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Elevational movement ecology and vegetational associations of birds in the Great Basin

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Elevational movement ecology and vegetational associations of birds in the Great Basin

By

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ABSTRACT

There is strong evidence that climate change has caused many species to shift their geographical distributions as suitable habitat changes both spatially and temporally. Determining mechanisms behind distributional shifts and understanding why some species are shifting while others are not, may offer clues about adaptive capacity and species persistence into the future. The research presented here examines shifts and variability in species' distributions in a community of birds in the Great Basin, USA using a long-term data set on avian abundance and novel occupancy and abundance modeling techniques.

Chapter one examined within breeding season elevational movement of 25 species of birds across two subregions of the Great Basin. This chapter examined the hypothesis that some species of birds disperse upslope as the breeding season progresses to track the distribution of higher-quality, late-season habitat as lower elevations become relatively hot and dry. Through the use of multinominal N-mixture models I examined 25 bird species over 7 years in two distinct regions of the Great Basin. I found evidence of upslope elevational dispersal in six species, and evidence of downslope elevational dispersal in one species, Green-tailed Towhee (*Pipilo chlorurus*). The results largely were consistent with the idea that environmental heterogeneity can drive dispersal. Changes in availability of six of the seven species (all except Broad-tailed Hummingbird [*Selasphorus platycercus*]) that dispersed within the season were associated significantly with shifts in primary productivity and food. The results of this chapter add to a growing body of research suggesting that within-breeding season dispersal is much more common than previously thought.

Chapter two assessed shifts in the elevational distribution of birds from 2001-2020. Although montane species are generally predicted to respond to climate change via upslope elevational movement, many populations and species are not moving in synchrony with increasing temperatures. This chapter examined 32 species of birds for evidence of elevational shifts at the upper and lower 25% of their elevational distribution as well as across the full elevational distribution. The elevational distributions of 19 species shifted, and the four shifts along the full elevational gradient were downslope. About half (46%) of the distributional shifts at the lower or upper elevational edges were upslope. Chapter two found evidence that elevational shifts in bird distributions may be a response to climate change, a signal detected over a relatively short time series (9 and 19 years).

Finally, chapter three examined associations of bird species with two different types of vegetational traits, plant physiognomy (characterized by functional groups) and plant floristics (characterized by plant species), in five biogeographically distinct subregions of the Great Basin. I hypothesized that plant physiognomy was significantly associated with bird occupancy across the Great Basin, while plant floristics were associated with occupancy within an individual subregion. This chapter found considerable variation among subregions with respect to which covariates were significantly associated with occupancy, and that the number and strength of bird-vegetation associations varied substantially between subregions. The results of this work suggest that for many bird species, vegetational associations are not transferrable across subregions, and that there is distinct geographical variation in vegetational preferences for some Great Basin bird populations.

INTRODUCTION

Since 1890, the average global ambient temperature has increased by 0.85°C (Pecl et al. 2017). Increases in temperature and other changes in climate, including climate variability, timing and intensity of storms, and changes in precipitation, are affecting organisms through shifts in distributions, relative abundances, and environmental associations. In general, when confronted with novel environmental conditions, organisms can either evolve, acclimate, or move. This research examines how movement at different spatial and temporal scales is utilized as an adaptive strategy. I investigate this idea by focusing on songbird communities in the mountain ranges of the Great Basin.

The Great Basin is the largest internally draining watershed in North America, stretching from the Sierra Nevada in the west to the Wasatch Range in the east (Grayson 1993). Distinct in its arid climate and sagebrush-steppe vegetation, there are over 300 mountain ranges in the Great Basin, most of which stretch north to south. The considerable topographic diversity contributes to variation in temperature and precipitation and to high species richness, including over 220 species of breeding birds. In three separate chapters I examine different aspects of species distribution in the montane avian community of the Great Basin.

Chapter one and two take advantage of elevational gradients in the Great Basin to examine how elevational changes in bird resources (e.g. plant phenology, insect biomass, and temperature) at multiple temporal scales effect bird dispersal. Through the use of multinominal N-mixture models and point count data, chapter one analyzes within-breeding season elevational movement, a poorly understood avian behavior. Chapter one hypothesizes that some species of birds will move upslope between breeding attempts to take advantage late-season high elevational resources. Chapter two examines elevational shifts over multiple years in an effort to understand if climate change has caused elevational range shifts in some bird species. Many studies have found evidence for upslope range shifts in variety of organisms, although evidence of downslope or lack of elevational shifts is becoming more widespread. Chapter two hypothesizes that the majority of elevational shifts observed would be upslope and would occur at the elevational range margins.

In addition to analyzing avian dispersal over elevational gradients, I wanted to understand if associations with plant species or plant functional groups were consistent across a large habitat gradient. Chapter three analyzed avian associations with vegetational attributes across five biogeographically distinct subregions of the Great Basin. I hypothesized that the bird species would be significantly associated with different plant species in each of the five subregions but would be significantly associated with the same vegetational functional groups. This chapter examines the well-recognized hypothesis that floristics is more important for bird distributions at local scales, but that physiognomy is more important at regional scales (MacArthur & MacArthur 1961, Robinson & Holmes 1984).

In the following text, each of the three chapters are treated as separate scientific papers, with separate corresponding figures, tables, and references. However, all three chapters examine the same community of Great Basin songbirds, and taken together have identified bird species that may have relatively large capacities to adapt to environmental change through resource tracking or habitat plasticity.

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CHAPTER 1

Within-season elevational dispersal of breeding birds in the Great Basin

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Abstract

A dominant paradigm in ornithology is that birds arrive on breeding grounds, establish a territory, and occupy that territory for the entire breeding season. However, a growing body of research suggests that not all species have fixed breeding territories. Territory switching during the breeding season, or what we refer to as *within-season dispersal,* is poorly understood, and numerous hypotheses aim to explain potential drivers of dispersal between nesting attempts. Our work identified avian species that dispersed elevationally within the breeding season and examined whether within-season dispersal was associated with regular, seasonal changes in resource availability or temperature. We hypothesized that some species of birds disperse upslope as the breeding season progresses to track the distribution of higher-quality, late-season habitat as lower elevations become relatively hot and dry. We applied two separate analyses to data on avian abundance and availability. First, we determined which species appeared to disperse along elevational gradients within the breeding season. Second, we examined whether environmental heterogeneity was associated with that dispersal. Through the use of multinominal N-mixture models we examined 25 bird species over 7 years in two distinct regions of the Great Basin. We found evidence of upslope elevational dispersal in six species, and evidence of downslope elevational dispersal in one species, Green-tailed Towhee (*Pipilo chlorurus*). Our results largely were consistent with the idea that environmental heterogeneity can drive dispersal. Changes in availability of six of the seven species (all except Broad-tailed Hummingbird [*Selasphorus platycercus*]) that dispersed within the season were associated significantly with shifts in primary productivity and food. These results add to a growing body of research suggesting that within-breeding season dispersal is much more common than previously thought.

Introduction

A dominant paradigm in ornithology is that birds arrive on breeding grounds, establish a territory, and occupy that territory for the entire breeding season (Greenwood and Harvey 1982). The assumption that territories are fixed throughout the breeding season affects research on avian distributions, occurrence and abundance, and habitat. For example, birds commonly are sampled repeatedly during the breeding season. The assumption of closure – that a species' presence or absence at a site does not change during the sampling period – follows from the belief that territories are fixed, and is fundamental to many models of occupancy and abundance (MacKenzie et al. 2003). However, a growing body of research suggests that not all species have fixed breeding territories (Betts et al. 2008, Gilroy et al. 2010, Brambilla et al. 2012, Cyzc et al. 2012).

Territory switching during the breeding season, or what we refer to as *within-season dispersal*, is poorly understood, and mainly has been observed in studies of a single or small set of bird species. Within-season dispersal most commonly refers to movement of adult breeding birds to a new territory after either nest failure (no offspring produced or fledged) or, in the case of species with multiple broods, after nest success (at least one offspring fledges). Birds also may disperse following a nest attempt or for reasons independent of reproduction, as discussed below. Many bird species attempt two or more clutches within a single season (Schmidt and Whelan 2019), and therefore have at least one opportunity to switch territories. Although it generally has been assumed that successive breeding attempts occur within the same territory and with the same mate (Feng et al. 2019), this may not be the case for all species.

Examination of within-season dispersal behavior may offer insights into the life histories of some bird species. Identifying species that disperse within a season and the associated drivers may elucidate territory choice, site fidelity, and seasonal shifts in avian community composition. Species that disperse within a season also may be more resilient to environmental change (Scheffers et al. 2017). For example, climate change has been linked to changes in the timing of seasonal events (i.e., phenology) of a variety of organisms (Helm et al. 2013). In response to increasing spring temperatures, spring migration of many bird species has advanced, some by as much as 2 days per C° (Lehikoinen et al. 2004). Phenological shifts could affect the probability of population or species persistence. To illustrate, among 100 species of European birds, timing of spring migration of species with declining population trends did not advance, whereas spring migration of species with stable or increasing populations advanced considerably (Møller et al. 2018). Although some species of migratory birds may be able to arrive earlier on their breeding grounds to track phenological advances, species in which within-season dispersal is common may be able to respond to spatial and temporal resource heterogeneity without changing the timing of migration. Changing the timing of migration is difficult because timing of long-distance migration mainly is controlled by photoperiod (Berthold 1996).

The prevalence of within-season dispersal also affects the accuracy of occupancy and abundance models that assume closure. Emigration or immigration of even a small proportion of birds can bias estimates of detection and abundance substantially (Hayes and Monfils 2015, Fogarty and Fleishman unpublished ms). Establishing which species or populations of birds disperse within a season can guide selection of statistical models and increase ecological understanding of both population and community dynamics. Here, we examine whether within-season dispersal along elevational gradients is occurring in a community of birds in the Great Basin, USA, and explore potential drivers of this behavior.

Drivers of within-season dispersal

There are numerous reasons why adult birds might disperse within a season including natal dispersal, or dispersal from the site of birth to that of first reproduction or attempted reproduction; and post-breeding dispersal, or interannual dispersal among breeding sites or groups (Greenwood and Harvey 1982, Howlett and Stutchbury 1997, Cline et al. 2013, Ganey et al. 2014). Additionally, because breeding and molting habitat differ, many species move to a new territory to molt after completion of breeding (*molt migration*) (Vega Rivera et al. 2003, Gow and Stutchbury 2013, Pyle 2018).

The best-studied potential drivers to explain dispersal between nesting attempts include dispersal to avoid predation, dispersal in response to changes in competition, and dispersal due to shifts in environmental heterogeneity. Examination of dispersal in response to predation suggested that an individual establishes a new territory after nest predation if the move reduces the likelihood of subsequent predation, and that the decision to disperse often depends on the timing of predation within the breeding cycle (Jackson et al. 1989). Support for this explanation is equivocal. Prairie Warblers (*Dendroica discolor*) were more likely to disperse after late-season nest predation (Jackson et al. 1989), and simulations indicated that predator characteristics, such as home-range size or identity, were associated with variation in dispersal distances (Powell and Frasch 2000). There was no significant difference in the distances that female Red-winged Blackbirds (*Agelaius phoeniceus*) moved between nests if their previous nest was unsuccessful due to predation or other causes (Beletsky and Orians 1991). Additionally, nest success of Northern Flicker (*Colaptes auratus*) pairs that either remained or switched territories after nest predation did not differ (Fisher and Wiebe 2006).

Relatively little research has examined avian dispersal in response to changes in the occurrence or abundance of conspecifics and heterospecifics during the breeding season. It is well known that competition can drive avian dispersal between breeding seasons (Waser 1985, Liu and Zhang 2008), but whether competition drives within-season dispersal is unclear. There was no effect of predation on dispersal of Hooded Warblers (*Setophaga citrina*) between breeding attempts, but dispersal of females was related to avoidance of fledglings that remained near the nest with the male (Howlett and Stutchbury 1997). Great Tits (*Parus major*) expanded their territories after removal of neighboring pairs mid-season, but there was no relation between density and fecundity (Both and Visser 2000).

Conditions in the territories of almost all bird species, such as weather or microclimate, vegetation growth and productivity, food availability, composition of the avian community, and the composition and abundance of natural enemies (e.g. predators, diseases, parasites), change within a single breeding season. Some species of birds, such as the nomadic Red Crossbill (*Loxia curvirostra*), can track resource abundance over large spatial extents and time their reproduction to coincide with resource pulses (Hahn 1998). Species that are not nomadic, but in which individuals disperse over relatively small spatial extents within a season, also may be able to take advantage of short-term shifts in habitat quality (Scheffers et al. 2017). For example, Black-throated Blue Warblers (*Setophaga caerulescens*) in New Hampshire moved to higher-quality habitat after initially settling in low-quality habitat (Betts et al. 2008). Female Wood Thrushes (*Hylocichla mustelina*) switched territories within their breeding season, presumably to seek higher-quality nesting vegetation (Gow and Stutchbury 2013). Similarly, over half of male Grasshopper Sparrows (*Ammodramus savannarum*) switched territories after a failed breeding attempt, potentially using cues such as conspecific density or resource availability to choose new territories (Willams and Boyle 2017).

There is some support for the theory that environmental heterogeneity might lead to within-season dispersal if local habitat quality changes within the breeding season and if establishment of subsequent territories in higher-quality locations maximizes reproduction. In the Swiss Alps, 57% of Grey Wagtail (*Motacilla cinerea*) females moved upslope within 10 days after their first brood fledges or is lost, and attempted their second brood at higher elevations (Klemp 2003). This movement was attributed to increased food availability at higher elevations later in the season (Klemp 2003). The nest-site associations of multiple-brooded Yellow Wagtails (*Motacilla flava*) in eastern England changed during the breeding season, perhaps to maximize the number of breeding attempts (Gilroy et al. 2010). Other biotic or abiotic factors also could lead to within-season dispersal. For example, stochastic natural events such as fire, extreme flooding, or storms could prompt dispersal away from affected areas.

We studied the within-season dispersal of 25 avian species over 7 years in two distinct regions of the Great Basin. Our study area consists of mountain canyons with an average elevational change of 400 m per canyon. Elevation is a good proxy for temperature, total radiation, and ultraviolet B radiation, and can be associated with precipitation and wind velocity (Körner 2007, Sundqvist et al. 2013). Elevational gradients indirectly affect a broad range of ecological phenomena, such as water availability, plant community composition (Sundqvist et al. 2013), and phenology of animals and plants (Hodkinson 2005, Ozgul et al. 2010, Richardson et al. 2013). Elevational movement within a single season has been examined in butterflies (Peterson 1997), and many ungulates, birds, and bats migrate along an elevational gradient between their breeding and non-breeding grounds (Hsiung et al. 2018). The phenology of many important resources for birds in the Great Basin is correlated with elevation (see Results section), allowing us to investigate environmental heterogeneity as a driver of within-season elevational dispersal. Our objectives were to identify avian species that dispersed elevationally within the breeding season and to examine whether within-season dispersal was associated with regular, seasonal changes in resource availability or temperature. We hypothesized that some species of birds disperse upslope as the breeding season progresses to track the distribution of higher-quality, late-season habitat as lower elevations become relatively hot and dry.

Methods

Study area

The Great Basin includes more than 300 mountain ranges and five or more centers of avifaunal differentiation (Behle 1963). Our work focused on two of these centers and six mountain ranges: the Sierra Nevada and Wassuk Range in the Inyo center (henceforth western Great Basin), and the Shoshone Mountains, Toiyabe Range, Toquima Range, and Monitor Range in the eastern center (henceforth central Great Basin) (Figure 1.1). Species richness of birds in the Great Basin is concentrated in riparian canyons. Therefore, we focused on 47 canyons, primarily riparian, in these mountain ranges (Fleishman 2019b,c). We sampled birds along the full elevational gradients of these canyons, from 1650 to 3200 m.

Field data

We sampled birds from late May through early July, which encompasses the breeding season of most birds in the region and ends before a high proportion of juveniles have fledged and before most movement to molting or wintering grounds. We sampled birds with 100-m fixed-radius point counts. In the western Great Basin, we sampled birds from 2012-2019 at a total of 168 points in 13 canyons (Fleishman 2019b). In the central Great Basin, we sampled birds from 2018-2020 at a total of 225 points in 19 canyons (Fleishman 2019c). Not all points or canyons were sampled in all years.

We visited each point three times during the breeding season, with ca. 10–14 days between visits, and recorded all birds detected by sight or sound that were using resources within the point during an eight-minute count. In almost all cases, we restricted sampling to the first four hours after sunrise. From 2012-2017, we recorded birds during consecutive 5-min and 3-min intervals (removal sampling; Farnsworth et al. 2002). From 2018-2020, we recorded birds during four consecutive 2-min intervals. We excluded fledglings and juveniles from our analyses.

Throughout the breeding seasons of 2018 and 2019, we collected data on insect biomass, plant phenology, and temperature at four locations in each of 10 canyons, five in the western Great Basin and five in the central Great Basin. These sampling locations spanned the elevational gradients of the canyons and were within the 100-m points at which we sampled birds. We collected data on insect biomass with 10 x 15 cm sticky traps set at a height of 1.2 m. Sticky traps are useful for estimating the local density and composition of flying insects (Leather 2005). We changed the traps every 8-10 days. We counted the insects on each trap, identified them to order, and weighed the traps to estimate relative insect biomass.

We tracked the phenology of individual plants of species that provide food for Great Basin bird species: bitterbrush (*Purshia tridentata*), aspen (*Populus tremuloides*), bitter cherry (*Prunus emarginata*), snowberry (*Symphoricarpus* sp.), and chokecherry (*Prunus virginiana)*. We tracked ten phenological stages: percentage of breaking leaf buds, young leaves, mature leaves, leaf death, flower buds, open flowers, pollen release, unripe fruits, ripe fruits, and fruit or seed drop. We chose to focus our analysis on two phenological stages that birds use as food during the breeding season: breaking leaf buds and ripe fruits. Our methods were based on those developed by the USA National Phenology Network, which standardized recording of the phenology of plants and animals (Schwartz et al. 2012, Denny et al. 2014). We deployed data loggers (HOBO Pendant MX Temperature/Light Data Logger) at each of the 40 locations to record temperature at 20-min intervals.

We used the normalized difference vegetation index (NDVI) to estimate primary productivity at each point during the breeding season. NDVI, an index of vegetation greenness, is a reliable measure of primary productivity (Wang et al. 2004) and is closely related to biological variables such as leaf area index, leaf cover, and chlorophyll per ground area (Gamon et al. 1995, Paruelo et al. 1997, Rundquist 2002). Additionally, NDVI is correlated positively with avian abundance and species richness in some arid ecosystems, including the central Great Basin (Seto et al. 2004, McFarland & van Ripper 2013). We extracted the maximum NDVI value at the centroid of each bird-survey point from 24 May through 14 July (the range of dates during which we sampled birds) of each year from the Application for Extracting and Exploring Analysis Ready Samples (AppEARS) database (https://lpdaacsvc.cr.usgs.gov/appeears/), resulting in one NDVI value per point per year. AppEARS derives NDVI from images captured every 16 days at 250-m resolution by the Moderate Resolution Imaging Spectroradiometer (MODIS). NDVI values are scaled from -1 to 1.

Analyses

We implemented single-species hierarchical models that integrated aspects of multinomial N-mixture models and temporary emigration models. Multinomial N-mixture models replace the binominal observation model of traditional N-mixture models with a multinomial observation model and include a model of local abundance (Kery and Royle 2016).

The multinomial classes usually correspond to distinct encounter histories (detected or not-detected) and reflect the probability that each encounter history occurs in a population of *N* individuals (Kéry and Royle 2016). As noted above, we collected count data with removal sampling, in which a population is sampled iteratively, and one records the time period during which each individual first is detected. For example, in data collected from 2018-2020, an individual bird first detected during the third minute of the point count was recorded as being detected during the second interval, regardless of whether it was detectable during subsequent intervals.

Incorporation of elements of temporary emigration models (Chandler et al. 2011) allowed us to relax the closure assumption of N-mixture models, which was necessary to test our hypothesis of elevational dispersal and to model abundance, availability, and detection separately. In temporary emigration models, availability is the probability that an individual is available to be sampled during a sampling period, and detection is the probability of detecting an individual given that it is available to be sampled. Changes in availability over time likely indicate emigration or immigration, whereas changes in detection over time likely indicate that birds are becoming more or less detectable due to behavioral changes.

We implemented two distinct single-species models. The first model identified species that dispersed along elevational gradients within the breeding season (henceforth referenced as the *within-season dispersal model*). The second model examined environmental heterogeneity as a potential driver of within-season elevational dispersal (henceforth referenced as the *environmental heterogeneity model*). There were two reasons why two distinct single-species models were necessary. First, we used different removal-sampling intervals to collect avian-abundance data from 2012-2017 and from 2018-2020, and these data could not be examined simultaneously in a single model. Second, data on temperature and phenology were only collected during the 2018-2019 seasons, therefore only avian survey data from 2018-2019 could be included in the environmental heterogeneity model. Finally, we implemented separate generalized linear models (GLMs) to identify shifts in avian resources along elevational gradients within the breeding season (henceforth referenced as the *phenology and temperature model*).

Within-season dispersal

The multinomial process in our within season dispersal model for each species was

$$y_{ijh} \mid n_{ij} \sim Multinom(n_{ij}, \pi^{c}{}_{i})$$

$$logit(\pi_{ij}) = \alpha_1 + \beta_1 * Visit_{ij} + \beta_2 * Elevation_{ij} + \beta_3 * Visit_{ij} * Elevation_{ij} + \beta_4 * Time_{ij} +$$

$$\beta_5 * (Time_{ij})^2 + \beta_{6ij} * Observer_{ij} + \beta_{7ij} * Point_{ij},$$

where y_{ijh} is the number of individuals detected at point i during removal sampling period h within visit j, n_{ij} is the number of individuals available to be sampled at point i during visit j, and $\pi^{c}{}_{i} = \pi_h / 1 - \pi_0$, where π_h is the probability of detection during removal sampling period h. By applying a logit link function to π_{ij}, we modeled relations between detection and elevation, visit number, and time of day. We also included random observer and point-level effects.

N (abundance) varies among visits, and is linked to the population M_i, or the total number of individuals that were available for detection at point i over the breeding season. We linked the multinomial process to the availability process through

$$n_{ij} \sim Binominal\ (N_{ij}, 1-\pi_0),$$

where π_0 is the sum of detection probabilities during each 2-min sampling period *h* at point *i*, and N_{ij} is the subset of the population present at point *i* during visit *j*. The availability process in the model was

$$N_{ij} \sim Binominal\ (M_i\,,\ \phi_{ij})$$

$$logit(\phi_{ij}) = \alpha_2 + \phi_1 {*} Visit_{ij} + \phi_2 {*} Elevation_{ij} + \phi_3 {*} Visit_{ij} {*} Elevation_{ij} + \phi_4 {*} Time_{ij} + \phi_5 {*} (Time_{ij})^2 + \phi_{6ij} {*} Point_{ij},$$

where M_i is the total population or the number of individuals that were available for detection at point *i* during the breeding season, and ϕ_{ij} is the probability that an individual was available at point *i* during visit *j*. We used a logit link function to model covariates of availability. We also included a random point-level effect. We modeled the effects of abundance on M_i as

$$M_i \sim Poisson\ (\lambda_i),$$

$$logit(\lambda_i) = \alpha_3 + \varpi_{1i} {*} Point_i + \varpi_{2i} {*} Canyon_i,$$

where λ_i is the expected count of individuals at point *i*. We used a logit link function to include random point-level and canyon-level effects in the abundance process model.

We modeled species in the western Great Basin and central Great Basin separately. We restricted our analyses to species with >50 annual detections in at least 3 of 6 years (western Great Basin, 20 species) or >40 detections in all 3 years (central Great Basin, 19 species) (Table 1.S1). These cutoffs were chosen arbitrarily, but we feel they selected the maximum number of species per region that could be modeled. We used vague prior distributions for intercepts, covariates, random effects, and mean imputation. We implemented models in JAGS (Plummer 2003) with the `jagsUI` package (Kellner 2019) in R (R Core Team 2020). We based posteriors on three chains of 50,000 iterations after a 5,000 sample burn-in and adaptive phase. We classified a model as converged if Rhat <1.01 (Gelman and Hill 2007). We calculated the collinearity of all pairs of candidate predictor variables. If collinearity >0.75, we excluded the variable of the pair that we deemed less ecologically relevant. We classified model fit as good, moderate, or poor on the basis of values of five metrics: Bayesian p-values for the availability, detection, and abundance submodels and estimates of mean detection and availability. Models with good fit were those for which Bayesian p-values for availability, detection, and abundance were 0.05-0.95, and posterior estimates of mean availability and detection were >15%. Models with moderate fit met three or four of the former criteria, and the remaining Bayesian p-values or posterior estimates of mean availability and detection were 0.015-0.985 or >10%, respectively. Models with poor fit are not reported.

In an effort to improve model fit, we reparametrized the abundance process to include a site suitability term. The site suitability term allowed the abundance process to have structural zeros in two circumstances: when the site was unsuitable, or when the site was suitable, but the species was not present. We modeled the reparameterization of the abundance process as

$$M_i \sim Poisson\ (\lambda_i),$$

$$\lambda_i = lam_i * S_i$$

$$S_i \sim Bernoulli(\dot{z})$$

$$log(lam_i) = \alpha_3 + \mho_{1i}*Point_i + \mho_{2i}*Canyon_i,$$

where λ_i is the expected count of individuals at point i conditioned on suitability (S_i), lam_i is expected count of individuals at point i given suitability, S_i is the suitability term, and $\dot{z}$ is a random variable defined by a normal distribution with a mean of 0 and variance of 1. To achieve convergence, we ran 100,000 iterations of the reparametrized models. This reparameterization can improve model fit by removing zeros from the Poisson process and transferring them to the Bernoulli process through the suitability term, therefore allowing the data to better fit the assumption of the Poisson distribution that the mean is equal to the variance. This reparameterization did not affect model inference, although the magnitude of estimates cannot be compared between models that included the reparameterization of the abundance process and models that did not. Therefore, we did not compare the magnitude of model estimates among species.

To determine whether species dispersed within the season, we compared four models with Watanabe-Akaike information criterion (WAIC; Watanabe 2013) values: intercepts only; all detection covariates, no availability covariates; all availability covariates, no detection covariates; and all detection and availability covariates (Tables 1.S2 and 1.S3). We report the model with the lowest WAIC score. Covariates included elevation, visit number, the interaction of visit number and elevation, time of day, and a quadratic term for time of day. All covariates were included in both the availability and detection processes. The interaction of elevation and visit number allowed us to determine whether elevation was more strongly associated with availability or detection as the season progressed. We included time of day and the quadratic effect of time of day to capture potential effects of survey time on detection probability. We aimed to identify species for which a model with covariates on the availability process was the best supported by the data. If the model best supported by the data was a model with covariates on the availability process, we evaluated whether the interaction of elevation and visit on the availability process was significant. Significance would indicate that availability, and not detection probability, changed along the elevational gradient throughout the season, potentially indicating upslope or downslope elevational dispersal. We included a point-level random effect in all detection and availability models, and an observer-level random effect in the detection models. If >90% of the posterior distribution of the interaction between elevation and visit number in the availability sub model of the best-supported model was above or below zero, we considered inferences about upslope or downslope movement to have high certainty. If 75-89% of the posterior distribution of the interaction was above or below zero, we considered inferences about upslope or downslope movement to have moderate certainty. These interactions indicated that point-level availability changed as the season progressed.

To estimate the horizontal or straight-line dispersal distances that corresponded to elevational dispersal distances, we first compared the mean elevation at which each species was detected during visit 1 and during visit 3. This yielded vertical or elevational dispersal distance. We then calculated the mean slope of the points at which we detected each species and performed a simple transformation to calculate the horizontal dispersal distance. The average interval between visit 1 and visit 3 was 34 days.

Environmental heterogeneity

The formulation of the environmental heterogeneity model was the same as that of the within-season dispersal model, except we restricted point-count data to those from 2018-2019, which corresponded to the period during which we collected data on phenology and temperature. We classified model fit and certainty of inferences with the same criteria as above.

Covariates included Julian date, insect biomass, mean temperature, NDVI, and total percentage of buds and fruits of all plant species examined. All covariates were centered and scaled to improve model fit and convergence. We calculated mean temperature during each of the three 24-hour dates on which we sampled birds at each point. We included interactions of each covariate with Julian date in both the availability and detection models to test whether associations changed during the breeding season. We included all covariates in both the detection and availability sub models. We calculated collinearity as above. The only collinearity >0.75 was between NDVI and mean temperature in the central Great Basin models. We excluded mean temperature (and its interaction with Julian date) from the final models for the central Great Basin.

Phenology and temperature

We used generalized linear models (GLMs) to assess whether insect biomass, mean temperature, onset of buds, onset of fruits, and NDVI changed along elevational gradients or over time in the western and central Great Basin. We implemented the GLMs with JAGS and used jagsUI in R to run three chains at 50,000 iterations each. We included canyon as a random effect. We modeled onset (the first day on which a given phenological stage was observed) of buds and of fruit as a function of year and elevation. Onset is a simple transformation of the total percentage of fruit and buds. We applied this transformation to avoid problems with modeling zero-inflated data. We modeled insect biomass as a function of elevation, the quadratic transformation of elevation, Julian date, the quadratic transformation of Julian date, year, and the interaction of elevation and Julian date. We included quadratic transformations of elevation and Julian date because species richness of some taxonomic groups of insects in some systems, including butterflies in the central Great Basin, peaks at intermediate elevations or in midsummer (Fleishman et al. 1998, McCoy 1990, Hodkinson 2005, Beck et al. 2017). If <5% of the posterior distribution of a variable overlapped zero, we considered the association between the variable and elevation or time to be significant.

Results

Within-season dispersal

Western Great Basin

In the western Great Basin, the average elevation at which we detected four species, Brewer's Sparrow (*Spizella breweri*), Green-tailed Towhee (*Pipilo chlorurus*), MacGillivray's Warbler (*Geothlypis tolmiei*), and Lazuli Bunting (*Passerina amoena*), changed within the breeding season (Table 1.1). Availability of Brewer's Sparrows, MacGillivray's Warblers, and Lazuli Buntings was positively associated with the interaction of visit and elevation in the within-season dispersal models, indicating upslope movement. Availability of Green-tailed Towhees was negatively associated with the interaction of visit and elevation, indicating downslope movement. The fit of models of Brewer's Sparrow, Green-tailed Towhee, Warbling Vireo (*Vireo gilvus*), and House Wren (*Troglodytes adeon*) was good. The fit of models of MacGillivray's Warbler, Western Wood-Pewee (*Contopus sordidulus*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Spotted Towhee (*Pipilo maculatus*), Yellow Warbler (*Setophaga petechia*), Yellow-rumped Warbler (*Steophaga coronate*), and Lazuli Bunting was moderate (Table 1.1).

The effect of the interaction of visit and elevation on availability of Brewer's Sparrows, MacGillivray's Warblers, and Lazuli Buntings was significant and positive (99%, 97%, and 99% of the posterior densities above zero, respectively), indicating high certainty that the average elevation at which each species was present increased during the breeding season. Certainty that the average elevation of Green-tailed Towhees decreased during the breeding season also was high (90% of the posterior density below zero). Brewer's Sparrows dispersed upslope by a horizontal distance of 273 m between visit 1 and visit 3. MacGillivray's Warblers dispersed upslope by a horizontal distance of 161 m, Green-tailed Towhees dispersed 84 m downslope, and Lazuli Bunting dispersed 705 m upslope. Horizontal dispersal estimates were calculated from the raw data (see Methods) because calculation of dispersal distances from the modeled results was not possible given the model's structure.

Examination of the raw data yielded similar inferences about elevational dispersal (Figure 1.2). Density curves of detections per meter during visits one and three, which were derived from the raw data, indicated upslope movement of MacGillivray's Warblers and Lazuli Buntings, and to a lesser extent Brewer's Sparrows. Because Lazuli Buntings in the western Great Basin occur at elevations below those of our lowest-elevation points, our data likely do not represent the full elevational range of Lazuli Buntings in that region. Therefore, the upslope movement of Lazuli Buntings may be greater than our analyses suggest.

Central Great Basin

In the central Great Basin, the average elevation at which we detected four species, Broad-tailed Hummingbird (*Selasphorus platycercus*), Vesper Sparrow (*Pooecetes gramineus*), MacGillivray's Warbler, and Yellow Warbler, increased within the breeding season (Table 1.1). Availability of all four species was positively associated with the interaction of visit and elevation in the within-season dispersal models, indicating upslope movement. The fit of the model of MacGillivray's Warbler was moderate, and the fit of models of the other three species was good. The fit of models of Dusky Flycatcher (*Empidonax oberholseri*) and Blue-grey Gnatcatcher (*Polioptila caerulea*) were good and moderate, respectively. Neither of the latter two species appeared to move along elevational gradients within the season.

More than 95%, 96%, and 91% of the posterior density of the interaction of visit and elevation on availability of Broad-tailed Hummingbirds, Vesper Sparrows, and MacGillivray's

Warblers, respectively, was above zero, indicating that the average elevation of each species' presence increased during the breeding season. The average elevation at which Yellow Warblers were detected also increased within the breeding season (77% of the posterior density above 0; moderate certainty). Broad-tailed Hummingbirds, Vesper Sparrows, MacGillivray's Warblers, and Yellow Warblers dispersed upslope by horizontal distances of 30 m, 237 m, 101 m, and 79 m, respectively.

Examination of the raw data again led to similar inferences about upslope dispersal (Figure 1.3). Density curves of detections per meter suggested that all four species dispersed upslope in the central Great Basin. We likely have not captured the full elevational range of Broad-tailed Hummingbirds or MacGillivray's Warblers in that region (Figure 1.3). Accordingly, the upslope dispersal distances of these species may be greater than our analyses suggest.

Environmental heterogeneity

Western Great Basin

Availability of the four species for which we detected elevational dispersal in the western Great Basin was associated with measured environmental covariates (Table 1.2). Availability of Brewer's Sparrows was positively associated with insect biomass (high certainty), the interaction of NDVI and Julian date (moderate certainty), and the interaction of temperature and Julian date (moderate certainty), and negatively associated with the interaction of insect biomass and Julian date (moderate certainty). Availability of Green-tailed Towhees was positively associated with total percentage of fruits and negatively associated with Julian date, insect biomass, and total percentage of buds, all with high certainty. Availability of MacGillivray's Warblers was positively associated with NDVI (high certainty), temperature (moderate certainty), and the interaction of temperature and Julian date (moderate certainty), and negatively associated with the total percentage of fruits (moderate certainty). Availability of Lazuli Buntings was positively associated with insect biomass, total percentage of fruits, and the interaction of total percentage of buds and Julian date, all with moderate certainty.

The fit of environmental heterogeneity models of 18 of 20 species in the western Great Basin was good. Availability of all 18 species was associated with measured environmental covariates, and associations for 15 of the 18 species had high certainty (Table 1.2).

Central Great Basin

Availability of three of the four species in the central Great Basin that appeared to disperse within the season was associated with measured environmental covariates (Table 1.3). Availability of Vesper Sparrows was positively associated with NDVI and the interaction of NDVI and Julian date, both with moderate certainty. Availability of MacGillivray's Warblers and Yellow Warblers was positively associated with NDVI, both with high certainty.

The fit of environmental heterogeneity models of all four species that appeared to disperse, and of models of an additional 10 species, was good. No environmental covariates were significantly associated with availability of Broad-tailed Hummingbirds. NDVI was associated with availability of the 13 other species.

Phenology and temperature

Examination of the raw data indicated that the phenology of individual plants was related to date and elevation. The phenology of high-elevation plants lagged behind that of low-elevation plants by as much as 57 days in some canyons (Figure 1.S1). In both the western and the central Great Basin, year was significantly and positively related to the date of onset of buds (Figure 1.4), indicating that date of onset of buds was later in 2019 than 2018. The effect of elevation on the date of onset of buds was significant and positive in the western Great Basin, and significant and negative in the central Great Basin (Figure 1.4). The breeding season in 2019 was unusually wet and cool, and plant development was delayed. The negative relation between onset of buds and elevation in the central Great Basin is surprising; we expected the relation to be positive. However, topography, aspect, and shading affect the relative photoperiod to which an individual plant is exposed, and the average photoperiod of our high-elevation plants may have been longer than that of our low-elevation plants in the central Great Basin. Phenology of bud burst is correlated with photoperiod in many plant species (Fracheboud et al. 2009, Basler and Korner 2014), whereas phenology of fruit development is more closely related to temperature and precipitation (Wadgymar et al. 2018). The effect of elevation on the date of onset of ripe fruits was positive in both the western and central Great Basin, although neither was significant (Figure 1.4).

Insect biomass in both the western and central Great Basin was significantly greater in 2019 than in 2018 (Figure 1.5). Nevertheless, neither Julian date nor elevation was significantly related to insect biomass. In both the western and central Great Basin, NDVI was significantly and positively related to year and elevation, and significantly and negatively related to the quadratic transformation of elevation (i.e., NDVI peaked at intermediate elevations). NDVI was higher in 2019 than in 2018, again likely reflecting that 2019 was unusually cool and wet.

Changes in temperature during the breeding season and along the elevational gradient were predictable in both regions of the Great Basin (Figure 1.S2). Temperature increased significantly over time at all elevations and decreased significantly as elevation increased.

Temperature also was significantly and negatively related to year. The interaction of Julian date and elevation was significantly and negatively associated with mean daily temperature in the central but not the western Great Basin.

Discussion

To our knowledge, this is the first study to examine within-season elevational dispersal in a community of birds in the United States. We estimated elevational shifts at the population level, where dispersal represents a change in the average elevation of a population. We applied two separate analyses to data on avian abundance and availability. First, we determined which species appeared to disperse along elevational gradients within the breeding season. Second, we examined whether environmental heterogeneity was associated with that dispersal. Of the 39 single-species within-season dispersal models, 17 had good or moderate fit, and of those, eight suggested within-season elevational dispersal. Six of the seven species represented in those models appeared to disperse upslope, and one species appeared to disperse downslope.

The fit of the majority (32 of 39) of the single-species environmental heterogeneity models was good or moderate, allowing us to make robust inferences about relations between availability and the temporal and spatial distribution of resources. Environmental covariates were significantly associated with availability in 31 of 32 of the former models (Tables 1.2 and 1.3). Our results largely were consistent with the idea that environmental heterogeneity can drive dispersal. Changes in availability of six of the seven species that dispersed within the season were associated significantly with shifts in primary productivity and food.

NDVI was significantly associated with availability in the greatest number of single-species models (26 of 32) (Tables 1.2 and 1.3). Given that NDVI is an index, birds likely are responding to variables highly correlated with NDVI, such as plant biomass, primary productivity (Carlson and Ripley 1997), water availability, and the abundance of plants that provide food or nest materials. Because we derived only one NDVI value per point per year, we can draw conclusions about elevational patterns in NDVI, but not temporal patterns. Our models indicated that in our study system, NDVI peaked at intermediate elevations. However, other studies have demonstrated that in general, primary productivity and plant biomass decrease as elevation increases (Sundqvist et al. 2013). A potential explanation for the mid-elevation peak in NDVI is that our data were collected during a period in which snow cover initially constrains productivity at high elevations and senescence increasingly constrains productivity at low elevations. Other studies have suggested that snowpack affects primary productivity over an elevational gradient. For example, in the Sierra Nevada, the relation between snowpack and productivity was strongest at intermediate elevations (Trujillo et al. 2012). Above 2100 m, temperature limited photosynthesis, and primary productivity sharply decreased (Trujillo et al. 2012). Others reported a strong negative relation between elevation and spring plant phenology (Vitasse et al. 2017, Richardson et al. 2019), which is consistent with our phenology analyses.

We found that plant phenology and temperature, but not insect biomass, changed predictably along elevational gradients throughout the season. The apparent lack of association between elevation and insect biomass during the breeding season may reflect our sampling methods. We sampled insect biomass at four locations over the elevational gradient in each canyon. Differences in insect biomass may occur at a much finer spatial resolution given that insect emergence times are affected by precipitation, day length, temperature, and, in some cases, host plant phenology (Hodkinson 2005, van Asch et al. 2007, Hodgson et al. 2011). Sampling insect biomass at a finer resolution, or even sampling directly in the territories of individual pairs of birds, could elucidate elevational or temporal patterns to which birds may be responding.

We acknowledge that our results cannot detect shifts in elevation of individual birds within the breeding season but instead offer insights into population-level shifts in availability. Therefore, we cannot rule out other mechanisms that might result in population-level elevational shifts. For example, arrival at high elevations of many new adults late in the season also would lead to inference of elevational dispersal. However, work that has tracked movement of individuals within the breeding season is consistent with our inference that within-season dispersal is occurring at the individual level (Klemp 2003, Gow and Stutchbury 2013, Williams and Boyle 2017). Additionally, our results cannot be linked directly to reproduction or recruitment. Future work might track individual birds throughout the breeding season and directly measure reproduction and resource availability in individuals' territories. Below, we further address the seven species that dispersed along elevational gradients within the breeding season.

Brewer's Sparrow

The average elevation of the presence of Brewer's Sparrows shifted upslope within the breeding season in the western Great Basin, with high certainty that availability was positively associated with insect biomass. Additionally, availability of Brewer's Sparrows was positively associated with the interaction of Julian date with NDVI and of Julian date with temperature, and negatively associated with the interaction of insect biomass with Julian date. During the breeding season, Brewer's Sparrows primarily eat arthropods associated with sagebrush (*Artemisia* spp.) (Stephens 1985). The negative association of availability with the interaction of insect biomass and Julian date suggests that as the season progresses, Brewer's Sparrows are moving away from areas with higher insect biomass. However, because we detected no elevational or temporal patterns in insect biomass, we cannot infer the cause of the movement. Instead, this relation may reflect that we recorded highest insect biomass in riparian vegetation, which is not associated with high abundance of Brewer's Sparrows.

The positive association of the interactions of Julian date with NDVI and with temperature suggests that the strength of Brewer's Sparrows' association with both temperature and NDVI increased as the season progressed. The positive relationship between Brewer's Sparrow availability and the interaction of Julian date with temperature indicates that Brewer's Sparrows are moving to areas with higher temperatures later in the breeding season. Our microclimate models found that temperature increased both with date and decreasing elevation, but that the interaction of elevation and date was not significantly related to temperature. The lack of a relationship between elevation, Julian date, and temperature likely indicates that temperatures at mid-elevations are warmer or cooler than would be expected in a linear relationship. Topography can highly modify the amount of solar radiation received by the surface, and highly heterogeneous topographical landscapes at our sites could cause mid-elevations to experience warmer or colder temperatures than expected (Bennie et al. 2008, Daley et al. 2010). Brewer's Sparrows disperse upslope within the breeding season, and the association with the interaction of temperature and Julian date may indicate movement upslope to warmer temperatures later in the season. Brewer's Sparrows lay multiple broods within a season. The species may establish late-season territories at relatively high elevations that become more productive as temperatures increase.

The positive association with the interaction of NDVI and Julian date suggests that as the season progresses, higher NDVI values become more strongly associated with Brewer's Sparrow site use or availability. These results may be explained by environmental heterogeneity. Because the relation between Brewer's Sparrow availability and NDVI strengthens over time, we can infer that Brewer's Sparrows may be moving to mid-elevation sites at which NDVI values increase later in the season. These results also reflect that the local population of Brewer's Sparrows spends longer periods of time in sites with higher NDVI values. For example, individuals that initially settled in sites with low NDVI values may move to sites with higher NDVI values later in the season, while individuals that initially settled in sites with high NDVI values do not disperse.

Vesper Sparrow

The average elevation at which Vesper Sparrows were present shifted upslope within the breeding season in the central Great Basin. Vesper Sparrows lay multiple clutches and, across the Great Basin, the habitat of Vesper Sparrows and Brewer's Sparrows is similar. Both species almost exclusively occupy sagebrush shrubsteppe, and in the western and central Great Basin, the abundance of both species is negatively associated with cover of pinyon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*, *J. occidentalis*), and positively associated with elevation (Fleishman et al. 2019a). We did not directly compare the two species in the western and central Great Basin because the fit of within-season dispersal models of Brewer's Sparrows in the central Great Basin and Vesper Sparrows in the western Great Basin was poor.

Our work is not the first to identify dispersal of multiple-brooded species within the breeding season. For example, three species of multiple-brooded European birds in agricultural landscapes moved upslope within the breeding season, apparently to track shifts in habitat quality due to farming practices (Brambilla et al. 2012). Movements of up to 28 km between clutches have been reported for Eurasian Bullfinches (*Pyrrhula pyrrhula*) (Newton 2000) and other European species, such as the Eurasian Penduline-tit (*Remiz pendulinus*) (Czyż et al. 2012). Four of the seven species that dispersed within seasons in the Great Basin (Brewer's Sparrow, Vesper Sparrow, Green-tailed Towhee, and Lazuli Bunting) lay multiple broods. Of the seven species in the Great Basin that did not appear to disperse within the season, four (Blue-gray Gnatcatcher, House Wren, Warbling Vireo, and Spotted Towhee) also have multiple broods. However, because abundances of both House Wren and Warbling Vireo are significantly correlated with presence of aspen in our study area (Fleishman et al. 2014), elevational movements of these species likely are limited by the scarcity of large aspen groves at high elevations.

The availability of Vesper Sparrows, like that of Brewer's Sparrows, was positively associated with the interaction of NDVI with Julian date. The conclusions we drew about the effect of the interaction of NDVI and Julian date on Brewer's Sparrow availability also may apply to Vesper Sparrow, as the two species have similar habitats and life histories. This association implies that the relation between Vesper Sparrow availability and NDVI strengthens with time, potentially indicating that another unmeasured variable is changing within the season, and leading Vesper Sparrows to move to sites with higher NDVI values later in the season.

Green-tailed Towhee

Green-tailed Towhee was the only species for which the average elevation of presence shifted downslope within the breeding season. Green-tailed Towhees are habitat generalists, and breed in or near transitions between shrubsteppe and other vegetation types in which tree density is low (Knopf et al. 1990). Availability of Green-tailed Towhees was associated with percentage of fruits (positive) and buds (negative), Julian date (negative), and insect biomass (negative). The opposing magnitude of associations with percentages of fruits and buds might be explained by elevational shifts in plant phenology in combination with downslope movement. For example, downslope dispersal implies that Green-tailed Towhees are moving toward relatively high fruit abundance at lower elevations and, perhaps incidentally, away from relatively high bud abundance at high elevations.

Availability of Green-tailed Towhees decreased as the season progressed in the western Great Basin, perhaps suggesting the beginning of molt migration (Morton 1991). The negative relation between insect biomass and availability is perplexing given that insects are a large part of most species' diets during the breeding season. Increased intraspecific competition for nest sites or other resources could be driving Green-tailed Towhee movement away from a resource-rich (e.g., high insect biomass) environment.

MacGillivray's Warbler

In both the western and central Great Basin, the average elevation of MacGillivray's Warbler presence shifted upslope during the breeding season. MacGillivray's Warblers lay a single clutch per year in dense riparian vegetation. In both regions, NDVI was positively associated with availability, and in the western Great Basin, percentage of riparian trees or shrubs was associated positively with abundance of MacGillivray's Warblers (Fleishman et al. 2019a). NDVI likely is a good proxy for productivity of riparian vegetation, and this association may indicate that MacGillivray's Warblers prefer riparian corridors within our sites. Our models suggest that NDVI values peak at intermediate elevations in both the western and central Great Basin. The positive association of MacGillivray's Warbler availability and NDVI indicates that birds that initially settled at sites with high NDVI values are more likely to remain at those sites throughout the season. Potentially, individuals that initially settled in sites with lower NDVI values moved upslope later in the season to sites with higher NDVI values.

In the western Great Basin, availability of MacGillivray's Warblers was positively associated with temperature and the interaction of temperature with Julian date, and negatively associated with total percentage of fruits. Our models indicate upslope elevational dispersal of MacGillivray's Warblers, and the association with the interaction of temperature and Julian date might be a product of movement upslope to sites with warmer temperatures later in the season. MacGillivray's Warblers are insectivores, and generally do not consume fruit during the breeding season (Hutto 1981). Their negative association with total percentage of fruits potentially reflects their upslope movement.

Yellow Warbler

The average elevation of Yellow Warbler presence shifted upslope within the breeding season in the central Great Basin. In both the western and central Great Basin, NDVI was positively associated with availability of Yellow Warblers (Tables 1.2 and 1.3). This result indicates that Yellow Warblers likely remain in sites with higher NDVI values for the majority of the season, which in our study system occur at intermediate elevations. Yellow Warblers lay one clutch per year. They are riparian obligates, and the riparian corridors in our canyons rarely extend to the highest elevations. Therefore, upslope dispersal of Yellow Warblers may be habitat limited. Yellow Warblers' association with willows (*Salix* spp.) (Heath and Ballard 2003) could explain their limited upslope dispersal: willows generally do not occur above 2500 m in our study areas in the central Great Basin. The upslope signal we detected may reflect migration from wetlands on the valley floor to mid-elevation riparian areas with high primary productivity.

Yellow Warblers and MacGillivray's Warblers have similar life histories and within-season dispersal patterns, and drivers of their movement may be the same. For example, availability of both species was positively associated with high NDVI values. The species' upslope dispersal could reflect movement after a failed breeding attempt, or movement of unpaired males to unoccupied, lower-quality habitat in the middle of the breeding season to avoid competition with paired males at lower elevations.

Broad-tailed Hummingbird

The average elevation of Broad-tailed Hummingbird presence shifted upslope within the season in the central Great Basin. No covariates were significantly associated with availability. This surprised us given that Broad-tailed Hummingbirds primarily eat nectar and small insects during the breeding season. However, our phenology data did not include the plants on which Broad-tailed Hummingbirds primarily feed, including scarlet gilia (*Ipomopsis aggregata),* Indian paintbrush (Castilleja *spp.),* and red columbine *(Aquilegia elegantula*) (McKinney et al. 2012). Nesting of Broad-tailed Hummingbirds coincides with availability of nectar (McKinney et al. 2012), and forbs at low elevations flower much earlier than those at high elevations. Because Broad-tailed Hummingbirds prefer to reproduce at higher elevations, they may remain at low elevations early in the season until productivity of nectar at high elevations increases. Male Broad-tailed Hummingbirds do not participate in parental care, and they attempt to mate with multiple females in a single season. The upslope elevational dispersal we detected may be due to male birds moving upslope to mate with unpaired females later in the season.

Lazuli Bunting

The average elevation of Lazuli Bunting presence shifted upslope within the breeding season in the western Great Basin. The dispersal distances of this species (705 m upslope) were at least three times greater than those of any other species we observed. Others also have observed within-season upslope dispersal of Lazuli Buntings. For example, data collected at radio frequency identification (RFID) feeders along an elevational gradient in Utah indicated that Lazuli Buntings move to higher elevations later in the breeding season (C. Rushing, personal communication). The distribution of Lazuli Buntings during the breeding season often is patchy, and apparent habitat often is unoccupied. Synchronous upslope movement may explain the strong upslope dispersal signal we detected in the western Great Basin. Availability of Lazuli Buntings was associated positively with insect biomass, total percentage of fruits, and the interaction of total percentage of buds and Julian date. During the breeding season, Lazuli Buntings feed on a wide variety of arthropods, and on the fruits and seeds of many plants (Greene et al. 2020). Our results suggested that upslope shifts in fruit and insect abundance may explain Lazuli Buntings' upslope movement.

Concluding Remarks

Spatial and temporal dispersal of birds throughout the breeding season may be applicable to inferences about species occurrence and abundance. To detect potential within-season dispersal with point-count data, we recommend adoption of removal sampling. Removal sampling allows calculation of availability for each sampling day and can reflect changes in the number of individuals available to be sampled throughout the breeding season (i.e., availability). Explicitly accounting for availability, or non-random movement between visits, can reduce bias in estimators of abundance.

Our results raise many questions about the population- and community-level effects of within-season dispersal. For example, it is unclear whether species consistently disperse within the breeding season, or whether dispersal is dependent on annual weather or local habitat quality (Morton 1991). Furthermore, there is little evidence to assess whether within-season dispersal is a population-level or individual-level trait. Dispersal of MacGillivray's Warblers and Yellow

Warblers in the western and central Great Basin was similar, but it is likely that dispersal of other species varies throughout their ranges.

Our results add to a growing body of research suggesting that within-breeding season dispersal is much more common than previously thought. Additionally, our work suggests that temporal and spatial shifts in resources over elevational gradients may in part be driving that dispersal. If such dispersal is associated with regional changes in resource distributions, then species able to disperse within the breeding season which species are better able to respond to the indirect effects of climate and land-use change.

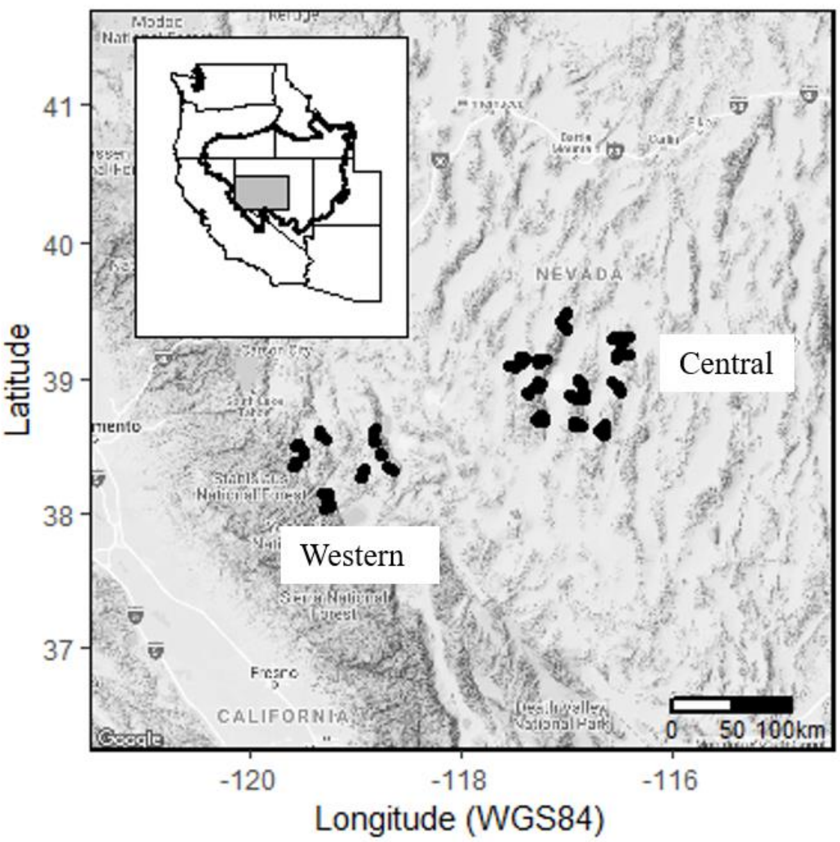

Figure 1.1. Locations at which we collected point-count data. Inset: Great Basin (thick black line) and the approximate study area (grey rectangle).

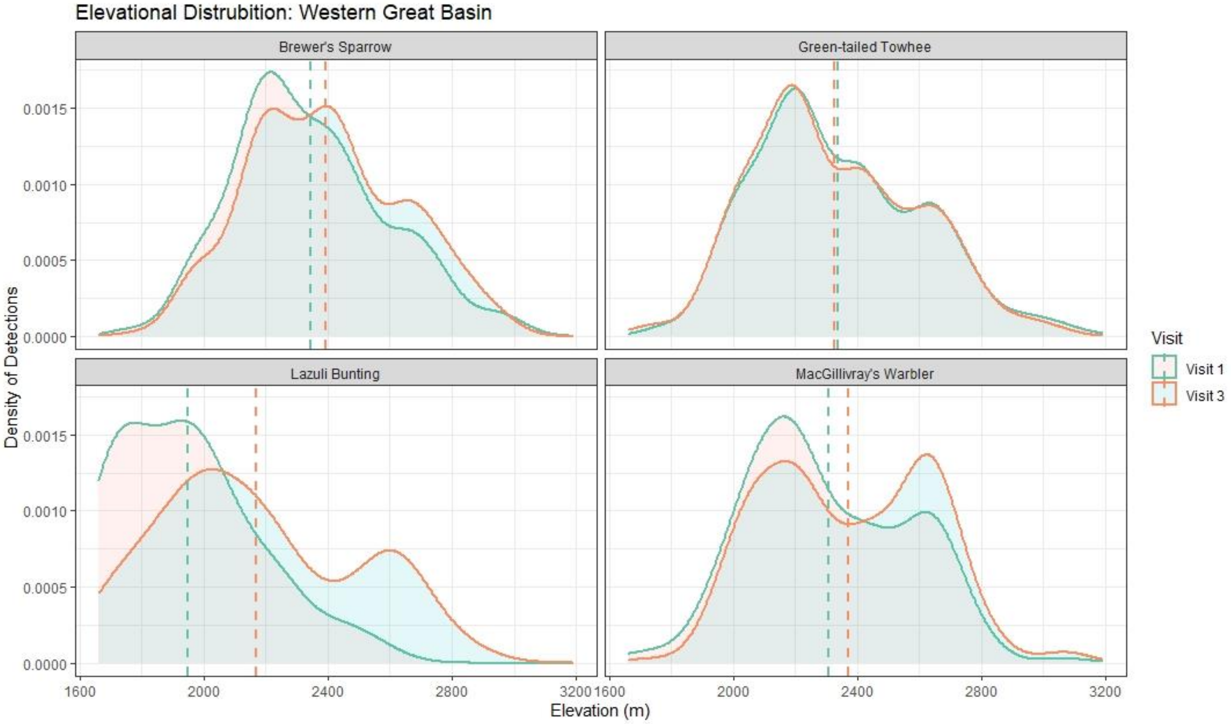

Figure 1.2. Density of detections per meter over the full elevational gradient in the western Great Basin between the first visit (earliest in the breeding season) and third visit (latest in the breeding season), calculated from our raw data. The area under each curve sums to 1. Dashed lines represent the mean elevation at which each species was detected during visit one and visit three. The difference between the two lines represents the vertical dispersal distance.

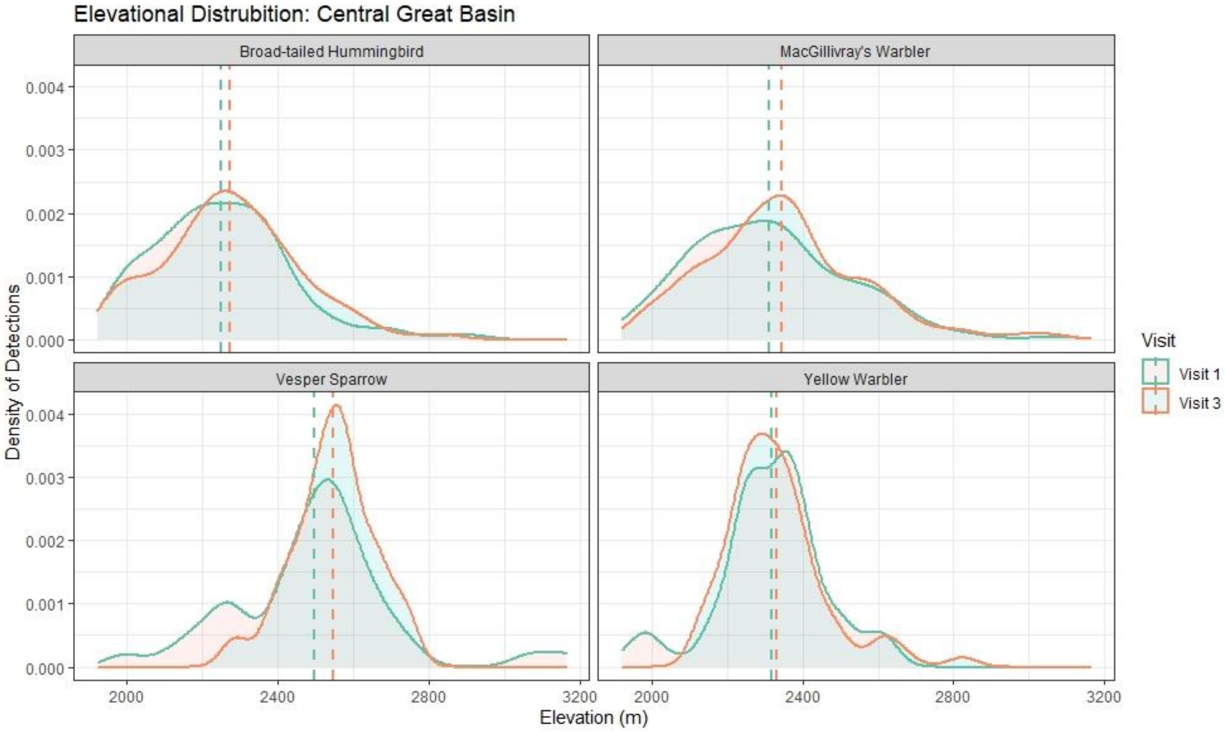

Figure 1.3. Density of detections per meter over the full elevational gradient in the central Great Basin between the first visit (earliest in the breeding season) and third visit (latest in the breeding season), calculated from our raw data. The area under each curve sums to 1. Dashed lines represent the mean elevation at which each species was detected during visit one and visit three. The difference between the two lines represents the vertical dispersal distance.

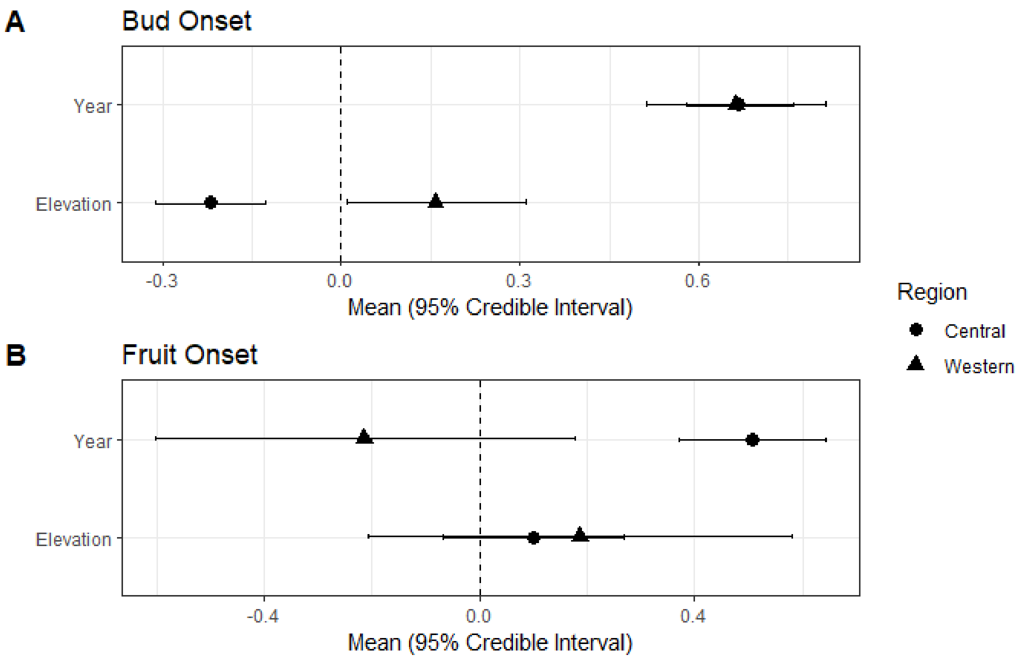

Figure 1.4. Associations of year and elevation with day of onset of buds (A) and fruits (B) in the western and central Great Basin.

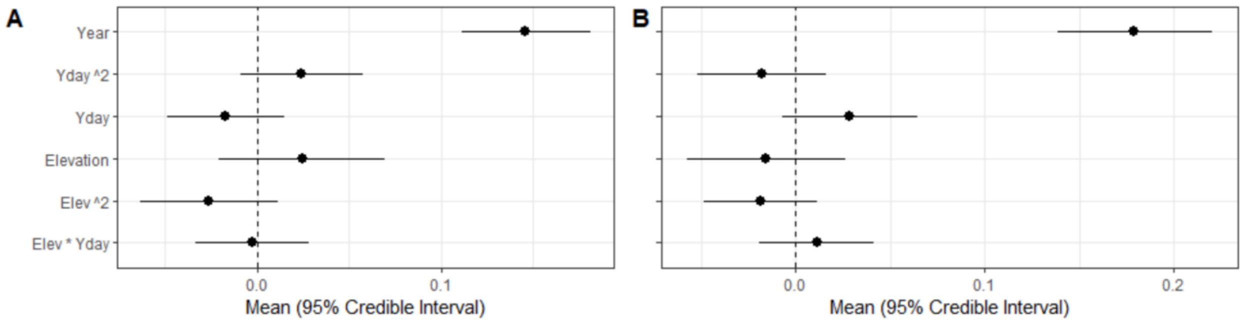

Figure 1.5. Associations of year, Julian date (Yday), and elevation (Elev) with insect biomass in the western Great Basin (A) and central Great Basin (B).

Table 1.1. Results of within-season dispersal models with good (**) or moderate (*) fit. If no mean or standard deviation (SD) is listed, no covariates of availability were included in the best model.

Species	Great Basin region	Interaction of visit and elevation with availability (mean, SD)	Direction of elevational movement
Broad-tailed Hummingbird	Central	(0.23, 0.14)**	Upslope
Western Wood-Pewee	Western		
Dusky Flycatcher	Central		
Warbling Vireo	Western		
House Wren	Western		
Blue-gray Gnatcatcher	Western	(0.02, 0.11)*	
Blue-gray Gnatcatcher	Central		
Brewer's Sparrow	Western	(0.28, 0.08)**	Upslope
Vesper Sparrow	Central	(0.84, 0.38)**	Upslope
Green-tailed Towhee	Western	(-0.06, 0.04)**	Downslope
Spotted Towhee	Western		
MacGillivray's Warbler	Western	(0.14, 0.07)**	Upslope
MacGillivray's Warbler	Central	(0.13, 0.09)**	Upslope
Yellow Warbler	Central	(0.09, 0.12)*	
Yellow Warbler	Western	(0.09, 0.23)*	
Yellow-rumped Warbler	Western		
Lazuli Bunting	Western	(0.35, 0.158)*	Upslope

Table 1.2. Results of environmental heterogeneity analyses for species in the western Great Basin. Numbers indicate the covariates' mean and standard deviation, respectively. Boldface indicates high certainty in associations with availability (>90% posterior distribution above or below zero). Certainty in other associations was moderate (75-89% posterior distribution above or below zero). A blank cell indicates no association of the variable with availability. The fit of models of Black-headed Grosbeak and Yellow-rumped Warbler was poor and the models are not reported. *Dispersed along elevational gradients within the season. NDVI, normalized difference vegetation index; Temp., temperature.

Species	Julian date	NDVI	Insect biomass	Total % fruits	Total % buds	Temp.	NDVI x Julian date	Insect biomass x Julian date	Total % fruits x Julian date	Total % buds x Julian date	Temp. x Julian date
Western Wood-Pewee		**0.72, 0.45**			0.76, 0.63			-0.45, 0.47	-0.4, 0.48		
Dusky Flycatcher	-0.35, 0.46	0.62, 0.68	**-0.51, 0.39**								
Warbling Vireo		**0.89, 0.67**	0.51, 0.62				**-0.72, 0.50**		0.45, 0.43	0.38, 0.45	
Mountain Chickadee		0.56, 0.64			-0.62, 0.63	**-0.89, 0.63**	-0.54, 0.53				
House Wren								-0.37, 0.52	**0.97, 0.56**		-0.39, 0.53
Blue-gray Gnatcatcher	-0.68, 0.70	-0.75, 0.81	**-0.84, 0.50**			0.94, 0.84		**-0.74, 0.49**			-0.69, 0.69
American Robin		**0.76, 0.48**	0.62, 0.55		**-0.09, 0.51**		**-0.74, 0.49**				**0.73, 0.54**
Cassin’s Finch	-0.65, 0.69	0.93, 0.76	-1.0, 0.85						0.69, 0.76		
Brewer’s Sparrow*			**0.97, 0.48**				0.42, 0.59	-0.49, 0.56			0.52, 0.56
Fox Sparrow		0.61, 0.61	0.64, 0.63	-0.63, 0.72	0.82, 0.66						
Song Sparrow				-0.76, 0.81			-0.61, 0.77	**-1.20, 0.85**			
Green-tailed Towhee*	**-0.57, 0.34**		**-0.61, 0.33**	**0.92, 0.56**	**-1.57, 0.64**						
Spotted Towhee	0.36, 0. 31	-0.72, 0.60	**-0.91, 0.14**	-0.47, 0.40	**-1.17, 0.55**		0.62, 0.52			0.35, 0.43	
MacGillivray’s Warbler*		**1.64, 0.87**		-0.77, 0.86		0.59, 0.74					0.82, 0.66

Yellow Warbler		**1.61, 0.89**		-0.67, 0.82							
Black-throated Gray Warbler				0.87, 0.85							
Western Tanager				-0.85, 0.71			**-0.88, 0.68**				
Lazuli Bunting*			0.63, 0.59	0.42, 0.55	-0.72, 0.95					0.90, 0.97	

Table 1.3. Results of environmental heterogeneity analyses for species in the central Great Basin. Numbers are mean and standard deviation, respectively. Boldface indicates high certainty in associations with availability (>90% posterior distribution above or below zero). Certainty in other associations was moderate (75-89% posterior distribution above or below zero). A blank cell indicates no association of the variable with availability. The fit of models of Mountain Chickadee, Bushtit, Mountain Bluebird, American Robin, and Green-tailed Towhee was poor and the models are not reported. *Dispersed along elevational gradients within the season. NDVI, normalized difference vegetation index.

Species	Julian date	NDVI	Insect biomass	Total % fruits	Total % buds	NDVI x Julian date	Insect biomass x Julian date	Total % fruits x Julian date	Total % buds x Julian date
Broad-tailed Hummingbird*									
Dusky Flycatcher	-0.57, 0.58	**0.88, 0.40**			-0.19, 0.28	**1.01, 0.52**			
Warbling Vireo		**1.10, 0.48**		-0.36, 0.35					
House Wren		**1.55, 0.87**			0.56, 0.52				
Blue-gray Gnatcatcher		-0.93, 0.84	0.55, 0.77			0.47, 0.64			
Cassin’s Finch		**1.16, 0.75**				-0.39, 0.44			
Brewer’s Sparrow	**0.62, 0.49**	**-0.69, 0.51**		0.45, 0.54	0.57, 0.66			0.88, 0.74	**0.97, 0.64**
Fox Sparrow	0.84, 0.67	0.55, 0.71	0.56, 0.78					0.76, 0.70	
Vesper Sparrow*		-0.89, 0.87				0.66, 0.85			
Dark-eyed Junco	-0.69, 0.61	(0.58, 0.60)				1.10, 0.85			0.75, 1.01
Spotted Towhee	**0.58, 0.38**	**0.94, 0.39**	0.46, 0.42	**-0.78, 0.32**		**0.35, 0.29**		**-0.56, 0.29**	0.46, 0.43
MacGillivray’s Warbler*		**1.01, 0.39**							
Yellow Warbler*		**1.39, 0.91**							
Black-throated Gray Warbler		**-0.66, 0.48**		0.74, 0.60					

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CHAPTER 2

Shifts in elevational distributions of Great Basin birds from 2001–2020

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Abstract

Montane species generally are predicted to respond to climate change via upslope elevational movement. However, many populations and species are not moving in synchrony with increasing temperatures, and either have not shifted or shifted downslope. Because abiotic and biotic processes at range edges may differ from those in the center, analyzing shifts at relatively low and high elevations in addition to those along the full elevational gradient may offer greater insight about potential mechanisms than analyzing shifts along the full gradient alone. We examined long-term avian point-count data in two regions of the Great Basin. We modeled occupancy of 32 bird species to assess elevational movement at three extents: the full elevational gradient (1650-3200 m) and the lowest and highest 25% of the elevational gradient. Additionally, we evaluated the effects of temperature, precipitation, and the Normalized Difference Vegetation Index (NDVI) to determine whether changes in climate or primary productivity were associated with elevational shifts. We found that the elevational distributions of 19 species shifted. The four shifts along the full elevational gradient were downslope. About half of the distributional shifts at the lower or upper elevational edges were upslope. Associations of climate variables or primary productivity with distributional shifts were inconsistent. Occupancy of 12 species with elevational distributions that shifted was associated significantly with precipitation. In 10 of those cases, the association was negative, suggesting that projected increases in precipitation in the Great Basin may have a detrimental effect on bird populations. Primary productivity (NDVI) was the only variable that increased with elevation over the past 9–20 years. Species with elevational distributions that shifted and were significantly associated with NDVI may be following food or other resources related to primary productivity.

Introduction

Changes in elevational distributions of diverse taxonomic groups are occurring globally, with the potential to reshape ecological communities, alter ecosystem function, and even affect climate (Pecl et al. 2017). Given that temperature generally decreases by 0.6°C per 100 m increase in elevation (Barry 2008), these shifts often are attributed to climate change. A dominant paradigm is that organisms move upslope in response to warming temperatures, reflecting an assumption that species distributions directly or indirectly are limited by temperature. The elevational ranges of montane animals, which may be limited by microclimate or by vegetation associations or other biotic interactions, may be especially likely to shift (Martin 2001, McNab 2003). Several reviews demonstrated general support for theories of upslope elevational shifts in multiple taxonomic groups (Chen et al. 2011, Freeman et al. 2018). However, many instances have emerged in which populations, species, or taxonomic groups are not moving in synchrony with warming temperatures and either have not shifted or shifted downslope (Campos-Cerqueira et al. 2017, DeLuca and King 2017). The interacting effects of changes in temperature, precipitation, and other attributes of climate could lead to large variations in the responses of species to climate change (Tingley et al. 2012). Direct or indirect effects of land use, such as shifts in hydrology, vegetation structure or composition, or the frequency of wildfire and other disturbances, also contribute to elevational shifts, whether in addition to or independent of climate change (Fleishman and Murphy 2012).

Shifts in elevational distributions of birds coincident with climate change have been relatively well studied. Birds, especially long-distance migrants, are highly vagile, and can track microhabitat both within breeding and overwintering grounds and across years (Greenwood and Harvey 1982, Cline et al. 2013, Gow and Stutchbury 2013). The elevational ranges of montane songbird species may be particularly likely to change due to their narrowness (McCain 2009) and the fact that climate variables at different elevations are not changing uniformly. For example, in some cases, high elevations are warming more rapidly than low elevations due to factors such as changes in snow albedo and surface-based feedbacks, water vapor, and radiative flux (Pepin et al. 2015). Precipitation rates also typically are greater at high elevations, and climate change is projected to strengthen this relation (Barry 2008, Van Tatenhove et al. 2019).

There is evidence that the distributions of some birds are shifting upslope. Through resurveying locations in the Sierra Nevada that were visited by Joseph Grinnell in the early 1900s, Tingley et al. (2012) found that the ranges of 84% of avian species documented by Grinnell shifted over the past 100 years. Of those species, 51% moved upslope and 49% moved downslope. A 16-year study in the northern Appalachian Mountains found that 9 of 16 low-elevation passerine species shifted an average of 99 m upslope, whereas 9 of 11 high-elevation species shifted an average of 19 m downslope (DeLuca and King 2017). Resurveys of a Puerto Rican bird community from 1998 through 2015 detected a significant shift in the ranges of eight (38%) of the species surveyed; the majority of elevational shifts were upslope and occurred at the lower limit of a species' elevational range (Campos-Cerqueira et al. 2017). In general, upslope movement is attributed to the direct and indirect effects of climate change. Indirect effects of climate change include elevational shifts of plant species, plant phenology, or primary productivity (Morison and Morecroft 2006, Lenior et al. 2008, Amano et al. 2010). In part because the geographic distribution of plants is strongly influenced by temperature and precipitation, plants often are more sensitive than vertebrates to changes in climate (Woodward 1987, Thackeray et al. 2016). Therefore, a primary mechanism of upslope elevational shifts of birds may be indirect, plant-mediated effects of climate change.

Numerous theories have emerged to explain downslope or lack of elevational movement in bird populations. One theory is that downslope movement results from biotic interactions such as predation or competition (Lenoir et al. 2010). For example, if the lower edges of species' ranges are limited by competition, and levels of disturbance, such as agricultural expansion, increase at lower elevations, then species may be released from competition (Lenoir et al. 2010). Theories regarding mechanisms of stable elevational distributions include temporal lags in response to climate and land-use change, stochastic fluctuations in population size, and small magnitudes of climate change (Parmesan et al. 2005, Tingley and Bessinger 2009, McCain et al. 2016).

Species- or population-level traits may explain variation in elevational shifts. Some work has suggested that low-elevation species are more likely than high-elevation species to move upslope due to their access to a larger amount of potential dispersal habitat (Mamantov et al. 2021). However, for many populations this is likely too simplistic of an explanation, in part because montane area does not necessarily decrease linearly with elevation. Others have proposed that thermal tolerances affect elevational movement. For example, high-elevation species and populations often have a greater range of thermal tolerance than those at low elevations, proportional to the magnitude of seasonal and diel thermal variation at high elevations (Janzen 1967, Deutsch et al. 2008), and are less likely to disperse in response to climate variability or change (Khaliq et al. 2014, Freeman 2016).

Examining shifts at the upper and lower edges of a species' elevational range can offer greater insight about potential range-shift mechanisms than analyzing shifts along the full elevational range alone. Demographic processes at elevational range edges may differ from those in the middle of the elevational range. Theoretically, differences in rates of climate change along elevational gradients, as noted above, may result in larger shifts at the upper than the lower edges of a species' elevational range. Additionally, biotic interactions, especially competition, may be stronger at lower range limits, and therefore stabilize ranges at the lower edge (Alexander et al. 2015).

From 1895-2011, mean annual temperatures across the Great Basin increased by an estimated 0.7-1.4°C (Snyder et al. 2019). Temperatures increased in all seasons, although the relative increase in winter was greater than in summer (Tang and Arnone 2013, Snyder et al. 2019). These trends are likely to continue. Mean annual temperatures across the southwestern United States, including the Great Basin, are projected to increase by 2.5-3°C, relative to 1971-2000, by the year 2065 (Abatzoglou and Kolden 2011). From 1951 through 2013, daily maximum precipitation and annual number of days with precipitation increased across the Great Basin (Xue et al. 2017). Interannual variation in precipitation is projected to increase in the region, as is cool-season (November – March) precipitation (Abatzoglou and Kolden 2011, Iknayan and Bessinger 2020). Furthermore, the frequency of precipitation events when minimum temperatures are above 0°C (implying precipitation falling as rain rather than snow) is projected to increase by 20-50%, relative to 1971-2000, across much of the Great Basin by the year 2050 (Abatzoglou and Kolden 2011).

Here, we examine two nearly continuous, long-term sets of avian point-count data in two regions of the Great Basin, a relatively under-studied region, to explore mechanisms of shifts in the elevational distributions of birds. We modeled occupancy of 32 species to investigate elevational movement at three spatial extents: the full elevational gradient and the lowest and highest 25% of the elevational gradient. Additionally, we explored the effects of temperature, precipitation, and primary productivity on single-species occupancy at these three extents to determine if shifts in these variables were associated with elevational movement. We hypothesized that shifts in primary productivity drive elevational shifts in bird distributions to a greater extent than shifts in temperature or precipitation.

Methods

Study area

The Great Basin includes more than 300 mountain ranges and five or more centers of avifaunal differentiation (Behle 1963). Our work focused on two of these centers and six mountain ranges: the Sierra Nevada and Wassuk Range in the Inyo center (henceforth western Great Basin), and the Shoshone Mountains, Toiyabe Range, Toquima Range, and Monitor Range in the eastern center (henceforth central Great Basin) (Figure 2.1). We restricted analyses to the 35 canyons in which we sampled at least 250 vertical meters of elevational change (Fleishman 2019a,b). Collectively, the full elevational gradients of these canyons ranged from 1650 to 3200 m. The main human disturbances in these areas of the Great Basin are livestock grazing, use of surface water and groundwater, and ground disturbances that facilitate expansion of non-native invasive plants (e.g., cheatgrass, *Bromus tectorum*). Our study areas generally are not used for growing crops, and have little human infrastructure such as roads, buildings, and traffic, which greatly can affect avian composition and abundance and movement of wildlife (Fahrig et al. 2009, Theobald et al. 2012, Clucas and Marzluff 2015). This relative lack of agriculture and urbanization allows for greater confidence in attributing changes in species' elevational distributions to climate change or its effects.

Field data

We sampled birds with 100-m fixed-radius point counts from late May through early July, which encompasses the breeding season of most birds in the region and ends before a high proportion of juveniles has fledged and before most movement to molting or wintering grounds. In the western Great Basin, we sampled birds from 2012-2020 at a total of 134 points in 10 canyons (Fleishman 2019a). We sampled 36 points in 8 years, and 121 for ≥5 years. In the central Great Basin, we sampled birds from 2001-2020, except 2016 and 2017, at a total of 303 points in 25 canyons (Fleishman 2019b). We sampled 230 of these points for ≥10 years.

We visited each point three times during the breeding season, with ca. 10–14 days between visits, and recorded all birds detected by sight or sound that were using resources within the point during an eight-minute count. In almost all cases, sampling was restricted to the first four hours after sunrise. We excluded fledglings and juveniles from analyses.

We extracted daily minimum temperature and daily precipitation at each bird survey point in each year from the Parameter-elevation Regressions on Independent Slopes Model data (PRISM, https://prism.oregonstate.edu/). From these data, which have a resolution of 4 km, we derived mean daily minimum spring (1 April – 30 June) temperature, cumulative daily winter (1 December – 31 March) precipitation, and cumulative daily spring precipitation, which we expected to limit breeding activity and food availability to a greater extent than temperature means or climate during other times of the year (Whitehouse et al. 2013, Visser et al. 2015, Messmer et al. 2021).

We used the normalized difference vegetation index (NDVI), a measure of vegetation greenness, to estimate primary productivity at each point (Wang et al. 2004). NDVI is closely related to biological variables such as leaf area index, leaf cover, and chlorophyll per ground area (Gamon et al. 1995, Paruelo et al. 1997, Rundquist 2002). Additionally, NDVI is correlated positively with avian abundance and species richness in some arid ecosystems, including the central Great Basin (Seto et al. 2004, McFarland and Van Riper 2013). We extracted the maximum NDVI value at the centroid of each bird survey point from 1 March through 30 June of each year from the Application for Extracting and Exploring Analysis Ready Samples (AppEARS) database (https://lpdaacsvc.cr.usgs.gov/appeears/). AppEARS derives NDVI from images captured every 16 days at 250 m resolution by the Moderate Resolution Imaging Spectroradiometer (MODIS). NDVI values are scaled from -1 to 1.

Analyses

We modeled single-species occupancy in the western and central Great Basin separately. Occupancy estimates the probability that a species is present while accounting for imperfect detection (MacKenzie et al. 2002, Royle and Nichols 2003). We built models for species with >30 detections in ≥4 of the 9 survey years in the western Great Basin (24 species) and >30 detections in ≥10 of the 18 survey years in the central Great Basin (23 species).

We compared three occupancy models for each species. The first model included data from the full elevational gradient sampled. The second and third models examined occupancy in the lowest and highest 25% (*lower and upper edges*) of the full elevational gradient. Because detection cannot be estimated if one excludes locations where the species has not been detected, and the elevations at which a given species was detected varied among canyons and years, we did not build models with species-specific elevational gradients. The three models had the same formulation and contained the same covariates. Model selection techniques differed between the full-gradient model and the edge models. We applied indicator variable selection to the full-gradient model, and the Watanabe-Akaike Information Criterion (WAIC) to the edge models. The edge models, which included much less data than the full-gradient model, did not converge when indicator variable selection was applied.

We modeled detection probability as

$$C_{ijk} \sim Binominal(p_{ijk}, Z_{ik})$$

$$logit(p_{ijk}) = \beta 1 + \beta 2 * jday_{ijk} + \beta 3 * time_{ijk} + \beta 4 * time^{2}_{ijk} + \alpha 1 * observer_{ijk},$$

$$\alpha 1 \sim Normal(0, tau1)$$

$$tau1 \sim Uniform(0,5),$$

where C_{ijk} is the observed presence or absence of the species at point i during visit j in year k, and p is the probability of detecting the species given its presence. We used a logit link function to model four detection covariates: Julian date (*jday*), time of day, the quadratic transformation of time of day, and a random, observer-level effect. $\beta 1$ is the mean point-level detection probability for a given species, and $\alpha 1$ is a random effect of observer identity on detection, with a mean of 0 and a precision of $tau1$.

We connected the detection process to the occupancy process through Z_{ik}, which we treated as a Bernoulli random variable governed by the success probability ψ:

$$Z_{ik} \sim Bernoulli(\psi_{ik})$$

$$logit(\psi_{ik}) = \beta 5 + \beta 6 * \mathbf{X}_{ik} + \alpha 2 * point_{ik} + \alpha 3 * canyon_{ik}$$

$$\alpha 2 \sim Normal(0, tau2)$$

$$tau2 \sim Uniform(0,1)$$

$$\alpha 3 \sim Normal(0, tau3)$$

$$tau3 \sim Uniform(0,1),$$

where Z_{ik} is the occupancy state (0 = absent, 1 = present) at point *i* in year *k.* We applied a logit link function to ψ to model occupancy covariates. In the indicator-variable selection process in the full-gradient model, $\boldsymbol{X_{ik}}$ represents the vector of covariate values at point i in year k. Indicator variables typically are used to track the posterior probability of the inclusion of a given covariate in a model. Covariates in X included year, elevation, the interaction of year and elevation, spring temperature, winter precipitation, spring precipitation, and NDVI. If the interaction of year and elevation was included in the best model, and if its posterior density did not overlap zero, we concluded that the mean elevational distribution of the species had shifted upslope or downslope across years. We included random effects on the occupancy process to account for unmeasured differences among points. α2 is a point-level random effect with a mean of 0 and precision of tau2, and α3 is a canyon-level random effect with a mean of 0 and precision of tau3. We used vague prior distributions for intercepts, covariates, and random effects.

We implemented models in JAGS (Plummer 2003) with the jagsUI package (Kellner 2019) in R (R Core Team 2020). We based posteriors on three chains of 50,000 iterations after a 10,000 sample burn-in and adaptive phase. We classified convergence as Rhat <1.15 (Gelman and Hill 2007). We calculated collinearity of all pairs of candidate covariates. A priori, we established that if collinearity >0.75, we would exclude the variable of the pair that we deemed less ecologically relevant. No variables were collinear. We examined model fit on the basis of separate Bayesian p-values for the detection and occupancy processes, and we estimated mean occupancy and detection. We classified the fit of models as good if both of the Bayesian p-values were 0.05-0.95 and estimated mean detection and occupancy were >15%.

We implemented a simple linear model that examined the effect of year on the mean elevation at which a species was observed. The resulting slope and intercept allowed us to calculate the average elevational shift over the survey period. We used standard error estimates to calculate the 95% confidence interval of the elevational shift.

To determine whether spring temperature, winter precipitation, spring precipitation, or NDVI changed over the survey period, we used generalized linear models (GLMs). We implemented GLMs for each variable in JAGS; we used jagsUI in R to run three chains of 5,000 iterations each. We included a point-level random effect and modeled all variables as a function of elevation, year, and the interaction of elevation and year.

We used our data on avian abundance, transformed to occupancy for the above analyses, to examine the elevational distribution of each species. We calculated the density of detections in each 50-m bin over the full elevational gradient surveyed in both the western and central Great Basin. We then computed a simple estimate of kernel density, which estimated the probability density function of the abundance data.

Plotting interaction effects is often useful for interpretation of covariate estimates. Therefore, we regressed predicted mean NDVI values against elevation and selected years in both regions.

Results

In the western Great Basin, the distributions of six species shifted along the full elevational gradient or at the edges of the elevational gradient from 2012-2020. The mean elevation at which we detected these six species was 2310 m, and we detected individuals along the full elevational gradient (1650-3200 m). Most individuals (94%) were detected from 1800-2800 m. In the central Great Basin, the elevational distributions of 14 species shifted over the past two decades. The mean elevation at which we detected these 14 species was 2350 m, and we detected individuals along the full elevational gradient (1900-3200 m). Most individuals (97%) were detected from 2000-2700 m.

In the western Great Basin, the distributions of three species shifted downslope along the full elevational gradient: House Wren (*Troglodytes aedon*) by 99 m, Black-headed Grosbeak (*Pheucticus melanocephalus*) by 65 m, and Lazuli Bunting (*Passerina amoena*) by 194 m (Table 2.1). In the central Great Basin, the mean elevational distribution of Gray Flycatcher (*Empidonax wrightii*) shifted downslope along the full gradient by 88 m (Table 2.2). There was no evidence that, along the full gradient, the mean elevational distribution of any species shifted upslope in either region.

Our results suggested that movement at the elevational range margins was more common than that along the full gradient, but the average distance moved was smaller. The average distance moved at the lower and upper edges was similar in the western Great Basin, but greater at the upper edge in the central Great Basin. In the western Great Basin, the absolute value of the average shift across the full elevational gradient was 119 m, compared to 49 m at the lower edge and 42 m at the upper edge (Table 2.1). In the central Great Basin, the absolute value of the shift across the full elevational gradient was 88 m (one species, Grey Flycatcher), compared to an average of 28 m at the lower edge and 53 m at the upper edge (Table 2.2).

In the western Great Basin, the distributions of five species, including the three that moved along the full elevational gradient, shifted within the lower edge of the elevational gradient. Black-headed Grosbeak, Bushtit (*Psaltriparus minimus*), and Warbling Vireo (*Vireo gilvus*) shifted upslope, whereas House Wren and Lazuli Bunting shifted downslope (Table 2.1). In the central Great Basin, the elevational distributions of eight species changed within the lower edge of the elevational gradient (Table 2.2). Brewer's Sparrow (*Spizella breweri*), MacGillivray's Warbler (*Geothlypis tolmiei*), Yellow Warbler (*Setophaga petechia*), and Lazuli Bunting shifted upslope. Broad-tailed Hummingbird (*Selasphorus platycercus*), Mountain Chickadee (*Poecile gambeli*), Black-throated Gray Warbler (*Setophaga nigrescens*), and Northern Flicker (*Colaptes auratus*) shifted downslope. Lazuli Bunting was the only species that shifted within the lower edge of the elevational gradient in both the western and central Great Basin. However, the species shifted downslope in the western Great Basin, and upslope in the central Great Basin.

The number of distributional shifts within the upper edge of the elevational gradient (9) was less than at the lower edge (13). In the western Great Basin, the elevational distributions of three species shifted within the upper edge. House Wren and Warbling Vireo shifted upslope, whereas Dark-eyed Junco (*Junco hyemalis*) shifted downslope (Table 2.1). In the central Great Basin, the elevational distributions of six species shifted within the upper edge. Mountain Chickadee, Rock Wren (*Salpinctes obsoletus*), and Vesper Sparrow (*Pooecetes gramineus*) shifted upslope, whereas Mountain Bluebird (*Sialia currucoides*), Chipping Sparrow (*Spizella passerina*), and Spotted Towhee (*Pipilo maculatus*) shifted downslope (Table 2.2).

Occupancy of 15 of the 19 species (79%) with elevational distributions that shifted was significantly associated with spring temperature, winter precipitation, spring precipitation, or NDVI (Tables 2.1 and 2.2). Occupancy of Spotted Towhee, Yellow Warbler, Black-throated Gray Warbler, and, in the western Great Basin, Lazuli Bunting was not associated with any of those four variables. Temperature, precipitation, or both were associated with shifts in elevational distributions of 15 species, whereas NDVI was associated with changes in the elevational distributions of 9 species.

Spring temperature was associated with shifts in the elevational distributions of 3 species, all in the central Great Basin. Winter or spring precipitation was associated with shifts in the elevational distributions of 12 species, and in 10 cases the association was negative. In the western Great Basin, occupancy of House Wren was positively associated with spring precipitation along the full elevational gradient, and negatively associated with winter precipitation at the lower edge of the elevational gradient. In both cases, the direction of elevational movement was downslope (Table 2.1). In the central Great Basin, occupancy of Lazuli Bunting also was positively associated with spring precipitation, and in no case was occupancy positively associated with winter precipitation. Similarly, the effect of precipitation on occupancy of the 22 species with elevational distributions that did not shift (18 in the western Great Basin and 9 in the central Great Basin; 5 species did not shift in either region) largely was significant. Winter or spring precipitation was significantly related to occupancy of 16 of those species (89%) in the western Great Basin and 6 (66%) in the central Great Basin. In the western Great Basin, the occupancy of 14 species (87%) was negatively related to precipitation. In the central Great Basin, no species had a strictly negative relation with precipitation, although two species were negatively associated with precipitation in at least one model (full elevational gradient or lower or upper edge).

NDVI was significantly related to occupancy of four species in the western Great Basin (three positively and one negatively) and five in the central Great Basin (three positively and two negatively) (Tables 2.1 and 2.2). In almost all cases, NDVI was associated with occupancy at the lower or upper edges of the elevational gradient. The exception was House Wren in the western Great Basin; NDVI was positively associated with occupancy within the lower edge and across the full elevational gradient.

In both the western and central Great Basin, temperature, winter precipitation, and spring precipitation were significantly and positively associated with year (Figures 2.2 and 2.3). In the western Great Basin, NDVI was negatively associated with the interaction of year and elevation (Figure 2.2). In the central Great Basin, by contrast, NDVI was positively associated with the interaction of year and elevation (Figure 2.3), although the effect was small. The interaction effect indicates that the relation between elevation and NDVI changed over time. Plotting predicted mean NDVI values against elevation in selected years similarly demonstrated that although NDVI increased with increasing elevation, the trend changed over time (Figure 2.4). The effect of elevation on mean NDVI decreased over time in the western Great Basin (Figure 2.4a) and slightly increased over time in the central Great Basin (Figure 2.4b).

Discussion

Our results are inconsistent with the paradigm that as the climate in the western United States becomes hotter and, in some areas, drier, the ranges of birds shift to cooler and wetter locations, including, in our case, higher elevations. The elevational occupancy of 19 of 32 species in two regions of the Great Basin—six in the western Great Basin and 14 in the central Great Basin—changed over the past one to two decades. This period of time is relatively short, but comparable to other studies of elevational shifts (Campos-Cerqueira et al. 2017, DeLuca and King 2017), and indicates considerably plasticity in elevational ranges. The elevational occupancy of one of the three species that we examined in both regions, Lazuli Bunting, shifted in both.

There was no apparent evidence of a widespread upslope shift in distribution, nor were associations between climate variables or primary productivity and distributional shifts consistent. All four distributional shifts along the full elevational gradient were downslope. Our results do not fully support our hypothesis that primary productivity is more likely than temperature or precipitation to be associated with elevational shifts in Great Basin bird populations. Elevational shifts of 15 of 19 species were associated with temperature or precipitation, whereas shifts of 9 species were associated with NDVI. Among the variables we examined, only NDVI changed over both time and elevation. Our results reinforce that not only are responses to climate species-specific, but birds respond to numerous and compounded types of environmental change.

About half (12 of 26 models) of the movement we observed at elevational range margins was upslope (Table 2.1 and 2.2). Our results contribute to a growing body of evidence that many species are moving downslope or not moving. The regional elevational ranges of some species, such as House Wren in the western Great Basin and Mountain Chickadee in the central Great Basin, seem to be expanding, with upper edges shifting upslope and lower edges shifting downslope. The regional elevational ranges of other species seem to be contracting. For example, in the central Great Basin, the upper edges of the ranges of Mountain Bluebird, Chipping Sparrow, and Spotted Towhee shifted downslope.

We found that the absolute distance of elevational shifts was greater at the upper edge compared to the lower edge in the central Great Basin. In the western Great Basin, there was no difference. Elevation was not related to trends in temperature or precipitation in either region, suggesting that rates of increase are similar along the elevational gradient. Elevation-mediated effects of climate change may be more prevalent in regions in which mean or maximum elevations are higher than those across most of the Great Basin (>4000 m), where the effects of changing snow-albedo feedbacks, water vapor, cloud cover, and radiative fluxes are more intense (Pepin et al. 2015).

In 10 of the 12 occupancy models in which winter or spring precipitation was significantly associated with occupancy, including three of the species with distributions that shifted along the full elevational gradient, the association was negative (Tables 2.1 and 2.2). Wet and cold conditions during the breeding season generally decrease bird survival and productivity (Kozlovsky et al. 2018, Zuckerberg et al. 2018). In the Great Basin, such conditions may be influenced by the El Niño-Southern Oscillation. For example, the El Niño from 2014-2016 was one of the strongest in the observational record (Rupic et al. 2018), and the El Niño during the winter of 2018-2019 resulted in extreme precipitation and flooding in the western and central Great Basin. These episodic events may have delayed the breeding season or decreased survival, leading to a decrease in occupancy. Projected increases in spring precipitation (Abatzoglou and Kolden 2011, Iknayan and Bessinger 2020) further may decrease occupancy of Great Basin bird species.

Increases in regional aridity, which are not necessarily correlated with precipitation, may affect primary productivity and vegetation structure and composition, particularly in riparian areas (Perry et al. 2011, Northrup et al. 2019). Altered precipitation and human water use in the Great Basin also may be causing shifts in canyon hydrology, which may affect bird distributions along elevational gradients. As the proportion of precipitation that falls as rain rather than as snow increases, snow depth decreases and water inputs to the soil become earlier and more sporadic (Abatzoglou and Kolden 2011, Petersky and Harpold 2018). Alternatively, the extent and vigor of riparian vegetation in the Great Basin may be changing in response to greater water-use efficiency as concentrations of carbon dioxide increase, especially as the intensity of livestock grazing decreases in some areas (Albano et al. 2020). Downslope expansion of riparian vegetation may contribute to the observed downslope elevational shifts of some bird species. Few elevational range shifts were significantly related to temperature. Diel temperature in our study canyons in the Great Basin during the breeding season is highly variable: day and night can differ by as much as 19°C (M. Zillig unpublished data). Therefore, Great Basin bird populations may have relatively broad thermal tolerances (Khaliq et al. 2014).

In both the western and central Great Basin, NDVI generally increased with elevation (Figure 2.4). However, other studies have demonstrated that primary productivity and plant biomass tend to decrease as elevation increases (Sundqvist et al. 2013). Our results may reflect the time period over which we extracted NDVI values (1 May – 30 June). During summer, NDVI at high elevations often is greater than at low elevations. In the Great Basin, this gradient could be due in part to midsummer senescence of low-elevation vegetation and to the expansion of cheatgrass, which is becoming more widespread and dense in mid- and low-elevation sagebrush shrubsteppe, coincident with increases in winter precipitation and in a positive feedback with more-frequent and larger fires (Bradley and Mustard 2005, Boyte et al. 2016, Williamson et al. 2020). Additionally, few of our sampling points are above tree line, where we would expect NDVI values to decrease dramatically.

Given that NDVI is an index, birds likely are not responding to NDVI per se but to resources highly correlated with NDVI, such as plant biomass, primary productivity (Carlson and Ripley 1997), water availability, or the abundance of plants that provide food or nest materials. Species that are shifting upslope within elevational edges in the central Great Basin may be tracking these resources. NDVI at all elevations increased over time, but in the western Great Basin, the difference in NDVI between high and low elevations decreased, perhaps suggesting that relative habitat quality is decreasing at high elevations, increasing at low elevations, or both.

PRISM data suggested that temperature and precipitation increased across the western and central Great Basin during winter and spring from 2001–2020 (Figures 2.2 and 2.3). We acknowledge that the resolution of the PRISM data (4 km) is relatively coarse given the resolution at which we sampled birds (~300 m). Additionally, the density of weather stations in the Great Basin, and therefore of the observations on which climate models are based, is relatively low. Birds likely are able to track climate at much finer resolutions than those at which most sources of gridded climate data are available (Frey et al. 2013). Furthermore, spatial variation in temperature and moisture availability in montane environments is much greater than in lowlands (Suggitt et al. 2011). For example, some narrow montane valleys are prone to temperature inversions, resulting in cooler temperatures in topographic concavities than in the surrounding area (Curtis et al. 2014, Rupp et al. 2020). As a result, short-distance movements in areas with complex topography may enable birds to access climate conditions favorable for feeding, nesting, or mating.

Our inferences might be biased if the elevational gradient we surveyed did not encompass each species' full elevational distribution in our study regions. However, our point-count locations appeared to capture the upper limits of each species' elevational distribution, and the lower elevational limits of most species (Figures 2.5 and 2.6). Our field observations indicate that Warbling Vireo, Rock Wren, Dark-eyed Junco, Spotted Towhee, and Lazuli Bunting occur in the valleys between mountain ranges, at lower elevations than we surveyed. As a result, true upslope shifts of Warbling Vireo and Lazuli Bunting within the lower elevational edge in the central Great Basin may be greater than we detected. In the western Great Basin, Lazuli Bunting occupancy shifted downslope along the full elevational gradient and in the lower edge. The signal we detected at the lower edge may be an artefact of the shift along the full elevational gradient.

Population variability also may bias our results. If variability in population sizes is high, upslope or downslope changes in occupancy may reflect natural fluctuations. For example, increases in population size may lead to colonization of unoccupied locations, whereas population declines may result in vacant lower-quality habitat (Thomas and Lennon 1999). Annual variability in abundance at the edges of species' elevational distributions may be especially high (McCain et al. 2016). Our analyses accounted for variability in population size by including year as a fixed effect, and in no case did year alone fully explain shifts in occupancy.

Although resurveying historical sampling locations can be useful, the unknown effects of population variability between two points in time impede strong inferences in many cases (Sparks and Tryjanowski 2005, McCain et al. 2016). We examined trends in occupancy over 9 or 19 years, a relatively long continuous survey effort for birds. Birds in the Great Basin may be responding to climate change through shifts within the lower and upper edges of the elevational gradient, yet the lack of a strong overall climate-response signal suggests that these populations may be relatively resilient to climate change.

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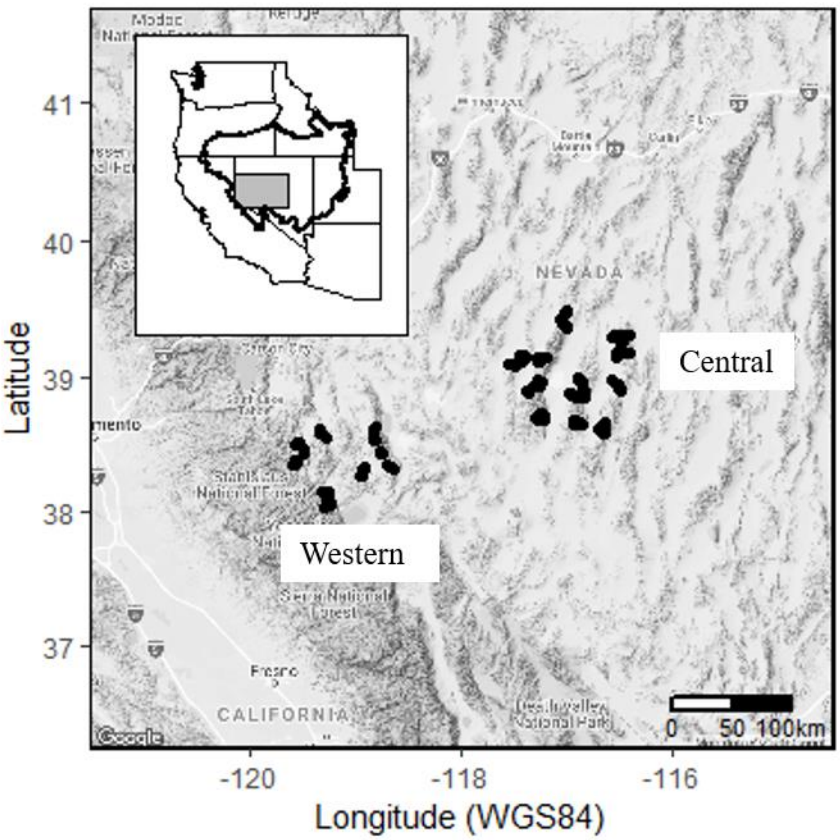

Figure 2.1. Locations at which we collected point-count data in the western and central Great Basin. Inset: Great Basin (thick black line) and the approximate boundaries of our study area (grey rectangle).

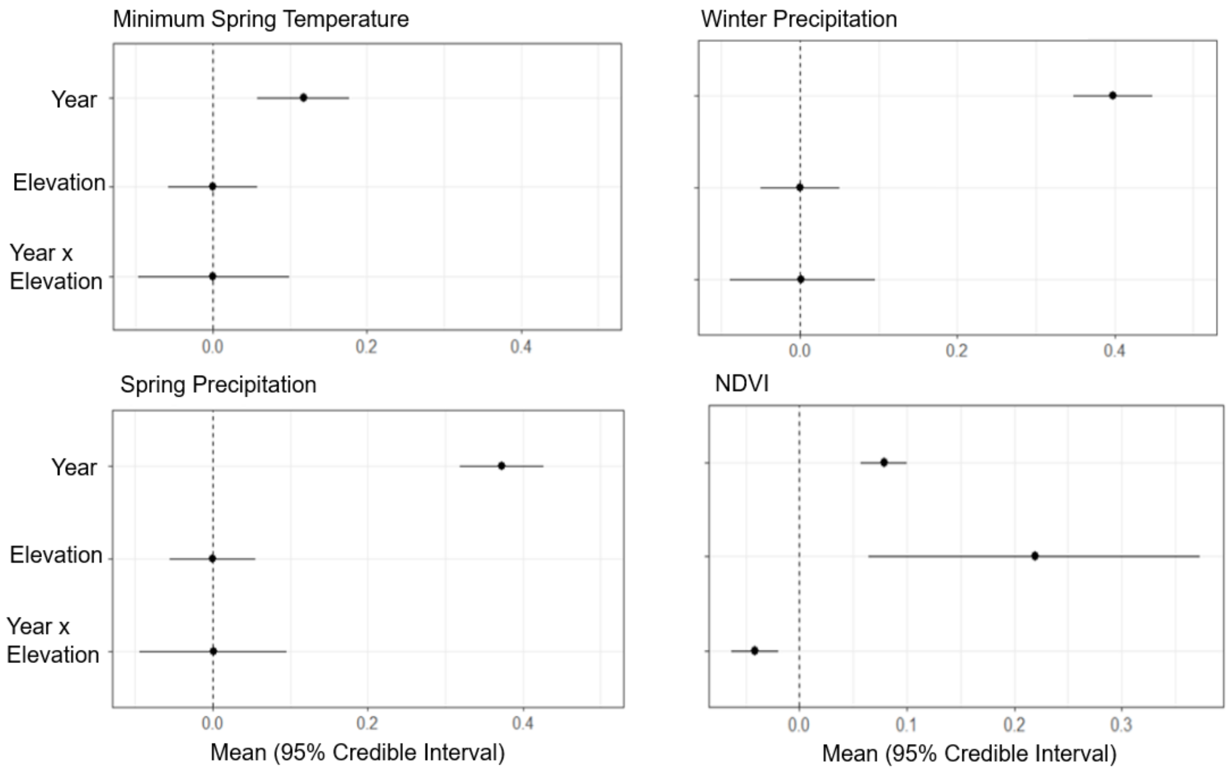

Figure 2.2. Mean estimates and 95% credible intervals of the effects of year, elevation, and their interaction on climate variables and the normalized difference vegetation index (NDVI) on occupancy of bird species in the western Great Basin.

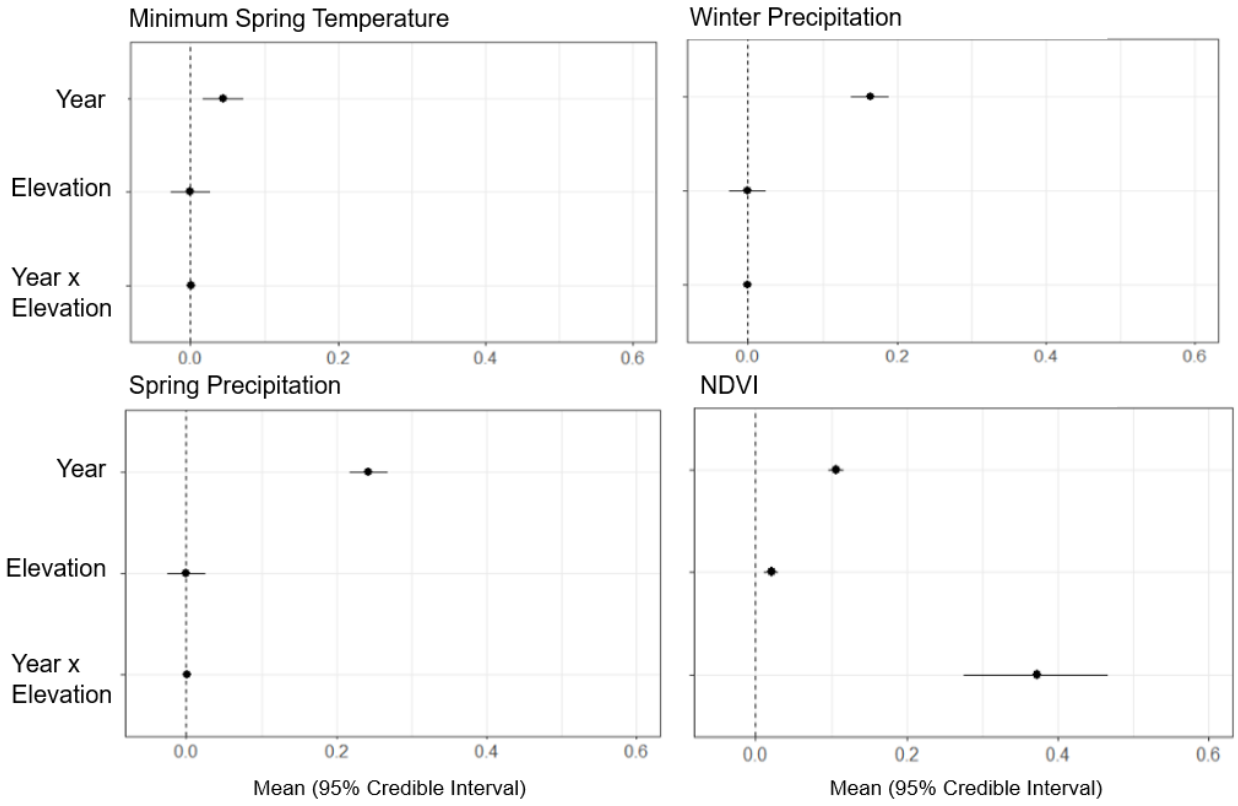

Figure 2.3. Mean estimates and 95% credible intervals of the effects of year, elevation, and their interaction on climate variables and the normalized difference vegetation index (NDVI) on occupancy of bird species in the central Great Basin.

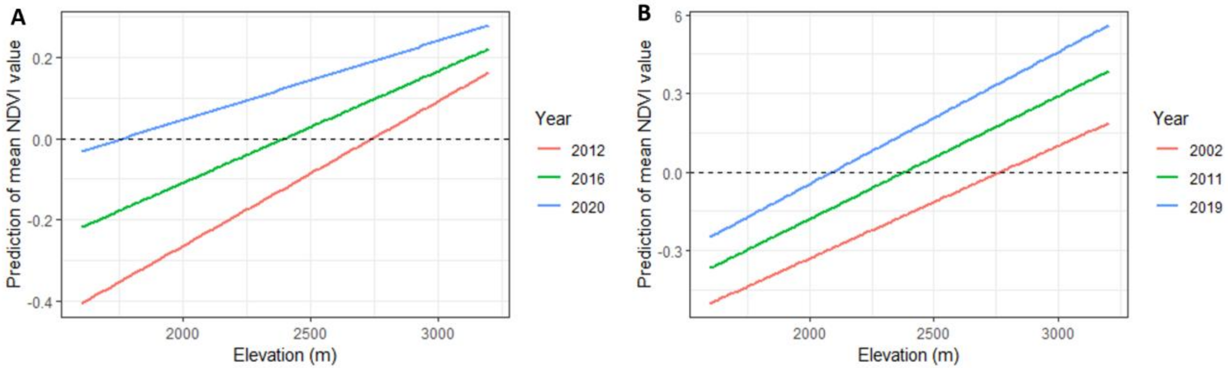

Figure 2.4. Predictions of mean NDVI values during three discrete years (early, intermediate, and late in our sampling periods) sampled from the posterior distribution of the interaction of elevation and year in a generalized linear model. A, western Great Basin; B. central Great Basin.

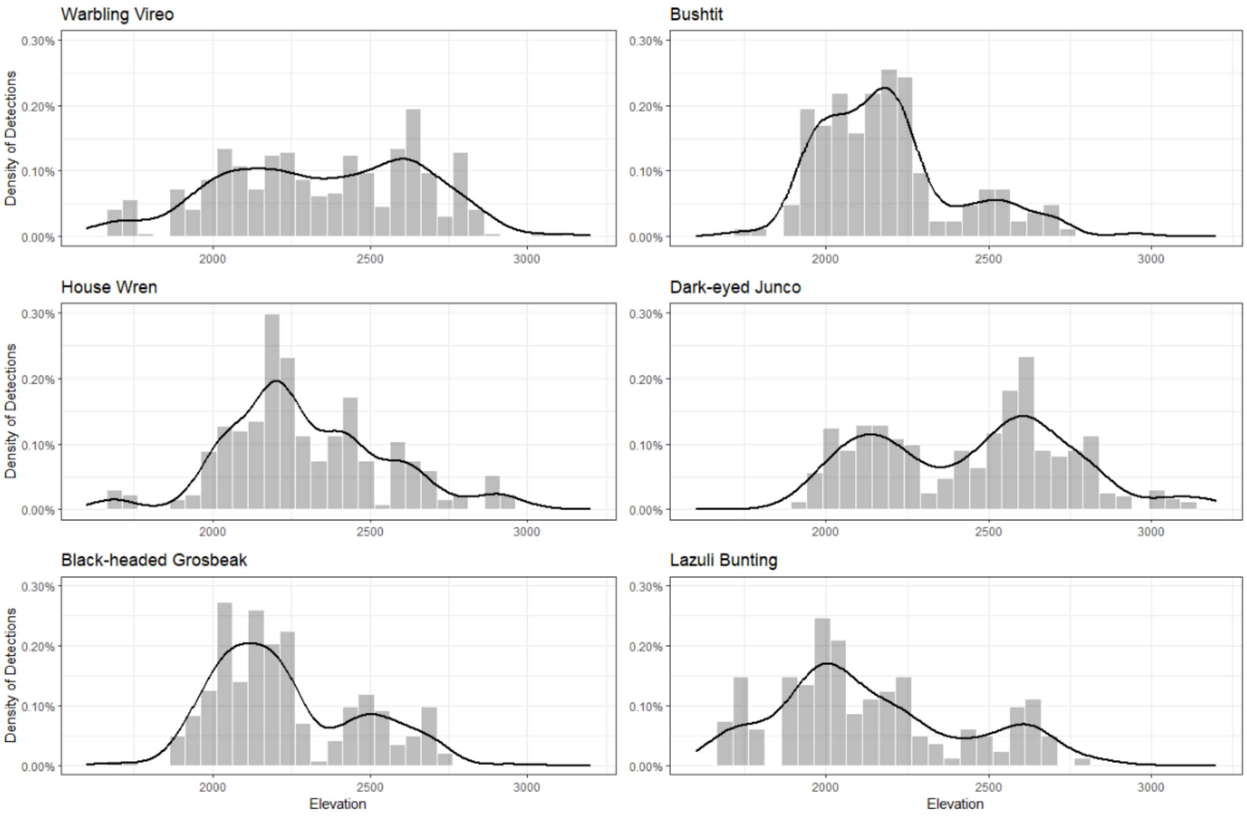

Figure 2.5. Density of detections extracted from abundance data over the full elevational gradient surveyed from 2012-2020 in the western Great Basin. Species are those with elevational ranges that shifted along the full gradient or the lower or upper 25% of the gradient.

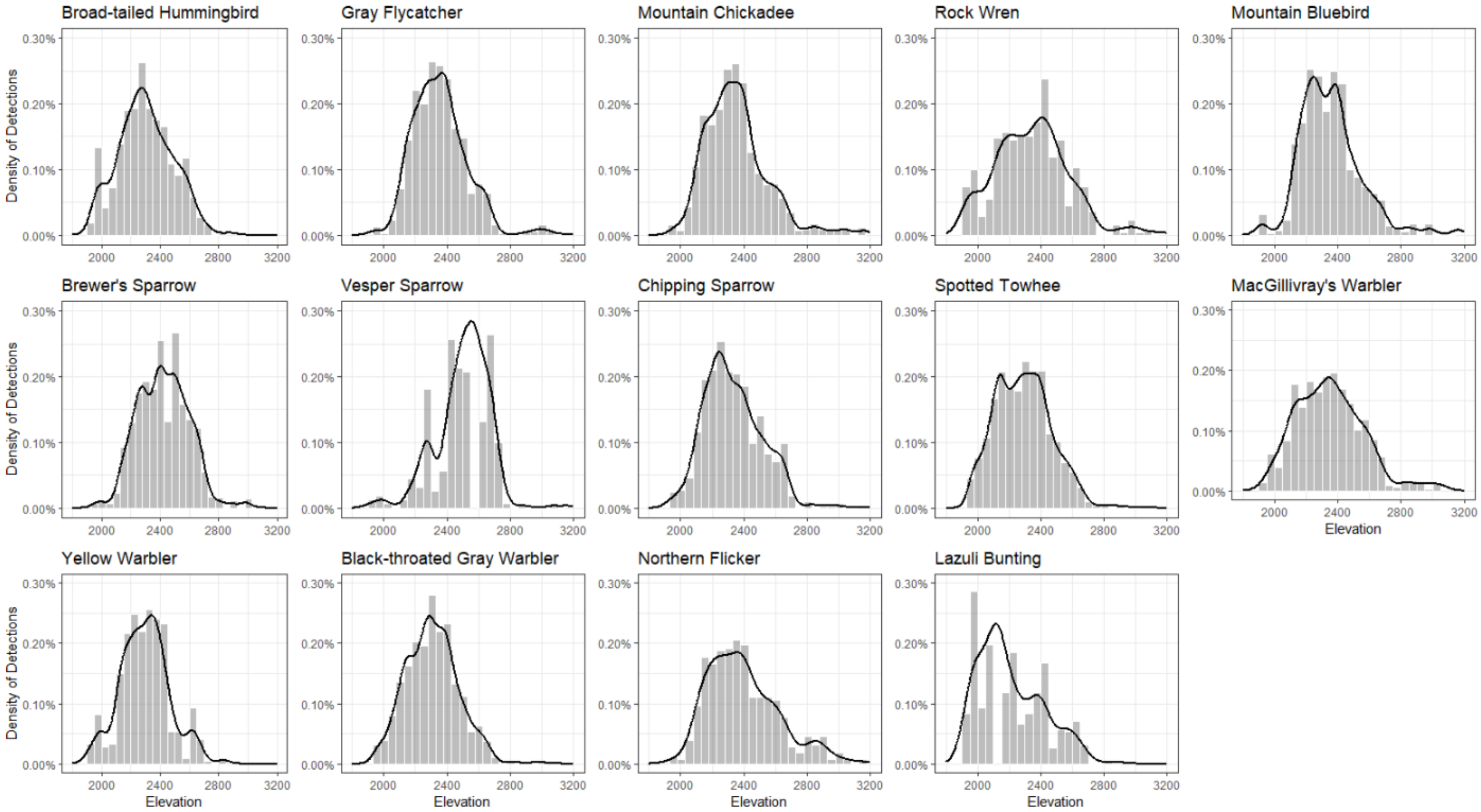

Figure 2.6. Density of detections extracted from abundance data over the full elevational gradient surveyed from 2001-2020 in the central Great Basin. Species are those with elevational ranges that shifted along the full gradient or the lower or upper 25% of the gradient.

Table 2.1. Elevational shifts in occupancy of breeding birds in the western Great Basin. Species reported are those for which the best model included the interaction of year and elevation and for which >90% of the posterior density of the interaction of elevation and year was above or below zero. Intercept and slope estimates were taken from simple linear models of the effect of year on mean elevation of occupancy.

	Full elevational gradient			**Lower edge**			**Upper edge**		
Species	Interaction of year and elevation with occupancy (mean, SD)	Estimated shift in m (95% CI)	Significant variables (mean, SD)	Interaction of year and elevation with occupancy (mean, SD)	Estimated shift in m (95% CI)	Significant variables (mean, SD)	Interaction of year and elevation with occupancy (mean, SD)	Estimated shift in m (95% CI)	Significant variables (mean, SD)
Warbling Vireo				0.61, 0.38	16 (-110, 143)	Spring precipitation (-1.38, 0.41)	0.48, 0.34	-21 (-98, 56)	NDVI (0.92, 0.53)
Bushtit				0.55, 0.41	1 (-74, 75)				
House Wren	-0.35, 0.15	-99 (-308, 111)	Spring precipitation (0.41, 0.17) NDVI (0.90, 0.32)	-0.53, 0.29	-89 (-259, 80)	Winter precipitation (-0.54, 0.36) NDVI (0.61, 0.53)	0.90, 0.39	59 (-95, 214)	
Dark-eyed Junco							-0.87, 0.55	-47 (-150, 56)	NDVI (1.11, 0.72)
Black-headed Grosbeak	-0.88, 0.37	-65 (-221, 91)	Spring precipitation (-0.78, 0.35)	0.52, 0.42	2 (-67, 71)	NDVI (-0.81, 0.53)			

Lazuli Bunting	-0.54, 0.18	-194 (-471, 84)	(-0.84, 0.48)	45 (-92, 183)	

Table 2.2. Elevational shifts in occupancy of breeding birds in the central Great Basin. Species reported are those for which the best model included the interaction of year and elevation and for which >90% of the posterior density of the interaction of year and elevation was above or below zero. Intercept and slope estimates were taken from simple linear models of effect of year on mean elevation of occupancy.

	Full elevational gradient			**Lower edge**			**Upper edge**		
Species	Interaction of year and elevation with occupancy (mean, SD)	Estimated shift in m (95% CI)	Significant variables (mean, SD)	Interaction of year and elevation with occupancy (mean, SD)	Estimated shift in m (95% CI)	Significant variables (mean, SD)	Interaction of year and elevation with occupancy (mean, SD)	Estimated shift in m (95% CI)	Significant variables (mean, SD)
Broad-tailed Hummingbird				-0.34, 0.16	-38 (-81, 5)	Winter precipitation (-0.37, 0.15) NDVI (0.91, 0.27)			
Northern Flicker				-0.5, 0.23	-39 (-77, -2)	Spring precipitation (-0.34, 0.24) NDVI (0.86, 0.33)			
Gray Flycatcher	-0.24, 0.4	-88 (-175, -1)	Spring precipitation (-0.29, 0.18)						
Mountain Chickadee				-0.35, 0.21	-17 (-50, 15)	Spring precipitation (-0.32, 0.23) Winter precipitation (-0.68, 0.2)	0.68, 0.28	8 (-80, 97)	Spring precipitation (-0.47, 0.21)

Rock Wren							0.51, 0.24	116 (244, -12)	Spring temperature (0.94, 0.26) NDVI (-0.88, 0.32)
Mountain Bluebird							(-0.45, 0.27)	-53 (-160, 55)	Winter precipitation (-0.85, 0.34) NDVI (-0.98, 0.4)
Brewer's Sparrow				0.51, 0.2	38 (0.4, 76.3)	Winter precipitation (-0.66, 0.17) Spring temperature (0.27, 0.17)			
Vesper Sparrow							(0.55, 0.24)	48 (-118, 23)	Winter precipitation (-0.27, 0.21)
Chipping Sparrow							(-0.4, 0.26)	-19 (-103, 66)	Spring temperature (-0.47, 0.29)
Spotted Towhee							(-0.43, 0.17)	-16 (-74, 42)	
MacGillivray's Warbler				0.29, 0.16	12 (-16, 40)	Winter precipitation (-0.32, 0.16) NDVI (0.87, 0.44)			
Yellow Warbler				0.28, 0.19	23 (-29, 74)				

Black-throated Gray Warbler		-0.24, 0.13	-4 (-36, 28)		
Lazuli Bunting		0.58, 0.19	31 (-11, 72)	Spring precipitation (0.4, 0.18)	

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CHAPTER 3

Geographical variation in vegetational associations of birds across the Great Basin

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Abstract

Characterization of differences in bird-habitat associations across the Great Basin may indicate how birds respond to environmental changes, including those caused by management actions. We examined associations of species and functional groups of plants with occupancy of 13 bird species across five biogeographic subregions of the Great Basin, USA. We hypothesized that plant physiognomy (characterized by functional groups) was associated significantly with occupancy across the Great Basin (all subregions), and that floristics (individual plant species) was associated with occupancy within subregions. We created single-species occupancy models that examined the effect of 13 habitat-structuring plant species and five functional groups on bird occupancy in each of the 5 subregions. We used two methods to evaluate differences in bird-vegetation associations across subregions. First, we examined which covariates had a significant effect on occupancy in each subregion. Second, for each bird species, we compared covariate estimates between each of the 10 pairs of subregions, and classified the effect of the covariate on occupancy in two subregions as significantly different if <5% of the posterior density estimates overlapped. We found considerable variation among subregions with respect to the covariates that were associated significantly with occupancy. Additionally, we found that the number of associations between occupancy and vegetation covariates, and the strengths of those associations, varied substantially among bird species and subregions. Our results did not support our hypothesis that associations between bird occupancy and plant species or plant functional groups differ depending on the spatial extent examined. We found that associations between bird occupancy and plant species were highly variable among subregions, and that associations between occupancy and functional groups were not consistent across the Great Basin. The high variability of bird-functional group and bird-plant species associations throughout the five

subregions indicates geographical variation in habitat for some bird species across the Great Basin.

Introduction

Identification of species-specific habitat requirements could improve habitat restoration and conservation efforts and may contribute to prediction of future species distributions in the face of climate and land-use change. The distribution of avian species is affected by numerous factors including climate, physiological tolerances, intrinsic limits to population growth, and resource availability (Gill 2007). At the local level, the species richness, abundance, and distribution of birds corresponds in large part to the complexity of vegetation. Vegetation structure and composition affect availability of nesting strata, food, and shelter; protection from predators; and cues about environmental conditions consistent with successful reproduction (James 1971).

Associations between vegetation and bird species have been relatively well studied, and much research has focused on the relative effects of plant physiognomy (vegetation structure) and floristics (vegetation composition) on bird distributions (MacArthur & MacArthur 1961, Robinson & Holmes 1984, Mac Nally 1990). In the western United States, grassland bird abundances were associated strongly with both physiognomy (Rotenberry & Wiens 1980) and floristics (Wiens & Rotenberry 1981). Relations with physiognomy were stronger over relatively large geographical extents (five states), whereas relations with floristics were stronger over smaller extents (southeastern Oregon). Subsequent work also indicated that physiognomy affects bird occurrence at the regional extent, and floristics affects occurrence at the local extent (Knopf et al. 1990). Across the Great Basin, vegetation composition was more strongly associated with species composition of birds than was vegetation structure or primary productivity (Fleishman & Mac Nally 2006), and in the Mojave Desert, species composition of birds was more closely related to floristics than to vegetation structure (Fleishman et al. 2003). However, a review of more than 45 years of research on birds in the western United States did not find consistent evidence of associations of floristics and physiognomy with avian distributions at various extents (Fisher & Davis 2014).

Encompassing more than 425,000 km^2 of internal drainage across California, Nevada, Utah, Idaho, and Oregon, the Great Basin is defined by aridity, expansive sagebrush-shrubsteppe ecosystems, and over 300 mountain ranges encompassing diverse ecological communities. More than 70% of the Great Basin is public land, and conservation priorities for wild animals are determined on a state-by-state basis and described in state Wildlife Action Plans and Conservation Plans (Wildlife Action Plan Team 2012, Utah Wildlife Action Plan Joint Team 2015, California Department of Fish and Wildlife 2015, Oregon Department of Fish and Wildlife 2016, Idaho Department of Fish and Game 2017). Goals for birds, and passerines in particular, are similar among the five state Wildlife Action Plans, and largely focus on protection of sagebrush-dominated ecosystems and restoration of riparian areas. The majority of plans emphasize management actions over extensive areas and do not recognize geographic variation in a species' habitat. Examples of management actions that span the majority of the Great Basin include reduction of cheatgrass (*Bromus tectorum*), a highly flammable, non-native invasive grass; fire suppression; restoration of sagebrush (*Artemisia* spp.); and increasing the sustainability of livestock grazing.

Management plans often assume that bird-environment relations that were characterized in one area of the Great Basin are representative of those relations across the entire ecoregion (e.g., Sage Grouse Initiative, https://www.sagegrouseinitiative.com/). However, differences in hydrology, vegetation composition, climate, geology, and insect and other animal communities across the Great Basin are well established (e.g., Brown 1978, Harper et al. 1978, Austin &

Murphy 1987, Grayson 1993, Riddle et al. 2014). For example, more precipitation falls in the northern Great Basin than in the central or southern Great Basin, and from 1951 through 2013, maximum precipitation increased significantly in the eastern and northern Great Basin, but not in the western or southern Great Basin (Xue et al. 2017). These differences have led researchers to divide the Great Basin into subregions on the basis of ecological and evolutionary processes and attributes, such as floristics, geology, and avian composition (Behle 1963, Holmgren 1972, Johnson 1978). Accordingly, it is reasonable to assume that the habitat of species that occur throughout the Great Basin varies regionally. Here, we investigate whether associations of floristics and physiognomy with bird occupancy change across five biogeographic subregions of the Great Basin (Figure 3.1). Understanding whether relations between birds and vegetation differ across vegetation gradients could indicate how birds respond to environmental or land-use changes, including those caused by management actions.

We examined avian associations with plant species and functional groups. Functional groups are sets of species with similar traits that relate to their ecological roles, and that respond to multiple environmental factors in similar ways (Lavorel et al. 1997, Diaz & Cabido 2001). Although functional groups are subjective, we considered traits that may be meaningful to birds (Lavorel et al. 1997), especially physical structure and association with riparian areas. We hypothesized that plant physiognomy (characterized by functional groups) was associated significantly with occupancy across the Great Basin (all subregions), and that floristics (individual plant species) was associated with occupancy within subregions.

Methods

Study system

Our work spanned five subregions of the hydrographic Great Basin, which we reference as central, western, Sierra Nevada, northern, and eastern (Figure 3.1). Our delineations, which primarily are based on vegetation, are generally consistent with ecoregions as defined by The Nature Conservancy (The Nature Conservancy of Nevada 2001) and the U.S. Environmental Protection Agency's Level 4 Ecoregions (Bryce et al. 2003). The Sierra Nevada subregion includes lodgepole pine (*Pinus contorta*), Jeffrey pine (*P. jeffreyi*), white fir (*Abies concolor*), and red fir (*A. magnifica*), and has expansive, closed-canopy, subalpine conifer forests. Conifers in the western and central subregions largely are dominated by juniper (*Juniperus osteosperma*) and single-leaf pinyon (*P. monophylla*). The northern subregion includes ponderosa pine (*P. ponderosa*) woodlands but few pinyon woodlands, whereas the eastern subregion includes plant species that are common in the Rocky Mountains but not much further west in the Great Basin, such as Douglas-fir (*Pseudotsuga menziesii*) (Grayson 1993).

Field data

We sampled birds with 100-m fixed-radius point counts from late May through early July, which encompasses the breeding season of most birds in the Great Basin and ends before a high proportion of juveniles have fledged and before most movement to molting or wintering grounds. In the Sierra Nevada and western subregions, we sampled birds from 2012-2020 at a total of 134 points in 10 canyons (Fleishman 2019a). In the central Great Basin subregion, we sampled birds from 2001-2020, except 2016 and 2017, at a total of 303 points in 25 canyons (Fleishman 2019b). In the northern and eastern subregions, we sampled birds from 2017-2018 in a total of 92 points in 5 canyons and 96 points in 6 canyons, respectively (Fleishman 2019c, d).

Each canyon had an average of 12 survey points, and the centers of almost all points were at least 350 m apart. Not all points or canyons were sampled in all years.

We visited each point three times during the breeding season, with ca. 10–14 days between visits, and recorded all birds detected by sight or sound that were using resources within the point during an eight-minute count. In almost all cases, sampling was restricted to the first four hours after sunrise. We excluded fledglings and juveniles from analyses.

To characterize vegetation structure and composition, we measured four radial 50-m lines, one in each of the cardinal directions, from the center of each point. At 5-m intervals along each line, we recorded the size of the closest tree within 1 m (either diameter at breast height or basal diameter, depending on plant morphology), canopy cover, and presence of dominant plant species (approximately 25 taxa; most grasses and forbs were not differentiated), for a total of 41 measurements at each point. These data were collected in 2013 in the central subregion, in 2016 and 2017 in the Sierra Nevada and western subregions, and in 2017 and 2018 in the northern and eastern subregions (Fleishman 2019e-h). Point-level abundances of tree and shrub species remained relatively stable over the period of this study.

We calculated the percentage similarity (*PS*) of tree, shrub, and bird species composition between subregions with Czekanowski's quantitative index,

$$PS = \frac{200\sum min(y_{ab}, y_{ac})}{\sum y_{ab} + \sum y_{ac}},$$

where y_{ab} is the abundance of species a in subregion b, and y_{ac} is the abundance of species a in subregion c. We excluded bird species that we observed less than twice in a subregion from the analysis. For the main analyses (see *Statistical Analyses*), we transformed avian abundance data into occupancy data due to lack of model fit to the abundance data. However, for the percentage similarity index, we used abundance data.

Functional group definitions

We defined five functional groups of plants on the basis of our 30 years of field experience and discussions with other scientists who are experts on the ecology of the Great Basin (Table 3.1). For example, we grouped sagebrush (*Artemisia tridentata* and *A. arbuscula*), rabbitbrush (*Ericameria* spp. and *Chrysothamnus* spp.), saltbush (*Atriplex* spp.), horsebrush (*Tetradymia* spp.), hopsage (*Grayia spinosa*), and bitterbrush (*Purshia tridentata*) in the low shrub functional group. We hypothesized that birds view these shrub species as functionally redundant given that they are relatively short, grow in dry microclimates, and may provide breeding habitat for birds that build their nests in shrubs. These functional groups are analogous to physiognomic groups used in previous studies of Great Basin bird-vegetation associations (Rotenberry & Wiens 1980, Fleishman & Mac Nally 2006).

Every functional group except montane conifers, which was not present in the northern subregion, was present in all subregions, but often included different species, reflecting geographic differences in vegetation composition. For example, in the central subregion, the riparian tree functional group included aspen (*Populus tremuloides*), cottonwood (*P. angustifolia*, *P. fremontii*), water birch (*Betula occidentalis*), and dogwood (*Cornus sericea*), whereas in the western subregion, the same functional group included aspen, cottonwood, dogwood, and alder (*Alnus* spp.). We examined associations between bird occupancy and the abundance of 13 plant species that occurred in at least three of the five subregions. For instance, of the riparian tree species, we examined the associations between cottonwood and aspen abundance and bird occupancy given that cottonwood and aspen occurred in five and four subregions, respectively.

Statistical analyses

We modeled bird occupancy across the five subregions in a single model to directly compare vegetation associations among subregions. Occupancy estimates the probability that a species is present while accounting for imperfect detection (MacKenzie et al. 2002, Royle & Nichols 2003). We built models of the occupancy of 19 species that were relatively abundant across the Great Basin (at least 40 individuals detected per subregion per year).

We modeled detection probability as

$$C_{ijk} \sim Binominal(p_{ijk}, Z_{ik})$$

$$logit(p_{ijk}) = \alpha 0 + \alpha 1 * observer_{ikj}$$

$$\alpha 1 \sim Normal(0, tau)$$

$$tau \sim Uniform(0,5),$$

where C_{ijk} is the observed presence or absence at point i during visit j in year k, and p represents the probability of detecting a species given its presence. We used a logit link function to model the random effects of observer on detection probability. $\alpha 0$ is the mean point-level detection probability for a given species, and $\alpha 1$ is a random effect of observer identity on detection, with a mean of 0 and a precision of *tau*.

We linked the detection process to the occupancy process through Z_{ik}, which we treated as a Bernoulli random variable defined by the success probability ψ:

$$Z_{ik} \sim Bernoulli(\psi_{ik})$$

$$logit(\psi_{ik}) = \beta 0_S + \beta 1 * year_{ik} + \beta 2 * point_{ik} + \boldsymbol{\beta 3_S} * \boldsymbol{X_{ik}},$$

$$\beta 0_S \sim Normal(mu, tau0)$$

$$mu \sim logit(mu0)$$

$$mu0 \sim Uniform\ (0,1)$$

$$tau0 \sim sd0^2$$

$$sd0 \sim Uniform\ (0,10)$$

$$\beta 2 \sim Normal(0, tau1)$$

$$tau1 \sim Uniform(0,1)$$

where Z_{ik} is the occupancy state (0 = absent, 1 = present) at point *i* in year *k.* We applied a logit link function to ψ to model occupancy covariates. $B0_S$ is an intercept that varies among subregions *S* and is defined by a normal distribution with a mean of *mu* and precision of *tau0*. $\beta 1$ is the fixed effect of year, and $\beta 2$ is a point-level random effect with a mean of 0 and precision of *tau1*. $\boldsymbol{B3_S}$ is a vector of covariate values indexed by subregion *S* for every variable in $\boldsymbol{X}$ at each point *i*. $\boldsymbol{X}$ is a matrix of point-level covariate estimates for each subregion. The variables in $\boldsymbol{X}$ were percent cover of the five plant functional groups (Table 3.1) and prevalence of 13 plant species or taxa: sagebrush, Woods' rose (*Rosa woodsii*), bitterbrush, desert peach (*Prunus andersonii*), rabbitbrush, aspen, cottonwood, pinyon, juniper, mountain mahogany (*Cercocarpus ledifolius*), willow (*Salix* spp.), limber pine (*Pinus flexilis*), and fir (*Abies* spp.). We classified a covariate as significant if >95% of its posterior distribution was above or below zero.

We implemented models in JAGS (Plummer 2003) with the `jagsUI` package (Kellner 2019) in R (R Core Team 2020). We based posteriors on three chains of 50,000 iterations after a 10,000 sample for both the burn-in and adaptive phase. We classified convergence as Rhat <1.10 (Gelman & Hill 2007). We calculated collinearity of all pairs of candidate covariates (those included in $\boldsymbol{X}$ and year). A priori, we established that if collinearity >0.75, we would exclude the variable of the pair that we deemed less ecologically relevant. No variables were collinear. We examined model fit on the basis of separate Bayesian p-values for the detection and occupancy processes, and estimated mean occupancy and detection. We classified the fit of models as good if both Bayesian p-values were 0.05-0.95 and estimated mean detection was >15%. Models of 13 of the 19 species passed all goodness of fit tests; we only report the results of those models. The 13 species represent a variety of ecological guilds (Gonzalez-Salazar et al. 2014) and land-cover associations.

We used two methods to evaluate whether estimated associations between the occupancy of a given species of bird and a particular covariate were significantly different between subregions. First, we examined which covariates had a significant effect on occupancy (>95% of the posterior distribution above or below zero) in each subregion. Significant associations with habitat variables (whether negative or positive) conventionally are used to inform or direct management actions for animal populations. Second, we compared covariate estimates between each of the 10 pairs of subregions. If the posterior densities in the two subregions overlapped by <5%, we classified the covariate's effect on bird occupancy in the two subregions as significantly different. The effect of a given covariate on occupancy could differ significantly between subregions regardless of whether it was significant in both subregions. For example, say 97% of the posterior distribution of a covariate in one subregion was above zero (significant, positive effect on occupancy), whereas 93% of the posterior distribution of the covariate in another subregion was above zero (non-significant effect on occupancy). Because the overlap between the two posterior distributions was <5%, we would not consider the covariate's effect on occupancy in the two subregions to be significantly different. Evaluation of subregional differences in bird-vegetation associations with this method allowed us to uncover relations that might not be apparent solely on the basis of significant vegetation associations with occupancy.

Results

Mean Great Basin-wide occupancy of the 13 species was 0.32, and mean subregion-level occupancy was 0.30-0.38 (Table 3.S1). Mean occupancy at the subregion level varied among species, from a low of 0.11 for House Wren (*Troglodytes aedon*) to a high of 0.82 for Green-tailed Towhee (*Pipilo chlorurus*). Occupancy of some species was relatively consistent among subregions (e.g., Green-tailed Towhee, Table 3.S1), whereas occupancy of others was more variable. For example, mean occupancy of Mountain Chickadee (*Poecile gambeli*) was 0.02 in the northern subregion and 0.82 in the Sierra Nevada subregion (Table 3.S1).

Species composition of birds and plants varied considerably among subregions. Mean similarity of avian species composition between pairs of subregions was 51% (range 42–60%) (Table 3.S2), and mean similarity of plant species composition between pairs of subregions was 53% (range 35–67%) (Table 3.S3). The central and northern subregions were the most similar with respect to avian composition (60%) but the least similar with respect to plant composition (35%).

Occupancy of none of the 13 bird species was associated significantly with the same plant species or functional group in more than three subregions (Figure 3.2). Three species, Warbling Vireo (*Vireo gilvus*), Brewer's Sparrow (*Spizella breweri*), and Green-tailed Towhee, were associated with the same plant species in three subregions (Figure 3.2), and the sign of the associations was the same (negative or positive). Of the 234 possible associations between a bird species and a plant species or functional group, 102 (44%) were significant in at least one subregion. Of those 102 associations, 18 (18%) were significant in more than one subregion, and four of those 18 associations had opposite signs in different subregions. For example, occupancy of Dark-eyed Junco (*Junco hyemalis*) was positively associated with the low shrub functional group in the central subregion, but negatively associated with that functional group in the Sierra Nevada subregion (Figure 3.2). Across all bird species and geographic subregions, 10% of possible associations between occupancy and plant species, and 13% of possible associations between occupancy and functional groups, were significant.

Associations between the occupancy of each bird species and an average of four plant species and three functional groups differed between subregions (Tables 3.2 & 3.3). Associations between occupancy of Dark-eyed Junco, Green-tailed Towhee, and Yellow-rumped Warbler (*Setophaga coronata*) and a given plant species or functional group in one of the subregions were significantly different from those in any other subregion. For example, the association between Green-tailed Towhee and the low shrub functional group in the Sierra Nevada was significantly more positive than that in any other subregion (Figure 3.3a). Similarly, the association between Green-tailed Towhee and sagebrush in the eastern subregion was significantly more negative than that in any other subregion (Figure 3.3c). With the exception of fir, which was not associated significantly with occupancy of any bird species, associations of all species of plants and functional groups with the occupancy of a given bird species varied between subregions (Table 3.4). The associations of occupancy with two plant species (juniper and pinyon) and four functional groups (all except riparian shrubs) differed significantly between pairs of subregions for more than 50% of bird species examined. Particular pairs of subregions dominated these differences. For example, associations of low shrubs with occupancy of six bird species differed between the Sierra Nevada and central subregions. Associations of montane conifers with occupancy of 10 bird species differed between the Sierra Nevada and western (six species) and Sierra Nevada and central (five species) subregions.

Associations between occupancy and plant species differed the least between the eastern and western subregions (4% of realized differences, Table 3.5), whereas associations between the Sierra Nevada and central or western subregions differed the most (16% each). Associations between occupancy and functional groups differed the least between the northern and western subregions (3%, Table 3.5), and differed the most between the Sierra Nevada and western (18%) and central (17%) subregions.

Discussion

We identified two types of differences in bird-vegetation associations across five subregions of the Great Basin. First, we found considerable variation among subregions with respect to the covariates that were associated significantly with occupancy. Second, we found that the number of bird-vegetation associations, and the extent to which those associations were positive or negative (differences in their posterior distributions), varied substantially among bird species and subregions. Significant differences in associations between occupancy of a given species and a given covariate among subregions would not have been apparent from analysis of significant occupancy associations alone. For example, the association between occupancy of Green-tailed Towhee and sagebrush was significant and negative in the eastern subregion and significant and positive in the central subregion (Figure 3.2). However, in addition to a significant difference between associations with sagebrush in the eastern and central subregions, associations in the northern, western, and Sierra Nevada were significantly different from that in the eastern subregion (Figure 3.3c). Our work did not yield evidence that associations between occupancy of birds and functional groups of plants were transferable among subregions.

Differences in associations between bird occupancy and plant species among subregions likely have multiple mechanisms. For example, the differences in part could be caused by subregionally distinct species richness, composition, and interspecific interactions of birds, which ultimately may reflect subregional differences in plant composition (MacArthur 1962, Rice et al. 1983). Differences in species composition of birds may be driven by competition and predation (Cody 1981, Martin 1993). Abundance of predators can influence selection of nest sites by females, and areas with low predator abundance may have characteristic but subregionally distinct vegetation (Lanyon 1981, LaManna et al. 2015). Similarly, in some subregions, sympatric species may be excluded from or avoid typical nesting strata because of competition (Wisz et al. 2013, Estevo et al. 2017).

There are at least three possible explanations why associations between occupancy and functional groups varied among subregions. First, our functional groups may not reflect traits or plant taxa that affect occupancy. We think this explanation is unlikely given that our functional groups included all dominant species of shrubs and trees, and the species in each group had similar structure and microclimate associations. Second, not all members of a given functional group occur or are equally abundant in all subregions. For example, water birch was abundant in the central subregion and absent from our survey locations in the other four subregions. Therefore, we included water birch in the riparian tree functional group in the central subregion only. As a result, associations between the riparian tree functional group and occupancy of any species that was attracted to or avoided water birch, and the direction of the associations, may have differed among subregions. Third, it is possible that species indeed are associated with different functional groups in different parts of the Great Basin. Our data support this hypothesis. Associations of occupancy of each bird species with at least one functional group differed among subregions. Similarly, the association between four of the functional groups with occupancy of ≥6 species varied between one or more pairs of subregions (Table 3.4). Our results suggested that relations between occupancy and functional groups in the Sierra Nevada subregion may be distinct from those in the western or central subregions, despite the fact that no more than 30 km separated many of our points in the western and Sierra Nevada subregions. Those differences may reflect differences in subregional climate, geology, and vegetation. The east slope of the Sierra Nevada captures considerably more precipitation from Pacific cyclonic storms than mountain ranges immediately to the east (Grayson 1993). Additionally, soils in the Sierra Nevada have low pH and low concentrations of extractable phosphorus, which supports ponderosa and Jeffrey pine woodlands that are absent further east (DeLucia et al. 1988, Schlesinger et al. 1989).

Associations with occupancy and subregional differences in the directions of those associations were highly species-specific. Occupancy of some species, such as Cassin's Finch (*Haemorhous cassinii*), Mountain Chickadee, and Spotted Towhee, was associated with relatively few covariates (Figure 3.2), and the directions of those associations differed little between subregions (Tables 3.2 & 3.3). These results suggest that the three species, none of which migrate far from the Great Basin, may have relatively similar and general vegetation associations across the ecoregion. Such generality is one way in which resident species may adapt to resource fluctuations across large areas (Martin & Fahrig 2018).

Occupancy of other species of birds was associated with different covariates in different subregions, and the directions of those associations differed considerably between subregions. For example, occupancy of Brewer's Sparrow was significantly associated with eight plant species and four functional groups. Its association with pinyon was significant and negative in the eastern, western, and Sierra Nevada subregions (Figure 3.2), and there was a significant difference between the eastern and western subregions in the effect of pinyon on occupancy (Figure 3.4c). Furthermore, the association of sagebrush with occupancy of Brewer's Sparrow in the central and northern subregions significantly differed, and only was strong and positive in the central subregion (Figure 3.4d). Additionally, Brewer's Sparrow was significantly and positively associated with the low shrub functional group in only the Sierra Nevada subregion, and the association in the Sierra Nevada subregion was significantly more positive than associations in the northern, eastern, and central subregions. This result may seem surprising given that Brewer's Sparrow is considered a sagebrush obligate, and its presence often is interpreted as an indication that sagebrush ecosystems are in good condition, particularly after a change in management (e.g., mechanical manipulation, changes in intensity of livestock grazing, expansion of non-native invasive species) (McAdoo et al. 1989, Magee et al. 2011, Golding & Dreitz 2017). However, in our experience, Brewer's Sparrow is most abundant in areas with few trees and many woody shrubs of moderate height. The lack of consistent associations with sagebrush and the low shrub functional group suggests that Brewer's Sparrows may not be responding to the presence of one or multiple arid shrub species, but instead to the presence of any low shrub species in addition to expansive, treeless habitat. Our results suggest that Brewer’s Sparrow may not be a sagebrush obligate throughout the Great Basin, especially at its edges.

Associations of occupancy with plant species and functional groups varied relatively strongly between the central subregion and other subregions (Table 3.5). Much of the Great Basin is similar to the central subregion with respect to vegetation, geology, and climate, whereas the other subregions are on the edges of the Great Basin (Figure 3.1) and more similar to adjacent ecoregions. For example, the northern subregion is cooler and has greater water availability than the other subregions (Xue et al. 2017). Although species composition of birds and plants differs among edges of the Great Basin, our results suggest that associations of occupancy with vegetation covariates may be more similar among edges than between edges and the center of the ecoregion.

Most efforts to characterize bird habitat in the Great Basin focused on sagebrush shrubsteppe and grassland communities (Knopf et al. 1990, Rotenberry & Wiens 1980, Wiens & Rotenberry 1981, but see Fleishman & Nally 2006). Our work is among the first to address habitat for bird species in both upland and riparian communities in the montane Great Basin. Our research adds to the large body of evidence that bird habitat varies among resolutions and extents (Weins et al. 1987, Kristan 2006, Chave 2013), and does not support the theory that physiognomy and floristics are more closely related to bird occurrence at large and small spatial extents, respectively.

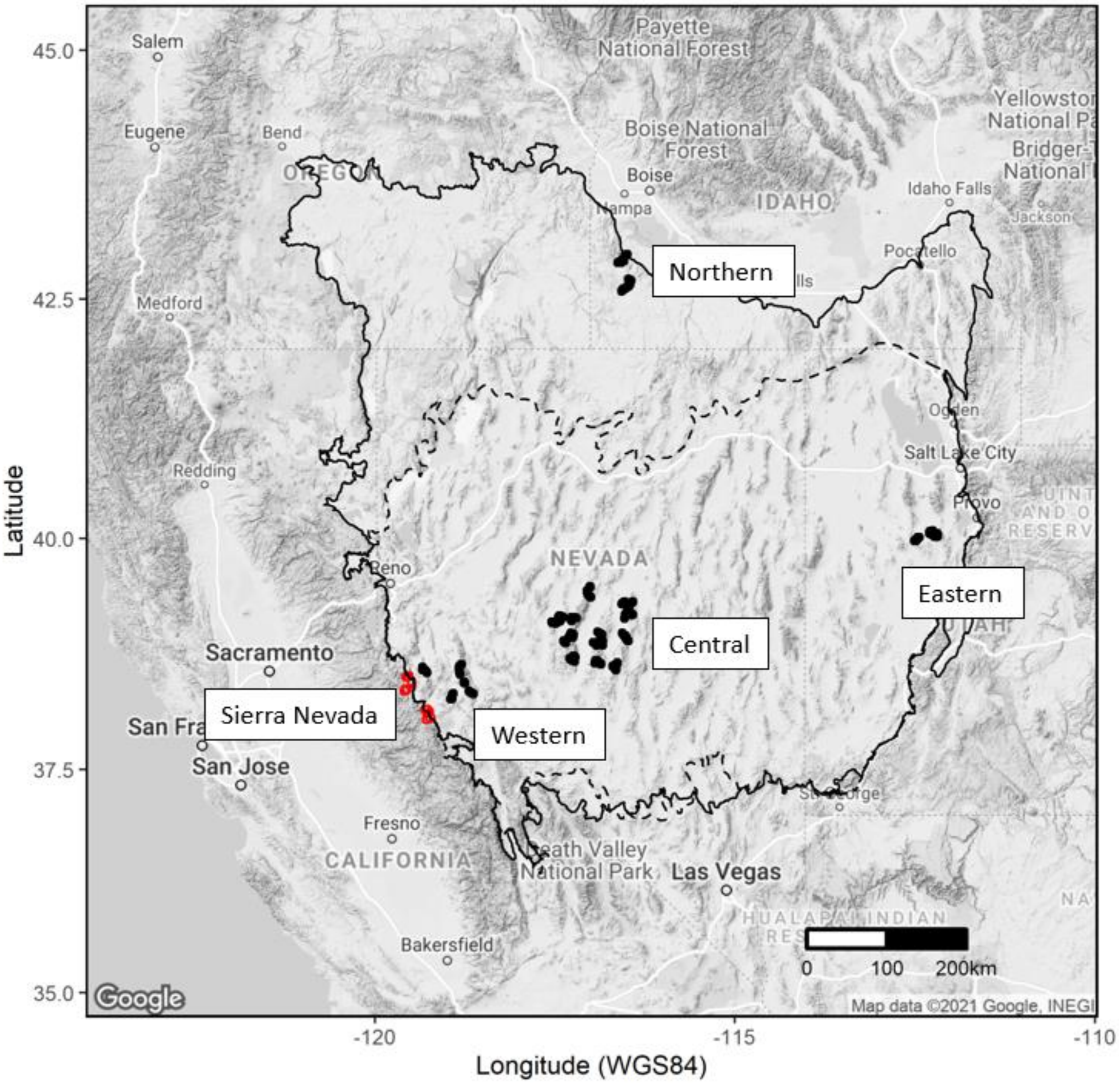

Figure 3.1. Great Basin and locations of survey points in each subregion. Points in the Sierra Nevada subregion are designated by red dots to better differentiate them from points in the western subregion. Dotted outline indicates The Nature Conservancy's designation of the Great Basin. Solid black outline indicates the U.S. Environmental Protection Agency's Subregion Level 3 designation of the Great Basin (Central Basin and Range and Northern Basin and Range).

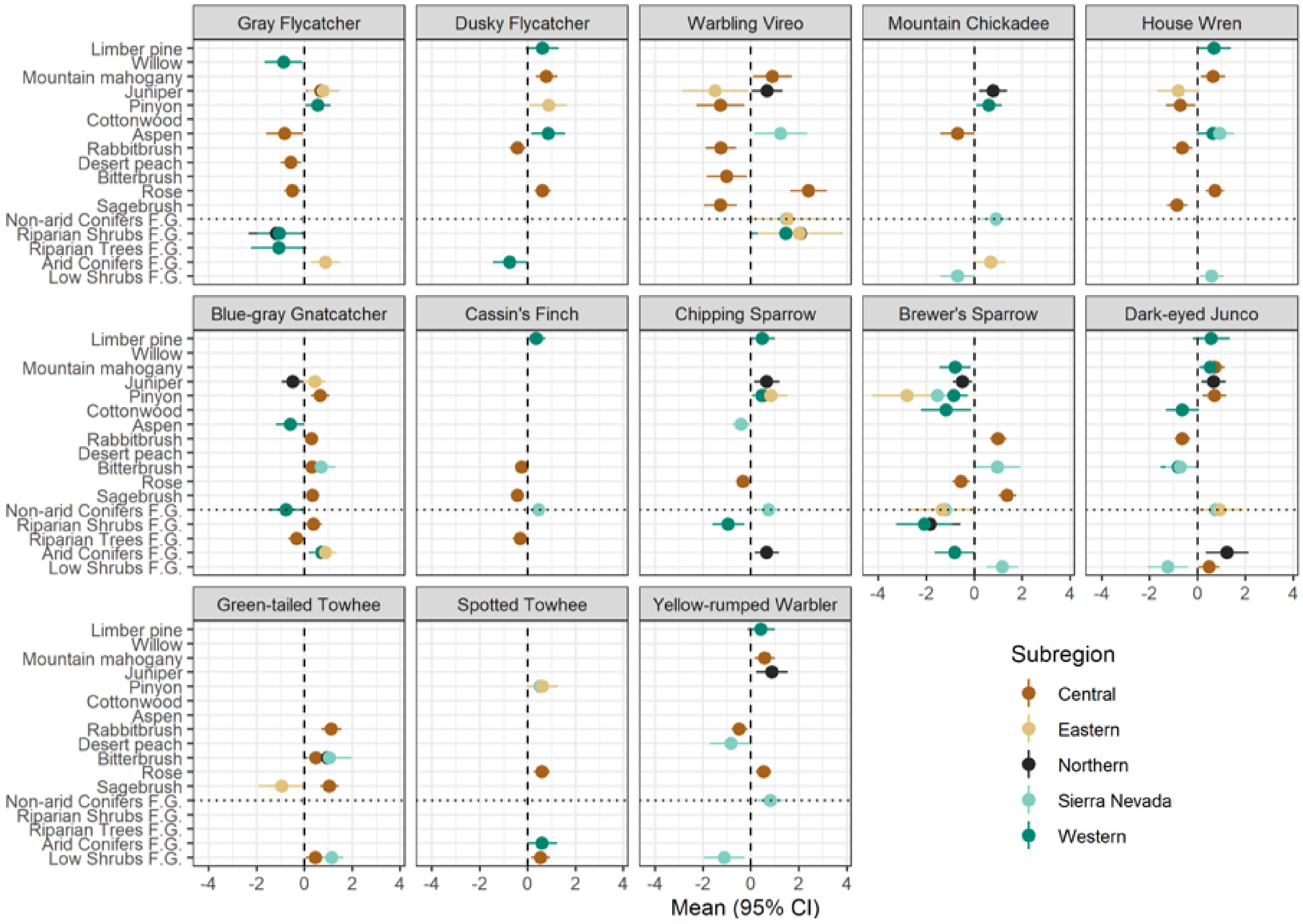
Gray Flycatcher
Dusky Flycatcher
Warbling Vireo
Mountain Chickadee
House Wren
Blue-gray Gnatcatcher
Cassin's Finch
Chipping Sparrow
Brewer's Sparrow
Dark-eyed Junco
Green-tailed Towhee
Spotted Towhee
Yellow-rumped Warbler
Limber pine
Willow
Mountain mahogany
Juniper
Pinyon
Cottonwood
Aspen
Rabbitbrush
Desert peach
Bitterbrush
Rose
Sagebrush
Non-arid Conifers F.G.
Riparian Shrubs F.G.
Riparian Trees F.G.
Arid Conifers F.G.
Low Shrubs F.G.
-4
-2
0
2
4
Mean (95% CI)
Subregion
● Central
● Eastern
● Northern
● Sierra Nevada
● Western

Figure 3.2. Model estimates of the effects of plant species and plant functional groups on bird occupancy in each subregion. Values are mean and 95% confidence intervals (CI) of associations for which >95% of the posterior density was above or below zero. F.G., functional group. Horizontal dotted line separates plant species and functional groups. No species' occupancy was associated significantly with fir.

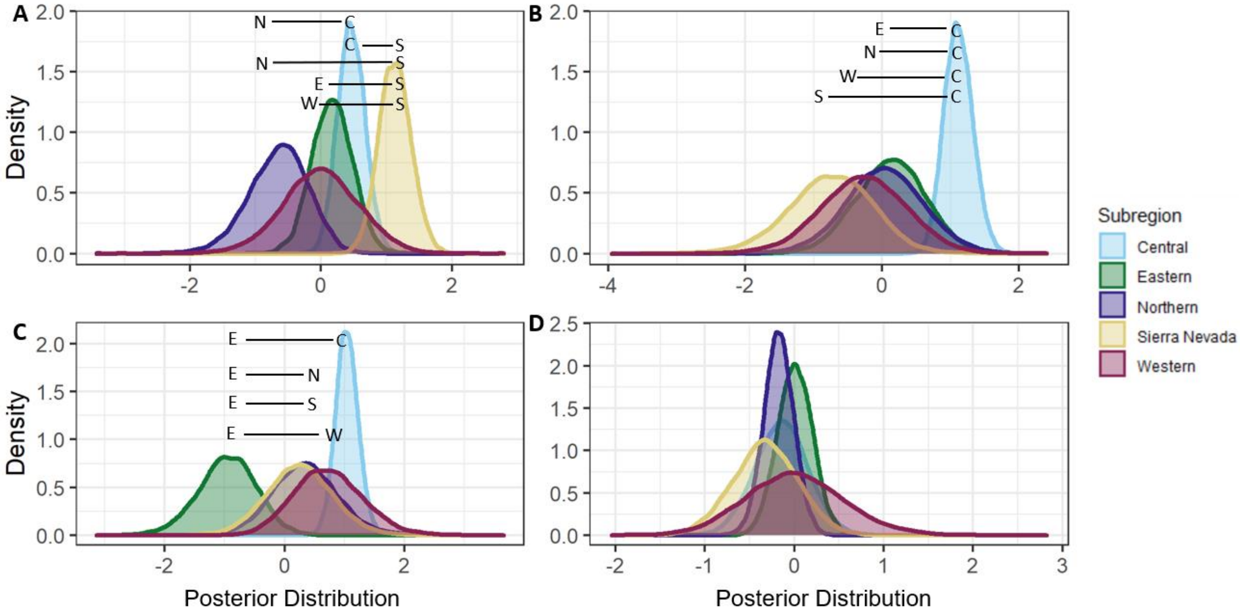

Figure 3.3. Posterior distributions of four covariates on Green-tailed Towhee occupancy. A, low shrub functional group; B, rabbitbrush; C, sagebrush; D, juniper. A line between two peaks indicates >95% confidence that the posterior distributions of two subregional estimates are significantly different. Letters indicate subregions that significantly differed: C = central, E = eastern, N = northern, S = Sierra Nevada, W = western.

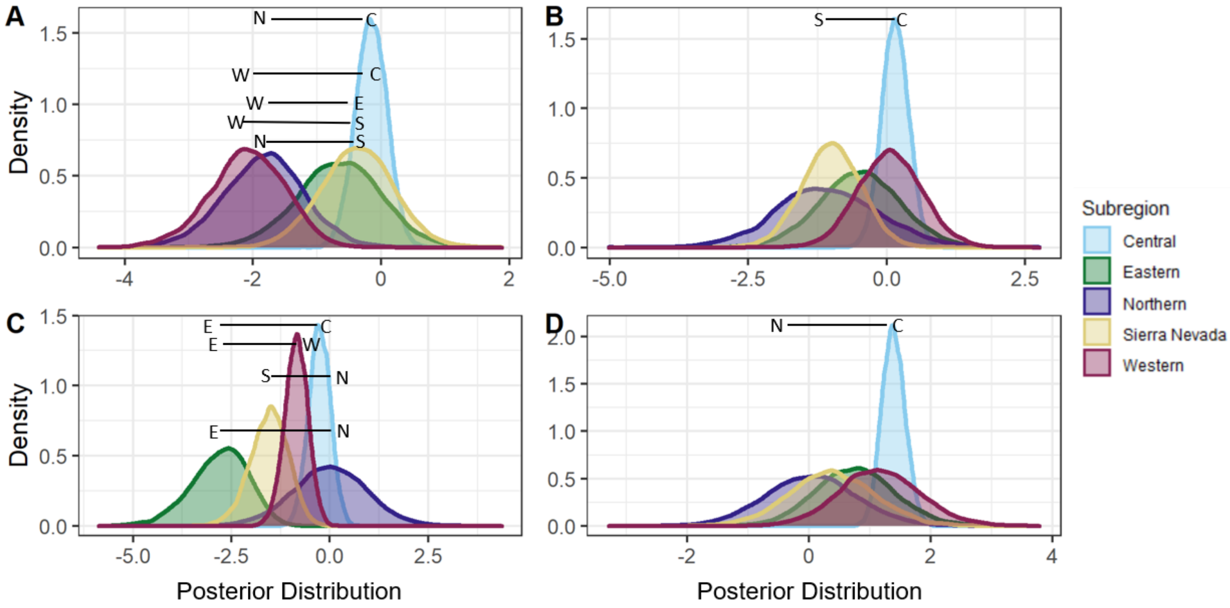

Figure 3.4. Posterior distributions of four covariates on Brewer's Sparrow occupancy. A, riparian shrub functional group; B, riparian tree functional group; C, pinyon pine; D, sagebrush. A line between two peaks indicates >95% confidence that the posterior distributions of two subregional estimates are significantly different. Letters indicate subregions that significantly differed: C = central, E = eastern, N = northern, S = Sierra Nevada, W = western.

Table 3.1. Functional groups of plants as defined in our analyses.

Species included	**Functional group**
All species of sagebrush, rabbitbrush, saltbush, bitterbrush, horsebrush, and hopsage	Low shrubs
Pinyon pine (*Pinus monophylla*), Utah juniper (*Juniperus osteosperma*)	Arid conifers
Aspen (*Populus tremuloides*), alder (*Alnus* spp.), water birch (*Betula occidentalis*), cottonwood (*Populus angustifolia*, *P. fremontii*)	Riparian trees
Chokecherry (*Prunus virginiana*), bitter cherry (*P. emarginata*), Woods' rose (*Rosa woodsii*), willow (*Salix* spp.)	Riparian shrubs
Limber pine (*Pinus flexilis*), Jeffrey pine (*P. jeffreyi*), lodgepole pine (*P. contorta*), Douglas-fir (*Pseudotsuga menziesii*), red fir (*Abies magnifica*), white fir (*A. concolor*)	Montane conifers

Table 3.2. Associations between bird occupancy and plant species that were significantly different between subregions. Letters indicate the subregions: C = central, E = eastern, N = northern, S = Sierra Nevada, W = western.

Species	Plant species	Pairs of subregions in which the difference was significant
Gray Flycatcher	Bitterbrush	C-N, N-E, W-N
	Willow	C-W
Dusky Flycatcher	Pinyon	C-E, W-E, S-E
	Rose	C-W
	Aspen	C-W, S-W
	Bitterbrush	C-S
	Rabbitbrush	C-S
	Willow	S-E, W-N
Warbling Vireo	Pinyon	C-E, C-W
	Juniper	N-E, C-N
	Aspen	C-S
	Rose	C-S, C-W, C-E
	Rabbitbrush	C-N
Mountain Chickadee	Juniper	N-E
	Aspen	C-W, C-S, C-E
House Wren	Pinyon	C-E, C-S
	Juniper	N-E, S-E
	Bitterbrush	C-N, C-S
	Mountain mahogany	C-S, S-N
Blue-gray Gnatcatcher	Pinyon	C-E, C-W
	Juniper	C-N, N-E
	Bitterbrush	C-W, W-E, S-W
	Aspen	S-W
	Willow	C-N, W-N
Cassin's Finch	Aspen	S-E
Chipping Sparrow	Pinyon	S-E
	Juniper	N-E, S-N, W-N
Brewer's Sparrow	Pinyon	C-E, C-S, N-E, W-E
	Bitterbrush	S-W
	Rabbitbrush	C-N, C-W
	Sagebrush	C-N
	Cottonwood	C-W
	Mountain mahogany	W-N
Dark-eyed Junco	Pinyon	C-S
	Juniper	C-N, N-E, S-N, W-N
	Rabbitbrush	C-S

	Cottonwood	C-W, S-W
	Aspen	C-W
	Willow	C-W
Green-tailed Towhee	Rabbitbrush	C-N, C-E, C-W, C-S
	Sagebrush	C-E, N-E, W-E, S-E
	Cottonwood	C-W
	Willow	C-N
Spotted Towhee	Willow	C-N, S-N
Yellow-rumped Warbler	Juniper	C-N, N-E, W-N
	Bitterbrush	C-E, S-E
	Rabbitbrush	C-S
	Desert peach	C-S

Table 3.3. Associations between bird occupancy and functional groups that were significantly different between subregions. Letters indicate the subregions: C = central, E = eastern, N = northern, S = Sierra Nevada, W = western.

Species	**Functional groups**	**Pairs of subregions in which the difference was significant**
Gray Flycatcher	Arid conifer Riparian tree	C-E, C-W, C-S C-W
Dusky Flycatcher	Arid conifer Riparian tree Riparian shrub Montane conifer	C-W, S-W C-E, C-W, C-S S-E, S-W W-E, S-W
Warbling Vireo	Riparian tree Montane conifer	C-W C-E, C-S, W-E, S-W
Mountain Chickadee	Low shrub Riparian tree Montane conifer	C-S C-S C-S, S-W, W-E
House Wren	Arid conifer	W-E
Blue-gray Gnatcatcher	Low shrub Arid conifer Riparian shrub Montane conifer	C-S C-E, C-W, N-E, S-E, S-W, N-W C-W, S-W S-E, S-W
Cassin’s Finch	Riparian tree Montane conifer	C-E S-W
Chipping Sparrow	Arid conifer Riparian shrub Montane conifer	C-N C-W, S-W S-W
Brewer’s Sparrow	Low shrub Arid conifer Riparian shrub Riparian tree Montane conifer	S-E, C-S, S-N C-W C-N, C-W, W-E, S-W, S-N C-S C-S
Dark-eyed Junco	Low shrub Arid conifer Montane conifer	C-N, C-S, N-E, S-N, S-W C-N, N-E, S-N, W-N C-N, C-S
Green-tailed Towhee	Low shrub Riparian shrub Riparian tree	C-N, C-S, S-N, S-W, S-E C-E, N-E, W-E C-E, W-E, S-E
Spotted Towhee	Low shrub Arid conifer Montane conifer	C-N, C-E, S-N N-E, S-W, W-N S-E
Yellow-rumped Warbler	Low shrub Montane conifer	C-S, S-E, S-W, S-N C-E, C-W, C-S

Table 3.4. Number and percentage of the 13 bird species for which associations with a given plant species or functional group differed significantly between at least two subregions.

	Number (percentage) of bird species
Limber pine	0
Willow	5 (38%)
Mountain mahogany	2 (15%)
Juniper	7 (54%)
Pinyon	7 (54%)
Cottonwood	3 (23%)
Aspen	6 (46%)
Rabbitbrush	6 (46%)
Desert peach	1 (7%)
Bitterbrush	6 (46%)
Rose	2 (15%)
Sagebrush	2 (15%)
Montane conifer functional group	10 (77%)
Riparian shrub functional group	5 (38%)
Riparian tree functional group	7 (54%)
Arid conifer functional group	8 (62%)
Low shrub functional group	7 (54%)

Table 3.5. Percentage of realized, significant differences in associations between bird occupancy and plant species (plain text) and functional groups (boldface) between subregions.

	Central	Western	Sierra Nevada	Eastern	Northern
Central	-				
Western	16, **13**	-			
Sierra Nevada	16, **17**	6, **18**	-		
Eastern	11, **11**	4, **8**	7, **10**	-	
Northern	15, **7**	8, **3**	6, **7**	11, **6**	-

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APPENDIX CHAPTER 1

Table 1.S1. All avian species modeled, and the Great Basin regions from which data were analyzed.

Scientific name	Common name	Great Basin regions
Selasphorus platycercus	Broad-tailed Hummingbird	Central
Contopus sordidulus	Western Wood-Pewee	Western
Empidonax oberholseri	Dusky Flycatcher	Central, western
Vireo gilvus	Warbling Vireo	Central, western
Poecile gambeli	Mountain Chickadee	Central, western
Psaltriparus minimus	Bushtit	Central
Troglodytes aedon	House Wren	Central, western
Setophaga petechia	Blue-gray Gnatcatcher	Central, western
Sialia currucoides	Mountain Bluebird	Central
Turdus migratorius	American Robin	Central, western
Haemorhous cassinii	Cassin’s Finch	Central, western
Spizella breweri	Brewer’s Sparrow	Central, western
Passerella iliaca	Fox Sparrow	Central, western
Contopus sordidulus	Vesper Sparrow	Central
Junco hyemalis	Dark-eyed Junco	Central
Melospiza melodia	Song Sparrow	Western
Pipilo chlorurus	Green-tailed Towhee	Central, western
Pipilo maculatus	Spotted Towhee	Central, western
Pheucticus melanocephalus	Black-headed Grosbeak	Western
Geothlypis tolmiei	MacGillivray’s Warbler	Central, western
Setophaga petechia	Yellow Warbler	Central, western
Setophaga coronata	Yellow-rumped Warbler	Western

Setophaga nigrescens	Black-throated Gray Warbler	Central, western
Piranga ludoviciana	Western Tanager	Western
Passerina amoena	Lazuli Bunting	Western

Table 1.S2. Watanabe-Akaike information criterion (WAIC) values for models of within-season dispersal of birds in the central Great Basin with good or moderate fit. Boldface indicates the lowest WAIC value.

Species	Availability covariates	Detection covariates	Intercept only	Availability and detection covariates
Broad-tailed Hummingbird	1127.9	1114.8	1127.6	**1093.3**
Dusky Flycatcher	2060.6	**2040**	2057.7	2042.6
Blue-gray Gnatcatcher	804.8	797.1	805.4	**787**
Vesper Sparrow	325.3	324.7	323.9	**320.2**
MacGillivray's Warbler	1509.1	1506.7	1508.9	**1492.2**
Yellow Warbler	**845.7**	863.1	856.1	853.1

Table 1.S3. Watanabe-Akaike information criterion (WAIC) values for models of within-season dispersal of birds in the western Great Basin with good or moderate fit. Boldface indicates the lowest WAIC value.

Species	Availability covariates	Detection covariates	Intercept only	Availability and detection covariates
Western Wood-Pewee	329.4	332.4	329.1	333.8
Warbling Vireo	637.7	**636.5**	**636.5**	641.4
Blue-gray Gnatcatcher	**288.8**	295.5	289	290.3
House Wren	445.8	447.3	**445.5**	449
Brewer’s Sparrow	606.4	607.3	614	**606.2**
Green-tailed Towhee	**1260.5**	1263.2	1260.6	1264.3
MacGillivray’s Warbler	**414.4**	419.2	414.5	424
Yellow Warbler	**200.7**	206.7	201.9	206.5

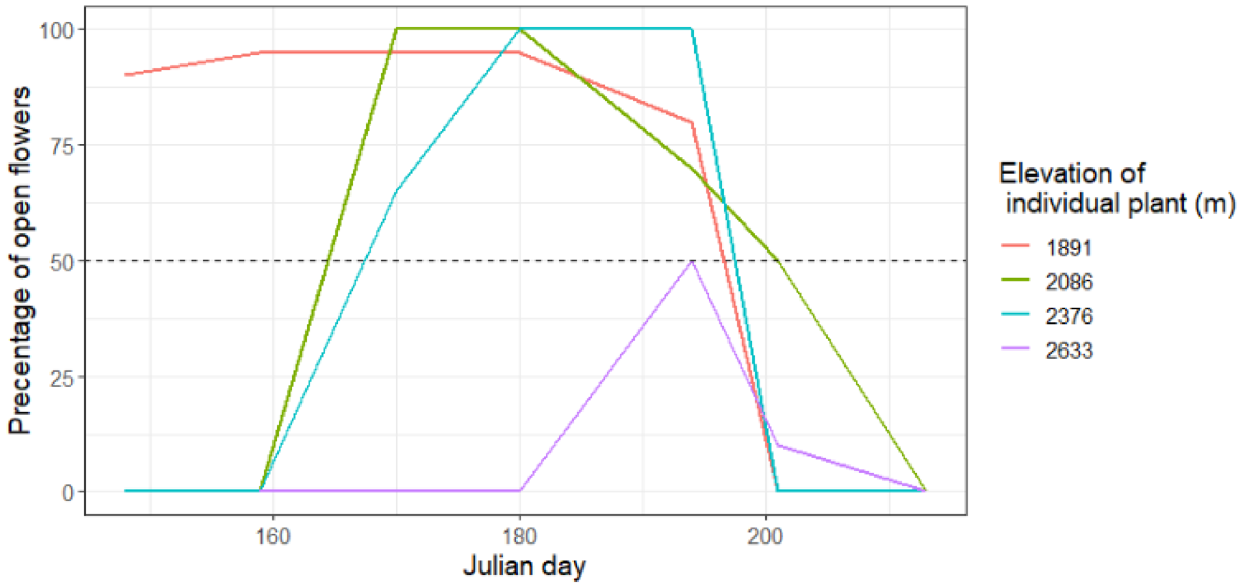

Figure 1.S1. The percentage of open flowers on four individual plants in Little Antelope Canyon in the western Great Basin in 2019. The dashed line represents 50% open flowers.

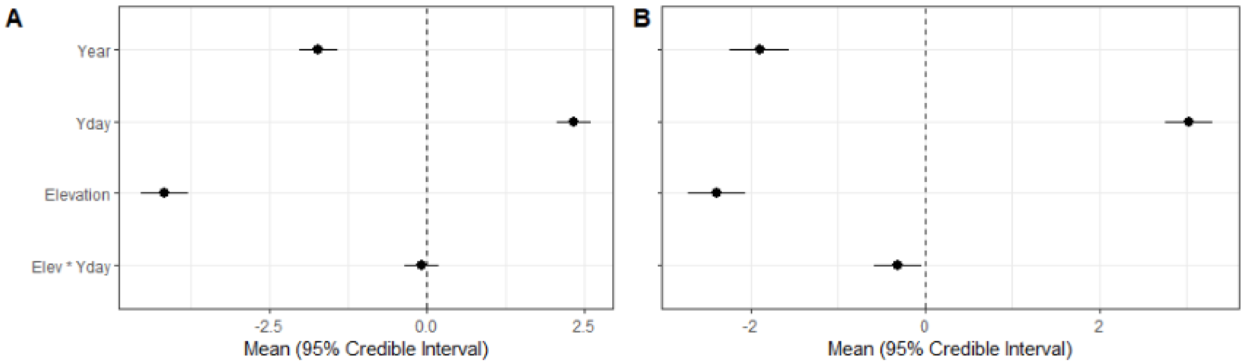

Figure 1.S2. Associations of year, Julian date (Yday), and elevation (Elev) with mean daily temperature in the western (A) and central (B) Great Basin.

APPENDIX CHAPTER 2

Table 2.S1. Association of variables with occupancy of breeding birds in the western Great Basin. n/a indicates that the model did not pass goodness of fit tests; results are not reported. *signifies that the elevational range of the species shifted. Precip., precipitation; temp., temperature; NDVI, normalized difference vegetation index. All values are mean, sd.

	Full elevational range				Lower edge				Upper edge			
Species	Spring precip.	Winter precip.	Spring temp.	NDVI	Spring precip.	Winter precip.	Spring temp.	NDVI	Spring precip.	Winter precip.	Spring temp.	NDVI
Western Wood-Pewee			-0.5, 1.5		-1.0, 0.4	-0.7, 0.4	-0.6, 0.4					
Dusky Flycatcher		-0.5, 0.2			n/a	n/a	n/a	n/a		-0.5, 0.4	-0.7, 0.5	
Warbling Vireo*	-0.5, 0.2			1.03, 0.3	-1.4, 0.4							0.9, 0.5
Mountain Chickadee	-1.2, 0.2			2.3, 0.6	-1.6, 0.5			1.5, 0.6	-0.8, 0.5			0.9, 0.7
Bushtit*									n/a	n/a	n/a	n/a
House Wren*	0.4, 0.2			0.9, 0.3		-0.5, 0.4		1.6, 0.5				
American Robin			0.5, 0.3	1.0, 0.4	-0.9, 0.4	0.6, 0.4	0.7, 0.5	1.0, 0.5				

Cassin’s Finch	-0.4, 0.2	-0.5, 0.2		1.4, 0.3	-1.8, 0.6						-0.7, 0.5	1.0, 0.6
Brewer’s Sparrow		-0.5, 0.2	-0.9, 0.2	-0.9, 0.4							-1.3, 0.5	-0.7, 0.5
Fox Sparrow				1.1, 0.4	n/a	n/a	n/a	n/a		-0.7, 0.4		
Chipping Sparrow					n/a	n/a	n/a	n/a		-0.8, 0.6		
White-crowned Sparrow					n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Dark-eyed Junco*				1.7, 0.3	-1.1, 0.4			1.4, 0.5				1.1, 0.7
Song Sparrow	0.6, 0.2				n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Green-tailed Towhee				-1.1, 0.3	-0.8, 0.4		0.7, 0.4					
Spotted Towhee	-1.2, 0.2	0.6, 0.4							-0.8, 0.4		0.8, 0.5	-0.8, 0.5
Black-headed Grosbeak*	-0.8, 0.4							-0.8, 0.5				
MacGillivray’s Warbler				0.9, 0.3				1.5, 0.5	-0.8, 0.4			
Yellow Warbler		0.8, 0.3			-0.8, 0.7							

Yellow-rumped Warbler	-1.0, 0.2			2.2, 0.4	-1.2, 0.5			1.7, 0.6			-0.8, 0.6	
Black-throated Gray Warbler					-1.0, 0.6		0.9, 0.6					
Western Tanager				1.5, 0.3	-1.1, 0.4			0.2, 0.4	n/a	n/a	n/a	n/a
Lazuli Bunting*									n/a	n/a	n/a	n/a
Steller’s Jay	-1.1, 0.2				-1.4, 0.4		0.9, 0.5	1.3, 0.5	n/a	n/a	n/a	n/a

Table 2.S2. Association of variables with occupancy of breeding birds in the central Great Basin. n/a indicates that the model did not pass goodness of fit tests; results are not reported. *signifies that the elevational range of the species shifted. Precip., precipitation; temp., temperature; NDVI, normalized difference vegetation index. All values are mean, sd.

	Full elevational range				Lower edge				Upper edge			
Species	Spring precip.	Winter precip.	Spring temp.	NDVI	Spring precip.	Winter precip.	Spring temp.	NDVI	Spring precip.	Winter precip.	Spring temp.	NDVI
Broad-tailed Hummingbird*				0.5, 0.4		-0.4, 0.2		0.9, 0.3	n/a	n/a	n/a	n/a
Dusky Flycatcher		-0.3, 0.1		0.9, 0.1					0.3, 0.2		-0.4, 0.1	1.3, 0.4
Gray Flycatcher*	-0.3, 0.2					-0.6, 0.2			n/a	n/a	n/a	n/a
Warbling Vireo	0.3, 0.1		-0.4, 0.1	0.8, 0.2	0.4, 0.2		-0.4, 0.2					
Mountain Chickadee*	-0.5, 0.1	-0.4, 0.1			-0.3, 0.2	-0.7, 0.2			-0.5, 0.2			
Bushtit									n/a	n/a	n/a	n/a
Rock Wren*	0.3, 0.3	0.8, 0.3		-0.7, 0.2	0.3, 0.2		0.7, 0.2	-0.9, 0.3			0.9, 0.3	-0.9, 0.3
Blue-gray Gnatcatcher	n/a	n/a	n/a	n/a					n/a	n/a	n/a	n/a
Mountain Bluebird*		-0.2, 0.1								-0.9, 0.3		-1.0, 0.4
American Robin		0.2, 0.5					0.4, 0.2	0.9, 0.3				1.1, 0.4
Cassin’s Finch		0.4, 0.1		0.5, 0.2			0.7, 0.3					0.6, 0.4

Brewer's Sparrow*						-0.7, 0.2	0.3, 0.2					
Vesper Sparrow*	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a		-0.3, 0.2		
Chipping Sparrow*				0.4, 0.1				0.6, 0.3			-0.5, 0.3	
Green-tailed Towhee							0.2, 0.1				0.2, 0.1	
Spotted Towhee*				0.7, 0.1	-0.4, 0.1		-0.2, 0.2	1.0, 0.30				
MacGillivray's Warbler*				1.2, 0.2		-0.3, 0.2		0.9, 0.4				
Yellow Warbler*	n/a	n/a	n/a	n/a					n/a	n/a	n/a	n/a
Yellow-rumped Warbler				1.4, 0.2	n/a	n/a	n/a	n/a		-0.5, 0.2	0.4, 0.2	1.8, 0.5
Black-throated Gray Warbler*				0.7, 0.2								
Northern Flicker*			0.4, 0.2	0.8, 0.2	-0.3, 0.2			0.9, 0.3	-0.4, 0.2	0.7, 0.3		1.5, 0.3
Lazuli Bunting*	n/a	n/a	n/a	n/a	0.4, 0.2				n/a	n/a	n/a	n/a
Woodhouse's Scrub-Jay						0.3, 0.2		0.6, 0.3	n/a	n/a	n/a	n/a

APPENDIX CHAPTER 3

Table 3.S1. Mean occupancy of bird species across the Great Basin and in each subregion.

Species	**Great Basin**	**Central**	**Western**	**Sierra Nevada**	**Northern**	**Eastern**
Gray Flycatcher	0.26	0.39	0.01	0.00	0.52	0.34
Dusky Flycatcher	0.45	0.43	0.13	0.76	0.64	0.64
Warbling Vireo	0.13	0.09	0.14	0.24	0.05	0.17
Mountain Chickadee	0.61	0.63	0.63	0.82	0.02	0.43
House Wren	0.05	0.03	0.10	0.12	0.33	0.06
Blue-gray Gnatcatcher	0.11	0.12	0.29	0.01	0.11	0.30
Cassin's Finch	0.63	0.69	0.28	0.61	0.49	0.15
Chipping Sparrow	0.27	0.29	0.10	0.10	0.50	0.76
Brewer's Sparrow	0.30	0.31	0.24	0.18	0.69	0.12
Dark-eyed Junco	0.10	0.06	0.30	0.66	0.06	0.09
Green-tailed Towhee	0.83	0.84	0.95	0.75	0.75	0.80
Spotted Towhee	0.57	0.64	0.31	0.96	0.05	0.51
Yellow-rumped Warbler	0.13	0.1	0.01	0.71	0.00	0.47
Mean	**0.34**	**0.36**	**0.27**	**0.46**	**0.32**	**0.37**

Table 3.S2. Czekanowski's similarity of avian species composition among subregions of the Great Basin.

	Central	Western	Sierra Nevada	Eastern	Northern
Central	-				
Western	48%	-			
Sierra Nevada	47%	57%	-		
Eastern	52%	54%	42%	-	
Northern	60%	44%	48%	57%	-

Table 3.S3. Czekanowski's similarity of tree and shrub composition among subregions of the Great Basin.

	Central	Western	Sierra Nevada	Eastern	Northern
Central	-				
Western	54%	-			
Sierra Nevada	47%	62%	-		
Eastern	43%	60%	60%	-	
Northern	35%	53%	47%	67%	-