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Source: *Ecological Monographs,* Vol. 79, No. 1 (Feb., 2009), pp. 77-108
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/27646167
Accessed: 22/04/2013 18:14

Incorporating ecological drivers and uncertainty into a demographic population viability analysis for the island fox

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Abstract. Biometricians have made great strides in the generation of reliable estimates of demographic rates and their uncertainties from imperfect field data, but these estimates are rarely used to produce detailed predictions of the dynamics or future viability of at-risk populations. Conversely, population viability analysis (PVA) modelers have increased the sophistication and complexity of their approaches, but most do not adequately address parameter and model uncertainties in viability assessments or include important ecological drivers. Merging the advances in these two fields could enable more defensible predictions of extinction risk and better evaluations of management options, but only if clear and interpretable PVA results can be distilled from these complex analyses and outputs. Here, we provide guidance on how to successfully conduct such a combined analysis, using the example of the endangered island fox (*Urocyon littoralis*), endemic to the Channel Islands of California, USA. This more rigorous demographic PVA was built by forming a close marriage between the statistical models used to estimate parameters from raw data and the details of the subsequent PVA simulation models. In particular, the use of mark–recapture analyses and other likelihood and information-theoretic methods allowed us to carefully incorporate parameter and model uncertainty, the effects of ecological drivers, density dependence, and other complexities into our PVA. Island fox populations show effects of density dependence, predation, and El Niño events, as well as substantial unexplained temporal variation in survival rates. Accounting not only for these sources of variability, but also for uncertainty in the models and parameters used to estimate their strengths, proved important in assessing fox viability with different starting population sizes and predation levels. While incorporating ecological drivers into PVA assessments can help to predict realistic dynamics, we also show that unexplained process variance has important effects even in our extremely well-studied system, and therefore must not be ignored in PVAs. Overall, the treatment of causal factors and uncertainties in parameter values and model structures need not result in unwieldy models or highly complex predictions, and we emphasize that future PVAs can and should include these effects when suitable data are available to support their analysis.

Key words: Aquila chrysaetos; density dependence; ecological drivers; Golden Eagle; island fox; mark–recapture; population viability analysis, PVA; process variance; stochasticity; uncertainty; Urocyon littoralis.

Introduction

Modeling the possible trajectories of rare and declining populations to predict future viability and identify management options has become a mainstay of conservation biology. Referred to as population viability analysis, or PVA, this approach has provided insights into some of the most controversial issues in conservation biology (e.g., Crouse et al. 1987, Lande 1988). These mathematical descriptions of population behavior replace simple statistical analyses and expert opinions, which are usually only indirectly or unquantifiably linked to current and future population dynamics. While PVA models can make direct quantitative predictions of stochastic population futures, uncertainties inherent to any model can decrease the reliability of these predictions if not accounted for properly (Taylor 1995, Beissinger and Westphal 1998, White 2000, Coulson et al. 2001*b*, Ellner et al. 2002, Doak et al. 2005). These uncertainties arise from many sources: field methods

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may yield imprecise or biased data, small sample sizes can produce large sampling variances around parameter estimates for demographic rates, short study durations can lead to imprecision or bias in estimates of the mean and process variance of demographic rates, and finally, the complexity of study systems will result in an incomplete knowledge of the best mechanistic model with which to describe and predict population behavior and management effectiveness.

Recent advances in analytical methods are providing a stronger foundation for quantifying both pattern and process in demographic rates, including associated estimates of uncertainty, although efforts to faithfully integrate these results into PVAs have lagged behind. For example, increasingly efficient methods are being developed to make robust demographic rate estimates from a diversity of data types (Easterling et al. 2000, Gross 2002, Morris and Doak 2002, Ellner and Fieberg 2003) including techniques for separating parameter uncertainty and process variation (Kendall 1998, Millar and Meyer 2000, White 2000, White et al. 2001). In some cases, likelihood methods can be used to take advantage of frequently ignored ancillary data, such as the use of stage-specific or whole population count data to refine demographic rate estimates and reduce their bias (Pascual and Adkison 1994, Besbeas et al. 2002, Holmes and York 2003, Gauthier and Lebreton 2004, Maunder 2004, Tinker et al. 2006). Information theory (IT) is becoming a widely accepted paradigm for statistical model selection using metrics such as Akaike's information criterion (AIC), which quantifies tradeoffs between the precision of simple models and the accuracy of complex ones (Burnham and Anderson 2002). While IT has more often been used to select a single best model to describe variation in demographic rates for population models (e.g., Lima et al. 1999, Kauffman et al. 2004), IT techniques can also quantify uncertainty in model selection, which can then be incorporated into models of population dynamics (e.g., Tinker et al. 2006).

In addition to the expanded use of new analytical techniques such as IT, PVA predictions may also be improved by the inclusion of covariates such as weather, conspecific densities, predators, or other ecological drivers of demographic rates (e.g., Franklin et al. 2000, Jones et al. 2002, Loison et al. 2002, Nicoll et al. 2003, Altwegg et al. 2005, Armstrong et al. 2005, Smith et al. 2005a). There have been several suggestions in the literature that incorporation of such ecological drivers of demographic rates could improve the ability of PVAs to simulate long-term temporal variance (e.g., Fieberg and Ellner 2001, Ellner 2003, Maunder and Watters 2003), but very few studies have done so convincingly (but see Beissinger 1995, Dennis and Otten 2000, Smith et al. 2005b) and fewer still have also included unassigned process variation to model the full range of stochasticity in population processes (for a partial example, see Gross et al. [1998]; see also Coulson et al. [2001a]).

The current situation is thus one in which far more sophisticated data analysis tools are available than are usually used in conjunction with PVAs. This mismatch is undoubtedly due to the daunting complexity both of current PVA models and of current analytical techniques to turn field data into parameter estimates. Successful merging of these different approaches will require rigorous matching of the structure and assumptions of population dynamics models to the outputs of parameter estimation methods, and also attention to the synthesis of the results, in order to prevent the increased complexity of the PVA predictions from needlessly obscuring their use in answering important biological questions.

Here, we present a framework for achieving this goal of building more reliable PVAs through the construction of models that faithfully reflect the output of advanced demographic analyses, especially those that quantify uncertainty (Fig. 1). To illustrate this approach, we build a PVA for the island fox (*Urocyon littoralis*) that accounts for a broad suite of uncertainties and ecological drivers and demonstrates how to manageably deal with these multiple issues, which improve but also complicate the construction of our PVA. The island fox is a rare island endemic that occurs as six distinct subspecies, each resident on one island off the southern coast of California, USA (Fig. 2; Gilbert et al. 1990, Wayne et' al. 1991). In 2004, four subspecies were listed as endangered under the Endangered Species Act after dropping to extremely low levels due to Golden Eagle (*Aquila chrysaetos*) predation on Santa Cruz, San Miguel, and Santa Rosa islands and disease on Santa Catalina Island (Roemer et al. 2004, U.S. Fish and Wildlife Service 2004). The island fox has been the subject of numerous prior demographic analyses (Roemer et al. 2001a, 2002, Angulo et al. 2007), including at least two studies that use one or more PVA methods (Roemer et al. 2001a, Kohlmann et al. 2005). However, none of these prior analyses has been able to use the amount of data available to us to test and refine model structures and parameter estimates, and hence to build as demographically realistic a model for this species as possible. We pay special attention to assessing and simulating the likely form and strength of density dependence, a particularly controversial and consequential issue in population viability modeling (Henle et al. 2004). Including uncertainty within PVA models could lead to a collision of statistical approximation with biological reality, when, for example, extreme values are randomly assigned to several demographic rates simultaneously. Thus, we also introduce a procedure to screen out parameter combinations that predict biologically implausible behaviors.

Our objective is to present an approach to the construction of PVAs that can serve as a roadmap for addressing past critiques of PVA methodologies, while still performing analyses that are biologically relevant and directly useful for conservation problem-solving

(Fig. 1). We focus on building models that (1) assign temporal variation in demographic rates to ecological drivers, (2) account for unassigned process variation, (3) specify and incorporate model selection and parameter uncertainty, (4) minimize bias and uncertainty in estimates of demographic rates by integrating ancillary data, and (5) produce biologically plausible population behaviors despite the inclusion of uncertainty. To illustrate the impact of our approach, we compare PVA outputs that include uncertainty in demographic estimates with results that ignore it. We also contrast the gains in understanding obtained by incorporating uncertainty with the results of simpler and more traditional PVA results, such as the sensitivity analysis of simple deterministic models. We concentrate our simulation modeling on two islands with contrasting situations: Santa Cruz Island, the largest island, which has maintained a small wild fox population, and San Miguel Island, the smallest island, which is currently rebuilding its wild population with released captives.

NATURAL AND UNNATURAL HISTORY OF THE ISLAND FOX

The endemic island fox inhabits the six largest of the Channel Islands (Fig. 2) and is the smallest canid in North America (mean = 1.9 kg [Roemer et al. 2001c]). Socially monogamous pairs defend exclusive territories (mean = 0.55 km² [Roemer et al. 2001c]). Island foxes subsist on a varied diet including insects, fruits, and small vertebrates (Crooks and Van Vuren 1995). Adult foxes have evolved with virtually no native predators (Red-tailed Hawks, *Buteo jamaicensis*, can take island fox pups [Moore and Collins 1995]) and their only native competitor, the island spotted skunk (*Spilogale gracilis amphiala*), occurs only on Santa Cruz and Santa Rosa islands. Fox courtship and breeding occur January through March, with pupping in late April and May, weaning in June and July, and dispersal from October through December (Laughrin 1977, Fausett 1993; D. Clifford, *personal communication*), although some pups remain on the natal territory through the second summer (Roemer et al. 2001c).

The Channel Islands have a maritime Mediterranean climate with periodic cool winter rains beginning in November and a hot dry summer beginning in May. Precipitation decreases along a southwesterly gradient with mean annual rainfall ranging from 50.4 cm on Santa Cruz Island to 19.1 cm on San Clemente Island (Table 1). For all our analyses, annual time steps start July 1, roughly corresponding to the biological year for foxes and the rain year for the region. Most of the islands support open grass and scrubland, but the larger and more topographically diverse islands of Santa Cruz and Santa Catalina have a range of vegetation types including oak woodlands, chaparral, and pine forest.

Although the habitat of the fox is largely undeveloped (Fig. 2), historical and current land uses have altered the ecological setting and endangered the fox. Most
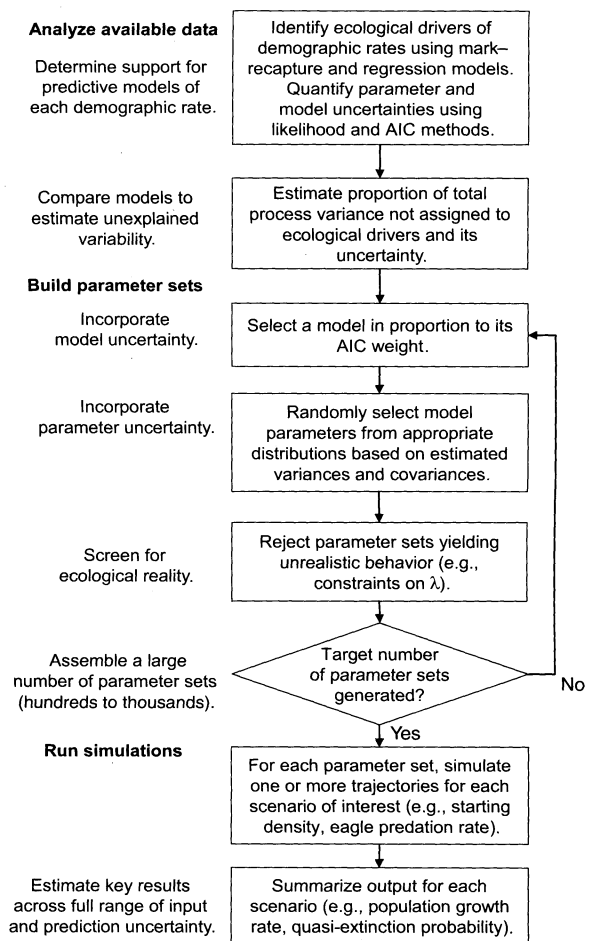

FIG. 1. Flow chart showing recommended process for incorporating uncertainty and both explained and unexplained variance into population viability analysis (PVA). Generalized steps are shown in the left column, and the specific approach taken in this study is shown in the right column..

critically, feral pigs (*Sus scrofa*) introduced to Santa Cruz Island in the 1800s and mule deer introduced to Santa Rosa in the early 1990s appear to have facilitated the growth of a substantial resident population of Golden Eagles throughout the northern Channel Islands during the 1990s (Roemer et al. 2001a, 2002, Collins and Latta 2006). A range of exotic herbivores have converted large areas of native shrublands to grasslands on all islands (Van Vuren and Coblentz 1987), reducing cover available to foxes and possibly increasing predation risk for the predator-naïve foxes. On Santa Cruz Island, estimated fox numbers exceeded 1300 in the early 1990s, but only about 130 remained by 1999, a decline believed to be largely or entirely due to eagle predation (Roemer et al. 2001a, 2002). The population remained at low levels on this island (Bakker et al. 2005) and a captive breeding program was initiated in 2002 as a safety net. Concurrently, the San Miguel and Santa Rosa island
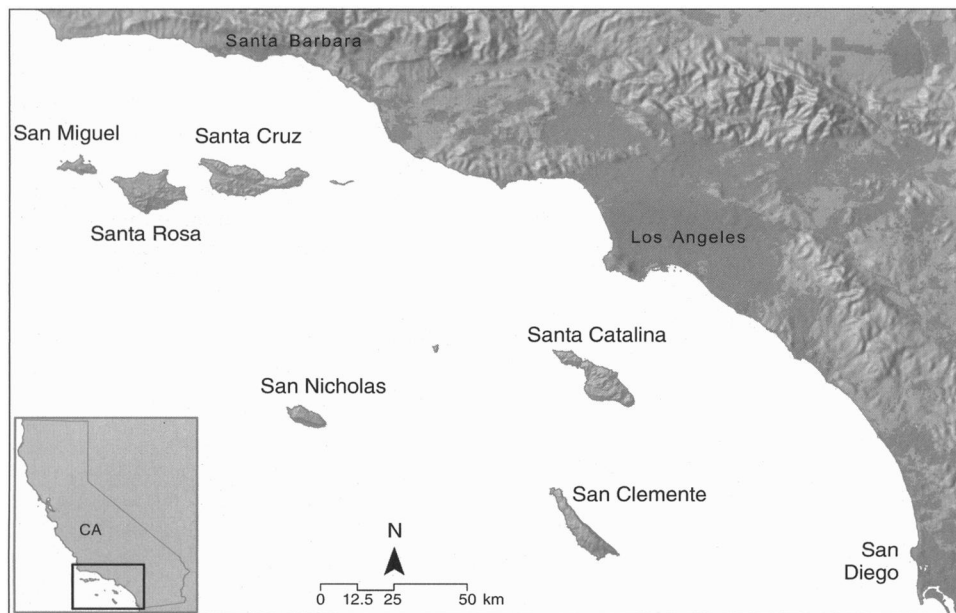
FIG. 2. The island fox (*Urocyon littoralis*) is found on six of the California (USA) Channel Islands. The three northern islands of Santa Cruz, San Miguel, and Santa Rosa are part of Channel Islands National Park or The Nature Conservancy's Santa Cruz Island Preserve. In the south, San Nicolas and San Clemente islands are operated by the U.S. Navy with limited land development, while 88% of Santa Catalina Island is protected by the Catalina Island Conservancy.

populations dropped to fewer than 30 foxes, and by 2000 virtually all wild individuals on these islands were removed to on-island captive breeding pens (Roemer et al. 2001a, Coonan 2003).

In response to these declines, land managers initiated several efforts to restore the Channel Islands ecosystem and reduce predation on foxes. Golden Eagles have been captured and relocated at great expense since 1999, but managers have been unable to keep the islands entirely free of these predators (Latta 2005). Beginning in 2002, territorial Bald Eagles (*Haliaeetus leucocephalus*) previously decimated by DDT poisoning (Kiff 1980) were reintroduced throughout the northern islands in hopes of making the environment more inhospitable to Golden Eagles (Dooley et al. 2005). And finally, to reduce the Golden Eagles' food supply, a feral pig eradication program commenced on Santa Cruz Island in 2005.

These efforts appeared to ease threats enough to justify the release of captive foxes on San Miguel and Santa Rosa islands by 2005, and thus small populations of wild foxes now occur on all three northern islands.

On the southern islands, where Golden Eagles are absent, diseases, competition from feral cats, and automobile strikes pose potential threats (Coonan 2003). On Santa Catalina Island, which hosts 5000 human residents and 1 000 000 visitors annually (Schuyler et al. 1988), canine distemper virus is the primary suspect in a crash of the fox population in 1999 (Timm et al. 2000) from approximately 1300 individuals to less than 100, which led to captive breeding of foxes on this island as well (Timm et al. 2002, Roemer and Donlan 2005). The wild fox population on Santa Catalina is now thought to exceed 300 (Kohlmann et al. 2005). On San Clemente and San Nicolas islands, foxes are not

TABLE 1. Pearson correlation coefficients (SAS Proc Corr) for annual rainfall (1 July–30 June) among the six Channel Islands (California, USA) inhabited by island foxes for ln-transformed values.

Island	Annual precipitation			Correlation coefficient, *r*			
	Mean (cm)	SE	*n* (yr)	Santa Catalina	San Clemente	Santa Cruz	San Miguel
Santa Catalina	32.1	1.7	61				
San Clemente	19.1	2.2	26	0.877			
Santa Cruz	50.4	2.3	102	0.847	0.775		
San Miguel	38.4	4.1	14	⋯	0.863	0.902	
San Nicolas	23.8	1.7	39	0.894	0.860	0.878	⋯
Santa Rosa	ND	ND	ND	ND	ND	ND	ND

Notes: No overlapping data were available for San Miguel and either Santa Catalina or San Nicolas islands. "ND" indicates that no data are available.

federally endangered and populations appear relatively stable (Schmidt et al. 2005, 2007*b*), although the IUCN has recommended that the San Clemente population be considered endangered and the San Nicolas population vulnerable (Roemer et al. 2004).

DATA SOURCES

Annual live trapping occurred on San Clemente, Santa Catalina, Santa Cruz, San Miguel, and San Nicolas islands on a total of 16 grids for various time periods from 1988 through 2004. Surveys were performed from July through September following the birth pulse using Tomahawk live traps (Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) spaced ~250 m apart and arrayed in grids ranging in size from 5 traps × 8 traps to 8 traps × 10 traps. On both Santa Cruz and San Miguel islands, trapping occurred on two grids before and during the population crash, but subsequently ceased due to extremely low densities (dates of trapping: Santa Cruz, 1993 and 1995–1999; San Miguel, 1993–1998). On Santa Catalina Island, three grids were trapped for two years (1989 and 1990). On San Clemente Island, trapping occurred at different intensities from 1988 through 2003 (three grids, 1988–1997 and 1999; four grids, 2000; six grids, 2001–2003). On San Nicolas Island, three grids were trapped from 2000 through 2004.

Field crews initially ear-tagged foxes and later implanted passive integrated transponder tags and recorded sex and age based on tooth wear patterns (Wood 1958, Collins 1993) for all captured foxes. Detailed accounting of female reproductive success was obtained for 30 grid-years on San Clemente Island, 9 grid-years on Santa Cruz Island, and 5 grid-years on San Miguel Island, with pups matched to females using one or more of the following techniques: capture locations of females and pups, range overlap based on telemetry, and genetic analyses. Reproductive data from San Clemente Island, however, were known to be substantially biased (Miller et al. 2003) and were excluded from our analyses. Trapping data from two grids on San Nicolas Island were censored from our analysis because foxes there occurred at densities as much as twice those found on any other island and appeared to respond differently to density-dependent factors by incorporating a large proportion of introduced food sources (ice plants and snails) into their diet and exhibiting reduced territoriality (D. Garcelon, *personal observation*). We also omitted the data from Santa Catalina Island because too few years were sampled to support survival rate estimates. A total of 1288 individual foxes (691 males:597 females) were captured on the 11 grids used in analyses.

Data were also available for three factors known or likely to be critical in driving survival and reproductive rates across time and space: conspecific densities, eagle numbers, and rainfall. Densities of adult foxes were calculated from grid population estimates based on capture–recapture data. Local population estimates were made using Program Capture (White et al. 1978), with model selection guided by Program Capture output (White et al. 1978, Menkens and Anderson 1988). In nearly all cases, model M(h) or M(bh) was used, consistent with the observed behavior of these foxes, which tend to be readily trappable on their territory. Local population estimates were converted to densities using a buffer strip width (Wilson and Anderson 1985) equal to the full mean maximum distance moved (MMDM) based on our observation that results using full MMDM (vs. the conventional 0.5MMDM) more closely approximate fox density estimates derived from telemetry (unpublished data) and supported by literature reports of similar improvements in accuracy with the use of full MMDM (Parmenter et al. 2003). Grid buffers had rounded corners (Parmenter et al. 2003) and were masked to avoid inclusion of ocean areas.

Although systematic Golden Eagle surveys and removals did not commence until 1999, the number of eagles present on the northern Channel Islands in each year was estimated retrospectively from 1990, the year of assumed colonization, onward (Latta 2005). To accomplish this, raptor experts from the Santa Cruz Predatory Bird Research Group (SCPBG) used the demographic characteristics of the surveyed eagle population, the number of nests found, and a reconstructed breeding history deduced from nest excavations. Aging was performed using plumage characteristics (juvenile, subadult I–III, adult [Bloom and Clark 2001]) and sex assignment was possible for captured eagles (based on tarsal measurements) or for non-captured eagles observed in proximity to the opposite sex (based on sexual dimorphism). After aging, individuals were assigned to a historically active nesting territory whenever plausible. Nest activity was determined by counting compressed nest layers, with each layer representing a single season's breeding attempt. The year that breeding commenced at each nest was deduced by assuming that breeders captured at nests had made annual breed attempts in prior years. Combined, these observations were adequate to characterize a plausible population trajectory that accounted for all eagles observed on the islands from 1999 through 2004, and that agreed with a simple population model for a single pair of adult eagles colonizing and initiating breeding in 1990, consistent with data from nest excavations.

For Santa Cruz Island, 102 years of continuous rainfall data were available; considerably fewer years, frequently discontinuous, were available for the other islands (Table 1). While mean rainfall varies substantially across the islands, inter-island variation in rainfall is highly correlated ($r \geq 0.775$; Table 1). Because only the Santa Cruz Island data set spanned all the years trapped, we applied these data to all islands. By using one data source to index rainfall on all islands, we were

TABLE 2. Symbols used in text.

Parameter	Description
λ_M	Matrix-derived population growth rate (lambda) based on survival rates estimated using ecological driver models and used in estimating F
λ_d	Density-derived population growth rate (lambda) based on annual estimates of grid density and used in estimating F
ϕ	Annual apparent survival rate, estimated using Cormack-Jolly-Seber open-population model
b_1, b_2	Parameters of the survival modifier F, used to correct apparent survival for emigration
B	Breeding rate, defined as the proportion of females producing litters
$\hat{c}$	Variance inflation factor, estimated as the deviance of the global survival model divided by the mean deviance of the simulated data sets
C	Process variance of the ecological driver models for annual survival probabilities
D	Estimated density of non-pup foxes
$d_{5.9}$	Binary control variable equal to 1 for densities ≤ 5.9 adult foxes per km^2 and 0 otherwise (survival modifier is applied only for $d_{5.9} = 1$)
EE	Eagle equivalent, the mortality rate equivalent to that caused by one eagle using space and employing predation behaviors comparable to those of the original colonizers
F	Modifier function to adjust annual apparent survival probability estimates to account for emigration
G	Process variance of the global survival model
L	Litter size, or the mean number of pups born to breeding females
i	Subscript indicating age-specific value
j	Subscript indicating grid-specific value
$\mathbf{M}$	Two-stage matrix model for island fox
N	Number of individuals
P_{re}	Annual recapture rate, estimated using Cormack-Jolly-Seber open population model
P_{qx}	Probability of quasi-extinction; in all cases, we defined quasi-extinction as ≤ 30 individuals
R	Annual female-only reproductive rate, defined as $B \times L$
S	Annual apparent survival probability
S_E	One minus the probability of eagle-caused mortality
S_{mod}	True annual survival rate, estimated as the annual apparent survival rate modified to account for emigration
S_N	Annual survival probability excluding eagle predation effects
S_{max}	The maximum survival probability, which occurs when density equals 5.9 foxes/km^2
U	Unassigned process variance associated with ecological driver models (i.e., $G - C$)
V_u	Unassigned process variance as a proportion of the maximum possible variance

able to assess the importance of temporal, but not spatial variation, in rainfall for fox demography.

DEMOGRAPHIC ANALYSIS METHODS

Environmental drivers and model selection uncertainty

We modeled annual apparent survival from capture–recapture data using the Cormack-Jolly-Seber module within Program MARK (White and Burnham 1999) and selected models based on quasi-Akaike information criterion corrected for small sample sizes and model lack of fit due to overdispersion (i.e., quasi-AIC$_c$, [Lebreton et al. 1992]). Because previous island-specific analyses indicated no differences in survival rates between the sexes or between yearlings and adults (Roemer et al. 2001a, Coonan et al. 2005; V. Bakker, unpublished data), we only considered differences between pups (i.e., <1 year old) and non-pups, which we refer to as adults.

Following Lebreton et al. (1992), we used a two-step procedure to identify the best model structure, first allowing survival (ϕ, see Table 2 for summary of symbols used in this paper) to vary fully by location, time, and age, as well as marked year to account for transients, and comparing full and reduced model structures for probabilities of recapture (P_{re}; see Appendix). We considered time-varying and constant recapture probabilities with interactive spatial effects. We tested for Markovian trap response in P_{re}, or the potential for P_{re}

to increase for individual foxes after a previous capture (i.e., trap happiness) by testing models that included an individual covariate indicating whether a fox was captured in the prior year (Lebreton et al. 1992). We did not vary recapture rates by age because pups were by definition adults by the time of their first recapture.

We then used the best model structure for recapture rates and compared full and reduced structures for survival, again examining time-varying and constant models with interactive and additive spatial, age, and marked year effects. We fit a total of 50 of these categorical effects models. We tested for goodness of fit of the global model by examining tests of model assumptions using Program U-CARE (Choquet et al. 2005) and by comparing the real deviance of the global model to those of 500 data sets simulated by Program MARK to match the release numbers and survival and recapture rates of the actual data, but without any violations of assumptions (White et al. 2001). The proportion of these bootstrapped goodness-of-fit simulations with deviances exceeding those of the global model can be considered a test of the null hypothesis that model fit is adequate. Simulations did not include a trap response because the distribution of this individual covariate in the population is unknown. Individual covariates, however, improve fit and decrease overdispersion, rendering our simulations conservative assessments of fit. Finally, we corrected for over-

dispersion using a variance inflation factor ($\hat{c}$), estimated as the deviance of the global model divided by the mean deviance of the simulated data sets (Lebreton et al. 1992, White et al. 2001).

To determine how ecological factors influenced survival rates, we next fit a series of models in which the time effect in the best model structure (and reduced structures) was replaced with covariates representing hypothesized ecological drivers; we refer to these models as "ecological driver models." Based upon the known and suspected determinants of fox performance, we considered a range of causal factors that might drive survival rates: eagle numbers as an index of predation intensity, fox density as a measure of competition, and both current and previous year's annual rainfall. Past rainfall, a proxy for vegetative conditions and their effects on fox food supplies, was expected to have positive effects on fox survival (Dennis and Otten 2000), while current year's rainfall was expected to decrease survival by reducing foraging opportunities during extended storms (Roemer 1999) or increasing risk-taking subsequent to storms (H. Swarts, *personal observation*). We included rainfall in our models as a categorical variable to distinguish the effects of large El Niño-Southern Oscillation (ENSO) events (annual rainfall > 80 cm), which occurred in 1994 and 1997, vs. more-normal rainfall years. We also tested for effects of ENSO events in the previous year. We evaluated a linear density term with and without a quadratic term to examine for possible Allee effects (Angulo et al. 2007).

We tested each covariate separately for interactions with island, island group (northern islands of San Miguel, Santa Cruz, and Santa Rosa vs. southern islands of San Clemente, San Nicolas, and Santa Catalina) and age, and also investigated whether environmental drivers acted only on specific ages or geographic locations, as suggested by a priori biological knowledge. Specifically, we suspected that current year's rainfall might increase mortality only in the northern islands where rainfall is higher while previous year's rainfall might increase survival only in the southern islands where rainfall is lower (Table 1). Similarly, any of the constraints might act disproportionately on pups because they have lower survival and are presumably more vulnerable to mortality factors in their first year (Roemer 1999). Finally we accounted for the number of foxes killed in 1998 and 1999 on San Clemente Island as part of a control program implemented to protect the endangered San Clemente Island Shrike. Our approach to building ecological driver models started with screening each potential driver for interactions with location and age in a total of 42 model forms, then using the best supported structures for individual drivers when building multi-driver models. We refit a subset of multivariate models with different univariate structures to test the validity of this approach. Finally, we assessed the information gained by including or excluding each of the four drivers.

We also fit models with other forms of environmental drivers, but these consistently yielded poor or biologically implausible fits, so we only briefly discuss them. These drivers include: rainfall as a continuous variable; a two-year lagged rainfall effect; an eagles × year interaction to test for changes in the effects of eagles on foxes over time, which might occur if foxes evolved behaviors that reduced predation risk (Roemer et al. 2002); an eagle × density interaction, which would occur if eagles exhibited a functional response to foxes (Holling 1959, Angulo et al. 2007); and, finally, the effects of grid-specific habitat differences. Grid-trapping data provided little basis for investigating habitat effects due to the limited spatial coverage, so we also assessed the effect of cover in the home range of radio-collared foxes on Santa Cruz Island from 2000 through 2004 using a Cox's proportional hazard model to identify predictors of survival time for individuals (Proc PHREG [SAS Institute 2005]). We found no support for a cover effect, likely due to the coarse mapping of habitat currently available, the small-scale patchiness and interspersion of habitat types, or, least plausibly, the lack of real effects on fox demography.

For breeding probabilities, we used logistic regression (SAS Proc Logistic) to compare models in which the likelihood of breeding varied fully by age, location, and time, as well as a series of reduced models. We approached model selection for mean litter sizes similarly (using SAS Proc GLM), but we did not look for age-specific variation because previous analyses based on the same data found no such differences (Roemer et al. 2001b). While we also investigated ecological driver models, there was poor support for these models and inconsistent relationships between environmental factors and reproductive performance, probably because the data set was relatively sparse and imprecise (Miller et al. 2003). As with survival analyses, we used AIC_c weights as a measure of model support.

We used analysis of deviance techniques to quantify the explanatory power of the ecological driver models (Skalski et al. 1993, Altwegg et al. 2003). This approach compares the proportion of overall variance in survival rates explained by an ecological driver model relative to that explained by a model with categorical year, grid, and island effects. We made these comparisons in two ways. First, we quantified the variance explained by different ecological driver models relative to a global, or fully parameterized categorical effects model, which essentially provides the best fit possible to the data:

$$\frac{\text{Dev(Const)} - \text{Dev(Driver)}}{\text{Dev(Const)} - \text{Dev(Global)}}. \tag{1}$$

Here deviance (Dev) is twice the negative log-likelihood, a measure of model fit (low deviance indicates better fit), Driver is the ecological driver models, Const is an intercept-only model, and Global is the global categorical effects model with variance by age, location, and

assess the proportion of variance explained by temporally varying ecological drivers relative to that explained by fitting a distinct categorical effect for each grid and year, controlling for all other factors. To achieve this we used the following equation:

$$\frac{\mathrm{Dev(Effects)} - \mathrm{Dev(Effects + Drivers)}}{\mathrm{Dev(Effects)} - \mathrm{Dev(Effects + Grid \times Year)}}. \quad (2)$$

Recalling that ecological driver models consist of categorical effects (e.g., age, marked year) and ecological drivers, either in additive or interactive forms, the Driver model from Eq. 1 above can be expressed as Effects + Drivers. Thus, here we include the same categorical effects (Effects) in each model and assess the reduction in deviance attained fitting a driver model (Effects + Drivers) to that achieved fitting a time-varying model that includes these categorical effects along with distinct effects for each grid and year (Effects + Grid $\times$ Year), both relative to a time-constant model that includes only these categorical effects (Effects).

Process variance

For any given time series of demographic data, observed year-to-year variance is approximately the sum of within-year sampling variance, a measure of uncertainty in measured rates, and true temporal, or process, variance. Thus, to estimate process variance, the directly estimated temporal variance should be discounted for the effects of sampling variance (mean rates also require adjustment; see Kendall 1998, White 2000, Morris and Doak 2002 for further discussion). We used random effects models in Program MARK to estimate the age- (i) and grid- (j) specific process variance, G_{ij} using the global model (White 2000, White et al. 2001, Burnham and White 2002); we summarized the overall global process variance for each age class, G_i, as the mean of these separate grid-specific estimates weighted by the inverse of the sampling variance of the estimate for each grid (Zhang 2006). To ensure that the population models based on ecological drivers accounted for the full global process variance, we estimated the unassigned age-specific temporal process variance, U_i, as the weighted average difference (Zhang 2006) between the process variance estimates of the global model, G_{ij}, and those of the covariate models, C_{ij}. We estimated C_{ij} as the simple variance of estimated rates across all years for each grid. For the purposes of the PVA model, we expressed each unassigned process variance, U_{ij}, as a proportion of the maximum possible variance, which for a survival rate is set by the mean, $\bar{S}$ (i.e., $\bar{S}[1 - \bar{S}]$) (Morris and Doak 2004; see *Simulation methods: Adding unassigned process variation*). Our overall estimate of V_u (unassigned process variance as a proportion of the maximum possible variance) for each age class was the mean of the grid-specific V_u values, weighted by the inverse of the sampling variance of the estimate for each grid (Zhang 2006). Process covariance between age-specific survival rates was imposed by covariance in the

fitted coefficients of the logistic functions that predict survival rates. We estimated covariance between other demographic rates as appropriate.

Parameter uncertainty

Uncertainty, or sampling variance, was estimated for all parameters in each of the best-fitting models for reproduction and survival. For the regression coefficients of the logistic survival models, we used estimates from the sampling variance-covariance matrix produced by Program MARK, which relies on central difference approximations to generate the Hessian matrix and inflates values to account for overdispersion by multiplying by $\sqrt{\hat{c}}$ (White et al. 2001). We estimated uncertainty in each grid-specific proportional unassigned survival process variance for each age class, V_{uij}, using a standard variance decomposition approximation (i.e., a delta approximation) as

$$\mathrm{var}(V_u) = \left[\frac{\mathrm{var}(G) + \mathrm{var}(C)}{(\bar{S} - \bar{S}^2)^2}\right]$$
$$+ \left[\frac{(G - C)(1 - 2\bar{S})}{(\bar{S} - \bar{S}^2)^2}\right]^2 \mathrm{var}(\bar{S}) \quad (3)$$

for each grid $\times$ age combination (subscripts omitted for clarity). We do not include covariance of G, C, or S in this approximation, as our model-fitting does not yield estimates for these terms and because there is no reason to expect any appreciable covariance to exist. Component variances were estimated using standard theory (i.e., var(S) [White 2000]; var(G), var(C) [Doak et al. 2005]). Variance of the overall V_u estimate for each age class was estimated as the inverse of the sum of the inverses of these grid-specific variances (Zhang 2006).

Estimating bias in apparent survival estimates

A widely known problem with survival rates derived from simple mark–recapture analyses is that permanent emigration is unaccounted for and can act to inflate mortality rate estimates (Conn et al. 2005). While the degree of bias may be negligible for highly philopatric species or studies extending over large areas, for island fox data, emigration may result in substantial bias due to the small size of grids relative to home range size, as is supported by the observation of an inter-grid movement rate ranging from 0% to 10% of animals captured on a grid (mean 0.6%). Over the broad range of densities seen in foxes, this bias is likely to change as a result of density effects on movement distances and probabilities. Our survival models ultimately predicted strong positive density dependence at low densities, in marked contrast to both the known natural history of island foxes and recent observations that very small and low-density reintroduced populations have maintained high survival rates (based on telemetry data, on San Miguel Island, where densities were less than ~1 adult fox/km^2, and annual survival exceeded 86% for 2 years) and can

increase rapidly in the absence of eagle predation (V. Bakker, *unpublished data*). Because the presence of transients in the sample can decrease apparent survival rates, increases in transients at low densities could produce this apparent positive density dependence. However, we included a transient class in our survival models, and the effect persisted.

To address this problem, we developed a new method to estimate emigration rates and correct for bias in our survival estimates. Some techniques have emerged recently to account for permanent emigration with mark–recapture data by combining data types or pooling data from different sites. Joint models, for example, use dead recovery or live resight data from outside the study area to estimate fidelity, and multistate models use data from multiple sites to estimate movement (Williams et al. 2002). As is commonly the case, we lacked adequate data to parameterize either of these model types (Conn et al. 2005). Nonetheless, we had relevant ancillary data, density estimates from daily trapping records (vs. survival estimates from annual trapping records), which were essentially independent and could be used to assess whether predicted densities based on survival models match those actually measured or whether an adjustment factor was supported. To accomplish this, we compared the annual rate of population change estimated from adult densities for each grid to rates estimated from demographic models built with our survival and reproduction parameter estimates coupled with a survival rate modifier function that re-assigns some natural (non-eagle-caused) apparent mortality to survival (i.e., emigration).

For each of the best ecological driver models of survival rates and the best estimates of breeding rates and litter sizes, we constructed a separate matrix model for each jth grid × year combination:

$$M_j = \begin{pmatrix} 0.5S_{1\text{mod}}B_1L & 0.5S_{2\text{mod}}B_2L \\ S_{1\text{mod}} & S_{2\text{mod}} \end{pmatrix} \quad (4)$$

where B_1 and B_2 are breeding probabilities, L is mean litter size, and $S_{1\text{mod}}$ and $S_{2\text{mod}}$ are modified survival probabilities for pups and adults, respectively (all equal to best estimates for the jth grid × year, subscripts suppressed for clarity). Apparent survival probabilities were modified by adjusting the natural, non-eagle survival rate upward. Specifically, $S_{ij\text{mod}} = S_{ij\text{E}}(S_{ij\text{N}} + F)$, where $S_{ij\text{E}}$ is one minus the risk of eagle-caused mortality for stage i in the jth grid × year, $S_{ij\text{N}}$ is the corresponding apparent survival rate accounting for all other mortality sources (all estimated from ecological driver models), and F is the modifier function that reassigns some part of apparent mortality to survival. We used the same modifier function for both pups and adults, as we have no additional data with which to fit stage-specific functions or parameters.

We initially evaluated three sets of modifier functions that differed in the maximum amount of apparent mortality that could be reassigned to survival. We present results for those in which

$$F_j = \frac{d_{5.9}(1 - S_{j\text{N}})}{(1 + \exp^{b_1 + b_2D_j})} \quad (5)$$

and for reduced models in which one of the coefficients b_1 or b_2 is set equal to zero; D_j is the density in the jth grid × year and $d_{5.9}$ is a binary control variable equal to 1 if densities were less than 5.9 adult foxes/km², the point at which estimated apparent survival is at its maximum (S_{max}), and equal to zero otherwise. We used the $d_{5.9}$ parameter to limit operation of the modifier function only to the low densities where apparent positive density dependence operated. We tested other model forms in which $(1 - S_{j\text{N}})$ was replaced with either the difference between apparent survival at a given density and S_{max}, or between apparent survival and a linear bound running between {5.9 foxes/km², S_{max}} and {0, 1}. Results from these alternative models are qualitatively identical and quantitatively extremely similar to those of the first set of models. Finally, we only present model fits for the northern islands. Model forms that applied to all islands or modified survival rates for high as well as low densities were uniformly less well supported.

Our approach to parameter estimation and model choice for the modifier function relies on a comparison between population growth estimates, λ_{M_j}, obtained from the population matrices M_j, built with the modifier functions (Eqs. 4 and 5), and those from the growth rate estimates arising from grid densities, λ_{d_j}. For each modifier function and its associated b_j parameter values we obtain a mean estimate, λ_{M_j} and an estimated variance, $\text{Var}(\lambda_{M_j})$, for each year × grid. $\text{Var}(\lambda_{M_j})$ arises from uncertainty in the survival and reproductive rates and was estimated using a delta approximation. Note that in making these λ_{M_j} estimates, we are implicitly assuming that in each year foxes in a grid are at the corresponding stable stage distribution (SSD) for that year's transition matrix. We eschewed the empirical stage distribution because the variable timing of grid trapping relative to parturition and the comparatively small number of pups captured each year make empirical estimates of stage distributions both imprecise and biased to an unknown degree. Given this problem and the relatively limited variance in likely stage structures, we accepted the SSD assumption as reasonable. To obtain a likelihood, ℓ, for F_j for a given year × grid transition we used normal probability density functions (pdf) to predict the corresponding λ_{d_j} value, which has its own uncertainty, $\text{var}(\lambda_{d_j})$, arising from uncertainty in density estimates. The likelihood of each F_j in the presence of $\text{var}(\lambda_{d_j})$ requires integrating over the range of possible λ_{d_j} values:

$$\ell(\lambda_{d_j}, \text{var}\lambda_{d_j} | \lambda_{M_j}, \text{var}\lambda_{M_j})$$
$$= \int_{\lambda_{j=0}}^{+\infty} \text{pdf}(\lambda_j | \lambda_{d_j}, \text{var}\lambda_{d_j})\text{pdf}(\lambda_j | \lambda_{M_j}, \text{var}\lambda_{M_j})d\lambda_j. \quad (6)$$

We used Matlab's symbolic math capabilities to solve this integral directly and sum the logs of the resulting likelihood values for each transition to obtain an overall negative log likelihood for each of the two best ecological driver models for survival rates. We then used a minimization routine to find the maximum likelihood estimates of the parameter values for each modifier function and compared the functions using AIC_c values and also the biological plausibility of the different predictions.

We also performed a check on this fitting procedure. Eq. 4 and 6 assume no estimation covariance either between or within the sets of λ_{d_j} or λ_{M_j} estimates, but both do, in fact, have substantial covariance structure. Both covariance matrices, however, are large and singular, making general formulae for the estimation of multivariate normal probabilities unworkable. To obtain an estimate of model fit that still considered covariance structure, we performed a simulation in which we drew 1000 values from the multivariate distributions of both λ_{d_j} and λ_{M_j} (while estimating multivariate pdf values of singular covariance matrices is difficult, selecting sets of random values in this situation is straightforward). For every combination of λ_{d_j} and λ_{M_j} values selected, we calculated the Euclidean distance in multivariate space as a measure of predictive accuracy and took the average of these distances over sets of lambda values as a measure of overall model fit. Using this metric to find the best parameters for the modifier function gave results that closely matched those of our more formal likelihood calculations and thus we proceeded with our initial approach that ignored covariances.

DEMOGRAPHIC ANALYSIS RESULTS

Environmental drivers and model selection uncertainty

The best model structure for recapture probabilities, P_{re}, included only a location effect, with differences between San Miguel Island and all other islands, and a positive response to trapping (trapresp), in which P_{re} increased for foxes captured in the previous year (Appendix). We considered our global model to be one in which survival rates, ϕ, varied by grid, year, age, and marked year but P_{re} took its most parsimonious form ϕ(grid $\times$ year $\times$ age $\times$ markedyear), P_{re} (miguel + trapresp) hereafter, Global model). We used this reduced parsimonious form for P_{re} due to the large number of unidentifiable parameters if P_{re} varied temporally, the limited a priori basis for suspecting substantial temporal variation in P_{re}, which integrates a week of trapping effort, and the absence of support for such a highly parameterized model. Simulations, which excluded trapresp and are thus conservative, did not support rejecting the null hypothesis that the model adequately described the data ($P = 0.07$) and indicated only minor overdispersion ($\hat{c} = 1.10$).

Using the most parsimonious structure for P_{re}, the best categorical effects structure for survival rates varied

by island and year and included marked year as an additive effect ϕ(isl $\times$ year + markedyear), P_{re} (miguel + trapresp). The marked year effect indicated lower apparent survival rates during the year following first capture and marking for both pups and adults. This pattern is likely attributable to the presence in the sample of transients captured once and never recaptured; the effect on survival estimation of transients moving out of the study area is identical to and indistinguishable from true mortalities.

Ecological driver models were initially built on the basic structure of this best categorical effects model (i.e., ϕ(isl + markedyear and drivers), P_{re}(miguel + trapresp)), with drivers considered as both interactive and additive effects. In univariate screening, models without island effects were also considered because one covariate, density, was grid-specific and might explain location effects adequately. In addition, because of the relatively high support for age effects and their potential importance to understanding population behavior, we also considered age effects in driver models. The best covariate forms identified in univariate screening were: a linear additive eagle effect (egl), linear and quadratic density effects with interactions by island group (i.e., density + density^2 + density $\times$ southern + density^2 $\times$ southern: this model is denoted as dns), current year's ENSO event acting only on pups in the northern islands (i.e., ENSO $\times$ northern $\times$ pup, denoted enso), and previous year's ENSO event with location-specific interactions (i.e., previous ENSO + previous ENSO $\times$ southern, denoted penso). Age effects improved support for all covariate models significantly while island effects reduced support; thus, we included the former and excluded the latter in all multivariate model building.

All of the best ecological driver models included a strong negative effect of eagle numbers. We refer to the units for this effect as eagle equivalents (EEs) to indicate a mortality rate equal to that caused by one eagle using space and employing predation behaviors comparable to those of the original colonizers for which we have data. Although it is not surprising that eagles have a consistently strong negative effect across all models considered, multivariate model building using Program MARK allowed us to quantify the strength of eagle predation while accounting for all other supported effects. Mean annual mortality rates corresponding to one EE are 0.033 $\pm$ 0.0005 (mean $\pm$ SE) for pups and 0.021 $\pm$ 0.0004 for adults, across a range of densities of 0.1–12.0 adult foxes/km^2 and of number of eagles present of 1 to 10 (because eagle effects are part of a multivariate logistic function, the relative per eagle risk varies as a function of other all other parameters in the model).

All the best models also included positive linear and negative quadratic terms for density (Appendix, Table 3). Apparent survival rate increased with density up until 5.9 adult foxes/km^2 then declined (Fig. 3), suggesting an Allee effect combined with negative

TABLE 3. Regression coefficients and standard errors (SE) for logistic functions to estimate annual survival probabilities based on environmental drivers.

Variable	Model 1			Model 2		
	Estimate	SE	CV	Estimate	SE	CV
Intercept	0.586	0.284	0.485	0.601	0.284	0.473
Marked year	−0.464	0.120	0.259	−0.455	0.120	0.263
Pup	−0.253	0.162	0.639	−0.318	0.157	0.492
Eagle	−12.041	2.060	0.171	−12.240	2.028	0.166
Density	60.700	11.801	0.194	60.122	11.520	0.192
Density^2	−5.002	0.982	0.196	−5.075	0.965	0.190
Previous ENSO	−0.720	0.327	0.454	−0.628	0.320	0.509
Previous ENSO × southern	1.215	0.420	0.346	1.115	0.413	0.370
ENSO × northern × pup	−0.931	0.548	0.589			

Notes: Coefficients are shown for the two best ecological driver models, which comprise 91% of the cumulative quasi-AIC$_c$ (QAIC$_c$) weight for all driver models considered. Eagle number, fox density (no. adults/km^2), and (fox density)^2 were rescaled by dividing by 100 to aid in numerical convergence. ENSO is the binary variable indicating an El Nino-Southern Oscillation (high rainfall), and previous ENSO is the occurrence of an ENSO event in the previous year. Proportional QAIC$_c$ weights, which rescale original QAIC$_c$ weights to sum to 1 and indicate the probability of selecting each model in simulations incorporating model selection uncertainty, were 0.62 (Model 1) and 0.38 (Model 2).

density dependence. Most well supported models also included a complex effect of previous year's ENSO that was negative in the wetter northern islands and positive in the drier southern islands, and many included a negative ENSO effect on pups in the northern islands (Table 3). Because there was strong support for a negative effect of the lethal control program on San Clemente Island, all models included this effect as a nuisance parameter. The two best supported models for survival probabilities using ecological drivers accounted for over 90% of the QAIC$_c$ weight (Appendix; Table 3) and provided good matches with the island- and year-specific predictions of the best categorical effects model (Fig. 4). Drivers in the best supported models explained ~52% of the variance accounted for by the year effects in the best categorical effects model and ~39% of overall variation (Table 4).

The two best models for breeding probability suggested differences by island and age, either additively or interactively (cumulative AIC$_c$ weight = 0.71, Tables 5 and 6), but there is some support for a third model in which breeding probability varies by age only (AIC$_c$ weight = 0.16). Litter sizes appear to be constant across space and time (AIC$_c$ weight = 0.58), although there is support for a model in which litter sizes vary by island (AIC$_c$ weight = 0.26; Tables 6 and 7).

Process variance and parameter uncertainty

The maximum likelihood estimate (MLE) for global process variance, G, was 0.029 for adults and 0.036 for pups. The estimated process variance of the best ecological covariate models, C, was 0.013–0.014 for adults and 0.010 for pups. Thus driver models accounted for a weighted mean of 52% of the process variance for adults and 34% for pups. The mean survival probabilities of the global model were 0.640 ± 0.045 for adults and 0.426 ± 0.035 for pups, and the maximum possible
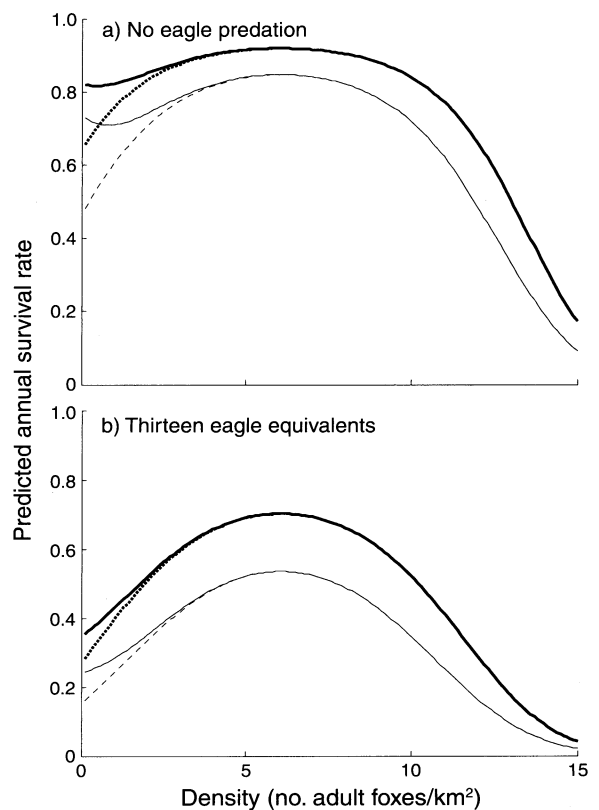

FIG. 3. Relationship between island fox survival probabilities and densities and the effect of a modifier function to correct for emigration off study grids, based on the best-supported models. Annual apparent survival estimates (dotted lines for adults, dashed lines for pups) and modified true survival rate estimates (solid lines) are shown for adults (thicker lines) and pups (thinner lines) for Santa Cruz Island (a) in the absence of ENSO events and with no eagles present, and (b) with the median number of eagles present during the population crash (13).
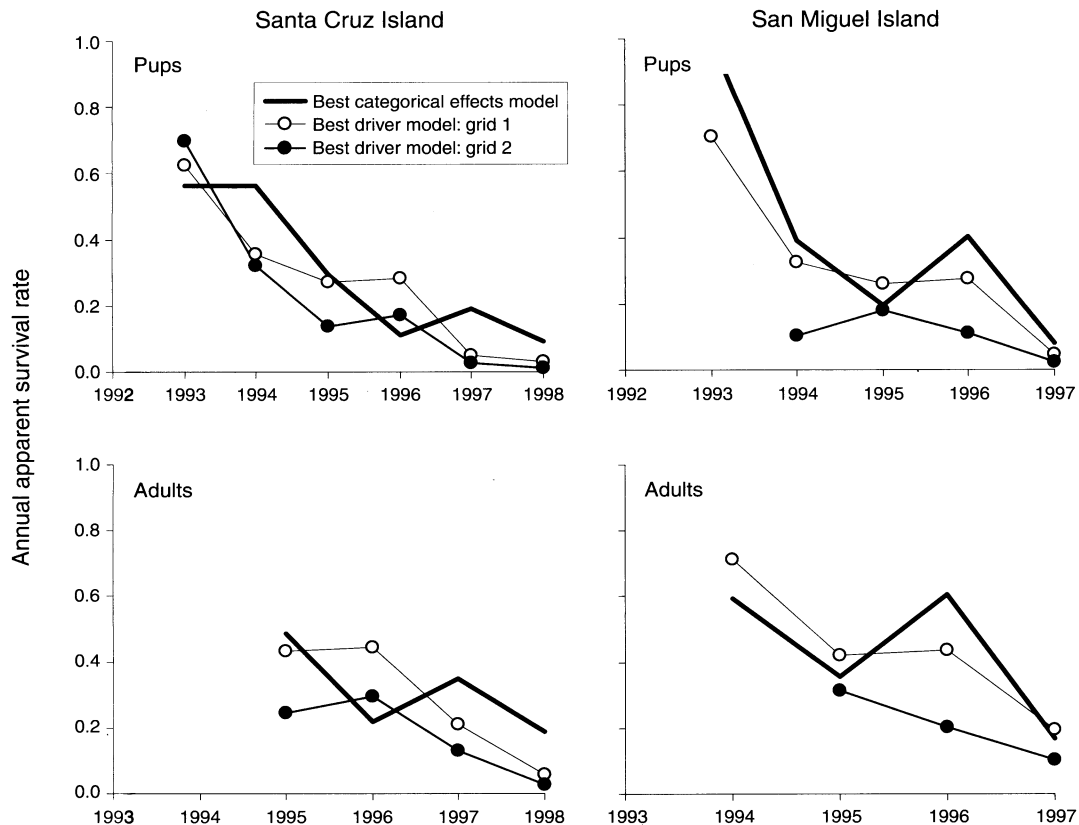
FIG. 4. Comparison of estimated survival probabilities from the best categorical effects model, ϕ(isl $\times$ year + markedyear), P_{re} (miguel + trapresp), and the best ecological driver model, ϕ(age + markedyear + egl + dns + penso + enso), P_{re} (miguel), for two islands and two age classes (see Table 2 for definition of symbols), where isl is island (Santa Cruz, San Miguel, San Nicolas, San Clemente), year is year of trapping, markedyear is a dummy variable indicating first year an individual was captured, miguel is a dummy variable indicating San Miguel Island, trapresp is a dummy variable indicating captured in previous year and used to model behavioral trap response, egl is estimated number of eagles present on the island, dns is density of adult foxes at annual summer surveys with a quadratic term and interactions by island group, enso is current year's ENSO event acting only on pups in the northern islands (i.e., current ENSO $\times$ northern $\times$ pup), and penso is previous year's ENSO event, with interactions by island group (i.e., previous ENSO, previous ENSO $\times$ southern).

process variances defined by these means were 0.231 and 0.245, respectively. Based on the difference in process variance between the global and ecological driver models, the weighted mean unassigned variance as a proportion of this maximum, V_u, was 0.046 $\pm$ 0.021 (model 1) and 0.048 $\pm$ 0.020 (model 2) for adults and 0.093 $\pm$ 0.030 (model 1) and 0.094 $\pm$ 0.030 (model 2) for pups.

We did not estimate process variance for reproductive rates because neither breeding rates nor litter sizes varied by year (Tables 5 and 7). Similarly, we did not estimate covariance between survival and reproductive rates, given the lack of process variance in the latter.

Estimating bias in apparent survival rate estimates

We found the strongest support for a logistic modifier function that contained a direct density effect but no constant term (Table 8). The predictions of this model result in essentially no change in survival until quite low densities are reached (Fig. 3). At these low densities, the

model corrected the predictions of extremely low survival rates, which are not in accord with observed growth of recent low density populations, and reduced but did not entirely eliminate the apparent Allee effect in survival estimates.

The next best modification model (with no direct density effect) has extremely small impacts on survival (results not shown); while this model has an AIC_c weight of 0.392 it does not correct the mismatch between the apparent survival and model predictions. Given the lower biological plausibility of the second best model, and the poor power of our data set to distinguish between models that differ in low density predictions (only a small number of grid by year combinations for which we have data were at low densities: 1 case with density $\leq$1.0 foxes/km^2 and 7 with density $\leq$ 1.5 foxes/km^2, out of 73 total cases), we used only the best supported model in our PVA simulations.

TABLE 4. The proportion of overall variance explained by survival models using ecological drivers as covariates.

Covariate models	Overall variance explained by covariate models	
	Ecological drivers vs. global model	Ecological drivers vs. year effects
$\phi_{egl\ dns\ enso\ penso}$	0.389	0.518
$\phi_{egl\ dns\ penso}$	0.382	0.506
$\phi_{egl\ dns\ enso}$	0.368	0.483
$\phi_{egl\ dns}$	0.363	0.476
$\phi_{egl\ enso\ penso}$	0.297	0.369
$\phi_{egl\ enso}$	0.286	0.350
$\phi_{egl\ penso}$	0.289	0.356
ϕ_{egl}	0.279	0.340
$\phi_{dns\ penso\ enso}$	0.296	0.367
$\phi_{dns\ penso}$	0.283	0.345
$\phi_{enso\ penso}$	0.231	0.261
ϕ_{penso}	0.212	0.230
$\phi_{dns\ enso}$	0.223	0.248
ϕ_{dns}	0.216	0.237
ϕ_{enso}	0.129	0.097

Notes: To assess the amount of overall variance accounted for by ecological driver models, we compared the reduction in deviance attained when fitting the ecological driver models compared to a constant (intercept-only) model, relative to the reduction attained by fitting the global model (comparison denoted: ecological drivers vs. global model). To compare the proportion of overall variance explained by ecological driver effects relative to year effects controlling for all other factors, we compared the reduction in deviance attained fitting a driver model (age + markedyear + ecological drivers) compared to a time-constant model with age and marked year effects only relative to a model with age, marked year, and grid × year effects (age + markedyear + grid × year) (comparison denoted: ecological drivers vs. year effects). Models are listed in order of descending $QAIC_c$ value (see Appendix). Definitions of variables: egl, estimated number of eagles present on the island; dns, density of adult foxes at annual summer surveys with a quadratic term and interactions by island group (southern vs. northern; i.e., density, density², density × southern, density² × southern); enso, current year's ENSO event (rainfall > 80 cm, 1 July–30 June) acting only on pups in the northern islands (i.e., Current ENSO × northern × pup); penso, previous year's ENSO event, with interactions by island group (i.e., Previous ENSO, Previous ENSO × southern).

The final step in our analysis was a direct search to define the likelihood surface for the single parameter value of the best modifier model for each of the two apparent survival models. The resulting surfaces, which quantify parameter uncertainty for the modifier, are highly asymmetric (results for the best apparent survival model shown in Fig. 5), and are skewed toward values that apply lower correction factors.

POPULATION SIMULATION METHODS

Basic model structure and demographic rates

Our models delineate four classes of foxes, defined by sex and two age-classes: pups and adults. The population matrix (Caswell 2001, Morris and Doak 2002) defining the average dynamics of the population assumes that each annual census occurs directly after spring reproduction:

$$\bar{M} = \begin{pmatrix} 0.5S_{1mod}B_1L & 0.5S_{2mod}B_2L & 0 & 0 \\ S_{1mod} & S_{2mod} & 0 & 0 \\ 0.5S_{1mod}B_1L & 0.5S_{2mod}B_2L & 0 & 0 \\ 0 & 0 & S_{1mod} & S_{2mod} \end{pmatrix}.$$

with column headers: female pups, female adults, male pups, male adults.

(7)

Here, S_{1mod} and S_{2mod} are the annual survival rates of pup and adult foxes, respectively; B_1 and B_2 are the probabilities of pup and adult females breeding in each year, and L is the mean litter size for all breeding females.

Survival probabilities for pups and adults for each year of each simulation were initially determined using one of the two best ecological driver models for survival, given a constant number of eagle equivalents, simulated random rainfall, and adult density. We accounted for potential transients by discounting the marked year for adults, thereby limiting survival estimation to known

TABLE 5. Comparison of logistic regression (SAS Proc Logistic) models predicting breeding probabilities, where "x" indicates components included in a particular model.

Island	Year	Age	Island × year	Island × age	Year × age	Island × year × age	AIC_c	Delta AIC_c	AIC_c weight
x		x		x			244.39	0.00	0.39
x		x					244.77	0.38	0.32
		x					246.17	1.77	0.16
x	x	x					248.87	4.47	0.04
x	x	x		x			248.90	4.51	0.04
x	x	x	x				249.88	5.49	0.02
x	x	x	x	x			251.17	6.77	0.01
	x	x					252.46	8.07	0.01
x	x	x		x	x		255.76	11.37	0.00
x	x	x			x		257.46	13.06	0.00
x	x	x	x		x		257.56	13.17	0.00
x	x	x	x	x	x		258.35	13.96	0.00
x	x	x	x	x	x	x	262.20	17.80	0.00
x							263.40	19.01	0.00
							263.71	19.32	0.00
	x						270.40	26.01	0.00

TABLE 6. Mean and sampling variance for breeding probabilities (probability that a female produces a litter) and litter sizes (mean number of pups per breeding female) for models with the greatest AIC_c weight.

Parameter, model, and island	Age	Mean	SE	CV	Proportional AIC_c weight
Breeding probability					
Model 1: Island + age + island × age					0.446
Santa Cruz	pup	0.429	0.089	0.207	
	adult	0.618	0.124	0.201	
San Miguel	pup	0.176	0.023	0.131	
	adult	0.571	0.039	0.068	
Model 2: island age					0.340
Santa Cruz	pup	0.346	0.048	0.139	
	adult	0.686	0.111	0.162	
San Miguel	pup	0.222	0.052	0.234	
	adult	0.541	0.010	0.018	
Model 3: age					0.184
All	pup	0.266	0.022	0.083	
	adult	0.586	0.034	0.058	
Mean litter size					
Model 1: constant					0.692
All	all	1.92	0.119	0.062	
Model 2: island					0.307
Santa Cruz	all	1.731	0.148	0.085	
San Miguel	all	2.028	0.208	0.103	

Notes: There was no process variance in either variable. Proportional AIC_c weights for these models rescale original AIC_c weights to sum to 1 and indicate the probability of selecting each model in simulations incorporating model selection uncertainty.

residents. For pups, however, we took a conservative approach in including the marked year effect in survival rate estimates because of the potential for high mortality during dispersal off the grid. These survival rate estimates were then corrected for emigration by our best density-dependent modifier function. Based on reproductive rate analyses, we modeled breeding probabilities and mean litter sizes as identical in all years but with the supported spatial or age effects (Table 6). We assumed based on limited evidence that island foxes are unlikely to breed successfully in the absence of an established mate. Although extra-pair fertilizations are not uncommon (Roemer et al. 2001c), females appear to have an induced estrus brought on by intersexual social interactions (Asa et al. 2007). Thus, to reduce the probability of female breeding in the presence of mate limitation, we used a marriage function based on limitation by the least abundant sex (Caswell 2001). When the number of female pups (N_{1Fem}) and adults (N_{2Fem}) exceeded the overall number

TABLE 7. Model comparison for estimating mean litter size (SAS Proc GLM), where "x" indicates components included in a particular model.

Island	Year	Island × year	AIC_c	Delta AIC_c	AIC_c weight
			−11.46	7.84	0.58
x			−9.85	6.22	0.26
	x		−7.89	4.26	0.10
x	x		−6.67	3.04	0.05
x	x	x	−3.63	0.00	0.01

Note: Data were for five years on two islands; $n = 55$.

of males (N_{Male}), we allocated males to adult females first, such that breeding probabilities for pups (B_1) and adults (B_2) were

$$B_{1,t} = B_1 \left(\frac{N_{Male,t} - B_{2,t}N_{2Fem,t}}{N_{F1,t}} \right) \qquad (8)$$

$$B_{2,t} = \min \left[(B_2), \left(B_2 \times \frac{N_{Male,t}}{N_{2Fem,t}} \right) \right]. \qquad (9)$$

We compared results using these functions to results of additional simulations using the harmonic mean marriage function and found no discernible differences.

Rainfall simulation

Because ENSO events are important drivers of survival, we sought to model realistic rainfall patterns on the Channel Islands to simulate variability in survival rates. Much of the literature on weather simulation begins with daily or even hourly rainfall records. Instead, we focus on total annual rainfall, since data on fox survival is taken at annual increments. Given the high correlation between annual rainfall on the different islands (Table 1), we used the 102-year record from Santa Cruz Island to analyze rainfall patterns. These data are normally distributed after a log-transformation ($P = 0.655$, Lilliefors test) and, surprisingly, show no evidence of significant autocorrelation or patterning at any lag up to 40 years using autocorrelations, partial autocorrelations, or Fourier analyses (all $P > 0.05$). Looking further, we found no graphical or statistical evidence for positive autocorrelation in drought years or negative autocorrelation between high and low rainfall

TABLE 8. Support for different survival modifier functions, F.

Modifier functions	k	Ecological driver model			
		1		2	
		AIC_c	AIC_c weight	AIC_c	AIC_c weight
$d_{5.9} \times (1 - S_{jN})/(1 + \exp[b_2 D_j])$	1	13.35	0.45	15.09	0.45
$d_{5.9} \times (1 - S_{jN}) \times b_1$	1	13.65	0.39	15.37	0.39
$d_{5.9} \times (1 - S_{jN})/(1 + \exp[b_1 + b_2 D_j])$	2	15.47	0.16	17.20	0.16

Notes: Modifier functions were used to remove bias in apparent survival estimates at low densities due to permanent emigration. AIC_c results arise from comparing population change, λ_{Mj}, based on demographic estimates for the jth grid × year to λ_{dj} based on 73 grid × year estimates of adult density (D_j). Note that $d_{5.9} = 1$ for $D_j \leq 5.9$ adult foxes/km^2, and 0 otherwise; k is the number of parameters in modifier function.

years, such as that produced by ENSO weather patterns. We found identical results for a 144-year record of annual rainfall from Los Angeles. Given these results, we simulated Santa Cruz rainfall as a normal independent, identically distributed (i.i.d) process. Based on our survival analyses, we then converted rainfall to a binary variable to indicate ENSO years (≥ 80 cm), which occur with a probability of 11% each year.

Unassigned process variance

Use of the logistic function to predict survival in response to environmental covariates alone ignores the remaining, unexplained process variance, but the best approach to incorporating this unassigned variability into PVA simulations is not well established. The most obvious way to combine these two types of variability is to first choose an expected survival rate, $\bar{S}_t$, using the logistic function and then to use the estimate of unassigned variability in combination with this mean to pick a random, realized survival rate for that year. But, this direct use of the estimated variability may violate limits on the maximum variability possible for random probabilities, as discussed above. Thus, in each year of our simulations we pick random values for pup and adult survival rates from beta distributions, using for each a mean determined by the expected rate, $\bar{S}_t$, estimated from our ecological covariate models, and a variance estimated as $V_u \bar{S}_t(1 - \bar{S}_t)$, which constrains unexplained variability to be less than or equal to its theoretical maximum in any year. This approach assumes that as annual values of a survival rate increase or decrease the unexplained variance, as a proportion of maximum possible variance, remains steady. While we do not have the data needed to test this assumption, it represents a logical assumption about variance–mean relationships for random probabilities (Morris and Doak 2004). To evaluate the effects of this unassigned process variance, we also ran simulations that did not include unexplained variance in survival rates (P_u) or included it in only adult or only pup survival rates.

Demographic stochasticity

In addition to annual environmental stochasticity in survival rates, we also incorporated demographic sto-

chasticity in survival and breeding rates by picking random binomial variates based on the mean rate and numbers of individuals in each year and age class. Similarly, we picked the sex of offspring using binomial probabilities with mean of 0.5. We invoked demographic stochasticity only when the numbers in any particular age and sex class fell below 20 animals, as initial model runs showed no significant changes in outcomes as a result of this speed-enhancing simplification. We also added minimal demographic stochasticity to total annual births, using as each year's realized rate a Poisson deviate based on the product of the number of females breeding and the annual expected value for litter sizes.

Model and parameter uncertainty

We ran four groups of models in order to compare our results with those from previous analyses and with assumptions made in simpler demographic PVAs. First, we ran no-uncertainty simulations based on the single best covariate model of survival probabilities, parameterized with the maximum likelihood parameter estimates (Table 3), and, similarly, the single best model structures and parameter estimates for breeding proba-
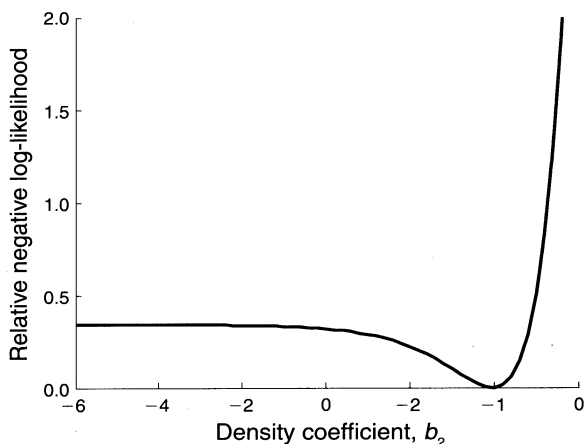

FIG. 5. Likelihood surface for the survival modifier parameter, b_2 (density coefficient) used to correct apparent survival estimates to account for permanent emigration.

bilities and litter size (Table 6). For each of these simulations, we assumed a constant number of eagle equivalents (i.e., constant eagle-driven mortality rates) ranging from 0 to 10 EEs. Because we have no estimates of how EEs or their effects on fox survival are likely to vary through time, we did not incorporate annual variation in eagle effects, above and beyond that created by the unassigned variance estimated from the ecological driver model. While these model runs include our best estimates of the manifold environmental effects on fox survival and reproduction, they do not account for any uncertainties in these estimated effects.

We also ran three sets of simulations incorporating either model uncertainty, parameter uncertainty, or both. In model-uncertainty simulations, we selected one of the two top survival models for each replicate simulation in proportion to its AIC_c weight, and similarly chose reproductive models for each replicate from the best two (litter size) or three (breeding rate) models using AIC_c weights (Tables 3 and 6).

For parameter-uncertainty simulations, we included uncertainty in parameter values but not in model selection by restricting ourselves to the best supported survival and reproductive models but choosing different, random sets of parameter values for each replicate run to reflect imprecision in parameter estimation. For survival models, we used the MLEs and approximate covariance matrix for the parameters of the logistic function and assumed a multivariate normal distribution for the coefficients. For the single parameter of the modifier function, which has a strongly asymmetrical distribution, we randomly picked parameter values bounded by the upper 95% likelihood confidence limit (0.25) and by a lower bound of -6.0 (corresponding to a minimal, 0.25%, change in survival rates at density $= 1$), with each value chosen in proportion to its relative likelihood. After picking a set of survival model parameters, we reestimated the mean and variance in proportional unassigned process variance, V_u, using the estimated explained process variance from the covariate model fit with these parameters (see *Process variance*): this procedure accounts for the effects of the survival model parameters on the estimation of assigned and hence unassigned process variance relative to that of the global model. For each set of parameters, we used the reestimated mean and variance to choose a random value for V_u to employ in the population simulation. We chose random values for breeding rates from beta distributions and for litter sizes from stretched beta distributions (Morris and Doak 2002) based on a maximum litter size of five (Moore and Collins 1995).

Finally, we introduced comprehensive uncertainty into the PVA model in full-uncertainty simulations by combining both model and parameter uncertainty. We accomplished this by randomly selecting the survival and reproductive models used for each replicate run, using the model-uncertainty simulation methods described above, and then introducing parameter uncer-

tainty into all variables of the selected models, according to the parameter-uncertainty simulation methods just outlined.

Screening for biological reality

Before using a parameter set to generate PVA predictions, we first tested each set to ensure that the incorporation of uncertainty did not result in biologically unrealistic population behavior. This is a simple form of Monte Carlo filtering that has occasionally been used in other ecological contexts (Van Winkle et al. 1997). We reasoned that in the absence of eagles or ENSO events, low to moderate density populations should be stable or growing on average. Thus, we discarded parameter sets in which deterministic lambda estimates were less than 1 at densities of 0.5 adult foxes/km^2. We did not screen for unrealistically high growth rates because all λ values were less than 1.6, even when assessed at S_{max}. For models with full uncertainty, screening to ensure biologically plausible behavior (i.e., growing populations at low densities in the absence of any threats in average years) eliminated about 57% of all potential parameter sets.

Simulation and analysis procedures

To help guide recovery planning for the fox, we ran simulations to assess the relative risk of extinction for different starting population sizes and numbers of eagles. Adult density in year one was determined based on starting population size, island area, and the stable stage distribution of the basic matrix model (Eq. 7) parameterized with the best-supported parameter values. Because short to medium-term risk analysis is most important for fox management, we ran each simulation for 50 years and used a quasi-extinction threshold of 30 foxes, set by the U.S. Fish and Wildlife Service island fox recovery team (*personal communication*), to further account for unidentified biological and sociopolitical uncertainties.

Each set of parameters, whether it incorporated model selection uncertainty, parameter uncertainty, or both, was used for an entire 50-year trajectory. To assess how much replication was needed to yield stable estimates of probability of quasi-extinction (P_{qx}), we compared predictions under a range of conditions and replication levels. Using parameter sets with full uncertainty, we assessed stability using the coefficient of variation (CV) and range of extinction risk predictions for ten replicate simulations at two EE levels (0 and 4) and two starting population sizes (100 and 400) for Santa Cruz Island. In each replicate, either 100, 200, 500, 1000, 2000, 5000, or 10 000 random parameter sets were used once. With full uncertainty simulations, probabilities of extinction stabilized at 1000 replicate parameter sets, at which point P_{qx} ranged ≤ 0.042 and the CV of P_{qx} was ≤ 0.077. Running multiple simulations with each parameter set (10, 20, or 50 times) had a negligible effect on estimator precision. Thus, for all

remaining analyses, we used 2000 replicate parameter sets to obtain viability estimates.

Sensitivity analyses

In addition to our simulations of population dynamics, we also conducted several analyses on the simple deterministic matrix models that correspond to asymptotic population behavior at fixed densities. These results are not designed to predict actual numbers or extinction risks but rather to aid in the interpretation of the stochastic behavior of simulated fox populations. For these analyses, we constructed models for Santa Cruz Island in the absence of ENSO conditions and without mate limitation. These models simplify to female-only matrices with two stages, pups and adults. We used these models to estimate asymptotic growth rates (λ) and also to calculate their sensitivity and elasticity values (Caswell 2001). We performed these analyses on matrices built with one EE (to allow an evaluation of sensitivity to eagle effects) at three fixed densities: 1 adult fox/km^2 (low), 5.9 adult foxes/km^2 (corresponding to the highest λ), and 11.4 adult foxes/km^2 (corresponding to $\lambda = 1$ or a stable population). Sensitivities for λ evaluated at this highest density are approximately equivalent to the sensitivity of equilibrium numbers (Caswell 2001). We performed these sensitivity analyses both for aggregate vital rates, stage-specific survival and reproduction (S_1, R_1 and S_2, R_2 for pups and adults, respectively), as well as for the lower-level parameters determining these vital rates.

We also investigated the sensitivity of stochastic risk predictions to individual parameters used to determine vital rates. Specifically, for each of 2000 parameter sets incorporating parameter uncertainty, we simulated 500 futures, then regressed (SAS Proc Reg) arcsine-square-root transformed extinction risk values on model parameters and generated squared semi-partial correlation coefficients (SSPCC) for each parameter. These SSPCCs indicate the amount of total variance explained by each variable above and beyond that accounted for by all other variables. Because parameter sets reflect actual parameter uncertainty, results indicate the influence of sampling variation in each parameter on estimated extinction risk.

We performed two additional analyses to assess the influence of parameter and model uncertainty on population growth and viability estimates. To examine how uncertainty altered the average performance of populations and also the variation over time in performance, we generated 500 λ values for each of 500 parameter sets for each type of uncertainty, all assuming a density of 5.9 and either 0 or 8 EEs. In addition, to investigate the distributions of risk predictions made by the individual parameter sets, which underlie the overall risk estimated under different forms of uncertainty, we summarized the results of 1000 replicate simulations for each of 1000 parameter sets

incorporating parameter uncertainty, model uncertainty, both, or neither.

POPULATION VIABILITY ASSESSMENT

Deterministic behavior and sensitivity results

A fox population model with no uncertainty exhibits weak positive density dependence and considerably stronger negative density dependence in deterministic λ, a pattern that changes little with increasing eagle-caused mortality rates (Fig. 6a, b). This negative density dependence is strong enough to produce low-amplitude, but sustained oscillations (Fig. 6c), indicated by the slope of the stock–recruitment curve of <-1 at the equilibrium population density (see Fig. 6b, May 1976). These deterministic, stable oscillatory dynamics are important in interpreting the instability of population numbers seen in our stochastic simulations (described in the following section).

We next consider the sensitivity of λ to stage-specific survival and reproductive rates for deterministic models estimated at three different densities (Fig. 7). At all densities, the greatest sensitivity and elasticity values are for adult survival rate, followed by pup survival and adult breeding rate (Fig. 7). At densities corresponding to lower λ values (i.e., 1.0 or 11.4 adult foxes/km^2), λ is slightly less responsive to reproductive rates than at densities where λ is high (i.e., 5.9 adult foxes/km^2; Fig. 7a, b).

In contrast to the minimal effect of density on the sensitivity of deterministic λ to survival and reproduction, there are strong effects of density on sensitivity to the underlying parameters that determine these rates (Fig. 8). Most marked is the increasing elasticity of population growth to the two density parameters at higher densities. At a density corresponding to maximal growth (5.9 adult foxes/km^2), λ has lowered sensitivity to most survival parameters but a higher sensitivity to all reproductive parameters (Fig. 8a). Nonetheless, when assessed on the scale of elasticities, all but the density parameters are little affected by changes in density (Fig. 8b). These results also show that the form and strength of density dependence in survival rates is the most important factor in understanding equilibrium numbers for fox populations, as indicated by the sensitivity results for λ at 11.4 adult foxes/km^2. At lower densities, where current at-risk populations reside, the intercept, which sets the mean survival rates prior to adding age and ecological driver effects, also has relatively large effects, as do adult breeding rates and mean litter sizes.

Stochastic results without uncertainty

Using only the best supported models for all demographic rates, our PVA model produced realistic population trajectories in the absence of uncertainty and with no eagle predation (Fig. 9a). As foreshadowed by our deterministic results, negative density dependence interacts with stochastic variation in demography to create substantial fluctuations in numbers for most population trajectories. For starting population sizes
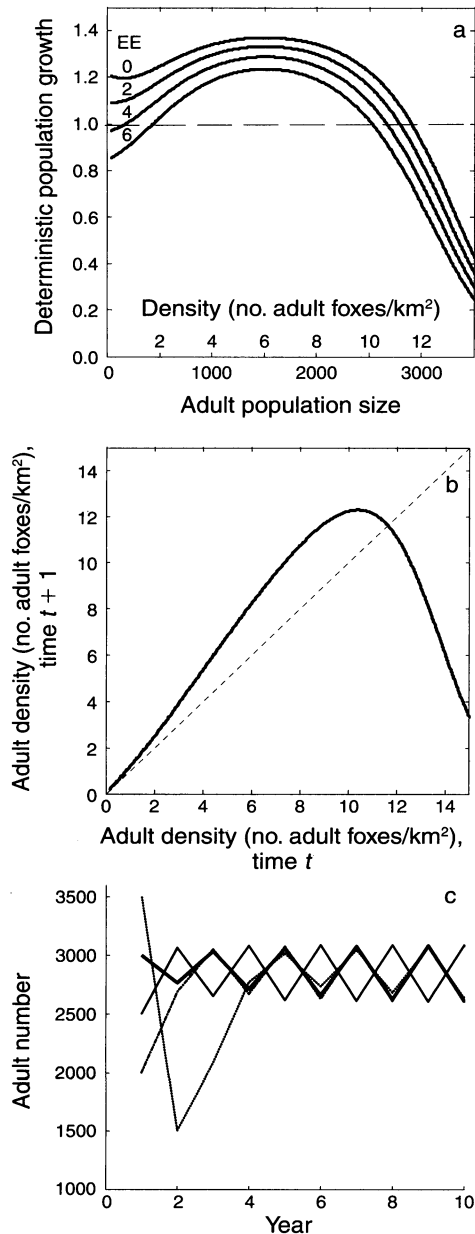
≥ 100, the risk of extinction over 50 years was low (~0) for both Santa Cruz and San Miguel islands (Fig. 10a, c). At very low starting population sizes of 50, extinction risk rose to 0.012 for Santa Cruz Island and 0.055 for San Miguel Island. Results were quite island-specific at small population sizes, apparently due to the higher breeding rates on Santa Cruz Island and the greater densities with lower population numbers on the much smaller San Miguel Island (Fig. 10, Table 6, Model 1).

At starting population sizes of 100, 1–2 EEs had only a slight impact on extinction risk for Santa Cruz Island foxes, and populations initialized with 650 foxes withstood up to 3 EEs without significant increases in risk (Fig. 11a, c). Each additional EE, however, posed substantial increased risk to fox populations and extinction was a near certainty when EEs exceeded

FIG. 6. Deterministic growth rate predictions for Santa Cruz Island, in the absence of ENSO events and using the best-supported model and parameter values: (a) population growth rates as a function of adult population size and eagle equivalents (EEs), with the double x-axis indicating corresponding adult density; (b) a stock-recruitment curve (density at time t vs. density at time $t + 1$) with no eagle predation, with dotted line showing points where density is identical from one year to the next; and (c) illustration of stable oscillations in deterministic fox dynamics for different starting population sizes.

FIG. 7. Deterministic sensitivity analysis results for basic demographic rates, evaluated at three densities. Population growth (a) sensitivities and (b) elasticities are shown for the major vital rates of a deterministic fox matrix evaluated at three adult densities: low (1.0), that resulting in the highest growth rate (5.9), and that resulting in stable numbers (11.4). Matrices were constructed for Santa Cruz Island and non-ENSO conditions and with predation of a single eagle equivalent. R_i is the age-specific annual female-only reproductive rate; S_i is the age-specific annual survival rate.
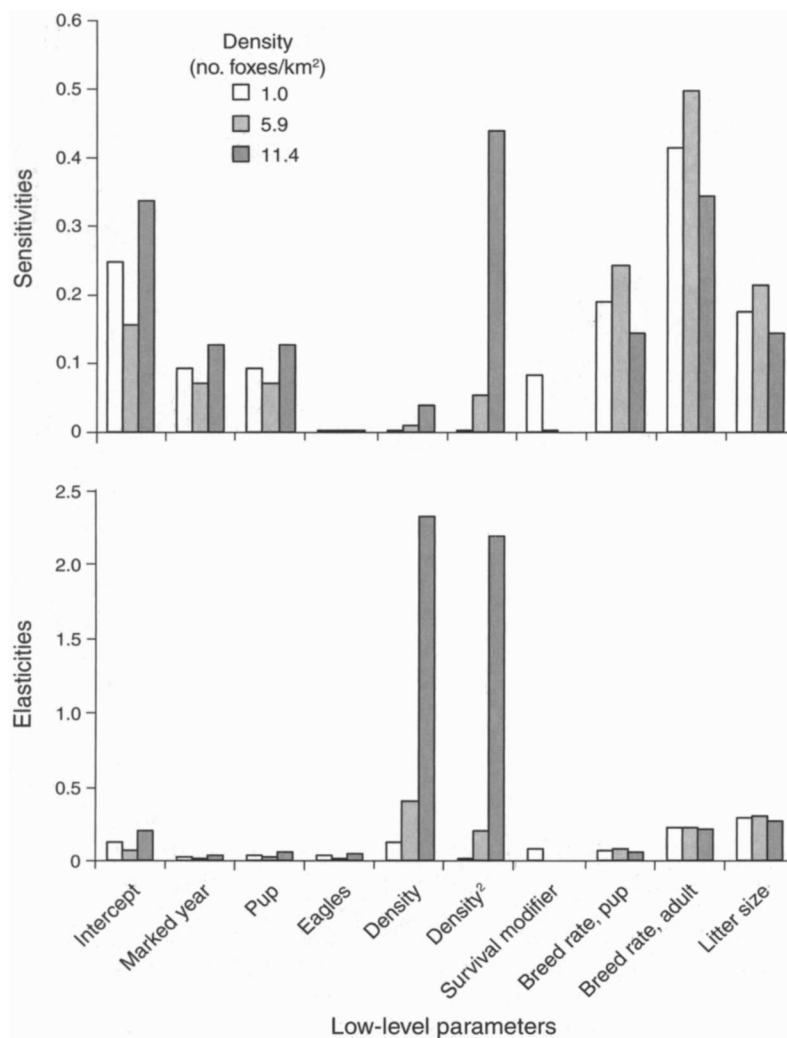
Fig. 8. Deterministic sensitivity analysis results for underlying parameter values evaluated at three densities. Population growth rate (a) sensitivities and (b) elasticities are shown for the low-level parameters governing survival and reproductive estimates of a deterministic fox matrix evaluated at three adult densities: low (1.0), that resulting in the highest growth rate (5.9), and that resulting in stable numbers (11.4). Matrices were constructed for Santa Cruz Island in non-ENSO conditions with a single eagle present. For ease of display, the sensitivity and elasticity for the survival modifier are shown for the negative of the value b_2 shown in Eq. 5.

seven. San Miguel Island fox populations responded similarly to eagle predation, but showed an even stronger influence of starting population size: starting populations of 100 foxes tolerated no more than 2 EEs, but at initial fox populations of 200 they withstood up to 5 EEs with minimal impact (Fig. 11e, g). Similarly, predicted extinction risk decreased steadily as starting population sizes increased on Santa Cruz Island in the presence of moderate eagle predation (4 EEs, Fig. 10e), but showed a threshold effect on San Miguel Island, dropping from 0.472 to 0.007 when starting population sizes increased from 100 to 200 foxes (Fig. 10g).

Accounting for uncertainty

Adding any type of uncertainty to simulations changed extinction risk predictions, sometimes markedly (Figs. 9–12). In the absence of eagles, uncertainty increased predictions of risk at low population sizes. For example, at starting population sizes of 50, the addition of full uncertainty elevated risk predictions from 0.012 to 0.049 on Santa Cruz Island and from 0.055 to 0.256 on San Miguel Island (Fig. 10).

Accounting for uncertainty, however, did not always increase estimated risk. Instead, incorporating full uncertainty narrowed the range of predicted extinction
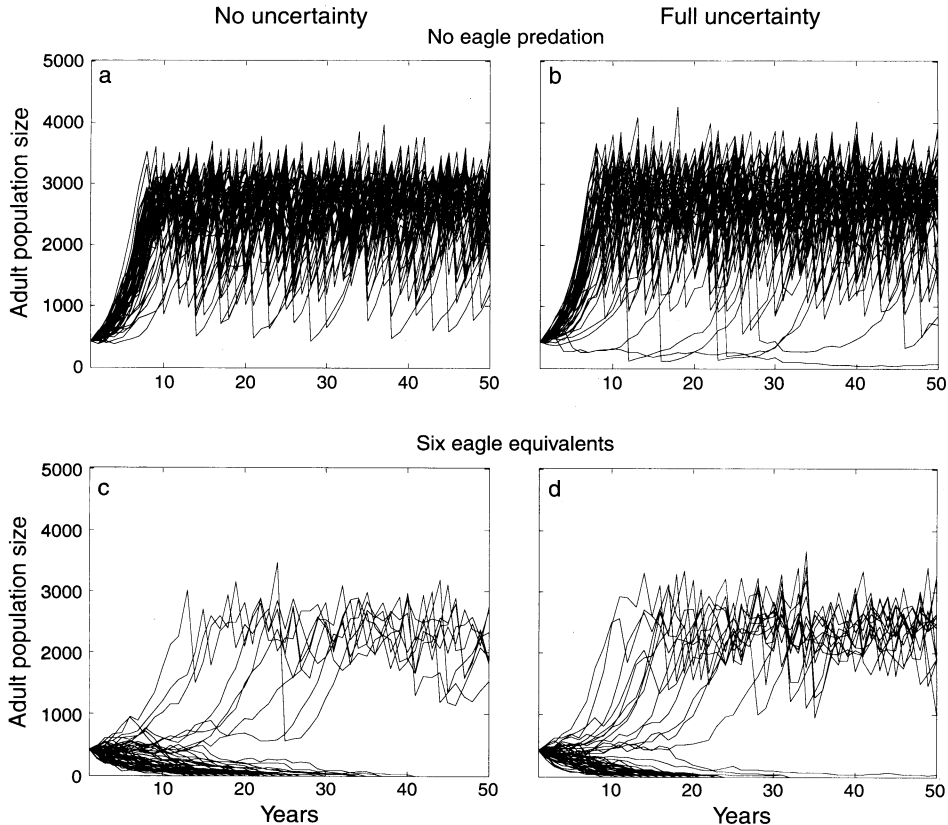
FIG. 9.   Population trajectories for island fox populations on Santa Cruz Island. Results are shown for 50 simulated futures for starting total population sizes of $n = 650$ (density $= 2.6$ foxes/km^2; at starting conditions, adults $= 0.65$ total) (a, b) in the absence of eagle predation and (c, d) with the addition of six eagle equivalents. Contrast trajectories for these conditions with no uncertainty (a, c) to those incorporating both model and parameter uncertainty (b, d). The quasi-extinction threshold was 30 for all runs.

risks associated with different levels of eagle predation (Fig. 11). On Santa Cruz Island, uncertainty decreased predicted extinction risk when EEs exceeded three and increased predicted risk when EEs numbered three or fewer at starting fox population sizes of 100; at starting population sizes of 650, risk predictions behaved similarly, but the cutoff point shifted to 5 EEs. Uncertainty had a similar effect on San Miguel Island. In general, when risk predictions ignoring uncertainty exceeded a P_{qx} of about 0.50, accounting for full uncertainty decreased predicted risk, and, conversely, if uncertainty-free predictions fell short of 0.50, adding uncertainty increased risk.

When fully accounting for uncertainty, even 1 EE markedly elevates the extinction risk at low starting population sizes of 100 on Santa Cruz Island ($P_{qx} = 0.093$), but at larger population sizes foxes tolerated the long-term presence of two to three EEs while maintaining similar predicted risk levels ($P_{qx} = 0.041 - 0.131$; Fig. 11b vs. 11d). Likewise, on San Miguel Island, at low population sizes of 100, 1 EE increased risk from 0.026 to 0.064 while at larger population sizes, extinction risk remained below 10% ($P_{qx} \leq 0.084$) until more than 5

EEs were added (Fig. 11f vs. 11h). These results also serve to illustrate the effects of numbers vs. density on the tolerance of fox populations to eagle predation; a starting population of 100 foxes on San Miguel Island is equivalent in density to 650 foxes on Santa Cruz Island (2.6 foxes/km^2 in both cases), yet the larger island with more foxes has considerably lower risk of extinction when eagles are present (Figs. 10f vs. 10h, 11d vs. 11f). Conversely, for population sizes over 50 and moderate eagle predation (≥ 2 EEs), extinction risks are lower on San Miguel than Santa Cruz island for the same number of foxes present (Figs. 10f vs. 10h, 11b vs. 11f).

The effect of different types of uncertainty varied with the degree of eagle predation threat (Fig. 12). Full and parameter uncertainty increased extinction risk when eagle predation was low and decreased it in when eagle predation was high, while model selection uncertainty increased extinction risk only at moderate eagle predation. Cumulative extinction curves reflecting full and parameter uncertainty were similarly shaped, and made nearly identical quantitative predictions of risk, while those reflecting model uncertainty corresponded closely to curves that ignored all uncertainty, with comparable
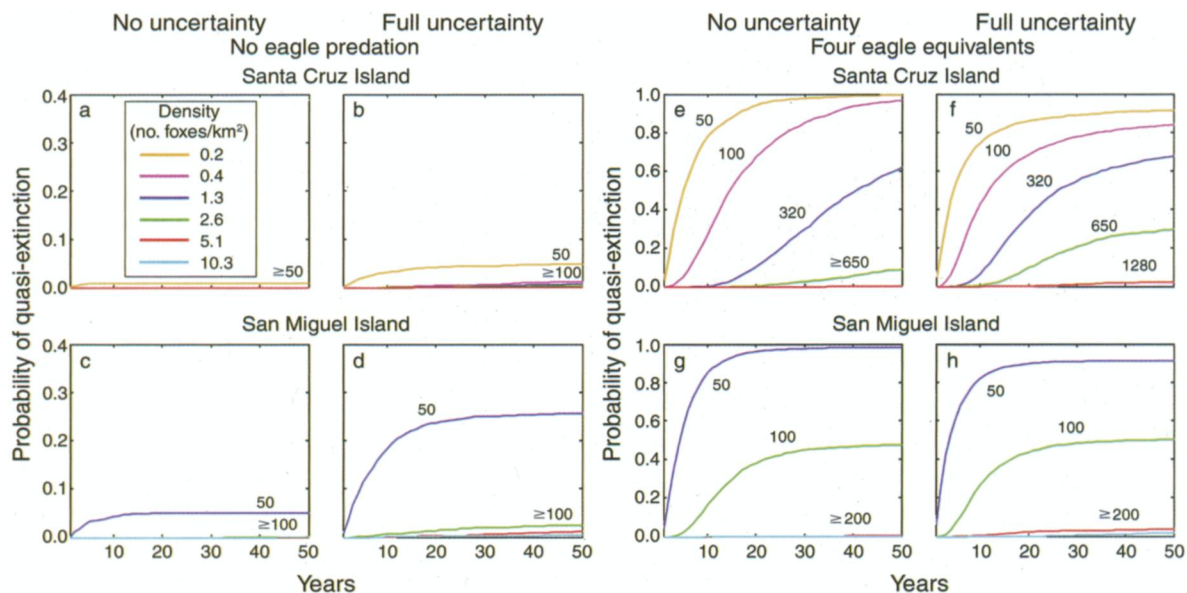
FIG. 10. Cumulative extinction curves for two islands at varying starting population sizes with and without uncertainty. Santa Cruz is the largest island (250 km²) with foxes, and San Miguel is the smallest island (39 km²) with foxes. Results are for 2000 replicate runs with a quasi-extinction threshold of 30. Numerical labels on lines show total starting numbers, while the key indicates the equivalent starting densities of foxes.

extinction risk predictions for most eagle predation rates. In most cases, extinction risks rose more quickly and reached an asymptote sooner for models that incorporated parameter and full uncertainty, relative to those including model uncertainty or no uncertainty (Fig. 12).

Examining the patterns of mean and variance in population growth rates and the distribution of risk predictions from individual parameters sets with different types of uncertainty helps to explain the varying effects of uncertainty on viability results. Adding model
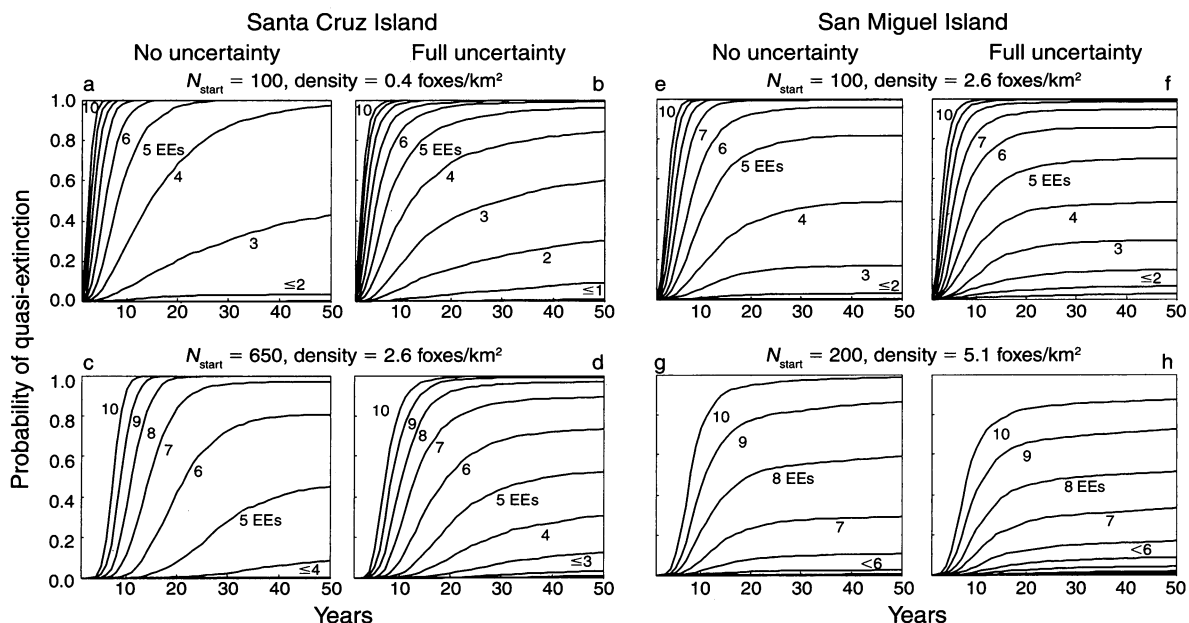
FIG. 11. Cumulative extinction curves showing the effects of 0–10 eagle equivalents (EEs) on the viability of fox populations on (a–d) Santa Cruz and (e–h) San Miguel islands without uncertainty and with full uncertainty. Results are for 2000 replicate runs with a quasi-extinction threshold of 30.

uncertainty, parameter uncertainty, or both, progressively and very substantially broadens the range of mean maximal λ between simulations and also its variance across time (Fig. 13). It similarly broadens overall risk predictions by individual parameter sets (Fig. 12). With low eagle predation (Figs. 12a, b and 13a) more uncertainty results in greater numbers of simulations with low means and high variances in λ, which put populations at greater risk of extinction. In contrast, with substantial eagle predation (Figs. 12d and 13b), when parameters without uncertainty result in high risks of extinction, adding uncertainty produces some simulations that are relatively safe, with high enough mean λ and low enough variance in λ to persist. Dissecting the effects of uncertainty underscores the fact that our overall extinction risk estimates summarize a range of possible population behaviors, especially at intermediate risk levels (e.g., Fig. 12).

Sensitivity analysis of stochastic models

Our analysis of how variation in different low-level coefficients influences extinction risk shows markedly different results than does the deterministic sensitivity analysis for population growth (Figs. 8 vs. 14). Some of these differences are due to parameters that only influence the stochastic models (e.g., those governing unassigned variance), but others are evaluated by both methods. Most importantly, extinction risk is strongly influenced by the survival modifier parameter, which has a very modest deterministic elasticity value. Another striking difference is the weak influence of parameters governing density dependence of survival for extinction risk, which contrasts with their large influence on deterministic λ. The differences in rankings of parameter importance when assessed via partial correlation coefficients and via deterministic sensitivity analysis arises from several sources, including the differing response variables (extinction probability vs. λ), the omission of density dependence from deterministic sensitivity results, and the substantial stochasticity of fox dynamics. However, a large component likely reflects a combination of the importance of parameters to extinction risk (as in traditional sensitivity analysis) interacting with uncertainty in our knowledge of these parameters. Thus, relatively large uncertainty in the survival intercept and survival modifier is reflected here (Fig. 14), but not in traditional sensitivity analyses, where parameters are varied only incrementally. Resolution of this uncertainty is thus critical for better determination of population viability. In contrast, while litter size and density effects were clearly important to fox dynamics by traditional sensitivity analysis, our parameter estimates are relatively precise for these variables (Tables 3 and 6), and thus they have less influence on variation in risk predictions.

We also performed simulations to test the importance of including unexplained variation in demographic rates in our extinction risk calculations. We found that omitting this variability greatly enhances the stability of fox numbers (Fig. 15 vs. Fig. 9a, b). These results also show that although population behavior is more sensitive to factors influencing adult survival rates, the greater value of V_u for pups means that inclusion of this factor produces similar variation in fox numbers to that of V_u of adults (Fig. 15a, d vs. b, e). With increasing eagle numbers, however, the influence of unexplained variability on dynamics is reduced, with most populations suffering rapid extinction regardless of the inclusion of this effect (results not shown).

DISCUSSION

Implications for island fox recovery

The immediate goal of our work was to yield useful guidance for management and monitoring of island foxes by developing a realistic characterization of their population behavior backed by careful analyses of all available data. Parameterizing our simulations using the survival rates predicted by ecological drivers such as predation, conspecific densities, and weather produces biologically plausible population trajectories. Population sizes oscillate around previously published estimates of carrying capacity for the islands (San Miguel Island, 577 adult foxes; Santa Cruz Island, 1540 adult foxes [Roemer et al. 2001a]), but are highly variable and prone to occasional crashes due to the interactions of negative density dependence with environmentally driven variance in survival and reproduction. Because the over-compensatory density dependence that creates these dynamics occurs at densities higher than those in our data sets, the functions we have fit and used may not be entirely accurate. However, numerous anecdotal observations (Holdredge 1954, Dawson 1990, Sheldon 1990a, b), prior assessments using live-trapping (Laughrin 1980, Kovach and Dow 1985), and recent genetic modeling (Aguilar et al. 2004) all indicate that fox population sizes have exhibited dramatic fluctuations historically, lending credence to these model predictions.

In spite of the predicted instability in fox numbers, our simulations also suggest that these populations are relatively safe from extinction risk once moderate population sizes are reached and if Golden Eagle predation is minimized. While we modeled numbers of eagles present on the northern islands, we have taken pains to refer to these as eagle equivalents or EEs to emphasize that we are simulating the estimated per capita impacts of eagles during the 1990s. We use EEs rather than eagle numbers, despite the intuitive appeal of the latter, because predator-prey dynamics have almost certainly changed with alterations of this ecological community, including the potential for increased per capita eagle predation rates with the decrease in the ungulate prey base across the northern islands (Courchamp et al. 2003) or for decreased predation efficacy with the acquisition of anti-predator behaviors by foxes (Roemer et al. 2002). Use of EEs also helps to emphasize the reliance of our model outputs on

the past space use patterns of eagles. For example, when our simulations suggest that populations of 200 adult foxes on San Miguel Island could withstand the presence of up to three eagles without significant increases in extinction risk, this eagle number refers to the historical impact of three eagles ranging throughout the entire northern islands, not three eagles living and preying continuously on San Miguel Island.

Our simulations suggest that fox populations exhibit resilience to eagle predation on the order of a few EEs. This does not offer island fox managers a reason to be complacent, given both the historical difficulties in finding and capturing Golden Eagles on the Channel Islands and the rapid rise in predicted extinction risks if eagle predation increases. However, it should provide some comfort that once fox populations are of sufficient size (which will differ by island), these avian predators are unlikely to decimate fox populations if managers maintain effective ongoing monitoring and control measures for eagles. Currently, Golden Eagles are thought to be present at very low levels in the northern Channel Islands (~1 eagle), and a small reintroduced population of 50 foxes on San Miguel Island had increased to approximately 180 by 2008 (T. Coonan, *unpublished data*), a size that represents relatively low risk. On Santa Cruz Island, fox populations were estimated at 207 adults in 2005 and 264 adults in 2006 (0.8 and 1.1 adult foxes/km^2, respectively [Schmidt et al. 2007*a*]), approaching conditions of relative safety from low rates of eagle predation. Interestingly, during 2005, three eagles were known to be present and preying upon a now intensively monitored fox population on Santa Cruz Island, taking at least 14 and possibly as many as 19 adults based on recovered carcasses of radio-collared and unmonitored foxes, resulting in a simple eagle mortality rate on adults of at least 0.022–0.031, consistent with the estimated rate of 0.027 for these conditions based on our ecological covariate models.

Our compilation of a species-wide data set and our approach to model building gave results that contrast with some findings of previous PVAs for the island fox (Roemer et al. 2001*b*, Kohlmann et al. 2005), but our work also confirms some basic conclusions of these analyses. Both previous analyses were applications of the program Vortex (Lacy et al. 1995), which limited the treatment of density dependence, ecological drivers, and unexplained stochasticity in fox demography, and prevented any systematic treatment of parameter and model uncertainty. Perhaps the most substantial difference between these past analyses and our current model is the greater flexibility to realistically assess population risk in a wide range of environmental conditions, which allows more refined management advice (Bakker and Doak, *in press*). We also predict somewhat greater extinction risk at low population sizes, suggesting a more cautious criterion for population safety, especially for small islands. For example, in their models for foxes on Santa Catalina Island, Kohlmann et al. (2005)

predicted that a starting population size of 80 ensured a 30-year extinction risk of 1% for the western end of the island, while our results for the similarly sized San Miguel Island predict a risk of quasi-extinction of 6% at 30 years for populations of 80. This difference likely results from our modeling of substantial random and also density-dependent variation in survival rates, which were not included in the simulations of Kohlmann et al. (2005). The simulations of Roemer et al. (2001*b*) are in general more comparable to ours, and they emphasize the importance of random variation in survival rates in governing population viability, as do we. However, our simulations generally show more safety at moderate population sizes in the absence of eagles, even with the inclusion in our models of parameter and model uncertainties. These differences arise mostly due to the flexibility we acquired to predict survival rates in the absence of eagle predation using our ecological driver models and to the importance of density-dependent survival changes in shaping population dynamics and hence extinction risk.

Taken together, integration of both ecological drivers and uncertainty into this island fox PVA has increased not only the realism of the models, but also their practical utility for management. Quantifying and incorporating the impact and uncertainty of the fox's current primary threat, Golden Eagles, has facilitated the comparison of relative extinction risks under a variety of eagle management scenarios (Bakker and Doak, *in press*). It has also aided in setting trigger points for alternative fox management based on observed eagle-driven mortality (Island Fox Recovery Coordination Group 2007). Finally, our approach has helped focus monitoring plans (Rubin et al. 2007). Biologists frequently recommend the collection of monitoring data to update PVAs for rare species (Morris et al. 2002), typically suggesting efforts targeted at the demographic rates most consequential to population growth rate. Here we show that to strengthen predictions of future iterations of this PVA, monitoring and research should also focus on parameters that exert a strong influence on population dynamics and extinction probability through a combination of high sensitivity value and large estimation uncertainty. Notably, we find, as have others (Ehrlén and Groenendael 1998, Benton and Grant 2000, Wisdom et al. 2000), that deterministic sensitivity values give very imperfect estimates of these overall importance values. This poor performance of deterministic sensitivity results arises from at least three differences between these analyses and the stochastic simulation analyses we report (Fig. 14): density dependence, environmental stochasticity, and parameter uncertainty. While the two differences in model structure assumptions certainly are important, our other results make clear that estimation uncertainty is also a critical issue when analyzing the importance of parameters for future dynamics. Not coincidentally, the issue of how parameter uncertainty
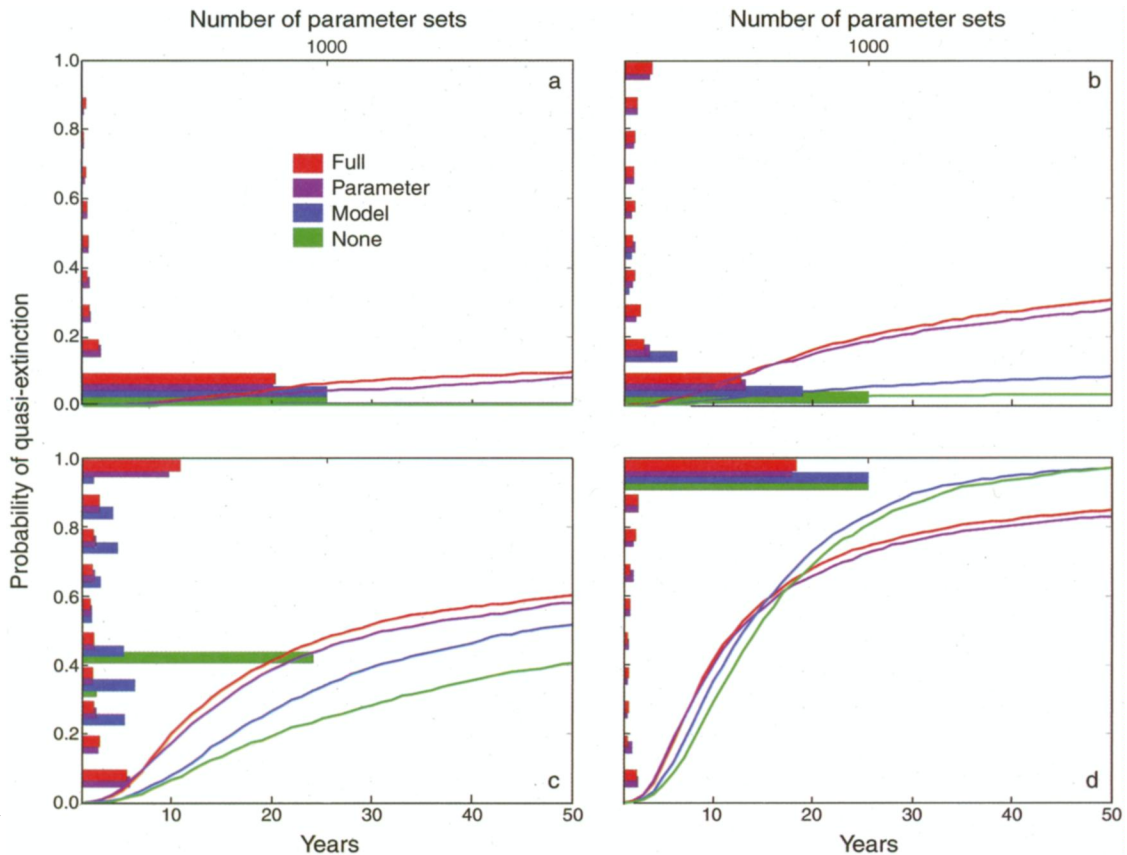
FIG. 12. The effects of incorporating different types of uncertainty into simulations of island fox population dynamics. Horizontal bars are histograms of predicted quasi-extinction risk at 50 years from 1000 trajectories run for each of 1000 parameter sets incorporating model uncertainty, parameter uncertainty, both (full), or neither (none). Histograms are binned by intervals of 0.1 on the y-axis and tallied on the upper x-axis. Lines show cumulative extinction curves (CEC) for 2000 50-year trajectories, each consisting of a random draw from a parameter set that incorporates model uncertainty, parameter uncertainty, both, or neither (i.e., identical to the approach used to generate Figs. 10 and 11). For CECs, corresponding time is on the lower x-axis, and extinction risk is on the y-axis. All simulations were for Santa Cruz Island with starting population sizes of 100 and four levels of eagle predation: (a) 1 EE, (b) 2 EEs, (c) 3 EEs, and (d) 4 EEs, all with a quasi-extinction threshold of 30.

influences viability assessments is also a key concern in prioritization of future research efforts.

Specific processes and parameters requiring further investigation to reduce uncertainty and thereby refine our understanding of risk for this species include density dependence in both survival and reproduction. For example, our PVA is built upon initial estimates of apparent survival that show strong and apparently unrealistic positive density dependence. While we develop a method to correct these estimates, there are still too few data for very low density populations in our data set to make reliable predictions of survival under these conditions, a problem that results in high uncertainty in the control parameter for this survival modification and consequently high sensitivity of model results (Fig. 14). A recent study (Angulo et al. 2007) reached different conclusions about density-dependent processes in island fox populations, highlighting the uncertainty and importance of this issue. Angulo et al.

(2007) found positive density dependence in survival, but only when eagles were present (thus they attribute this Allee effect to eagle predation) with no corresponding negative density dependence at higher densities. Our study used a larger data base and a comprehensive survival analysis technique to separate effects of eagle numbers (which historically increased as fox mortality rose and densities declined) from the effects of density on survival. We infer that positive density dependence in apparent survival is most likely due to emigration, based not only on this analysis, but also data indicating that emigration is not uncommon and exhibits negative density dependence, as well as mismatches at low densities between annual changes in grid densities and apparent survival estimates. Continued monitoring of and research on now-recovering fox populations should provide more information with which to address this problem.

Identifying relationships between habitat and fox densities or, minimally, understanding variation in densities across islands, may also refine our estimates of fox viability. Historical grids may have been sited in areas of higher fox densities and yet our models assume uniform densities and processes across each island. For some islands, especially those with considerable habitat variation such as Santa Cruz, our models are likely to overestimate equilibrium population sizes. Nonetheless, considering the general similarity in predicted tolerances of EEs between populations on large and small islands and the lower risk for populations on smaller islands for any given population size, we do not expect any overestimate of equilibrium numbers to substantially bias risk predictions downward. Finally, our analyses highlight adult breeding rates as a demographic parameter that is both relevant to population dynamics and imprecisely understood. Ideally, researchers would identify important ecological drivers of breeding rates, including the form and strength of any density dependence (Angulo et al. 2007). While random environmental drivers such as weather are unlikely to alter risk predictions, differing strength or forms of density dependence could increase or decrease extinction risk, and in particular, an Allee effect in reproduction could increase risk.

General implications for the construction and analysis of PVAs

The broader goal of our work was to develop and present effective methods for integrating advanced demographic analysis techniques into population models, and in particular to aid others seeking to provide guidance to managers that properly reflects variation and uncertainty but that can also be presented clearly enough to allow useful biological interpretation. One major component of our analysis approach was to identify important ecological drivers of fox demography and then use these drivers to simulate more realistic population dynamics. After eagle predation, density dependence is the most important of these drivers of demographic variation in foxes, and it is clearly critical in understanding plausible population growth rates and extinction risks for potentially fast-growing populations such as these. Many PVA models, even for species with similar life histories, do not include density dependence (or feature only a ceiling on numbers), usually due to a simple lack of data with which to estimate density-dependent effects. We do not advocate including density dependence in PVAs when there is no information with which to parameterize these effects (Caswell 2001, Morris and Doak 2002, Henle et al. 2004, Sabo et al. 2004). However, for species such as the fox, which over even the short time horizons we modeled can grow from small numbers to densities at which demographic rates are substantially influenced by negative density effects, at least some exploratory consideration of density dependence is probably warranted in almost any PVA.
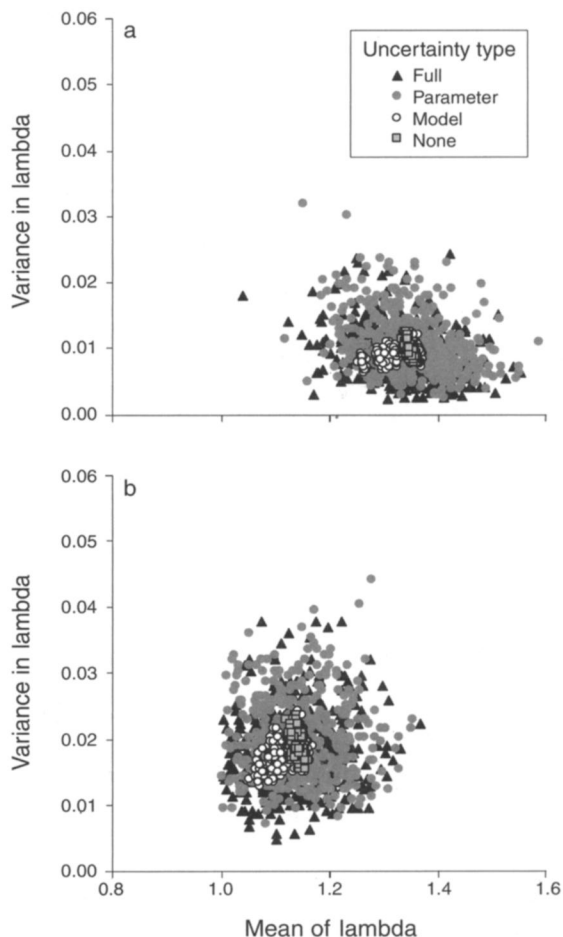

Fig. 13. Mean and variance in peak annual λ values by uncertainty type. For each of 500 parameter sets incorporating model uncertainty, parameter uncertainty, both (full), or neither (none), 500 random annual population growth rates were generated, all assuming an adult density of 5.9 foxes/km^2, and the means and variances of these λ values are plotted. Results are for (a) no eagle predation and (b) eight eagle equivalents.

Certainly the dynamics we simulate here, including extinction risk estimates under different eagle predation rates and on different islands, could not be adequately captured by models that ignored the strong density dependence that appears to operate within island fox populations.

ENSO events are the other major driver of temporal variability in fox numbers. Here too, we found significant effects, and an added complexity in the negative effects of ENSO on survival specific to pups in the wetter northern islands and variable effects of previous year's ENSO, being positive in the drier south and negative in the wetter north. One key complication that we anticipated but did not find was strong autocorrelation in these weather events, a result which should be of general interest to ecologists. We usually
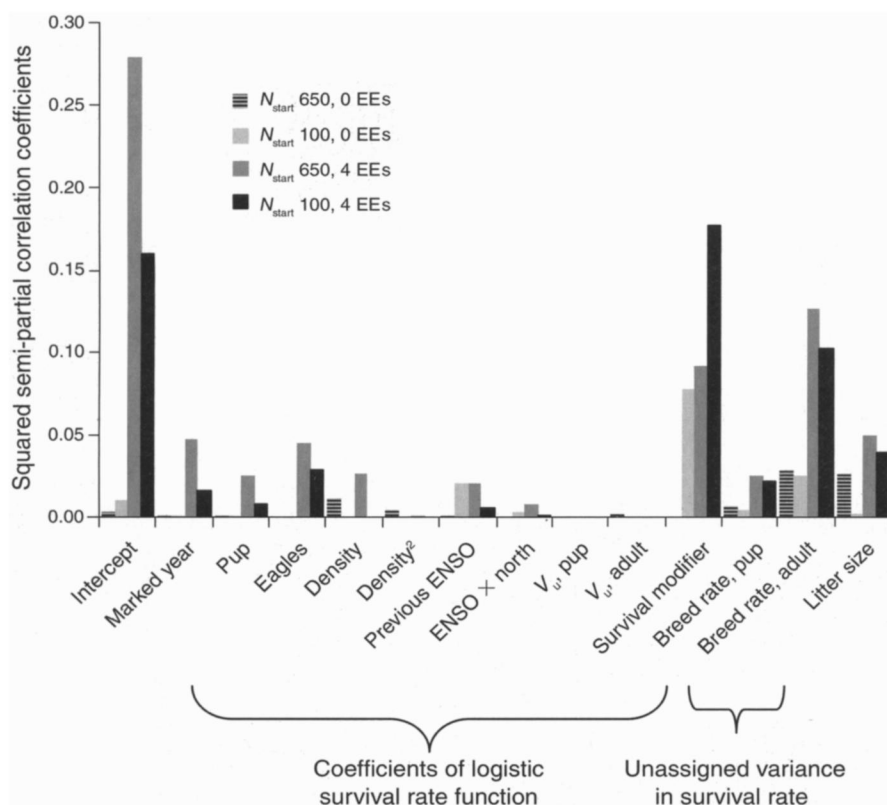
FIG. 14.   Stochastic sensitivity analyses at two starting population sizes (100 vs. 650 foxes) and two eagle predation levels. Shown are squared semi-partial correlation coefficients for regressing parameter values reflecting parameter uncertainty for the best survival and reproductive models against probability of quasi-extinction P_{qx} based on 500 replicate runs for each random parameter set. Results reflect a combination of the influence of each low-level parameter as well as its degree of uncertainty. V_u is unassigned process variance as a proportion of the maximum possible variance.

assume that weather patterns discussed by climatologists are directly relevant to the biological processes in which we are interested, and thus that climate is essentially always autocorrelated. In the case of the southern California region, climate does indeed show substantial evidence of long- and short-term correlations in rainfall patterns (Ropelewski and Halpert 1986, Latif and Barnett 1996, Dettinger et al. 1998). However, these climate analyses typically describe temporally smoothed data aggregated from weather stations arrayed over large areas; the broad cyclicity seen in such data sets may be exceptionally weak for a population living in any particular locale. While many regional weather data sets clearly show strong temporal patterning, our findings suggest that ecologists should not assume that this super-annual structuring of weather is a strong driver of local population dynamics. This same reasoning also suggests caution in our own use of rainfall data from only a single island to characterize conditions for multiple populations separated in space, based on imperfect correlations. Island-specific, or even intra-island-specific data, if available, might have revealed clearer weather-driven patterns, including relationships

between demographic rates and continuous rainfall rather than only extreme events.

While identifiable drivers of survival parameters are crucial determinants of fox dynamics, an equally important force is unexplained variability in demography that cannot be tied to any of the measured ecological drivers. This unaccounted-for process variation comprised 48% of the total estimated process variance for adult survival and 66% for pup survival. This unexplained variation can also be considered another form of uncertainty, and as such, indicates our lack of understanding of key ecological drivers controlling survival rates, especially for pups. Simulations that ignored this variability resulted in far more stable numbers (Fig. 15). Thus, while incorporation of environmental drivers of demographic rates into PVAs may improve their realism, this approach should not supplant the simulation of stochasticity per se: random variation in rates that we can estimate but can't assign to a cause. In this work, we have far more data with which to isolate and estimate drivers of demographic variation than are typical in PVA studies, so we would expect the
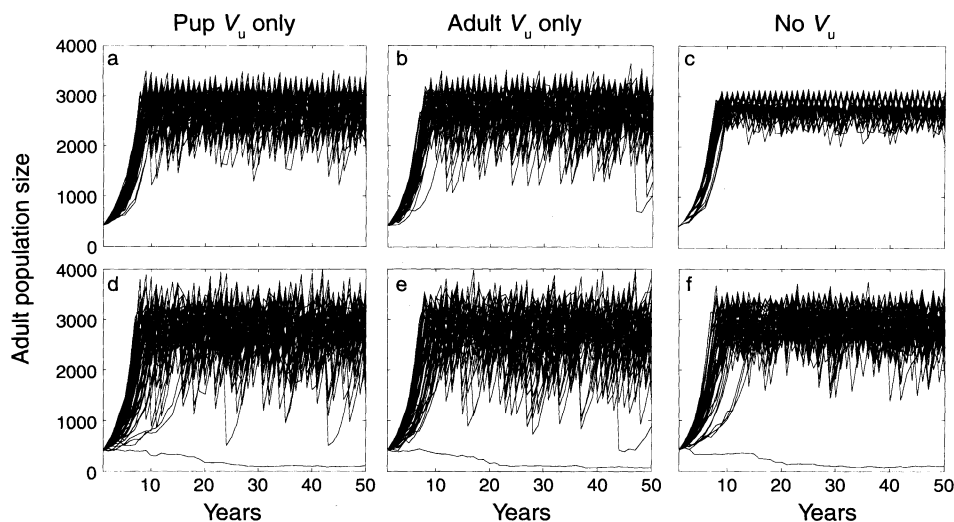
FIG. 15. Sample population trajectories to show the importance of including unexplained variation, V_u, in survival rates. Each panel shows 50 simulated futures for starting total population sizes of $n = 650$ (density = 2.6 foxes/km^2; at starting conditions, adults = 0.65 total) on Santa Cruz Island in the absence of eagle predation, with panels differing in the inclusion of unexplained variance and of uncertainty. The top row shows trajectories with no uncertainty while the bottom row includes full uncertainty. Panels (a) and (d) show trajectories that exclude adult V_u, (b) and (e) exclude pup V_u, and (c) and (f) exclude all V_u. Compare to Fig. 9a, c for trajectories with unexplained variation in both adult and pup survival rates.

percentage of unexplained variation to be higher in many other analyses for rare species.

The other broad class of complications we sought to address is uncertainty in model form and parameter values. Here too, we tried to build results of survival and reproductive analyses directly into our PVA models. Even for this well-studied species, uncertainty in parameter values was substantial, resulting in strong variation in extinction risk estimates between parameter sets. In general, adding uncertainty into the structure and parameters of population models tended to moderate overall predictions of extinction risk, increasing risks assigned to seemingly safe conditions (i.e., high starting numbers and low Golden Eagle numbers) and decreasing risks for apparently dangerous conditions. For example, absent uncertainty, all simulated Santa Cruz Island fox populations at moderate densities quickly go extinct in the presence of eight EEs, but with the addition of uncertainty, a small number of populations persist. Similarly, without uncertainty, all populations persist with three EEs, but with uncertainty, a small number go extinct (Fig. 11c vs. 11d). While adding full uncertainty interjects approximately symmetrical variability into estimates of mean λ and its variance (Fig. 13), the consequences of this variation for viability estimates are usually asymmetrical. Despite a decrease in mean λ when accounting for full uncertainty under an eight EE threat level, overall extinction risk is reduced due to the increase in variance of λ (Fig. 13): some random parameter sets now produce more pessimistic behavior, with no net effect on risk predictions in these already pessimistic scenarios, but

some sets yield more optimistic behavior to reduce net extinction risk. Conversely, without uncertainty, most populations at larger starting sizes and low eagle numbers persist. In this case, adding uncertainty creates some simulations with even more optimistic parameters, which don't influence viability estimates, but others with more pessimistic parameter sets that inject extra extinctions into the estimates of overall viability (Figs. 9–11). This increased variance results in cumulative extinction curves that asymptote more quickly for simulations incorporating full or parameter uncertainty in high risk conditions (Figs. 10–12).

Despite its moderating influence, by increasing the risks estimated under safer conditions, uncertainty has the practical effect of favoring more conservative management for the endangered fox. Because even the dampened risks of extinction posed by high EEs are unacceptably high, only the increase in risks at low eagle levels will meaningfully alter management options. Thus, the net result of adding uncertainty is to increase caution toward eagle presence, relative to PVA predictions ignoring uncertainty. While this conclusion is not unexpected, it is surprising how modest the effects of the substantial uncertainty are for overall viability predictions; careful inclusion of uncertainty did not doom the PVA to make ridiculously dire predictions or otherwise to lose its relevance for the guidance of management.

An even broader lesson from our work is that uncertainty can be incorporated into the structure and results of PVA models without making them substantially more complex or confusing. While we have presented many additional results and analyses here in

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order to illustrate the effects of parameter and model uncertainty, simply presenting the results for models with full uncertainty would suffice for a basic PVA to more accurately reflect our understanding of population behavior for species of concern. Thus, PVAs can account for uncertainty without becoming hopelessly difficult to understand or to present and in doing so can address a key long-running criticism of the PVA approach (Taylor 1995, Ludwig 1996, 1999, Beissinger and Westphal 1998, White 2000, Coulson et al. 2001b, Brook et al. 2002, Ellner et al. 2002, Ellner and Fieberg 2003, Harwood and Stokes 2003, McCarthy et al. 2003).

The comparison of extinction risk predictions from simulations with different types of uncertainty suggests that, at least for our system, parameter uncertainty is of far greater importance than model uncertainty. While we do not expect that model uncertainty will always have such a minimal effect, we suggest that in most circumstances its influence will tend to be smaller than that of parameter uncertainty. When data are sufficient to give strong support only to models with quite similar structures and predictions, as in this study, then the minimal effects of model uncertainty seem predictable. With less informative data, models with very different structures and predictions may have substantial support, giving model uncertainty more influence over PVA predictions. However, in these cases, parameter uncertainty within each model is also likely to be high, again reflecting the poor power of the data to resolve different causal factors and their strengths. Overall, then, we expect that parameter uncertainty will nearly always be critical in shaping PVA results, even in cases where it is unclear whether alternative model structures must be investigated. For island foxes, model selection uncertainty increased risk predictions because the best supported models tended to be somewhat more optimistic than less supported models, although this will not always be the case.

A key part of our strategy to incorporate parameter uncertainty into our PVA was to "screen" the resulting models for a minimal level of biological realism. This step is really an application of the general model testing and building philosophies of information theory: we try to limit the model forms we consider to ones that seem at least somewhat plausible, based on our general understanding of the study system (Van Winkle et al. 1997, Burnham and Anderson 2002). Thus, our screening criterion enforced a boundary on parameter uncertainty in a manner analogous to truncating the lower confidence limit on population size at the minimum number known alive; one could also argue that this approach follows directly from a Bayesian philosophy of using prior data to inform parameter and model estimation. Here, we apply this approach to generating sets of parameter values to reflect uncertainty. Ideally, our model forms and estimated parameter uncertainties would constrain all resulting simulations to have at least plausible behavior, but this ideal will not

generally be met in any demographic study. Thus, the best solution appears to be the application of a relatively simple criterion that ensures plausible population behavior, such as the one we adopted here (positive population growth from low densities in average years when no eagle threat is present). Given the importance of including parameter and model uncertainty into future PVAs, this type of screening procedure is also likely to become a necessary and common aspect of PVA methods.

While the population model we developed incorporates the lion's share of estimable model and parameter uncertainty into the PVA simulations, it is also worth noting the sources of uncertainty not included. For example, we only have data from one eagle colonization event and thus have no information on process variance in predation rates by colonization. It is unknown how fox populations would be affected if the size of the colonizing population varied or if the starting fox populations were small. Similarly, as noted above, we do no yet know how the removal of feral pigs from the island might change predation behavior (Courchamp et al. 2003, Dratch et al. 2004) or if the foxes have decreased susceptibility to eagles through evolved or learned antipredator responses such as increased nocturnality (Roemer et al. 2002). Disease outbreaks have afflicted island fox populations in the past (Timm et al. 2000, Clifford et al. 2006) and pose a serious threat for the future, but the frequency of recorded epizootics has been so low that any inclusion of them in our models would require undue guesswork. However, we do recognize disease as significant threat for the fox and elsewhere investigate alternative monitoring and management methods to reduce this threat. Habitat differences are also almost certain to influence fox demography, but we currently have too little information to see evidence of such effects. This laundry list of possible complications—typical of any predictive analysis—should not suggest that this or other PVAs are useless, but rather serve as a reminder that while we can account for many complexities, and in particular, uncertainties, in a formal way, we will never be able to fully quantify all the ecological forces that may impinge on our study systems, and should thus advance the viability and management recommendations that come from these analyses cautiously (Doak et al. 2008).

Conclusions

Altogether, these models give us better insight into the future viability of fox populations, and especially the forces that will interact with ongoing threats and continuing management to jointly influence their dynamics. Fox populations appear able to withstand very low levels of eagle predation in perpetuity, suggesting that ongoing monitoring for and removal of Golden Eagles is both necessary and sufficient to ameliorate the eagle threat. Our analyses have also highlighted important weaknesses in our knowledge, revealing that

increasing the utility of this PVA as a management tool will require greater understanding of density dependent processes in survival and reproduction.

More broadly, we believe that the set of modeling structures we present, starting with data analyses and ending with extinction risk predictions, show a general strategy by which ecological complexities and limitations of knowledge can be folded together into a PVA that is scientifically defensible and useful to managers. In many cases, PVAs can only be built with pre-digested data or information borrowed from other species, making some of the ways we analyze and treat ecological drivers and uncertainty difficult or impossible to perform. But often there is an opportunity to conduct or adapt data analyses to directly shape the structure of a PVA. As we hope to have illustrated here, careful integration of more complex demographic analyses can improve both the rigor of PVA results and also our understanding of populations of concern.

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APPENDIX

Model selection for estimation of survival rates for island foxes (*Urocyon littoralis*) based on annual capture–recapture data from 11 grids on four islands using Program MARK (*Ecological Archives* M079-003-A1).