

Shifts in elevational distributions of montane birds in a temperate, arid ecosystem

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January 30, 2023

Abstract

Montane species are generally predicted to respond to climate change via upslope movement. In birds, these potential elevational range shifts have primarily been examined in tropical regions. Although desert bird species may be at the edge of their aridity tolerances, elevational range shifts of desert bird species rarely have been studied. Here, we examine shifts in the elevational distributions of breeding birds from two regions of the Great Basin, a desert in the western United States, over 10 to 20 years. We collected data annually from 2001-2020, a relatively long time series that is uncommon in research on distributional shifts. We used single-species occupancy models of 32 bird species to examine elevational shifts at three extents: the full elevational gradient (1650-3200 m) and the lowest and highest edges (25%) of the gradient. We then conducted simulations to test whether population stochasticity could confound inferences about shifts. We examined whether temperature, precipitation, and primary productivity (normalized difference vegetation index) were associated with occupancy and shifts. The elevational distributions of 19 species shifted, and simulations indicated that shifts in the distributions of 12 species were unlikely to be stochastic. The three shifts along the full elevational gradient were downslope, and the majority of distributional shifts occurred at the elevational range edges. Occupancy of 10 species with elevational distributions that shifted was associated significantly with precipitation, and 8 of those associations were negative. Although we found that climate changed considerably even over the short temporal extent of our study, our results suggested that this community of desert birds is relatively resilient to the direct effects of climate change.

Introduction

Changes in elevational distributions of diverse taxonomic groups are occurring globally, with the potential to reshape ecological communities, alter ecosystem function, and affect climate (Pecl et al. 2017). Given that temperature generally decreases by 0.6°C per 100 m increase in elevation (Barry 2008), and the assumption that species distributions are limited by temperature, a dominant paradigm suggests that montane animals and plants will move upslope in response to climate change (Martin 2001, McNab 2003). Theories of upslope elevational shifts in multiple taxonomic groups are often supported by field data (Chen et al. 2011, Freeman et al. 2018). However, in many instances, populations and species are not moving in synchrony with warming temperatures and either have not shifted or shifted downslope (Tingley et al. 2012, Campos-Cerqueira et al. 2017, DeLuca and King 2017, Freeman et al. 2018). The interacting effects of temperature, precipitation, and other climatic variables could lead to large variation in interspecific or intraspecific responses to climate change (Tingley et al. 2012). The direct or indirect effects of land use may further lead to unpredictable shifts in species' distributions (Fleishman and Murphy 2012).

Understanding mechanisms of elevational range shifts is complicated by the fact that climate variables are not changing uniformly across elevational gradients. For example, in some cases, high elevations are warming

more rapidly than low elevations (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). Theoretically, differences in rates of climate change along elevational gradients may result in larger distributional shifts at the upper edges than at the lower edges of a species' elevational distribution. Additionally, biotic interactions, especially competition, may be stronger at lower distributional limits, stabilizing distributions at the lower edge (Alexander et al. 2015). Conversely, high-elevation taxa often have greater thermal tolerance than low-elevation taxa, proportional to the magnitude of seasonal and diel thermal variation at high elevations (Janzen 1967, Deutsch et al. 2008). High-elevation species' physiology may therefore result in relatively small elevational range shifts.

Birds, especially long-distance migrants, are highly vagile, and can track microhabitats within and across years (Greenwood and Harvey 1982, Cline et al. 2013, Gow and Stutchbury 2013). Elevational range shifts of birds have primarily been examined in tropical regions, as species richness and endemism of birds often is concentrated in tropical mountains. Tropical species are generally more physiologically sensitive to temperature than temperate species, and the extent of temperature tracking may be stronger in tropical than in temperate bird species (Pollock et al. 2020, Freeman et al. 2021). However, temperate regions are warming at a faster rate than tropical regions (Friedman et al. 2013), and research on the effects of climate change on non-tropical montane species is essential to understanding how elevational shifts may affect global responses to climate change. Recent research on bird species in North America has identified a variety of elevational shifts. The distributions of 84% of avian species in the Sierra Nevada that were documented by Grinnell in the early 1900s shifted over the past 100 years, with 51% of species moving upslope and 49% moving downslope (Tingley et al. 2012). Over 16 years, 9 of 16 low-elevation passerine species in the northern Appalachian Mountains 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). In the Adirondack Mountains, repeat surveys found that abundance-weighted mean elevational distributions of 42 species shifted upslope by 83 m over 40 years, with shifts observed at the both the upper and lower elevational range edges (Kirchman & Van Keuren 2017). Although elevational shifts in temperate bird communities appear to be more variable than those in tropical communities (Freeman et al. 2021), sizable yet unexplained variation among species is apparent in both temperate and tropical regions.

Mechanisms of elevational range shifts in birds are difficult to investigate, in part due to data or sampling constraints. Particularly among resurveys of historical sampling locations, variation in distribution or abundance between two time points can impede strong inferences (Sparks and Tryjanowski 2005, McCain et al. 2016). In general, upslope shifts are attributed to the direct and indirect effects of climate change, such as changes in the composition of plant species, plant phenology, or primary productivity (Morison and Morecroft 2006, Lenior et al. 2008, Amano et al. 2010). Downslope shifts in bird populations are often attributed to changes in the predator community or other shifts in interspecific competition (Lenoir et al. 2010). Theorized mechanisms of stable population distributions include temporal lags in species' responses to climate and land-use changes, stochastic fluctuations in population size, and small magnitudes of climate change (Parmesan et al. 2005, Tingley and Bessinger 2009, McCain et al. 2016).

However, if variability in population size is high, upslope or downslope changes in occupancy may reflect stochastic fluctuations. For example, stochastic increases in population size may lead individuals to colonize unoccupied locations, whereas population declines may result in vacant lower-quality habitat (Thomas and Lennon 1999). Annual variability in abundance may be especially high at the edges of species' elevational distributions (McCain et al. 2016). Therefore, accounting for population fluctuations is necessary to detect a deterministic distributional shift. Population fluctuations can be identified through long-term data, which can capture annual oscillations that often are undetectable in studies comparing two time points, and by inclusion of tests for population variability in statistical analysis.

We examined whether the elevational distributions of two communities of birds in the Great Basin are shifting. The Great Basin is a cold desert characterized by extensive sagebrush shrubsteppe and variable topography. We are aware of few studies that examined shifts in the elevational distributions of birds in arid

ecosystems (Iknayan and Bessinger 2020), where species may be at the edges of both their thermal and xeric tolerances. We examined data from long-term, nearly continuous avian point-count surveys in two regions of the Great Basin to explore potential mechanisms of the shifts. These data span a considerably larger area (>100 km) and greater number of elevational transects (35), and characterize annual variability in occupancy more rigorously, than most resurveys of birds and other taxonomic groups (e.g., Moritz et al. 2008, Tingley et al. 2012). We used single-species occupancy models of 32 species to examine elevational movement at three spatial extents: the full elevational gradient and the lowest and highest 25% of the elevational gradient. Additionally, we examined the effects of temperature, precipitation, and primary productivity on single-species occupancy and elevational movement.

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). We collected data in 35 canyons in these six mountain ranges. The elevation gradient of our study canyons collectively ranged from 1650 to 3200 m. Our study areas generally are not used for agriculture and have little infrastructure, such as roads and buildings, which can greatly affect faunal composition and movement (Fahrig et al. 2009, Theobald et al. 2012, Clucas and Marzluff 2015), allowing for greater confidence in attributing changes in species' elevational distributions to climate change.

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, especially summer (Tang and Arnone 2013, Snyder et al. 2019). 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 1951–2013, 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 when minimum temperatures are above 0°C (implying 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).

Field data

We sampled breeding birds with eight-minute, 100-m fixed-radius point counts from late May through early July. 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 for 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. We excluded fledglings and juveniles from analyses.

We extracted daily minimum temperature and daily precipitation at each 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) to estimate primary productivity at each point (Wang et al. 2004). 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 annual maximum NDVI value at the centroid of each survey point from 1 March–30 June from the Application for Extracting and Exploring Analysis Ready Samples (AppEARS) database (<https://lpdaacsvc.cr.usgs.gov/appears/>). AppEARS derives NDVI from images captured every 16 days at 250 m resolution by the Moderate Resolution Imaging Spectroradiometer (MODIS).

Analyses

We modeled detection-weighted, single-species occupancy (MacKenzie et al. 2002, Royle and Nichols 2003) in a Bayesian framework in the western and central Great Basin separately. 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 included data from all points sampled along the full elevational gradient. The second and third examined occupancy in the lowest and highest 25% (*lower and upper edges*) of the gradient. The three models had the same formulation and covariates. All continuous covariates were scaled and centered around zero. 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, which did not converge when indicator variable selection was applied.

We modeled detection probability as

$$C_{ijk} \sim \begin{cases} \text{Bernoulli}(p_{ijk}) & \text{if } Z_{ik} = 1 \\ 0 & \text{if } Z_{ik} = 0 \end{cases}$$

$$\text{logit}(p_{ijk}) = \beta_1 + \beta_2 * jday_{ijk} + \beta_3 * time_{ijk} + \beta_4 * time^2_{ijk} + \alpha_1 * observer_{ijk}$$

$$\alpha_1 \sim \text{Normal}(0, \tau_1)$$

$$\tau_1 \sim \text{Uniform}(0, 5),$$

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 a species given its presence. We used a logit link function to model four detection covariates: Julian date ($jday$), time of day and its quadratic transformation, and a random, observer-level effect. β_1 is the mean point-level detection probability for a given species, and α_1 is a random effect of observer identity on detection, with a mean of 0 and a precision of τ_1 .

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 :

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

$$\text{logit}(\psi_{ik}) = \beta_5 + \beta_6 * \mathbf{X}_{ik} + \alpha_2 * point_{ik} + \alpha_3 * canyon_{ik}$$

$$\alpha_2 \sim \text{Normal}(0, \tau_2)$$

$$\tau_2 \sim \text{Uniform}(0, 1)$$

$$\alpha_3 \sim \text{Normal}(0, \tau_3)$$

$$\tau_{3} \sim \text{Uniform}(0, 1)$$

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. X_{ik} represents the vector of covariate values at point i in year k . 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 its posterior density estimate 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. a_2 is a point-level random effect with a mean of 0 and precision of τ_{2} , and a_3 is a canyon-level random effect with a mean of 0 and precision of τ_{3} . We used vague prior distributions for intercepts, covariates, and random effects. All covariates were centered and scaled.

We conducted simulations to test whether species' elevational distributions shifted linearly over time or were consistent with stochastic processes, such as random chance or population variability. For each species for which a significant interaction was included in the best model, we constructed a null distribution for the time trend by randomly permuting the year variable in 100 copies of the dataset. The model previously identified as best was estimated on these simulated data sets. We then conducted a two-tailed test of whether the estimated mean of (year x elevation) in each simulation was greater than the absolute value of the estimate from the original model. For example, if the estimated effect of year x elevation on occupancy was 0.65, we determined the percentage of simulations in which the mean estimate of the interaction term was greater than 0.65 or less than -0.65. We would expect >90% of simulations to include a mean estimate that was equal to or greater than the absolute value of the observed estimate if the effect was not a product of stochasticity.

We implemented all 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 $R_{\text{hat}} < 1.15$ (Gelman and Hill 2007). No pairs of candidate covariates 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 0.15.

We implemented a simple linear model of 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 distance that the species' distribution shifted over the survey period, which was not possible to estimate from the results of the occupancy model. 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 included a point-level random effect and modeled all variables as a function of elevation, year, and their interaction.

Results

Our original models suggested that the elevational distributions of 19 of the 32 species shifted (Tables S1-S4). Simulations indicated high confidence that the shifts of 12 species were not an artifact of stochasticity (Table S5 and S6). Further discussion focuses on these 12 species.

In the western Great Basin, the elevational distributions of four species shifted. 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 1). At the lower edge of the elevational gradient, the distributions of three species, including two that shifted along the full elevational gradient, changed. Warbling Vireo (*Vireo gilvus*) shifted upslope, whereas House Wren and Lazuli Bunting shifted downslope (Table 1, Figure 2). At the upper edge of the elevational gradient, the distribution of House Wren shifted downslope.

In the central Great Basin, no species shifted along the full elevational gradient. However, movement at the edges of the elevational ranges was relatively common. At the lower edge of the elevational gradient, five species' distributions changed. Brewer's Sparrow (*Spizella breweri*) and Lazuli Bunting shifted upslope, whereas Broad-tailed Hummingbird (*Selasphorus platycercus*), Mountain Chickadee (*Poecile gambeli*), and Northern Flicker (*Colaptes auratus*) shifted downslope (Table 2, Figure 3). 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. At the upper edge of the elevational gradient, the elevational distributions of five species changed. Mountain Chickadee, Rock Wren (*Salpinctes obsoletus*), and Vesper Sparrow (*Poocetes gramineus*) shifted upslope, whereas Mountain Bluebird (*Sialia currucoides*) and Spotted Towhee (*Pipilo maculatus*) shifted downslope (Table 2, Figure 3).

The average distance moved was smaller at elevational edges than along the full gradient. In the western Great Basin, the absolute value of the average elevational shift across the full elevational gradient was 119 m, compared to 50 m at the lower edge and 59 m at the upper edge (Table 1). In the central Great Basin, the absolute value of the average elevational shift was 33 m at the lower edge and 48 m at the upper edge (Table 2).

Irrespective of distributional shifts, many of the associations between bird occupancy and temperature or precipitation were statistically significant, and this information is relevant to understanding species' responses to climate variables. However, given that the effect of elevation on temperature or precipitation did not change through time (e.g., higher elevations do not seem to be warming faster than lower elevations, or receiving more or less precipitation through time), these associations should not necessarily be interpreted as drivers of the observed distributional shifts. Occupancy of 10 of the 12 species with elevational distributions that shifted was significantly associated with winter or spring precipitation (Tables 1 and 2). Spring temperature was associated with shifts of 2 of the 12 species, and NDVI was associated with shifts of 5 of those species. Only occupancy of Spotted Towhee in the central Great Basin and Lazuli Bunting in the western Great Basin was not significantly associated with any of those four variables. Both associations with spring temperature were positive. In all but two cases (House Wren in the western Great Basin and Lazuli Bunting in the central Great Basin), the association with precipitation was negative. NDVI was significantly related to occupancy of House Wren in the western Great Basin both across the full elevational gradient and within the lower edge (positive association; Table 1), and with occupancy of four species in the central Great Basin (two positively and two negatively; Table 2).

Over the study period, spring temperature, winter precipitation, and spring precipitation increased significantly in both the western and central Great Basin (Figure 4). NDVI also changed, but not in a uniform manner. In the western Great Basin, NDVI was negatively associated with the interaction of year and elevation, whereas in the central Great Basin, the association was the opposite (Figure 4); both effects were small. Over time, NDVI decreased as elevation increased in the western Great Basin, and slightly increased with elevation in the central Great Basin.

Discussion

Our results add to a growing body of evidence that many temperate bird species are not consistently shifting upslope as climate changes. Elevational distributions of bird species in the western and central Great Basin shifted in a variety of ways, with a greater number of distributional shifts occurring at the edges of the elevational gradient than along the full gradient. All three distributional shifts along the full elevational gradient were downslope. Our results also illustrate the importance of assessing population variability in conjunction with range shifts. In 7 of 19 cases, what initially appeared to be a deterministic elevational shift is likely attributable to stochasticity. Although bird occupancy was strongly associated with climate variables, there was little consistency between an elevational shift and temporal changes in temperature, precipitation, or primary productivity. The duration of our time-series data was relatively short, but comparable to other studies of elevational shifts (Campos-Cerqueira et al. 2017, DeLuca and King 2017), and indicated considerable plasticity in elevational distributions.

Our simulations explicitly tested whether the linear effect of year was driving significant interactions between year and elevation, which we interpreted as evidence of elevational shifts. Although we did not collect demographic data, we found that observed shifts of seven species could reflect stochastic changes in temporal and elevational occupancy. There are two main reasons why a significant interaction term in the original model might not be consistent with simulation results. First, mean occupancy at high or low elevations might differ between the latest and earliest years, in effect driving a linear trend. Second, annual mean occupancy of some species is highly variable, and the apparent linear trend may have been coincidental. Annual variability in abundance or occupancy of passerines can be caused by factors including conditions at overwintering grounds, cyclic weather events, or variable migration mortality. Population dynamics are rarely considered in studies of distributional shifts, but likely influence the accuracy of detected shifts (McCain et al. 2016).

Among the environmental variables we examined, only NDVI changed over both time and elevation. This may be due to the resolution at which the climate variables and NDVI were measured. Because the resolution of the climate variables was 4 km, some of our survey points within a canyon fell within the same pixel. By contrast, because the resolution of the NDVI data was 250 m, each survey point had a unique value, allowing for finer-resolution changes in NDVI to be captured in our analysis. Additionally, 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 canyons are prone to temperature inversions (Curtis et al. 2014, Rupp et al. 2020). As a result, microclimate in areas with complex topography may be unpredictable, and short-distance movements may be sufficient for birds to access microclimates favorable for feeding, mating, or nesting.

The majority of observed elevational shifts occurred at range edges. Distributional shifts may be more common at elevational edges than along the full elevational gradient due to higher rates of climate change at higher elevations and reduced competition at lower elevations (Alexander et al. 2015). In our study system, plant phenology at higher elevations can be 21 days later than at lower elevations (Zillig, unpublished manuscript). As climate change results in increasing temperatures and earlier snowmelt, birds may shift upslope to take advantage of habitat that is becoming available earlier in the breeding season, resulting in changes in species-level occupancy. For example, Rock Wren and Vesper Sparrow, both of which nest on the ground, moved upslope at the upper edge of their elevational ranges. Individuals may have dispersed into nesting habitat that previously was covered in snow or did not green up until late in the breeding season.

At the lower range edges, elevational movement may be driven by downslope expansion of riparian vegetation. About 60–70% of the vertebrate species native to the Great Basin, including most of the birds that breed in the region, are associated with riparian areas (Brussard et al. 1998, Poff et al. 2011). NDVI significantly increased during the time span of our study, with NDVI at higher elevations increasing faster in the central Great Basin and NDVI at lower elevations increasing faster in the western Great Basin (Figure 4). The primary productivity and extent of riparian areas may be expanding in some parts of the Great Basin in response to greater water-use efficiency as concentrations of carbon dioxide increase, especially where the intensity of livestock grazing is decreasing, as it is in our study system (Dwire et al. 2018, Fesenmyer et al. 2018, Albano et al. 2020). In the western Great Basin, species that nest in riparian vegetation, such as Lazuli Bunting and House Wren, may be moving downslope in response to expansion of that nesting habitat at the lower edge of their elevational ranges.

In all but two of the 13 instances in which winter or spring precipitation was significantly associated with occupancy, the association was negative (Tables 1 and 2). In general, one would expect bird communities in arid ecosystems to respond positively to increased precipitation, as many species may be limited by water availability (Bolger et al. 2005, Riddell et al. 2019). Our counterintuitive result may be explained by climate change-driven changes in precipitation across the Great Basin. Increased winter and spring precipitation across much of the western United States, including the Great Basin (Chambers 2008), is driven in part by increasingly severe storms (Xue et al. 2017), which could affect birds adversely. Increases in precipitation also may have delayed the breeding season or decreased survival or reproduction, leading to a decrease in

occupancy (Kozlovsky et al. 2018, Zuckerberg et al. 2018). Moreover, the proportion of precipitation that falls as rain rather than as snow is increasing, resulting in decreases in snow depth, earlier snowmelt, and water inputs to the soil becoming earlier and more sporadic (Abatzoglou and Kolden 2011, Petersky and Harpold 2018).

Our inferences might be biased if the elevational gradient we surveyed did not encompass species' full elevational distributions 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 S1 and S2). Of the 32 bird species we examined, the elevational ranges of 12 appeared to shift. With the exception of a 194 m downslope shift by Lazuli Bunting in the western Great Basin, the shifts were less than 100 m. The breeding ranges of all species examined extend beyond our study system. We acknowledge that the bird populations we examined may be responding to climate change differently than populations in wetter, less topographically diverse systems, and do not suggest that population-level responses we observed are necessarily indicative of species-level responses.

Although temperature and precipitation changed considerably even over the 10-20 years of our study, few elevational shifts were significantly related to temperature. Diel temperature in our study canyons during the breeding season is highly variable: day and night differ by as much as 19°C (M. Zillig unpublished data). We suspect that Great Basin bird populations have relatively broad thermal tolerances, consistent with higher tolerances of temperate than tropical bird species to high and low temperatures after controlling for body mass and experiential humidity (Pollock et al. 2020). The elevational shifts that we observed were relatively rapid. The lack of consistent associations between elevational shifts and temperature or precipitation suggest that birds may be responding to elements of habitat that are indirectly associated with our measured variables or with those that we did not measure, such as competition or quantity and quality of food.

We are aware of no other studies that examine elevational range shifts in arid bird populations. Our results reinforce that not only are responses to climate species-specific, but birds respond to numerous and compounded types of environmental change. Great Basin bird populations may be responding to climate change through shifts within the 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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Table 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 (interaction), >90% of the posterior density of the interaction was above or below zero, and simulations indicated that the interaction was likely not a product of stochasticity (see Supporting Information, Tables 1 and 3).

	Full elevational gradient	Full elevational gradient	Full elevational gradient	Lower edge	Lower edge	Lower edge	Upper edge	Upper edge	Upper edge
Species	Interaction (mean, SD)	Estimated shift in m (95% CI)	Significant variables (mean, SD)	Interaction (mean, SD)	Estimated shift in m (95% CI)	Significant variables (mean, SD)	Interaction (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)			
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)	
Black-headed Grosbeak	-0.88, 0.37	-65 (-221, 91)	Spring precipitation (-0.78, 0.35)						
Lazuli Bunting	-0.54, 0.18	-194 (-471, 84)		(-0.84, 0.48)	45 (-92, 183)				

Table 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 (interaction), >90% of the posterior density of the interaction was above or below zero, and simulations indicated the interaction was

likely not a product of stochasticity (see Supporting Information, Tables 2 and 4). No shifts occurred along the full elevational gradient.

	Lower edge	Lower edge	Lower edge	Upper edge	Upper edge	Upper edge
Species	Interaction (mean, SD)	Estimated shift in m (95% CI)	Significant variables (mean, SD)	Interaction (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)			
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)
Spotted Towhee				(-0.43, 0.17)	-16 (-74, 42)	
Lazuli Bunting	0.58, 0.19	31 (-11, 72)	Spring precipitation (0.4, 0.18)			

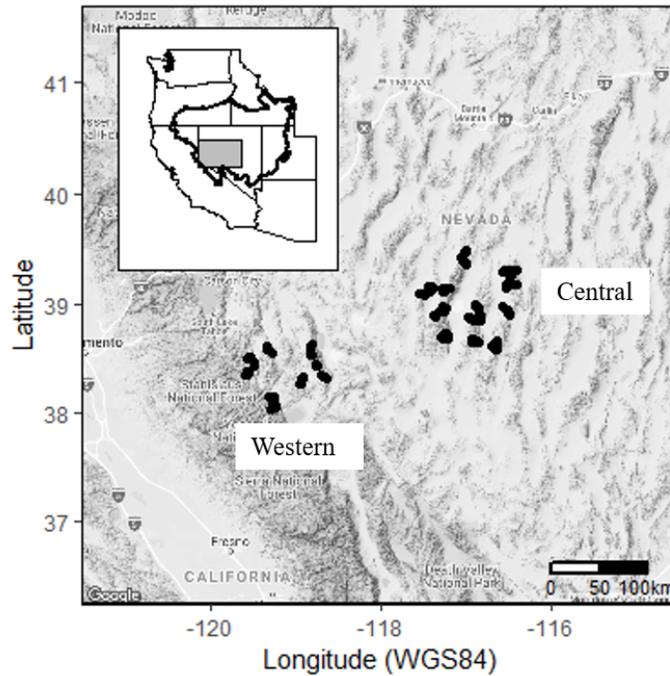


Figure 1. Locations at which we collected point-count data in the western and central Great Basin. Inset: Great Basin (thick black line) and the approximate boundaries of our study area (grey rectangle).

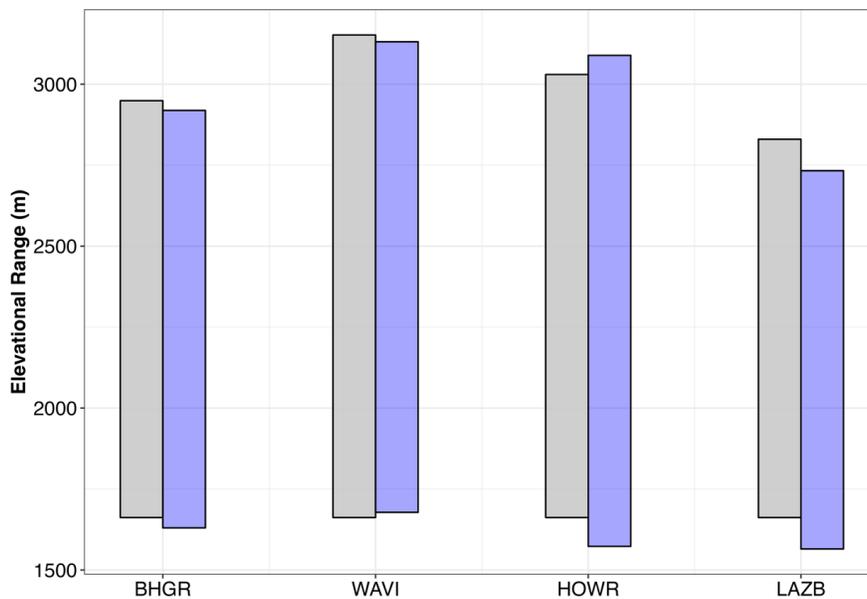


Figure 2. Shifts in elevational distributions of breeding birds in the western Great Basin, 2012–2020. Light blue bars indicate the observed range shift. Grey bars represent the elevational range over which we detected each species. BHGR, Black-headed Grosbeak; WAVI, Warbling Vireo; HOWR, House Wren; LAZB, Lazuli Bunting.

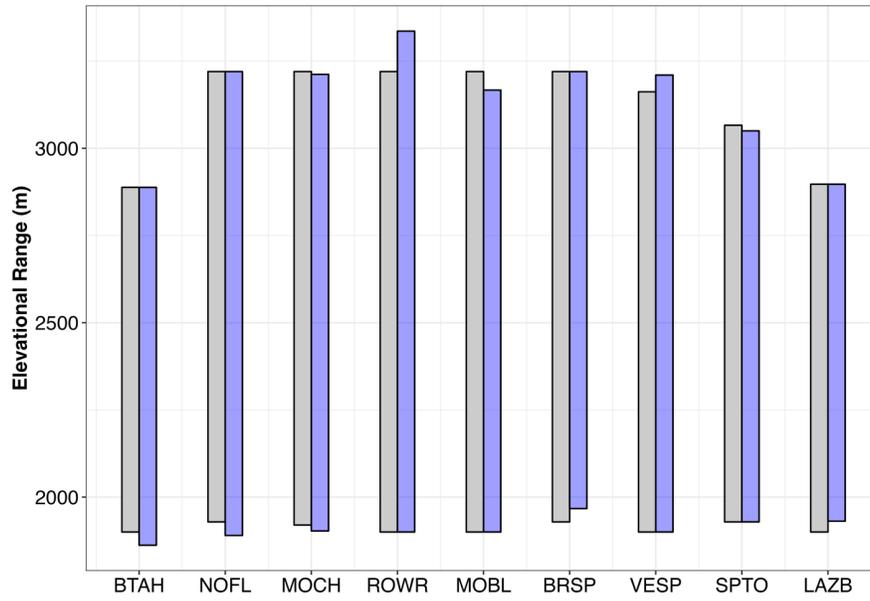


Figure 3. Shifts in elevational distributions of breeding birds in the central Great Basin, 2001–2020. Light blue bars indicate the observed range shift. Grey bars represent the elevational range over which we detected each species. BTAH, Broad-tailed Hummingbird; NOFL, Northern Flicker; MOCH, Mountain Chickadee; ROWR, Rock Wren; MOBL, Mountain Bluebird; BRSP, Brewer’s Sparrow; VESP, Vesper Sparrow; SPTO, Spotted Towhee; LAZB, Lazuli Bunting.

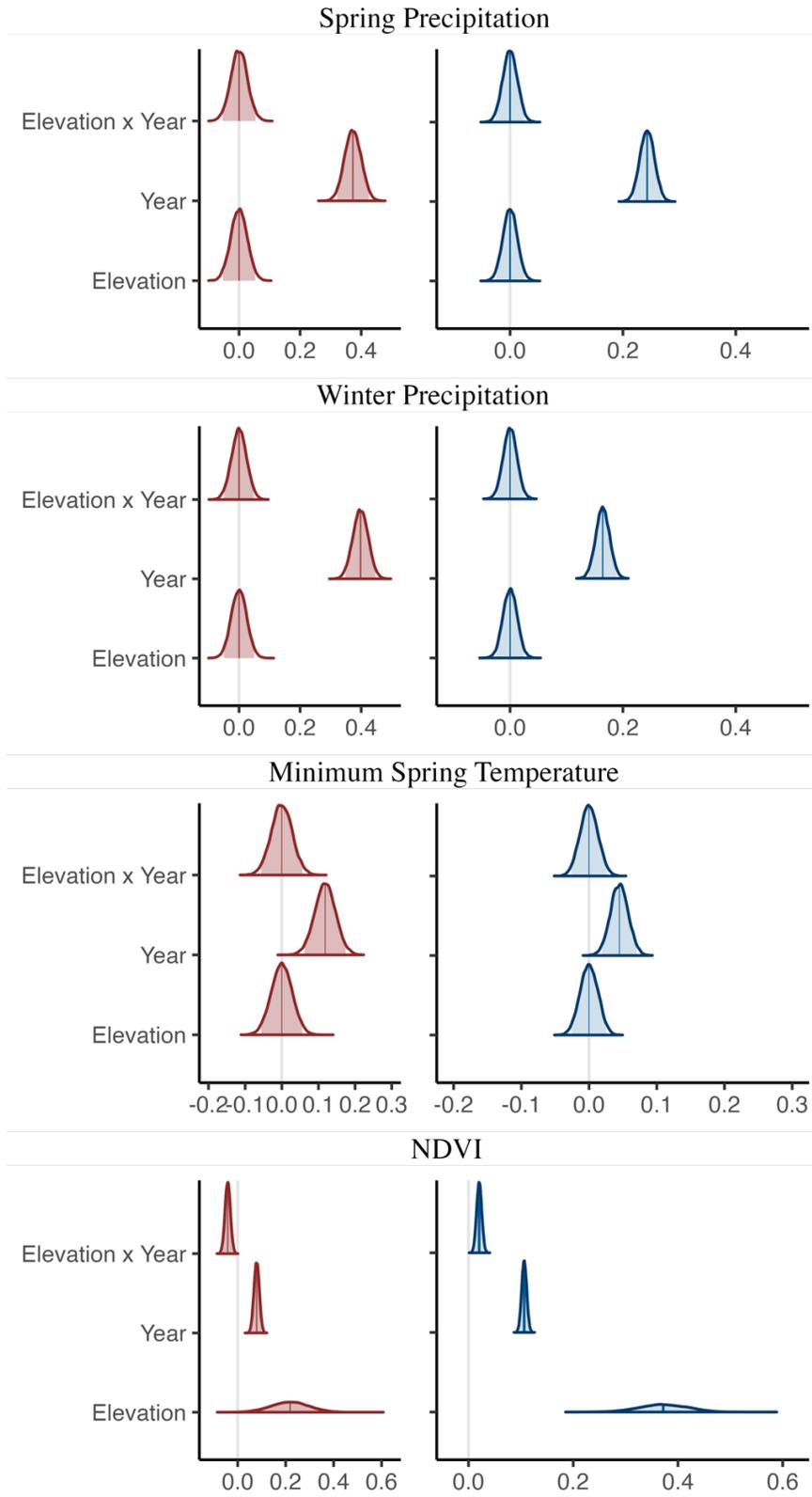


Figure 4. Posterior density estimates of the effects of year, elevation, and the interaction of year and elevation on total spring precipitation, total winter precipitation, minimum spring temperature, and the normalized difference vegetation index (NDVI) in the western Great Basin (red) and central Great Basin (blue).