

Projecting demographic responses to climate change: adult and juvenile survival respond differently to direct and indirect effects of weather in a passerine population

KRISTEN E. DYBALA*, JOHN M. EADIE*, THOMAS GARDALI†, NATHANIEL E. SEAVY† and MARK P. HERZOG‡

*Department of Wildlife, Fish and Conservation Biology, University of California, One Shields Avenue, Davis, CA 95616, USA, †PRBO Conservation Science, 3820 Cypress Drive #11, Petaluma, CA 94954, USA, ‡Western Ecological Research Center, Davis Field Station, US Geological Survey, University of California, One Shields Avenue, Davis, CA 95616, USA

Abstract

Few studies have quantitatively projected changes in demography in response to climate change, yet doing so can provide important insights into the processes that may lead to population declines and changes in species distributions. Using a long-term mark-recapture data set, we examined the influence of multiple direct and indirect effects of weather on adult and juvenile survival for a population of Song Sparrows (*Melospiza melodia*) in California. We found evidence for a positive, direct effect of winter temperature on adult survival, and a positive, indirect effect of prior rainy season precipitation on juvenile survival, which was consistent with an effect of precipitation on food availability during the breeding season. We used these relationships, and climate projections of significantly warmer and slightly drier winter weather by the year 2100, to project a significant increase in mean adult survival (12–17%) and a slight decrease in mean juvenile survival (4–6%) under the B1 and A2 climate change scenarios. Together with results from previous studies on seasonal fecundity and postfledging survival in this population, we integrated these results in a population model and projected increases in the population growth rate under both climate change scenarios. Our results underscore the importance of considering multiple, direct, and indirect effects of weather throughout the annual cycle, as well as differences in the responses of each life stage to climate change. Projecting demographic responses to climate change can identify not only how populations will be affected by climate change but also indicate the demographic process(es) and specific mechanisms that may be responsible. This information can, in turn, inform climate change adaptation plans, help prioritize future research, and identify where limited conservation resources will be most effectively and efficiently spent.

Keywords: California, climate change, direct and indirect effects, juvenile survival, mark-recapture, Palomarin, weather

Received 3 July 2012 and accepted 21 March 2013

Introduction

The projected effects of climate change on wildlife populations are frequently in the form of changes in species' distributions, which have included dramatic shifts and contractions in species' ranges (e.g., Thomas *et al.*, 2004; Stralberg *et al.*, 2009). These studies suggest that many local populations will decline as range limits retreat, but they reveal little about the processes that may produce these declines and range shifts. Deeper insight may be obtained by projecting the effects of climate change on demographic rates (McLaughlin & Zavaleta, 2012; Peery *et al.*, 2012). Yet, despite a long history of examining the role of weather in regulating populations (Andrewartha & Birch, 1954), and the effects of weather on survival (Grosbois *et al.*, 2008),

only a small number of studies have quantitatively projected changes in demography in response to climate change (Jenouvrier *et al.*, 2009; Wolf *et al.*, 2010; Barbraud *et al.*, 2011).

Thus far, efforts to project the effects of climate change on demographic rates and population growth have generally been limited to the effects a single, overwhelmingly important weather factor. These include the effects of sea surface temperatures or sea ice extent on polar species (e.g., Jenouvrier *et al.*, 2009; Hunter *et al.*, 2010; Barbraud *et al.*, 2011), and the effects of precipitation on organisms in arid environments (e.g., Tews & Jeltsch, 2004; Altwegg & Anderson, 2009; Jonzén *et al.*, 2010). However, in most climatic regions, there are likely to be multiple effects of weather on survival throughout the annual cycle (Silllett *et al.*, 2000; Robinson *et al.*, 2007), including both direct and indirect effects (McCarty, 2001; Stenseth *et al.*, 2002). Furthermore, the magnitude and direction of these effects may

Correspondence: Kristen E. Dybala, tel. +1 415 218 9295, fax +1 530 752 4154, e-mail: kedybala@ucdavis.edu

vary by life stage, each of which will contribute to variation in the population growth rate to varying degrees (Sæther, 1997; Gaillard *et al.*, 1998; Coulson *et al.*, 2001; Altwegg *et al.*, 2005; van de Pol *et al.*, 2010). Therefore, in most climatic regions, studies that focus only on the effects of a single weather factor or on a single life stage will result in an incomplete understanding of the influence of climate change on the population as a whole (Ådahl *et al.*, 2006; Seavy *et al.*, 2008; Rogers *et al.*, 2011; McLaughlin & Zavaleta, 2012).

We projected the demographic effects of climate change on a population of Song Sparrows (*Melospiza melodia*) in central coastal California for the climatic conditions expected by the year 2100 under two climate change scenarios. Our objectives were to: (i) examine the relative importance of direct and indirect effects of weather on adult and juvenile survival, complementing earlier work on the effects of weather on seasonal fecundity (Chase *et al.*, 2005); (ii) project the effects of climate change on survival in each age class and on seasonal fecundity; and (iii) project the consequences of changes in these demographic rates for the population's growth rate.

Materials and methods

Study site, species, and data collection

Our study was conducted at the Palomarin Field Station, located in the Point Reyes National Seashore, 20 km north of San Francisco, California (37°56'N, 122°45'W). The climate is Mediterranean, typically with cool, rainy winters and warm, dry summers. Total precipitation and high and low temperatures are collected on-site daily. The habitat in the 36 ha study area consists of coastal scrub with an increasing abundance and density of Douglas fir (*Pseudotsuga menziesii*), which has coincided with a steady decline in the density of Song Sparrow breeding territories since 1980 (Chase *et al.*, 2005). Song Sparrows are a common passerine found throughout North America, and the local population (*Melospiza melodia gouldii*) is nonmigratory (Arcese *et al.*, 2002). Year-round constant-effort mist-netting began in 1979, and all Song Sparrows captured in mist-nets are given a unique combination of colored leg bands (DeSante & Geupel, 1987). Since 1980, the entire study area has been intensively searched for color-banded individuals, breeding territories, and nests, and all nests are monitored to determine their success or failure in fledging young (Geupel & DeSante, 1990; Chase *et al.*, 2005). Further details about the study area, flora, and field methods have been described elsewhere (Nur *et al.*, 2004; Jennings *et al.*, 2009).

Annual adult and juvenile survival

We modeled the annual survival of juvenile and adult Song Sparrows using R 2.15.1 with the package RMark 2.1.1 to write Cormack-Jolly-Seber models for Program MARK 6.1 (Lebreton

et al., 1992; White & Burnham, 1999; Laake, 2013; R Core Development Team, 2012). We defined each year as beginning 1 April, early in the breeding season, and ending 31 March of the following calendar year, and we considered all birds to be juveniles (J) from fledging until 1 April of the following year, when they became adults (A). We constructed annual encounter histories for all individuals captured in the mist-nets as juveniles between 1979 and 2011, and included all subsequent mist-net captures and encounters of color-banded individuals in the study area.

We initially modeled apparent survival (ϕ) and recapture (P) probabilities solely in terms of fixed effects of age class (J or A) and year (t) to establish a baseline model structure. We tested the fit of the general model, $\phi (J_t + A_t) P (t)$, with full year-dependent survival for each age class and year-dependent recapture probabilities using U-CARE 2.3.2 (Choquet *et al.*, 2009). There was evidence for trap-dependence, so we allowed recapture probability to vary by year and time since marking (m), grouped by 1 or 2+ years after initial capture. We used the median- \hat{c} method implemented in Program MARK 6.1 to estimate overdispersion in the new general model, $\phi (J_t + A_t) P(m_t)$, which was estimated to be low ($\hat{c} = 1.09$). Adjusting for overdispersion had no effect on model-selection results, and we present unadjusted results below.

We defined two additional survival models, each constraining one of the age classes to have constant survival probability. We also defined two additional recapture models, with constant or time-varying survival. We fit all nine combinations of the three survival and three recapture models to the mark-recapture data, and used the model-selection results to calculate model-averaged survival rates for each age class in each year. The model with the most support, which included effects of year on adult and juvenile survival and on recapture probability, hereafter Ref_t , became the primary reference model to which we compared models including effects of the candidate weather and density variables (Grosbois *et al.*, 2008). We also refer to the nested models, Ref_J and Ref_A , each of which constrained survival in one age class to be constant.

Weather and density variables

We defined four hypotheses for the effects of population density and the direct and indirect effects of weather on survival rates (summarized in Table 1). First, we considered direct effects of weather as weather conditions that induce immediate physiological stress and contribute to mortality (McCarty, 2001; Stenseth *et al.*, 2002). We hypothesized direct effects of heat (H1), which was measured as the average of the daily high and low temperatures during the summer (June–August), and winter weather (H2), which was measured as the combination of average temperature during the winter (December–February) and total precipitation during the winter rainy season (October–March). Extended periods of heat are known to cause physiological stress and mortality in birds and mammals (Welbergen *et al.*, 2008; McKechnie & Wolf, 2010), and winter is frequently expected to be the season of highest adult mortality in passerines (Lack, 1954; Newton,

Table 1 Hypotheses for the effects of density and the direct and indirect effects of weather on adult and juvenile survival rates

Hypotheses	Representative variables	Notation
Direct effects of weather		
H1. Heat	Summer (June–August) average temperature	Summer Temp
H2. Winter weather	Winter (December–February) average temperature and rainy season (October–March) precipitation	Winter Temp + Rain
Indirect effects of weather		
H3. Prior winter weather (on food availability and predation risk)	Prior winter (December–February) average temperature and prior rainy season (October–March) precipitation	Winter _{t-1} Temp + Rain
Population density		
H4. Relative territory density	Residuals of the annual breeding territory count from a declining trend	Density

The set of models representing each hypothesis included the linear and quadratic effects of each variable on either adult or juvenile survival. For the indirect effects of prior winter weather, we use the subscript $t-1$ to indicate the use of temperature and precipitation values from the previous survival year. All other models used temperature, precipitation, and density values from the same survival year (1 April–31 March).

1998). Therefore, we expected survival to be lower in years with relatively hot summers or cold, wet winters.

The indirect effects of weather on survival include the effects of weather on competitors, predators, parasites, and prey, and may include time lags (Stenseth *et al.*, 2002). In the Mediterranean climate of central coastal California, primary and secondary productivity is characteristically limited by water availability (Roy *et al.*, 1995). Wet winters generally benefit subsequent plant growth and insect populations, which can, in turn, provide increased cover and food resources for birds throughout the following spring and summer (Bale *et al.*, 2002; Bolger *et al.*, 2005; Kreyling, 2010). In addition, cold, wet winters may negatively affect the survival of Song Sparrow predators, reducing predation risk during the following year. Nest success rates in this population were also higher following wet years, further suggesting increased resources and/or reduced predation risk (Chase *et al.*, 2005). Therefore, we hypothesized an indirect, time-lagged effect of weather during the previous winter on survival rates (H3). Finally, we also examined support for density-dependent survival (H4). We measured population density in terms of the number of Song Sparrow territories in the study area each breeding season. However, because the territory density has been steadily declining as the habitat has changed, we examined an effect of territory density relative to this declining trend, calculated as the residuals between the number of territories observed and the number predicted from the trend.

We considered effects of all four hypotheses on both adult and juvenile survival. However, across taxa, juvenile survival is often reported to be more variable and more sensitive to environmental conditions than adult survival (Gaillard *et al.*, 1998; Portier *et al.*, 1998; Altwegg *et al.*, 2005; Oro *et al.*, 2010). Adult survival often contributes more than juvenile survival to variation in population growth, so this relative lack of adult sensitivity to environmental variability helps limit variation in adult survival and subsequently population growth (Sæther & Bakke, 2000; Gaillard & Yoccoz, 2003; Forcada *et al.*, 2008). Moreover, from a behavioral perspective, adults may have the necessary experience and skill to compensate for variation in

environmental conditions such as food availability or predation risk, experience and skill juveniles have not yet acquired (Marchetti & Price, 1989; Weathers & Sullivan, 1989). Consequently, we expected juvenile survival to be more strongly affected by variation in population density and weather, particularly the indirect effects of weather on food availability or predation risk (Adams *et al.*, 2006; Schmidt *et al.*, 2008), whereas we expected adult survival to be affected primarily by the direct effects of extreme conditions.

We calculated the Pearson's correlation coefficient (r) among all the variables under consideration to identify any evidence of multicollinearity, and conducted a regression analysis to identify any linear or quadratic trends in each of the variables (reported below). To allow for comparisons between the estimated effect sizes of each variable on survival, we standardized all of the variables to have a mean of 0 and a SD of 1. Because daily high and/or low temperature data were missing for more than 20 days in five of the summer seasons and four of the winter seasons, we used 0 as the average temperature during these seasons (equivalent to the standardized mean). We took this approach because Program MARK does not allow missing values, and because it should result in conservative estimates of the effect of each variable on survival. However, we also checked the sensitivity of our results to these missing values by recalculating our results using values of +2, +1, -1, or -2 for the missing values (equivalent to 1 or 2 SDs above or below the mean). For both adults and juveniles, varying these missing values had no effect on which hypothesis had the most support, and there were no differences in the estimated effect sizes of each weather variable in the top models (Fig. S1). Because 95% of the missing weather values will fall between -2 and +2 SDs, we are confident that these missing values did not affect our results.

Effects of weather and density on survival

We modeled the effects of each of the weather and density variables to determine how well each hypothesis accounted for the annual variation in adult or juvenile survival that was

estimated by Ref_i , the primary reference model that included effects of year on survival. Thus, for each age class, we compared the fit of Ref_i with models that replaced the fixed effect of year with an effect of one of the hypotheses, in essence, adding linear or quadratic fixed effects of each variable to the respective baseline reference models (Ref_j or Ref_A). We then calculated the fraction of the variation in annual juvenile or adult survival accounted for by each variable (R^2_{Dev}) as the difference between the model deviances of the baseline reference model and the model including the variable, in proportion to the difference between the model deviances of the baseline reference model and Ref_i , the most general model (Skalski, 1996; Grosbois *et al.*, 2008). We considered variables in models with $R^2_{Dev} > 0.20$ to have support (Grosbois *et al.*, 2008).

To check for the presence of spurious correlations between weather variables and survival due solely to similar trends in each, we re-examined the effects of weather variables with significant linear or quadratic trends by first identifying whether there was support for a similar trend in survival, and then including the detrended weather variable in a model that also accounted for the trend in survival (Grosbois *et al.*, 2008). This approach allowed us to determine whether an effect of the detrended weather variable on survival was still supported, as well as how much of the variation around the trend in survival was accounted for by the variation around the trend in the weather variable.

Finally, as a result of modeling the effects of each hypothesis separately for adults and juveniles, we identified different weather variables as having strong effects on each age class. This suggests either that the variables had different effects on each age class, or that the effects were similar, but there was more uncertainty in the effect on one of the age classes. To help distinguish between these possibilities, we compared the fit of two final models that combined the effects of all of the supported variables. The first model allowed effects of each variable to vary by age class, and the second model constrained the effect of each variable to be the same for each age class.

Seasonal fecundity and postfledging survival

To complete the parameterization of a population model (described below), we drew on previous studies at Palomarin that have examined seasonal fecundity and postfledging survival in this population of Song Sparrows. Chase *et al.* (2005) reported a strong, positive relationship between precipitation during the previous biyear (July–June) and seasonal fecundity (total fledglings produced per female per breeding season; their Fig. 3; $\beta = 0.013 \pm 0.0049$ fledglings cm^{-1}). Because most of the biyear precipitation falls during the rainy season (October–March), and to match the variables we used in the survival analysis, we recalculated the relationship to reflect the effect of prior rainy season precipitation (October–March) on seasonal fecundity. We also divided seasonal fecundity in half, to reflect the number of females fledglings produced per female, assuming a 50 : 50 sex ratio.

We also considered juvenile survival during the postfledging stage, when juveniles are dependent on parental care and

are extremely vulnerable to predation. Dybala *et al.* (2013) examined the survival of dependent fledglings in Song Sparrows at Palomarin, and found that survival during the first 3 weeks after fledging averaged 0.53 (95% CI: 0.49–0.57). However, our estimates of annual juvenile survival are based on individuals captured in mist-nets, most of whom are likely to be independent and to have already survived this stage (Johnson & Geupel, 1996; Gardali *et al.*, 2003). Consequently, our estimates of juvenile survival likely do not account for postfledging survival and may be overestimated. Because Dybala *et al.* (2013) also found no effect of weather on postfledging survival, we incorporated the mean postfledging survival rate into the population model.

Projecting survival, fecundity, and population growth under future climate conditions

We obtained recent climate change projections for Northern California through the year 2100 using the NOAA Geophysical Fluid Dynamics Laboratory CM2.1 (GFDL) climate model and based on the B1 (low emissions) and A2 (medium-high emissions) scenarios as defined by the Intergovernmental Panel on Climate Change (IPCC, 2007; Cayan *et al.*, 2008). Using the top model describing the effects of weather on adult or juvenile survival, we calculated the expected mean adult and juvenile survival rates (ϕ_A and ϕ_J , respectively) over a range of values for each weather variable, including the values projected under each climate change scenario. Similarly, we used the relationship between prior rainy season precipitation and seasonal fecundity to calculate the expected mean seasonal fecundity (F) over a range of precipitation values.

We used the projected survival and fecundity rates, along with the mean postfledging survival rate (ϕ_{PF}), to parameterize a simple two age-class population model, based on the model described by Donovan & Thompson (2001), in which $n_{J,t}$ and $n_{A,t}$ represent the number of juveniles and adults in the population at time t , respectively, and $n_{J,t+1}$ and $n_{A,t+1}$ represent the same at time $t+1$:

$$\begin{bmatrix} n_{J,t+1} \\ n_{A,t+1} \end{bmatrix} = \begin{bmatrix} F\phi_{PF} & F\phi_{PF} \\ \phi_J & \phi_A \end{bmatrix} \times \begin{bmatrix} n_{J,t} \\ n_{A,t} \end{bmatrix}$$

We used this population model to calculate the expected deterministic population growth rate (λ) under the current mean climatic conditions, as well as for the future mean conditions under both the B1 and A2 climate change scenarios. We used a parametric bootstrap procedure with 10 000 replicates to calculate 95% bootstrap intervals for λ under each scenario, drawing ln-transformed fecundity and logit-transformed survival parameters from normal distributions with their respective means and standard deviations, back-transforming, and calculating λ . Because there is uncertainty in the climate projections themselves, particularly in projections of precipitation (Dettinger, 2005), we also calculated the expected λ over a range of temperature and precipitation values, to explore the effects of a range of climatic conditions on population growth (Seavy *et al.*, 2008). Our estimates of λ are likely to be underestimated because our estimates of survival incorporate emigration (Lebreton *et al.*, 1992), and we do not have estimates of

immigration to include in the model. However, if we assume no strong effect of weather on the immigration rate, the direction of the projected change in λ will still be informative.

Results

Annual adult and juvenile survival

The data set for the survival analysis included 3027 individuals captured as juveniles between 1979 and 2011. A total of 846 (28%) were recaptured in at least one subsequent year, with individual cohort recapture rates ranging from 2.6 to 90.3%. The most general model (Ref_t) had strong support (Akaike weight = 0.960), indicating considerable annual variation in both adult and juvenile survival (Table 2a). Model-averaged annual juvenile survival rates ranged from a high in 1980 of 0.51 (95% CI: 0.41–0.61) to a low in 1990 of 0.09 (95% CI: 0.03–0.24), with an overall mean of 0.30 (95% CI: 0.27–0.33; Fig. 1). Model-averaged annual adult survival rates were higher, ranging from a low of 0.45 (95% CI: 0.32–0.59) in 1982 to a high of 0.82 (95% CI: 0.62–0.93) in 1986, with an overall mean of 0.66 (95% CI: 0.63–0.69).

Weather and density variables

The mean summer (June–August) average temperature during the study period was 15.4 °C, and the mean winter (December–February) average temperature was

10.2 °C (Fig. 2). There were weak, but significant, quadratic trends in average temperatures during both seasons ($P < 0.05$), peaking in the mid-1990s, which resulted in a strong positive correlation between these variables (Pearson's $r = 0.42$). However, after removing the quadratic trends, they were no longer strongly correlated ($r = 0.25$). Precipitation during the winter rainy season (October–March) was highly variable, ranging from 0.38 to 1.39 m, with a mean of 0.78 m. There was no evidence for a linear or quadratic trend in winter precipitation ($P > 0.8$), and it was not strongly correlated with either summer or winter average temperature ($r < 0.3$). In contrast, Song Sparrow territory density declined steadily by 0.03 territories ha⁻¹ yr⁻¹ ($P < 0.001$). We calculated relative territory density as the difference between the density observed and the declining trend, and relative density ranged from 0.42 territories ha⁻¹ fewer than expected to 0.36 territories ha⁻¹ more than expected from the declining trend.

Effects of weather and density on survival

Of the four hypotheses, a direct effect of winter weather (H2) had the strongest support for an effect on adult survival, with the combined Akaike weights of all models representing hypothesis H2 totaling 0.9999 (Table 2b). Winter weather accounted for 44% of the total variation in annual adult survival. Consistent with hypothesis H2, adult survival rates were higher in years with relatively warm, dry winters, but the effect

Table 2 Model-selection results for the analysis of juvenile and adult survival

Survival (ϕ)	k	AICc	Δ AICc	w	Dev	R^2_{Dev}	H#
(a) Reference models, including effects of age and year							
Ref _t = A _t + J _t	95	8383.72	0.00	0.960	1430.02		
Ref _j = A _t + J	64	8392.25	8.53	0.013	1502.65		
Ref _A = A + J _t	65	8393.09	9.37	0.009	1501.45		
(b) Effects of weather on adult survival							
Ref _A + Winter Temp + Rain	67	8365.87	0.00	0.518	1470.11	0.44	H2
Ref _A + Winter Temp ² + Rain	68	8367.61	1.73	0.218	1469.79	0.44	H2
Ref _A + Winter Temp + Rain ²	68	8367.92	2.05	0.186	1470.10	0.44	H2
Ref _A + Winter Temp ² + Rain ²	69	8369.63	3.76	0.079	1469.76	0.44	H2
Ref _t	95	8383.72	17.85	0.000	1430.02	1.00	–
(c) Effects of weather on juvenile survival							
Ref _j + Winter _{t-1} Temp + Rain ²	67	8378.12	0.00	0.684	1482.36	0.28	H3
Ref _j + Winter _{t-1} Temp ² + Rain ²	68	8380.11	1.99	0.253	1482.29	0.28	H3
Ref _t	95	8383.72	5.60	0.042	1430.02	1.00	–

Only reference models and models with $R^2_{\text{Dev}} > 0.20$ are shown. See Table S3, for the complete results. All of the models shown included full year-dependent recapture probability. Survival model notation includes juvenile (J) and adult (A) age classes, with the subscript denoting year-dependent (t) or constant (no subscript) survival. For (b–c), we added linear or quadratic effects of each variable to Ref_A and Ref_j, the baseline reference model for each age class from (a). We present models including quadratic effects with a shortened notation, but these models do include both the linear and quadratic terms. See Table 1, for the definition of each variable, and the hypothesis (H#) it represents.

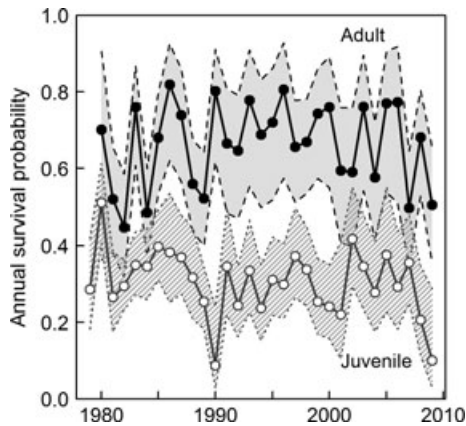


Fig. 1 Model-averaged survival estimates for adults and juveniles, 1979–2009, shown with 95% CI.

of winter temperature ($\beta = 0.32$, 95% CI: 0.19–0.45) was stronger than the effect of precipitation ($\beta = -0.17$, 95% CI: -0.27 to -0.05 ; Fig. 3). Because there was a quadratic trend in winter average temperature, we also checked for trends in adult survival, and we found strong support for a quadratic trend in adult survival (Table S1). After accounting for this trend, there was still strong support for a direct effect of the detrended winter weather on adult survival. Therefore, the relationship between winter weather and adult survival was not simply the result of similar trends in each.

For juveniles, an indirect effect of prior winter weather (H3) had the strongest support, with a combined Akaike weight of 0.951 (Table 2c). Prior winter weather accounted for 28% of the variation in annual juvenile survival rates, and was primarily due to a strong quadratic effect of prior winter precipitation (linear term $\beta = 0.28$, 95% CI: 0.14–0.43; quadratic term $\beta = -0.16$, 95% CI: -0.25 to -0.07) rather than the linear effect of prior winter temperature ($\beta = -0.07$, 95% CI: -0.15 –0.02). Consistent with hypothesis H3, and an effect of prior winter weather on food availability and/or predation risk, juvenile survival was lowest after dry winters (Fig. 3). Again, because there was a quadratic trend in winter average temperatures, we checked for a similar trend in juvenile survival. We found weak support for a linear declining trend, but no support for a quadratic trend (Table S1). Consequently, the observed relationship between prior winter weather and juvenile survival was also not simply the result of similar trends in each.

By comparing the fit of two final models combining the direct and indirect effects of winter weather (H2 and H3), we found much stronger support for the model that allowed each effect to vary by age class relative to the model that constrained the effects to be the same on both age classes (Akaike $w = 1.00$; Table S2),

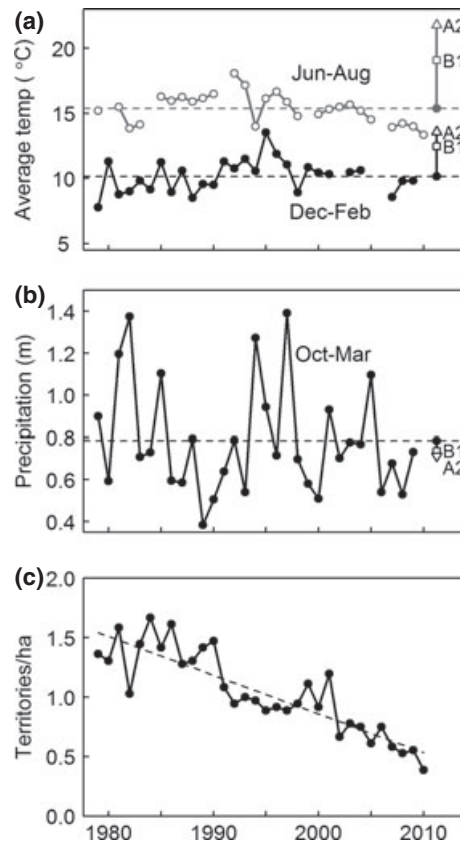


Fig. 2 Annual variation in (a) summer (June–August) and winter (December–February) average temperatures, (b) total precipitation during the winter rainy season (October–March), and (c) density of Song Sparrow breeding territories in the 36 ha study area. The dashed lines denote (a–b) the 1979–2010 mean values, and (c) the declining trend. In (a–b), the open points along the right edge of each plot display the projected changes in mean temperature and precipitation under the B1 and A2 scenarios (Cayan *et al.*, 2008).

providing further support that adult and juvenile survival rates responded differently to these weather variables. Finally, for both adults and juveniles, none of the models representing effects of extreme heat (H1) or density (H4) was competitive ($\Delta\text{AICc} < 10$) or accounted for more than 20% of the variation in annual survival (Table S3).

Seasonal fecundity

Drawing on the relationship reported by Chase *et al.* (2005) between biyear precipitation (July–June) and seasonal fecundity in Song Sparrows (their Fig. 3), we found a significant positive relationship between prior rainy season precipitation (October–March) and the ln-transformed number of female fledglings produced per adult female (linear regression; $\beta = 0.00059 \pm 0.00019$; $P = 0.007$; $r^2 = 0.32$).

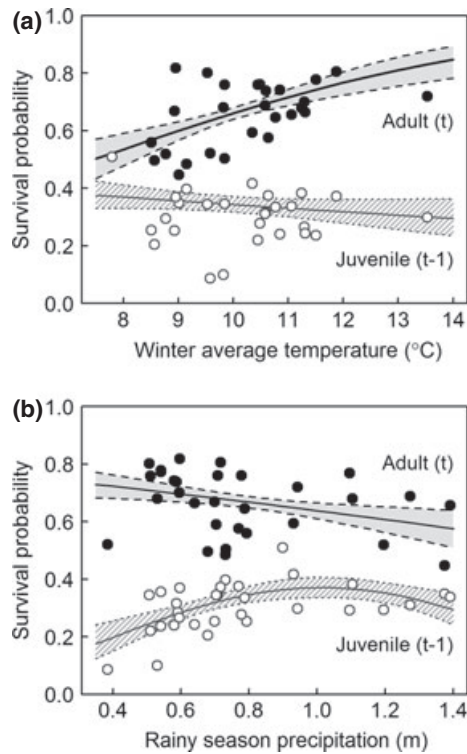


Fig. 3 Expected and estimated adult and juvenile survival rates over a range of current (t) and prior ($t-1$) winter weather conditions, respectively: (a) winter (December–February) average temperature ($^{\circ}\text{C}$) and (b) total precipitation (m) during the winter rainy season (October–March). The lines and shaded areas represent the expected survival rate and 95% CI over the range of weather conditions shown. The filled and open points mark the observed weather conditions in each year and the corresponding model-averaged adult and juvenile survival estimates, respectively. For clarity, CI are not shown for the annual survival estimates, but are shown in Fig. 1.

Projecting survival, fecundity, and population growth under future climate conditions

The climate change projections we obtained from the literature for Northern California under the B1 and A2 climate change scenarios included substantial increases in mean winter temperatures of 2.3 and 3.4 $^{\circ}\text{C}$, representing increases of 1.85 and 2.74 SDs from the current mean, respectively (Fig. 2; Cayan *et al.*, 2008). Only slight decreases in mean winter precipitation of 6% and 9% were projected, representing decreases of 0.18 and 0.27 SDs from the current mean, respectively.

Due to the positive effect of winter temperature on adult survival, we projected increases in mean adult survival under both scenarios, from the current expected mean of 0.67 (95% prediction interval: 0.65–0.69), to 0.79 (0.74–0.83) under the B1 scenario, and 0.84 (0.78–0.88) under the A2 scenario (Fig. 4a). In contrast,

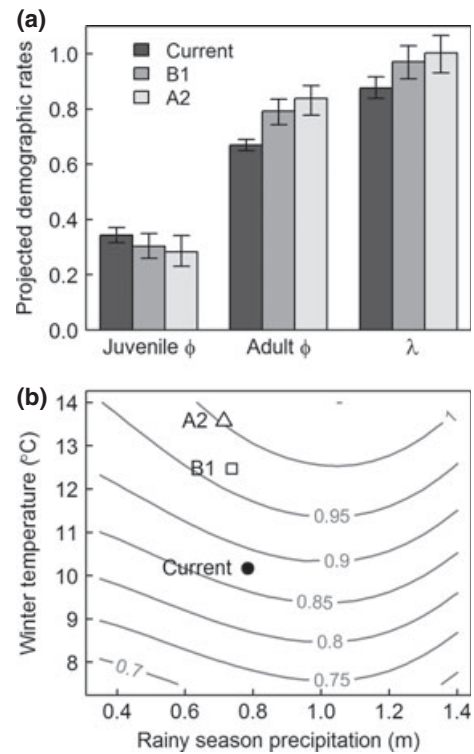


Fig. 4 Current and projected demographic rates. (a) Current expected mean survival and population growth rates based on current (1979–2010) climatic conditions, and projected mean survival and population growth rates under B1 and A2 climate change scenarios. (b) Projected population growth rates (λ) over a range of climatic conditions. Population growth rates were calculated using a population model that incorporated the effects of weather on juvenile and adult survival rates from this study, and on seasonal fecundity as reported in a prior study (Chase *et al.*, 2005; their Fig. 3), as well as the previously reported mean postfledging survival rate (Dyballa *et al.*, 2013). See text, for details.

due to the relatively weak effect of prior winter temperature on juvenile survival and the small changes projected in mean precipitation, we projected slight declines in mean juvenile survival from the current expected mean of 0.34 (95% prediction interval: 0.32–0.37), to 0.30 (0.26–0.35) under the B1 scenario, and 0.28 (0.23–0.34) under the A2 scenario. Similarly, we projected slight declines in mean seasonal fecundity from the current expected mean of 1.13 (95% prediction interval: 0.67–1.91) female fledglings per female to 1.11 (0.66–1.87) under the B1 scenario, and 1.09 (0.65–1.85) under the A2 scenario. As a result of the projected increase in adult survival and slight declines in fecundity and juvenile survival, our population model projected an increase in λ from a current expected mean of 0.88 (95% bootstrap interval: 0.84–0.92) under current climatic conditions, to 0.97 (0.91–1.03) under the B1

scenario, and 1.00 (0.93–1.07) under the A2 scenario. Furthermore, even if precipitation under each climate change scenario becomes much drier or wetter than currently projected, we would still project an increase in the population growth rate (Fig. 4b).

Discussion

By conducting a comprehensive study of the effects of weather on both adult and juvenile survival rates, we were able to quantitatively project changes in demography in response to climate change. We considered multiple, direct, and indirect effects of weather on both life stages, and identified strong differences between the effects of weather on adult and juvenile survival, resulting in strong differences in their projected responses to climate change. Our results contribute to the substantial body of literature that has reported differences in the effects of environmental conditions on different life stages (Gaillard *et al.*, 1998; Portier *et al.*, 1998; Altwegg *et al.*, 2005; Oro *et al.*, 2010). Furthermore, our results indicate that juvenile survival was more sensitive to the indirect effects of weather on food availability, whereas adult survival responded primarily to the direct effects of extreme weather.

The indirect effect of prior winter weather accounted for 28% of the variation in annual juvenile survival (Table 2b), and is consistent with the hypothesis that rainy season precipitation is related to increased food availability and/or reduced predation risk during the following spring and summer. However, prior winter weather had little effect on adult survival (Table S3). These results suggest that adults may be able to compensate for reduced food availability or increased predation risk after dry winters, whereas juveniles lack the necessary foraging and predator-avoidance skills. In contrast, adults are likely unable to compensate for the direct, physiological stress of colder winters, and the direct effect of winter weather accounted for 44% of the variation in annual adult survival in this population. Although it was surprising that there was little support for a similar direct effect of winter weather on juvenile survival (Table S3), this does not necessarily mean that juveniles are less sensitive than adults to cold weather. Instead, this result suggests that much of the variation in juvenile survival happens earlier in the year, when the youngest juveniles are especially vulnerable to starvation or predation, and thus especially sensitive to variation in food availability or predation risk. By winter, there may be relatively little variation in juvenile survival remaining that could be accounted for by the direct effects of winter weather. Therefore, even though a warm, dry winter might have a positive direct effect on juvenile survival, as it does for adults, this effect is

outweighed by their sensitivity to the indirect effect of prior winter weather on food availability or predation risk earlier in the year.

Because warm, dry winters were associated with higher adult survival whereas cool, wet winters were associated with higher juvenile survival in the following year (Fig. 3), we projected differences in the response of adult and juvenile survival to climate change (Fig. 4a). When we integrated changes in these demographic rates in a population model, we projected a significant increase in the population growth rate under both the B1 and A2 climate change scenarios. In the absence of immigration, for which our models cannot account, the population is currently expected to decline rapidly ($\lambda = 0.88$), with reproduction rates too low to offset mortality and emigration rates, and consistent with the observed decline in population density (Fig. 2c). Yet, in a future with significantly warmer winters, and all else being equal, the projected increase in adult survival may be sufficient to stabilize or even reverse the declining trend in this population.

Our results underscore the importance of considering multiple effects of weather, as well as differences in the response of each life stage to climate change. If we had assumed that juvenile survival had the same response to warmer winter weather as adults, we would have projected an increase in juvenile survival rates and even larger increases in λ . On the other hand, if the climate model we used had projected a much drier future, we would have expected a stronger decline in both seasonal fecundity and juvenile survival, and thus a smaller increase in the population's growth rate (Fig. 4b). Therefore, we recommend that future efforts to project the effect of climate change on demography: (i) examine the effects of weather on all age classes; (ii) consider multiple direct and indirect effects of weather throughout the annual cycle; and (iii) integrate climate model projections to quantitatively explore the effects of a range of future climate conditions. However, we also recommend keeping in mind that these demographic projections will depend on the accuracy of the climate models on which they are based, and will need to be updated as climate models continue to improve and as different climate scenarios become more likely. In addition, these projections must necessarily assume that all other critical factors influencing the population do not change significantly, such as changes in habitat type or quality, or the introduction of new competitors and predators. Finally, it will be essential to continue monitoring populations to identify changes in the current relationships between weather and demographic processes, such as threshold responses to new climate conditions (Burkett *et al.*, 2005), shifts in plant and insect phenology (Parmesan,

2006), or the evolution of the population itself, as selection pressures change with the climate (Nevoux *et al.*, 2010; Reed *et al.*, 2011).

Although few studies have quantitatively projected changes in demography in response to climate change, this approach provides important insights into the processes that may lead to the expected changes in species distribution. In addition to identifying populations that will be positively, negatively, or neutrally affected by climate change, this approach can identify the demographic process(es) that will be most influenced by climate change as well as indicate the specific mechanisms that may be responsible. While it may be impossible to influence the effects of some of these mechanisms, such as the direct effects of weather on physiological stress, it may be feasible to mitigate some of the indirect effects of weather, such as changes in food availability. Knowing which mechanisms and demographic processes to target will be critical to the development of effective climate change adaptation plans, helping to prioritize future research and identify where limited conservation resources will be most effectively and efficiently spent.

Acknowledgements

This manuscript benefited from comments by M. Holyoak, J. Ackerman, and anonymous reviewers. We are grateful to L. R. Mewaldt, C. J. Ralph, D. DeSante, and G. R. Geupel for establishing and maintaining long-term monitoring at the Palomar Field Station, and to the staff and interns for their contributions to data collection and methodologies. The continued operation of the field station has been made possible by the support of the Point Reyes National Seashore, the members of PRBO, the PRBO Board of Directors, the late Dorothy Hunt, the Chevron Corporation, the Bernard Osher Foundation, the Gordon and Betty Moore Foundation, the National Park Service Inventory and Monitoring Program, the Karen A. & Kevin W. Kennedy Foundation, the Kimball Foundation, the DMARLOU Foundation, a grant from the National Science Foundation (DBI-0533918), and anonymous donors. K. E. Dybala was supported by the UC Davis Graduate Group in Ecology, ARCS Foundation scholarships via the Eileen and Lisa Ludwig Foundation, the National Park Service's G. M. Wright Climate Change Fellowship, the American Ornithologists' Union, the Dennis G. Raveling Endowment, the Selma Herr Fund for Ornithological Research, an Ernest E. Hill Fellowship, the American Museum of Natural History's F. M. Chapman Memorial Fund, and the Western Bird Banding Association. The use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US Government. This is PRBO contribution number 1931.

References

- Adahl E, Lundberg P, Jonzén N (2006) From climate change to population change: the need to consider annual life cycles. *Global Change Biology*, **12**, 1627–1633.
- Adams AAY, Skagen SK, Savidge JA (2006) Modeling post-fledging survival of Lark Buntings in response to ecological and biological factors. *Ecology*, **87**, 178–188.
- Altwegg R, Anderson MD (2009) Rainfall in arid zones: possible effects of climate change on the population ecology of blue cranes. *Functional Ecology*, **23**, 1014–1021.
- Altwegg R, Dummermuth S, Anholt BR, Flatt T (2005) Winter weather affects asp viper *Vipera aspis* population dynamics through susceptible juveniles. *Oikos*, **110**, 55–66.
- Andrewartha HG, Birch LC (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago, IL.
- Arcese P, Sogge MK, Marr AB, Patten MA (2002) Song Sparrow (*Melospiza melodia*). In: *The Birds of North America*, No. 704 (eds Poole A, Gill F). The Birds of North America, Inc., Philadelphia, PA.
- Bale JS, Masters GJ, Hodkinson ID *et al.* (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1–16.
- Barbraud C, Rivalan P, Inchausti P, Nevoux M, Rolland V, Weimerskirch H (2011) Contrasted demographic responses facing future climate change in Southern Ocean seabirds. *Journal of Animal Ecology*, **80**, 89–100.
- Bolger DT, Patten MA, Bostock DC (2005) Avian reproductive failure in response to an extreme climatic event. *Oecologia*, **142**, 398–406.
- Burkett VR, Wilcox DA, Stottemyer R *et al.* (2005) Nonlinear dynamics in ecosystem response to climatic change: case studies and policy implications. *Ecological Complexity*, **2**, 357–394.
- Cayan DR, Maurer EP, Dettinger MD, Tyree M, Hayhoe K (2008) Climate change scenarios for the California region. *Climatic Change*, **87**, 21–42.
- Chase MK, Nur N, Geupel GR (2005) Effects of weather and population density on reproductive success and population dynamics in a Song Sparrow (*Melospiza melodia*) population: a long-term study. *Auk*, **122**, 571–592.
- Choquet R, Lebreton JD, Gimenez O, Reboulet AM, Pradel R (2009) U-CARE: utilities for performing goodness of fit tests and manipulating CAPTURE-RECAPTURE data. *Ecography*, **32**, 1071–1074.
- Coulson TN, Catchpole EA, Albon SD *et al.* (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, **292**, 1528–1531.
- DeSante DF, Geupel GR (1987) Landbird productivity in central coastal California: the relationship to annual rainfall, and a reproductive failure in 1986. *The Condor*, **89**, 636–653.
- Dettinger MD (2005) From Climate-Change Spaghetti to Climate-Change Distributions for 21st Century California. *San Francisco Estuary and Watershed Science*, **3**, Article 4.
- Donovan TM, Thompson FR III (2001) Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. *Ecological Applications*, **11**, 871–882.
- Dybala KE, Gardali T, Eadie JM (2013) Dependent vs. independent juvenile survival: contrasting drivers of variation and the buffering effect of parental care. *Ecology*, **94**, 1584–1593.
- Forcada J, Trathan PN, Murphy EJ (2008) Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Global Change Biology*, **14**, 2473–2488.
- Gaillard J-M, Yoccoz NG (2003) Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, **84**, 3294–3306.
- Gaillard JM, Festa-Bianchet M, Yoccoz NG (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, **13**, 58–63.
- Gardali T, Barton DC, White JD, Geupel GR (2003) Juvenile and adult survival of Swainson's Thrush (*Catharus ustulatus*) in coastal California: annual estimates using capture-recapture analyses. *Auk*, **120**, 1188–1194.
- Geupel GR, DeSante DF (1990) Incidence and determinants of double brooding in Wrentits. *The Condor*, **92**, 67–75.
- Grosbois V, Gimenez O, Gaillard J-M *et al.* (2008) Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews*, **83**, 357–399.
- Hunter CM, Caswell H, Runge MC, Regehr EV, Amstrup SC, Stirling I (2010) Climate change threatens polar bear populations: a stochastic demographic analysis. *Ecology*, **91**, 2883–2897.
- IPCC (2007) *Climate Change 2007: Synthesis Report*. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.
- Jennings S, Gardali T, Seavy NE, Geupel GR (2009) Effects of mist netting on reproductive performance of Wrentits and Song Sparrows in central coastal California. *The Condor*, **111**, 488–496.
- Jenouvrier S, Caswell H, Barbraud C, Holland M, Stroeve J, Weimerskirch H (2009) Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 1844–1847.

- Johnson MD, Geupel GR (1996) The importance of productivity to the dynamics of a Swainson's Thrush population. *The Condor*, **98**, 133–141.
- Jonzén N, Pople T, Knape J, Sköld M (2010) Stochastic demography and population dynamics in the red kangaroo *Macropus rufus*. *Journal of Animal Ecology*, **79**, 109–116.
- Kreyling J (2010) Winter climate change: a critical factor for temperate vegetation performance. *Ecology*, **91**, 1939–1948.
- Laake JL (2013) RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Report 2013-01. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, Seattle, WA.
- Lack D (1954) *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.
- Marchetti K, Price T (1989) Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biological Reviews*, **64**, 51–70.
- McCarty JP (2001) Ecological consequences of recent climate change. *Conservation Biology*, **15**, 320–331.
- McKechnie AE, Wolf BO (2010) Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*, **6**, 253–256.
- McLaughlin BC, Zavaleta ES (2012) Predicting species responses to climate change: demography and climate microrefugia in California valley oak (*Quercus lobata*). *Global Change Biology*, **18**, 2301–2312.
- Nevoux M, Forcada J, Barbraud C, Croxall J, Weimerskirch H (2010) Bet-hedging response to environmental variability, an intraspecific comparison. *Ecology*, **91**, 2416–2427.
- Newton I (1998) *Population Limitation in Birds*. Academic Press, San Diego, CA.
- Nur N, Geupel GR, Ballard G (2004) Estimates of adult survival, capture probability, and recapture probability: evaluating and validating constant-effort mist netting. *Studies in Avian Biology*, **29**, 63–70.
- Oro D, Torres R, Rodríguez C, Drummond H (2010) Climatic influence on demographic parameters of a tropical seabird varies with age and sex. *Ecology*, **91**, 1205–1214.
- Parnesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.
- Peery MZ, Gutiérrez RJ, Kirby R, LeDee OE, LaHaye W (2012) Climate change and spotted owls: potentially contrasting responses in the Southwestern United States. *Global Change Biology*, **18**, 865–880.
- van de Pol M, Vindenes Y, Sæther B-E, Engen S, Ens BJ, Oosterbeek K, Tinbergen JM (2010) Effects of climate change and variability on population dynamics in a long-lived shorebird. *Ecology*, **91**, 1192–1204.
- Portier C, Gaillard J, Jorgenson JT, Yoccoz NG (1998) Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *Journal of Zoology*, **245**, 271–278.
- R Core Development Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reed TE, Schindler DE, Waples RS (2011) Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. *Conservation Biology*, **25**, 56–63.
- Robinson RA, Baillie SR, Crick HQP (2007) Weather-dependent survival: implications of climate change for passerine population processes. *Ibis*, **149**, 357–364.
- Rogers LA, Stige LC, Olsen EM, Knutsen H, Chan K-S, Stenseth NC (2011) Climate and population density drive changes in cod body size throughout a century on the Norwegian coast. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 1961–1966.
- Roy J, Aronson J, di Castri F (eds) (1995) *Time Scales of Biological Responses to Water Constraints: The Case of Mediterranean Biota*. SPB Academic Publishing, Amsterdam.
- Sæther B-E (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology & Evolution*, **12**, 143–149.
- Sæther B-E, Bakke Ø (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, **81**, 642–653.
- Schmidt KA, Rush SA, Ostfeld RS (2008) Wood thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. *Journal of Animal Ecology*, **77**, 830–837.
- Seavy N, Dybala KE, Snyder MA (2008) Climate models and ornithology. *Auk*, **125**, 1–10.
- Sillett TS, Holmes RT, Sherry TW (2000) Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science*, **288**, 2040–2042.
- Skalski JR (1996) Regression of abundance estimates from mark-recapture surveys against environmental covariates. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 196–204.
- Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292–1296.
- Stralberg D, Jongsomjit D, Howell CA, Snyder MA, Alexander JD, Wiens JA, Root TL (2009) Re-shuffling of species with climate disruption: a no-analog future for California birds? *PLoS ONE*, **4**, e6825.
- Tews J, Jeltsch F (2004) Modelling the impact of climate change on woody plant population dynamics in South African savanna. *BMC Ecology*, **4**, 17–28.
- Thomas CD, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Weathers WW, Sullivan KA (1989) Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecological Monographs*, **59**, 223–246.
- Welbergen JA, Klose SM, Markus N, Eby P (2008) Climate change and the effects of temperature extremes on Australian flying-foxes. *Proceedings. Biological Sciences/The Royal Society*, **275**, 419–425.
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46** (Suppl.): 120–138.
- Wolf SG, Snyder MA, Sydeman WJ, Doak DF, Croll DA (2010) Predicting population consequences of ocean climate change for an ecosystem sentinel, the seabird Cassin's auklet. *Global Change Biology*, **16**, 1923–1935.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Sensitivity to missing values of the estimated effects of weather variables on survival.

Table S1. Model-selection results for the presence of long-term trends in Song Sparrow survival.

Table S2. Model-selection results for the difference in effects of weather on adult and juvenile survival.

Table S3. Model-selection results for effects of age, year, weather, and density on survival.