

Breeding birds of high-elevation mixed-conifer forests have declined in national parks of the southwestern U.S. while lower-elevation species have increased, with responses to drought varying by habitat

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ABSTRACT

Climate change is considered a major driver of recent avian population declines, particularly in the drought-stricken southwestern United States. Predicting how bird populations will respond requires understanding the climatic drivers influencing population density across the region's diverse habitats. We modelled breeding-season densities of 50 bird species in relation to spring and summer drought and the timing of North American monsoon rainfall over a 12-year period (2007–2018) and across 4 habitats comprising an approximately 1,500 m elevational gradient. We estimated annual breeding-season population density in relation to climate in the previous year by fitting a Bayesian hierarchical *N*-mixture model to point-count data from each of 6 national parks on the Colorado Plateau. Specifically, we asked whether (1) population trends were stable, increasing, or decreasing in the focal parks; (2) breeding densities were affected by drought or the timing of monsoon rains; and (3) climatic effects differed across habitat types and among species that molt on the breeding grounds, the nonbreeding grounds, or stopover in the monsoon region of northwestern Mexico (molt migrants). Population trends varied with habitat. Species of high-elevation mixed-conifer forest declined over the study period, matching regional Breeding Bird Survey trends, likely in response to climate-related habitat loss and disturbance. By contrast, lower-elevation pinyon-juniper and grassland-shrubland species density generally increased. Effects of drought varied by habitat with elevation: mixed-conifer species responded positively to drought in the previous year, likely due to earlier snowmelt and breeding phenology, whereas pinyon-juniper species were unaffected, and grassland-shrubland species responded negatively, perhaps due to reduced nest survival. Later arrival of monsoon rains, a common prediction of climate models, had a positive effect on grassland bird densities, but a negative effect on molt-migrant densities. Late monsoon rains may result in a phenological mismatch between migration timing and the pulse of resources required to molt.

Keywords: climatic moisture deficit, long-term monitoring, mixed-conifer forest, national parks, pinyon-juniper woodlands, riparian woodlands, Southwestern grasslands

How to Cite

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LAY SUMMARY

- Changes to the timing and intensity of climate events are key causes of bird population declines, but it is unclear how these effects change across habitat types.
- We asked how drought and monsoon rain timing affected the breeding densities of 50 bird species in 4 habitats across 1,500 m of elevation in Colorado Plateau, USA, national parks.
- Effects of drought varied with elevation: high-elevation conifer-forest bird species responded positively to drought, while middle-elevation species were unaffected and low-elevation grassland species responded negatively.
- Later arrival of the monsoon had a positive effect on grassland birds, but a negative effect on species that stopover in the monsoon region of northwestern Mexico to molt while migrating south; species may mistime this “molt migration” in years when monsoon rains are late.
- Birds of high-elevation conifer forest showed declining populations during the study period (2007–2018), likely due to drought- and wildfire-related deaths of conifer trees.

Las aves reproductoras de los bosques mixtos de coníferas de elevaciones altas han disminuido en los parques nacionales del suroeste de EEUU mientras que las especies de elevaciones más bajas han aumentado, con respuestas a la sequía que varían según el hábitat

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RESUMEN

Se considera que el cambio climático es un importante impulsor de las recientes disminuciones poblacionales de las aves, especialmente en el suroeste de Estados Unidos, afectado por la sequía. Predecir cómo responderán las poblaciones de aves requiere comprender los impulsores climáticos que influyen en la densidad poblacional a través de los diversos hábitats de la región. Modelamos las densidades durante la temporada de cría de 50 especies de aves en relación con la sequía de primavera y verano y con el momento de las lluvias monzónicas de América del Norte, durante un período de 12 años (2007–2018) y en cuatro hábitats que comprenden un gradiente altitudinal de ~1500 m. Estimamos la densidad poblacional anual durante la temporada de cría en relación con el clima del año anterior, ajustando un modelo jerárquico bayesiano de mezcla N a datos de conteo de puntos provenientes de cada uno de los seis parques nacionales del Plateau de Colorado. Específicamente, preguntamos si (1) las tendencias poblacionales eran estables, aumentaban o disminuían en los parques focales; (2) las densidades de cría se veían afectadas por la sequía o el momento de las lluvias monzónicas; y (3) los efectos climáticos diferían según los tipos de hábitat y entre especies que mudaban en las zonas de cría, en las zonas no reproductivas o las que hacían escala para mudar en la región de monzones del noroeste de México (aves migratorias en muda). Las tendencias poblacionales variaron según el hábitat. Las especies de los bosques mixtos de coníferas de elevaciones altas disminuyeron durante el período de estudio, coincidiendo con las tendencias regionales del Censo de Aves Reproductoras, probablemente en respuesta a la pérdida y los disturbios del hábitat relacionados con el clima. Por el contrario, la densidad de especies de pino enebro y pastizales arbustivos de elevaciones más bajas aumentó en general. Los efectos de la sequía variaron según el hábitat y la elevación: las especies de bosques mixtos de coníferas respondieron positivamente a la sequía del año anterior, probablemente debido al deshielo temprano y la fenología de cría, mientras que las especies de pino enebro no se vieron afectadas y las especies de pastizales arbustivos respondieron negativamente, tal vez debido a la reducción de la supervivencia de los nidos. La llegada tardía de las lluvias monzónicas, una predicción común de los modelos climáticos, tuvo un efecto positivo en las densidades de aves de pastizal, pero un efecto negativo en las densidades de las aves migratorias en muda. Las lluvias monzónicas tardías pueden resultar en una falta de sincronización fenológica entre el momento de la migración y el pulso de recursos requeridos para mudar.

Palabras clave: bosque mixto de coníferas, bosques de pino enebro, bosques ribereños, déficit de humedad climática, monitoreo a largo plazo, parques nacionales, pastizales del suroeste

INTRODUCTION

Ongoing vertebrate population declines underpin the current biodiversity crisis (Dirzo *et al.* 2014), and have been particularly alarming for birds in North America, where roughly 60% of species have declined since 1970 (Rosenberg *et al.* 2019, North American Bird Conservation Initiative 2022). Climate change is a major driver of declines (Bohning-Gaese and Lemoine 2004), jeopardizing an estimated two-thirds of North American bird species (Bateman *et al.* 2020b). While long-term climate shifts can cause range expansions and contractions (Sohl 2014, Roberts *et al.* 2019a), the increased frequency or variability of extreme short-term climate events, such as heat waves or droughts, may influence population trends (Bateman *et al.* 2016, Taff and Shipley 2023). These short-term effects of climate change on birds are especially pronounced in aridland ecosystems (Bateman *et al.* 2020a), where species live close to their physiological limits. For example, extreme heat waves caused the collapse of bird populations in the Mojave Desert (Iknayan and Beissinger 2018). Arid southwestern North America is a climate change hotspot (Diffenbaugh *et al.* 2008) currently facing a multi-decade megadrought (Williams *et al.* 2020), which amplifies the effects of extreme climate events.

Predicting how bird populations will respond to climate change in the Southwest requires understanding the climatic drivers influencing population density. Of these, drought, particularly when combined with abnormally high temperatures, often has negative effects on bird abundances in the western United States (Albright *et al.* 2010a, 2010b, Cady *et al.* 2019, Roberts *et al.* 2021). Indeed, the effects of extreme spring heat and drought are predicted to pose the greatest climate risk for North American birds (Bateman *et al.* 2020a). Drought affects populations in a variety of ways. Direct mortality may occur when individuals cannot effectively thermoregulate during heat waves, leading to lethal dehydration (McKechnie and Wolf 2010, Albright *et al.* 2017). However, indirect effects of drought on bird demography might be even more pronounced. For example, drought can delay the onset of breeding activity, leading to reduced nest success (Bolger *et al.* 2005, McCreedy and van Riper 2015, Cruz-

McDonnell and Wolf 2016) and productivity (Saracco *et al.* 2018). Drought can also alter plant communities that serve as breeding habitat, for example, by causing tree die-off and die-back (Williams *et al.* 2013) and stand-destroying wildfires (Mueller *et al.* 2020).

Another climatic variable that could potentially affect bird populations is the North American monsoon, a pulse of heavy rainfall between July and September that affects the southwestern United States and northwestern Mexico (Adams and Comrie 1997). The timing and intensity of the monsoon varies from year to year, largely in response to the El Niño Southern Oscillation (Pascale *et al.* 2019). Earlier monsoon rains (i.e., more rain in June and July) are believed to benefit many bird populations, as the annual pre-basic molt and fall migratory movements of many species take place in July and August (Pyle *et al.* 2018). Many climate models suggest that monsoon rains will be increasingly delayed, however, with reduced rainfall in June and July and increased rainfall in September and October (Grantz *et al.* 2007, Cook and Seager 2013, Torres-Alavez *et al.* 2014). Many migratory birds in western North America stopover for several months during their southward migrations to molt in monsoonal areas of Mexico and the southwestern United States before migrating again to nonbreeding ranges farther south (Rohwer *et al.* 2009b, Chambers *et al.* 2011, Siegel *et al.* 2016, Pyle *et al.* 2018), a phenomenon known as molt migration. Species that have evolved this stopover molt strategy molt faster than those that molt on the breeding or nonbreeding grounds (de la Hera *et al.* 2012), and time their arrival on the molting grounds with peak green-up (Siegel *et al.* 2016). Earlier monsoon rainfall on the molting grounds is therefore more likely to lead to a successfully timed molt and has resulted in higher recruitment in at least one molt-migrant species (Saracco *et al.* 2022). Even for species that do not undertake molt migrations, earlier monsoon rains on the breeding grounds lead to earlier seed masting in some western conifers (Wion *et al.* 2021) and higher primary production in aridland plant communities (Forzieri *et al.* 2014). Monsoon rain timing therefore likely influences arthropod food availability (Uhey *et al.* 2020) and post-fledging mortality, and some species raise

second broods in July after the onset of the rains (Rohwer *et al.* 2009a). As such, survival and productivity of both molt-migrant and resident species is predicted to increase in years with earlier monsoon rainfall on the breeding and molting grounds. Despite its potential importance, however, the timing of monsoon rains has received little attention in studies of bird populations.

The effects of climate, particularly drought, on bird population trends can vary considerably across habitats by elevation (Cady *et al.* 2019, Roberts *et al.* 2021). Low-elevation grassland species are more negatively affected by drought compared to species that use closed-canopy habitats (Skagen and Adams 2012, Conrey *et al.* 2016). Reduced grass biomass during drought may reduce vegetation structure (Winter *et al.* 2005) and nest concealment (Fogarty *et al.* 2017), with negative consequences for habitat quality and nest success. By contrast, montane forest species often exhibit higher densities following drought (Ray *et al.* 2017, Saracco *et al.* 2019), perhaps due to earlier snowmelt in drought years leading to earlier nest initiation and greater reproductive output (Smith and Andersen 1985, Saracco *et al.* 2019). Species responses to drought were less uniform in middle-elevation habitats on the northern Colorado Plateau (Roberts *et al.* 2021), however, suggesting that community composition might shift with drought “winners” and “losers.” The effects of monsoon timing should also vary by habitat along the elevational gradient. For many grassland birds, extreme rainfall events reduce daily nest survival (Fisher *et al.* 2015, Oberg *et al.* 2015, Conrey *et al.* 2016, Ruth and Skagen 2018), and later monsoon rains are therefore predicted to increase population densities. By contrast, earlier monsoon rains may benefit high-elevation mixed-conifer forest birds, as late-breeding-season monsoon rainfall can increase nesting productivity (Saracco *et al.* 2018) and breeding bird densities (Smith 1982) through a variety of mechanisms (see above). Because the large elevational gradient in the Southwest contains a diversity of habitat types, a better understanding of elevation- and habitat-specific responses to climate variables is needed for the region.

In this study, we modelled breeding-season densities of birds in relation to spring and summer drought and the timing of monsoon rainfall using Bayesian hierarchical *N*-mixture models. Using point count data collected over a 12-year period (2007–2018) in 6 national parks in the southwestern United States, we estimated changes in breeding-season population density over time, and in relation to climatic conditions during the previous year. Our study sites spanned a large elevational gradient (approximately 1,400–2,900 m above sea level [m.a.s.l.]) and 4 habitat types: arid grasslands and shrublands, riparian woodlands, pinyon-juniper woodlands, and mixed-conifer forest. Specifically, we asked whether (1) population trends were stable, increasing, or decreasing, (2) breeding densities were affected by drought or the timing of monsoon rains in the previous year, and (3) climate effects differed across habitats and among species with differing migratory strategies. We predicted that bird species breeding in montane mixed-conifer forest, many of which reach the southern extreme of their breeding range in this region, should be the most vulnerable to climate change, and the most likely to show long-term declines. Paradoxically, we predicted that montane bird densities would increase following drought due to earlier snowmelt, while negative effects were predicted for open-habitat species in arid grasslands. Finally, we predicted

that earlier monsoon rains would benefit forest species more than open-habitat species and migrants more than residents. Many molt migrants time their southward movements to coincide with a seasonal pulse of resources in the monsoon region, while resident species could presumably benefit from monsoon-related resources whenever they arrive.

METHODS

Study Sites and Sampling Design

Breeding season survey data were collected at national parks and monuments (hereafter “parks”) within the Southern Colorado Plateau Inventory & Monitoring Network (SCPN), located in the Four Corners region of the southwestern United States (Figure 1). We used data collected as part of the network’s long-term vital signs bird monitoring program (Holmes *et al.* 2015) in 6 parks across Colorado, New Mexico, and Arizona: Bandelier NM (BAND), Canyon de Chelly NM (CACH), Grand Canyon NP (GRCA), Mesa Verde NP (MEVE), Petrified Forest NP (PEFO), and Wupatki NM (WUPA). In each park, 1 focal habitat of conservation concern was selected for long-term monitoring (2 habitat types were monitored at GRCA); overall, 4 habitat types were sampled: mixed grassland and shrubland (PEFO, WUPA), riparian woodland (CACH), pinyon-juniper woodland (GRCA, MEVE), and mixed-conifer forest (BAND, GRCA). These habitats span the full elevational gradient on the Colorado Plateau and include a full gradient of canopy cover and vegetation structure (Table 1). Because each habitat is restricted to specific elevations in this region, habitat and elevation were strongly correlated and elevation could not be used as a covariate in our models (see below). The sampling frame for monitoring, each park’s focal habitat, was determined by overlaying National Park Service vegetation classification maps and soil classification maps to identify areas of overlap between soil layer(s) associated with the focal habitat (see Table 1) and areas mapped as containing the focal plant community (“ecological sites”; see DeCoster *et al.* 2012; Supplementary Material). The sampling frame was further reduced by removing areas near roads, human structures, and archaeological sites; areas with a slope of > 30%; inaccessible areas > 2 hr away from crew campsites; and areas that experienced high-severity wildfire (Holmes *et al.* 2015; Supplementary Material for full description of sampling frame delineation). All survey locations were ground-truthed prior to establishment to ensure they fell within the focal habitat.

The spatial sampling design varied by park and habitat type and fell into 4 categories (Table 1, Figure 1). (1) In parks where the sampling frame was relatively large, point count stations were randomly placed in 3 × 3 regular clusters (Figure 1A) using the generalized random tessellation stratified (GRTS) algorithm (Stevens and Olsen 2004). (2) When the center point of a cluster fell within an irregularly shaped portion of the sampling frame, the central station plus 8 nearest possible stations were selected to form irregular clusters. (3) Where the sampling frame was more limited in spatial extent, count stations were placed as a regularly spaced grid (Figure 1C). Finally, (4) transects of evenly spaced count stations were placed along the streambed at CACH to sample riparian habitat (Figure 1B). We treated each grouping of stations on the same stretch of the streambed and each cluster of stations

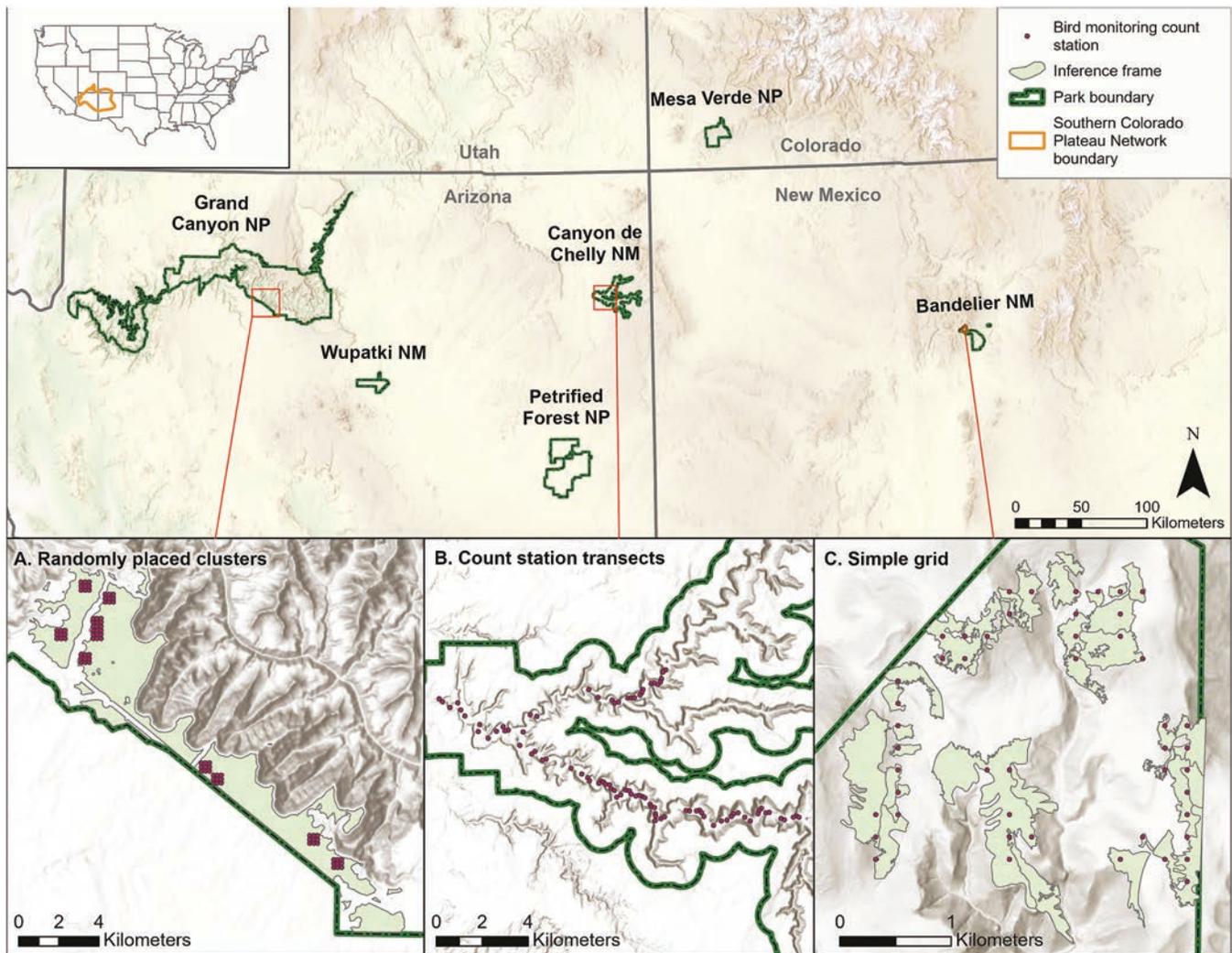


FIGURE 1. Locations and spatial sampling designs in six Southern Colorado Plateau Network national parks. Monitored parks are bounded in dark green and labeled. Filled polygons in panels (A) and (C) represent the sampling frame (i.e., area of inference for the habitat type selected for monitoring) in three parks and represent the variation in sampling designs across parks. See Methods for sampling frame in Canyon de Chelly NM. Points represent individual count stations, which were arrayed as randomly placed clusters (A), linear transects (B), or simple grids (C) in each park.

as a spatially cohesive “transect.” The minimum distance between stations varied by park (see Table 1), ranging from 150 to 300 m. All count stations were surveyed in each year that a park was sampled. For additional detail on the sampling design and changes to station sample sizes across years, see [Supplementary Material](#).

Point Count Surveys

Breeding bird densities in each focal habitat were sampled using 8-min, unlimited-radius point counts paired with distance sampling following [Holmes et al. \(2015, Standard Operating Procedure #4\)](#). Each single-observer point count survey took place between a half hour before and 4 hr after local sunrise. For each detection, observers recorded the minute of first detection (1–8) and the horizontal distance (in meters [m]) from the observer to the location of first detection (estimated with the help of a laser rangefinder). At each count station, observers recorded environmental covariates including background noise (0–3 scale) and cloud cover to the nearest 10%. Each count station was visited at least twice in each year it was surveyed,

with visits 3–4 weeks apart. Lower elevation parks were always surveyed before higher-elevation parks, and the timing of surveys was consistent across study years. Low elevation sites (PEFO, WUPA) were surveyed in early- to mid-May and again in late-May to early June. High elevation sites were surveyed in late May and again in mid-to-late June. Each park was sampled every 3 years from 2007 to 2018, with 2–4 parks surveyed per year ([Supplementary Material Table 1](#)). Because of this schedule, no parks were sampled in 2010, 2013, or 2016.

Prior to analysis, taxonomic nomenclature of detected species was updated for consistency with the American Ornithological Society checklist. We also removed all detections of individuals flying over the point but not interacting with the focal habitat (“flyovers”), and excluded species which form large flocks during the early breeding season that violate the assumptions of our model. We included data from the first two surveys conducted at each count station in each survey year, omitting data from an incomplete set of third surveys. We only modelled species with a sample size of at least 100 detections across the time series.

TABLE 1. Focal habitats, spatial sampling design, and sampling frames for six national parks in the Southwestern United States. Four-letter park abbreviations are described in the text. *N* refers to the species richness of birds detected during point counts in each focal habitat. Sampling frame is the area considered to be part of the focal ecological site at each park (see Methods for sampling frame delineation). Elevational range corresponds to the approximate maximum and minimum elevations of count stations. For a description of the three spatial sampling designs, see Methods.

Park	Focal habitat	Count stations	<i>N</i>	Sam-pling frame (ha)	Eleva-tional range (m)	Soil type(s)	Spatial sam-pling	Station spacing (m)	Habitat description
BAND	Mixed-conifer forest	100	70	150.60	2,690–2,950	Multiple, primarily Calaveras soil component	Grid	200	Closed canopy forest dominated by an association of ponderosa pine (<i>Pinus ponderosa</i>), Douglas fir (<i>Pseudotsuga menziesii</i>), white fir (<i>Abies concolor</i>), blue spruce (<i>Picea pungens</i>), Engelmann spruce (<i>Picea engelmannii</i>), limber pine (<i>Pinus flexilis</i>), and quaking aspen (<i>Populus tremuloides</i>)
CACH	Riparian woodland	91	76	159.12	1,690–1,780		Linear	150	Riparian areas dominated by various combinations of Russian olive (<i>Elaeagnus angustifolia</i>), tamarisk (<i>Tamarix ramosissima</i>), Goodding's willow (<i>Salix goodingii</i>), boxelder (<i>Acer negundo</i>), and cottonwoods (<i>Populus</i> spp.). Variable degrees of canopy and shrub cover
GRCA	Mixed-conifer forest	90	48	5363.00	2,550–2,780	Loamy Hills Cold and Loamy Hills	Cluster	200	See above
	Pinyon-juniper woodland	90	45	2138.68	1,950–2,020	Limestone Upland	Cluster	200	Overstory comprised of Utah juniper (<i>Juniperus osteosperma</i>) and twoneedle pinyon (<i>Pinus edulis</i>) with an understory of big sagebrush (<i>Artemisia tridentata</i>), Stansbury cliffrose (<i>Purshia stansburiana</i>), muttongrass (<i>Poa fendleriana</i>), and blue gramma (<i>Bouteloua gracilis</i>)
MEVE	Pinyon-juniper woodland	86	72	459.48	2,080–2,320	Loamy Mesa Top and Shallow Loamy Mesa Top	Grid	200	Woodland dominated by twoneedle pinyon (<i>Pinus edulis</i>) and juniper (<i>Juniperus</i> spp.) in the overstory (15–65% cover). The shrub layer contains antelope bitterbrush (<i>Purshia tridentata</i>) and Utah service-berry (<i>Amelanchier utahensis</i>), while mountain mahogany (<i>Cercocarpus montanus</i>), big sagebrush (<i>Artemisia tridentata</i>), fendlerbush (<i>Fendlera rupicola</i>), and Gambel oak (<i>Quercus gambelii</i>) are uncommon elements. A sparse herbaceous layer, prickly-pear cacti (<i>Opuntia</i> spp.), and Datil yucca (<i>Yucca baccata</i>) are also frequent
PEFO	Grass-land and shrubland	100	41	3515.21	1,640–1,760	Sandy Loam Upland and Clayey Fan	Cluster	250	Little to no tree cover (<10%). Includes both grasslands and mixed shrublands often dominated by alkali sacaton (<i>Sporobolus airoides</i>), but also including snakeweed (<i>Gutierrezia sarothrae</i>), prickly pear (<i>Opuntia</i> spp.), galleta (<i>Hilaria jamesii</i>) and grama grasses (<i>Bouteloua</i> spp.). Shrublands also occur dominated by sand sagebrush (<i>Artemisia filifolia</i>) and/or four-wing saltbush (<i>Atriplex canescens</i>), with or without an herbaceous layer
WUPA	Grass-land and shrubland	150	61	2598.15	1,390–1,730	Volcanic Upland and Loamy Upland	Grid	300	Mix of grass and shrubs with little to no woody vegetation. Common shrubs include fourwing saltbush (<i>Atriplex canescens</i>), rubber rabbit-brush (<i>Ericameria nauseosa</i>), snakeweed (<i>Gutierrezia sarothrae</i>), sand sagebrush (<i>Artemisia filifolia</i>) and Apache plume (<i>Fallugia paradoxa</i>). Dominant grasses are blue grama (<i>Bouteloua gracilis</i>) and James' galleta (<i>Pleuraphis jamesii</i>)

Climatic Covariates

We obtained climatic variables representing spring and summer drought and the timing of monsoon rainfall for each count station from ClimateNA (version 7.10), which produces locally downscaled point estimates of monthly historical climate data from gridded precipitation and temperature data (Wang *et al.* 2016). The downscaling accounts for both the latitude and elevation of the point location, and can produce estimates that closely match local weather station data in montane conifer forests (Ye *et al.* 2022). Because drought and heat waves often act in concert to affect avian densities (Albright *et al.* 2010b), we quantified drought using the Hargreaves climatic moisture deficit (hereafter CMD; Hargreaves 1994). CMD quantifies the amount of water lost to evapotranspiration (in millimeters) that is not replaced by precipitation; higher values therefore reflect both higher temperatures and reduced precipitation. We summed two historical seasonal CMD measures for the spring (March–May) and summer (June–August) periods from ClimateNA to obtain a single measure of drought stress during the nesting and fledging periods. While a second precipitation pulse may occur on the Colorado Plateau during the winter months (December–February), we did not include winter precipitation in our models because it was mechanistically unclear how this variable would directly affect breeding densities of migratory species (a majority of our study species) that are not present in the focal habitats during this time period. To quantify monsoon timing, we followed Saracco *et al.* (2022) in calculating the ratio of early season (June and July) to late season (August and September) historical monthly precipitation for a site; higher values therefore indicate an earlier onset of the monsoon rains. Because drought should affect nesting and fledging success, resulting in a 1-year lag between drought metrics and avian occupancy (Cady *et al.* 2019), we used CMD and monsoon timing from 2006 to 2017 in models of 2007–2018 adult density. Each lagged metric was also standardized by subtracting its 30-year (1971–2000) normal value for each count station.

Modelling Breeding-season Densities

Following Ray *et al.* (2017), we estimated trends in breeding adult density for each of 50 species by adapting a Bayesian hierarchical mixture model developed by Amundson *et al.* (2014) to data from the first 2 surveys conducted at each count station in each survey year. This approach combines an N -mixture model of abundance (Royle 2004) with models of detection based on time removal and distance sampling (Farnsworth *et al.* 2002) to allow for estimation of (1) availability or the probability that an individual was available for detection (p_a) by signaling its presence, (2) perceptibility or the probability that an available individual was perceived by the observer (p_d), and (3) true abundance during survey k (N_k). N_k was modeled as a Poisson random variable with mean λ_k (k in 1, ..., K surveys, where $K = \text{years} * \text{stations} * \text{surveys/station/year}$), and was related to the survey-specific count (y_k) as

$$y_k \sim \text{Binomial}(p_{d[k]}, n_k)$$

$$n_k \sim \text{Binomial}(N_k, p_{a[k]})$$

where n_k enumerates individuals available for detection.

We modeled survey-specific heterogeneity in p_a and p_d as detailed by Amundson *et al.* (2014). In brief, we assumed individuals were available with probability a during each time interval (each minute of an 8-minute survey), such that availability during interval j of survey k is $\pi_{jk} = a_k(1 - a_k)^{j-1}$, with corresponding conditional probability $\pi_{jk}^c = \pi_{jk}/p_{a[k]}$, where $p_{a[k]} = \sum_j \pi_{jk}$ is the probability of an individual being available during at least one interval of survey k . We modeled heterogeneity in availability using survey-specific covariates x as $\text{logit}(1 - a_k) = \beta_0 + \sum_x \beta_x x_k$. In the full model, we included 4 covariates of availability: minute of day, ordinal date (linear and quadratic terms), and cloud cover (less than or greater than 50%). To model perceptibility, we used observed horizontal detection distances and considered the probability that a bird was detected in distance bin $b = 1, \dots, B$ of survey k as $p_{d[bk]} = \sum_b \pi_{d[bk]}^c$, with corresponding conditional probability $\pi_{d[bk]}^c = \pi_{d[bk]} / \sum_b \pi_{d[bk]}^c$. We assumed a half-normal distribution of detection distances, $\pi_{d[bk]} = \exp(-r_b^2/2\sigma_k^2) / (2r_b\sigma_k) \exp(-r_b^2/2\sigma_k^2)$, where r_b is the midpoint distance of bin b , δ_b is the width of bin b , σ_k shapes the decline in detection with distance, and r_{\max} is the species-specific truncation radius or maximum detection distance. To avoid fitting sparse data from the tail of the detection-distance distribution, we omitted approximately 10% of the farthest observations of each species, or more if necessary to ensure that detection interval and detection-distance bin were statistically independent. To test for independence, we used analysis of variance and a conservative alpha value (0.10) whenever feasible, or the standard alpha value (0.05) when needed to avoid excessive truncation. We then modeled heterogeneity in p_d as $\text{log}(\sigma_k) = \text{log}(\sigma_0) + \sum_x \beta_x x_k$. In the full model, we included a fixed effect of environmental noise during the survey, and a random effect of surveyor.

Heterogeneity in mean population size was modeled as

$$\text{log}(\lambda_k) = \beta_{0k[\text{transect}[\text{station}]]} + \beta_1 t + \beta_2 \text{park}_k + \beta_3 t \text{park}_k + \beta_4 \text{CMD}_k + \beta_5 \text{monsoon timing}_k,$$

including a random effect of station nested within (riparian or cluster) transect, a global trend effect of year t , a fixed park effect, an interaction between park and year, and the year- and station-specific climatic variables described above. We reported the mean population density (number per hectare) across the sampled plots at each park, accounting for variation among species in sampled area (determined by the species-specific r_{\max}) as $\text{mean}(N_{k[\text{park}]}) / [\pi r_{\max}^2 / 10,000]$. We then calculated an overall density across parks as a weighted average based on the proportion of the total sampling frame area that occurred within each park (see Table 1 for sampling frame areas in ha). Because the closure assumption of N -mixture models is violated by individuals with home ranges that only partially overlap the survey area (determined by r_{\max}), our estimates of N_k and consequently of park-specific and overall density, are best interpreted as measures of the number of individuals using the sampling area rather than permanently present therein (Latif *et al.* 2016).

Parameter Estimation

All analyses were conducted in JAGS version 4.3.0 (Plummer 2003), called remotely using R version 4.1.1 (R Core Team 2021). Prior to analysis, we standardized each continuous covariate (setting mean = 0, SD = 1) to facilitate model convergence and comparison of effect sizes across variables. Kendall's rank correlation was <0.4 for all covariates except those

sampled in BAND; for analyses of species only encountered in that park, correlation was < 0.5 . We used vague normal priors with a mean of 0 and precision 0.001 for fixed effects and uniform priors bounded at 0 and 10 for the variance of random effects. We assumed random effects were normally distributed with mean 0 and precision τ ($\tau = 1/\text{variance}$). We drew posterior estimates from 3 Markov chains of 40,000 samples each with a burn-in of 10,000 samples and a thinning rate of 1 in 10, yielding a joint posterior distribution of 9,000 samples. We assessed the convergence of parameter estimates through inspection of Markov Chain Monte-Carlo summaries and the Gelman-Rubin potential scale reduction parameter, \hat{r} ; we considered chains to have converged for $\hat{r} < 1.2$ (Kéry and Schaub 2012). We measured goodness of fit for the availability and perceptibility sub-models using Bayesian P -values generated from posterior distributions, as suggested by MacKenzie *et al.* (2017) and as detailed by Amundson *et al.* (2018). We assumed a good fit for P -values near 0.5 and inadequate fit where $P < 0.2$ or $P > 0.8$. We assessed support for the effect of each covariate on abundance, availability, or perceptibility using the highest-density 95% Bayesian credible interval (BCI) on the estimate of its coefficient (β); a relationship was considered supported if the 95% BCI on β did not contain zero.

RESULTS

Over 9 survey years during the 12-year time series, 22 observers detected 57,834 individual birds of 134 species (a full list of species detected is available in the [Supplementary Material](#)) during 5,640 point-count surveys at 777 unique count stations grouped into 60 transects. We modeled breeding densities of 50 species (listed in [Figure 2](#)) after excluding those with insufficient sample size, those with social behaviors that violate model assumptions, and those for which models did not converge. For all modeled species except Western Meadowlark (*Sturnella neglecta*), we fitted the full model; for this species, we dropped all covariates of p_a (availability) and p_d (perceptibility) to obtain model convergence. For seven additional species that were encountered in one park each, we dropped the park and year * park terms. On average, we truncated $13.04 \pm 1.22\%$ (mean \pm SE; [Supplementary Material Table 2](#)) of the farthest distance estimates prior to analysis. The maximum effective detection distance (i.e., truncation distance) was 121.38 ± 10.96 m (mean \pm SE), though this value was highly variable across species (range: 41–400 m; [Supplementary Material Table 2](#)).

For modeled species, availability (0.77 ± 0.17 ; mean \pm SD of median values of p_a) was higher than perceptibility (0.41 ± 0.15 ; mean \pm SD of median values of p_d ; [Supplementary Material Table 2](#)). Bayesian P -values indicated adequate goodness of fit for sub-models of both p_a and p_d for all species ($0.2 < \text{Bayesian } P < 0.8$). Goodness of fit was generally good, with 46 and 48 species (of 50) having a Bayesian P -value between 0.4 and 0.6 for p_a and p_d respectively ([Supplementary Material Table 2](#)). We found supported effects for the 5 covariates included in the detectability sub-models, though effect sizes were generally small, and direction of effects differed considerably across species ([Supplementary Material Table 3](#)).

Trends in Population Density

Population density was highly variable across species and habitat categories (0.92 ± 1.36 individuals ha^{-1} , mean \pm SD of

median values; see [Figure 2](#), [Supplementary Material Table 4](#)). The effect of year on density was positive on average (0.19 ± 0.74 ; mean \pm SD of median β values), and we interpret the year effect as a population trend across all parks in which we modelled a given species' density ([Figure 2](#), [Supplementary Material Table 4](#)). Based on 95% BCIs, we found support for 13 population declines (26% of species) and 18 population increases (36% of species) across parks, and these trends were dependent upon habitat associations. Species sampled only in mixed-conifer forest ($n = 15$) were predominantly declining (-0.32 ± 0.67 ; mean \pm SD of median β values), with 8 supported population declines (2 supported population increases). Three generalist species (i.e., those encountered in 2 or more habitat types) typically associated with montane mixed-conifer forest also showed supported declines: Warbling Vireo (*Vireo gilvus*; -0.16), Western Tanager (*Piranga ludoviciana*; -0.26), and Mountain Chickadee (*Poecile gambeli*; -0.55 , median β values). By contrast, we found supported population increases for many bird species found only in grassland-shrubland ($n = 9$; 0.39 ± 0.91 , mean \pm SD of median β values; 5 supported population increases, 1 supported decline) and pinyon-juniper woodlands ($n = 7$; 0.89 ± 0.68 , mean \pm SD of median β values; 4 supported population increases, 1 supported decline). A notable exception to this trend was Brewer's Sparrow (*Spizella breweri*), a shrubland-associated species, which declined in density by $\sim 79\%$ over the monitoring period (-1.59 , median β). Most generalist species ($n = 16$) also showed a positive, if smaller, effect of year (0.21 ± 0.41 ; mean \pm SD of median β values), with 8 supported population increases. In many cases, we also observed differences in the sign or magnitude of the effect across parks, with supported park effects and park * year interactions ([Supplementary Material Table 5](#) and [Figures 3–5](#)).

Our park-level estimates correlated closely ([Figure 3](#)) with regional Breeding Bird Survey trend estimates for the Colorado Plateau (BCR S16; [Sauer *et al.* 2020](#)) over the same time interval ($n = 46$ spp., $\beta = 0.07$, $t = 2.40$, $P = 0.02$; linear model). Species declining in our focal parks but increasing regionally were Red-breasted Nuthatch (*Sitta canadensis*) and Ruby-crowned Kinglet (*Corthylio calendula*), both associated with montane spruce-fir forests. Conversely, species increasing in the parks but declining regionally tended to favor open woodlands and/or shrublands: White-breasted (*Sitta carolinensis*) and Pygmy Nuthatch (*Sitta pygmaea*), Black-throated Gray Warbler (*Setophaga nigrescens*), Bewick's Wren (*Thryomanes bewickii*), Chipping Sparrow (*Spizella passerina*), Blue-gray Gnatcatcher (*Poliophtila caerulea*), Gray Flycatcher (*Empidonax wrightii*), and American Robin (*Turdus migratorius*; [Figure 3](#)).

Climate Effects on Breeding Densities

We found support for both lagged climate effects (drought and monsoon timing in the year before sampling) on avian breeding densities, though the sign and magnitude of effects varied across species ([Figure 4](#), [Supplementary Material Table 6](#)). Drought, quantified as CMD, had an overall positive effect on avian densities (0.22 ± 0.56 ; mean \pm SD of median β values), with 21 supported positive effects (42% of species) and 6 supported negative effects. Once again, however, the effect size varied considerably by habitat type. Species found in high-elevation mixed-conifer forest responded positively

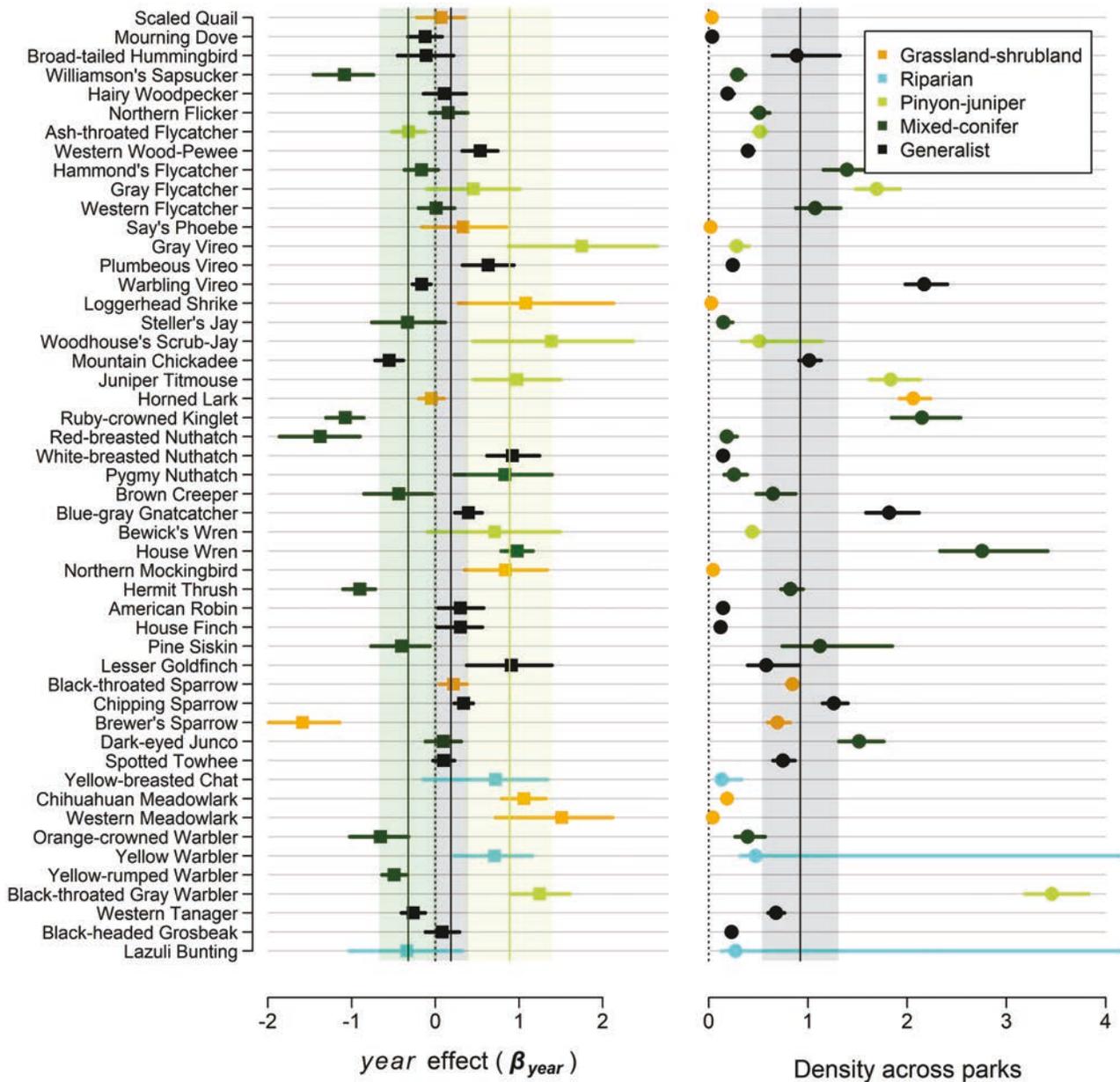


FIGURE 2. Across-park year effects (population trend estimates) and densities (birds ha⁻¹) for 50 Southwestern bird species. The year effect refers to the effect of increasing year over the timeseries on breeding densities after controlling for park and climate effects. The median value and 95% Bayesian credible interval are plotted for each species; species are listed in taxonomic order. Vertical lines and shading represent the mean and standard error for (1) all species (black line and gray shading), (2) pinyon-juniper species (light green line and shading), and (3) mixed-conifer species (dark green line and shading). The plotted habitat groupings showed large average effect sizes of year.

(0.33 ± 0.39 ; mean \pm SD of median β values, 11 supported positive responses), while species of middle-elevation pinyon-juniper woodland showed no effect (0.06 ± 0.21 ; mean \pm SD of median β values, 0 supported responses). Species of the low-elevation grassland-shrubland biome showed the most negative response to drought (-0.01 ± 0.89 ; mean \pm SD of median β values, 4 supported negative responses), though the effect sizes were more variable than in other habitat types. Most of the “generalist” species that occur in two or more habitat types were detected at higher elevations on average than the habitat specialists of the lowlands, and also showed a positive response (0.29 ± 0.35 ; mean \pm SD of median β values, 9 supported positive responses, 1 supported negative response). When we compared the drought response of a spe-

cies to the average elevation at which it was detected during surveys (a measure of its average breeding elevation on the Colorado Plateau), we found a trend of increasingly positive drought effects with increasing elevation (Figure 5A). After removing two outlier species with large effect sizes and very wide credible intervals (Scaled Quail [*Callipepla squamata*] and Yellow-breasted Chat [*Icteria virens*]), this relationship was statistically significant ($n = 48$ spp., $\beta = 0.0005$, $t = 3.28$, $P = 0.002$; phylogenetic linear model).

The effect size of monsoon timing on breeding densities the following year was near-zero when averaged across all modelled species (-0.01 ± 0.28 ; mean \pm SD of median β values; Figure 4). This result, however, belies the large number of supported positive (17) and negative (15) effects. Species of

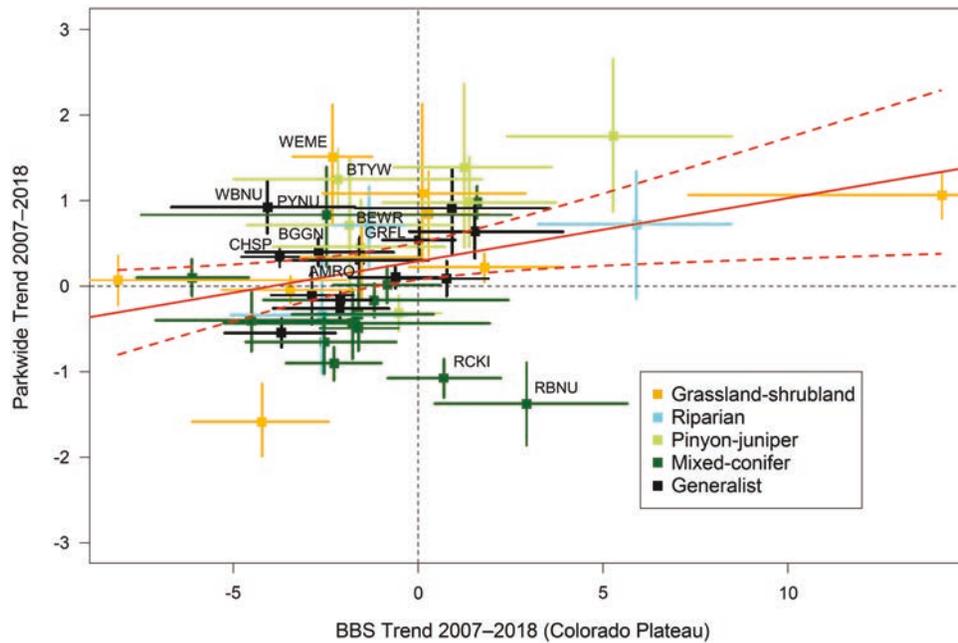


FIGURE 3. Local (parkwide) bird population trends reflect regional (Colorado Plateau) trends. Plotted points represent median (for parkwide trends) and mean (for regional trends) trend estimates, while vertical and horizontal lines represent the 95% BCIs. Regional trends correspond to trends for the Colorado Plateau/Southern Rockies Bird Conservation Region (S16) of the continent-wide Breeding Bird Survey (BBS), derived from [Sauer et al. \(2020\)](#). Trend line and confidence intervals are from a linear model of local trends as a function of regional trends. Labeled species indicate those declining locally but increasing regionally (lower right quadrant) and vice versa (upper left quadrant). Species codes are: AMRO = American Robin, BEWR = Bewick's Wren, BGGN = Blue-gray Gnatcatcher, BTYW = Black-throated Gray Warbler, CHSP = Chipping Sparrow, GRFL = Gray Flycatcher, PYNJU = Pygmy Nuthatch, RCKI = Ruby-crowned Kinglet, RBNU = Red-breasted Nuthatch, WBNU = White-breasted Nuthatch, WEME = Western Meadowlark.

grassland-shrubland tended to respond negatively to earlier monsoon rains (-0.26 ± 0.24 ; mean \pm SD of median β values, 6 supported negative responses), while species of the mixed-conifer forest responded positively to earlier monsoon rains (0.15 ± 0.26 ; mean \pm SD of median β values, 7 supported positive responses). By contrast, we found relatively small effect sizes for the generalist (-0.07 ± 0.27 ; mean \pm SD of median β values), and pinyon-juniper (0.002 ± 0.14 ; mean \pm SD of median β values) species. When we compared the effect size of monsoon timing against a measure of species-specific molt migration propensity from [Pyle et al. \(2018\)](#), we found that molt migrants were more likely to show positive effects of earlier monsoon rains than species that predominantly molt on the breeding ground ([Figure 5B](#)). After removing three molt migrants that are not known to molt in the monsoon region, the relationship was significant ($n = 26$ spp., $\beta = -0.53$, $t = -3.14$, $P = 0.004$; phylogenetic linear model). The 3 notable exceptions to this trend were Western Tanager (-0.16), Lesser Goldfinch (*Spinus psaltria*; -0.36), and Western Wood-Pewee (*Contopus sordidulus*; -0.52 , median betas).

DISCUSSION

We documented numerous supported effects of climatic variables on breeding bird densities, but with effect sizes and signs that varied by habitat association along a $\sim 1,500$ m elevational gradient. Species of montane mixed-conifer forest, both residents and migrants, showed declines in breeding density from 2007 to 2018, which generally matched regional population declines. By contrast, many species of grassland-shrublands and pinyon-juniper woodlands increased on the study plots. Species favoring woodlands and

shrublands increased locally despite regional declines, while spruce-fir associated mixed-conifer species (found at higher elevations) declined in the parks despite regional increases. As predicted, drought effects were increasingly positive at higher elevations: mixed-conifer forest species benefited from drought, while middle-elevation pinyon-juniper species were unaffected and grassland-shrubland species at the lowest elevations were negatively affected. Similarly, effects of monsoon timing were highly variable across habitat types and molt locations (breeding grounds, nonbreeding grounds, or monsoonal region of Mexico). Species of open grassland-shrubland responded negatively to earlier monsoon rains, while molt migrants benefited from earlier rains.

Declines of Mixed-Conifer Bird Species: Climate Effects on Conifer Forests

We found supported declines for 11 species that commonly use montane mixed-conifer forest in the southwestern United States, a result that corroborates the findings of [Rosenberg et al \(2019\)](#) of approximately 30% population declines in western North American forests. These declines at Bandelier NM and Grand Canyon NP match regional declines of mixed-conifer bird species across the Colorado Plateau and, given that they occur in large protected-areas, we believe they are primarily due to climate-driven habitat change. Western conifer forests have exhibited heightened tree mortality and dieback following extreme drought and subsequent bark beetle and disease outbreaks ([Williams et al. 2013](#), [Allen et al. 2015](#), [Goulden and Bales 2019](#)), which led to bird population declines in California's Sierra Nevada ([Roberts et al. 2019b](#)). These mortality events differentially affect different tree species and size categories, with many subalpine tree

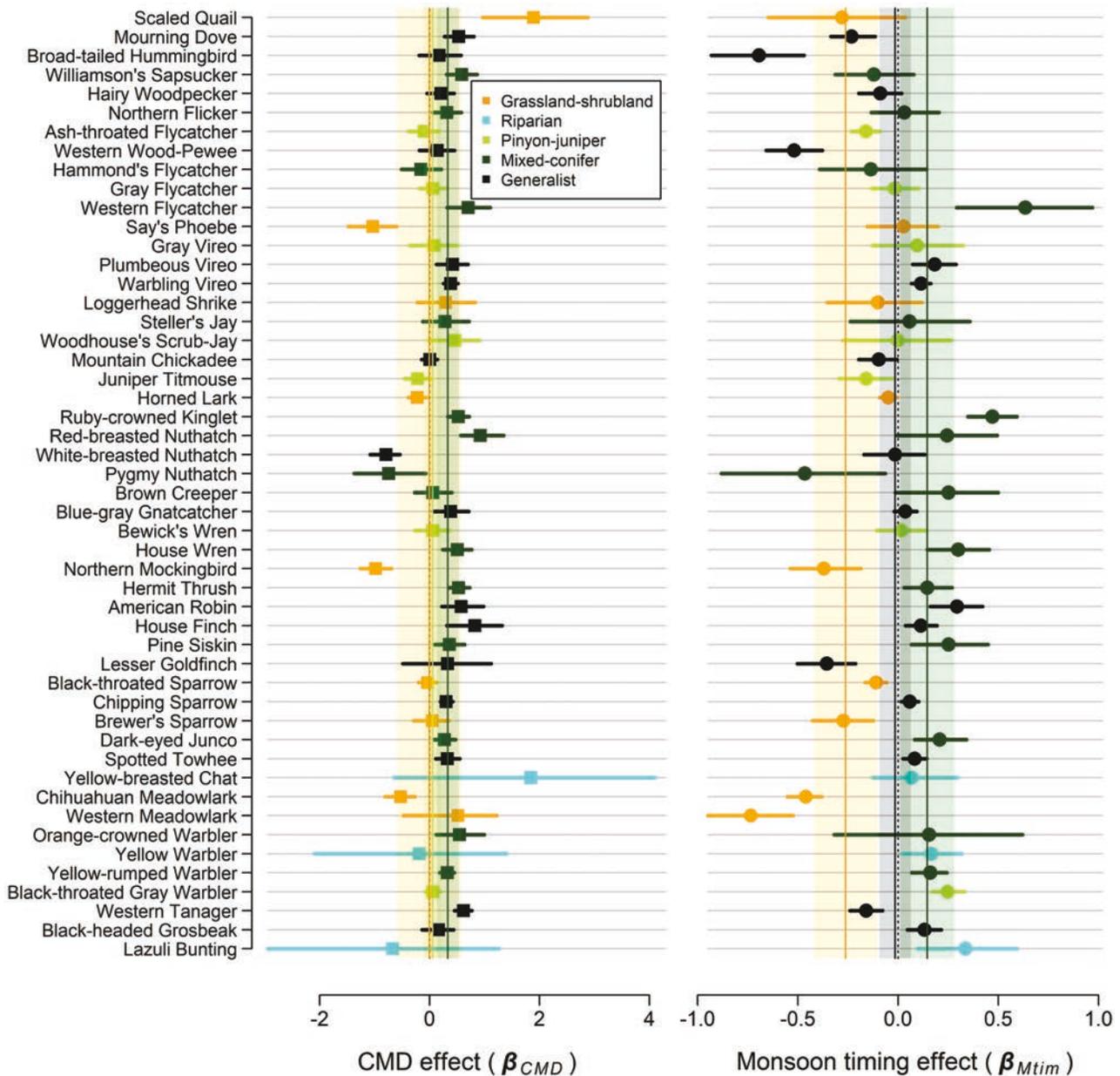


FIGURE 4. Effects of lagged spring and summer drought (CMD) and timing of monsoon rains on breeding densities of 50 Southwestern birds. Higher values of CMD indicate a warmer and drier spring and summer (March–August), while higher values of monsoon timing indicate earlier monsoon arrival (more precipitation in June and July). The median value of the posterior distribution and 95% Bayesian credible interval are plotted for each species; species are listed in taxonomic order. Vertical lines and shading represent the mean and standard error for all species (black line and gray shading), grassland-shrubland species (orange line and shading), pinyon-juniper species (light green line and shading) and mixed-conifer species (dark green line and olive shading).

species, such as Engelmann spruce (*Picea engelmannii*), and “corkbark” subalpine fir (*Abies lasiocarpa* var. *arizonica*; Ganey and Vojta 2011, Kane *et al.* 2014, Mathys *et al.* 2017), as well as large-diameter, old-growth trees (Ganey and Vojta 2011, Bennett *et al.* 2015) being more sensitive to drought stress. Thus, drought-associated mortality may disproportionately affect birds that associate with fir and spruce, such as Red-breasted Nuthatch and Ruby-crowned Kinglet, as well as species dependent upon old-growth conifers, such as Brown Creeper (*Certhia americana*). Drought-related mortality may also affect recruitment of young conifers (Ganey and Vojta 2011, Fettig *et al.* 2019), particularly white fir, which may be detrimental to species such as Hermit Thrush

and Orange-crowned Warbler that nest in young, dense fir stands. Periods of extreme drought also result in fewer, or less regular, conifer masting events (Woodward *et al.* 1994, Keyes and Gonzalez 2015), with negative consequences for species such as Mountain Chickadee, Pine Siskin (*Spinus pinus*), and Steller’s Jay (*Cyanocitta stelleri*) that rely on seed crops as energy sources during the fall and winter. Finally, drought-related floristic and structural changes to mixed-conifer forests may promote more open, park-like habitat (Clark *et al.* 2016) that benefits species such as Dark-eyed Junco (*Junco hyemalis*), Chipping Sparrow, American Robin, and Pygmy Nuthatch; these species all increased in the parks despite regional declines on the Colorado Plateau.

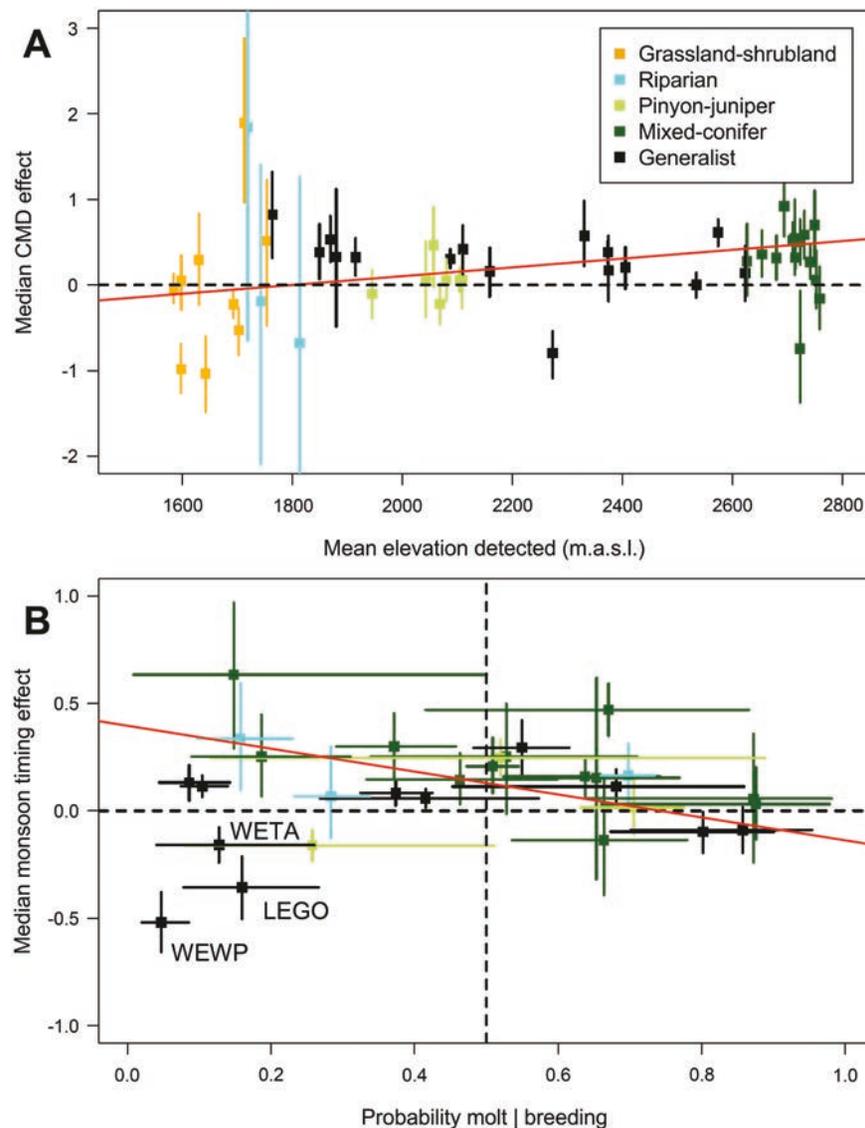


FIGURE 5. Breeding elevation and molt migration propensity influence the relationship between climatic variables and breeding densities. **(A)** Spring and summer drought (CMD) had an increasingly positive effect with average elevation of detection (a proxy for breeding elevation). High-elevation mixed-conifer forest birds responded positively to drought in the previous year, while pinyon-juniper species showed no response and grassland-shrubland species were negatively affected. **(B)** Earlier monsoon rains (higher monsoon timing values) are associated with increased densities of molt migrants in the following year, while species molting on the breeding or overwintering grounds tended to be unaffected or negatively affected. The measure of molt migration propensity (probability of molt | breeding) is from Pyle *et al.* (2018); only species included in that analysis ($n = 29$) are plotted. Notable exceptions to this trend are labeled. Trend lines are derived from phylogenetic linear models run using the *phylolm* package with a Brownian motion evolution model. Species codes are: LEGO = Lesser Goldfinch, WETA = Western Tanager, WEWP = Western Wood-pewee.

A second major threat to bird communities in Western montane conifer forests is the increasing prevalence of stand-replacing megafires (Mueller *et al.* 2020, Haggmann *et al.* 2021). For example, the 2011 Las Conchas Fire destroyed approximately 156,000 ha of predominately forest habitat in the Jemez Mountains (in and around BAND), while the 2006 Warm Fire burned 15,800 ha on GRCA's Kaibab Plateau. Such fires may destroy large expanses of mixed-conifer forest, fragment remaining habitat into patches, homogenize tree species composition by removing subalpine species (Cassell *et al.* 2019), and result in delayed tree mortality in the decades following the fire (Stoddard *et al.* 2018). While wildfire is a natural component of Southwestern conifer forest ecology, recent megafires, often in association with climate-driven changes to aridity, are causing regeneration failures in

burn patches that have resulted in type conversion to non-forest habitat (Stevens-Rumann *et al.* 2022), or changes in dominance to quaking aspen (*Populus tremuloides*) stands (Kulakowski *et al.* 2013). Wildfires can initially lead to several years of elevated productivity for mixed-conifer forest bird species (Saracco *et al.* 2018), though these effects vary across avian foraging guilds, and, where they burn at high severity and induce type conversions, may be counterbalanced by negative effects of habitat loss, habitat fragmentation, and floristic homogenization. For instance, high-severity megafires have destroyed approximately 19% of the habitat of Dusky Grouse (*Dendragapus obscurus*), a mixed-conifer forest specialist, in southern New Mexico since 2000 (Youtz *et al.* 2022). Other species, such as Yellow-rumped Warbler, Red-breasted Nuthatch, and Western Tanager responded

negatively to increased habitat fragmentation of montane conifer forest (Hejl *et al.* 2002), perhaps driving declines in fragmented post-fire forests. Still other species of woodpeckers, thrushes, finches, and sparrows may preferentially select for burned forests, however (Hutto *et al.* 2020).

Drought Effects on Birds Vary with Elevation

We found that lagged temperature and precipitation, as measured by CMD, were good predictors of avian densities in the succeeding year, echoing previous findings throughout the western United States (Albright *et al.* 2010b, Ray *et al.* 2017, Roberts *et al.* 2021). Like Albright *et al.* (2010a) and Cady *et al.* (2019), we found that drought effects on avian densities varied by elevation, with negative effects for grassland species in the lowlands and generally positive effects for montane forest birds. These positive effects of drought on montane communities are unlikely to be the result of an interaction between the CMD and year terms because drought conditions decreased over the timeseries (Pearson's $r = -0.36$ across all count stations). Instead, this result is likely driven by demographic effects of earlier snowmelt, which can positively influence western montane bird abundance and density (Hejl *et al.* 1988, Ray *et al.* 2017, Saracco *et al.* 2019). In the Sierra Nevada, for instance, earlier snowmelt led to an 18-day earlier breeding phenology (Saracco *et al.* 2019), which allows for second broods in some species, such as Dark-eyed Junco (Smith and Andersen 1985). In a population of single-brooded Dusky Flycatcher (*Empidonax oberholseri*) breeding in the Sierra Nevada, delayed nest initiation due to high snowpack led to smaller clutch sizes and reduced nest success (Pereyra 2011). Other negative effects of cold, wet springs on mixed-conifer bird populations may include higher mortality during spring cold snaps, and reduced recruitment of second-year birds (Desante 1990). While our result indicates that moderate spring and summer drought can have positive effects on western montane bird populations, this is not always likely to be the case. For example, positive effects of drought during the early breeding period may be offset by negative effects during the post-fledging period (Albright *et al.* 2010b) or reduced adult survival (Saracco *et al.* 2018). At longer timescales, the negative indirect effects of tree mortality may also counteract short-term demographic gains from drought (Roberts *et al.* 2019b; previous section). Reconciling the negative indirect effects of drought on habitat (tree die-off) with positive direct demographic effects is key for predicting future population trends of montane mixed-conifer birds in the Southwest.

Our finding that arid grassland-shrubland bird densities were negatively affected by drought is also well supported in the literature (George *et al.* 1992, Albright *et al.* 2010a, Conrey *et al.* 2016, Cady *et al.* 2019), and these negative effects are more pronounced for ground-nesting species (Albright *et al.* 2010b). Two ground-nesting birds, Chihuahuan Meadowlark (*Sturnella liliana*) and Horned Lark (*Eremophila alpestris*), showed supported negative drought effects, while other shrub-nesting passerines, including Black-throated Sparrow (*Amphispiza bilineata*) and Brewer's Sparrow, did not. Western Meadowlark (*Sturnella neglecta*), which prefers more mesic habitats bordering washes in the southwest, also appears to be more drought tolerant (this study, Roberts *et al.* 2021). Additionally, two aerially foraging species, Say's Phoebe (*Sayornis saya*) and Northern Mockingbird (*Mimus*

polyglottos), showed negative effects of drought, perhaps because aerial prey insects may be more sensitive to climate variables (Wheelwright *et al.* 2022).

The negative drought effect on ground nesters is likely driven by two concurrent mechanisms. First, drought reduces the height and density of grasses during the nesting season, and many species select for, and have higher nest survival in (Winter *et al.* 2005, Skagen *et al.* 2018, Bernath-Plaisted *et al.* 2021), taller and/or more extensive grass cover. This microhabitat likely allows for greater nest concealment from predators (Ruth and Skagen 2018) and reduces exposure of the nest (Hartman and Oring 2003). Second, days with high temperatures directly reduce nest success of grassland birds (Conrey *et al.* 2016, Zuckerberg *et al.* 2018, Gaudet *et al.* 2020). These effects may be due to both direct mortality of nestlings and eggs from heat stress, reduced provisioning behavior of heat-stressed parents (Ruth *et al.* 2020), and nest abandonment during extreme conditions (George *et al.* 1992). Shrubs are thought to act as thermal refugia in Southwestern grasslands (Ruth *et al.* 2020), and their deeper root systems are less influenced by short-term drought (Hoover *et al.* 2017), which may explain why shrub-nesting species are relatively drought-tolerant. The increased prevalence of spring drought and hot days during the breeding season is therefore expected to have negative effects on ground-nesting birds, yet populations of these species may recover quickly with a more favorable climate (George *et al.* 1992). While these negative effects of drought may appear to contrast with observed population increases of many grassland species we observed, they may be explained by the relative drought tolerance of shrub-nesting species and the positive effect of later monsoon rain timing (next section).

Location and Timing of Molt Explain Effect of Monsoon Rain Timing

We found a significant trend of molt migrants responding positively to earlier monsoon rains, while species that molt predominantly on the breeding ground showed non-supported or negative effects. Stop-over molt migration in the North American monsoon region before continuing to nonbreeding ranges further south is common in birds of western North America (Rohwer *et al.* 2009b, Chambers *et al.* 2011, Pyle *et al.* 2018), particularly in species that breed in more arid habitats (Pageau *et al.* 2020). Earlier monsoon rains likely lead to an earlier summer green-up and pulse of food on the molting grounds, which is important for stopover molt migrants that molt rapidly (de la Hera *et al.* 2012), and time their arrival on the molting grounds with historical peak green-up (Siegel *et al.* 2016). Delayed arrival of monsoon rains projected by some climate models could therefore result in a "phenological mismatch" between the arrival of molt migrants in the monsoon region and the peak pulse of food resources needed to molt. Many young-of-year of molt migrant species migrate to the molting grounds later than adults and appear in some cases to molt faster (Carlisle *et al.* 2005, Butler *et al.* 2006); the constraints of a faster molt might be more costly when the monsoon food pulse arrives late. In support of this theory, Saracco *et al.* (2022) found higher recruitment of Black-headed Grosbeak (*Pheucticus melanocephalus*) in years following earlier arrival of rains on the monsoon-region molting grounds. In earlier, wetter monsoon seasons, molt migrants also use a greater diversity of habitats on the molting grounds

(Chambers *et al.* 2011), perhaps decreasing inter- and intra-specific competition. The 3 exceptions to the above trend are species that do not molt in the monsoon region (Figure 5B). Western Wood-Pewee molts on its nonbreeding grounds in South America (Bemis and Rising 2020), interior populations of Lesser Goldfinch molt after the monsoon rains in October and November (Watt and Willoughby 2020), and many Western Tanager, particularly young-of-year, molt in montane habitats on the breeding range (Butler *et al.* 2002). Therefore, the effects of monsoon timing on avian densities in the Southwest appear to be driven by dynamics on the molting ground rather than the breeding ground.

By contrast, negative effects of earlier monsoon rains were primarily observed for species that breed in grassland-shrublands. Precipitation during the breeding season, particularly intense storms, has been linked to reduced daily nest survival in many grassland birds (Skagen and Adams 2012, Conrey *et al.* 2016, Ruth and Skagen 2018, Zuckerberg *et al.* 2018). Monsoon storms might negatively affect nest success through a variety of mechanisms. For one, nestlings of ground-nesting species may face direct mortality from flooding of the nest or hypothermia during violent storms (Fisher *et al.* 2015). Second, rainstorms reduce parental provisioning of young in the nest, causing food limitation (Fisher *et al.* 2015, Oberg *et al.* 2015). Frequent provisioning visits after heavy rainfall events may also increase nest conspicuousness, leading to increased predation. Third, the higher winds and humidity associated with storm events may increase the olfactory conspicuousness of nests, leading to higher predation, though empirical evidence for this hypothesis is limited (Ruzicka and Conover 2011). Because both ground-nesting and shrub-nesting species showed negative effects of monsoon rains, it is likely that direct nestling mortality from storms is not the sole mechanism. Later monsoon rains are therefore expected to increase populations of grassland-shrubland species in the Southwest, though it is unclear if monsoon effects will counteract the negative effects of drought.

Conclusions

Drought and the changing timing of monsoon rains are both positively and negatively impacting the breeding densities of birds in national parks of the southwestern United States. Climate effects on breeding densities varied along the elevational habitat gradient, indicating that a habitat-specific approach (or species-by-habitat approach; Roberts *et al.* 2021) may be most productive for understanding how birds of the region will respond to future climate scenarios. Mixed-conifer forest species at the southern, “warm edge” limits of their breeding ranges appeared to be declining as the result of climate-change-related habitat changes, and there is an urgent need to understand the mechanisms linking changes in forest structure and floristics to reduced habitat suitability. Paradoxically, the lower snowpack associated with drought years appears to help populations of mixed-conifer birds, though additional work testing whether this remains true during severe drought, and how much drought-associated tree mortality counteracts this phenomenon, is needed. We also found the potential for both drought and monsoon timing to impact densities of arid grassland-shrubland birds, with negative effects of drought and positive effects of later monsoon rains. Further work examining how drought and monsoon

timing effects interact, and what mechanisms (i.e., adult survival, nest success, fledgling survival) are responsible for these effects are needed to help conserve declining grassland bird populations in the Southwest. Finally, later monsoon rain arrival has the potential to create a phenological mismatch between migration timing and the pulse of monsoonal resources for molt migrant species. However, the movement ecology of molt migrants is still poorly known and highly variable across age classes and populations of the same species, complicating our understanding of climate effects (Pyle *et al.* 2018). The molting grounds are rarely incorporated into conservation plans for Neotropical migrants or discussed in the context of climate change (Leu and Thompson 2002), yet our results indicate an imperative need to better understand this little-known period of the yearly cycle and account for changes to the North American monsoon in conservation planning for migratory birds.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

Field data collected for this study were observation only, and no birds were captured or manipulated. Research permits were approved by all national parks prior to conducting field surveys.

Conflict of interest statement

The authors have no conflicts of interest to declare.

Author contributions

H.J. and R.S. formulated the research questions and hypotheses. C.R. developed the analytical framework, and H.J. and C.R. analyzed the data. M.J. contributed substantial resources, data, and funding. H.J. wrote the paper, and all co-authors reviewed and substantially edited drafts of the manuscript.

Data availability

Analyses reported in this article can be reproduced using data and code archived on the Integrated Resource Management Applications (IRMA) repository. The data is available at <https://doi.org/10.57830/2302328> and the code (R scripts) is available at <https://doi.org/10.57830/2302329>.

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