

WILEY



Avian demographic responses to drought and fire

Author(s): James F. Saracco, Stephen M. Fetting, George L. San Miguel, David W. Mehlman, Brent E. Thompson and Steven K. Albert

Source: *Ecological Applications*, OCTOBER 2018, Vol. 28, No. 7 (OCTOBER 2018), pp. 1773-1781

Published by: Wiley on behalf of the Ecological Society of America

Stable URL: <https://www.jstor.org/stable/10.2307/26623272>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

Wiley and Ecological Society of America are collaborating with JSTOR to digitize, preserve and extend access to *Ecological Applications*

Avian demographic responses to drought and fire: a community-level perspective

JAMES F. SARACCO^{1,6} ,^{1,6} STEPHEN M. FETTING,² GEORGE L. SAN MIGUEL,³ DAVID W. MEHLMAN,⁴ BRENT E. THOMPSON,⁵ AND STEVEN K. ALBERT¹

¹The Institute for Bird Populations, P.O. Box 1346, Point Reyes Station, California 94956 USA

²Migratory Bird Program, Pacific Southwest Region, U.S. Fish and Wildlife Service, 2800 Cottage Way, W-1916, Sacramento, California 95825 USA

³Mesa Verde National Park, P.O. Box 8, Mesa Verde, Colorado 81330 USA

⁴The Nature Conservancy, Migratory Bird Program, 316 Osuna Rd NE, Suite 400, Albuquerque, New Mexico 87107 USA

⁵Los Alamos National Laboratory, Mailstop: J978, PO Box 1663, Los Alamos NM 87545

Abstract. Drought stress is an important consideration for wildlife in arid and semiarid regions under climate change. Drought can impact plant and animal populations directly, through effects on their physiology, as well as indirectly through effects on vegetation productivity and resource availability, and by creating conditions conducive to secondary disturbance, such as wildfire. We implemented a novel approach to understanding community-level demographic responses of birds and their habitats to these stressors in the context of climate change at 14 study sites in the Four Corners region of the southwestern United States. A large wildfire affecting three of the sites provided a natural experiment for also examining fire effects on vegetation and the bird community. We assessed (1) trends in drought and end-of-century (2071–2100) predicted average drought conditions under mid-range and high greenhouse gas concentration trajectory scenarios; (2) effects of drought and fire on habitat (vegetation greenness); and (3) effects of drought and fire on community-level avian productivity and adult apparent survival rates. Drought has increased and is expected to increase further at our study sites under climate change. Under spring drought conditions, vegetation greenness and avian productivity declined, while summer drought appeared to negatively affect adult apparent survival rates. Response to fire was mixed; in the year of the fire, avian productivity declined, but was higher than normal for several years post-fire. Our results highlight important links between environmental stressors and avian vital rates that will likely affect population trajectories in this region under climate change. We suggest that the use and continued development of community-level demographic models will provide useful tool for leveraging sparse species-level data to provide multi-species inferences and inform conservation.

Key words: avian demography; capture–recapture; drought; fire; hierarchical model; MAPS program; mist-netting; productivity; survival; vital rates.

INTRODUCTION

Anthropogenically caused climate and habitat changes are expected to cause widespread wildlife population declines, range shifts, and loss of biodiversity (Bellard et al. 2012). Approaches to understanding ecological responses to environmental change have largely been based on models relating species occurrence or abundance to current environmental conditions and predicting responses under environmental change scenarios (Berry et al. 2002, Pearson and Dawson 2003, Albright et al. 2009). These models have yielded important insights and have provided inferences for a variety of ecological responses, including species distribution and abundance, richness, and community composition (Hijmans and Graham 2006, Stralberg et al. 2009). Nevertheless, these models lack ecological detail (Mustin et al. 2007) and demographic mechanisms, by which populations and communities respond to their environment, remain poorly understood (McMahon et al. 2011, Selwood et al. 2015).

Approaches that model responses of demographic rates as functions of environmental covariates offer an alternative that may provide a more mechanistic understanding population dynamics under environmental change. However, ecological inferences from these models have generally been restricted to population-level parameters. Demographic responses at the community level may also be of interest, but there are currently few examples of multi-species demographic models in ecology (Lahoz-Monfort et al. 2011, Lloyd et al. 2014). Development of community-level demographic models in the context of multi-species monitoring efforts, where there are typically insufficient data for developing models of individual species, offers the opportunity to improve our understanding of higher-level ecological responses to environmental change and provide greater insights for conservation planning and adaptation.

Here, we develop community-level models of demographic rates within a Bayesian hierarchical modeling framework to understand avian responses to drought and fire in the Four Corners region of the semiarid southwestern United States. Precipitation has declined while temperatures have risen in this region over the past century. These conditions have led to increased severity and frequency of drought, a trend that is expected to worsen in the coming decades (Seager et al. 2007, Diffenbaugh et al. 2008). Drought can depress avian

Manuscript received 13 December 2017; revised 20 April 2018; accepted 27 April 2018. Corresponding Editor: Dianne Brunton. [Correction made 30 August, 2018: Author Brent E. Thompson was added after the article was published.]

⁶E-mail: jsaracco@birdpop.org

abundance and richness at local and regional scales (George et al. 1992, Albright et al. 2009) and may be an important driver of demographic rates and population viability (Selwood et al. 2015, Cruz-McDonnell and Wolf 2016). Drought may affect demographic rates directly through increased mortality or lowered reproductive investment due to dehydration and physiological stress (Albright et al. 2017) or indirectly through effects on habitat and food resources (Assal et al. 2016). Drought can also lead to secondary disturbances that further impact populations, such as fires, insect outbreaks, or tree mortality events. All of these events are expected to become larger, more frequent, and more intense under climate change (Dale et al. 2001, Kolb et al. 2016).

To better understand historical and potential future effects of drought on habitat and bird communities across our study region, we leveraged data collected at 14 study sites as part a large cooperative demographic monitoring effort, the Monitoring Avian Productivity and Survivorship (MAPS) program (Saracco et al. 2008) and remote-sensed habitat (Glenn et al. 2008) and climate (Wang et al. 2016) data to model relationships among drought, fire, vegetation, and avian demography. We assessed (1) trends in drought and end-of-century (2071–2100) predicted average drought conditions under mid-range and high greenhouse gas concentration trajectory scenarios; (2) effects of drought and fire on habitat (vegetation greenness); and (3) effects of drought and fire on avian productivity and adult apparent survival rates.

MATERIALS AND METHODS

Study areas and field methods

Study sites were in two protected areas, Bandelier National Monument (BNM) and Mesa Verde National Park (MVNP), and in eight nearby areas (<200 km from park sites) not currently experiencing major land-use change (Fig. 1). The eight nearby, relatively undisturbed sites provide important context, monitoring, and management opportunities for understanding population and community responses to environmental change (Baron et al. 2009, Monzón et al. 2011). We operated three mist-netting stations in BNM and three stations in MVNP during the breeding seasons (May–August) of 2010–2015 according to protocols of the MAPS program (DeSante et al. 2004, DeSante and Kaschube 2009). The additional eight MAPS stations followed the same operating protocols for varying numbers of years between 1998 and 2015 (Appendix S1). Stations spanned a gradient of montane woodland, meadow, and forest habitats of the southern Rockies and Colorado Plateau of the United States. Habitats at all but the BNM stations were relatively stable throughout the years they were operated. In contrast, the BNM stations were subject to large-scale habitat change when impacted by the Las Conchas fire starting in late June 2011.

Each mist-netting station consisted of 10–13 12 × 2.5 m, 30-mm mesh, four-tier nylon mist nets operated within the central 8 ha of an approximately 20-ha sampling area. With few exceptions, nets were opened for approximately 6 h (beginning at about local sunrise) once per 10-d sampling period between 9 May and 6 August (8–10 sampling days

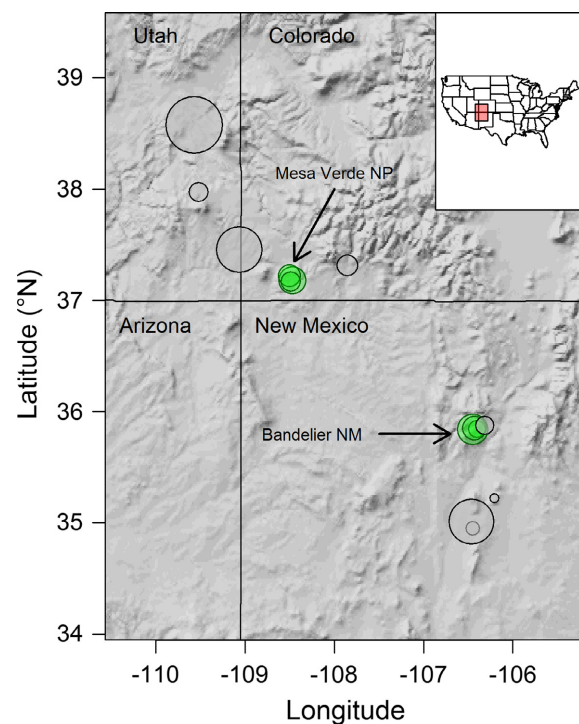


FIG. 1. Locations of Monitoring Avian Productivity and Survivorship (MAPS) stations included in the analysis. Stations in Bandelier National Monument (New Mexico, USA) and Mesa Verde National Park (Colorado, USA) are indicated with green circles. Additional stations used in the analysis within 200 km of these sites in Utah, Colorado, and New Mexico are indicated with gray circles. Symbols are scaled by sample size (total year-unique captures). See Appendix S1: Table S1 for additional detail.

per station per year). Mist-netting stations at MVNP were limited to 4 h per day for the safety of the birds because morning temperatures increase rapidly in the pinyon-juniper habitats where these stations were located. With few exceptions, we identified all birds captured in mist nets to species, age (young, hatching year; adult, after hatching year), and sex (based on Pyle 1997) and banded them with U.S. Geological Survey numbered aluminum leg bands. We recorded band numbers of all recaptures. This research was conducted in compliance with *Guidelines to the use of wild birds in research* (Fair et al. 2010), and all required permits were obtained by the authors and collaborators in the MAPS program.

Climate and vegetation data

We characterized drought conditions using Hargreave's climate moisture deficit (CMD; Wang et al. 2012), a derived variable in the ClimateNA data base (*available online*).⁷ ClimateNA uses bilinear interpolation of monthly gridded climate data and local elevation adjustments to provide "scale-free" climate metrics for individual points (Wang et al. 2016). CMD was calculated as the monthly summed difference between atmospheric evaporative demand (E_{ref} ; Hargreaves and Samani 1982) and precipitation. We

⁷<https://sites.ualberta.ca/~ahamann/data/climatena.html>

extracted spring (March–May) and summer (June–August) CMD values for the 14 MAPS stations for all years available in the ClimateNA data base (1902–2015), for the years 1981–2010 to compute reference values, and for expected CMD values for 2071–2100 based on model-averaged predictions from 15 atmosphere–ocean global climate models (AOGCMs) of the Climate Model Intercomparison Project (Knutti et al. 2013, IPCC 2014). For the future time period (2071–2100), we considered two greenhouse gas concentration trajectory scenarios (Representative Concentration Pathways [RCPs]; Taylor et al. 2012, IPCC, 2014), RCP 4.5 and RCP 8.5. Under RCP 4.5, considered a mid-range emissions reductions scenario, greenhouse gas emissions peak around 2040 and then decline, while under RCP 8.5, a high-emissions scenario, emissions continue to rise throughout the 21st century.

Because our stations spanned a variety of habitat types and we were primarily interested in assessing climate effects on vital rates, rather than habitat effects, we calculated CMD covariates as deviations from 1981–2010 reference values for both spring (CMDsp.dev) and summer (CMDsm.dev).

One way in which drought is expected to affect bird habitat is through limiting the amount of vegetation growth in spring and summer. To better understand the relationship between spring and summer CMD deviations (CMDsp.dev and CMDsm.dev) and vegetation greenness, we used Enhanced Vegetation Index (EVI) data from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument of NASA's Terra satellite summarized at 0.25-km resolution (MODIS product MOD13Q1; EVI data available online).⁸ EVI is a composite metric that incorporates structural and seasonal components of vegetation greenness, including primary productivity (leaf chlorophyll content), leaf area, canopy cover, and vegetation complexity (Glenn et al. 2008, Potithepa et al. 2010). We extracted interpolated bimonthly EVI values averaged over the 81 pixels within 1 km of station coordinates using the MODISsubsets function of the R package MODISTools (Tuck et al. 2014). To relate EVI to the spring CMD deviation (CMDsp.dev), we created a spring EVI deviation response variable, EVIsp.dev, by averaging EVI for each station across dates corresponding to 24 May and 9 June of each year from 2000 to 2015 (the entire MODIS-EVI time series) and then subtracting these year-specific values from the station average EVI values for these dates across all years. We calculated an analogous EVI deviation value for summer (EVIsm.dev) using EVI dates of 11 and 27 July.

Statistical analyses

Historical trends in drought.—We implemented regressions of spring and summer drought deviations as linear functions of year to infer historical trends in drought. Autocorrelograms suggested no significant temporal autocorrelation in drought deviations for any station; thus, we assumed independence of residuals in the standard linear regression context.

⁸ <http://terra.nasa.gov/>

Drought and fire effects on vegetation greenness.—We examined relationships between drought and fire and vegetation greenness deviations with linear mixed effects models. We regressed EVI deviations (EVIsp.dev_{j,t} and EVIsm.dev_{j,t}, where *j* indexes station and *t* indexes year) on standardized CMD deviation covariates (CMDsp.dev_{j,t} and CMDsm.dev_{j,t}) and covariates representing initial fire impact (fire_{j,t}; where fire_{j,t} is a 0–1 indicator variable denoting post-fire years at the BNM stations) and linear trend in fire effect in the years following the fire (fire.tr_j; is a linear year effect following the fire at the BNM stations). We allowed intercepts and slopes to vary randomly by station

$$\text{EVIsp.dev}_{j,t} = \beta_{0,j} + \beta_{1,j} \times \text{CMDsp.dev}_{j,t} + \beta_{2,j} \times \text{fire}_{j,t} + \beta_{3,j} \times \text{fire.tr}_{j,t} + \epsilon_j$$

and

$$\text{EVIsm.dev}_{j,t} = \beta_{0,j} + \beta_{1,j} \times \text{CMDsm.dev}_{j,t} + \beta_{2,j} \times \text{fire}_{j,t} + \beta_{3,j} \times \text{fire.tr}_{j,t} + \epsilon_j.$$

Drought and fire effects on avian productivity.—We implemented a multi-species generalized linear mixed effects model to examine the relationship between drought and avian productivity. We included 51 species with ≥50 yr-unique (i.e., individual × year) captures in the analysis (Appendix S3: Table S1). We modeled the probability of a captured bird (indexed by *i*) being a young (hatching year) bird ($p[Y_{i,j,s,t}]$) as a logit-linear function of a random species intercept ($\beta_{0,s}$), spring drought ($\beta_{1,s} \times \text{CMDsp.dev}_{j,t}$), initial impact of the fire at the BNM sites ($\beta_2 \times \text{fire}_{j,t}$), post-fire year effects at the BNM sites ($\beta_{3,s} \times \text{fire}_{j,t}$), post-fire trend ($\beta_{4,s} \times \text{fire.tr}_{j,t}$, where fire.tr_{j,t} is a linear year effect following the fire at the BNM stations), and random station-scale error (ϵ_j)

$$\text{logit}(p[Y_{i,j,s,t}]) = \beta_{0,s} + \beta_{1,s} \times \text{CMDsp.dev}_{j,t} + \beta_2 \times \text{fire}_{j,t} + \beta_{3,s} \times \text{fire}_{j,t} + \beta_{4,s} \times \text{fire.tr}_{j,t} + \epsilon_j.$$

Drought and fire effects on avian survival.—We implemented a multi-species version of a Cormack-Jolly-Seber (CJS) model allowing for transients in the data set (Saracco et al. 2010) to model adult apparent survival rates. For the CJS model, we included adult (after hatching year) capture history data for a reduced set of 29 species with ≥5 between-year recaptures at 13 stations with ≥2 yr of data (Appendix S3: Table S2). For the survival component of the model, we defined a logit-linear model allowing survival probability, $\phi_{i,j,s,t}$ to vary as a function of a random species intercept ($\text{logit}(\phi_{0,s})$), summer drought ($\beta_{1,s} \times \text{CMDsm.dev}_{j,t}$), initial fire impact over the interval between the summer of the BNM fire and the following summer ($\beta_2 \times \text{fire}_{j,2011}$), and zero-mean random station × species error ($\epsilon_{j,s}^\phi$)

$$\text{logit}(\phi_{i,j,s,t}) = \text{logit}(\phi_{0,s}) + \beta_{1,s} \times \text{CMDsm.dev}_{j,t} + \beta_2 \times \text{fire}_{j,2011} + \epsilon_{j,s}^\phi.$$

Recapture data were too sparse to support species-specific fire effects or additional fire covariates. In addition to the

model for survival, the CJS model requires sub-models for two nuisance parameters, probability of predetermining a resident, ρ , and recapture probability, p , as well as an additional parameter, π , representing the probability of a newly marked bird in the sample being a resident individual. We allowed each of these parameters to vary by species but added no additional constraints. For p , we included an additional zero-mean random station $\times$ species effect, $\varepsilon_{j,s}^p$, analogous to that which we included in the survival model.

Note that for our multi-species avian productivity and survival models, we assumed a general model structure that allowed all intercepts and covariate relationships to vary by species, except for initial fire effects on productivity in the year of the Las Conchas fire (which we assumed would be similarly negative among species) and for the fire interval effect on survival (for which species-level recapture data were sparse). These model structures represented what we viewed as the most parsimonious representation of our hypotheses, given the data available. For all models, we assumed β s to be distributed according to $\text{Norm}(\mu_\beta, \sigma_\beta^2)$. We used vague prior distributions for hyperparameters of the model random effects. For the CJS model, we used $U(0, 1)$ prior probabilities for the predetermined residency and residency parameters (ρ_s and π_s) as well as for recapture and survival probability intercepts on inverse-logit scale (i.e., on the scale of the real parameters). We implemented models in JAGS (Plummer 2003) using the `jagsUI` package (Kellner 2015) in R (R Core Team 2015). We obtained posterior distributions by sampling the full conditional distributions using Markov chain Monte Carlo (MCMC) methods (Gilks et al. 1996) as implemented in JAGS (Plummer 2003). Posteriors were based on four chains of 30,000 iterations after discarding the first 10,000 iterations and thinning by three.

RESULTS

Moisture deficit conditions have tended to increase over the past century (1902–2015; Appendix S2), were high during the study period (1998–2015) relative to the 1981–2000 reference values (mean CMDsp.dev and CMDsm.dev all >0) and are expected to increase further for the 14 study areas under climate change regardless of the emissions reduction scenario used (Fig. 2). Annual drought conditions were significant predictors of relative vegetation greenness (deviations in the enhanced vegetation index (EVI) in both spring ($\hat{\mu}_{\beta_1} = -0.009$; 95% credible interval: $-0.013, -0.006$; Fig. 3A) and summer ($\hat{\mu}_{\beta_1} = -0.006$; 95% credible interval: $-0.009, -0.002$; Fig. 3B). In addition, vegetation greenness sharply declined in spring from the previous year following the Las Conchas fire at BNM sites ($\beta_2 = -0.083$; 95% credible interval: $-0.112, -0.054$; Fig. 3C), and in the summer of the fire ($\beta_2 = -0.197$; 95% credible interval: $-0.227, -0.167$; Fig. 3D). Vegetation greenness has since increased in both spring ($\beta_2 = 0.009$; 95% credible interval: $0.003, 0.016$) and summer ($\beta_2 = 0.041$; 95% credible interval: $0.033, 0.048$). Estimated spring EVI levels were still slightly low compared to pre-fire values (mean = 0.003 ; 95% credible interval: $-0.109, -0.051$ pre-fire vs. mean = -0.023 ; 95% credible interval = $-0.044, -0.001$ in 2015), while summer EVI estimates exceeded those observed prior to the Las Conchas fire by the end of the study (mean = 0.004 ; 95%

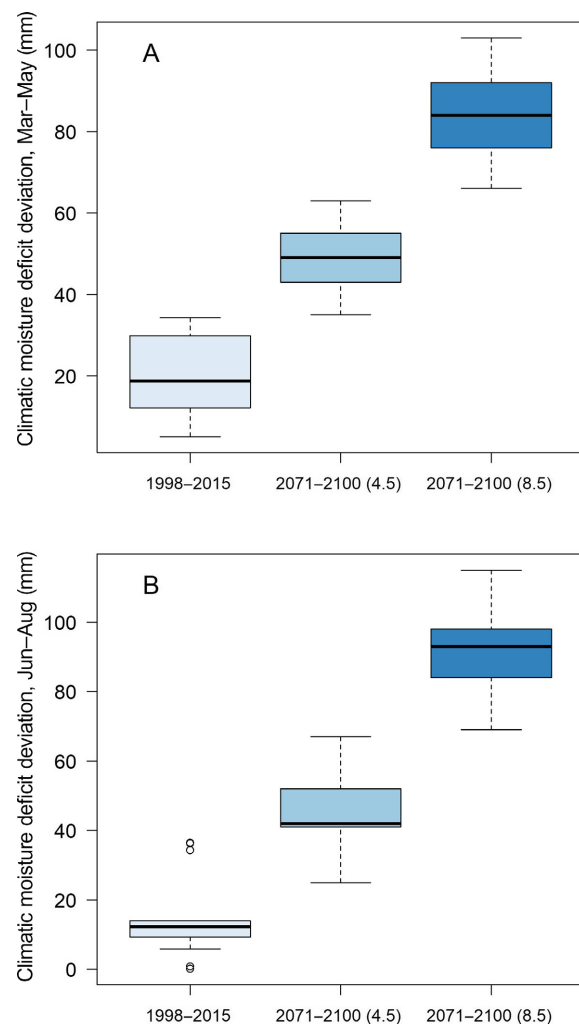


FIG. 2. Drought conditions in (A) spring (March–May) and (B) summer (June–August) at MAPS sites on the Colorado Plateau. Drought conditions are presented as deviations from 1981–2000 reference values of Hargreaves climatic moisture deficit derived from the ClimateNA data set (<http://www.climatewna.com>) for annual mean values from the current period during which MAPS stations were operated (1998–2015; light blue) and for predicted mean values for 2071–2100 under two greenhouse gas emission scenarios, RCP 4.5 (medium blue) and RCP 8.5 (dark blue). Boxplots delineate medians (mid line), quartile limits (upper and lower box edges), $1.5 \times$ interquartile range (IQR; whiskers) and outliers ($>1.5 \times$ IQR; points).

credible interval: $0.002, 0.010$ pre-fire vs. mean = 0.040 ; 95% credible interval $0.016, 0.065$ in 2015).

Avian productivity declined as a function of relative spring drought severity ($\hat{\mu}_{\beta_1} = -0.298$; 95% credible interval: $-0.421, -0.173$; Fig. 4A; Appendix S3: Table S1). Model predictions suggest that average avian productivity might decline by 16% (RCP 4.5) to 33% (RCP 8.5) by the end of the century under climate change. Bird species showing the strongest negative effects of drought on productivity included a nectarivore (Bullock's Oriole), ground foragers (American Robin, Song Sparrow), and an insectivore (Ruby-crowned Kinglet; all with $\beta_1 < 0.6$). Among bird species with productivity apparently least affected by drought ($\hat{\beta}_1 > 0$) were species that fed on conifer seeds (Mountain

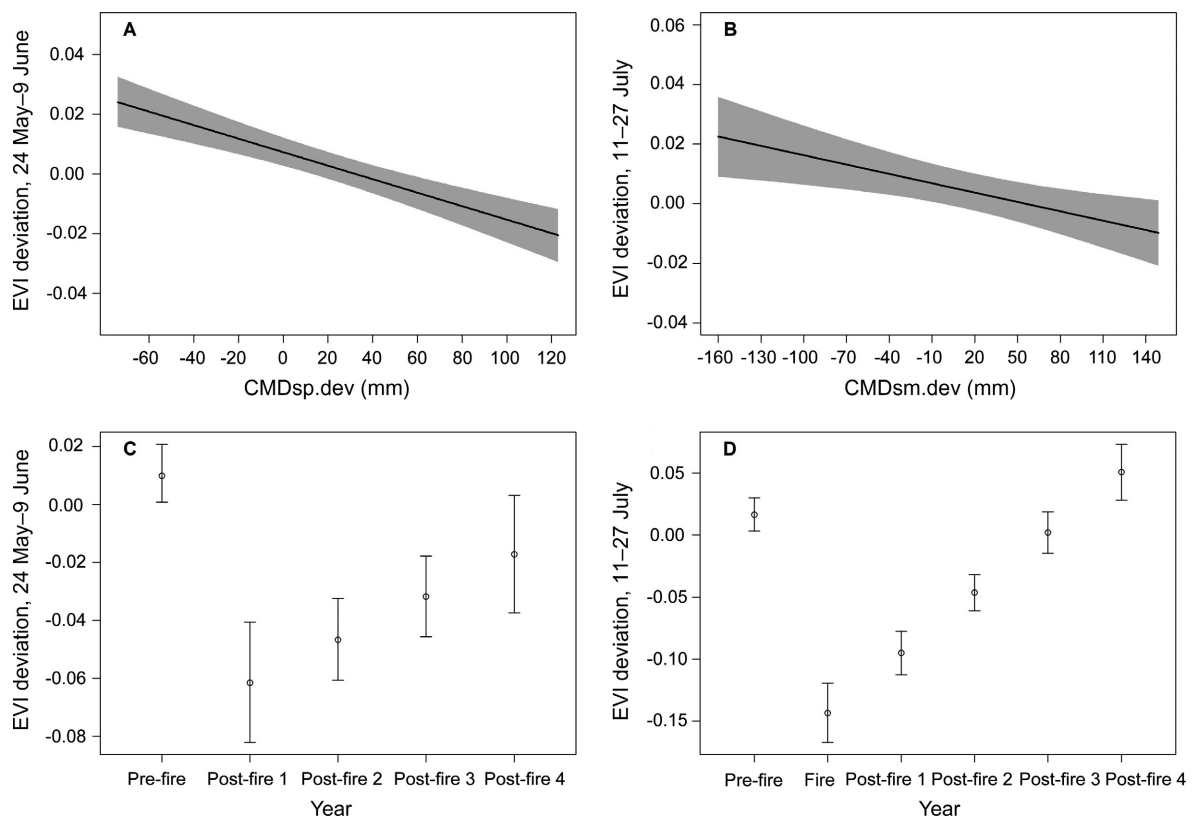


FIG. 3. Relationship between relative drought conditions and vegetation greenness during (A) spring (March–May) and (B) summer (June–August) and estimated effects of fire on vegetation greenness during (C) spring and (D) summer. Drought conditions in spring (CMDsp.dev) and summer (CMDsm.dev) are represented as deviations from 1981–2000 reference values of Hargreaves climatic moisture deficit derived from the ClimateNA data set (<http://www.climatewna.com>). Vegetation greenness was calculated as annual deviations from mean 2000–2015 values; EVI, enhanced vegetation index. Fire effects in panels C and D were estimated based on data from the BNM sites in the year of the Las Conchas Fire (summer only; D), and in years following the fire (Post-fire 1, 2, etc.). Gray areas (A and B) and error bars (C and D) delineate 95% credible intervals.

Chickadee, House Finch) and several warbler species (Orange-crowned Warbler, MacGillivray's Warbler, and Wilson's Warbler).

We found effects of fire at BNM both in the year of its occurrence and for several seasons afterward (Fig. 4B; Appendix S3: Table S1). After initial decline in avian productivity in the year of the Las Conchas fire ($\hat{\beta}_2 = -1.847$; 95% credible interval: $-3.364, -0.645$), productivity increased sharply in the following year ($\hat{\mu}_{\beta_3} = 1.962$; 95% credible interval: $0.338, 2.628$), then gradually declined ($\hat{\mu}_{\beta_4} = -0.522$; 95% credible interval: $-0.737, -0.296$) to near the pre-fire mean by the fourth year post-fire (Fig. 4B). The increase in avian productivity in the year following the fire was consistently strong among species, ranging from $\hat{\beta}_3 = 1.04$ (95% credible interval: $-0.43, 2.30$) for American Robin to a high of $\hat{\beta}_3 = 2.78$ (95% credible interval: $2.02, 3.60$) for Chipping Sparrow. The decline following this post-fire pulse in avian productivity was also relatively consistent among species ranging from $\hat{\beta}_3 = -0.31$ (95% credible interval: $-0.67, 0.20$) for Mountain Chickadee to a relatively steep decline for Pine Siskin $\hat{\beta}_3 = -0.83$ (95% credible interval: $-1.55, -0.40$) (Appendix S3: Table S1).

Estimates of adult apparent survival probability were relatively consistent among species, averaging 0.51 (95% credible

interval: 0.33, 0.68), and ranging from a low of $\hat{\phi}_{0,s} = 0.42$ (95% credible interval: 0.26, 0.59) for Bushtit to a high of $\hat{\phi}_{0,s} = 0.58$ (95% credible interval: 0.42, 0.73) for Ash-throated Flycatcher (Appendix S3: Table S2). As for productivity, mean adult apparent survival rates also appeared to depend on drought conditions ($\hat{\mu}_{\beta_1} = -0.233$; 95% credible interval: $-0.452, -0.022$; Fig. 5A). These results suggest that average adult apparent survival would decline by about 7% (RCP 4.5) to 16% (RCP 8.5) due to climate change. Negative effects of drought on survival were relatively strong for several resident and short-distance migrant species, including Gray Vireo, Black-capped Chickadee, House Wren, Spotted Towhee, and Dark-eyed Junco (Appendix S3: Table S2). Fire did not appear to affect survival in the year of the fire ($\hat{\beta}_2 = 0.310$; 95% credible interval: $-0.291, 0.949$; Fig. 5B).

DISCUSSION

Approaches to assessing ecological impacts of anthropogenic change have largely been based on models of distribution or abundance data or on data on the phenology of life history events (Walther et al. 2002, Miller-Rushing et al. 2010, McMahon et al. 2011, Bellard et al. 2012). Given the

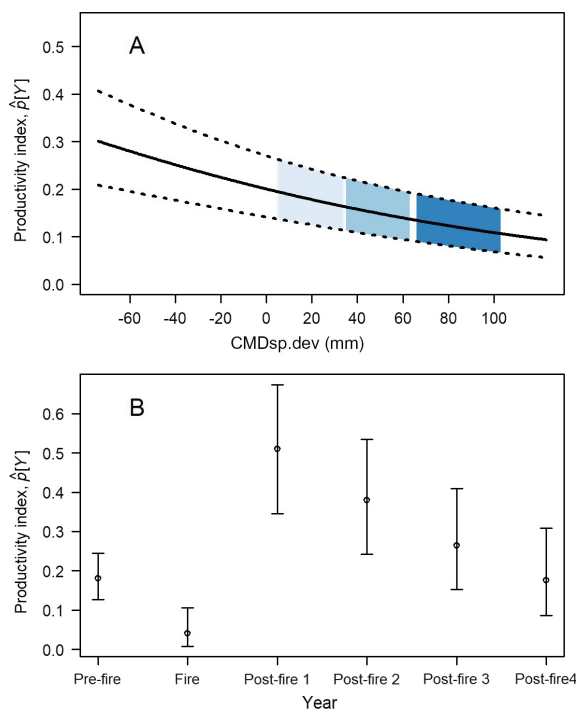


FIG. 4. Relationship between avian productivity, $\hat{p}(Y)$, and (A) spring drought conditions (CMDsp.dev) and (B) fire disturbance. Dashed lines (A) and error bars (B) delineate 95% credible intervals. Ranges of average current (light blue) and future (medium blue [4.5] and dark blue [8.5]) drought conditions are indicated in panel A to provide perspective on how average productivity may be expected to change under average future conditions (see Fig. 2). Fire effects were estimated based on data from the BNM sites following the Las Conchas Fire in June 2011. Postfire 1, 2, etc. in panel B indicate years since the Las Conchas Fire.

typically greater cost in data generation, demographic data (i.e., data on vital rates, such as productivity, recruitment, and survival) are available for a relatively small number of taxa and geographic regions. However, when available, linking such data to environmental change offers a potentially powerful tool for providing a more mechanistic understanding of how populations and communities respond to changing environments. Avian monitoring programs based on capture-recapture methods have been implemented at continental scales for decades (Robinson et al. 2009) and offer the opportunity to develop models of demographic responses to climate and habitat change. Typically, data from such programs are insufficient for estimating vital rates at spatial scales of individual study areas or even small clusters of study areas for most species sampled. Our multi-species modeling approach allowed us to take advantage of the relatively sparse data available for individual species and make broader inferences about community demographic responses to environmental covariates (Ovaskainen and Soininen 2011). Such models have so far received little attention in ecology (Lahoz-Monfort et al. 2011, Lloyd et al. 2014), but with the advent of Markov chain Monte Carlo methods for estimating parameters of these models in a hierarchical modeling framework, these models have become an approachable avenue for developing community-level demographic models (Kéry and Schaub 2011, Kéry and Royle 2016). A core assumption of our model is a unimodal

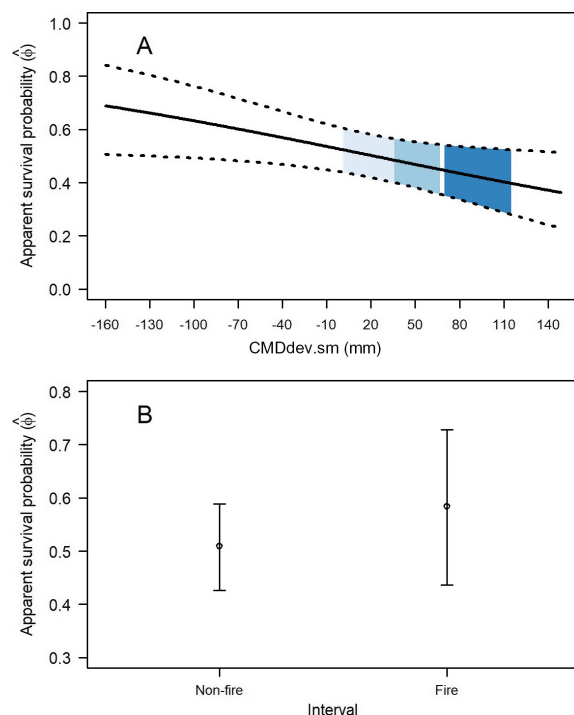


FIG. 5. (A) Relationship between adult apparent survival probabilities and summer drought conditions (CMDsm.dev) and (B) estimated mean adult apparent survival probabilities ($\pm$ 95% credible intervals) during non-fire and fire intervals. The solid line in panel A shows mean predictions; dashed lines indicate 95% credible intervals. Ranges of average current (light blue) and future (medium blue [RCP 4.5] and dark blue [RCP 8.5]) drought conditions are included in A to provide perspective on how average survival may be expected to change under average future conditions (see Fig. 2).

response of species' demographic rates to covariates. Although this assumption may not always be reasonable, we believe that it is an accurate portrayal of the avian communities represented here.

We showed that early spring drought conditions in the Four Corners region of the southwestern United States influence vegetation greenness later in spring when most birds initiate breeding activities. In drier years with lower vegetation greenness, community avian productivity was comparatively low. This provides context for other studies that have reported negative drought effects on avian productivity of individual species at local scales (George et al. 1992, Cruz-McDonnell and Wolf 2016) and effects of drought on community-level metrics, such as declines in abundance or species richness and changes in community composition at landscape and regional scales (Smith 1982, Albright et al. 2009). We found the strongest negative effects of drought for the nectarivorous Bullock's Oriole and the most positive effects on Mountain Chickadee and House Finch. This is consistent with Smith (1982) who found nectarivores to disappear completely during a drought year and positive responses of granivores to increased cone crops following drought in subalpine habitats of Utah and Idaho.

Drought conditions later in summer also appeared to have negatively affected apparent survival rates of adult birds. This was interesting given that survival of many migrant

songbirds is generally thought to be driven largely by non-breeding season conditions (Sillett et al. 2000, Faaborg et al. 2010). However, it should be noted that individual species drought effects showed low precision and all had 95% credible intervals that overlapped zero. Low precision may have been due in part to relatively few between-year recaptures and low recapture probability (mean ~ 0.25) but also potentially to heterogeneity among individuals of each species in responses to drought. In addition, species that showed strongest effects of summer drought on survival were residents or short-distance migrants that may have been affected by regional climate patterns that were similar between breeding and wintering areas and across seasons.

Despite variability in bird communities, habitats, and local climate conditions among study sites, we were able to detect a common signal in the responses of vegetation greenness and avian demography to climate variation. We suggest that this common signal reflects such processes as early spring precipitation determining levels of understory growth, which in turn can affect availability of potential nest sites as well as food resources. Nevertheless, habitat variation may also play an important role in how resilient sites are to variable climate conditions. For example, sites dominated by Utah juniper (*Juniperus osteosperma*) may be expected to be more heavily impacted by depressed summer precipitation than mixed conifer sites, due to the relatively shallow root system of that species. We suggest that identification of habitat features that mitigate against potential negative consequences of drought on ecological communities should be a priority for future research.

The Las Conchas fire at the BNM study sites allowed us to also incorporate fire effects into our demographic models. Although avian productivity was very low in the year of the fire, it spiked in the following year and remained relatively high until the fourth year post-fire (Fig. 4A). The positive effect of fire on overall avian productivity in the initial years following fire may have resulted from enhanced understory growth and food resources in those initial years (Bock and Block 2005). It should be noted, however, that the Las Conchas fire in the area of the BNM study sites was not an intense stand-replacing event. Thus the habitat and avian community remained relatively intact. Wildfires of higher intensity could have changed the habitat structure of these sites much more dramatically. Although a variety of studies have assessed responses of avian abundance or occupancy to fire, we are unaware of studies linking avian productivity to fire. Furthermore, despite the importance of fire in shaping historical Southwestern ecosystems, there are relatively few data available for assessing avian responses to this disturbance type (Bock and Block 2005, Dickson et al. 2009, Kalies et al. 2010). The need for better information on drought and secondary disturbances, such as fire, is critical given the likely increased role these factors will play in shaping vegetation and wildlife habitat in the coming decades due to climate change (Seager et al. 2007, Diffenbaugh et al. 2008).

By taking advantage of remote-sensed vegetation data and a multi-site, multi-species monitoring data set that spanned a range of drought conditions and included a natural fire disturbance, we gained insight into how these factors can change the state and trajectory of habitats and the vital

rates of the bird community that depends on them. For our multi-species demographic models, we only considered a single representation of covariate effects on affect responses that reflected our initial hypotheses about drought and fire effects on demographic rates. However, we suggest that additional development of these methods in a multi-hypothesis model-selection framework would further broaden the potential of these models. In addition, these applications can be developed further in the context of predicting average population changes for groups of species based on vital rate-environment relationships under different management or climate change scenarios. Applications such as this thus provide important additional suite of metrics for guiding wildlife management in the context of future environmental change.

ACKNOWLEDGMENTS

Danielle Kaschube and Ron Taylor vetted and prepared MAPS data. We are grateful to those who contributed to MAPS data collection, especially station managers A. Anderson, S. Cox, C. Hathcock, J. Harris, L. Kamees, S. Milligan, J. Parrish, L. Smith, H. White, and L. Wickersham. We express thanks to the National Park Service (NPS) Office of International Affairs, Mesa Verde National Park, Bandelier National Monument, Pajarito Environmental Education Center, University of Arizona, Northern Arizona University, and the Rio Grande Bird Research, for providing valuable assistance and support for data collection. The paper benefited from comments of two anonymous reviewers. This project was supported with funding from the NPS, especially from the Intermountain Region's International Conservation Program Office, through The Nature Conservancy's Migratory Bird Program. Any use of trade, product, website, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is publication no. 586 of The Institute for Bird Populations. J.F.S., S.M.F., G.L.S.M., D.W.M., and S.K.A. conceived the study. B.E.T. and S.M.F. contributed field data. J.F.S. analyzed the data and wrote the manuscript with contributions from S.M.F., G.L.S.M., D.W.M., and S.K.A. All authors approved the final version of the manuscript.

LITERATURE CITED

- Albright, T. P., A. M. Pidgeon, C. D. Rittenhouse, M. K. Clayton, C. H. Flather, P. D. Culbert, B. D. Wardlow, and V. C. Radeloff. 2009. Effects of drought on avian community structure. *Global Change Biology* 16:2158–2170.
- Albright, T. P., D. Mutibwa, A. R. Gerson, E. K. Smith, W. A. Talbot, J. J. O'Neill, A. E. McKechnie, and B. O. Wolf. 2017. Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences USA* 114:2283–2288.
- Assal, T. J., P. J. Anderson, and J. Sibold. 2016. Spatial and temporal trends of drought effects in a heterogeneous semi-arid forest ecosystem. *Forest Ecology and Management* 365:137–151.
- Baron, J. S., L. Gunderson, C. D. Allen, E. Fleishman, D. McKenzie, L. A. Meyerson, J. Oropeza, and N. Stephenson. 2009. Options for national parks and reserves for adapting to climate change. *Environmental Management* 44:1033–1042.
- Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters* 15:365–377.
- Berry, P. M., T. P. Dawson, P. A. Harrison, and R. G. Pearson. 2002. Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography* 11:453–462.
- Bock, C. E., and W. M. Block. 2005. Fire and birds in the southwestern United States. *Studies in Avian Biology* 30:14–32.

- Cruz-McDonnell, K. K., and B. O. Wolf. 2016. Rapid warming and drought negatively impact population size and reproductive dynamics of an avian predator in the arid southwest. *Global Change Biology* 22:237–253.
- Dale, V. H., et al. 2001. Climate change and forest disturbances. *BioScience* 51:723.
- DeSante, D. F., and D. R. Kaschube. 2009. The monitoring avian productivity and survivorship (MAPS) program 2004, 2005, and 2006 report. *Bird Populations* 9:86–169.
- DeSante, D. F., J. F. Saracco, D. R. O'Grady, K. M. Burton, and B. L. Wal. 2004. Methodological considerations of the monitoring avian productivity and survivorship (MAPS) program. *Studies in Avian Biology* 29:28–45.
- Dickson, B. G., B. R. Noon, C. H. Flather, S. Jentsch, and W. M. Block. 2009. Quantifying the multi-scale response of avifauna to prescribed fire experiments in the southwest United States. *Ecological Applications* 19:608–621.
- Diffenbaugh, N. S., F. Giorgi, and J. S. Pal. 2008. Climate change hotspots in the United States. *Geophysical Research Letters* 35: L16709.
- Faaborg, J., et al. 2010. Conserving migratory land birds in the New World: Do we know enough? *Ecological Applications* 20:398–418.
- Fair, J., E. Paul, and J. Jones, editors. 2010. Guidelines to the use of wild birds in research. Ornithological Council, Washington, D.C., USA. <http://www.nmnh.si.edu/BIRDNET/guide/>
- George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. *Ecological Applications* 2:275–284.
- Gilks, W. R., S. Richardson, and D. J. Spiegelhalter. 1996. Introducing Markov chain Monte Carlo. Pages 1–20 in W. R. Gilks, S. Richardson, and D. J. Spiegelhalter, editors. *Markov chain Monte Carlo methods in practice*. Chapman and Hall, New York, New York, USA.
- Glenn, E. P., A. R. Huete, P. L. Nagler, and S. G. Nelson. 2008. Relationship between remotely-sensed vegetation indices, canopy attributes and plant physiological processes: what vegetation indices can and cannot tell us about the landscape. *Sensors (Basel, Switzerland)* 8:2136.
- Hargreaves, G. H., and Z. A. Samani. 1982. Estimating Potential Evapotranspiration. *Journal of the Irrigation and Drainage Division* 108:225–230.
- Hijmans, R. J., and C. H. Graham. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* 12:2272–2281.
- IPCC. 2014. Climate Change 2014: Synthesis Report. Pages 151 in Core Writing Team, R. K. Pachauri, and L. A. Meyer, editors. *Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, Switzerland.
- Kalies, E. L., C. L. Chambers, and W. W. Covington. 2010. Wildlife responses to thinning and burning treatments in southwestern conifer forests: A meta-analysis. *Forest Ecology and Management* 259:333–342.
- Kellner, K. 2015. jagsUI: A Wrapper Around “rjags” to Streamline “JAGS” Analyses. R package version 1.4.4. <https://CRAN.R-project.org/package=jagsUI>
- Kéry, M., and J. A. Royle. 2016. Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS. Volume 1. Elsevier, San Diego, California, USA.
- Kéry, M., and M. Schaub. 2011. Bayesian population analysis using WinBUGS. First edition. Academic Press, Waltham, Massachusetts, USA.
- Knutti, R., D. Masson, and A. Gettelman. 2013. Climate model genealogy: generation CMIP5 and how we got there. *Geophysical Research Letters* 40:1194–1199.
- Kolb, T. E., C. J. Fettig, M. P. Ayres, B. J. Bentz, J. A. Hicke, R. Mathiasen, J. E. Stewart, and A. S. Weed. 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. *Forest Ecology and Management* 380:321–334.
- Lahoz-Monfort, J. J., B. J. T. Morgan, M. P. Harris, S. Wanless, and S. N. Freeman. 2011. A capture-recapture model for exploring multi-species synchrony in survival. *Methods in Ecology and Evolution* 2:116–124.
- Lloyd, P., F. Abadi, R. Altwegg, and T. E. Martin. 2014. South temperate birds have higher apparent adult survival than tropical birds in Africa. *Journal of Avian Biology* 45:493–500.
- McMahon, S. M., et al. 2011. Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology & Evolution* 26:249–259.
- Miller-Rushing, A. J., T. T. Høye, D. W. Inouye, and E. Post. 2010. The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B* 365:3177–3186.
- Monzón, J., et al. 2011. Climate change and species range dynamics in protected areas. *BioScience* 61:752–761.
- Mustin, K., W. Sutherland, and J. Gill. 2007. The complexity of predicting climate-induced ecological impacts. *Climate Research* 35:165–175.
- Ovaskainen, O., and J. Soininen. 2011. Making more out of sparse data: hierarchical modeling of species communities. *Ecology* 92:289–295.
- Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12:361–371.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003)*, March 20–22, Vienna, Austria.
- Potithea, P., N. K. Nasaharab, H. Muraokac, S. Nagaia, and R. Suzukia. 2010. What is the actual relationship between LAI and VI in a deciduous broadleaf forest? *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Science* 38:609–614.
- Pyle, P. 1997. Identification guide to North American birds, part 1. Slate Creek Press, Bolinas, California, USA.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Robinson, R. A., R. Julliard, and J. F. Saracco. 2009. Constant effort: Studying avian population processes using standardised ringing. *Ringing & Migration* 24:199–204.
- Saracco, J. F., D. F. DeSante, and D. R. Kaschube. 2008. Assessing landbird monitoring programs and demographic causes of population trends. *Journal of Wildlife Management* 72:1665–1673.
- Saracco, J. F., J. A. Royle, D. F. DeSante, and B. Gardner. 2010. Modeling spatial variation in avian survival and residency probabilities. *Ecology* 91:1885–1891.
- Seager, R., et al. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316:1181–1184.
- Selwood, K. E., M. A. McGeoch, and R. Mac Nally. 2015. The effects of climate change and land-use change on demographic rates and population viability. *Biological Reviews* 90:837–853.
- Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288:2040–2042.
- Smith, K. G. 1982. Drought-induced changes in avian community structure along a Montane sere. *Ecology* 63:952–961.
- Stralberg, D., D. Jongsomjit, C. A. Howell, M. A. Snyder, J. D. Alexander, J. A. Wiens, and T. L. Root. 2009. Re-shuffling of species with climate disruption: a no-analog future for California birds? *PLoS ONE* 4:1–8.
- Taylor, K. E., R. J. Stouffer, and G. A. Meehl. 2012. An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society* 93:485–498.

- Tuck, S. L., H. R. Phillips, R. E. Hintzen, J. P. Scharlemann, A. Purvis, and L. N. Hudson. 2014. MODISTools - downloading and processing MODIS remotely sensed data in R. *Ecology and Evolution* 4:4658–4668.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Wang, T., A. Hamann, D. L. Spittlehouse, and T. Q. Murdock. 2012. ClimateWNA—high-resolution spatial climate data for western North America. *Journal of Applied Meteorology and Climatology* 51:16–29.
- Wang, T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE* 11: e0156720.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1751/full>

DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.09j26sv>.