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Understanding extinction risk and resilience in an extremely small population facing climate and ecosystem change

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Abstract. San Nicolas Island (SNI) foxes historically had the highest densities of the six subspecies of Channel Island fox, four of which were listed as endangered in the 1990s. As an island species, SNI foxes are inherently vulnerable because they evolved in isolation from many potential threats, and their small range features relatively simple and degraded habitats, limiting their population size and heightening susceptibility to climate-driven habitat changes. In the past decade, the SNI fox population has decreased by nearly half, spurring concern. Our analyses of 18 yr of trapping data suggest that both drought and density dependence contributed to this decline. Density dependence in survival acted on older individuals and its strength doubled after recent drought-induced habitat changes. Annual precipitation was a strong driver of pup production, but density dependence moderated precipitation benefits. Using a stochastic model with island-specific drivers of demography, we developed a risk isocline tool to predict 50-yr quasi-extinction risk based on population size and mortality. Predicted extinction risk for SNI foxes is currently <5% and expected to decrease. Compared to the previously listed subspecies, risk isoclines indicate the SNI subspecies is more resistant to quasi-extinction at moderate population sizes and mortality rates, but quasi-extinction risk does not decline as rapidly at higher population sizes or lower mortality rates. Thus, limiting human-caused mortality and monitoring for novel threats such as exotic disease remain important. The ability of SNI foxes to increase pup production following high-rainfall low-density years is a key feature stabilizing their dynamics. Habitat- and location-specific dynamics produce substantial portfolio effects, whereby asynchrony in growth rates stabilizes overall population numbers, and restoration efforts that increase food resources and habitat diversity will further enhance the resilience of this population. Although the SNI fox appears to be rebounding, its recent decline may foreshadow future dynamics and serves as a cautionary tale for stewards of island species facing unprecedented climatic conditions, especially those inhabiting small and less diverse systems. Finally, our analyses highlight limitations in applying risk analyses from one population to related species, or even the same species in different habitat settings.

Key words: carnivores; climate change; demographic model; extinction risk; insular endemics; portfolio effects; *Urocyon littoralis*.

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INTRODUCTION

Island endemics, which mostly consist of small and isolated populations, have proven especially vulnerable to near or complete extinction (Alcover et al. 1998), and they are disproportionately targets of urgent conservation concern. Climate change has increased this concern because warming may interact with a host of other anthropogenic threats and with intrinsic vulnerabilities. While these vulnerabilities are well documented (Simberloff 2000), we often know fairly little about the specific dynamics of island species and the factors that have allowed them to persist, making analysis of their true status difficult and predictions of their future safety in shifting conditions unclear.

The endemic San Nicolas Island (SNI) fox (*Urocyon littoralis dickeyi*) faces several intrinsic vulnerabilities common to island populations. First, the subspecies is confined to a small land area (57 km^2), limiting its potential maximum population size. With an island-wide carrying capacity likely well under 1000 individuals, it is and will remain one of world's rarest carnivores. Second, SNI is a relatively simple terrestrial ecosystem hosting a low diversity of food resources and habitats, and much of the island's vegetation is sparse and anthropogenically degraded. Climate change could increase variability or trigger declines in the fox's food supply (Drost and Fellers 1991, Cypher et al. 2017), with little apparent scope for differential habitat responses across the island. Finally, genetic isolation (Funk et al. 2016) has heightened the fox's behavioral and physiological vulnerability to introduced predators, competitors, and pathogens, and to human mortality sources.

Despite these concerns, over its recent history the SNI fox population has been among the densest of the six subspecies of island fox, apparently due to abundant introduced food sources, and it has never been listed under the US Endangered Species Act (ESA). However, beginning in 2009, SNI foxes initiated an apparent multi-year decline. Island fox managers and biologists are vigilant stewards, not only because of the fox's theoretical island-associated vulnerabilities, but also because the real events of the late 1990s crystalized the seriousness of these risk factors when four island fox subspecies declined catastrophically and were listed as federally endangered in 2004. Predation by non-native golden eagles reduced fox populations to ~15 on San Miguel and Santa Rosa islands and ~55 on Santa Cruz Island (Roemer et al. 2001*a*, US Fish and Wildlife Service 2012), while on Santa Catalina Island an outbreak of exotic canine distemper virus lowered fox populations to ~100 (Timm et al. 2009). Foxes on SNI were considered "dense and stable" at the time these other subspecies were ESA-listed (US Fish and Wildlife Service 2012), with population size estimated at ~550 in 2004 (Garcelon and Schmidt 2005).

A population viability management framework guided recovery planning for the ESA-listed subspecies, and they were delisted in 2016, the fastest recovery in the history of the ESA. Underpinning this framework was a demographic model that incorporated uncertainty and carefully quantified environmental drivers of demographic rates and hence population health (Bakker et al. 2009, US Fish and Wildlife Service 2012). This population model was used to develop risk isoclines depicting the probability of future (50-yr) quasi-extinction (<30 foxes) predicted by different adult mortality rates and population sizes. These risk isoclines provided a biologically meaningful metric for tracking the status of the ESA-listed foxes (Bakker and Doak 2009) and formed the basis of their key recovery criteria (Bakker et al. 2009, US Fish and Wildlife Service 2012). Monitoring data from SNI foxes were censored from the demographic analyses used to parameterize the Bakker et al. (2009) model because at that time SNI foxes "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 (Bakker et al. 2009)." However, if tailored to its unique dynamics, the modeling approach developed for the other fox populations can serve as a useful framework with which to analyze the status of the SNI fox, allowing us to leverage substantial past scientific and policy work on risk thresholds.

Unlike the island fox declines of the 1990s, no driver of decline like golden eagles or CDV has been identified for SNI foxes, suggesting more indirect or multifactorial causes. SNI is unusual among the fox-inhabited islands in its small size (comparable to 38 km^2 San Miguel Island but much smaller than the remaining four, which range 147–250 km^2), its ecosystem simplicity, with only shrub and grassland but no forested habitats, and its degree of monodominance by only a few plant species, mostly invasives (Schoenherr et al. 1999). Accordingly, the SNI fox has historically been the subspecies most reliant on non-native food resources, in particular, ice plant (*Carpobrotus* spp.) fruits and exotic garden snails (*Cornu aspersum*), which have made up about half its diet during certain times of year (Cypher et al. 2014). Given the relative simplicity and small size of SNI, warming temperatures and changing precipitation regimes have the potential to substantially heighten the future vulnerability of this fox by decreasing the spatial extent or temporal reliability of the habitats or resources it depends upon, and to do so earlier and more extensively than on the other Channel Islands, making the SNI fox a potential bellwether for the effects of climate change on island fox populations more broadly. From fall 2011 to fall 2015, California experienced the driest and hottest weather on record (Williams et al. 2015, Hanak et al. 2016). Drought conditions on SNI led to a die-off of the widespread, drought-tolerant *Carpobrotus*, leaving behind extensive areas of dead thatch (Cypher et al. 2018). Island fox biologists hypothesized that density-dependent forces or other threats initiated the SNI fox decline and the extended drought and resulting habitat changes prolonged and exacerbated it.

In addition to climatic effects, several other drivers of mortality and reproduction have the potential to influence recent dynamics of the SNI fox population. Foxes on SNI experienced unusually low survival in 2009, coincident with an island-wide cat eradication effort that likely disturbed foxes due to the presence of leghold traps and tracking dogs. Only four fox mortalities were directly attributable to this carefully monitored effort, and its effect on fox population dynamics is generally assumed to be negligible (Hanson et al. 2015), but no studies have evaluated potential indirect or unobserved effects on fox survival. Finally, the greatest cause of known mortalities is vehicular trauma, although foxes killed along roadways are more likely to be discovered than those dying elsewhere of other causes.

Here, we assess population status and trends for the SNI fox to identify the most important environmental drivers of demographic rates, considering the influence of ecosystem-scale events such as recent drought and habitat alteration, as well as density dependence, intrinsic factors, and the role of cat eradication. We make use of 18 yr of annual trapping data spanning non-drought and drought conditions (i.e., 2000–2017), and use our island-specific analyses to modify the previous island fox population model (Bakker et al. 2009) for SNI foxes. Using this model, we investigate the influence of climate and related habitat changes on the population dynamics and future extinction risk of SNI foxes and develop tailored risk isoclines to assess its current status, using population size and mortality as predictors of risk consistent with recovery criteria developed for the other subspecies. In addition, we explore the roles of both density-dependent processes and habitat- and location-specific dynamics (i.e., portfolio effects; Schindler et al. 2015) in stabilizing this population, adding to our general understanding of how small and isolated populations are able to persist. Finally, the extensive data and analyses available for island foxes on different island allow us to assess the generality of viability patterns and the drivers of population dynamics.

DENSITY AND VITAL RATE ESTIMATION: METHODS

Study system

Island foxes, small canids weighing 1–3 kg and standing 12–15 cm tall, are habitat and diet generalists (Moore and Collins 1995, Hofman et al. 2016). On SNI, common diet items are arthropods (>90% of scats), European garden snails (*C. aspera*, ~40-50% of scats), fruits (~50–60% of scats) including those of non-native ice plants (*Carpobrotus* spp.) and Australian saltbush (*Atriplex semibaccata*), and vertebrates (up to ~60% of scats), including deer mice (*Peromyscus maniculatus*), birds, and lizards (Cypher et al. 2014, Cypher et al. 2017). Deer mouse abundance on the island is positively correlated with precipitation (Cypher et al. 2017); other food sources are likely to be positively affected by rainfall as well, although these relationships have not been quantified.

Island foxes are territorial and form mated pairs. They breed in February and March, parturition occurs in April and May, with litter sizes averaging 2–3 (range 1–5), and offspring disperse in their first or second year (Moore and Collins 1995). Similar to other island populations, island fox home range sizes are small (~0.5 km^2), and dispersal distances are short relative to mainland canids (Roemer et al. 2001*b*). Pups are known to breed at the end of their first year but at a lower rate than older foxes (Moore and Collins 1995).

Feral cats were present on SNI from the start of the study until they were eradicated in 2009–2010. Island foxes were frequent non-target captures in the leghold traps used for cat eradication (Hanson et al. 2015), and although captured foxes were released from these traps, generally without obvious trauma, foxes experienced low survival in the years cat eradication efforts took place. Vehicular trauma is the largest source of known mortality to foxes (74% of documented mortality events), and interactions with human structures also cause substantial mortalities (e.g., entrapment, drowning, electrocution: 11% of documented mortality). Considerable traffic and human activity occur between Nictown, where personnel live, and the airport (Fig. 1a). There is also a road network across the island, such that most foxes live in relatively close proximity to roads; however, traffic data are unavailable.

Annual precipitation, which is the second lowest of all the Channel Islands, was recorded by the Navy from 1948 to 2005. Subsequently, the time series was extended based on a correlation with precipitation data from Los Angeles (rain year July–June, C. Drost, *unpublished data*; Fig. 1 b). When simulating future fox dynamics, we make predictions using two different assumptions about future precipitation: (1) long-term a, in which future precipitation is simulated by the mean and variance of the 69-yr record from 1948 through 2017 ($\bar{x}$ = 20.05, σ = 10.61), or (2) recent-reduced, in which future precipitation is simulated by the mean and variance of the 19-yr record from 1998 through 2017, when precipitation has been unusually low ($\bar{x}$ = 16.71, σ = 7.60), but which may more accurately reflect future patterns associated with climate change. Precipitation and other project data and code are archived at Dryad (Appendix S1: Table S1).

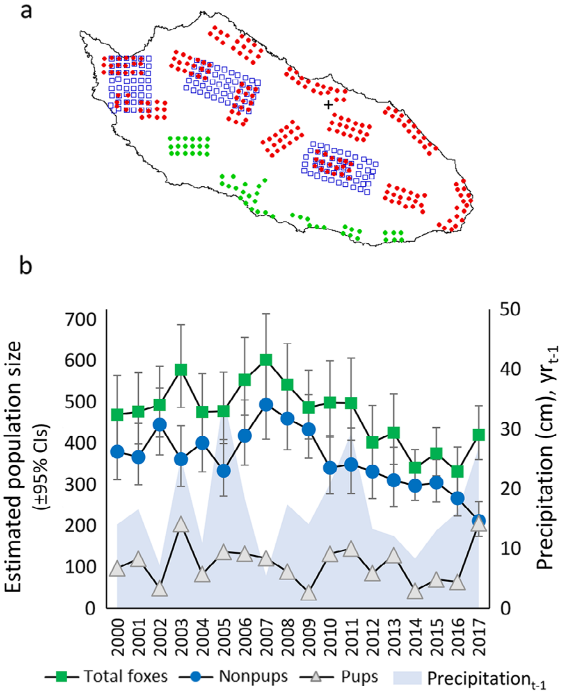

Fig. 1. Island-wide monitoring and population size estimates for island foxes on San Nicolas Island, 2000–2017. (a) Locations of large monitoring grids (blue squares), trapped 2000-2014, minigrids (red circles), trapped 2014–2017, and discontinued minigrids, trapped in 2014 only (green circles), + represents Nictown. (b) The estimated number of total foxes, nonpups, and pups, based on analyses of trapping data using the best-supported covariate model: D_{np} ~ Year × NW + Tallshrub g0 ~ *B* + *Sex* σ ~ *B* + Sex, pmix(Sex) ~ 1 and D_{tot} ~ Year × NW + Tallshrub g0 ~ *B* × Pup σ ~ *B* × Pup, pmix(Pup) ~ Year.

Monitoring

The SNI fox has been monitored annually from 2000 to 2017 using mark–recapture trapping methods. Trapping methodologies evolved over the timeframe of the study due to efforts to maximize both the robustness and efficiency of sampling schemes. Specifically, from 2000 to 2014, three large grids (6 × 8, 5 × 10, 5 × 10, Fig. 1a) were monitored annually. From 2014 to 2017, minigrids, consisting of 18 traps (3 × 6 or 2 × 9), were dispersed throughout accessible portions of the island (Fig 1a). The minigrid approach followed recommendations of an all-island monitoring plan (Rubin et al. 2007) developed to facilitate robust population size estimates and to assess attainment of the risk-based ESA recovery criteria established for the listed subspecies (Bakker and Doak 2009). Minigrid trap layout was designed for use with spatially explicit capture–recapture methods based on observed fox movement and detection behavior.

For all years, trap spacing was ~250 m. During 2014, both the three large grids and the 15 minigrids were trapped to allow comparisons of density estimates; thereafter only the minigrids were trapped. Starting in 2015, three minigrids were discontinued due to logistical and operational challenges (Fig. 1a).

Density

Because density-dependent regulation was documented for other island fox populations and was a key component of the Bakker et al. (2009) island fox model, we estimated annual island-wide population size in part to support analyses of density dependence in survival and reproduction. Identifying habitat or geographic covariates of fox density was critical to allowing extrapolation of local density estimates to island-wide abundance due to the changes in trapping locations through time.

To estimate density, we used spatially explicit maximum-likelihood-based capture–recapture models (Royle et al. 2013) to fit distance-dependent detection probabilities as defined by a detection function relative to home range centers. Home range centers are assumed to follow a Poisson process, inhomogeneous if density covariates are modeled, although the method is robust to evenly dispersed centers associated with territorial species (Efford 2004). To implement this approach, we used the R package secr (secr version 3.1.3, R version 3.3.3, Efford 2017), which models capture events as a joint function of density (D), detection (g0), and movement (σ) parameters. Package secr constructs objects defining the spatial locations of detectors (i.e., traps), individual capture histories at detectors, a habitat mask represented by a meshed grid delineating overall habitat and the spatial variation in potential covariates of D, g0, and σ. User-specified submodels describe detection of individual i at detector d on occasion s, based on spatial, temporal, and behavioral covariates of D, g0, and σ.

We explored models that included behavioral responses to trapping such that g0 and σ changed after first capture each year. We also considered time-varying models in which D, g0, and σ varied or remained constant across grids and/or years and assessed support for several potential covariates of detection and movement, including sex and timing of trapping. The heterogeneity of habitat on the island relative to trap spacing (~250 m) makes it difficult to use trapping data to identify fine-grained associations between fox densities and habitat. However, we investigated whether coarse-scale associations existed between habitat or geography and the densities of foxes by assessing whether model fit improved when using general habitat attributes at detectors as covariates of density, including Tallshrub (>0.5 m, reflecting the existence of some patches of taller and denser vegetation on the island, primarily *Coreopsis gigantea*, *Lupinus albifrons*, and *Baccharis pilularis* associations), distance to shore (Dist2shore, reflecting access to marine resources), distance to Nictown (Dist2nic, reflecting a presumed gradient in human-fox interactions), and northwesterliness (NW, reflecting the direction of prevailing winds and hence local climate effects, Appendix S1: Table S3). Island-wide population size estimates were generated using secr's Region.N function to extrapolate year- and covariate-specific density functions based on covariate attributes in the island-wide mask generated using GIS habitat mapping (1996), with a grid cell size of 100 m.

One mechanism that can generate stability in population numbers is the portfolio effect, which occurs when different segments of a population fluctuate asynchronously (Schindler et al. 2015). Recent work in multiple populations has shown that such effects can be strongly stabilizing, including for rare and restricted species, and even when fluctuations are positively correlated (Schindler et al. 2010, Moore et al. 2014, Abbott et al. 2017, Dibner et al. 2019, Waddle et al. 2019). We expected that the homogeneity of habitats across the island would weaken any portfolio effects, but tested for such effects by dividing the island into four categories of latitude and four of longitude, for a total of 14 sections (two combinations did not contain any land), summing the predicted densities for each section in each year, and then estimating the synchrony index, ϕ, the ratio of observed aggregate variance to maximum aggregate variance (Loreau and de Mazancourt 2008) across all sections (Appendix S1).

Vital rates

Because the timing of trapping varied across years and grids and we lacked data that linked females to pups, we did not estimate breeding probability and litter size as in the Bakker et al. (2009) model, but instead used the ratio of pups to nonpups as a measure of annual pup production (Repro). Pups per nonpup was derived from secr analyses of total fox densities using a hybrid mixture model that specified pups and nonpups as two classes of individuals. We used multiple linear regression models (R version 3.5.1) to investigate ecological drivers of Repro, considering density in the previous year (total, D_{tot_t-1}, and nonpup, D_{np_t-1}), precipitation in the previous year (Rain_{t-1}), timing of trapping (average day of trapping in months after June 21, Seasontiming), and proportion of non-yearlings in the nonpup segment of the population (Propnonyrl), using AICc to compare model fit. While these Repro ratios have associated uncertainties, we follow other researchers in using standard linear models to predict these values without considering estimation uncertainty in either independent or dependent variables. We estimated annual unexplained process variance in Repro by comparing total process variance from annual Repro estimates (White 2000) to the realized variance of the predicted Repro estimates from the best covariate model (Bakker et al. 2009).

To identify ecological drivers of annual survival, we built Cormack-Jolly-Seber (CJS) open population models in Program MARK using annual trapping observations. The variation in monitoring schemes, the complexity of the CJS model structure, and the number of different covariates considered required a sequential model selection procedure. First, we used a highly parameterized survival model (S ~ Year + Markyear + Male:Markyear + Age + Age^2 + D_{np} + D_{np}^2 + Drought:D_{np} + Drought:D_{np}^2) to explore different recapture models (sensu, Lebreton et al. 1992). Year is categorical year effects, Markyear is a binary time-varying individual covariate indicating the year of marking, which helps account for transients, and Male:Markyear allows for sex differences in transients. Age is a discrete time-varying individual covariate, with pups in their first year classified as age 0, and Drought is a binary time-varying covariate indicating the years from 2012 onward when drought altered island vegetation and food resources. This model structure was selected based on previous analyses for other subspecies (Bakker et al. 2009) coupled with knowledge of the fox's biology and of habitat changes on San Nicolas Island. We considered interactions of density and drought because biologists hypothesized that both drought-driven habitat changes and high fox densities contributed to recent decreases in survival.

Next, using the best model structure for recapture probability, we tested the following model structures for survival: (1) age and stage structure (2) ecological drivers, including time-varying covariates (D_{np}, Rain_{t-1}, Drought) and time-varying individual covariates (Markyear, Dist2nic, the mean distance to Nictown from capture traps each year, Tallshrub, and Leghold, one or more captures in a leghold trap, and LegholdN, the number of captures in a leghold trap, testing for an influence of leghold captures on survival from 2009 to 2010 only), and (3) combinations of the best-supported age/stage structure and environmental drivers with and without annual variance (i.e., Year). For all model building, we selected models based on Akaike information criterion corrected for small sample sizes (i.e., AICc, Lebreton et al. 1992). We estimated unexplained process variance in survival probability as the difference in the process variance of the global model and the realized variance of the estimates from the best driver model over the same time period, averaged across ages. See Appendix S1 for expanded vital rate estimation methods.

DENSITY AND VITAL RATE ESTIMATION: RESULTS

Island fox density and population size

*Model selection.—*We fit a total of 35 secr models for nonpup densities (Appendix S1: Table S4). The best structure for behaviors included effects of sex on both detection and movement and a transient trap response (g0 ~ B + Sex σ ~ B + Sex, pmix(Sex) ~ 1, Appendix S1: Table S4). Specifically, for all foxes, detection probability temporarily increased following capture, suggesting short-term trap happiness, and males were more trappable than females, a pattern also observed on Santa Cruz Island (unpublished data). In addition, for all foxes, distance moved following capture temporarily decreased, again suggesting short-term trap happiness, and distance moved was lower for males than females. The density component of the best secr model was D_{np} ~ Year × NW + Tallshrub; nonpup fox densities were highest in tall shrub habitat, varied by year, and increased in a northwesterly direction, with the strength of that gradient varying across years, indicating asynchronous density dynamics across space and time. The best nonpup covariate model captured 74% of the variation of the global model (year- and grid-specific estimates, Appendix S1: Fig. S6), and bias appeared minimal (slope of 1.01).

We fit an additional 29 models for total fox captures (pups and nonpups, D_{tot}). The best structure for behaviors included differences between pups and nonpups with an interactive transient trap response in both detection and movement (i.e., g0 ~ B × pup σ ~ B × pup, Appendix S1: Table S6). As with nonpup-only models, nonpups exhibited a temporary increase in detection and decrease in movement following capture. In contrast, pups had higher detection probabilities and moved shorter distances relative to nonpups but did not alter movements after capture. The best structure for the density component of the total fox secr model was the same as the nonpup-only model. (D_{tot} ~ Year × NW + Tallshrub). There was strong support for annual variation in the ratio of pups to nonpups (pmix(Pup) ~ Year).

*Population size.—*Applying the selected models to the spatial attributes of SNI yielded annual population size estimates. The estimated total number of nonpups was generally stable at about 400 from 2000 to 2006, then increased to a maximum of 495 (95% CI: 411, 596) in 2007 before slowly decreasing to a low of 213 (95% CI: 175, 259) in 2017 (Fig. 1b, Appendix S1: Table S8). The estimated number of total foxes island-wide followed a similar pattern, increasing from 470 (95% CI: 391, 565) in 2000 to a maximum of 603 (95% CI: 508, 715) in 2007 and then slowly decreasing to a low of 332 (282, 392) in 2016 (Fig. 1b). Extremely high pup production in 2017 led to an increase in total fox numbers in 2017 to 421 (95% CI: 361, 492). The distribution of foxes across the island varied through time (Fig 2), with densities more variable and generally high on the west end, but relatively constant and generally low on the east end (Fig. 2).

*Effects of habitat- and location-specific dynamics in stabilizing numbers.—*As shown in Fig. 2, the effects of Tallshrub and NW and especially the interaction of Year and Tallshrub led to somewhat asynchronous dynamics across the island. We found that there was a substantial portfolio effect, with observed variance only 69% of the maximum expected if all fluctuations were synchronous. Further, from 2009 onwards, the portfolio effect was stronger, with observed variance only 62% of the maximum predicted value. Thus, even with a degraded and fairly homogeneous set of habitats, the SNI fox population appeared to benefit from the habitat differences that still exist, especially during the drought period.

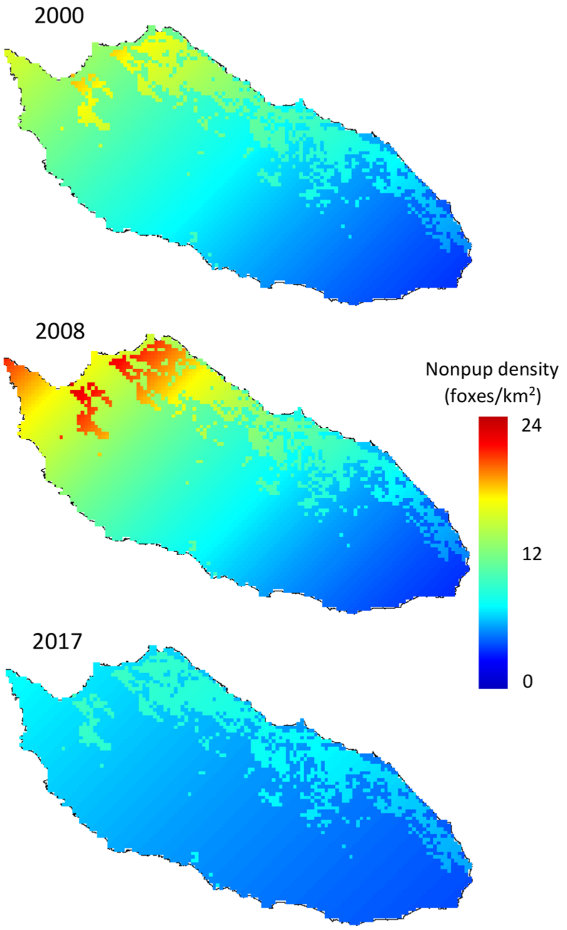

Fig. 2. Spatial and temporal trends in the density of nonpup island foxes on San Nicolas Island. Island-wide population size estimates were made by applying the best nonpup density (D_{np}) covariate model (see Fig. 1 legend) to island-wide attributes.

Reproduction

The number and proportion of pups in the population varied considerably through time (Fig. 1b, 3a). Pup numbers peaked in 2003 (205) and 2017 (207) and were notably low in 2002 (49), 2009 (39), and 2014 (43). The proportion of pups followed a generally similar pattern, with pups making up their smallest fraction of the population in 2002 (0.10), 2009 (0.08), and 2014 (0.13), and their largest fraction in 2003 (0.35) and 2017 (0.49).

A substantial amount of the variance (adjusted $R^2 = 0.73$) in Repro was explained by annual precipitation and total fox density in the preceding year ($\text{Repro} \sim \text{Rain}_{t-1} + D_{\text{tot}\_t-1} + \text{Rain}_{t-1} \times D_{\text{tot}\_t-1}$, $P = 0.0001$, Fig. 3, Appendix S1: Table S11). Precipitation was positively related to Repro and total fox densities were negatively related, with a strong negative interaction such that the highest pup production only occurred when precipitation was high and fox densities were low. When annual precipitation was low or when fox density was high, Repro tended to be low. The best covariate model accounted for 90% of the process variance of the global model.

Despite the clear support for the $\text{Repro} \sim \text{Rain}_{t-1} + D_{\text{tot}\_t-1} + \text{Rain}_{t-1} \times D_{\text{tot}\_t-1}$ model (DAIC 11.2, AICc wt 0.99), the very high Repro datapoint in 2017 following a low-density, high-rainfall year had large influence in this analysis. Excluding this datapoint, the best fitting model was simply $\text{Repro} \sim \text{Rain}_{t-1}$, with no support for a density effect.

Survival

The best-supported model structure for annual apparent survival was $S \sim$ Year2009 + Markyear + Male: Markyear + Ageif≥4 + Dist2nic + Ageif≥4 × D_{np_t} + Ageif≥4 × Drought: D_{np_t}. This model included an effect of year of marking, with sex-specific differences, indicating lower apparent survival in the year of marking, especially for males. We attributed these marked year effects to the presence of transients that only appear once in the sample, with males more likely to be transients. The best age structure indicated there is a prime age for foxes when survival is high and constant extending from age-zero pups in their first summer/fall through age three, after which foxes experience survival senescence (Figs. 4, 5b). Negative density dependence acted only on post-prime-age foxes and its strength increased during and after drought years (Figs. 4, 5b) and associated island changes beginning in 2012.

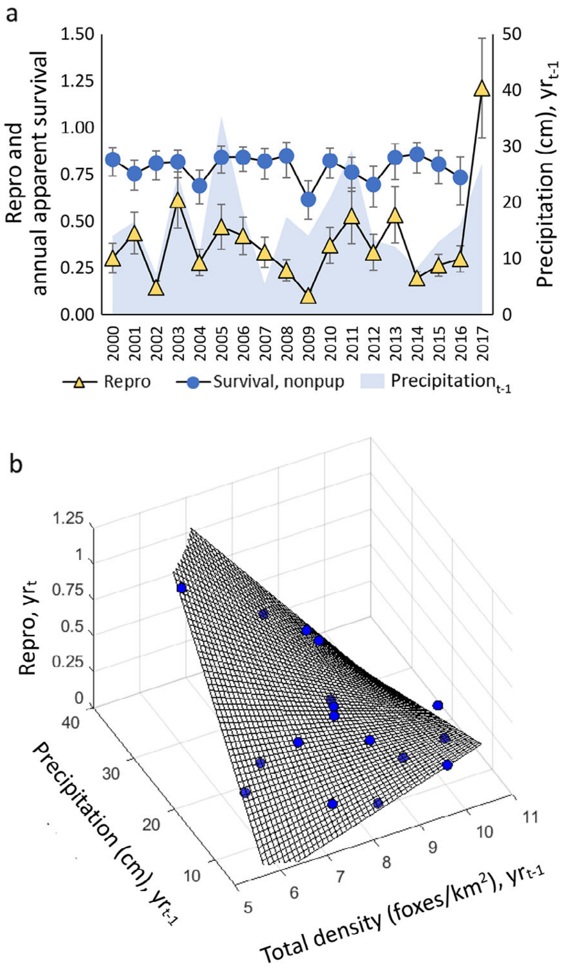

Fig. 3. Relationship between precipitation, density, and island fox demographic rates on San Nicolas Island. (a) Precipitation in the preceding year was strongly correlated with pups per nonpup (Repro) at summer/fall trapping but did not predict annual apparent survival (Tables S11–S12); survival estimates for nonpups are from the $S \sim$ Year + Markyear + Male:Markyear + Nonpup model. (b) Reproduction was best predicted by both precipitation and total fox density in the preceding year (Appendix S1: Table S11).

There was a positive survival effect of distance to Nictown, indicating lower survival for foxes living in closer proximity to Nictown. There was no support for an effect of previous year's

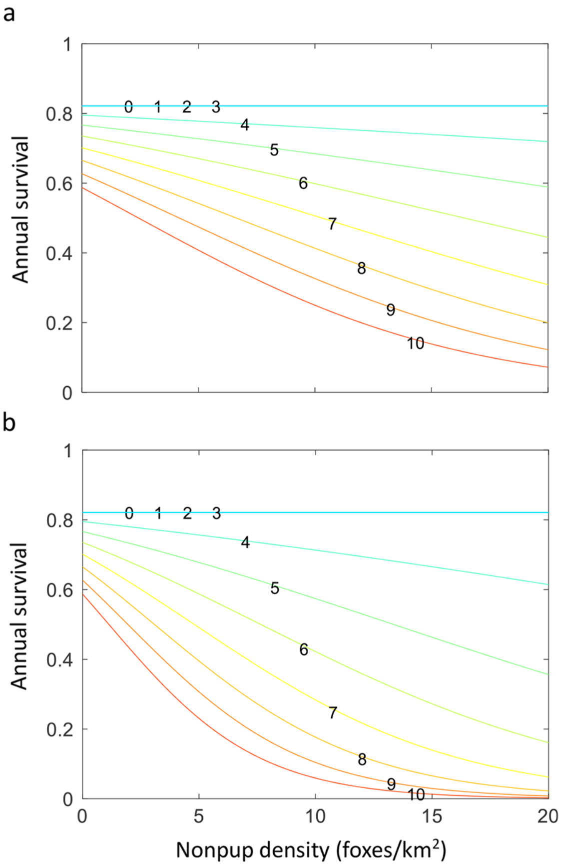

Fig. 4. Relationship between survival, density, and drought for island foxes on San Nicolas Island. Nonpup density predicted annual apparent survival for older than prime age (foxes beyond their fourth year) and the strength of the negative density dependence increased from the time period (a) before drought-associated habitat changes to (b) the years following drought-associated habitat change. Labels on lines indicate age in years.

precipitation on survival. There was no negative survival effect of capture in a leghold trap in 2009–2010, or of the number of times captured in a leghold trap. However, foxes experienced unusually low survival in 2009, an effect that could not be accounted for by other covariates (Appendix S1: Table S12).

The best recapture model was: *R* ~ Yearmod + Age + D_{np_t} + Discontinued + LegholdN. There was a permanent negative effect of number of times captured in a leghold trap in 2009–2010 on future recapture probability. Other factors predicting recapture probability included a negative effect of age, a positive effect of nonpup density, and a negative effect of previous capture only in discontinued traps (Fig. 1). Because of the known annual variation in trapping protocols, we included a year effect, except for the years 2015 to 2017, when 12 minigrids were systematically run and we set recapture rates as equal (i.e., Yearmod, Appendix S1: Table S12).

Our goal in this survival analysis was to identify the best driver model consisting only of variables that could be specified in simulations. Thus, we chose the model that best accounted for annual stochastic variance without using year effects (*S* ~ Markyear + Male:Markyear + Ageif≥4 + Dist2nic + Ageif≥4 × D_{np_t} + Ageif≥4 × Drought:D_{np_t}). We used this driver model to simulate survival, and to fully account for stochastic variance, we estimated process variance using the global model (*S* ~ Year + Markyear + Male:Markyear + Ageif≥4 + Dist2nic + Ageif≥4 × D_{np_t} + Ageif≥4 × Drought:D_{np_t}) and added unexplained process variance to the simulations. The best covariate model including Year2009 accounts for 60% of global process variance for prime age foxes and 55-100% of older foxes, but omitting Year2009, it accounts for only ~1% and 2–28% of process variance in prime age and older fox survival. Note, however, that survival models accounted for variation in survival relative to density and distance to Nictown, which varies across the island but is averaged across the island to estimate process variance. There was relatively little variation in island-wide density during the study, although greater density variation and thus greater survival variation is realized in population simulations.

Simulation Models and Risk Isoclines: Methods

We modified the island fox stochastic demographic matrix population model described in Bakker et al. (2009) to fit the demographic rates and drivers observed on San Nicolas Island. Unlike the Bakker et al. (2009) model, which was a four-stage demographic matrix model with two age classes (pup and nonpups) and two sexes, we took advantage of our evolving understanding of fox dynamics to refine this matrix to a female-only model with 12 age classes to reflect

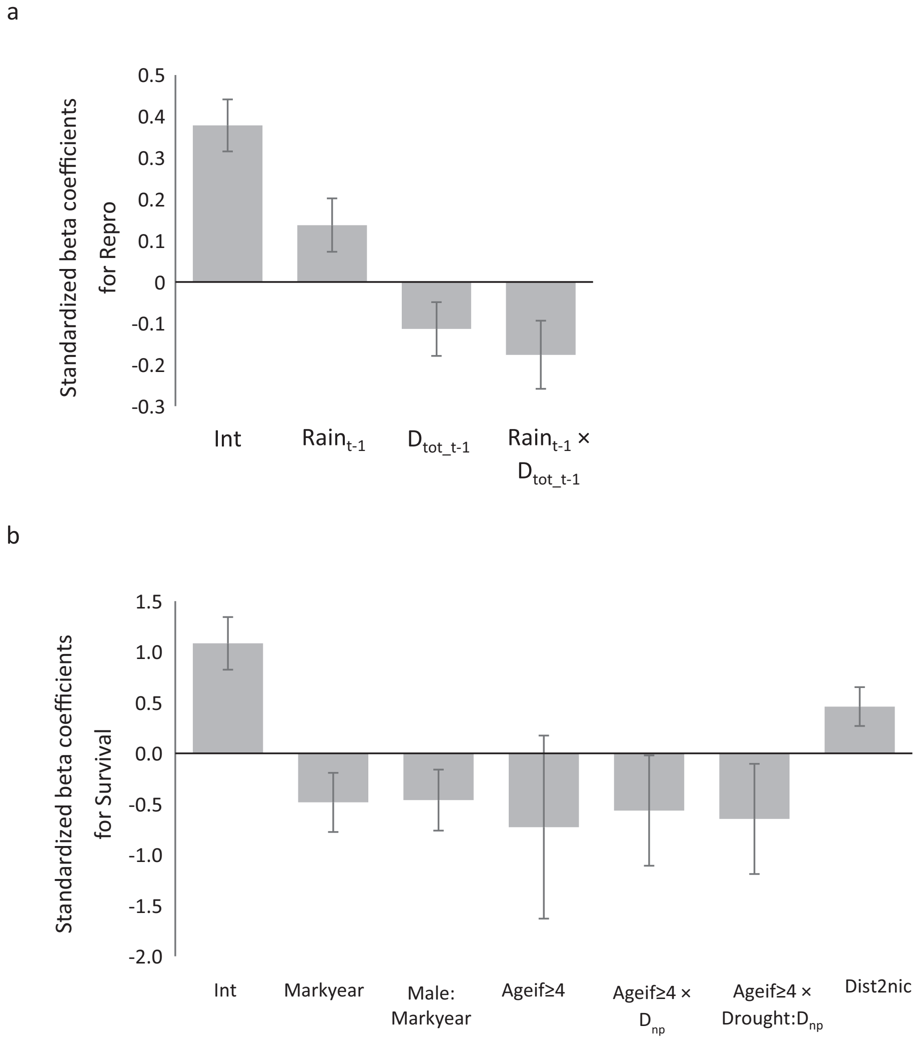

Fig. 5. Predictive equations for demographic rates. Standardized beta coefficients for (a) linear regression relationship between ecological drivers and Repro using *z*-score transformation (b) and logistic regression relationship between ecological drivers and annual apparent survival, with variables transformed by dividing by two standard deviations. See text for variable descriptions. Int is model intercept.

the evidence for significant declines in survival with increasing age (survival senescence; Figs. 4, 5, Tables S11–S12). As with the Bakker et al. (2009) model, we simulated demographic rates (survival and reproduction) based on the best-supported covariate models. We incorporated parameter uncertainty and unexplained stochastic variance but did not include model uncertainty as previous work suggested parameter uncertainty accounted for a substantial majority of total variance in model predictions (Bakker et al. 2009). We incorporated demographic stochasticity in all simulations.

We ran simulations for a total of 10 scenarios (Table 1). In the default scenario (scenario 1), we assumed future precipitation followed the recent-reduced precipitation pattern to reflect the likelihood that climate change will lead to more frequent drought conditions (Williams et al. 2015). We also assumed that the effects of density dependence in survival observed during recent drought conditions persisted and that density

Table 1. Scenarios used in stochastic population model to simulate future population dynamics for the San Nicolas Island fox.

Scenario	Precipitation	Island conditions defining survival density dependence	Drivers of reproductive rates	Form of added mortality	Notes
1	Recent-reduced	Drought	Precipitation and density	Proportional increase	Default assumption for risk isoclines (Figs. 6, 7a, 8, 9a, Appendix S1: Figs. S8a, S11a)
2	Long-term mean	. . .	. . .	. . .	(Figs. 6b, 7b, 9b, Appendix S1: Fig. S8a)
3	Recent-reduced	. . .	. . .	Quadratic density function	Added mortality is highest at low and high densities, same as golden eagle mortality on northern islands (Bakker et al. 2009) (Appendix S1: Fig. S12c)
4	Long-term mean	. . .	. . .	. . .	Appendix S1: Fig. S12d
5	Recent-reduced	. . .	. . .	Constant increase with age and density	Appendix S1: Fig. S12a
6	Long-term mean	. . .	. . .	. . .	Appendix S1: Fig. S12b
7	Recent-reduced	Pre-drought	. . .	Proportional increase	Appendix S1: Figs. S8b, S13
8	Long-term mean	. . .	. . .	. . .	Appendix S1: Fig. S8c
9	Recent-reduced	Drought	Precipitation only	Proportional increase	Appendix S1: Figs. S9a, c
10	Long-term mean	. . .	. . .	. . .	Appendix S1: Figs. S9b, d

Notes: The population model was parameterized based on demographic analyses that identified drivers of survival and reproduction. This model was then run to simulate replicate population trajectories for each of a range of scenarios. The simulated trajectories were used to identify population sizes and mortality rates associated with future risk of extinction and to develop risk isoclines. Our analyses indicated survival of older foxes was driven in part by density dependence, which was strongest in drought conditions, and reproductive rates were driven by previous year's precipitation and density dependence. Precipitation in the past two decades has been below average (1998–2017, recent-reduced rate: $\bar{x}$ = 16.7 cm, σ = 7.6, vs. 1948–2017, long-term mean rate: $\bar{x}$ = 20.1 cm, σ = 10.6) and drought conditions occurred on the island at the end of the observed time series, with drought-associated habitat change starting in 2012. It is unclear whether these precipitation and habitat conditions best characterize future conditions or are atypical. Thus, we simulated futures under different scenarios for precipitation and drought-associated island conditions. Finally, to allow prediction of risk for a wide range of mortalities and population sizes, we evaluated scenarios using baseline mortality and a range of added mortality. Because added fox mortality could occur due to golden eagle predation or a variety of other known or unknown threats, we explored different scenarios for the functional form of added mortality (see *Simulation Models and Risk Isoclines: Methods*). For all scenarios, we present simulated population trajectories, comparisons to observed data, and/or resulting risk isoclines in figures as indicated in Notes column. ". . ." indicates same as above.

dependence in reproduction also continued. To thoroughly investigate the role of future climate on extinction risk, we also considered scenarios in which future precipitation followed the long-term mean. For long-term mean climate scenarios, we ran simulations in which density dependence was weaker, as observed in years prior to the drought, as well stronger, as estimated for the years subsequent to the drought. Finally, given the large influence of the Repro datapoint from 2017 in supporting a Repro model that included D_{tot_t-1} and Rain_{t-1}, we ran a subset of models in which Repro was driven by Rain_{t-1} alone.

To allow prediction of risk isoclines across a range of threat conditions, we ran each future scenario incorporating proportional increases in mortality of 0.1–1 times baseline predicted mortality rates, such that relative age-specific patterns of density-dependent mortality remained the same. In the northern Channel Islands, Bakker et al. (2009) simulated mortality based on the observed pattern of golden eagle predation, which averaged ~2% island fox mortality per eagle but exhibited curvilinear density dependence, being highest at low and high fox densities. To compare the effect of different possible patterns in density-dependent

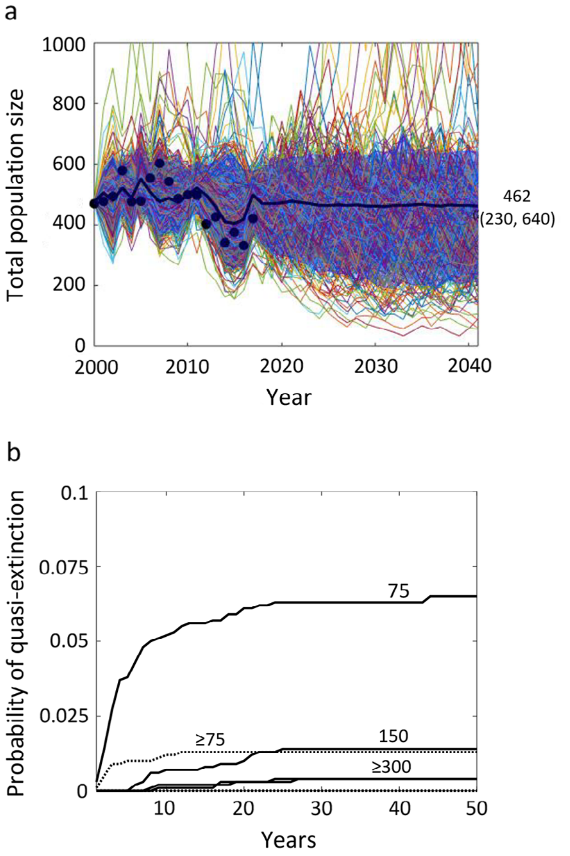

Fig. 6. Basic output from stochastic demographic matrix model simulations: (a) Comparison of observed and predicted numbers of foxes when the simulation model is initiated at the observed year 2000 size and age structure and with observed precipitation imposed through 2017. After 2017, reproduction is driven by simulated fox density and random rainfall, assuming the recent-reduced precipitation persists ($\bar{x}$ = 16.7 cm, σ = 7.6), and survival is driven by simulated density assuming post-drought conditions persist. Plots show results of 1000 replicate trajectories (colored lines), their median and 95% confidence region (solid line and blue shaded region), and observed data (dots). (b) Quasi-extinction risks for a range of starting population sizes (75, 150, 300, 600) assuming recent-reduced (solid line) and long-term mean (dotted line) precipitation, based on 1000 replicate runs for each scenario.

mortality, we also simulated this pattern of mortality (range 1 to 10 eagles), representing the introduction of a novel threat with density-dependent mortality. Finally, we ran a third scenario in which mortality associated with 1–10 golden eagles occurred but was imposed as 2% island fox mortality per eagle exerted equally across all fox densities and ages.

To investigate basic population dynamics, we simulated 1000 replicate trajectories over 50 yr for a range of starting population sizes (75, 150, 300, 600) assuming current mortality and drought-associated habitat conditions persist, coupled with recent-reduced and long-term-mean precipitation. For all isocline scenarios, we simulated a range of starting population sizes (50, 100, 150, 200, 250, 300, 350, 400, 450, 500), running 500 replicate trajectories for each starting population size and mortality level over a 100-yr time horizon, consistent with the approach used to develop recovery isoclines for other island fox subspecies (US Fish and Wildlife Service 2012). For each of the first 50 yr, we recorded population size and mortality rate for nonpups and total foxes and whether the population reached quasi-extinction within 50 yr. Using these simulated data, we built risk isoclines that used observed population size and mortality to predict future 50-yr quasi-extinction risk. We predicted risk using generalized linear models with a binomial response, employing AICc to compare models with annual data vs. two- and three-year-averaged data, and total fox abundance vs. nonpup abundance. As with the development of recovery criteria for other island fox populations (Bakker and Doak 2009), we considered only nonpup mortality because of the logistical challenges of radiocollaring growing pups in their first year, as well as the challenge of estimating ages of foxes not captured as pups in their first fall. We used a piece-wise fitting approach to capture nonlinearities in the relationship between risk and predictor variables, fitting the relationship between mortality, population size, and extinction risk for population size intervals of 100 (Bakker and Doak 2009). We did not plot isocline segments if predictor variables were not significant across a given population interval.

Simulation Models and Risk Isoclines: Results

Model simulations initiated at the observed population size and age structure in 2000 and imposing the observed annual precipitation and density-weighted mean Dist2nic through 2017

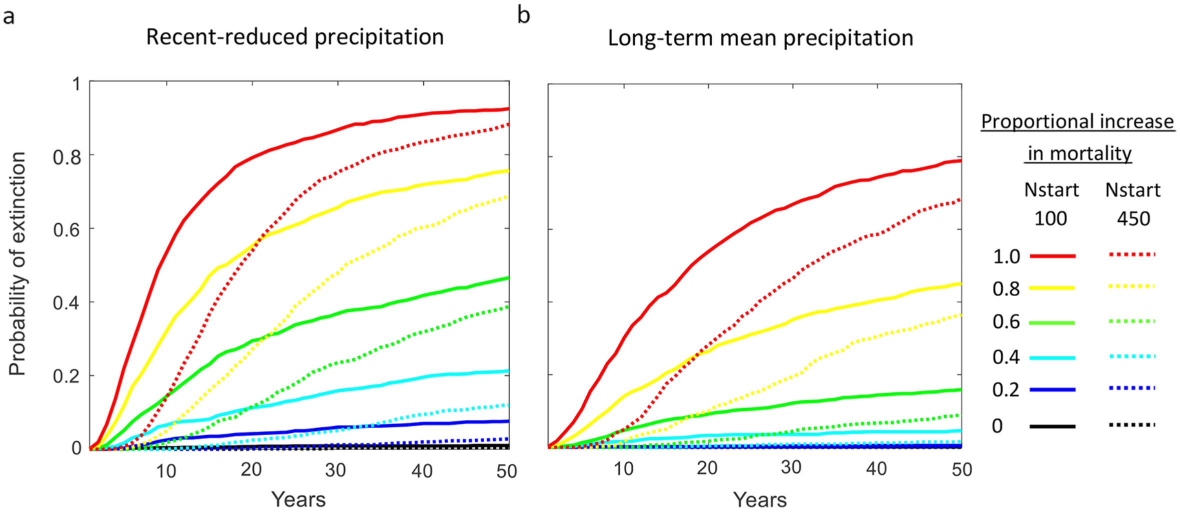

Fig. 7. Predicted risk of quasi-extinction for SNI foxes with increases in mortality. Cumulative risk of quasi-extinction with proportional increases in existing mortality of 0–1.0 assuming (a) recent-reduced (Table 1, scenario 1), or (b) long-term mean ($\bar{x}$ = 20.1 cm, σ = 10.6) precipitation characterizes future conditions (Table 1, scenario 2) for starting population sizes of 100 and 450, based on 1000 replicate runs.

yield population trajectories that follow the same approximate pattern as the observed population estimates (Fig. 6a), generally increasing from 2000 through 2005, followed by a slow decline that accelerates in 2012, and ending with an increase in 2017. When we simulated populations after 2017 assuming recent-reduced precipitation and persistent drought-associated habitat changes, trajectories increase and stabilize at a median of ~460 foxes. Maintaining drought-associated habitat change but assuming the return of long-term mean precipitation increases carrying capacity, with the median population size stabilizing at ~490 foxes, and variability decreases (Appendix S1: Fig. S8a). Imposing the weaker density dependence that appears to characterize pre-drought conditions also results in a modestly higher median population size but does not reduce variability (Appendix S1: Fig. S8b). The shared reliance of simulated reproduction and survival on density (previous year for reproduction and current year for survival) imposes a stabilizing effect such that high mortality years are non-randomly followed by years of higher reproductive success. Simulations that assumed Repro was driven by precipitation alone (i.e., using Repro models fit to data excluding the year 2017) resulted in unstable trajectories that did not match the observed population (Appendix S1: Fig. S9). Because density dependence is stabilizing for this population, isoclines based on precipitation-only Repro models predict greater extinction risk for any given population size and mortality (Appendix S1: Fig. S9).

San Nicolas Island foxes had a low risk of quasi-extinction when starting population sizes were ≥150 assuming recent-reduced precipitation, or when starting populations were ≥75 assuming long-term mean precipitation (Fig. 6b). A proportional increase in mortality of 0.2 or more increased 50-yr extinction risk to greater than 5% even at large population sizes assuming recent-reduced precipitation (Fig. 7a). Long-term mean precipitation reduced quasi-extinction risk for all population sizes and mortality levels (Fig. 7b).

Overall, population size was a stronger predictor of 50-yr extinction risk than mortality, but the best model included an interaction between non-pup mortality and total population size (Appendix S1: Table S14, Fig. 8). The shape of both the overall predictive relationship (Fig. 8) and the shape of the risk isoclines (Fig. 9) indicate that population size is a better predictor of future risk at small population sizes, and mortality rate is a better predictor at large population sizes, due to

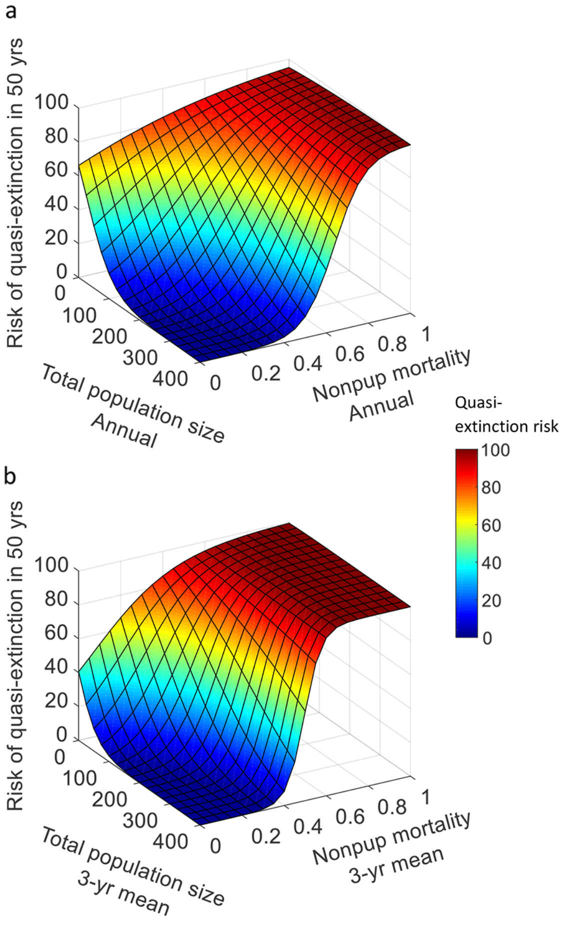

Fig. 8. Predictors of 50-yr quasi-extinction risk. Precision of risk prediction (a) based on annual nonpup mortality and total population size ($M_{\mathrm{np\_1yr}} + N_{\mathrm{tot\_1yr}} + M_{\mathrm{np\_1yr}} \times N_{\mathrm{tot\_1yr}}$) compared to (b) three-year-averaged nonpup mortality and total population size ($M_{\mathrm{np\_3yr}} + N_{\mathrm{tot\_3yr}} + M_{\mathrm{np\_3yr}} \times N_{\mathrm{tot\_3yr}}$). See Appendix S1: Table S14.

higher sensitivity of risk to shifts in these variables in these conditions. Consistent with previous analyses (Bakker and Doak 2009), models in which monitoring data were averaged over 3 yr received more support.

Assessing the SNI fox population status using isoclines derived from scenarios in which recent-reduced precipitation and related drought conditions persist on the island, we can conclude it was safely below the 5% quasi-extinction threshold in early 2000 but approached this level more

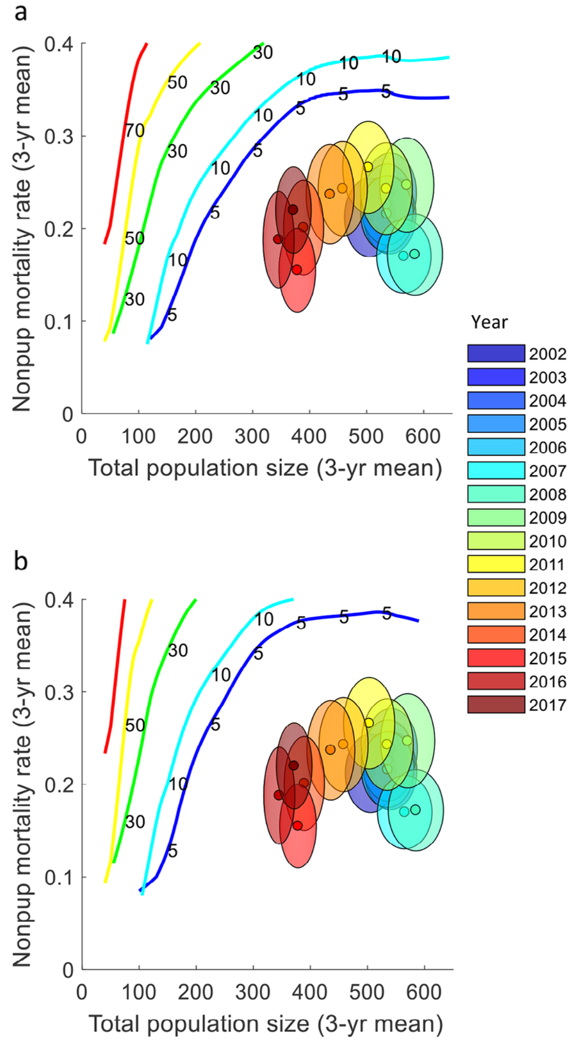

Fig. 9. Risk isoclines: Risk of the fox population on San Nicolas Island declining to quasi-extinction (30 foxes) within 50 yr for a range of nonpup mortalities and total population sizes, each averaged over three years. Plots shown depict risk assuming (a) recent-reduced precipitation and drought-associated island conditions persist in the future, and (b) long-term mean precipitation conditions occur in the future. Plots also show observed monitoring data from 2000 through 2017, with 80% confidence ellipses. For the purposes of plotting monitored nonpup survival on risk isoclines, we used a simplified survival model, which included only marked year structure and pup/nonpup effect for age (S ~ Markyear + Male: Markyear + Nonpup).

recently (Fig. 9a), remaining generally equidistant from the 5% risk threshold from 2012 through the end of the time series (i.e., at or near the 2.5% risk level, Fig S11a). Predictions for 2011, the year the population was closest to the 5% risk isocline, included the very high mortality year of 2009, when adult mortality was 38%. Subsequent years had lower mortality but also lower population sizes. Simulations that assumed long-term mean precipitation in the future resulted in isoclines in which risk was lower for the same population sizes and mortalities (Fig. 9b). The form of added mortality had relatively little effect on risk isoclines (Appendix S1: Fig. S12).

Discussion

Until recently, San Nicolas Island foxes exhibited some of the highest densities of all Channel Island fox subspecies, but abundances changed substantially over the past two decades. After reaching a peak of 603 individuals (mean island-wide density of 10 foxes/km^2) in 2007, numbers slowly declined and by 2016 the population had dropped by nearly half, to 332. These changes in total numbers reflect the sum of significant spatial asynchrony through time, with fox densities on the northwestern side of the island fluctuating even more dramatically than these island-wide abundances indicate, while densities on the southeastern side remained relatively constant (Fig. 2). Our analyses of 18 yr of annual trapping data suggest that both drought and density dependence interacted to drive SNI fox demographic rates and likely contributed to this decline. Simulations based on these drivers predict that reduced precipitation increases the likelihood of SNI fox populations declining to small sizes and increases their predicted risk of extinction. Although the SNI fox appears to be rebounding, its recent decline may foreshadow dynamics that could become more common in the future and serves as a cautionary tale for stewards of all island fox subspecies facing unprecedented climatic conditions. These analyses complement other recent analyses of avian species on the Channel Islands facing climate-related threats (Thomsen and Green 2019, Bakker et al. 2020) and, more broadly, document how climate change may interact with other forces shaping the population dynamics of many island species (Leclerc et al. 2020). Our SNI fox analyses suggest species inhabiting smaller and less diverse island systems may be particularly vulnerable. Recent efforts to restore a more natural and diverse set of vegetation communities on the island may help buffer fox populations against future climate change.

Survival analyses supported the hypothesis that negative density dependence more strongly impacted survival rates starting in 2012, essentially doubling in strength, after drought led to widespread changes in habitat conditions. However, negative density dependence acted only on foxes beyond prime age (in their fifth year and older), and unlike the Bakker et al. (2009) analyses, there was no support for a direct effect of annual precipitation on survival. In contrast, precipitation was a particularly strong driver of pup production, and precipitation interacted with negative density dependence such that the highest pup productivity occurred following years with high annual precipitation and low fox densities. High precipitation likely supports a flush of food resources, from *Peromyscus* to invertebrates to edible fruits (Cypher et al. 2017), and low fox densities reduce competition for these resources, amplifying the bounty. Accordingly, low total fox densities on the island in 2016 coupled with high annual precipitation from 2016 to 2017 favored very high pup production in 2017, resulting in an increase in total population size (Fig. 1b). Despite the increase in total numbers of foxes in 2017, the number of nonpups continued to decline, following several years of very low pup production (2014–2016, Fig. 1b, 3a) and relatively low nonpup survival (Fig. 3a). Thus, based on observed fox numbers alone, the status of this population remains unclear.

The evident role of precipitation and drought-associated island conditions in driving fox dynamics underscores the importance of understanding the current risk status and likely future trajectory of this population. We used these documented drivers of demographic rates, and their uncertainties and unexplained variation, to build stochastic simulation models to explore population futures. Initiating populations at the observed conditions in 2000 and imposing the observed annual precipitation, the median trajectory is generally consistent with the observed trajectory (Fig. 6a). Thus, observed rainfall and density dependence appear sufficient to produce trajectories similar to the observed dynamics. Simulating the return of long-term mean precipitation regimes and pre-drought survival density dependence in the future, the median population trajectory stabilizes at ~500 foxes (Appendix S1: Fig. S8c), compared to ~460 foxes (Fig. 6) assuming recent-reduced precipitation and post-drought density dependence, a decrease of ~8%. More importantly, decreasing precipitation increased stochastic variance in population futures and increased the number and extent of declines in population trajectories, thereby increasing the size of the lower 95% confidence interval by over 20% (Appendix S1: Fig. S8c). Similarly, simulating the continuation of the recent-reduced precipitation regime decreased the resilience of the SNI fox to increased mortality, increasing extinction risk at all population sizes (Fig. 7). The high-rainfall, low-density year of 2017 has outsized effects in the real dataset, and instances of partial overlap of high precipitation and low density in the simulations are a key factor driving population rebounds even when these conditions are less extreme.

We recommend that SNI fox managers rely on risk isoclines built with the assumption that the recent low-precipitation regime and drought-associated habitat conditions persist (Fig. 9a). These more cautionary isoclines indicate that in the absence of even greater changes to the island and climate, quasi-extinction risk for SNI foxes will remain below 5%, the level established as a recovery criterion for the federally listed island foxes (US Fish and Wildlife Service 2012). The quasi-extinction risk associated with currently observed demographic rates is <2% for starting population sizes ≥150 for all precipitation scenarios (Fig. 6b), similar to quasi-extinction risk predictions for Santa Cruz and San Miguel islands in the absence of eagle mortality (Bakker et al. 2009). Although increased nonpup mortality and decreased total population size beginning in the late 2000s elevated the risk of extinction for SNI foxes starting in 2011, their risk does not appear to be trending upward, and indeed, the most recent monitoring data, from 2017, suggest declining risk.

Compared to the convex-shaped risk isoclines produced for the other subspecies (Appendix S1: Fig. S11b) (Bakker et al. 2009, US Fish and Wildlife Service 2012), the more concave-shaped SNI risk isoclines suggest somewhat lower risk at the mid-range population sizes and mortalities exhibited by the SNI population currently. However, the isoclines indicate less of a risk refuge at high population size and at low mortality. These differences result from the different ecological drivers identified for SNI foxes. The greater resilience to mortality for SNI foxes at moderate population sizes arises from the stabilizing effects of density-dependent reproduction. Model runs in which reproduction was driven by precipitation alone produce isocline plots more similar in shape to the isoclines derived from the Bakker et al. (2009) model (Appendix S1: Fig. S9c–d vs. Fig. S11b). However, density-dependent reproduction interacting with precipitation-driven changes in prey abundance is consistent with observations of other small canids (White and Garrott 1997, Dennis and Otten 2000). On the larger islands, such as Santa Cruz and Santa Catalina, habitat diversity may buffer cycles in food availability and the effects of variation in precipitation. While there is evidence of an influence of rainfall on pups per nonpup on Santa Cruz Island, there is currently no evidence for density-dependent reproduction (unpublished data). The Santa Cruz Island fox population has also been recovering from extreme declines and may not yet have reached a point where density-dependent forces curtail reproduction.

Our analyses provide several insights for increasing the resiliency and reducing the extinction risk of SNI foxes. First, the strong support for distance from Nictown as a positive predictor of survival suggests that interactions with human activity, likely vehicle mortalities, is associated with decreased survival, and efforts to minimize human-fox conflict should be continued. There is currently no major identified threat to SNI foxes, and thus, the simulated increases in mortality risk are hypothetical, and we do not know the form any increases in mortality would take. However, mortality comparable to observed golden eagle predation on the northern Channel Islands, which exhibited positive density dependence at low densities, or an Allee effect (Angulo et al. 2007, Bakker et al. 2009), resulted in higher predicted extinction risk (Appendix S1: Fig. S10). Traffic deaths have the potential to exert an apparent Allee effect if habitat value along roadways is high and vacancies after vehicle mortalities are filled, placing additional foxes at risk. With higher densities, a smaller fraction of individuals would be exposed to road mortality, reducing population-wide mortality rates.

A second management approach to increase the resiliency of the population is habitat restoration. We found fox densities were highest in tall shrub habitats, the plant associations that tend to be most complex and diverse on the island, and that habitat productivity appears to drive reproduction. In addition, location (northwesterliness) interacts with year effects to influence fluctuations in densities. Although we have not identified the specific factors along the northwesterly gradient that influence fox dynamics, given that this gradient corresponds with the prevailing winds, we hypothesize it serves as another proxy for habitat quality. The joint effects of these habitat-driven differences in dynamics lead to substantial portfolio effects, stabilizing total population numbers. These effects are weaker than those seen in some other populations, in which portfolio effects can often result in variance values less than 10% of the theoretical maximum (Abbott et al. 2017, Dibner et al. 2019, Waddle et al. 2019, but see Satterthwaite and Carlson 2015) but are still surprisingly strong given that SNI lacks sharply different habitats and is regarded as highly invaded and degraded. Currently, personnel on the island are engaged in several efforts to restore plant communities that are more diverse, native-rich, and of greater height than the invasive communities that dominate much of SNI. Our results suggest that these efforts are likely to benefit fox populations, although the limited extent of these habitats within the existing fox monitoring sites make it impossible to fully quantify benefits for viability with existing data.

The unusually low survival of SNI foxes in 2009–2010 could not be directly attributed to cat eradication activities, nor to other identified drivers of annual survival. The eradication effort appears to have reduced recapture rates for foxes experiencing capture in leghold traps; the conditioned aversion of SNI foxes to leghold traps has been documented (Jolley et al. 2012), but permanent generalized trap avoidance following capture has not been shown before. The type of unexplained stochastic variance in survival observed in 2009 could be due to an episodic threat, such as an undetected disease, although there is no direct evidence for such an effect from field work done at that time. We do not have complete cause-specific mortality data for that timeframe and thus cannot rule out unidentified indirect effects of cat eradication activities on fox survival.

Island fox populations have exhibited pronounced population fluctuations in the past on SNI (Cypher et al. 2017 and references therein) and all islands (Bakker et al. 2009 and references therein), similar to those produced by the density-dependent and precipitation drivers simulated here, and climate change is likely to induce greater temporal variation. Thus, one key to ongoing fox management is differentiating normal population fluctuations from those indicating serious extinction risk. Developing and refining tools such as the risk isoclines presented here provide a quantitative basis for such assessments. Although we incorporated unexplained variance in survival in our simulation models to account for the type of events observed in 2009–2010, we did not simulate, and thus our isoclines do not account for, disease outbreaks that might result in more rapid and pronounced declines, such as canine distemper virus or rabies (Doak et al. 2013). As with the formerly ESA-listed species, ongoing surveillance for diseases is recommended, especially since some disease threats can increase at high densities and cause rapid declines (Doak et al. 2013).

The SNI fox may serve as a bellwether for island foxes as they face changing climatic conditions. Shifting temperature and precipitation regimes resulting in lower rainfall and increased probability of drought and habitat alteration, similar to that observed since 2012, could pose increasing risk for the SNI fox. The resilience of this population to added mortality decreases substantially when precipitation is lower (Fig. 7). An increase in food resources following years of high precipitation coupled with reduced competition when population densities are low appear to fuel bonanza years that allow declining populations to rebound. However, the changes in island conditions associated with the recent drought decreased simulated carrying capacity and increased the strength of density dependence on SNI foxes, and more frequent and severe droughts could further transform the island environment (Williams et al. 2015). Indeed, the simplicity of habitats on SNI likely increases the vulnerability of species inhabiting it to climate-driven ecosystem change. To counter these trends, the US Navy has been working to restore native habitat with more varied and temporally variable food resources for the fox. Diversifying and enriching fox habitat on San Nicolas Island should help ameliorate the population stressors associated with decreasing precipitation for island foxes and other island species.

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Data Availability

Data are available from Dryad: https://datadryad.org/stash/share/JTLQU4jIjAh1wRx6FIDmVo61Q2FbG864PyXY3yEzD00, https://datadryad.org/stash/share/5a-qySV9abrTUF3_deeuf1RJ6zVk990msxuAnnxhRRA, https://datadryad.org/stash/share/LOysS4gC7Q0iGppYid0BBY7QDYnh33Qyf-4Uh1UG_ac, https://datadryad.org/stash/share/E8kqgPXdWegR5CGAtpyyJ2-h1R4tvAsnxb3DkrEncAU with the exception of daily capture location data for this state-threatened species and Department of Defense species-at-risk/species of special concern. These data may be obtained from Victoria J. Bakker.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3724/full