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Research article

Shifts in elevational distributions of montane birds in an arid ecosystem

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Montane species are generally predicted to respond to climate change via upslope movement. Elevational range shifts of birds rarely have been examined in arid regions. Here, we examine shifts in the elevational distributions of breeding birds from two regions of the Great Basin, a desert in the western USA, over 10 to 20 years. We collected data annually from 2001 to 2020, a relatively long and consistent time series that is uncommon in research on distributional shifts. We used single-species occupancy models of 32 bird species to examine shifts along the full elevational gradient (1650–3200 m a.s.l.) and within 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 23 species shifted, and simulations indicated that shifts in the distributions of 18 species were unlikely to be stochastic. The majority of shifts in the western Great Basin were downslope, whereas those in the central Great Basin were upslope. More shifts occurred at the edges of the elevational gradient than along the full gradient. Elevational shifts lacked a consistent climate-response signal, but those of some species appeared to follow changes in primary productivity. We found regional differences in elevational shifts and climate associations, and our work suggests that these desert bird populations may be relatively resilient to climate change.

Keywords: Climate change, elevation, Great Basin, occupancy model, point count, precipitation, primary productivity, range shift, temperature

Introduction

Changes in elevational distributions of diverse taxonomic groups are occurring globally, with the potential to reshape ecological communities and alter ecosystem function (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 in part by temperature, a dominant paradigm suggests that montane animals and plants will move upslope in response to climate change (Martin 2001, McNab 2003). However, in many instances, populations and species are not moving in synchrony with warming temperatures and either have not shifted or shifted downslope (Chen et al. 2011, Tingley et al. 2012, Auer and King 2014, Campos-Cerqueira et al. 2017, DeLuca and King 2017, Neate-Clegg and Tingley 2023). The interacting effects of temperature, precipitation, and other climate variables could lead to large variation in interspecific or intraspecific responses to climate change (Tingley et al. 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. Biotic interactions, especially competition, may be stronger at the highest or lowest elevations, potentially precluding species from expanding upslope or downslope if an aggressive competitor is present (Terborgh and Weske 1975), or resulting in competitive release and consequent shifts if a competitor is extirpated (Freeman et al. 2022). High-elevation taxa often have greater thermal tolerances than low-elevation taxa, proportional to the magnitude of seasonal and diel thermal variation at high elevations (Janzen 1967, Deutsch et al. 2008, Khaliq et al. 2014, Sunday et al. 2019). High-elevation species' physiology therefore may result in relatively small elevational range shifts (Mamantov et al. 2021).

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). Research on avian elevational shifts is biased towards temperate regions (Neate-Clegg and Tingley 2023), but little research has examined whether elevational shifts are occurring in temperate arid systems (Hargrove and Rotenberry 2011). Deserts globally and in the contiguous USA have warmed more rapidly in the last 50 years than other ecoregions, and this trend is predicted to continue through the end of the century (Dominguez et al. 2010, Zhou et al. 2015). Species in arid systems may be on the edges of their thermal and hydric limits, and indirect effects of climate on water and food availability may further threaten population persistence in desert mountain ranges. Research in the USA has identified elevational shifts in bird species, although the directions of the shifts are inconsistent. For example, 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, repeated surveys indicated that abundance-weighted mean elevational distributions of 42 species shifted upslope by 83 m over 40 years, with shifts observed at both the upper and lower elevational range edges (Kirchman and Van Keuren 2017).

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 temperature, changes in the composition of plant species, plant phenology, or primary productivity (Menzel and Sparks 2006, Lenoir et al. 2008). Downslope shifts in bird populations are often attributed to changes in predation or other forms of interspecific competition (Lenoir et al. 2010). Changes in precipitation may drive upslope or downslope shifts directly, for example when extremely high or low precipitation damages nests and reduces survival; or indirectly, such as through the effects of precipitation on plants and insects that provide food for birds (Tingley et al. 2012, Neate-Clegg and Tingley 2023). 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).

If variability in population size is high, then 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 low-quality habitat (Thomas and Lennon 1999). Annual variation 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 when comparing two time points, and by testing population variability in statistical analyses.

We examined whether the elevational distributions of species in two communities of birds in the Great Basin are shifting. The Great Basin is a cold desert with extensive sagebrush *Artemisia* spp. 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). We examined data from long-term, nearly continuous avian point-count surveys in two regions of the Great Basin to explore potential distributional shifts and their mechanisms. We used single-species occupancy models of 32 species to examine elevational movement along the full elevational gradient and within the lowest and highest 25% of

the elevational gradient. We then conducted simulations to test whether population stochasticity could confound inferences about shifts. We examined the highest and lowest 25% of the elevational gradient because distributional shifts may be greater, or more consistent, at the range edges than along the full gradient (Lenoir and Svenning 2014). Additionally, overall stability of elevational ranges may mask variability at elevational range edges. 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 eight mountain ranges: the Sierra Nevada, Wassuk Range, Sweetwater Range, and Bodie Hills (henceforth western Great Basin) and the Shoshone Mountains, Toiyabe Range, Toquima Range and Monitor Range (henceforth central Great Basin) (Fig. 1). We collected data in 38 canyons in these eight mountain ranges. Most canyons extend from the base to the crest of the mountain range, collectively covering an elevational gradient from 1650 to 3200 m a.s.l. We distributed survey points along the elevational gradient in each canyon, and separated the centers of survey points by at least 300 m (Supporting information). We recorded the coordinates of each point's centroid with a handheld global positioning system (GPS) and returned to the same points each year. 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 and Rytwinski 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 to 2011, mean annual temperatures across the Great Basin increased by an estimated 0.7–1.4°C (Snyder et al. 2019). Mean annual temperatures across the southwestern USA, 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 to 2013, daily maximum precipitation and the 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). These results suggest

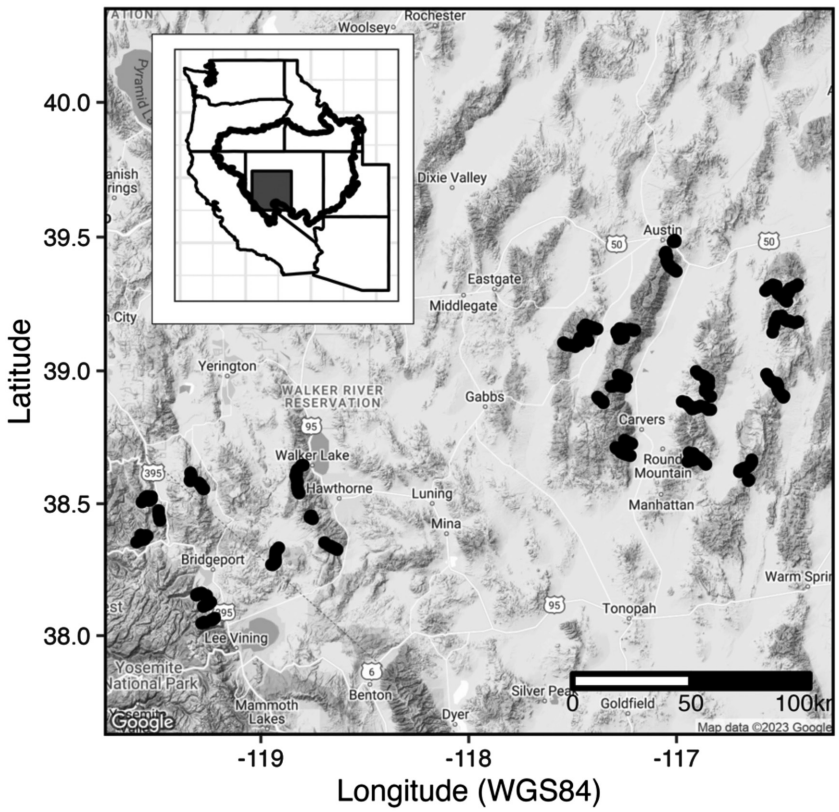

Figure 1. Locations at which we collected point-count data in the western and central Great Basin. Inset: Great Basin (thick black line) and the approximate boundaries of our study area (gray square).

that bird populations in our study canyons were exposed to warming temperatures and, at least indirectly given the timing of migration, changes in the seasonality and intensity of precipitation during the study period (2001–2020). We therefore collected data on temperature, precipitation, and the normalized difference vegetation index (NDVI) to examine potential direct and indirect effects of climate on bird occupancy.

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 to 2020 at a total of 134 points in 13 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 to 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, juveniles, and fly-over detections 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). Because the centers of almost all of our survey points were a minimum of 300 m apart and the resolution of our climate data was 4 km, the values of some climate variables were applicable to more than one point. Most canyons overlapped 2–4 PRISM pixels.

We used 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 to 30 June from the Application for Extracting and Exploring Analysis Ready Samples (AppEARS) database (https://lpdaac-svc.cr.usgs.gov/appeears/). AppEARS derives NDVI from images captured every 16 days at 250 m resolution by the Moderate Resolution Imaging Spectroradiometer (MODIS). Therefore, virtually all survey points had a unique NDVI value.

Analyses

We modeled detection-weighted, single-species occupancy (MacKenzie et al. 2002, Royle and Nichols 2003) in a Bayesian framework. We modeled the western and central Great Basin data 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 (24 species). These cutoffs were arbitrary, but included enough data to achieve model fit and convergence. In total, we modeled occupancy of 32 species, 16 of which occurred in both the western and central Great Basin (Supporting information).

We examined three occupancy models for each species. The first model included data from all points sampled along the full elevational gradient, and examined shifts along that full gradient. The second and third models examined potential elevational shifts in the lowest and highest 25% (lower and upper edges) of the elevational gradient. The elevational gradients were consistent among species and models; we did not exclude points that fell outside a species' apparent elevational range. The elevational ranges of all species we examined extended into the upper and lower 25% of the elevational gradient (Supporting information). The three models had the same formulation and covariates. All continuous covariates were scaled and centered around zero. We used the Watanabe–Akaike information criterion (WAIC) to select and compare four models: an intercept only model; a model with elevation, year, and the interaction of elevation and year as covariates on the occupancy submodel; a model with spring and winter temperature and spring and winter precipitation as covariates on the occupancy submodel; and a model that included all covariates above on the occupancy submodel (for WAIC scores see the Supporting information).

We modeled the observation process as:

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

$$\text{logit}\left(p_{ijk}\right) = \beta_1 + \beta_2 \times \text{jday}_{ijk} + \beta_4 \times \text{time}_{ijk} + \beta_4 \times \text{time}^2{}_{ijk} + \text{observer}_{ijk}$$

$$\text{observer} \sim \text{Normal}\left(0, \tau_1\right)$$

$$\tau_1 = \sigma_1^{-2}$$

$$\sigma_1 \sim \text{Student}\left(0,1,6\right)\text{T}\left(0,\right)$$

where Y_{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 observer is a random intercept 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:

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

$$\text{logit}(\psi_{ik}) = \beta_5 + \beta_6 \times \mathbf{X_{ik}} + \text{point}_i + \text{canyon}_i$$

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

$$\tau_2 = \sigma_2^{-2}$$

$$\sigma_2 \sim \text{Student}(0,1,6)\text{T}(0),$$

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

$$\tau_3 = \sigma_3^{-2}$$

$$\sigma_3 \sim \text{Student}(0,1,6)\text{T}(0,)$$

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. $\mathbf{X_{ik}}$ represents the vector of covariate values at point i in year k. Covariates in $\mathbf{X}$ included year, elevation, the interaction of year and elevation, spring temperature, winter precipitation, spring precipitation, and NDVI, depending on which of the four models were being examined (above). 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. *point* is a point-level random intercept with a mean of 0 and precision of τ_2, and canyon is a canyon-level random intercept with a mean of 0 and precision of τ_3. We used weakly informative prior distributions, which assign greater prior probability near zero, for intercepts, covariates, and random effects. Our data are stacked: each row of data represents a single survey point-year combination. This model structure, and the inclusion of a point-level random effect, accounts for potential psuedoreplication caused by including multiple years in a single model. We chose this approach for two reasons. First, we were not interested in dynamic parameters, such as colonization and extinction, which require multilevel occupancy models to analyze. Second, we feel that this approach is biologically realistic given that our species of interest, short-lived passerines, have high temporal turnover in our study system (Yen et al. 2018).

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 data. We estimated the model previously identified as best on these simulated data. We then conducted a two-tailed test of whether the estimated mean of the interaction of year and elevation in each simulation was greater than the absolute value of the estimate from the original model. For example, if the estimated effect of the interaction of year and 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 2023) with the jagsUI package (Kellner 2019) in R (www.r-project.org). We based posteriors on three chains of 60 000 iterations after a 10 000 sample burn-in and adaptive phase. We classified convergence as Rhat < 1.15 (Gelman and Hill 2007). No pair of candidate covariates was 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 (Supporting information) and estimated mean detection and occupancy were > 0.15. All model code and model outputs for species with statistically significant elevation movements are at https://github.com/MarthaZillig/elevational_shifts_code.

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 23 of the 32 species shifted. Five species shifted downslope and nine shifted upslope over the full elevational gradient. Twelve species shifted at the lower edge (seven upslope and five downslope), and 12 species shifted at the upper edge (six upslope and six downslope) (Supporting information). Simulations indicated high confidence that the shifts of five species (American robin *Turdus migratorius*, bushtit *Psaltriparus minimus*, chipping sparrow *Spizella passerina*, MacGillivray's warbler *Geothlypis tolmiei*, and yellow-rumped warbler *Setophaga coronata*) were likely an artifact of stochasticity (Supporting information). Further discussion focuses on the 18 species for which simulations indicated movement likely was not an artifact of stochasticity.

In the western Great Basin, the elevational distributions of seven species shifted. The distributions of four species shifted downslope along the full elevational gradient: house wren *Troglodytes aedon* by 76 m, Brewer's sparrow *Spizella breweri* by 106 m, yellow warbler *Setophaga petechia* by 184 m, and lazuli bunting *Passerina amoena* by 194 m (Table 1). One species, black-throated gray warbler *Setophaga nigrescens*, shifted upslope (81 m) along the full elevational gradient. 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, Fig. 2a). At the upper edge of the elevational gradient, the distribution of house wren shifted upslope, and the distribution of dark-eyed junco *Junco hyemalis* shifted downslope (Table 1).

In the central Great Basin, the elevational distributions of 15 species shifted (Table 2). Six species shifted along the full elevational gradient, all upslope: Woodhouse's scrub-jay *Aphelocoma woodhouseii* (48 m), mountain chickadee *Poecile gambeli* (10 m), fox sparrow *Passerella iliaca* (56 m), vesper sparrow *Pooecetes gramineus* (68 m), spotted towhee *Pipilo maculatus* (90 m), and yellow warbler (16 m). At the lower edge of the elevational gradient, four species' distributions changed. Brewer's sparrow shifted upslope, whereas broad-tailed hummingbird *Selasphorus platycercus*, mountain chickadee, and black-throated gray warbler shifted downslope (Table 2, Fig. 2b). At the upper edge of the elevational gradient the distributions of nine species changed, including three species that shifted over the full gradient. Gray flycatcher *Empidonax wrightii*, blue-gray gnatcatcher *Polioptila caerulea*, mountain bluebird *Sialia currucoides*, and spotted towhee shifted downslope, while warbling vireo, mountain chickadee, rock wren *Salpinctes obsoletus*, vesper sparrow, and green-tailed towhee *Pipilo chlorurus* shifted upslope (Table 2, Fig. 2b). The distributions of four species shifted in both the western and central Great Basin: warbling vireo shifted upslope in both regions, Brewer's sparrow shifted downslope in the western and upslope in the central Great Basin, yellow warbler shifted downslope in the western and upslope in the central Great Basin, and black-throated gray warbler shifted upslope in the western and slightly downslope in the central Great Basin.

In both regions of the Great Basin, 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 133 m, compared to 50 m at the lower edge and 46 m at the upper edge (Table 1). In the central Great Basin, the absolute values of the average elevational shift across the full elevational gradient, lower edge, and upper edge were 72, 32, and 44 m, respectively (Table 2).

Over the study period, spring temperature, winter precipitation, and spring precipitation increased significantly in both the western and central Great Basin (Fig. 3). NDVI also changed, but not in a uniform direction. 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 positive (Fig. 3); both effects were small, but significant. Over time, NDVI decreased as elevation increased in the western Great Basin, and increased as elevation increased in the central Great Basin.

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 eight of the 18 species with elevational distributions that shifted was significantly associated with winter or spring precipitation (Table 1, 2). Spring temperature was associated with shifts of eight of the 18 species, and NDVI was associated with shifts of 10 of the 18 species. In both regions, all associations with spring precipitation (two species in the western and three in the central Great Basin) were negative and were associated with shifts upslope. In the central Great Basin, the five significant associations with spring temperature also were negative. Of the eight associations with NDVI in the central Great Basin, five were positive and three were negative. Of the four significant associations with NDVI in the western Great Basin, three were positive; only occupancy of Brewer's sparrow was negatively associated with NDVI. The four associations with NDVI in the western Great Basin corresponded to downslope elevational movement. Winter precipitation was associated positively with movement of two species in the central Great Basin, both upslope.

Discussion

Our results add to a growing understanding that many temperate bird species are not consistently shifting upslope as climate changes, and provide compelling evidence that the direction of elevational movement may be population- or region-specific. In the western Great Basin, more shifts occurred along the full elevational gradient than at the edges. By contrast, in the central Great Basin, a greater number of distributional shifts occurred at the edges of the elevational gradient than along the full gradient. Additionally, four of five shifts across the full gradient in the western Great Basin were downslope, whereas all six shifts in the central Great Basin were upslope. Our results also illustrate the importance of assessing population variability in conjunction with range shifts. In five of 23 cases, what initially appeared to be a deterministic elevational shift was likely attributable to stochasticity or population trends over large areas. Although bird occupancy was strongly associated with climate variables, most elevational shifts were not associated with deterministic changes in temperature, precipitation, or primary productivity. The duration of our

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 (Supporting information).

	Full gradient			Lower 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				0.59 (0.38)	16 (−110, 142)	Spring precip. (−1.42, 0.43)			
House wren	−0.27 (0.12)	−76 (−253, 100)	NDVI (0.74, 0.28)	−0.53 (0.29)	−90 (−259, 80)	NDVI (1.69, 0.56)	0.7 (0.36)	43 (−85, 171)	None
Brewer's sparrow	−0.23 (0.13)	−106 (−294, 83)	Spring temp. (−0.76, 0.19); Winter precip. (−1.04, 0.23); NDVI (−0.85, 0.34)						
Dark-eyed junco							−0.54 (0.43)	−38 (−128, 52)	NDVI (1.56, 0.75)
Yellow warbler	−0.56 (0.17)	−184 (−492, 124)	Spring temp. (0.89, 0.23); Winter precip. (0.7, 0.28)						
Yellow-rumped warbler	0.28 (0.16)	−8 (−197, 178)	Spring precip. (−1.04, 0.23); NDVI (2.19, 0.31)						
Black-throated gray warbler	0.37 (0.22)	81 (−101, 264)	Spring precip. (−0.74, 0.24); Spring temp. (0.54, 0.26); Winter precip. (0.87, 0.34)						
Lazuli bunting	−0.52 (0.16)	−220 (−494, 53)	Spring temp. (−0.43, 0.21)	−0.87 (0.38)	−45 (−91, 182)	N/A			

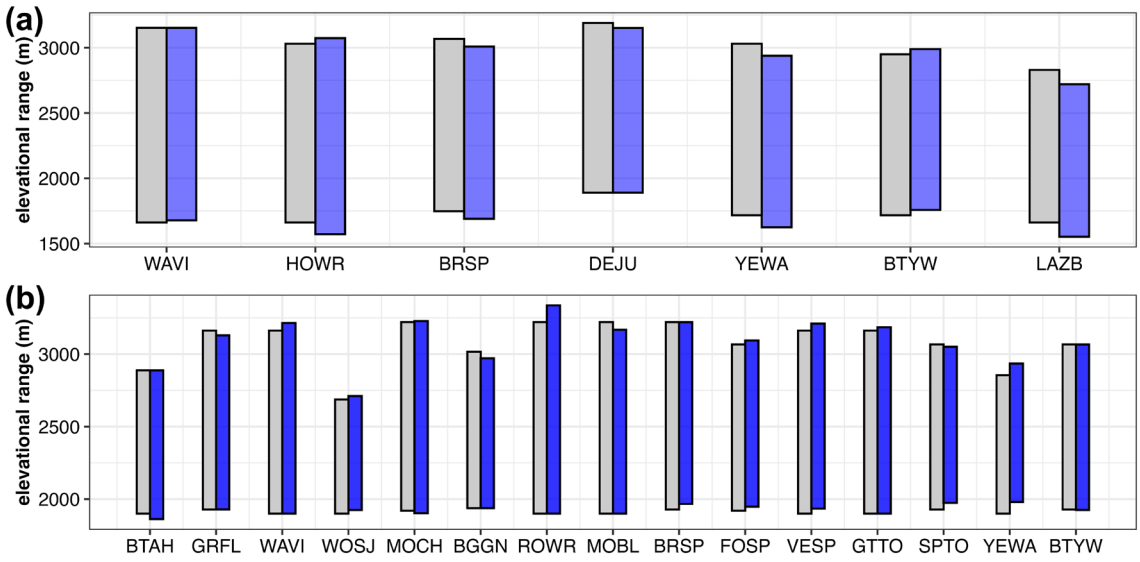

Figure 2. Shifts in elevational distributions of breeding birds in the western Great Basin from 2012 to 2020 (A) and in the central Great Basin from 2001 to 2020 (B). Gray bars represent the elevational range over which we detected the species, and light blue bars represent the addition (or subtraction) of elevational range on the basis of modeled elevational shifts (Table 1, 2). BTAH, broad-tailed hummingbird; GRFL, gray flycatcher; WAVI, warbling vireo; WOSJ, Woodhouse's scrub-jay; HOWR, house wren; MOCH, mountain chickadee; BGGN, blue-gray gnatcatcher; ROWR, rock wren; MOBL, mountain bluebird; BRSP, Brewer's sparrow; FOSP, fox sparrow; VESP, vesper sparrow; SPTO, spotted towhee; GTTO, green-tailed towhee; DEJU, dark-eyed junco; YEWA, yellow warbler; YRWA, yellow-rumped warbler; BTYW, black-throated gray warbler; LAZB, lazuli bunting.

time-series data was relatively short, but comparable to other studies of elevational shifts (Campos-Cerqueira et al. 2017, DeLuca and King 2017), and indicates considerable plasticity in elevational distributions.

Our simulations explicitly tested whether the linear effect of year drove 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 five 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, driving a linear signal despite considerable noise in the intervening years. Second, annual mean occupancy of some species is highly variable, and the apparent linear trend may have been coincidental and weak but still significant. Annual variability in abundance or occupancy of passerines can be caused by factors including conditions at overwintering grounds, episodic weather events or climate cycles, 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).

Population dynamics across large areas may influence our inferences about stochasticity, particularly if there are significant decreases or increases in population size. Therefore, we examined population trends of the 23 species that originally appeared to move along elevational gradients in the 1966–2019 North American Breeding Bird Survey (Sauer et al. 2019). Of the five species for which observed elevational shifts were likely due to stochasticity, continental population trends of three were estimated to be decreasing around −0.7% per year (bushtit, chipping sparrow, and MacGillivray's warbler), while populations of American robin and yellow-rumped warbler increased by 0.1% per year (Sauer et al. 2019). We recognize that regional trends may differ from continental trends (Murphy and Jarzyna 2023). However, trends in population size in the Great Basin Bird Conservation Region are difficult to assess reliably on the basis of community observations given the paucity of established survey routes and low density of human residents.

Continental population trends also have the potential to influence the significant, non-stochastic observed elevational shifts. For example, species with positive population trends may be better able to track environmental variables and expand their niches than species with negative population trends (Ralston et al. 2016). Of the four species for which we observed range expansions (warbling vireo in the central Great Basin, mountain chickadee, rock wren and house wren; Fig. 2), warbling vireo and house wren had significantly positive population trends across the continent, whereas population trends of the other two species were significantly negative (Sauer et al. 2019). The significant and positive continental trend in warbling vireo and house wren populations may in part explain the elevational range expansions we observed, but population trends likely do not explain the range expansions of the other two species. Similarly, decreasing population size may correspond with range contractions (Fuller et al. 1995, Rodriguez 2002). Of the six species for which we observed elevational range contractions (blue-gray gnatcatcher, mountain bluebird, dark-eyed junco, Brewer's sparrow, green-tailed

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 (Supporting information).

	Full gradient			Lower 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)
Broad-tailed hummingbird				−0.34 (0.15)	−38 (−81, 4)	Spring temp. (−0.34, 0.14); NDVI (0.82, 0.23)			
Gray flycatcher							−0.69 (0.45)	−33 (−118, 52)	None
Warbling vireo							0.36 (0.16)	52 (−22, 126)	NDVI (1.56, 0.37)
Woodhouse's scrub-jay	0.26 (0.13)	48 (−21, 117)	Winter precip. (0.26, 0.13)						
Mountain chickadee	0.18 (0.1)	10 (−67, 87)	Spring precip. (−0.49, 0.12); Spring temp. (−0.43, 0.1)	−0.34 (0.2)	−17 (−50, 15)	Spring temp. (−0.69, 0.19)	0.68 (0.29)	8 (−80, 97)	Spring precip. (−0.44, 0.2)
Blue-gray gnatcatcher							−0.43 (0.35)	−45 (−142, 51)	None
Rock wren							0.39 (0.23)	116 (−12, 243)	Winter precip. (0.93, 0.26); NDVI (−1.2, 0.34)
Mountain bluebird							−0.49 (0.28)	−52 (−160, 55)	Spring temp. (−0.75, 0.33); NDVI (−0.82, 0.34)
Brewer's sparrow				0.49 (0.2)	38 (0, 76)	Spring temp. (−0.66, 0.17)			
Fox sparrow	0.22 (0.11)	56 (−79, 191)	N/A						
Vesper sparrow	0.3 (0.12)	68 (−34, 170)	N/A				0.58 (0.24)	48 (−23, 118)	None
Green-tailed towhee							0.26 (0.16)	23 (−16, 63)	NDVI (−0.65, 0.29)
Spotted towhee	0.16 (0.07)	90 (28, 151)	NDVI (0.71, 0.14)				−0.38 (0.18)	−16 (−74, 42)	NDVI (0.46, 0.23)
Yellow warbler	0.46 (0.11)	161 (68, 254)	Spring precip. (−0.24, 0.11); NDVI (0.67, 0.2)						
Black-throated gray warbler				−0.24 (0.14)	−4 (−36, 28)	None			

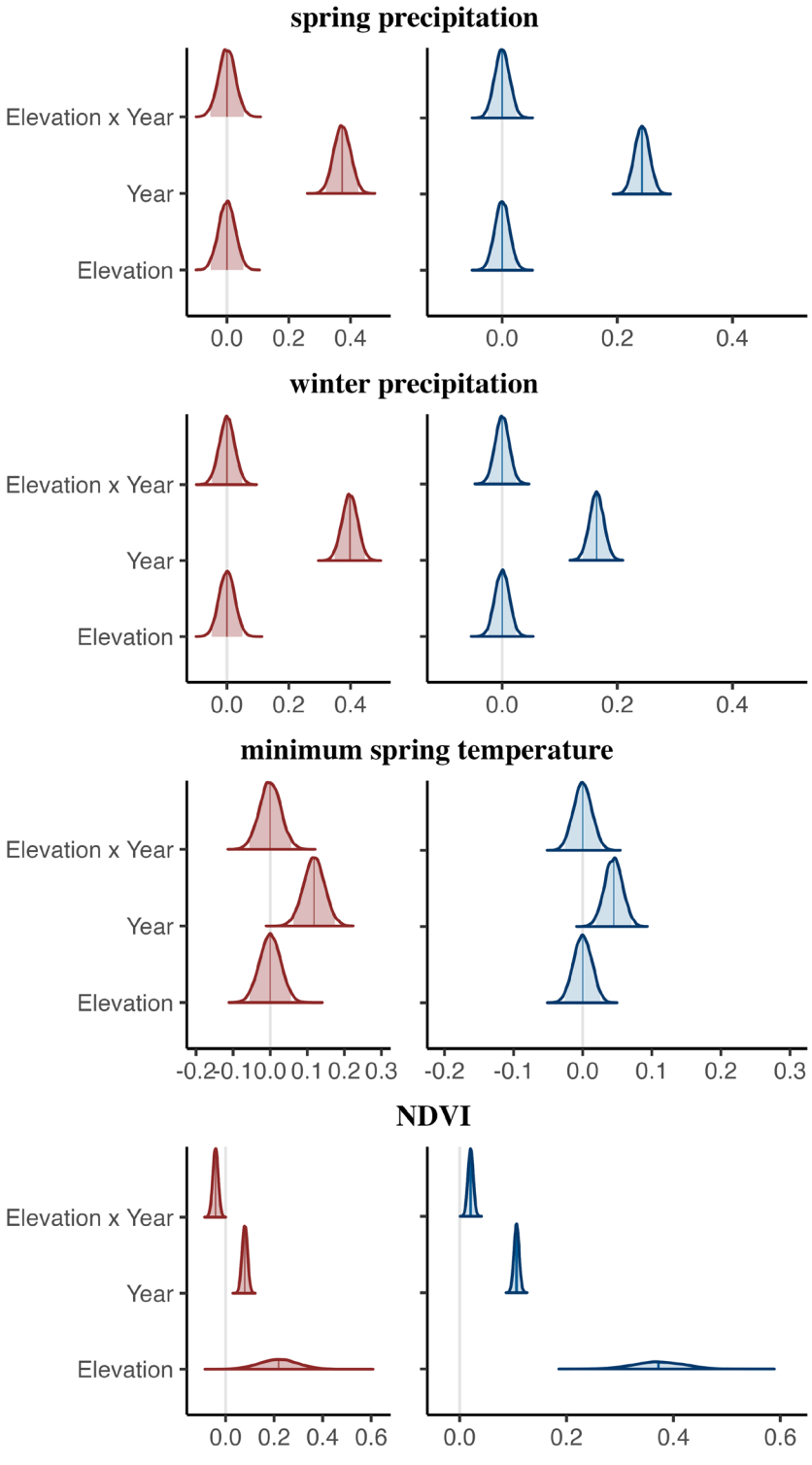

Figure 3. Posterior density estimates of the effects of year, elevation, and the interaction of year and elevation on total spring precipitation, total winter precipitation, minimum spring temperature, and the normalized difference vegetation index (NDVI) in the western Great Basin (red) and central Great Basin (blue).

towhee and spotted towhee; Fig. 2), four had significantly negative continental population trends, and populations of the other two species (blue-gray gnatcatcher and spotted towhee) were stable (Sauer et al. 2019).

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. At the time of our analysis, finer-resolution climate data that covered the extent of our survey areas were not freely available to us. Because the resolution of the climate variables was 4 km, some of our survey points within a canyon fell within the same pixel, and therefore had the same value of a climate variable. By contrast, because the resolution of the NDVI data was 250 m, each survey point could have a unique value. 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 elevational shifts we observed in the western Great Basin were downslope (five of seven shifts), whereas 10 of the 15 shifts we observed in the central Great Basin, including all six shifts along the full elevational gradient, were upslope. These opposing trends may be due to differences in biogeography and productivity between the two regions. Our survey points in the western Great Basin are on the western boundary of the hydrographic Great Basin and most are in riparian canyons. The vegetation surrounding these canyons is heterogeneous and, particularly in the Sierra Nevada, relatively productive and diverse. Our survey points in the central Great Basin sites are also in mountain canyons, but not all are riparian, and the surrounding vegetation generally is less hospitable to breeding passerines than that in the western Great Basin (Johnson 1975, Fleishman and Mac Nally 2006). Species in the central Great Basin may be shifting upslope to access higher-productivity habitat, whereas species in the western Great Basin may encounter areas with high productivity across the elevational gradient, or by moving downslope. Consistent with this theory, NDVI is increasing more rapidly at higher elevations in the central Great Basin and more rapidly at lower elevations in the western Great Basin (Fig. 3). In the central Great Basin, three riparian species, warbling vireo, spotted towhee, and yellow warbler, shifted upslope, and the shifts were significantly and positively associated with NDVI.

Elevational changes in NDVI and downslope bird movement in the western Great Basin may be driven by downslope expansion of riparian vegetation. 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 (Perry et al. 2012, 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 house wren, yellow warbler, and lazuli bunting, may be moving downslope in response to expansion of that nesting habitat at the lower edge of their elevational ranges.

In the central Great Basin, the majority of observed elevational shifts occurred at range edges. This result is consistent with the theory that the edges of species' elevational distributions are more responsive to direct and indirect effects of climate change than the centers of the distributions (Rumpf et al. 2018). For example, high elevations may be warming faster than lower elevations (Pepin et al. 2015), resulting in more pronounced distributional shifts at high elevations. In our study system, plant phenology at higher elevations can be 21 days later than at lower elevations (Zillig unpubl.). 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. 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.

Occupancy was significantly associated with winter or spring precipitation in ten instances, and in seven instances, including the five with spring precipitation, the association was negative (Table 1, 2). The fact that multiple survey points fell within the same PRISM grid cell potentially resulted in underestimation of the effects of temperature and precipitation on occupancy. We expect that finer-resolution climate data would result in even greater effects of precipitation on occupancy given that precipitation is highly variable in montane landscapes (Buytaert et al. 2006, Lopez-Moreno et al. 2007). In general, one would expect bird communities in water-limited arid ecosystems to respond positively to increased precipitation (Bolger et al. 2005, Riddell et al. 2019). The negative associations we found may be explained by climate change-driven changes in precipitation across the Great Basin. Increases in winter and spring precipitation across much of the western USA, including the Great Basin (Chambers 2008), are driven in part by increasingly severe storms (Xue et al. 2017), which could affect birds, especially residents or short-distance migrants, 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 earlier and more sporadic water inputs to the soil (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 (Supporting information). Most elevational

shifts were relatively small, but the distributions of four species shifted by more than 100 m: rock wren (+116 m), Brewer's sparrow (−106 m), yellow warbler (−184 m in the western Great Basin, +161 in the central Great Basin), and lazuli bunting (−220 m). The difference between regions in the direction of elevational movement of Yellow Warbler is striking, and with no shared associations with climate variables, suggests that populations are responding to environmental conditions in different ways across their breeding range.

Spring temperature increased considerably even over the 10–20 years of our study (Fig. 3), and seven of nine associations between bird occupancy and spring temperature were negative (Table 1, 2). We did not find evidence that changes in temperature differed along the elevational gradient (Pepin et al. 2015), but this again may be an artifact of multiple survey points falling within the same PRISM cell.

Associations of bird populations with vegetation composition and structure differ among regions of the Great Basin (Zillig et al. 2023), and our results suggest that bird populations also have spatially variable responses to climate. Additionally, no bird species is known to breed exclusively in the Great Basin. Therefore, the population-level responses we observed are not necessarily indicative of species-level responses. The elevational shifts we documented occurred over a relatively short period of time (10–20 years), although this duration is comparable to that of other studies on elevational movement (DeLuca and King 2017). We found that Great Basin bird populations are capable of responding quickly to environmental change through relatively short-distance elevational movements, suggesting that these desert populations may be relatively resilient to climate change.

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Author contributions

Martha W. Zillig: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (equal). **Wesley Brooks**: Formal analysis (supporting); Methodology (supporting); Writing – review and editing (supporting). **Erica Fleishman**: Conceptualization (supporting); Funding acquisition (lead); Project administration (equal); Supervision (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Forest Service Research Data Archive: https://www.fs.usda.gov/rds/archive/catalog/RDS-2011-0002-4, https://www.fs.usda.gov/rds/archive/catalog/RDS-2015-0031-2 (Zillig et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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