Research Article

Shifting Threats Faced by the San Clemente Sage Sparrow

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ABSTRACT Threats to a species' persistence are likely to change as conservation measures reduce some threats, while natural and anthropogenic changes increase others. Despite a variety of potential underlying mechanisms, extinction threats will be manifested through one of the 3 components of population dynamics: reducing population growth potential, increasing population variability, or lowering the population ceiling. Consequently, effective management can be guided by monitoring programs and population models that examine each of these components. We examined the potential for a coupled monitoring and modeling effort to guide management of species-at-risk while accounting for evolving risks using the case study of the threatened San Clemente sage sparrow (*Amphispiza belli clementeae*). Originally listed due to a low population ceiling imposed by severe habitat loss, we found that the major threat to San Clemente sage sparrow persistence has shifted to low population growth potential driven by high juvenile mortality. We further found that successful mitigation of high juvenile mortality will shift the primary threat to drought frequency, which is predicted to increase on San Clemente Island as a consequence of global climate change. The latter shift is a consequence of the boom-bust ecology exhibited by San Clemente sage sparrows in response to rainfall—likely a common characteristic of short-lived terrestrial vertebrates in arid environments. Our ability to successfully recover this species hinges on a comprehensive monitoring and modeling program incorporating all 3 components of population dynamics informing changes in management priorities to reflect shifting threats. Our study indicates that the next critical step to recovering sage sparrows is to understand and mitigate the causes of high juvenile mortality. In response to these predictions, the United States Navy has funded a radio-telemetry study to determine the cause(s) of juvenile mortalities. © 2011 The Wildlife Society.

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Extinction threats are varied and complex. For example, though island birds are particularly at risk (Johnson and Stattersfield 1990), threats faced by individual species are diverse and include introduced competitors, predators, disease, habitat destruction, and global climate change. These threats influence population size and variability and interact with species and island characteristics in ways that make determining the relative vulnerability of a species difficult

(Karr 1982, Pimm et al. 1988, Tracy and George 1992, Vucetich et al. 2000). Identifying the key factors influencing population dynamics is critical to developing a framework for evaluating threats to extinction (Lande 1998). Population dynamics can be described by 3 salient components: the potential (or maximum) growth rate of the population, variability in realized population growth rates, and the population ceiling (i.e., the largest population size that can be sustained given existing environmental conditions). Lower population growth rates, greater variability in population growth rates, lower population ceilings, and interactions between those components are all associated with greater extinction risk (Karr 1982, Morris and Doak 1992, Fagan et al. 1999).

Although effective management of at-risk species depends on understanding the full range of threats, most studies focus only on one component of population dynamics. Focusing on one component can be useful in guiding conservation efforts (Crowder et al. 1994, Heppell et al. 1994, McLaughlin et al.

2002) only if the appropriate risk has been identified. For example, although much of the early population viability analyses (PVA) focused on small populations limited by a low population ceiling, many species-at-risk may be more threatened by negative population growth (Caughley 1994). Recent efforts have shifted the focus towards issues of declining populations (Beissinger and Westphal 1998, Beissinger 2002), but few studies have examined the role of population variability in determining extinction risk (Sæther et al. 1998, Fagan et al. 1999, McLaughlin et al. 2002, Reed et al. 2003, Wichmann et al. 2003). Narrowly focused PVAs also limit our ability to predict how threats may shift under changing conditions. Evaluating impending threats is especially critical for successful conservation efforts given recent studies suggesting that global climate change may have negative impacts on many populations (Walther et al. 2002, Crick 2004, Sekercioglu et al. 2008).

The case of the San Clemente sage sparrow (*Amphispiza belli clementeae*) highlights both how extinction threats change through time and the importance of considering each aspect of population dynamics as part of a comprehensive conservation program. When San Clemente sage sparrows were listed as threatened under the Endangered Species Act, habitat loss caused by introduced livestock (Doran 1980) and predation risk from introduced cats (United States Fish and Wildlife Service [USFWS] 1977) were identified as the primary threats to the population. Introduced herbivores were removed from San Clemente Island (SCI) by 1993, and the United States Navy, which owns and manages the island, initiated habitat restoration efforts, potentially removing the threat posed by limited available habitat (i.e., low population ceiling). However, increased drought frequency associated with global climate change (Hayhoe et al. 2004) may emerge as a new threat to the San Clemente sage sparrow by increasing variability in population growth rates.

San Clemente sage sparrows (hereafter, sage sparrows) are resident endemics to San Clemente Island, California (Grinnell 1897). Adults breed from January through mid-July depending on winter rains (Kaiser et al. 2009). During good years, pairs may attempt up to 5 clutches of 1–5 eggs; in poor years few pairs reproduce (see below). There is no sexual dimorphism in plumage, but singing and territory defense is performed by males. Birds disperse across the island in the fall and winter, although some individuals remain near their breeding territories year-round (Kaiser et al. 2009; T. Docherty, Institute for Wildlife Studies, personal communication). Surviving adults reestablish exclusive breeding territories 1–2 weeks before nesting (F. Beaudry and S. Kaiser, Institute for Wildlife Studies, personal observations). Juveniles disperse up to 16 km from their natal territories (Munkwitz 2004).

We used a detailed population model based on intensive monitoring of sage sparrow ecology to 1) evaluate the influence of moderate changes in habitat availability on sage sparrow extinction risk, 2) determine what factor(s) have the greatest influence on extinction risk and should be targeted by management, and 3) determine how the influences

on extinction risk would change if the primary threat can be mitigated successfully. As part of intensive ongoing monitoring, we examined how extinction risk was affected by each of the 3 components of population dynamics: population ceiling determined by the amount of available habitat, potential population growth determined by demographic rates, and population variability determined by drought frequency. We used demographic and climatic data to examine how variation in rainfall and sage sparrow density influenced survival and fecundity and to inform a stochastic population model reflecting the impacts of demographic rates, drought frequency, and habitat availability on potential population growth, variation in population growth, and the population ceiling. We evaluated the model to assess the most pressing threats to sage sparrow persistence.

STUDY AREA

Our study took place on San Clemente Island, located approximately 103 km from the coast of southern California, United States (118°30′ W, 33°00′ N). The island is 33.6 km long and covers 14,764 ha. The island experienced a Mediterranean climate with mild winters and cool summers. Most precipitation fell between November and April, with minimal rain during June, July, and August.

Sage sparrows bred in maritime desert scrub, which covered approximately 2,100 ha along marine terraces on the west shore of the island. Sage sparrows built open cup nests in a variety of plants, but boxthorn (*Lycium californicum*) was the predominant nesting substrate and was the dominant plant species in most breeding areas (Kaiser et al. 2009). Sage sparrow density varied across the maritime desert scrub vegetation community, with highest densities occurring in the lower elevation terraces and decreasing density with greater elevation, generally, but not always, following patterns of boxthorn density (Turner 2009).

METHODS

Monitoring

Population size.—We estimated sage sparrow abundance using both distance sampling line transect surveys (2000–2008) and spot mapping territories on plots (2000–2007). We established approximately 45 km of transects in 2000. We divided the study area into high-, medium-, and low-density habitat types based on historically consistent differences in relative sage sparrow densities (Beaudry 2004) and placed transect segments of 2–6 km in a stratified random design constrained so that each segment was entirely within a habitat type and that transects did not interfere with military operations. We modified transects in 2002 to more equally represent different habitat types on the island (with 15 km in each habitat type) and again in 2006 due to restricted access.

A trained observer surveyed each transect monthly from March to May by continuously walking along the route between sunrise and 1100 hr. With the aid of binoculars and a range-finder, observers mapped the location of sage sparrows observed within 100 m of the transect, and, when possible, recorded the age class (hatch-year [HY] or after-

hatch-year [AHY]), sex (based on behavior or known identity), and color band combination of birds. We estimated detection probabilities and the density of adult males in each habitat (and associated 95% CIs) using distance sampling techniques implemented in Program DISTANCE (DISTANCE Version 5.0, www.ruwpa.st-and.ac.uk/distance/, accessed 04 Nov 2009). We calculated annual density estimates of adult male sage sparrows in each habitat as the average of the 3 monthly density estimates from monthly surveys of transects within that habitat. Because we rarely observed unpaired adult birds, we assumed a 1:1 sex ratio and estimated island-wide population size as twice the sum of the products of the estimated density of males in each habitat and the area covered by that habitat.

We also monitored 6 study plots established in 2000. Plots were located using a stratified (by habitat type) random design constrained to areas where the entire plot would be within one habitat type, would be within 30-min hiking distance from a road, and would not interfere with military activity. In 2002, we added one plot, removed one, and refined the boundaries of established plots because of improved knowledge of sage sparrow distribution and density patterns.

The sizes of plots after 2002 ranged from 20 ha to 60 ha; 2 plots were in each of the high, medium, and low density habitats. Plots located on the same habitat were 2–4 km apart, and plots in different habitats were >50 m apart. Trained observers visited each plot every 1–5 days to map territories by recording individual and pair locations and interactions with neighboring individuals. Because sage sparrow breeding habitat has little vertical structure and neighboring males engage in frequent antagonistic interactions, it was easy to map territory boundaries and observe the activities of breeding pairs. We calculated plot-specific densities by dividing the number of adult birds with territories ≥50% within each plot by the area of the plot.

Breeding biology.—We monitored breeding each year by following nesting pairs in the study plots described above. We located nests by observing behavioral cues such as adults carrying nesting material, transporting food, or removing fecal sacs and by following incubating females returning to their nests. We monitored active nests every 2–5 days until the brood fledged or failed. For each nest, we recorded clutch size and the number of nestlings fledged.

We examined 2 aspects of sage sparrow breeding biology based on nest monitoring in intensively surveyed plots: breeding success and the productivity of successful breeders. We measured breeding success as the proportion of pairs observed on study plots producing ≥1 fledgling in a breeding season. We conducted analyses on study plots, treating each study plot and year as independent samples. We measured productivity of successful breeders as the number of fledglings produced per successfully breeding pair.

Because years of low rainfall coincided with large sage sparrow population sizes during the period we monitored the population, we examined relationships between density and breeding parameters separately for years with high and low rainfall. We defined annual rainfall as the total accumu-

lation from 1 August of the year preceding a breeding season to 31 July of the following year, which measures rainfall that may influence plant productivity and ecological conditions during the breeding season. We separated drought years (years with <45 mm annual rainfall) from normal years (years with >110 mm annual rainfall). There were no years during our study when rainfall totaled between 45 mm and 110 mm.

We examined whether rainfall affected breeding success with an analysis of covariance (ANCOVA), using a drought term and a drought by density interaction term. We then examined the effect of density on breeding success in normal years ($n = 10$ [5 years × 2 plots] in each habitat) by regressing annual breeding success in each plot against plot density. We conducted separate analyses for each habitat type. We performed all analyses using the GLM procedure in SAS (SAS Institute, Cary, NC).

We took advantage of spatial variation in adult density within habitat classes to test for density effects on productivity (i.e., the number of fledglings per successfully breeding pair) after accounting for year-to-year (i.e., climate-driven) differences. For each plot in each year, we calculated residual productivity as the difference between observed number of young fledged by successful breeders in the plot and mean fledgling production by all successful breeders within the same habitat type. We then regressed these residuals against plot-specific densities using the REG procedure in SAS. This analysis assumes that birds distribute themselves randomly with respect to resource availability. We conducted separate regressions for each habitat because we defined habitat classes based on consistent historic differences in sage sparrow densities; it is therefore unlikely that the random distribution assumption is met across habitat types. In contrast, within each habitat the ranking of plots with respect to sage sparrow densities varied from year to year. Although we cannot rule out the possibility that important resources varied within plots in ways detectable to sage sparrows when they settled on breeding territories, we argue it is unlikely for 2 reasons. First, distribution of boxthorn, which provides the primary nesting substrate and is associated with gross differences in sage sparrow densities among habitat classes, does not vary much from year to year, as it is a slow-growing perennial shrub. Second, insect abundances, which likely vary from year to year in response to rain-driven differences in plant productivity, may change substantially during the breeding season.

To determine rainfall effects on productivity, we first graphically confirmed a linear relationship between fledgling production and adult density and then used the resulting regression equations to generate expected numbers of young produced by pairs in each plot based solely on its density. We calculated the plot residuals as the difference between observed and expected productivity and regressed productivity residuals against annual rainfall. We conducted all fecundity-related analyses separately for each habitat type.

Survival.—Between June 1999 and July 2007, we color banded 262 adults and 1,663 nestlings, fledglings, and juveniles with unique combinations of 4 bands (2 per leg): 3 color

bands and one USFWS metal band. From February through July of each year, we captured adults and juveniles with mist nets and banded nestlings in their nests within plots, along transect routes, and opportunistically throughout the habitat when we encountered unbanded individuals. We banded nestlings approximately 7–10 days post-hatching.

We estimated adult and juvenile survival from annual resight histories of color-banded birds using the Cormack–Jolly–Seber model implemented within Program MARK (White and Burnham 1999). We compared a set of a priori models that included all combinations of constant and age effects (HY vs. AHY) on survival and detection probability and constant or fully time-dependent models. We also included models in which detection probability varied by whether birds were banded as HY or AHY, as the latter were more likely to maintain territories in or adjacent to frequently visited study plots. We examined the effects of rainfall and density on survival by including annual precipitation and island-wide adult population density as covariates. Rainfall data were collected from a weather station located on SCI (H. Cox, California State University, Northridge, unpublished data). We selected the best model based on Akaike's Information Criteria (AIC).

We collected resight data from both transect and plot surveys and from opportunistic surveys in remaining sage sparrow habitat. Plot and transect surveys covered 55% of sage sparrow habitat, with some overlap (overlap area comprised approx. 30% of plot area and approx. 6% of transect area). Although resight probabilities were much greater for adult birds breeding in intensively studied plots the previous years, using separate resight probabilities for plot adults versus other adults did not change estimated survival probabilities (B. Hudgens, Institute for Wildlife Studies, unpublished data). For simplicity, we did not separate adult birds marked on plots from non-plot birds in the analyses except as noted above.

Dispersal.—Because demographic rates may vary across different habitat types, we examined dispersal among habitat types. We conducted intensive resight surveys in 2001 and 2002 to locate breeding territories of birds banded as nestlings. During these surveys, a trained observer walked a zigzag line through a limited area recording the identity and location of banded birds. Intensive resight surveys covered 60% of sage sparrow breeding habitat in 2001 and all known sage sparrow breeding habitat in 2002. We calculated dispersal rates among habitats as the proportion of banded sage sparrows fledged in habitat i observed nesting in habitat j.

Modeling

We conducted a population viability analysis (PVA) on sage sparrows to assess the contribution of different threats to extinction risk and to determine the influence of demographic parameters on persistence. We simulated sage sparrow population dynamics using the VORTEX individual-based modeling package (VORTEX v.9.7.2, http://www.vortex9.org/vortex.html, accessed 30 Apr 2007). We chose VORTEX to facilitate comparison to a preliminary PVA conducted in

2004 (Beaudry 2004). The package VORTEX is an accessible, widely used, flexible Monte Carlo simulation program that models deterministic and stochastic processes and allows a wide range of functional forms for demographic rates and their associated variances (Lacy 1993, 2000). The program has been tested against field data and found to produce reasonably accurate predictions for a variety of species (Lindenmayer et al. 2003).

The simulation tracks breeding success, productivity, survival, and juvenile dispersal across the 3 habitat types. We modeled expected breeding success and productivity of successful breeders as functions of local (i.e., habitat specific) density. Fecundity was further modified by weather corresponding to habitat specific reductions during minor and major droughts. We modeled survival as dependent on age but not dependent on density, rainfall, or breeding habitat. Juvenile dispersal in the simulation depended on natal habitat but not on local density or rainfall. We began with a baseline model using parameter estimates from our monitoring efforts (Table 1, see Supporting Appendix, available online at www.onlinelibrary.wiley.com).

To evaluate the predictive efficacy of the model, we compared observed population growth to that predicted from the equations underlying the simulation. We parameterized model equations using observed mortality, rainfall, and plot density and compared the predicted change in population size the following year to growth rates ($\lambda = N_t/N_{t-1}$; where λ = proportional change in the population from year t to year $t + 1$, N = population size and t = time) estimated from transect surveys. These surveys were independent of the plot data we used for most of the model's parameters. The exception is that birds observed on transects were included in estimated annual mortality rates input to the model. However, because year-to-year fluctuations in population size are primarily driven by annual variation in fecundity, which is wholly determined from study plots, and not well correlated with annual variation in mortality rates, we believe the comparison was a good test of the model's predictive ability. We limited the comparison to the period between 2002 and 2008, after we designated final plot and transect locations. We tested for systematic differences in predicted and observed growth rates using a paired t-test. Because the geometric mean growth rate is more informative than the arithmetic mean in the context of population viability (Morris and Doak 1992), we performed the test on log-transformed data. We considered the model to be reasonably accurate if 1) predicted and observed growth rates were tightly and positively correlated, with predicted variation in λ accounting for >50% of observed variation in λ (i.e., $r^2 > 0.50$; corresponding to $r > 0.71$); 2) the Pearson correlation coefficient, r, was significantly positive; and 3) there was no systematic difference between predicted and observed λ (i.e., the mean predicted and observed growth rates were similar). We judged the third criteria to be violated if a paired t-test indicated a significant difference between predicted and observed annual growth rates.

We conducted an elasticity analysis to evaluate the sensitivity of sage sparrow population persistence to various

Table 1. Parameter values input to baseline model used to conduct a 50-year population viability analysis of San Clemente sage sparrows on San Clemente Island, California.

Parameter label	Value in high density habitat	Value in medium density habitat	Value in low density habitat	Comments
$b1$ (%)	108	100	116	Habitat specific percentage of adults that successfully breed at low densities in normal years[a]
$b2$ (%)	23.8	5.2	60	Rate at which percent adults successfully breeding decreases with increasing density
A (ha)	373	667	1,053	Area covered by each habitat type[b]
K (birds)	361	543	593	Variable population ceiling (varies among simulations mimicking habitat addition or destruction)[b]
Kb (birds)	361	543	593	Baseline population ceiling (constant for all simulations)[b]
s (b)	10.5	4.7	14	Habitat specific standard deviation in proportion of breeders during normal years
$f1$ (fledglings)	5.78	6.95	7.06	Habitat specific number of young produced per breeding pair at low densities
$f2$ (fledglings)	1.54	3.41	8.26	Habitat specific rate at which young produced per breeding pair decreases with increasing density
s (F)	0.43	0.43	0.43	Standard deviation in number young produced per breeding pair
$m(j)$ (%)	72	72	72	Juvenile mortality
$s(mj)$	22.2	22.2	22.2	Standard deviation in juvenile mortality
$m(a)$ (%)	56	56	56	Adult mortality
$s(ma)$	15	15	15	Standard deviation in adult mortality
p_{d1}	25	25	25	Annual probability of minor drought
$d1$	0.43	0.22	0.66	Habitat specific proportional amount by which the mean number of young per breeding pair is reduced during minor drought years
p_{d2}	15	15	15	Annual probability of major drought
$d2$	0.05	0	0	Habitat specific proportional amount by which the mean number of young per breeding pair is reduced during major drought years
N_0 (birds)	168	238	140	Initial population size in each habitat
D_h[c]	40	35.56	24.44	Percentage of young born in high density habitats dispersing to each habitat type
D_m[c]	31.25	62.5	6.25	Percentage of young born in medium density habitats dispersing to each habitat type
D_l[c]	41.67	33.33	25	Percentage of young born in low density habitats dispersing to each habitat type

[a] Values of $b1 > 100$ result in 100% breeding until $b1 - b2 \times$ (density) < 100; see footnote b.

[b] We calculated density as $N/(A \times K/Kb)$, where the true area of each habitat is $A \times (K/Kb)$. A is the baseline area for each habitat and Kb is the baseline population ceiling so that the term K/Kb scales the area of each habitat in simulations mimicking habitat addition or destruction.

[c] Multinomial 95% confidence limits for estimated dispersal rates to high, medium, and low density habitats are ±14%, ±13.6%, ±12.3%, respectively, for birds born in high density habitat, ±22.2%, ±23.1%, ±11.6%, respectively, for birds born in medium density habitat, and ±19.2%, ±18.4%, ±16.9%, respectively, for birds born in low density habitat.

aspects of the species' ecology corresponding to the 3 components of population dynamics. We examined the effects of the potential population growth rate on model output by varying each demographic parameter and assessing its effect on extinction risk. We assessed variability in population growth by examining both changes in the variation of demographic parameters and changes in drought frequency on extinction risk. Finally, we evaluated the effect of changes in the population ceiling on extinction risk. For each test, we modified the values of habitat specific parameters (Table 2) by the same proportion in all habitats. Because the baseline model predicted extremely high extinction risk (see below), we modified parameters to decrease extinction risk and calculated elasticities as the proportional decrease in extinction risk divided by the proportional change in parameter values. The exception to this was breeding success at low density, which was already maximized at 100% and could not be increased further. We therefore modified maximum breeding success downward, which would be expected to increase extinction risk. For each parameter tested, we assessed a range of changes (10%, 20%, and 50%). If a 50% change

in a parameter resulted in a <0.5% decrease in extinction risk we did not assess the effect of 10% or 20% changes in that parameter. We also assessed the effect of doubling the initial population size to ensure that our results were robust to initial conditions.

We further examined 2 sets of model parameters to address specific management questions. First, we reduced habitat-specific carrying capacities to understand the potential consequences of habitat loss. Second, we examined the potential impact of future global climate change by increasing the annual probability of major and minor droughts to 25% and 33%, respectively. These frequencies are similar to what would be expected if rainfall in southern California were to decrease by amounts predicted by the most pessimistic 20% of climate models (Maurer et al. 2007). Because global climate change is likely to affect both major and minor drought frequencies simultaneously, we changed both rates together. Because high juvenile mortality rates might mask the effects of habitat loss or increased drought frequency, we repeated these analyses assuming that juvenile mortality was reduced by 10%.

Table 2. Elasticity analysis results of simulation model used to conduct a 50-year population viability analysis of San Clemente sage sparrows on San Clemente Island, California. Scenario column describes which parameter(s) were modified, followed by the proportion of the baseline value by which the parameters were changed, the predicted extinction risk (i.e., the fraction of simulations ending in qausi-extinction [$p[E]$]), the mean time to extinction (TTE), the difference in predicted extinction risk ($\Delta p[E]$) and the elasticity of predicted extinction risk to the modification.

Scenario (modified parameter[s])[a]	Proportional change[b]	$p[E]$	TTE[c]	$\Delta p[E]$[d]	Elasticity of $p[E]$[e]
Baseline		0.99	15		
Reduced frequency of major drought ($p(d2)$)	0.2	0.97	15.5	−0.01	0.061
	0.5	0.96	17	−0.03	0.063
Reduced frequency of minor drought ($p(d1)$)	0.2	0.98	15.5	−0.01	0.041
	0.5	0.96	15.9	−0.02	0.047
Reduced juvenile mortality ($m(j)$)	0.1	0.81	21.8	−0.18	1.818
	0.2	0.49	24.7	−0.49	2.505
	0.5	0.11	25.2	−0.88	1.785
Reduced adult mortality ($m(a)$)	0.1	0.93	19.1	−0.05	0.527
	0.2	0.78	23.5	−0.21	1.07
	0.5	0.1	29.9	−0.88	1.789
Reduced variation in mortality rates ($S(m(j))$, $s(m(a))$)	0.2	0.93	19.6	−0.05	0.269
	0.5	0.59	28.9	−0.39	0.795
Reduced maximum breeding success ($b1$)	0.5	0.98	15.1	[f]	0.004
Reduced variation in breeding success ($s(b)$)	0.5	0.98	14.9	[f]	0.006
Increased mean productivity ($f1$)	0.5	0.87	19.2	−0.11	0.231
Reduced impact of increased adult density on productivity ($f2$)	0.5	0.98	15.3	−0.01	0.016
Reduced variation in productivity $s(F)$	0.5	0.99	15.1	[f]	0.002
Double initial population size ($N(0)$)	1	0.98	16.1	[f]	0.003
Double available habitat (K)	1	0.98	15.7	−0.01	0.009

[a] We report only scenarios resulting in a change in the probability of quasi-extinction ($p[E]$) of ≥0.01 or reflecting the largest magnitude change in the affected parameters.
[b] Proportion of baseline values by which parameters were changed increased or reduced, as indicated by the scenario title.
[c] Mean time to quasi-extinction for runs dropping below 10 birds.
[d] Difference in the quasi-extinction risk between the scenario and baseline scenario.
[e] Calculated as ($\Delta p[E]/0.99$)/(proportional change in parameters).
[f] $0 > \Delta p[E] > −0.01$.

RESULTS

Monitoring

The sage sparrow population estimated from transects declined by an average of 40% a year (mean $\lambda = 0.60 \pm 0.212$ SD) during 3 drought years (2002, 2004, 2007). In contrast, populations grew rapidly during the 5 wetter years (mean $\lambda = 1.46 \pm 0.736$ SD).

Survival rates fluctuated during our study (Fig. 2), but we found no relationship between apparent survivorship and rainfall (Table 3), density, or subsequent population growth (Figs. 1 and 2). Notably, juvenile survival peaked in 2001–2002, steadily declined to 3% by 2005, and remained low through 2007.

Fecundity was influenced by both rainfall and adult density. Breeding success was generally high during normal rainfall years but was severely reduced during drought years (Table 4 and Fig. 3). Breeding success in study plots ranged between 0% and 80% in minor drought years (rainfall from 40 to 45 mm) and was below 5% in major drought years (rainfall <40 mm). Breeding success was negatively correlated with density during non-drought years (Table 4). Successful breeders produced up to 15 young in one breeding season, with the number of fledglings produced by successful

Table 3. Cormack–Jolly–Seber adult and juvenile survival model selection examining the effect of age and banding age (hatch year vs. after hatch year), time, density, and rainfall on survival probability and detection probability of San Clemente sage sparrows on San Clemente Island, California, 2000–2007. For each survival and detection model, we present the quasi Aikaike's Information Criterion corrected for small sample size and an overdispersion factor of 1.15 (QAIC$_c$), the difference in QAIC$_c$ compared to the model with the lowest QAICc (ΔQAICc), Akaike weight (w_i), model likelihood, number of estimable parameters (K) and model deviance. We report only models with a likelihood of ≥0.01.

Survival	Detection	QAIC$_c$	ΔQAIC$_c$	w_i	Model likelihood	K	Deviance
Age × year	Banding age	832.89	0	0.432	1.00	18	37.582
Age × year	Age × banding age	833.89	1	0.262	0.61	19	36.541
Age × year	Constant	835.46	2.57	0.120	0.28	17	42.185
Age, density (s_{AHY} only)	Age × banding age	835.73	2.84	0.104	0.24	11	54.627
Age × density	Age × banding age	837.72	4.83	0.039	0.09	6	66.697
Age × density	Age × banding age	839.51	6.62	0.016	0.04	7	66.47
Age × density	Age × year	840.17	7.28	0.011	0.03	18	44.859
Age × year	Year	840.93	8.04	0.008	0.02	23	35.419
Age, density (s_{AHY} only)	Age × year	841.55	8.66	0.006	0.01	23	36.043
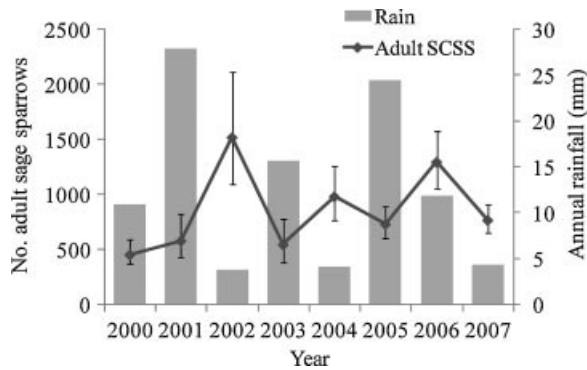
Figure 1. Annual rainfall (bars) and San Clemente sage sparrow (SCSS) population estimates (line), from San Clemente Island, California, 2000–2007. Error bars on sage sparrow population estimates represent 95% confidence intervals.

breeders negatively influenced by density but not affected by rainfall (Fig. 4).

Birds hatched in high- or medium-density habitats were most likely to remain in their natal habitats, whereas birds hatched in low-density habitats were most likely to disperse into high-density habitat (Table 1). Birds were least likely to disperse to low-density habitat regardless of where they hatched (Table 1).

Modeling

Predicted population growth based on observed rainfall, plot density, and mortality rates was strongly correlated with observed population growth ($r_5 = 0.835$, $p < 0.01$, Fig. 5). In addition, the model estimates appeared to be unbiased as paired observed and predicted growth rates were very similar (geometric mean ± SD; predicted $\lambda = 0.81 \pm 0.368$; observed $\lambda = 0.84 \pm 0.598$; $t_7 = -0.062$, $p = 0.952$).

Predicted extinction probabilities were high and most sensitive to changes in juvenile mortality, followed by adult mortality and the magnitude of annual variation in mortality rates (Table 4). A 20% decrease in juvenile mortality lowered extinction risk 40 times more than did a 20% decrease in major drought frequency, 49 times more than a 50% reduction in the impact of density, and >250 times more than doubling the amount of habitat. Model predictions were least
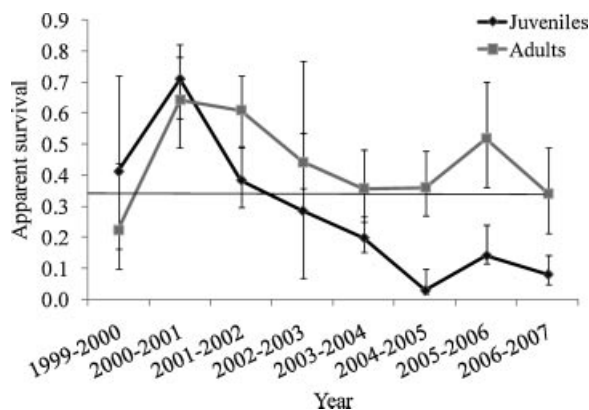
Figure 2. Adult and juvenile annual apparent survival (±SE) of San Clemente sage sparrows on San Clemente Island, California, 1999–2007.

sensitive to changes in initial population size, density dependence, and amount of habitat (i.e., population ceiling).

Habitat loss and global climate change (measured via increased drought frequencies) changed predicted extinction risk by <2% when assuming baseline demographic rates (Fig. 6). The negative impact of habitat loss and increased drought frequency was, however, limited by the already high extinction risk predicted by the baseline model. When we reduced juvenile mortality, the potential impact of increased drought frequency was much greater, leading to a 17% increase in the extinction risk compared to a 1.3% increase under baseline assumptions. Habitat loss reducing the population ceiling by 50%, in contrast, still changed predicted extinction risk by 5% (Fig. 6).

DISCUSSION

San Clemente sage sparrow populations exhibit large year-to-year fluctuations driven by the effects of rainfall on productivity. The climate-driven nature of sage sparrow population dynamics means that persistence of the species depends on the interplay between the growth potential of the population and drought frequency. Historic concerns of low population ceiling imposed by limited available habitat (USFWS 1977) appear to be a minor concern at present. Sensitivity analysis of our population model indicates 1) the immediate conservation priority for San Clemente sage sparrows is to increase apparently low juvenile survivorship and 2) that with current demographic rates, sage sparrow extinction risk is not affected by increased drought associated with climate change (Hayhoe et al. 2004). If, however, low juvenile survivorship is mitigated, the balance between growth potential and population variability means that the fate of the population will depend on the extent to which drought frequency increases under the influence of global climate change. The shifting nature of threats acting on sage sparrow population ceiling, growth potential, and variability highlights how management actions and changing environmental conditions interact in complex ways to shift conservation priorities.

One of the most striking observations from our study is the widely fluctuating nature of the San Clemente sage sparrow population. Although density dependence does act to reduce sage sparrow fecundity at high densities, variation in sage sparrow growth is primarily driven by density-independent variation in winter rainfall through its influence on breeding success. As a consequence, habitat availability, in as much as its effects are limited to determining the population ceiling, is likely only to impact San Clemente sage sparrow persistence when the amount of habitat available is very small. It appears that the threat imposed by historic habitat loss has been abated in the 15 years of habitat recovery since introduced herbivores have been removed from SCI. Indeed, our results suggest that moderate amounts of habitat loss are unlikely to increase extinction risk, which is reflected in recent biological opinions granting the Navy greater flexibility in using sage sparrow habitat during training exercises (USFWS 2009).

Table 4. Modeled effects of drought and density on the fraction of adult birds breeding successfully, by habitat of San Clemente sage sparrows on San Clemente Island, California, 2000–2008. We built models using a general linear model for adults successfully producing at least one fledgling.

Habitat	Parameter	Estimate[a]	t[b]	Error df	p
High	Drought[c]	−1.61	−3.78	12	<0.01
	Density[d]	−0.257	−1.91	9	0.093
Medium	Drought	−1.37	−7.04	12	<0.001
	Density	−0.053	−1.81	9	0.11
Low	Drought	−1.35	−3.73	10	<0.01
	Density	−0.603	−0.309	9	0.02

[a] We took estimates from untransformed data.
[b] We based t-statistics and associated p values on arcsin(square root) transformed data.
[c] SAS proc GLM model was % birds breeding = $a + b1 \times$ drought $+ b2 \times$ density $+ b3 \times$ drought $\times$ density. We ran separate analyses for each habitat. Negative parameter estimates indicate lower breeding success in drought years than nondrought years. There was a significant ($p < 0.05$) interaction term in all cases.
[d] SAS proc GLM model was % birds breeding = $a + b1 \times$ density. We conducted separate models for each habitat in non-drought years.

The primary factor influencing San Clemente sage sparrow extinction risk has thus shifted to the link between juvenile survivorship and the ability of the population to recover quickly from drought. Of particular concern is the decline in apparent juvenile survival we observed from 2001 through 2005 and its subsequent stabilization below 15%. This juvenile survival rate is less than half the estimated juvenile survival rates for mainland sage sparrows (Akçakaya et al. 2005) and the similar-sized Bachman's Sparrow (*Peucaea*

aestivalis, Pulliam et al. 1992). In addition the 34–52% adult survival we observed for San Clemente sage sparrows in the last 5 years of our study is well below the estimated 60% adult survival in their mainland counterparts (Pulliam et al. 1992, Akçakaya et al. 2005).

The main conclusions from our model analysis were quite robust to changes in both the functional form and values of demographic and environmental parameters included in the model. In addition to the analyses we reported, we ran the
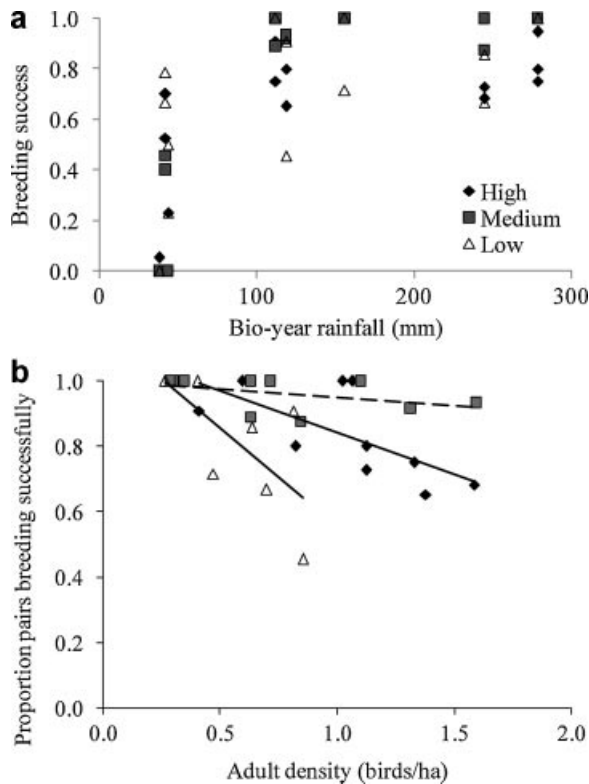

Figure 3. Sage sparrow breeding success of San Clemente sage sparrows on San Clemente Island, California, 2000–2007. (a) The proportion of pairs in study plots producing ≥1 fledgling was typically high but declined sharply when annual rainfall was <50 mm. (b) During years with high annual rainfall (>100 mm) breeding success was density-dependent and the relationship between breeding success and local density varied among habitats with birds in high density habitat (diamonds) showing an intermediate response compared to birds in medium (triangles) or low (squares) density habitats.
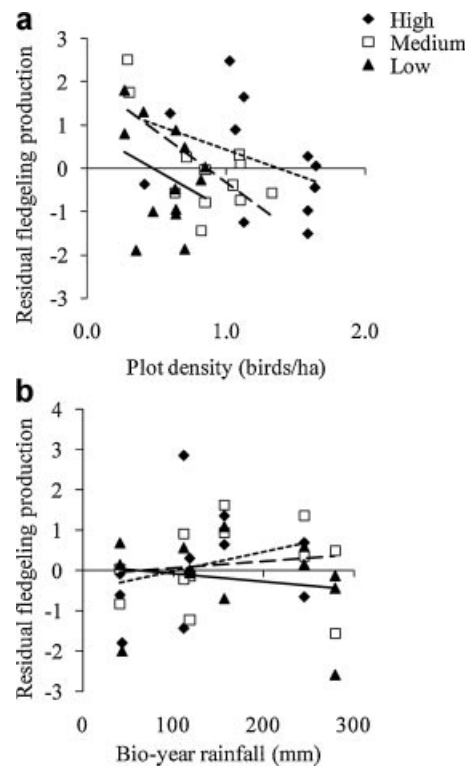
Figure 4. Residual effects of (a) density and (b) annual rainfall on fledgling production of San Clemente sage sparrows on San Clemente Island, California, 2000–2007. Points indicate plot mean differences between observed and expected fledgling production by successfully breeding birds after accounting for (a) annual rainfall or (b) density effects. Lines show linear trends within high (diamonds), medium (triangles), and low (squares) density habitats.
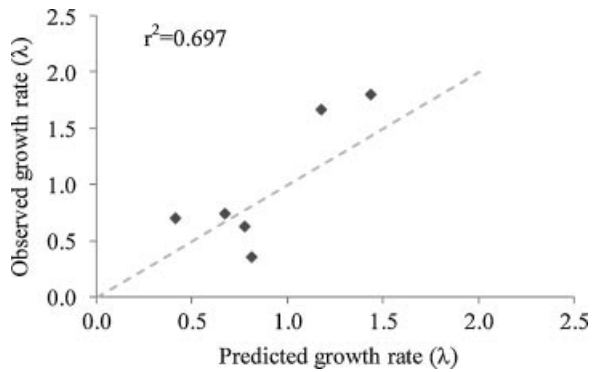
Figure 5. Predicted versus observed annual population growth (λ) of San Clemente sage sparrows on San Clemente Island, California, from 2002 to 2008. We calculated predicted growth as the population size in year t as predicted by the equations underlying the population viability analysis model and observed annual rainfall, density in year $t - 1$, and survivorship from year $t - 1$ to year t divided by the population in year $t - 1$. Dotted line reflects 1:1 match.

model assuming no density dependence in breeding success, variable effects of minor droughts on fecundity, and with the parameter estimates based only on data through 2004. Beaudry (2004) ran preliminary models using substantially different functional forms for survival (assumed to be density-dependent), fecundity, and the effects of drought parameterized from data collected through 2002. Although models based only on data collected when both juvenile and adult survival were high predict lower extinction risk than our model, in all cases the major results we presented have been upheld; sage sparrow extinction risk is closely tied to juvenile mortality rates and is insensitive to moderate habitat loss.

Since we reported our findings to the United States Navy, it has focused research efforts on determining why apparent juvenile survival has fallen since 2001. One possible reason our survival estimates were so low was that we relied on
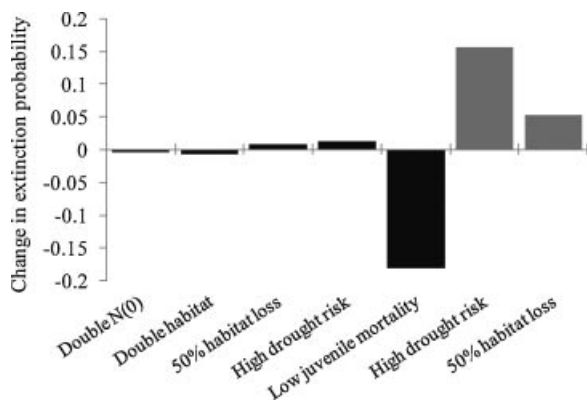
Figure 6. Change in predicted 50 years extinction risk of San Clemente sage sparrows on San Clemente Island, California associated with changes in juvenile mortality, drought frequency and available habitat. The high drought risk scenario assumed annual probabilities of 0.25 and 0.33 for major and minor droughts, respectively. Low juvenile mortality scenarios assumed a 10% reduction in juvenile mortality ($m(j) = 0.648$). The 2 rightmost bars indicate the change in extinction risk relative to simulations with low juvenile mortality.

mark-resight surveys, which do not account for emigration outside the surveyed area. However, emigration is unlikely to affect estimates of adult survival because adults are faithful to their breeding territories (Munkwitz 2004). Furthermore, we attempted to minimize bias on estimates of juvenile survival by searching all available sage sparrow habitat when time allowed each year. Statistical models allowing both survival and detection probability to vary by age and year did reveal a signature of greater detection probabilities during years with intensive search efforts to measure natal dispersal (2001 and 2002) or years when low breeding allowed more time to conduct range-wide surveys (2004 and 2007). But variation in detection probabilities does not explain the large drop in estimated survival during the later part of our study. Incorporating annual variation in detection probability into survival estimates actually resulted in reduced estimated juvenile survival for 2001 and 2002 and little change ($\Delta < 0.01$) in estimated survival for other years. In a more directed effort, in 2009 the United States Navy initiated a radio-telemetry study in collaboration with the Institute for Wildlife Studies to track juveniles through their first fall and winter to identify mortality risks.

San Clemente sage sparrows typify the ecological characteristics of species on the edge between what Fagan et al. (1999, Fig. 3) termed "short-term viable" and "dispersal dependent" populations, the former describing populations likely to persist the latter describing populations that face high risk of local extinction within the next 20–200 years. The position of sparrows on the extinction-risk continuum is driven by those factors that reduce sage sparrow numbers sufficiently to make them susceptible to demographic and environmental stochastic events (Pimm et al. 1988, Tracy and George 1992). The time that sage sparrow populations remain at dangerously low population size is driven by a balance between drought frequency and the ability for populations to recover rather than the amount of available habitat, which is characteristic of species on the short-term viable, dispersal dependent continuum (Fagan et al. 1999).

It is likely that rapid recovery potential is a key to the persistence of many small passerines, particularly island endemics. Despite widespread examples of climate variables exerting a strong influence on reproductive rates and population dynamics of many passerines (Boag and Grant 1984, Arcese et al. 1992, Bolger et al. 2005, Chase et al. 2005), this group lacks buffers such as long-lived adults or a resistant life history stage for coping with frequent disturbances (Gray 1981, Sæther and Bakke 2000). Consequently, in the absence of spatial population structuring, populations facing frequent climate disturbances will depend on the ability to recover quickly from population crashes (Fagan et al. 1999, Haddad et al. 2008). One potential mechanism promoting recovery is the ability to produce multiple clutches in good years, particularly if foregoing breeding in 1 year allows for enhanced productivity the following year (Boag and Grant 1984, this study). Such compensatory breeding may have caused population growth 2 years after the 2002 and 2004 droughts to be higher than predicted (the uppermost 2 points in Fig. 5).

Disturbance tolerant species such as San Clemente sage sparrows are not likely to be as threatened by habitat loss as from threats such as introduced predators or disease, which tip the balance between disturbance and recovery. Consequently, the most relevant impact of global climate change on such species may not be associated changes in vegetative communities, but changes in the frequency of extreme climatic events, such as droughts or excessively rainy years. Such generalizations should be taken with caution, however, as the underlying mechanisms will be varied and complex, making it challenging to predict their impact on any particular population (Walther et al. 2002). However, threats imposed by global climate change, like all threats to a species' persistence, will ultimately act through their effect on a population's growth potential, variability, or population ceiling. Thus, models and monitoring programs addressing these 3 components of population dynamics will provide a ready framework for detecting and managing shifting threats throughout a species' trajectory from at-risk to recovery.

Successful adaptive management requires understanding and managing for multiple and changing risks. Informing such management demands the use of complex modeling techniques to separate the underlying mechanisms and integrate the effects of different aspects of population dynamics on a species extinction risk. The oft-cited weakness of complex population models—the intensive data requirements to determine parameter values and how they are influenced by environmental factors—is also their strength. When built around a solid empirical understanding, the flexibility of complex models allows the kinds of explorations necessary to predict how present management and future environmental conditions will interact to change conservation priorities.

MANAGEMENT IMPLICATIONS

The primary management implications of our findings are that 1) moderate habitat loss will have a minimal impact on sage sparrow extinction risk, 2) understanding and mitigating causes of juvenile mortality are key to managing the species, and 3) recovery goals for the species need to consider the potential for increased drought frequency associated with global climate change. The management focus for San Clemente sage sparrows has been, for a few decades now, raising the population ceiling through habitat recovery and protection. The elimination of introduced herbivores and subsequent habitat recovery has been successful to the point where moderate habitat loss will have a minimal impact on sage sparrow extinction risk, and it is now time for management efforts to switch focus. In recognition of the key assumption in our model that habitat degradation or destruction does not influence demographic rates in remaining areas, any new activity resulting in loss of sage sparrow habitat should be coupled with monitoring designed to detect changes in demographic rates in nearby undisturbed areas. The most immediate next step to successfully recovering the San Clemente sage sparrow is to continue investigations of the causes and develop management strategies to reduce juvenile mortality. Looking further ahead, and assuming juvenile mortality rates are successfully reduced,

recovery goals should be based on the balance between expected drought frequency and recovery potential rather than population trajectories or population size.

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