative hypotheses that might explain the observed survival patterns. Although we found no evidence supporting any of the alternative hypotheses, we could not rule any out as making some contribution to observed patterns of fox apparent survival because monitoring was not specifically designed to address them.

A potential sublethal impact of cat trapping on island foxes was the temporary removal of foxes from their territories, leading to home range shifts (Alberts et al. 2002). Not only were trapped foxes prevented from maintaining territorial boundaries during their time in the trap, but some trapped animals were held for days to treat injuries. Moa et al. (2001) found that trapped lynx avoided returning to trapping locations for over a year, so it is not unreasonable to consider that cat-trapping in 2009 could result in home range fluidity for some foxes in 2010. If so, small homer-range shifts could have taken animals out of the effective trap area covered by mini-grids. Although we did not directly determine fox home ranges, we found no evidence of increased movement within or between trapping grids associated with cat trapping. Consequently we conclude it is unlikely that observed dips in apparent survival was due to patterns of emigration out of trapped areas. However, because we did not track foxes during the period of cat removal we cannot evaluate if temporary removal of foxes led to home-range shifts.

The most difficult alternative hypothesis to assess is the possibility of a disease epidemic. The potential for disease epidemics to cause significant population declines in island foxes is well documented (Timm et al. 2009). Disease is suspected to have led to a severe reduction of the San Nicolas Island fox population (Aguilar et al. 2004). That the dip in survival rates in 2009 occurred where fox densities are greatest is consistent with expected patterns of disease spread (Sanchez 2012). The disease with the greatest known virulence to island foxes is Canine Distemper, with virulent strains responsible for causing a severe fox population crash on Santa Catalina Island (Timm et al. 2009). However, nonvirulent strains of CDV are endemic to all of the island fox populations (Munson 2010). A mutation in nonvirulent CDV circulating in San Nicolas Island foxes could have led to a virulent or moderately virulent strain. If a virulent strain CDV were the agent responsible for reduced adult survival, an epidemic may have run its course–increasing in prevalence then fading out as infections reduced the local density of susceptible hosts–within several months (Sanchez 2012) without being detected in annual surveys. However, given the relatively low antibody titers for CDV in the San Nicolas Island fox population in 2010 (Garcelon and Hudgens 2011) compared to what was observed during the CDV outbreak on Santa Catalina Island (Timm et al. 2009), it is unlikely that CDV was implicated. Alternatively, other disease agents, especially pathogens with short durations of clinical disease, may have gone unnoticed in the absence of efforts to specifically monitor for them. Proper monitoring to detect a disease epidemic would have required a sample of 60-100 frequently monitored radio-collared foxes (Ferrara and Hudgens 2008, Hudgens et al. 2011).

Although we could not assign the observed declines in adult survival to the effects of density dependence, weather, or fox health alone, we cannot rule out influences of these factors alone or in concert. Fox populations on the western monitoring grids were the largest on record (Garcelon and Hudgens 2012), and as a consequence, nonlinear density dependent effects on survival may have played a role while being difficult to detect statistically. Interactions between density dependence, weather and fox health, especially nonlinear interactions, may have also resulted in 2009 being a "perfect storm" year where multiple stressors come together to impact survival (Stone et al. 2001).

Two additional alternative hypotheses that were not tested relate to human activities on the island. The first is increased road mortalities associated with more intensive use of the island for military activities. Road mortalities are the most common mortality factor affecting young adult foxes on San Nicolas Island (Hudgens et al. 2007, 2008). However, road mortalities are typically associated with animals living between the airport and NicTown, as traffic volume is substantially lower on the western end of the island. The second possibility is cumulative stress to foxes associated with multiple captures. Because foxes are trap-happy (e.g., probability of first capture=0.25/night, probability of recapture=0.42/night paired t-test t=9.5; p<0.001) and relatively docile in the trap, it is generally assumed that island foxes do not suffer stress from capture in box traps. However, capture may cause internal physiological stress reactions without external signs of stress. We must therefore acknowledge there is a possibility that intensive trap-based monitoring before, during and immediately after cat-removal led to animals being captured multiple times within the year and suffering cumulative effects of stress leading to increased mortality risk (Cabezas et al. 2007).

Conclusions

Cat-removal activities may or may not have had a short-term impact on island fox survival and population size, but the effects did not carry through beyond 2010. The ability to isolate the impacts of cat-trapping on island foxes would have been enhanced had there been a number of frequently-monitored radio-collared foxes distributed across the island through the period of removal. While there is no reason to believe that invasive species removal on other islands will necessarily pose a threat to fox populations, the San Nicolas Island cat removal experience suggests that a high-frequency monitoring program should be in place to inform an adaptive response if required.

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Appendix 1. Statistical Methods Used to Evaluate Alternative Hypotheses Explaining Observed Spatio-Temperal Patterns of Depressed Adult Survival and Population Size of San Nicolas Island Foxes from 2009-2012.

We note here that these are all post-hoc analyses of data not designed to explicitly evaluate these hypotheses. As such, we describe results that lend support for or against the hypothesis as a contributing mechanism or, if applicable, can rule out the hypothesis.

H1: Cat trapping increased fox mortality. Analysis 1: Comparison of grid-specific survival rates in 2009 relative to other years. If cat trapping was a contributing factor, we would expect the magnitude of the decreased survival in 2009-2010 to be greatest for foxes captured on Sklyine grid, where cat trapping was most intense, and least for foxes captured on Redeye grid, where there was little cat-trapping effort. Decreased survival on Redeye and Tuft's grids but not Skyline grid would provide evidence against this hypothesis.

Analysis 2: Comparison of recapture rates for foxes captured in leg hold traps to foxes not previously captured in leg hold traps. For this comparison, foxes must have been captured on long-term grids in 2008 or 2009. Lower survival of foxes captured in leg hold traps would provide evidence for this hypothesis; other results would provide evidence against this hypothesis. This analysis has been previously reported (Garcelon 2011)

H2: Cat trapping led to greater fox movement because foxes captured in leg hold traps left areas where they were trapped or foxes held at the fox hospital led to disrupted territorial boundaries. Analysis 1 : Comparison of the distance moved between the mean trap locations of foxes captured in consecutive years from 2009-2010 and 2000-2008. Greater distances in 2009-2010 than the 2000-2008 average would support this hypothesis. Because increased movement may be restricted to movements larger than the grid size, other results provide no evidence against the hypothesis.

Analysis 2: Comparison of temporary emigration in 2009 to previous years. We estimated temporary emigration as the proportion of foxes captured in 2009, not recaptured in 2010, and subsequently recaptured in 2011 or 2012. This analysis only includes fox captures on the long-term monitoring grids. Greater temporary emigration rates in 2009 would support this hypothesis. Because temporary emigration is rare, this analysis lacks the power to provide evidence against the hypothesis.

Analysis 3: Comparison of inter-grid dispersal in 2009-2010 to other years. We estimated dispersal rates as the proportion of foxes captured on the long-term monitoring grids in one year that were either captured on multiple grids in that year or on a different grid the following year. Animals not captured the following year, but were next captured on a different in a subsequent year were also considered to have dispersed. Greater dispersal rates in 2009 would support this hypothesis. Because dispersal is rare, this analysis lacks the power to provide evidence against the hypothesis.

Analysis 4 : Comparison of inter-grid dispersal within 2010 for foxes captured on mini-grids with high and low intensity cat trapping. We used binomial regression to assess whether foxes captured on mini-grids in intensively cat-trapped areas were more likely to be captured on multiple grids than foxes not captured in intensively cat-trapped areas. Because few animals were captured on multiple grids, this analysis lacks the power to provide evidence against the hypothesis.

H3: Density dependent survival coupled with unusually high fox densities. Analysis: We tested for negative correlations between adult annual survival rates and estimated population size on long-term monitoring grids. In keeping with the best models for adult survival (see below), we did separate analyses for young and old adult foxes, for animals captured on Redeye or Tuft's grids, and animals captured on Skyline grid. If we found a significantly negative Pearson's correlation coefficient for the Redeye/Tuft's population at the $\alpha=0.10$ level, we would reanalyze the mark-recapture data to include models with survival as a function of local population size. A negative correlation between adult fox population size and apparent annual survival would provide weak evidence in support of this hypothesis. Subsequent superior rankings of mark-recapture models specifying survival as a (decreasing) function of adult population size would provide stronger evidence in support of this hypothesis. A lack of a negative correlation would provide evidence against this hypothesis as the mechanism leading to the observed decline in 2009, but would not rule out fox density as a factor influencing survival.

H4: A disease epidemic impacted the fox population. This hypothesis was suggested when noting that young adult survival rates dipped on Skyline grid in 2007-2008 and 2008-2009, with survival dipping in Tuft's and Redeye the next year, consistent with what might happen if a disease were to spread across the island. A disease would also be expected to have a greater impact in Redeye/Tuft's, where fox densities are substantially greater than on Skyline.

Analysis: Comparison of disease prevalence for three pathogens (Canine Adenovirus, Canine Distemper, Canine Parvovirus) monitored from 2008-2012. Relatively high prevalence in Skyline animals in 2008 and/or in Redeye/Tuft's animals in 2009 would support this hypothesis.

Analysis: Comparison of fox weights of animals captured in 2007-2008 on Skyline and 2009 on Redeye/Tuft's grids to weights of animals from the same grids in other years. Decreased weights in proposed years of epidemic would be consistent with unhealthy (sick) animals and support this hypothesis.

Analysis: Comparison of effect of fox weight on survival probabilities in epidemic years compared to other years. We used logistic regression models to ask if fox return probabilities were affected by weight, and if there was an interaction with weight and epidemic year. Because diseases may disproportionately affect already stressed animals, an interaction increasing the effect of weight on survival in epidemic years would support this hypothesis.
A decrease in fox weights or an increase in the influence of fox weight on survival in 2009 could also signal the impact of extreme weather (H5 below).
Negative results from any of these analyses would not provide evidence against this hypothesis.

H5: Extreme weather such as prolonged drought or an unusually wet and cold winter. Analysis: Comparison of rainfall from Nov 2009-April 2010 to similar periods in other years. Most rainfall in southern California, including on San Nicolas Island for periods when records are available, falls between November and April. We accessed precipitation data from the National Climatic Data Center (http://gis.ncdc.noaa.gov/map/viewer/#app=cdo) accessed March 25, 2013. Unfortunately, rainfall data for SNI are only available from 1934-1976, with data missing for several months within this period. We first identified two nearby coastal NOAA weather stations with monthly precipitation records going back to at least 1945 and coverage through April 2012, the Santa Barbara Airport (SBA), and Los Angeles International Airport (LAX). We next established whether rainfall was tightly, positively correlated between the coastal stations and SNI over 43 (LAX)-55 (SBA) months from 1941-1976. In order to avoid a biasing this evaluation by including months when rainfall is rare across the region, we only included December-March, when rainfall is most variable from year to year (Figure A1). After establishing that monthly rainfall at both sites (SNI-LAX correlation: r^2=0.73; SNI-SBA: r^2=0.80) was tightly correlated with monthly rainfall on SNI, we checked if winter/spring (i.e., November-April) rainfall from 2000-2012 was correlated with adult survival, and if 2009-2010 represented an unusually wet or unusually dry year. If 2009-2010 was unusually wet, the hypothesis would be supported. Because much of the island, particularly the west end, may receive significant moisture from fog drip, assessing whether or not drought conditions were present on the island would require the use of NDMI satellite imagery to measure patterns of primary productivity.

Temperature data was available from the National Climatic Data Center (http://gis.ncdc.noaa.gov/map/viewer/#app=cdo; accessed March 25, 2013) for San Nicolas Island from 2005-2013. If 2009-2010 was unusually cold the hypothesis of extreme weather would be supported. We used two measures to determine how “cold” a winter was: the average daily temperature from November –April 30, and the proportion of days during that period where the average daily temperature was in the coldest 5% (below 51.9° F) of records for the period.

Figure A1. Mean monthly rainfall on San Nicolas Island (1933-1978).