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Authors: Porzig, Elizabeth L., Seavy, Nathaniel E., Eadie, John M., Gardali, Thomas, Humple, Diana L., et al.

RESEARCH ARTICLE

There goes the neighborhood: White-crowned Sparrow nest site selection and reproductive success as local density declines

Elizabeth L. Porzig,[1,2]* Nathaniel E. Seavy,[1] John M. Eadie,[2] Thomas Gardali,[1] Diana L. Humple,[1] and Geoffrey R. Geupel[1]

[1] Point Blue Conservation Science, Petaluma, California, USA
[2] Department of Wildlife, Fish and Conservation Biology, University of California, Davis, California, USA
* Corresponding author: eporzig@pointblue.org

ABSTRACT
Changes in climate, vegetation, and land use are recognized as important drivers of changes in the distribution and abundance of wildlife. However, the behavioral and demographic mechanisms through which these changes affect populations have received less attention. Identifying these mechanisms is an important component of predicting the impacts of increasing environmental change. We used 30 yr of nest monitoring data at a study site where White-crowned Sparrow (*Zonotrichia leucophrys*) breeding density declined 85% to evaluate factors influencing habitat selection and reproductive success. Rapid secondary plant succession occurred at our study site, but the rate of change was faster in some areas than others. White-crowned Sparrows exhibited strong patterns of nest site selection, preferring open shrub vegetation and avoiding forest. As a result, many parts of the study area that were used for nesting early in the study period were no longer occupied by the end of the study period. Over the course of the study, both the weather conditions and the vegetation structure and composition around nests varied. Across the range of occupied habitat, we found no effect of vegetation structure on reproductive success. We also found no support for effects of temperature and rainfall on nest survival, and only weak and inconsistent effects of temperature on clutch size and the number of fledglings per nest. These results indicate that vegetation change drove changes in the nest sites used through habitat selection, and that habitat selection appeared to ameliorate any potential negative effects of vegetation change on per capita reproductive success. Hence, the population's response to rapid vegetation change was driven, at least in part, by site selection, rather than by a decline in reproductive success. In light of increasing environmental variation, it will be important to partition the effects of environmental change on habitat use and reproductive success to predict population viability and extinction risk.

Keywords: environmental change, demography, habitat selection, reproductive success, vegetation succession, White-crowned Sparrow, *Zonotrichia leucophrys*

Ahí va el vecindario: selección del sitio de anidación y éxito reproductivo de *Zonotrichia leucophrys* a medida que disminuye la densidad local

RESUMEN
Se reconoce que los cambios en el clima, la vegetación y el uso del suelo son impulsores importantes de los cambios en la distribución y la abundancia de la vida silvestre. Sin embargo, los mecanismos del comportamiento y demográficos a través de los cuales estos cambios afectan las poblaciones han recibido menos atención. La identificación de estos mecanismos es un componente importante para predecir los impactos del aumento del cambio ambiental. Para evaluar los factores que influencian la selección de hábitat y el éxito reproductivo, usamos 30 años de datos de monitoreo de nidos en un sitio de estudio donde la densidad reproductiva de *Zonotrichia leucophrys* ha disminuido en un 85%. En nuestra área de estudio ha ocurrido una rápida sucesión vegetal secundaria, pero algunas partes cambiaron más rápido que otras. Los individuos de *Z. leucophrys* mostraron fuertes patrones de selección del sitio de anidación, prefiriendo vegetación arbustiva abierta y evitando el bosque. Como resultado, muchas partes del área de estudio que fueron usadas para anidar al principio del período de estudio no fueron ocupadas luego hacia el final del periodo de estudio. Durante el transcurso del estudio, tanto las condiciones climáticas como la estructura y la composición de la vegetación alrededor de los nidos variaron. A lo largo del rango del hábitat ocupado, no encontramos un efecto de la estructura de la vegetación en el éxito reproductivo. Tampoco encontramos apoyo a un efecto de la temperatura y la precipitación en la supervivencia del nido, y solo efectos débiles e inconsistentes de la temperatura sobre el tamaño de la nidada y el número de volantones por nido. Estos resultados indican que los cambios en la vegetación impulsan cambios en los sitios de anidación usados a través de la selección de hábitat, y la selección de hábitat parece mejorar cualquier efecto negativo potencial del cambio de la vegetación en el éxito

reproductivo per cápita. Por lo tanto, la respuesta poblacional al rápido cambio de la vegetación está impulsada, al menos en parte, por la selección del sitio en lugar de una disminución en el éxito reproductivo. A la luz de un aumento en la variación ambiental, será importante separar los efectos del cambio ambiental en el uso del hábitat y el éxito reproductivo para predecir la viabilidad poblacional y el riesgo de extinción.

Palabras clave: cambio ambiental, demografía, éxito reproductivo, selección de hábitat, sucesión de la vegetación, *Zonotrichia leucophrys*

INTRODUCTION

As the rate of environmental change has increased as a result of climate and land use change, there has been an increasing focus on how animals track these changes in time and space. Distributional modeling using occurrence or abundance data has been widely adopted as a way of predicting wildlife responses to future environmental change (Seoane et al. 2004, Stralberg et al. 2009, 2015, Wiens et al. 2009). Most of these models have been built independently of demographic mechanisms that can drive distributional shifts. To improve predictions of how species may respond to change, a clearer understanding of how and at what spatial and temporal scale species track changes in habitat is needed (Ackerly et al. 2010).

One approach to gain such insight is to study how dynamic habitat conditions affect the underlying behavioral and demographic mechanisms of population change: habitat selection decisions and resultant fitness consequences. We use standard terminology of habitat use, or the presence of animal in a habitat, and habitat selection, or the use of a habitat disproportionate to its availability (Lele et al. 2013, Northup et al. 2013). For birds, the decision of where to build a nest and the resultant fitness consequences of this decision are important aspects of habitat suitability and a species' ability to respond to habitat change (Martin 1993, Johnson 2007). Because nesting behavior such as nest site use has fitness consequences, habitat selection should be adaptive (Misenhelter and Rotenberry 2000, Latif et al. 2012). However, there are many examples of cases in which habitat selection is not adaptive, particularly when habitat is rapidly altered by human impacts (Pulliam and Danielson 1991, Kristan 2003).

Congruence or mismatch between habitat selection and reproductive outcome in dynamic conditions can indicate a bird's ability to track environmental change. For example, if there is selection for habitat along a gradient (i.e. some habitat types are used more frequently than others), and there is no effect of the selected habitat on observed reproductive success, this can be interpreted as evidence that birds are making adaptive resource selection decisions such as those seen in an adaptive peak or plateau (Fisher 1930, Latif et al. 2012). Alternatively, when birds nest across a gradient of habitats and have lower nest success in some habitat types than others, this can indicate that birds are not responding to environmental cues adaptively. Such behaviors are seen in nonideal habitat selection or ecological traps (Battin 2004, Arlt and Pärt 2007). Time lags in tracking suitable environmental conditions can lead to increased extinction risk (Urban et al. 2012); thus, it is increasingly important to identify the degree of congruence or mismatch between habitat selection and reproductive success in dynamic environments.

For most landbird species (passerines and near-passerines), as well as most terrestrial wildlife, vegetation community and structure are the dominant components of habitat because they affect most environmental components necessary for reproduction and occupancy (Felix et al. 2007, Johnson 2007). Thus, habitat suitability is strongly influenced by vegetation community dynamics. These dynamics range from severe (e.g., fire) to seasonal (e.g., flooding, deciduous cycles), irruptive (e.g., masting), and directional (e.g., succession) change. While studies examining reproductive success in relation to vegetation characteristics are legion and have been reviewed several times (Jones 2001, Stephens et al. 2004, Chalfoun and Schmidt 2012), important new information could be gained from resolving how long-term habitat dynamics drive demographic outcomes of habitat selection (Arlt and Pärt 2007, Koenig et al. 2011).

Understanding the impact of habitat change on reproductive success requires evaluating habitat characteristics in the context of other environmental variables. For landbirds, there is abundant evidence that seasonal weather patterns influence nest success (Rotenberry and Wiens 1991, Chase et al. 2005, Skagen and Adams 2012, Grisham et al. 2016). Variation in weather and changes in habitat characteristics can result in behavioral and demographic responses by animals because they can act at different temporal and spatial scales. For example, transitions within the vegetation community typically occur on a slower time scale than weather variation, and thus landbird populations are able to respond through individual sampling of the physical habitat or through conspecific or heterospecific cues (Chalfoun and Schmidt 2012). If cues are reliable, this information may allow individuals to select more suitable habitat rather than incur a demographic cost. On the other hand, changes in weather may be less predictable, resulting in a higher risk of incurring a demographic cost. It is thus informative to

compare the relative importance of vegetation change on reproductive success in the context of weather variation.

Long-term monitoring of territories, nest locations, and reproductive success of a landbird community has been conducted at the Palomarin Field Station in central coastal California, USA, since 1980. Previous research has demonstrated an 85% decline in territory density of White-crowned Sparrows (*Zonotrichia leucophrys*) and a relationship between this decline in territory density and vegetation change at the scale of the entire field station (Porzig et al. 2014). Palomarin Field Station has undergone secondary succession since the mid-1960s due to a lack of vegetation disturbance. These changes have not been homogeneous across the field station; in some areas, coastal scrub has been converted to conifer forest, whereas in other areas the vegetation structure and composition (coastal scrub) has been maintained but has become more mature. As a result, it is possible to understand not just the aggregate response of the landbird community to vegetation change (Porzig et al. 2014), but also the responses of individuals and the impact of these changes on fitness components across a gradient of habitat conditions.

Our goals were to combine an examination of the responses of birds to habitat change and the effect of environmental variation on reproductive success. We investigated the influence of 30 yr of vegetation succession and weather variation on the habitat selection and reproductive success of White-crowned Sparrows. We evaluated 3 measures of reproductive effort (nest survival, clutch size, and the number of chicks fledged) to allow for the possibility that vegetation and rainfall variables had different effects on separate stages of the nesting cycle. Because White-crowned Sparrows prefer early successional habitat, we hypothesized that, over the course of the study, this habitat preference would result in similar per capita reproductive success irrespective of the amount of suitable habitat available. We predicted (1) a positive relationship between the proportion of early successional habitat within the overall study site and breeding density, (2) preferential use of early successional habitat for nesting, (3) no relationship between nest survival and successional state at the nest site (as would be consistent with adaptive habitat selection), and (4) a greater relative influence of weather variables than vegetation variables on reproductive success as measured by nest survival, clutch size, and the number of chicks fledged.

METHODS

Study System

Nuttall's White-crowned Sparrows (*Z. l. nuttalli*) inhabit the California coastal zone from Cape Mendocino to Point Conception. This resident subspecies is found in mixed shrub and grassland habitats (Mewaldt and King 1977).
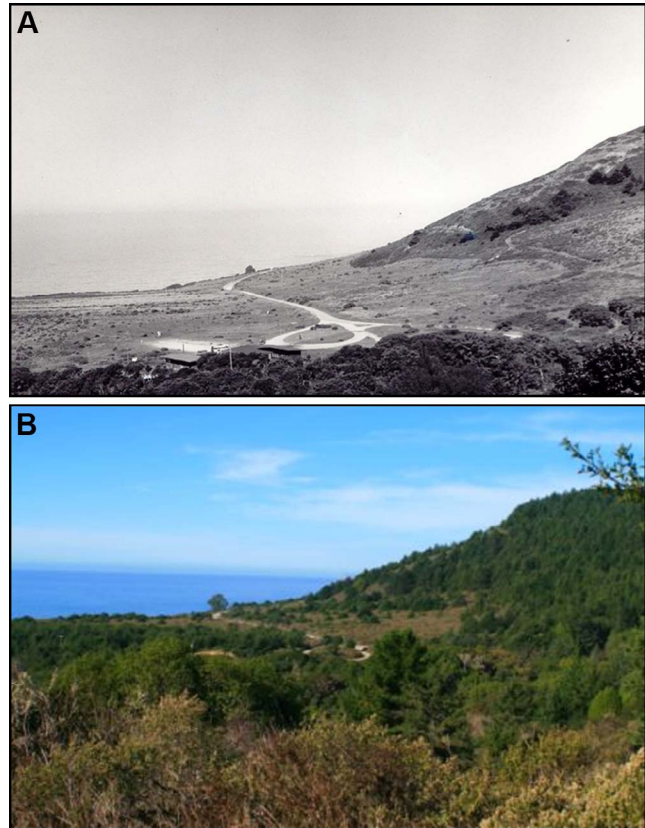
FIGURE 1. Photos of Palomarin Field Station, Marin County, California, USA, (**A**) circa 1970 and (**B**) circa 2008, where we examined nest site selection and reproductive success of White-crowned Sparrows in relation to changes in vegetation.

Since the 1960s, territory dynamics and reproductive success of White-crowned Sparrows have been monitored at the Palomarin Field Station, operated by Point Blue Conservation Science (formerly Point Reyes Bird Observatory [PRBO]; see Porzig et al. 2011 for details). Much of the 36-ha study area at the southern end of the Point Reyes National Seashore was in agricultural cultivation or disturbed by other human use and activity until the mid-1960s. After incorporation into the Point Reyes National Seashore in 1965, vegetation in the study area was left largely undisturbed, resulting in succession from a grassland–shrub landscape to mature coastal scrub dominated by coyotebrush (*Baccharis pilularis*) and encroaching Douglas-fir (*Pseudotsuga menziesii*) forest (Figure 1; Porzig et al. 2014).

Data Collection

Since 1981, field biologists have mapped breeding territories of White-crowned Sparrows annually in the 36-ha study area using a combination of sightings of individually color-banded individuals, singing birds, and movements (Ralph et al. 1993). To facilitate mapping,

uniquely marked stakes have been placed every 30 m across the study area. Over the course of the study, the number of White-crowned Sparrow territories declined from 27 in 1982 to 4 in 2010 (Porzig et al. 2014; Figure 1). Territory density from 1981 was excluded due to less thorough coverage of the study area in the initial year.

Since 1980, nests in the study site have been located and monitored using methods described by Martin and Geupel (1993). Once found, nests were generally visited at least once every 4 days (mean interval = 2.41 ± 1.38 SD days; range = 1–13 days). For nests observed across nesting stages (building, egg laying, incubation, nestlings), we estimated the age of the nest at each visit by assuming 12 days of incubation and fledging by nestlings on day 10 (DeSante and Baptista 1989, Chilton et al. 1995). When nests were found and failed within a stage, we estimated the age of the nest at each visit by taking the total time that the nest was observed to be active and centering this interval within the stage that it was observed. When the nest became inactive, the outcome was determined by a combination of sightings of fledglings, behavioral cues of adults, timing, and any physical evidence at the nest as to whether the nest fledged or was depredated (Martin and Geupel 1993, Ball and Bayne 2012). We include nesting data from 1981 onward in this analysis.

Biologists measured changes in plant cover and composition at 40 locations throughout the 36-ha study area at 3 time points: 1981–1982, 2000, and 2008. Locations were chosen from a random subset of the uniquely marked stakes (G. Geupel and D. DeSante personal communication). At each location, vegetation was measured along 4 10-m transects that extended from the center point in the northwest, northeast, southeast, and southwest directions. We measured the height, length along the transect line, and maximum width perpendicular to the transect line for each shrub or tree that intersected the transect line.

Weather data, including rainfall and temperature (high and low), were recorded daily on site. We aggregated daily weather records to generate annual rainfall (from July 1 to June 30), breeding season (April 1–July 31) mean high temperature, and breeding season mean low temperature. In 5 of our study years, there was insufficient data to estimate mean temperatures, thus we used zero (the standardized mean) for these values. For all analyses, rainfall and temperature were scaled and centered by subtracting the mean rainfall or temperature from each value and dividing the result by the standard deviation.

Data Analysis

Field observations and preliminary analyses identified coyotebrush height, mean Douglas-fir height, and the number of Douglas-firs as variables that were large contributors to the successional changes at the Palomarin Field Station. We used Principal Components Analysis to reduce the dimensionality of these 3 variables into 1 variable describing successional state. We then interpolated this value across the study area using ordinary kriging for each of the 3 sampling years using the 'predict' function in the gstat package in R 3.3.3, specifying a 10-m grid (Pebesma 2004, R Core Team 2017). From these interpolated surfaces, we estimated vegetation characteristics across the study area in the other years of the study using linear regression for each 10-m grid cell. Using these spatial and temporal interpolations, we assigned each nest location a continuous value representing an estimated successional state in the 10-m grid cell at that location in each year. We were also interested in the effect of the rate of vegetation change at the nest site, so in addition to the successional stage for each nest in each year, we estimated the successional rate at each nest using the slope of the interpolated regression line at each nest location. We confirmed our calculated successional values by visually comparing our interpolated maps to patterns visible in historic satellite imagery available through Google Earth (Google, Mountain View, California, USA), as well as using personal observation. While small discrepancies between the interpolated successional values and the historical satellite imagery existed, the 2 images agreed on general patterns and heterogeneity in successional change

We calculated resource selection ratios following Manly et al. (2002) using package adehabitatHS 0.3.6 (Calenge 2006) in R 3.3.3 (R Core Team 2017). While not often used to evaluate nest site selection in territorial passerines, resource selection ratios are a commonly used and useful tool for identifying the proportion of habitat that is used relative to what is available (Northup et al. 2013). We divided the available successional types from all years in the study area into 4 categories of equal range of successional state (early, middle, late, and very late) and assigned a category to each nest location. We then calculated the ratio of used nest locations within each of the 4 successional states to the proportion of that state available. There was evidence of habitat selection if the selection ratio differed significantly from 1. To visually evaluate modeled changes in successional state and nest locations, we mapped the distribution of nests in 6 equally spaced years (1985, 1990, 1995, 2000, 2005, and 2010).

We analyzed nest survival using logistic exposure, a generalized linear model with a binomial response and a modified logit link that treats the interval between each nest visit as an independent sampling unit (Shaffer 2004). Because not all nests are found at the beginning of the nesting cycle, nests are observed for different lengths of time. By treating the interval between each visit as the individual sampling unit and modeling daily survival rate

as the response variable, logistic exposure avoids bias that results from observing nests for different lengths of time.

Continuous time-varying factors, such as the day of the nesting cycle and day of the season, can affect daily survival rates in linear or nonlinear ways (Grant et al. 2005). Thus, including these variables and in different forms (i.e. linear, quadratic, and cubic) can improve estimates of parameters of interest (Skagen and Adams 2012). We analyzed daily survival rate using a 2-step process. First, we found the best base model by evaluating the following 2 covariates separately and in combination: day of the nesting cycle and day of the season, in linear, quadratic, and cubic forms, and their linear interaction. We selected the best base model using Akaike's information criterion corrected for small sample size (AIC_c). In the second step, we took the best base model and added combinations of the 3 weather variables (annual rainfall, breeding season mean high temperature, and breeding season mean low temperature) and the 2 variables describing vegetation change (successional state and successional rate). We included a quadratic term for annual rainfall because this has been shown to be a significant predictor of the reproductive success of Song Sparrows (*Melospiza melodia*) in our study site (Chase et al. 2005). We did not explicitly include year as a covariate because year was correlated with vegetation change. We fit 48 candidate models and calculated model-averaged estimates of daily survival rate for the range of successional rates using package nestsurvival 0.85 (M. Herzog personal communication) in R. Functions in this software build candidate models following methods described by Shaffer (2004) and Rotella et al. (2004) and estimate model-averaged predictions and variance based on Akaike model weights as described by Burnham and Anderson (2002; M. Herzog personal communication).

We evaluated the effect of weather variation and vegetation change on clutch size and the number of fledglings using an information-theoretic approach (Burnham and Anderson 2002) and stepwise linear modeling. For clutch size, we only included data from nests that were observed with eggs, and for which timing or behavioral observations indicated that the clutch was complete. For the number of fledglings, we only included data from nests that successfully fledged at least one young. The number of young fledged was obtained by using the last count of nestlings observed prior to fledging or, in some cases, by visually confirming the exact number of fledglings. We established a base model for each response by comparing an intercept-only model with a model that included nest initiation date (clutch size model) or clutch size (number of fledglings model). We identified the best overall base model structure for
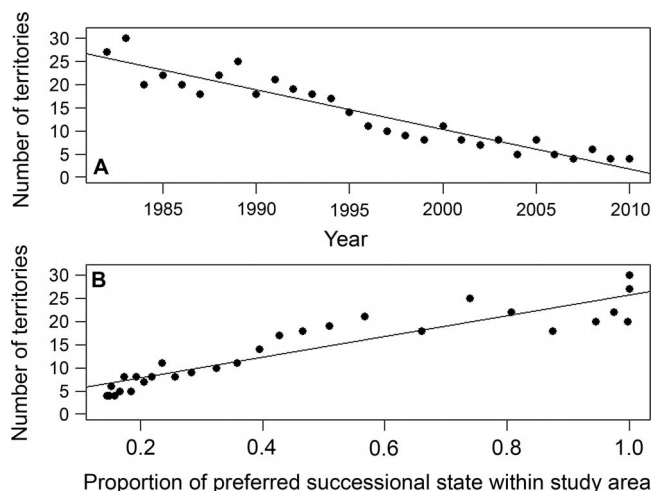

FIGURE 2. (**A**) Number of White-crowned Sparrow breeding territories through time in the study site at the Palomarin Field Station, Marin County, California, USA. (**B**) Number of White-crowned Sparrow territories as a function of the proportion of the study area that was in the preferred successional state (early successional vegetation, i.e. grassland and small coastal shrubs).

each response by comparing model AIC_c values. We then formulated balanced candidate model sets (i.e. variables of interest were equally represented among the candidate models for each response) with the weather and vegetation covariates: annual rainfall, seasonal mean high temperature, seasonal mean low temperature, successional state, and successional rate. We calculated Akaike weights and model-averaged coefficients for the effects of weather and vegetation variables on the response variables using R package AICcmodavg 1.3 (Mazerolle 2013).

RESULTS

Over the course of the 30-yr study period, White-crowned Sparrow territory density declined significantly (Figure 2A; linear regression model: number of territories = 1718.70 − 0.85 × year; $F_{1,27} = 232.3$, $P < 0.001$, $R^2 = 0.89$). Territory density over the course of the study period was positively associated with the proportion of the study area that was classified as early successional habitat (Figure 2B; linear regression model: number of territories = 3.3 + 22.5 × proportion of preferred habitat; $F_{1,27} = 147.1$, $P < 0.001$, $R^2 = 0.84$). As the vegetation community transitioned from early successional coastal scrub to later successional scrub and Douglas-fir forest, there was a reduction in the overall availability of preferred habitat (Figure 3).
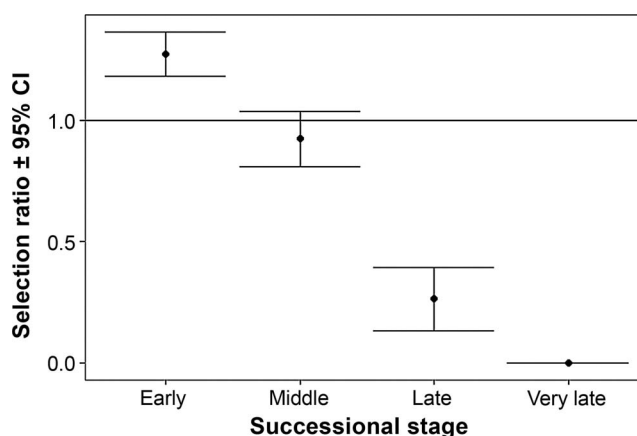
Resource selection ratios indicated that habitat selection over the course of the entire study period was nonrandom; White-crowned Sparrows selected the earliest successional habitat and avoided later successional habitat (Figure 4).
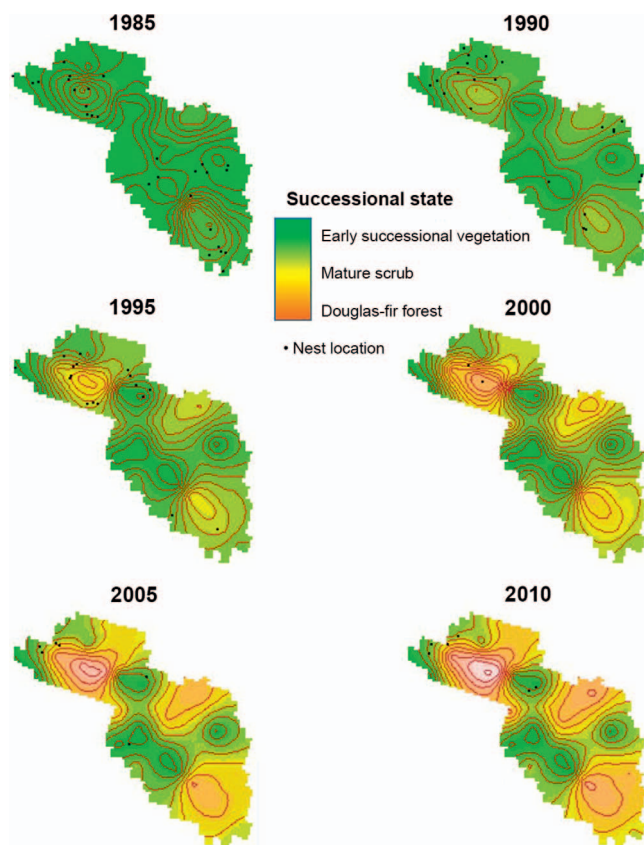
FIGURE 3. Maps of the study area (Palomarin Field Station, California, USA) showing successional state and nest locations of White-crowned Sparrows at 6 time points throughout the study period. Colors are approximately analogous to different successional stages: greens represent early successional stages (grassland and early successional coastal scrub), yellow represents mature coastal scrub, and oranges and reds represent Douglas-fir forest.

FIGURE 4. Manly Design I selection ratios and 95% confidence intervals for White-crowned Sparrow nest locations from 1981 to 2010 in each of 4 successional stages at Palomarin Field Station, California, USA. Selection ratios significantly higher than 1 indicate selection for that habitat type, while selection ratios significantly lower than 1 indicate avoidance of that habitat type. 'Early' represents the earliest successional stage observed in the study area, corresponding with early successional scrub and grassland. 'Very late' represents the latest observed successional state, corresponding with Douglas-fir forest.

During the last decade of the study, the vegetation at most of the nest sites used in the first year of the study was in a later successional state than the vegetation at sites that continued to be used (Figure 3).

We evaluated the nest success of 447 nests. The best base model contained a quadratic nest age effect (number of model parameters = 3, AIC_c = 1314.2, Akaike model weight = 0.72). The next-best base model contained a cubic nest age effect (number of model parameters = 4, AIC_c = 1316.1, Akaike model weight = 0.28). We found little evidence that either weather or nest site vegetation influenced nest success (Table 1, Figure 5). Models including weather and vegetation covariates were not better supported than the base model (although some of these models were competitive: $\Delta AIC_c \leq 2$; Table 1). Model weights of the top models were low (Table 1), indicating a low degree of support for any one of these models. Model-averaged coefficients for weather and vegetation variables were close to zero and had 95% confidence intervals that overlapped zero (Figure 6A).

We evaluated the clutch size of 273 nests. Variation in clutch size was low (mean = 3.23 ± 0.60 SD eggs; range = 1–4 eggs). There was no support for using nest initiation date as a covariate for modeling clutch size ($\Delta AIC_c > 2$), so the candidate models consisted only of the environmental predictors of interest. Model-averaged coefficients and 95% confidence intervals indicated that breeding season mean high temperature was the only variable with a significant effect on clutch size, with warmer temperatures resulting in smaller clutch sizes (Figure 6B).

We evaluated the number of fledglings produced by 262 nests. Variation in fledgling numbers was low (mean = 2.66 ± 0.85 SD chicks; range = 1–4 chicks). The base model included a linear effect of clutch size. Model-averaged coefficients and 95% confidence intervals indicated that breeding season mean high and mean low temperatures had significant and opposing effects on the numbers of fledglings produced, with a positive effect of high temperature and a negative effect of low temperature (Figure 6C). The effect of high temperature on fledgling numbers was the opposite of its effect on clutch size (Figure 6).

DISCUSSION

Our results provide insight into the behavioral responses of landbirds to rapid environmental change that drives

TABLE 1. Model results of logistic exposure analysis of nest success of White-crowned Sparrows at the Palomarin Field Station, California, USA, 1981–2010. The model shown in bold font is the best base model. Models are ranked by differences in Akaike's information criterion corrected for small sample size (ΔAIC_c) and Akaike model weights (w_i). The number of parameters (K), maximized log likelihood ($-2logL$), and cumulative weight ($\sum w_i$) are also included. Models summing to a cumulative w_i of 0.90 are shown (differences between $\sum w_i$ and adding of w_i occur due to rounding). 'High temp' = breeding season mean high temperature, 'Low temp' = breeding season mean low temperature, 'Nestday' = the day of the nesting cycle, 'Rainfall' = annual rainfall from July 1 to June 30, 'Slope' = vegetation successional rate at the nest site, and 'Succession' = vegetation successional state at the nest site.

| Model	K	ΔAIC_c	$-2logL$	w_i	$\sum w_i$
Nestday + Nestday^2	**3**	**0.00** [a]	**1216.22**	**0.11**	**0.11**
Nestday + Nestday^2 + Rainfall	4	0.38	1214.59	0.09	0.20
Nestday + Nestday^2 + Succession	4	1.46	1215.67	0.05	0.25
Nestday + Nestday^2 + Low temp	4	1.51	1215.73	0.05	0.31
Nestday + Nestday^2 + High temp	4	1.92	1216.13	0.04	0.35
Nestday + Nestday^2 + Rainfall + High temp	5	1.98	1214.18	0.04	0.39
Nestday + Nestday^2 + Slope	4	1.99	1216.20	0.04	0.43
Nestday + Nestday^2 + Rainfall + Succession	5	2.03	1214.23	0.04	0.47
Nestday + Nestday^2 + Rainfall + Low temp	5	2.18	1214.38	0.04	0.51
Nestday + Nestday^2 + Rainfall + Rainfall^2	5	2.24	1214.45	0.04	0.54
Nestday + Nestday^2 + Rainfall + Slope	5	2.37	1214.57	0.03	0.58
Nestday + Nestday^2 + High temp + Low temp	5	2.56	1214.76	0.03	0.61
Nestday + Nestday^2 + Rainfall + High temp + Low temp	6	2.79	1212.97	0.03	0.63
Nestday + Nestday^2 + Low temp + Succession	5	3.28	1215.48	0.02	0.66
Nestday + Nestday^2 + High temp + Succession	5	3.41	1215.62	0.02	0.68
Nestday + Nestday^2 + Succession + Slope	5	3.44	1215.64	0.02	0.70
Nestday + Nestday^2 + Low temp + Slope	5	3.51	1215.71	0.02	0.71
Nestday + Nestday^2 + Rainfall + High temp + Succession	6	3.70	1213.89	0.02	0.73
Nestday + Nestday^2 + Rainfall + Rainfall^2 + High temp	6	3.71	1213.90	0.02	0.75
Nestday + Nestday^2 + High temp + Slope	5	3.90	1216.10	0.02	0.76
Nestday + Nestday^2 + Rainfall + Rainfall^2 + Succession	6	3.93	1214.12	0.02	0.78
Nestday + Nestday^2 + Rainfall + High temp + Slope	6	3.95	1214.14	0.02	0.80
Nestday + Nestday^2 + Rainfall + Low temp + Succession	6	3.99	1214.18	0.01	0.81
Nestday + Nestday^2 + Rainfall + Succession + Slope	6	4.03	1214.22	0.01	0.82
Nestday + Nestday^2 + Rainfall + Rainfall^2 + Low temp	6	4.10	1214.29	0.01	0.84
Nestday + Nestday^2 + Rainfall + Low temp + Slope	6	4.17	1214.36	0.01	0.85
Nestday + Nestday^2 + Rainfall + Rainfall^2 + Slope	6	4.24	1214.43	0.01	0.87
Nestday + Nestday^2 + High temp + Low temp + Slope	6	4.50	1214.69	0.01	0.88
Nestday + Nestday^2 + High temp + Low temp + Succession	6	4.58	1214.77	0.01	0.89
Nestday + Nestday^2 + Rainfall + Rainfall^2 + High temp + Low temp	7	4.62	1212.80	0.01	0.90

[a] The AIC$_c$ of the top model = 1222.23.

population change. Consistent with our predictions, White-crowned Sparrows showed strong selection for nest sites in early successional habitat (Figure 4), and there was a positive effect of the amount of early successional habitat on territory density (Figure 2B). Furthermore, successional stage was not a good predictor of variation in measures of reproductive success (Figures 5 and 6). These results indicate that individual White-crowned Sparrows track suitable nesting habitat and suffer no detected per capita fitness cost of habitat change as measured by reproductive success.

The strong relationship between nest site selection and successional state provides an example of a bird species' response to habitat change at the scale of the individual territory. This pattern, coupled with no effect of vegetation change on reproductive success, suggests that White-crowned Sparrows are adjusting to changes in habitat through behavioral decisions rather than incurring a reproductive cost. Our results suggest that at least some songbirds have the behavioral plasticity to respond to rapid habitat change of the type, rate, and magnitude observed in our study site.

From a conservation and management perspective, breeding density and reproductive rate are often used as indicators of habitat quality; however, both empirical and theoretical evidence provide examples and mechanisms to the contrary (Johnson 2007, Skagen and Adams 2011). For example, high-quality habitats will not necessarily show a positive relationship with density or fitness measures when the population becomes limited by density dependence (e.g., psuedosinks; Watkinson and Sutherland 1995). In light of increasing environmental dynamism, the focus needs to shift from inferring information about the quality of habitat from density or reproductive success and toward evaluating density, reproductive success, and patterns of habitat selection
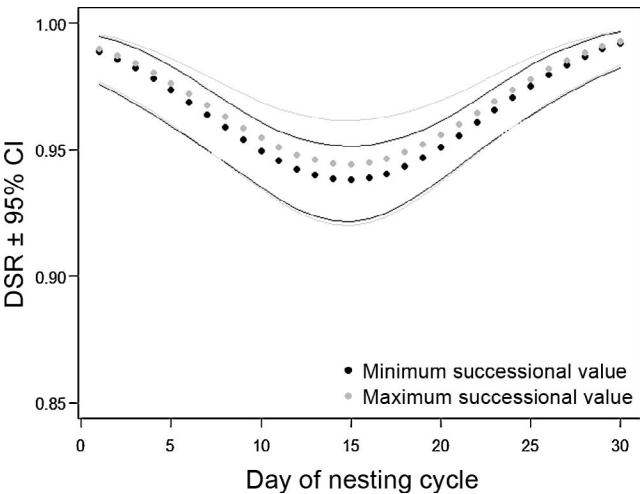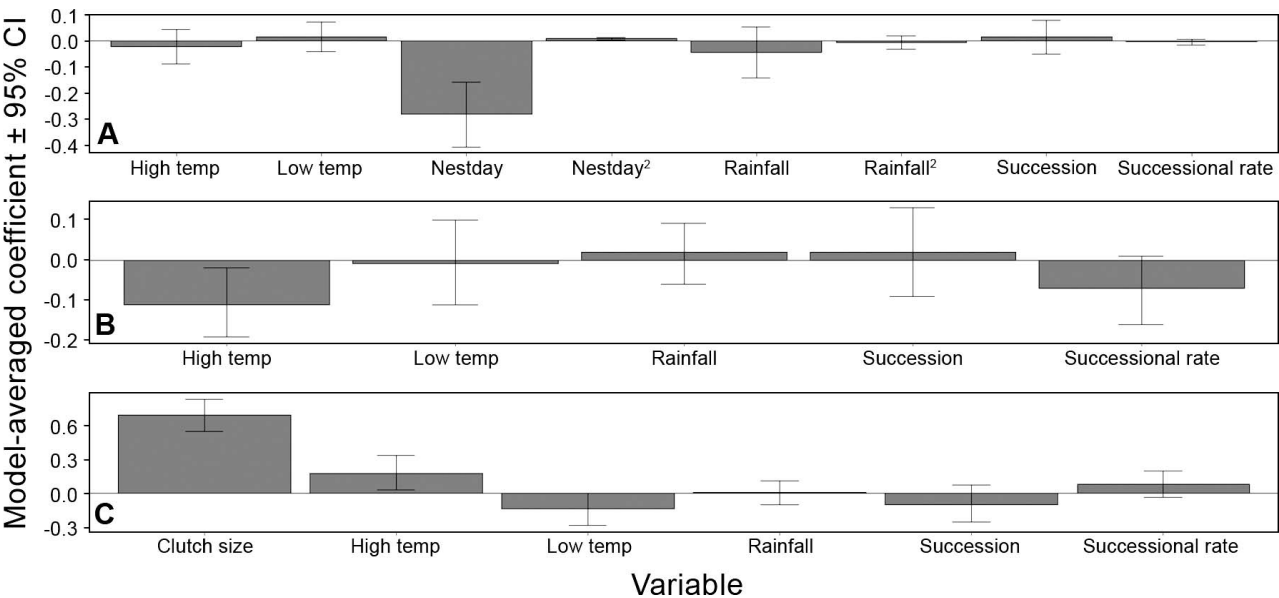
FIGURE 5. Daily survival rates (DSR) and 95% confidence intervals throughout the course of the White-crowned Sparrow nesting period at the minimum (black) and maximum (gray) observed successional states at Palomarin Field Station, California, USA. The minimum observed successional state was early successional scrub and grassland, and the maximum observed successional state was Douglas-fir forest.

increasing environmental dynamism and thus inform conservation and management.

There are several possible mechanisms by which White-crowned Sparrows might select breeding locations. While direct sampling of environmental conditions has been invoked most often, there is increasing evidence that indirect sampling through conspecific cues is more prevalent than previously appreciated (Ahlering and Faaborg 2006, Chalfoun and Schmidt 2012). Similarly, informed site fidelity, or the win–stay lose–switch rule (Schmidt 2004), and natal habitat preference induction (Davis and Stamps 2004) are other mechanisms through which suitable habitat can be selected (Chalfoun and Schmidt 2012).

The influence of weather on the daily nest survival of passerines has been widely demonstrated (Martin 2001, Chase et al. 2005, Skagen and Adams 2012), yet we detected a very limited influence of variation in weather on the reproductive success of White-crowned Sparrows. Thus, our prediction that there would be a greater influence of weather variables on reproductive success compared with vegetation variables was only weakly and inconsistently supported. Breeding season mean high temperature had a negative influence on clutch size, but it influenced fledgling numbers positively. Breeding season mean low temperature had a negative influence on fledgling numbers. Variation in both clutch size and the

in concert to understand how well populations adjust to different rates and types of environmental change. Rather than a static view of habitat quality, this approach will provide insight into population viability in the face of

FIGURE 6. (**A**) Influence and 95% confidence interval of the day of the nesting cycle (Nestday), rainfall, successional rate, successional state (Succession), breeding season mean low temperature (Low temp), and breeding season mean high temperature (High temp) on daily nest survival; (**B**) Influence and 95% confidence interval of rainfall, breeding season mean high temperature (High temp), breeding season mean low temperature (Low temp), successional rate, and successional state (Succession) on clutch size; and (**C**) Influence and 95% confidence interval of rainfall, clutch size, breeding season mean high temperature (High temp), breeding season mean low temperature (Low temp), successional rate, and successional state (Succession) on the number of fledglings of White-crowned Sparrows at the Palomarin Field Station, California, USA, 1981–2010.

number of fledglings was relatively low, thus the biological significance of these results is uncertain. Effects of weather on White-crowned Sparrow reproduction have been reported in other studies conducted at higher latitudes and elevations (Morton 2002, Wingfield et al. 2003). Yet, latitudinal and elevational gradients in weather patterns are not the only factors that can affect the sensitivity of reproductive success to weather variation. For Song Sparrows in our study site, Chase et al. (2005) found a positive effect of rainfall on nest success and a negative influence of high summer temperature on fledgling numbers. However, the primary cause of nest failure for this species was predation, and there would have been only indirect effects of weather. Differences in weather effects on White-crowned Sparrow and Song Sparrow reproductive success in our study site could be explained by differences in weather-mediated predation susceptibility or phenological differences in breeding behavior.

The ability of populations to track suitable environments in increasingly dynamic conditions will be a critical component in determining population persistence and extinction or extirpation risk (Williams et al. 2008). Our study suggests that White-crowned Sparrows have been able to track their suitable niche in current and recent environmental conditions, which supports the use of distribution modeling to guide management for this species under future climate and land use scenarios. While it may be encouraging that species can track changes in suitable vegetation, as found in this study, it is important to maintain an appropriate amount and configuration of suitable habitat in order to conserve species.

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