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A population viability analysis for the Island Fox on Santa Catalina Island, California

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Abstract

The island fox (*Urocyon littoralis*) on Santa Catalina Island is among the most imperiled species on the Channel Islands due to a recent outbreak of canine distemper virus (CDV). The western subpopulation, which was not exposed to CDV, is a crucial element in the recovery of foxes by providing a source of animals for translocation and captive breeding. Using the program VORTEX, we developed a population viability analysis for the Santa Catalina Island fox to (1) address the likelihood of population persistence, (2) estimate the current susceptibility of the population to catastrophic events, and (3) evaluate the efficacy of current restoration strategies of releasing captive bred foxes and transplanting wild animals. Overall, we found the population to be susceptible to catastrophic events; a 50% increase in mortality every 20 years was sufficient to elevate the extinction risk above 5%. Current management activities entail the transplanting of 12 juvenile foxes annually, which may reduce the viability of the western subpopulation. A minimum population size of at least 150 foxes should be maintained in each subpopulation to reduce the risk of extinction due to demographic stochasticity. Releases of translocated and captive bred animals affect the speed of recovery on the eastern half of Catalina Island, but not the probability of extinction, which is near zero under current conditions. We conducted a sensitivity analysis for demographic parameters by incrementally varying survival, fecundity and density-dependence parameters, while holding all other parameters constant. Sensitivity analyses identified mortality and mean litter size as the most sensitive parameters, while the implementation of density-dependence and environmental variation of model parameters did not seem to affect population performance. We conclude that the population of island foxes on Santa Catalina is currently at a critically low population level, but recovery of the species appears possible.

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Keywords: Island fox; Logistic regression; Management; MARK; Population viability; Sensitivity analysis; Survival; *Urocyon littoralis*; VORTEX

1. Introduction

The persistence of species on oceanic islands has played an important role in the development of ecological theory, especially biogeography and conserva-

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Fig. 1. Location of Santa Catalina Island among the Channel Islands off the coast of California.

tion biology (McArthur and Wilson, 1967). Islands often harbor a unique assemblage of endemic species resulting from rapid evolutionary adaptation and low competition from new immigrant species. As a result, biodiversity and endemic species on islands are often negatively affected by introduced exotic organisms (Coblentz, 1990). Consequently, many island species present pressing conservation problems due to their unique adaptation, their limited ability to compete with non-native species, their geographical and taxonomic isolation, and their vulnerability to localized stochastic events.

An example for such a vulnerable island endemic is the island fox (*Urocyon littoralis*), a relative of the mainland gray fox (*Urocyon cinereoargenteus*). This territorial and monogamous carnivore is endemic to six of the eight California Channel Islands (Fig. 1), with each island supporting a genetically unique subspecies. Weighing only 1.4–2.7 kg, it is the smallest fox species

in the United States, but still the largest native land mammal on the Channel Islands. It has been classified as threatened by the California Department of Fish and Game and is currently under review for federal listing. Four of the six island fox subspecies have experienced catastrophic declines in the recent past. Populations on San Miguel, Santa Rosa, and Santa Cruz islands have declined by as much as 95% since 1993, probably due to predation by non-native golden eagles (*Aquila chrysaetos*; Coonan et al., 1998; Roemer, 1999).

The population on Santa Catalina Island has experienced precipitous declines in 1999 and 2000 due to an outbreak of CDV. Apparently, the western part of the island was spared from the CDV epidemic, suggesting that the lack of dispersal of foxes may have prevented the spread of CDV to the western part of Santa Catalina. A narrow isthmus separates fox populations on the eastern part of Santa Catalina Island (EAST) from the smaller western part (WEST, Fig. 2).

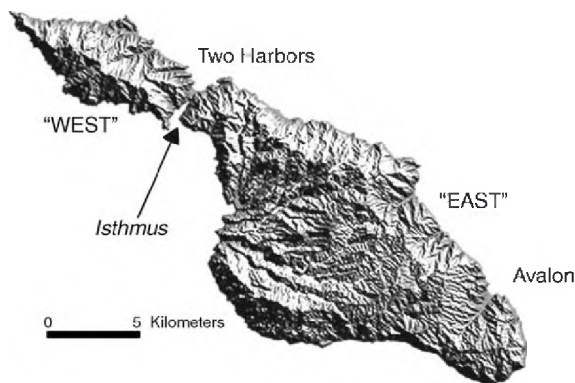


Fig. 2. Map of Santa Catalina Island, California, showing the location of the isthmus separating the subpopulations of island foxes. CDV affected only the EAST end of the island.

The isthmus has a dense population of humans and pet dogs, which may deter foxes from crossing. Within a 3-year observation period, only one animal had moved across the isthmus (Institute for Wildlife Studies, unpublished data). This unique land barrier has apparently created two subpopulations on the island.

In response to the recent catastrophic declines an experimental CDV vaccine was tested on wild foxes on Santa Catalina Island (Timm et al., 2002). Current island fox conservation efforts on Santa Catalina focus on (1) an intensive mark-recapture program to estimate population development, (2) translocation of radio-collared juvenile foxes from the WEST to the nearly extirpated EAST population, (3) inoculation of the entire island fox population with the experimental CDV vaccine, and (4) a captive breeding program to provide juveniles for release in the EAST population (Timm et al., 2002). However, the effectiveness of these conservation actions is difficult to estimate, given the relative paucity of pre-decline data for Santa Catalina Island foxes and the uncertainty of many relevant parameters (e.g., the frequency and severity of another CDV outbreak, and the survival of translocated foxes).

In this study, we investigated the viability of the Santa Catalina Island fox population. We employed population viability analysis (PVA; Boyce, 1992; Beissinger, 2002; Morris and Doak, 2002) to estimate the vulnerability of island fox populations on Santa Catalina Island to extinction and to assess the efficacy of conservation effort. PVA includes an array of quantitative methods and is a commonly used modeling tool

for assessing population status, estimating extinction risks, and developing conservation strategies for endangered or threatened species (Boyce, 1992; Lindenmayer and Possingham, 1996; Beissinger and Westphal, 1998). The predictive accuracy of PVA has been shown to be high (Brook et al., 2000a,b).

Specifically, we sought to (1) estimate the long-term persistence of the species given the two-component metapopulation structure of Santa Catalina Island, (2) simulate population dynamics under various frequencies of catastrophes (e.g., CDV outbreaks), and (3) determine how translocation of wild foxes and supplementation by captive-bred individuals affects the long-term stability of the population.

2. Methods

2.1. Study area and field methods

Santa Catalina Island (hereafter Catalina), located near Long Beach, California, is 34 km long, 0.8–13 km wide and covers 194 km². Elevations range from 0 to 648 m. Topographical relief is pronounced due to numerous canyons and steep-sided ravines dissecting the island (Fig. 2). The island has a Mediterranean climate with mean temperatures ranging from 12 to 20 °C and an average annual rainfall of 31 cm. The vegetation of Santa Catalina Island is dominated by grasslands and low scrub and oak woodlands (Thorne, 1967).

An intensive mark-recapture study was initiated on Santa Catalina Island in the fall of 1999 to determine the post-CDV outbreak population size and to inoculate remaining foxes with a CDV vaccine (Timm et al., 2000). Foxes were captured in modified single-door live traps (Model No. 106, Tomahawk Live Trap Co., Tomahawk, WI, USA) baited with canned cat food and a loganberry paste (Knobb Mountain Fur Co. Berwick, PA, USA) as an attractant (Timm et al., 2000).

Captured foxes were sexed, aged and weighed and marked with colored ear tags and PIT tags (Biomark Inc., Boise, ID, USA). Traps were placed 320 m apart, across the entire island along ridgelines and established roads, but some areas were too rugged or hazardous to be sampled. Based on previous studies, we believed that each trap had an effective area of 500 m radius. Thus, we estimated trap coverage at 81% of the western half and 73% of the eastern half of Santa Catalina

Island, respectively. Traps were operated on average for three consecutive nights. The main mark-recapture effort occurred during the summer and early fall. A less intensive trapping session (primarily to capture individuals for translocation) occurred in late fall and winter. Thus, we had two capture occasions per year with varying recapture probabilities.

2.2. Population estimation

To estimate the population size in each year we used the minimum number known alive (MNKA) from the island wide trapping and applied a joint hypergeometric likelihood estimator (JHE; White, 1996) to annual mark-recapture data. Because, we could not assess the exact number of marked animals alive at the beginning of each summer capture period, we used the MNKA (total of marked animals) from the previous year as an estimate of the number of marked animals available. This is most likely an overestimate of the true number of marked animals alive, and thus causes population estimates to be biased high when recapture probabilities are low.

2.3. Survival rate analysis

Using the capture–recapture data, collected from 1999 through the summer of 2002 on the west end of Santa Catalina Island, we constructed capture histories for each individual with an approximate time step of 6 months. We did not use data from the eastern subpopulation, because sample sizes were small. Assigning exact ages to captured foxes was difficult, hence we classified individuals either as pups or adults, based on dentition characteristics, and as male or female. Capture histories for 188 individuals (33 male pups, 39 female pups, 56 adult males, 60 adult females) were available for survival estimation. We used the “recapture only” subprogram of MARK (White and Burnham, 1999) to obtain maximum-likelihood estimates of age-, class-, and sex-specific survival rates. We modeled recapture rates with sex, age, and season as covariates, to account for the variability in recapture probabilities due to seasonally varying trapping efforts. Model selection was based on Akaike’s Information Criterion (AIC), which weighs the deviance of a model by the number of parameters (Burnham and Anderson, 1998). We corrected AIC values for overdispersion in the data

and used QAIC values to select the best model that contained all parameters of interest (i.e., age- and sex-specific survival rates). Alternative models, including those with and without interaction terms, were explored to ascertain that model parameters were estimated from the “best” biologically meaningful model.

2.4. Population viability analysis

We defined ‘population viability’ as a 95% probability of the fox population persisting at a minimum population size of at least 50 animals for at least 100 years. We used model VORTEX (Lacy, 1993, 2000; Lindenmayer et al., 2000) to simulate the dynamics of the Catalina fox population. VORTEX is an individual-based stochastic metapopulation model (Miller and Lacy, 1999). It generates a virtual population of N individuals, each with its own characteristics (sex, age, parentage, and location within the metapopulation). Implementation of density dependence in VORTEX is achieved by adjusting the number of breeding females in the population as population size increases (Lacy, 2000). In addition, VORTEX allows also for a quasi-density-dependence by a simple truncation of the population size when it exceeds the user-specified carrying capacity. The truncation in VORTEX abruptly removes all animals above a specific population size (K_{mod}). Although convenient, this is not realistic because it lacks the negative feedback on population growth as the population approaches K . For a logistically growing spatially closed population, mortality (D) and reproduction (B) cancel each other out at K , resulting in a zero growth of the population. The truncation may mask the true “effective carrying capacity” when reproduction is density-dependent and where K_{eff} occurs when $B = D$.

Unfortunately, elimination of the truncation in VORTEX is not straightforward. One possible way is to set the model’s truncation threshold (K_{mod}) at a higher value than the estimated K_{eff} . However, the proportion of females breeding at K_{eff} must be specified to adjust the density-dependent reproduction function. In our study, $P(K_{\text{eff}})$, i.e., the proportion of females breeding at K_{eff} was not known. The easiest way to estimate $P(K_{\text{eff}})$ is by linear regression analysis involving: (a) setting $P(K_{\text{mod}})$ to zero and changing the model’s parameter estimate for K (K_{mod}) incrementally, recording the effective carrying capacity (K_{eff}) at which the population growth is zero, (b) estimating the parameters

Table 1
Simulation model parameters for the island fox metapopulation on Santa Catalina island, California

Parameter/variable	Value
Replications	500
Generations (years)	30, 50 and 100
Extinction definition	$N < 50$
Populations	2 (EAST and WEST)
Inbreeding depression	N
Correlation between survival and reproduction	1.00
Breeding system	Long-term monogamous
Age at first breeding	2
Maximum breeding age	8
Sex ratio among pups	0.5
Mean litter size	1.58
S.D. of litter size	0.47
Dispersal ages	1
Dispersal survival	0.8
Percent dispersing	1%
Annual percent mortality (pup)	31.3 ± 5.9
Annual percent mortality (adult female)	16.8 ± 4.7
Annual percent mortality (adult male)	25.2 ± 6.0
Stable age distribution	Yes
Catastrophes	Local
K (EAST)	800 ± 80
K (WEST)	300 ± 30
Trend in K	No
Supplementation to	EAST
Removal from	WEST
Years of management	10
Age class supplemented/harvested	1

for the linear model $K_{\text{eff}} = a + b(K_{\text{mod}})$, (c) calculating $P(K_{\text{eff}})$ as:

$$P(K_{\text{eff}}) = P(0) - \frac{P(0)}{K_{\text{mod}}} K_{\text{eff}} \quad (1)$$

and (d) substituting the estimated carrying capacity for the population for K_{eff} and solving Eq. (1) for K_{mod} . This provided model parameters K and $P(K_{\text{mod}})$ for the linear density-dependent reproduction functions.

For the estimation of population persistence, we modeled the population with a linear density dependent reproduction. Whenever possible, we estimated the parameters required by VORTEX from field data (Kohlmann et al., 2003) and a previous intensive study of island Foxes (Roemer, 1999; Table 1). We simu-

lated the population for 100 years, repeating each run 500 times to obtain probabilities of extinction events. The fox population on Catalina was represented in VORTEX as a two-element (i.e., WEST and EAST) metapopulation. The two-population model structure allowed the specification of population parameters for each subpopulation. From the model output, we recorded the stochastic rate of change (λ), the probability of quasi-extinction, and mean and variance of population size for extant populations and the metapopulation.

2.5. Effects of environmental variation

The frequency and severity of environmental variation, such as an outbreak of disease, drought or a large fire is a potentially important factor determining the fate of the island fox. Although, VORTEX does not explicitly model disease transmission, its “catastrophe” feature may be used for this purpose. VORTEX allows the user to change the frequency at which catastrophic events occur, and their severity in regard to survival. For example, a severity factor of 30% means that a catastrophe—when it occurs, will reduce the survival rate of adult males to $83.18\% \times (1 - 0.3) = 58.22\%$. We modeled a combination of severity factors, ranging from 10 (nearly total mortality of all individuals) to 90% (i.e., 10% reduction of survival), and frequencies of occurrence (ranging from 1 to 20% of the time). We recorded the probability of quasi-extinction and the mean time to extinction (for populations going extinct) for each parameter combination.

2.6. Management scenarios

Ultimately, we were interested in evaluating the current conservation efforts and whether alternative management strategies may be effective in the protection and restoration of island foxes. We first explored a range of translocation and supplementation scenarios under the given population sizes on WEST and EAST and for a time horizon of 25 years. Management scenarios included the translocation of 0–12 juveniles from WEST to EAST and the release of 0–12 captive bred pups in EAST annually for 10 years. We also assessed the effect of translocating foxes for a range of population sizes, and used linear regression to estimate the relationship between population size and the number

Table 2

Model characteristics for three alternative VORTEX models differing in type and assumptions about density-dependence

Parameter	Model 1	Model 2	Model 3
Percent females breeding	Variable	Constant (95%)	Variable
Density-dependence in breeding?	Yes, $P(K) = 0$	No	Yes, $P(K) = 58\%$
Effective K (truncation threshold)?	Not effective	Yes	Yes

of pups that can be maximally translocated without exceeding a 5% risk of quasi-extinction. Lastly, we estimated the size of the EAST population resulting from various translocation and supplementation measures.

2.7. Sensitivity analysis

As the complexity of a natural system is reduced to a few estimable parameters in simulation models, uncertainty is of major concern in the assessment of model predictions. Thus, an important part of model validation is assessing the sensitivity of the developed model to variations in input parameters and assumptions. Sensitivity analysis is a quantitative assessment of the population response (e.g., the change in the population growth rate or extinction risk) when a parameter in the model is altered. The source of uncertainty in our PVA may be related to (i) model uncertainty, i.e., the number and characteristics of parameters to include in the model, (ii) data uncertainty, i.e., the accuracy and precision of parameter estimates, and (iii) environmental uncertainty, i.e., how environmental variability and the frequency of catastrophes affects population persistence. To explore the implications about different forms of density dependence in VORTEX, we developed two additional models (one with non-linearity in the reproductive function and K -truncation, and a simple density-independent with K -truncation only, Tables 2 and 3).

We evaluated the sensitivity of the VORTEX model by a conventional “manual perturbation” (Beissinger, 1995), and by logistic regression (Cross and Beissinger, 2001). Manual perturbation involves systematically

changing the values of each input variable in stepwise proportional increments while holding all other variables constant. We selected several model parameters for sensitivity analysis (Table 4) and changed each parameter incrementally by 0.1 starting at zero. In addition to changing each model parameter separately, we also examined the model’s sensitivity to global changes in the mortality regime affecting all age and sex classes simultaneously. This was implemented by including a mortality multiplier as a state variable in model VORTEX, calculating mortality as a product of the normal rate and the mortality multiplier, and by repeating simulations while varying the multiplier from 0 to 4.0 in increments of 0.1 (i.e., 10%). The same procedure was followed for the mortality variability parameter (EV) in VORTEX. Variable scenarios were simulated for 50 years and 500 replications each. To facilitate the running of models with successive incremental changes of a single input parameter in VORTEX, we developed a computer program that automatically creates batch input files for program VORTEX with varying parameter values (Table 4). This program is available from the authors upon request.

To assess the relative effect of proportional changes (10%) in input parameters on model output, we estimated the proportional sensitivities of each input variable as:

$$S_{\text{PROP}} = \frac{\lambda_{x-0.1x} - \lambda_{x+0.1x}}{0.2\lambda_{\text{original}}}$$

where $\lambda_{x+0.1x}$ is the new stochastic λ from model VORTEX output as the input variable x is increased or decreased by 10% (Heppell et al., 2000). S_{PROP} is equivalent to the slope of the change in the stochastic λ as the parameter of the model changes from -10 to $+10\%$. We ranked each variable according to the mean S_{PROP} across subpopulations and the three models. To address the relationship between an incremental change in the input variable Δx and the relative change of the population growth rate $\Delta \lambda$ calculated

Table 3

Parameter estimates for density-dependent reproduction in model VORTEX (see text for explanation of parameters)

Population	K_{eff}	K_{mod}	$P(K_{\text{eff}})$	$P(K_{\text{mod}})$
WEST	300	778	58.38	0
EAST	1300	3094	55.05	0

Table 4
VORTEX model parameters used in sensitivity analysis and their minimum and maximum values

Description	Minimum	Maximum	Applicable models
Mean litter size	0	4.584	1, 2, 3
S.D. of litter size	0	12.764	1, 2, 3
Dispersal (%)	0	3.0	1, 2, 3
Survival during dispersal (%)	0	96	1, 2, 3
Mortality multiplier (applied to all mortality rates simultaneously)	0	3.5	1, 2, 3
Adult male mortality	0	75.51	1, 2, 3
Adult female mortality	0	50.43	1, 2, 3
Pup mortality	0	93.84	1, 2, 3
S.D. of mortality for adult males	0	18.03	1, 2, 3
S.D. of mortality for adult females	0	14071	1, 2, 3
S.D. of mortality for pups	0	17085	1, 2, 3
Females breeding (constant, %)	0	100	2
Standard deviation of females breeding (%)	0	37.5	1, 2, 3
Females breeding at $N = 0$ (%)	0	100	3
Females breeding at K (%)	0	100	3
Carrying capacity, K	0	1400/2600	3
S.D. of K	0	150/300	3
Under-population (Allee)-effect	0	4.0	3
B , curvature of the density-dependent reproduction function	0	50	3
Concordance between survival and reproduction	0	1	1, 2, 3

Because of differences in the density dependence of reproduction among models, not all parameters apply to all models.

as $(\lambda_{\text{modified}} - \lambda_{\text{original}}) / -\lambda_{\text{original}}$ (Mills et al., 1999), we plotted the relative change in the model's growth rate ($\Delta\lambda$) over the proportional change in the input parameter (Δx) to examine the linearity of these relationships. Because our three models were complex and contained different assumptions about density-dependence and non-linearity in the density-dependent feedback, we expected these elasticities to be non-linear over the range of parameter perturbations (Mills et al., 1999). In addition, we were interested not only in the response of the stochastic λ_s , but also in the change in the risk of extinction to each subpopulation as parameter values changed. Thus, we employed logistic regression as an additional method of sensitivity analysis (McCarthy et al., 1995, 1996; Cross and Beissinger, 2001). The method involves recording the population's fate after simulation of 50 years as a binary variable (extinct or extant) and applying logistic regression analysis to address the relative importance of different variables. Prior to logistic regression analysis, we examined the relationship between each input parameter and the logits of the resulting probability of extinction for non-linearity. No parameter was rejected due to apparent violation of the linearity assumption of the logits. We accepted a model if it showed (1) a minimum difference of 2.0 units in AIC between a model containing the inter-

cept only and the "full" model containing the intercept and the independent variable and (2) a non-significant P -value for the Hosmer–Lemeshow goodness of fit test (Hosmer and Lemeshow, 1980). We also inspected the regression diagnostics suggested by Pregibon (1981) as displayed by SAS PROC LOGISTIC for obvious extreme points that may have affected the fitted model. Any variable that did not meet these requirements was excluded from further consideration in sensitivity analysis. We used the standardized regression coefficient (McCarthy et al., 1996; Cross and Beissinger, 2001) to estimate the contribution of each variable to the probability of a population going extinct. We also compared the exponent of the slope (i.e., the odds ratio) as an indicator of the sensitivity. Odds ratios describe the proportionate rate at which the predicted odds change with each successive change in the independent variable (i.e., the change in the odds of the population going extinct after a 1-unit change in the demographic parameter). Lastly, we examined the adjusted coefficient of determination (R -adj; Nagelkerke, 1991) and the Receiver-Operating-Characteristic (ROC) curve as an indicator of the predictive accuracy of the logistic model (Hanley and McNeil, 1983). However, ROC curves are not very sensitive measures for comparing models, hence, we simply ascertained that these curves

indeed rose quickly and that the area under the curve (c) was closer to 1 than 0.5.

3. Results

3.1. Population parameters

During summer 2002, 178 marked foxes were verified to be alive in the wild on Santa Catalina. After accounting for known mortalities and removals from the wild for captive breeding purposes, a conservative estimate of the current minimum population of wild

foxes on Santa Catalina Island is 161 foxes (94 WEST, 67 EAST). Adjusting this number for the proportion of the island sampled provides an island-wide population estimate of 214 animals (94 WEST, 67 EAST). The JHE population estimate was 140 (95% CI: 133–151) for WEST and 67 (95% CI: 67–68) for EAST. While the population estimate for WEST was probably biased high due to an unknown number of marked animals alive prior to the summer trapping in 2002, the EAST population estimate is identical to the MNKA. Sex ratios were 42:52 M:F for WEST and 33:34 M:F for EAST, respectively.

Results from Program MARK suggested that recapture rates of island foxes on Santa Catalina Island (WEST) were highly variable and differed among seasons, sex and age class. After controlling for this “nuisance parameter”, survival estimates in the model with the lowest AIC value differed among pups and adults and among the sexes for adults, but not between male and female pups. Seasonal effects did not explain significant variation in mortality rates. Confidence intervals of mortality estimates overlapped considerably among the different age classes (Fig. 3). The test of the global model via the GOF parametric bootstrap test suggested that overdispersion of our data was mild ($\hat{c} = 1.0440$). Only 1 acceptable competing model (based on QAIC) was identified, but it did not include age- or sex-specific mortality estimates. This was not useful for the purpose of this analysis (i.e., the parameterization of model VORTEX), and hence, we ignored the competing model.

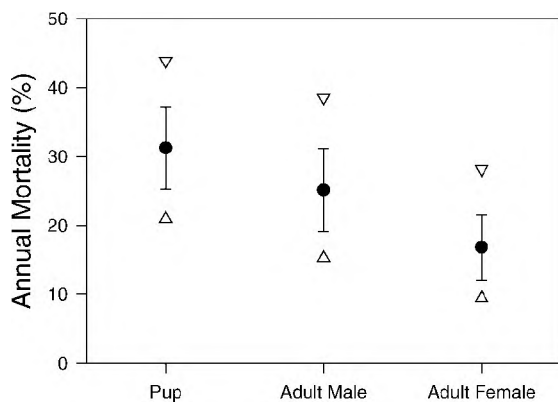


Fig. 3. Mortality estimates (mean, S.E.) by age and sex classes of island foxes, for the western subpopulation on Santa Catalina Island, California, 1999–2002. Triangles indicate upper and lower confidence intervals.

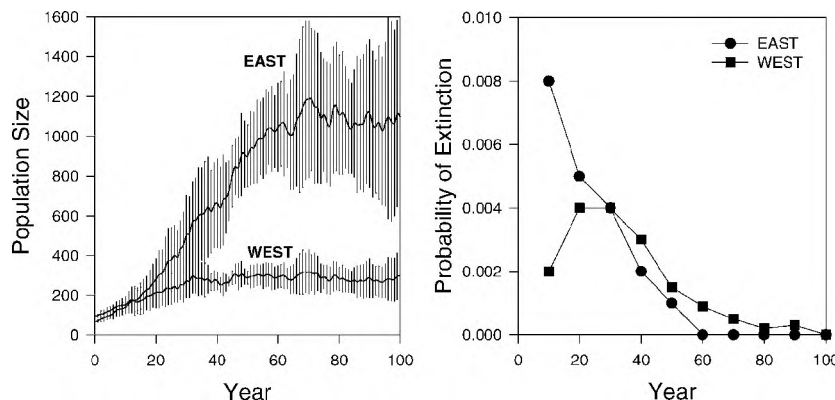


Fig. 4. Simulated population trajectories (left) and probability of extinction (right) for two subpopulations of island foxes on Santa Catalina Island, from VORTEX two simulation with no catastrophes or management actions (Model 1).

Table 5

Parameter estimates from logistic regression for the effects of population size and length of simulation (time span) on the probability of extinction of two subpopulations of Island fox on Santa Catalina Island, California

Parameter	d.f.	Estimate	Standard error	χ^2	P	Standardized estimate
Intercept	1	4.2349	0.0834	2576.3	<0.0001	
Population size	1	−0.1158	0.00164	4985.3	<0.0001	−1.6479
Time span	1	−0.0826	0.00272	923.6	<0.0001	−0.372
Population	1	0.2706	0.042	41.6	<0.0001	0.0746

3.2. Population persistence

Simulating the Santa Catalina Island fox population with VORTEX revealed a steadily increasing population when catastrophic events or management actions were excluded (Fig. 4). Under these conditions, the probability of extinction was less than 1% for both subpopulations. However, the EAST population had a higher probability of going extinct than the WEST population, especially during the first 20 years. After 30 years of simulation, the extinction risk for the WEST population was higher due to an overall smaller population size. Both populations showed a distinct return tendency around the estimated K_{eff} , which was far below the truncation parameter K_{mod} of program VORTEX. The mean time to extinction was 9.3 and 23.4 years for the EAST and WEST populations, respectively. Stochastic rates of change were positive for all models and did not differ significantly among the two subpopulations and between models (Fig. 5)

3.3. Effect of initial population size

To address the risk of extinction associated with small population size, we modeled the same parameters with initial population sizes ranging from 10 to 90. The risk of populations going extinct increased rapidly with declining starting population sizes for both subpopulations. Persistence was also a function of time: extinction risk declined with the number of generations these populations were simulated (Table 5 and Fig. 6).

3.4. Effects of catastrophic events

Including catastrophes into the model resulted in a rapid exponential increase in the risk of extinction when

frequency of catastrophic events exceeded 5% (i.e., one catastrophe every 20 years) and when the severity factor was greater than 50% (Fig. 7). As severity and frequency of catastrophes increased, the extinction risk

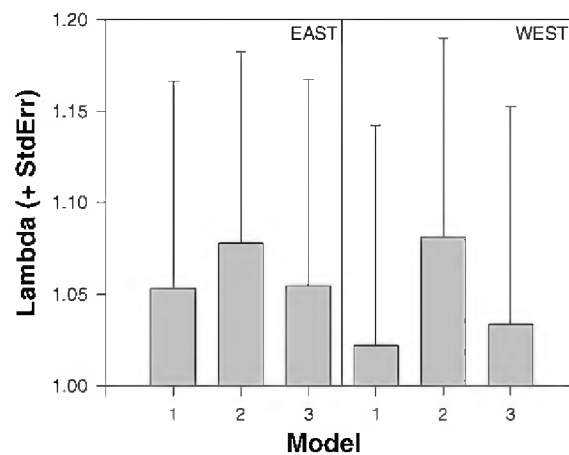


Fig. 5. Growth rate (λ) for two subpopulations of island foxes on Santa Catalina Island, California. For definitions of models, see text.

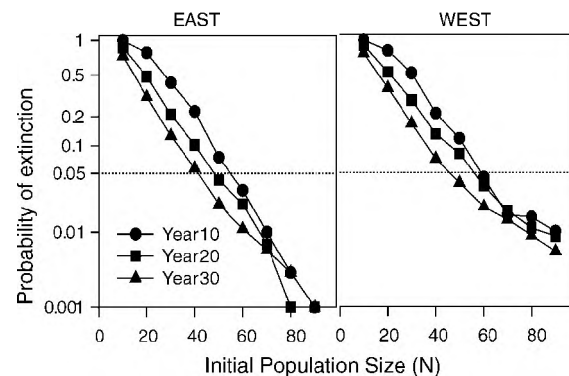


Fig. 6. Effect of varying initial population size for the two subpopulations of Island foxes on Santa Catalina Island, California: probability of subpopulations surviving a predetermined time span under simulations with different initial starting conditions (Model 1).

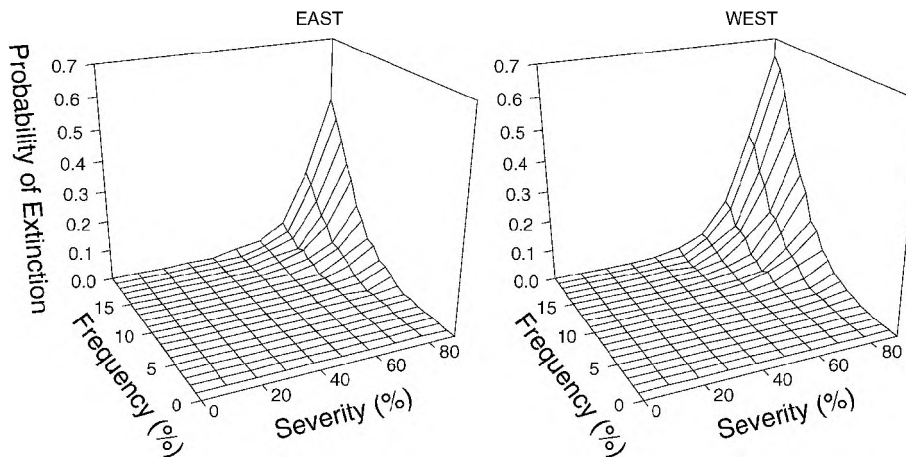


Fig. 7. Risk of quasi-extinction for island fox sub-populations on Santa Catalina Island, California, for varying degrees of frequency and severity (i.e., reduction in survival) of catastrophic events (Model 1).

Table 6

Parameter estimates from logistic regression for the effects of frequency and severity of catastrophic events on the probability of extinction of two subpopulations of Island fox on Santa Catalina Island, California

Parameter	d.f.	Estimate	Error	χ^2	P	Odds Ratio		
						Point estimate	95% Confidence limits	
EAST								
Intercept	1	−14.0831	0.1412	9946	<0.0001			
Frequency	1	0.2868	0.0045	4052	<0.0001	1.332	1.320	1.344
Severity	1	0.9193	0.0138	4448	<0.0001	1.096	1.093	1.099
WEST								
Intercept	1	−18.9653	0.2740	4792	<0.0001			
Frequency	1	0.3628	0.0077	2228	<0.0001	1.437	1.416	1.459
Severity	1	1.2522	0.0269	2174	<0.0001	1.107	1.104	1.110

increased faster in the western subpopulation than in EAST. Odds ratios from logistic regression were higher for frequency than for severity, suggesting that the odds of a subpopulation going extinct increased faster with a 1% change in frequency than with a 1% increase in severity. Confidence intervals of point estimates of odds ratios did not overlap among populations or parameters, suggesting that these differences were significant (Table 6).

Although, we did not include inbreeding into our models, mean genetic heterogeneity (H) was significantly correlated with population size N and N^2 (WEST: $H = 710.8 + 1.4673 \times N - 0.002283 \times N^2$, $F_{2,197} = 14242$, $P < 0.0001$, $R^2 = 0.9950$; EAST: $H =$

$811.8 + 0.1923 \times N - 0.000063 \times N^2$, $F_{2,197} = 19717$, $P < 0.0001$, $R^2 = 0.9931$; Fig. 8).

3.5. Management scenarios

The current recovery strategy for the Santa Catalina Island fox population calls for the release of the entire annual production of captive bred juveniles and the translocation of up to six male and six female juvenile foxes from the western subpopulation to the eastern half of the island. In 2002, eight captive bred pups were produced and released to the east end of Santa Catalina Island and 12 wild born juvenile foxes were translocated from WEST to EAST. Under the current

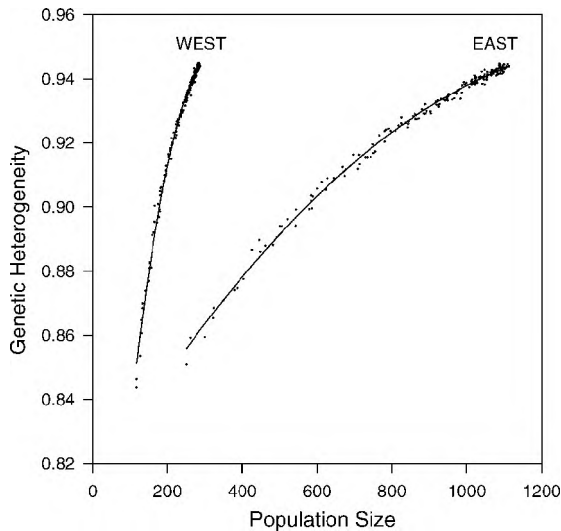


Fig. 8. Genetic heterogeneity as a function of population size for two subpopulations of island fox on Santa Catalina Island, California (Model 1).

conditions, the risk of a quasi-extinction within 30 years resulting from the removal of pups from WEST and translocating them to EAST increased with the number of pups removed (Fig. 9). Likewise, the mean number of foxes on the EAST end of Santa Catalina Island for a 30-year period increased with the number of fox pups released there (Fig. 9). For both measures, the number of foxes translocated was a significant factor affecting the risk of extinction and the mean population size ($P < 0.0001$).

The 5% isocline of the extinction risk associated with the annual removal of pups ($N_{\text{pups},0.05}$) increased

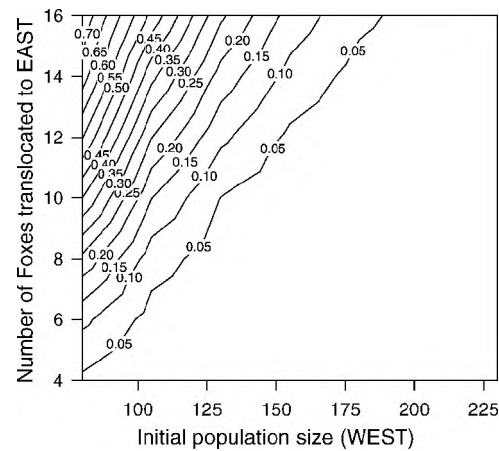


Fig. 10. Five percent isoclines for extinction risk of the WEST subpopulation of island foxes on Santa Catalina Island, California (Model 1).

linearly with the initial population size N_{init} ($N_{\text{pups},0.05} = -4.90776 + 0.1107N_{\text{init}}$; $R^2 = 0.9978$, $F_{1,21} = 5500$, $P < 0.0001$, Fig. 10). Similarly, when translocations occurred in alternate years the 5% extinction risk isocline also increased linearly with the number of pups removed and increasing population size ($N_{\text{pups},0.05} = -2.5819 + 0.1026N_{\text{init}}$; $R^2 = 0.9918$, $F_{1,12} = 2160.09$, $P < 0.0005$). The slopes of the two lines were not significantly different ($P = 0.64$). The release of pups into the eastern subpopulation did not affect the risk of extinction due to the already low probability of extinction. However, population sizes for the eastern subpopulation after 25 years were highly dependent on the number of pups released (Fig. 11). A third-order polynomial explained most of the variation for

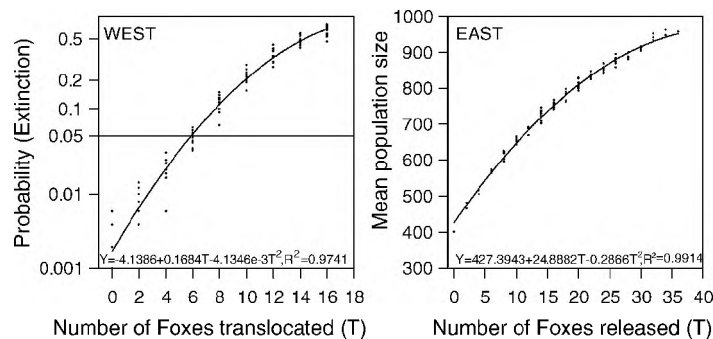


Fig. 9. Effects of translocation of foxes on the probability of extinction for the western subpopulation (left) and on the mean population size for the eastern subpopulation (right) of island foxes on Santa Catalina Island, California (Model 1).

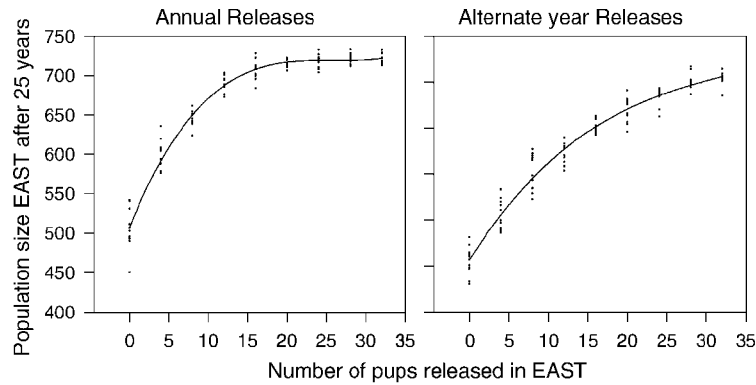


Fig. 11. Mean population size for the eastern subpopulation of island foxes on Santa Catalina Island after 25 years under different release strategies.

the annual release ($N_{25,EAST} = 507.23 + 24.77N_{Released} - 0.9636N_{Released}^2 + 0.01246N_{Released}^3$, $R^2 = 0.9662$) and for the alternate release ($N_{25,EAST} = 506.506 + 13.511N_{Released}^2 - 0.0031N_{Released}^3$, $R^2 = 0.9635$).

3.6. Sensitivity analysis

Manual perturbation of several demographic parameters resulted in significant changes in population

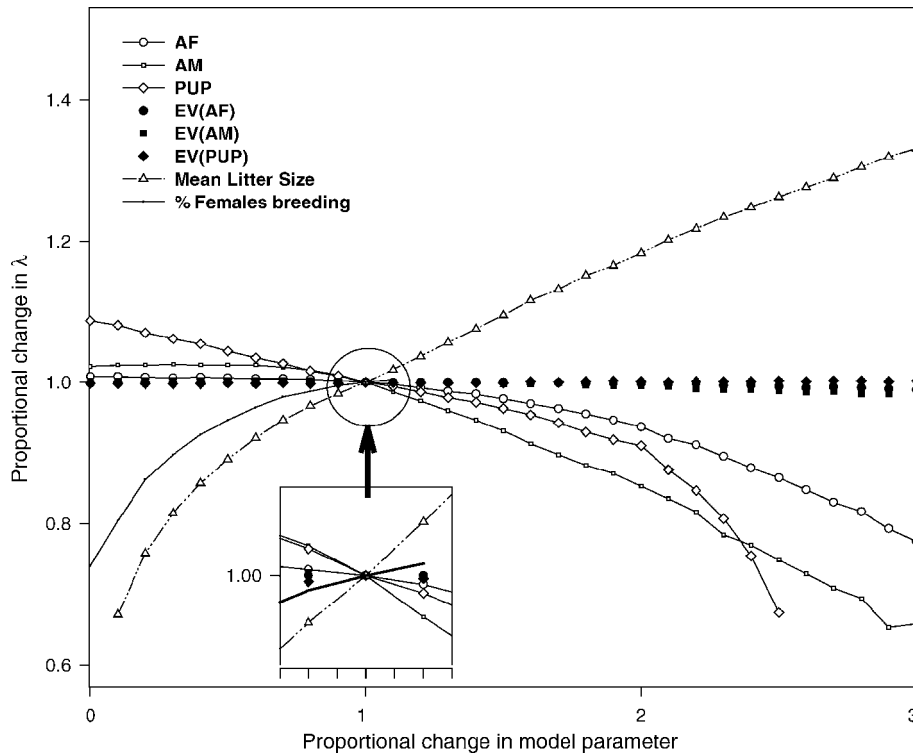


Fig. 12. Example of elastograms for eight demographic parameters showing the relative response in the population growth parameter λ to an incremental proportional change in the demographic parameter for the WEST subpopulation (Model 3). The steepest slope (see inset) indicates the most influential parameter.

Table 7

Elasticity estimates for demographic parameters of three population models for island foxes on Santa Catalina island, California

Rank	Parameter	Model 1		Model 2		Model 3	
		EAST	WEST	EAST	WEST	EAST	WEST
1	Curvature (B)	–	–	–	–	–0.3095	–0.2188
2	Total mortality	0.1674	0.0967	0.3825	0.4101	0.2374	0.2642
3	Mean litter size	–0.1566	–0.0864	–0.2879	–0.3098	–0.1885	–0.1745
4	Mortality (adult male, %)	0.1202	0.0611	0.2479	0.2592	0.1466	0.1229
5	Females breeding (%)	–	–	–0.1235	–0.1401	–	–
6	Mortality (Pup, %)	0.0786	0.0408	0.1347	0.1459	0.0734	0.0769
7	Females breeding at $N = 0$ (%)	–	–	–	–	–0.0633	–0.0464
8	Females breeding at K (%)	–	–	–	–	–0.0317	–0.0670
9	Carrying capacity (K -truncation)	–	–	–	–	–0.0158	–0.0155
10	Mortality (Adult female, %)	0.0052	0.0102	0.0162	0.0216	0.0105	0.0257
11	Survival (dispersants, %)	0.0000	–0.0051	–0.0162	–0.0162	0.0000	–0.0103
12	Environmental variation (total mortality)	0.0053	0.0051	0.0108	0.0054	0.0106	0.0052
13	Environmental variation mortality-adult male)	0.0105	0.0051	0.0000	0.0054	0.0052	0.0051
14	Allee-effect	–	–	–	–	–0.0053	–0.0051
15	Environmental variation (K)	–	–	–	–	–0.0053	–0.0051
16	Environmental variation (mortality-adult female)	–0.0052	–0.0051	0.0054	0.0000	–0.0052	0.0000
17	Environmental variation (mortality-pup)	0.0000	0.0000	0.0054	0.0054	0.0000	–0.0052
18	Std (litter size)	0.0000	0.0000	0.0054	0.0000	0.0000	0.0000
19	Environmental variation (% females breeding)	0.0052	0.0000	–0.0054	0.0000	0.0052	0.0000
20	Correlation (survival and reproduction)	–0.1436	–0.3046	0.1491	0.2790	0.0678	–0.0463
21	Dispersal (%)	0.0052	0.0000	0.0000	–0.0162	0.0105	0.0000

Elasticity estimates were calculated as the relative change in the population's growth rate when a demographic parameter was changed by 10% above and below the normal value. Model assumptions were: density-dependent reproduction, no K -truncation (Model 1); density-independent reproduction and K -truncation (Model 2); and density-dependent reproduction and K -truncation (Model 3). Ranks of parameters are based on mean absolute elasticity.

growth rates (Fig. 12). Elasticity values for a 10% change of demographic parameters (S_{PROP} , Table 7) differed among populations and models (i.e., the assumptions about density dependence; Table 7). At this scale of perturbation (i.e., observed vital rate $\pm 10\%$), the most influential parameters affecting the relative change in λ across all models were total mortality and mean litter size. Among the different sex and age categories, adult male mortality was the most influential parameter, followed by pup mortality and adult female mortality (Table 7). Increasing the environmental variation of demographic parameters did not affect proportional changes in λ greatly (Table 7). Of the parameters affecting the shape of the density-dependent reproduction function in Model 3, a minute change in

curvature (B) had a greater effect on stochastic growth rates than the inclusion of an Allee-effect. Proportional changes in λ were non-linear as demographic parameters changed systematically by 10% of their mean (e.g., Fig. 12), which rendered S_{PROP} a poor predictor of the parameter's elasticity. Therefore, we compared the results from a linear elasticity analysis with logistic regression analysis, where we modeled the effects of proportional changes in the vital rates on quasi-extinction risks for each subpopulation. Our requirements for AIC, Hosmer–Lemeshow goodness of fit test and regression diagnostics were met by 8 of the 18 parameters (Table 8), suggesting that the remaining 10 parameters either did not affect the extinction risk significantly or violated some of the assumptions of lo-

Table 8

Logistic regression results for sensitivity analysis of three models (1: density-dependent reproduction, no K -truncation; 2: constant reproduction, K -truncation, and 3: density-dependent reproduction and K -truncation)

Model	Parameter	WEST				EAST			
		STB	C	Odds ratio	R -adj	STB	C	Odds ratio	R -adj
1	Mean litter size	−16.70	0.99	0.00	0.97	−17.60	0.99	0.00	0.97
	Mortality (AM, %)	10.22	0.99	2.28	0.96	—	—	—	—
	Mortality (AF, %)	5.90	0.99	1.88	0.94	6.13	0.99	1.93	0.94
	Mortality (pup, %)	5.86	0.99	1.55	0.93	5.78	0.99	1.54	0.93
	Mortality total (%)	22.10	0.99	—	0.98	21.88	0.99	—	0.98
	Environmental variation — % mortality (AM)	2.63	0.98	1.57	0.84	2.43	0.97	1.52	0.82
2	Mean litter size	−17.49	0.99	0.00	0.97	−17.54	0.99	0.00	0.97
	Mortality (AM, %)	10.08	0.99	2.26	0.96	10.54	0.99	2.34	0.96
	Mortality (AF, %)	8.05	0.99	2.36	0.95	7.66	0.99	2.27	0.95
	Mortality (pup, %)	6.17	0.99	1.58	0.93	6.16	0.99	1.58	0.94
	Mortality total (%)	22.74	0.99	—	0.98	25.98	1.00	—	0.98
	Environmental variation — % mortality (AM)	2.55	0.97	1.55	0.83	2.36	0.97	1.50	0.81
3	Mean litter size	−17.63	1.00	0.00	0.97	−16.91	0.99	0.00	0.97
	Carrying capacity (K -truncation)	−9.47	0.99	0.91	0.92	−13.03	0.99	0.97	0.91
	Mortality (AM, %)	9.67	1.00	2.18	0.96	9.49	0.99	2.15	0.96
	Mortality (AF, %)	6.84	1.00	1.87	0.94	6.74	1.00	1.85	0.94
	Mortality (pup, %)	5.55	0.99	1.54	0.93	5.50	0.99	1.53	0.93
	Mortality total (%)	21.45	0.99	—	0.98	21.59	0.99	—	0.98
	Females breeding (%)	−4.03	0.99	0.80	0.90	−4.33	0.99	0.79	0.91
	Environmental variation — % mortality (AM)	2.62	0.98	1.57	0.84	2.45	0.97	1.52	0.82
	Environmental variation — % mortality (AF)	2.42	0.97	1.70	0.81	2.42	0.97	1.70	0.80

Demographic parameters (VAR) were varied systematically from 0 to 400% of the normal value and simulated for 50 years and 500 replications. Regression statistics include the standardized slope estimates (STB), the area under the ROC curve (c), the odds ratio and the adjusted coefficient of determination (R^2 -adj).

gistic regression analysis (e.g., convergence criteria). The most influential parameter affecting the risk of extinction was mean total mortality, followed by litter size, mortality of adult males, adult female mortality, pup mortality and the environmental variation in adult male mortality rates. This sequence was identical for Models 1 and 2. Thus, both sensitivity analyses identified the mean litter size as the most sensitive parameter in our simulations. Likewise, in all analyses adult male mortality ranked before adult female and pup mortality, while environmental variation in mortality seemed influential only for adult male mortality. Standardized estimates of the regression coefficient were not different between EAST and WEST ($T = 0.2610$, d.f. = 34, $P = 0.7956$). Rankings based on the mean standardized slope estimate remained consistent among the different models, despite the variation in underlying assumptions of the different models. The density-dependent model with carrying capacity truncation (Model 3) was quite sensitive to a lowering of the truncation level.

Model 3 was also the only model to respond to the percentage of females breeding at low population sizes ($P(0)$) in VORTEX. The form of density dependence in our three models did not affect the mean growth rate under normal parameter values (i.e., without manual perturbations; Fig. 5)—the density-dependent model with K -truncation (Model 3) produced similar growth rates as the density-independent model (Model 2) or the “realistic model” (Model 1).

4. Discussion

Our PVA of the island fox on Santa Catalina Island contains three major elements: estimates of vital rates and relationships that served as input for our models, simulated dynamics of the fox population and the sensitivity of the model, and management recommendations for the recovery of the species. Certainly, the accuracy of our predictions is a function of how accurate model

input parameters and assumptions are. For example, survival estimates were derived from only three years of data collected on the west end of Catalina Island where the population density was probably at or near carrying capacity. Thus, our survival estimates may underestimate the survival of foxes in the low-density population on the EAST end of Santa Catalina Island. Preliminary data indicate that survival of translocated and released captive-bred juveniles on the EAST is comparable, if not higher than that of wild foxes on the WEST end of Santa Catalina Island (Kohlmann et al., 2003). However, mean pup survival on Santa Catalina Island was 35% higher and mean adult survival up to 50% higher compared with nearby San Clemente Island (Roemer, 1999). Mortality of all age classes was the most significant factor affecting the viability of the Santa Catalina island fox population. Adult mortality was higher in male foxes than in females, perhaps due to the risk of injury related to frequent territorial disputes among males. Interestingly, the number of male foxes found with bite wounds, cuts and abrasions of the head and ears is rather large and may indicate intense aggressive interactions among individuals (Kohlmann et al., 2003). Male mortality appeared to have the greatest effect on population growth and extinction risk. Mortality of different age and sex classes within a population is usually correlated in wild populations, hence examining the model's sensitivity towards mortality rates for a single cohort is not very informative. However, the predominant sensitivity of the model towards male mortality may also point to an artifact related to the strictly monogamous breeding system of the individual-based VORTEX model. The model assumes long-term monogamy, which may be less flexible than the actual mating system of foxes in the wild. Thus, the model may have included an additional limiting factor (male availability for breeding). Unfortunately, no field data exist to test this hypothesis. Mean litter size significantly affected the sensitivity of all models. Our model estimate of mean litter size was based on the lowest reported data and hence was very conservative (1.58 ± 0.42 ; Coonan et al., 1998) but most studies show that litter size can be substantially larger. Litter sizes on San Miguel Island from 1993 to 1998 averaged 2.21 ± 0.66 (Coonan et al., 1998). Five wild foxes on Santa Catalina Island produced litters with 1.8 ± 0.45 pups, while seven captive foxes had 2.0 ± 0.57 pups each (Institute for Wildlife Stud-

ies, unpubl. data). Because of the model's sensitivity to litter size estimates, underestimation may produce growth rates that are substantially lower, and thus may predict a less optimistic recovery potential.

Model behavior did not change with model structure, i.e., our choice of how density dependence was implemented. Stochastic growth rates were similar for all models, suggesting that eliminating the artificial truncation in program VORTEX did not affect model predictions. The inclusion of carrying capacity (K_{mod}) in Model 3 as one of the most sensitive model parameters highlights its impact on the effective carrying capacity and the necessity to estimate it carefully. K_{mod} essentially determines the slope of the density-dependent reproduction function, thus a change of K_{mod} affects the strength of the negative feedback at high population densities. Reducing K_{mod} is equivalent to making that slope steeper, and thus increasing the risk of extinction. With the exception of the sensitivity of Model 3 to K_{mod} , the different models did not affect rankings of individual parameters.

Our analyses indicate that the status of the Santa Catalina Island fox population is critical due to a significant risk of extinction, small population size and high susceptibility to catastrophic events. The model suggests that even a relatively "mild" (e.g., 50%) increase in mortality occurring once every 20 years may increase the probability of extinction beyond 5%. Currently, little is known about the frequency of catastrophic events (e.g., disease, fire, drought) on Santa Catalina Island and their effects on fox populations. In the past 140 years, over 200 fires were documented on Catalina (Catalina Conservancy, personal communication) and severe 12-month drought conditions with a Standardized Precipitation Index (McKee et al., 1993) of <-1.5 occur on average once every 20 years (author's unpublished data). As the recent CDV outbreak demonstrated, diseases can have a devastating effect on island fox populations. Antibodies to canine distemper have not been found in any of the fox populations on the Channel Islands. This suggests that either distemper has never before been introduced to island fox populations, or that island foxes are extremely susceptible to distemper and none survived exposure (Garcelon et al., 1992). Captive island foxes used in a preliminary study in 2000 showed good antibody production to a Canary Pox vectored recombinant Canine Distemper Virus vaccine (CPV-CDV, Merial Ltd., Athens, GA)

but declines in antibody titers were measured at 12–14-month post-vaccination in these same animals (Timm et al., 2002). To date, over 400 doses of the CPV-CDV vaccine have been given to Santa Catalina Island foxes and no mortalities, illness or secondary effects have been attributed to the vaccine. Although vaccinated animals have yet to be challenged by exposure to CDV, it is likely that vaccination will reduce the morbidity of a new CDV outbreak. Hence, we recommend continuing the vaccination of all wild captured and captive foxes on Santa Catalina Island.

Current recovery actions on Santa Catalina include the translocation of wild-born yearlings between subpopulations and the release of captive bred pups to the EAST end of the island. Our simulations suggested that the WEST population currently is not large enough to sustain the planned translocation of 12 animals per year. Instead, we recommend a rule-based translocation strategy that recognizes an acceptable risk of extinction (5%) over a long-term (>25 years) time horizon. This is perhaps overly cautious, because most likely managers would curtail the translocation as soon as a decline in the source population is evident. Likewise, it would be difficult to obtain the number of yearling translocates at low population size. Although, an aggressive translocation program poses a significant risk to the WEST end population, the potential for a rapid recovery of the EAST subpopulation is large, even without any management. The growth rate of the EAST subpopulation is positive (regardless of assumptions on density dependence) and larger than for the WEST population. This is probably related to the current population size relative to the estimated carrying capacity. The WEST population is closer to the estimated carrying capacity (31% of K) and hence has lower potential for population growth than the EAST population, which is currently estimated at approximately 7% of K .

It is important to note that our sensitivity analysis was prospective, thus cannot elucidate why and how parameters or population behavior may have changed in the past. Obviously, the paucity of pre-decline data prevented us from a detailed retrospective analysis of the variation of population parameters and its influence on population dynamics and extinction probability. Our sensitivity analysis explored how stochastic growth rates (λ) and quasi-extinction probabilities

changed with a systematic change in vital rates, and thus may elucidate how management actions may contribute achieving recovery goals (Caswell, 2001). Because of the non-linear elasticities of λ , the effect of changing vital rates on the stochastic growth rate is difficult to quantify in individual-based models. Thus, we used logistic regression to obtain relative measures of extinction risk associated with changes in model parameters. Results from our logistic regression model (Table 8) mirrored the results of the sensitivity analysis of stochastic growth rates, but offered additional advantages. First, standardized regression coefficients of a logistic regression model are unitless estimates of the importance of model parameters (predictor variables) affecting the population's performance index. Because the standardized regression coefficient is scaled by an estimate of parameter variability (i.e., the standard error of the model estimate) it includes uncertainty originating from process error and the sampling error contained in the parameter estimate (White et al., 2002). Although we were not able to remove sampling error from our estimates, we addressed the sensitivity of the model to changes in the variation of parameter estimates. Surprisingly, increasing the variation of parameter estimates had a lesser effect on extinction risk than a change in mean vital rates. It remains to be shown if the difference between standardized regression coefficients for mean and variance of a population parameter can identify the importance of different sources of error in PVA. Secondly, using logistic regression allowed us to evaluate the relative importance of vital rates not only by quantitative comparisons, but also by examining the reliability of information contained in these estimates. Logistic regression provides estimates of information criteria, such as AIC, by which the significance of individual parameters can be addressed. Lastly, logistic regression addresses the interaction of continuous variables without requiring their explicit expression in the model. Interactions with categorical variables can be modeled relatively easily (Jaccard, 2001), which facilitates an in-depth examination of model behavior (McCarthy et al., 1995). However, it is presently unclear if standardized regression coefficients are comparable among different studies or organisms (Cross and Beissinger, 2001).

Various PVA packages exist today, including individual-based programs, such as GAPPS (Harris et al., 1986) and VORTEX (Lacy et al., 1995), and matrix-

based models INMAT (Mills and Smouse, 1994), RAMAS[®] Metapop (Akçakaya and Atwood, 1997), and RAMAS[®] Stage (Ferson, 1994; Inouye, 1994). Although each was designed with slightly different objectives in mind (see Lindenmayer et al., 1995), these simulation programs provide a convenient toolbox for building predictive models based on the life history traits, deterministic factors, and stochastic processes that together control the dynamics of natural populations (Gilpin and Soulé, 1986). We chose to conduct our PVA with a generic population simulation model (program VORTEX). Other workers have used species-specific PVA models, especially for some high-profile species (e.g., Northern spotted owl; Boyce, 1994). However, such specially developed models are usually expensive and time consuming to construct. In addition, they are rarely used for more than one study or data set, thus possible flaws may remain undetected. Commercially available “generic” PVA packages offer an excellent opportunity for improving PVA, because they are scrutinized, evaluated and iteratively developed by a variety of modelers (Brook et al., 1997). Although, conservation biologists increasingly recognize the importance of habitat-based models by incorporating habitat relationships and landscape characteristic into the metapopulation dynamics (Akçakaya, 2000), the paucity of landscape-related information for the Santa Catalina Island fox did not permit addressing landscape level processes and their uncertainty.

White et al. (2002) postulated that rigorous estimates of viability are contingent upon knowledge of the status of population at a fixed point in time and its dynamics over a certain time frame. Both requirements were met in our analysis: a rigorous mark-recapture program allowed us to estimate the current population size, structure and survival with high precision. Parameters that were less well-known were conservatively estimated, which increased the estimated risk of extinction, but at the same time prevented us from overly optimistic predictions. Our 2 methods of sensitivity analysis provided us with a clearer understanding how minute changes in mean or variance of model parameters affect measures of population performance. Hence, we feel confident that our assessment of the population viability of the island fox on Santa Catalina Island has important implications for management and the recovery of the species.

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