Molting strategy influences vulnerability to climate change in migratory birds

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Manuscript elements: Figure 1, figure 2, figure 3, figure 4, figure 5, figure 6, supplemental PDF. Figure 1 is to print in color.

Keywords: molt, migration, phenological mismatch, climate change, North American monsoon, community science.

Manuscript type: Major article.

Prepared using the suggested LaTeX template for *Am. Nat.*

Abstract

Molting, the process by which birds replace their feathers, is a necessary annual event with major ramifications for fitness. However, few studies have described threats to birds during molt. Here, we combine long-term climate and bird occurrence datasets to investigate the potential for ongoing anthropogenic shifts in precipitation volume and phenology in southwestern North America to influence bird populations that molt in the region. Our analyses of eBird records reveal intraspecific variation in molting location, which may heighten resistance to interannual variation in precipitation. However, we demonstrate widespread declines among molt-migrant populations following weak and late monsoons, suggesting that this variation is insufficient to buffer many against the current rate of environmental changes. We hypothesize that deviations from historical precipitation regimes increasingly deprive birds of sufficiently predictable resources to supply molt, elevating mortality. Finally, we present associations between sensitivity to precipitation variation and recent population trends, demonstrating that anthropogenic shifts in resource availability during molt have already contributed to population declines and pose a growing threat to western North American birds. Overall, our study demonstrates that anthropogenic shifts away from historical patterns of resource availability may compromise the self-maintenance and recovery of individual organisms, representing an overlooked threat to biodiversity.

Introduction

By altering weather patterns, temperatures, and precipitation regimes more rapidly than ever before in the history of life on earth (Cook and Seager, 2013; Shuman, 2012; Trenberth, 2011), anthropogenic climate change poses an unprecedented threat to biodiversity (Bellard et al., 2012). While some taxa appear relatively resilient to the impacts of climate change (Moritz and Agudo, 2013), others are extremely sensitive (Benkman, 2016; Brawn et al., 2017; Cleland et al., 2012). If we hope to mitigate future biodiversity loss associated with climate change, there is an urgent need to identify which taxa are most threatened by climate change and to understand the reasons for their vulnerability (Qvarnström et al., 2016).

Many previous studies have demonstrated that anthropogenic climate change can threaten populations by imparting phenological mismatch between individual life history events and optimal environmental conditions (Zimova et al., 2019). For example, advancing spring green-up increasingly challenges animals to align migration and breeding with necessary pulses in resource availability, reducing individual fitness and contributing to population declines (Aikens et al., 2020; Møller et al., 2008; Senner et al., 2017). The extent of phenological mismatch depends on individual flexibility, intraspecific variation, and rates of adaptive evolution (Zimova, 2016). Therefore, without adequate understanding of natural history variation throughout the year, we may fail to appreciate the true toll of phenological mismatches on wild populations. Current knowledge gaps reflect historical research biases; across taxa, most studies have focused on the most accessible populations, life stages, and periods of the annual cycle (Ådahl et al., 2006; Marra et al., 2015; Paaijmans et al., 2007; Small-Lorenz et al., 2013). Thankfully, novel datasets and new technology have enabled researchers to begin addressing historically neglected subjects.

While the vast majority of studies in ornithology have focused on breeding populations (Kiat, 2023; Leu and Thompson, 2002), recent efforts to strengthen conservation strategies have sparked an explosion of research on migrating and overwintering populations in the past decade (Leu and Thompson, 2002). This effort has been described as a “full annual cycle” approach to conservation (Hostetler et al., 2015). For instance, long term datasets, such as eBird, have enabled ornithologists to describe shifts in migratory phenology and behavior in response to climate change (Covino et al., 2020; Wilson, 2017). Additionally, increasing accessibility to techniques such as individual tracking and year-round genetic sampling is rapidly illuminating migratory routes, nonbreeding sites, and stopover locations for a variety of species (Kramer et al., 2018; Linscott et al., 2024; Ruegg et al., 2020; Tonra et al., 2019). With a growing understanding of the habitats bird populations rely on throughout the year, researchers have been able to prioritize specific locations for protection and to explore connections between nonbreeding habitat quality, individual fitness, and population trends (Kramer et al., 2018; Powell et al., 2021; Rushing et al., 2015).

While these studies are rapidly filling gaps in our understanding of nonbreeding ecology, we still know little about molt (Kiat, 2023; Leu and Thompson, 2002; Pillar et al., 2015). Molt, the process by which birds systematically lose and replace their feathers, is an understudied life history trait with important ramifications for fitness and conservation (Kiat, 2023; Tonra and Reudink, 2018). Birds rely on feathers for a wide variety of functions critical for survival and reproduction, including flight, communication, and thermoregulation (Benton et al., 2019; Chen et al., 2021; Gill, 2007; Terrill and Shultz, 2023). Because exposure to the sun, abrasive vegetation, and parasites wear feathers down over time, most birds molt body and flight feathers at least once per year to maintain sufficient feather function (Howell, 2010; Terrill et al., 2020). This annual full-body molt (hereafter prebasic molt), which typically occurs following breeding, represents one of the most metabolically demanding events in the avian annual cycle (Murphy and Taruscio, 1995). Dolnik and Gabrilov observed Chaffinches (*Fringilla coelebs*) to increase their caloric intake by approximately 50% during molt (1979). This increase supplies not only feather keratin synthesis, but also associated physiological processes (e.g., heightened whole-body protein synthesis during molt) (1995). The high metabolic demands of feather protein synthesis have selected for populations to molt at times and locations with high resource availability and to minimize temporal overlap between molt and other expensive life history events (i.e., reproduction and migration). These temporal constraints are especially pronounced for migratory populations, which must complete molt outside of externally determined migratory and physiological transition periods

(Ramenofsky and Wingfield, 2006; Terrill, 2018).

Because molt is necessary, metabolically demanding, and temporally restricted, a potential process through which anthropogenic climate and landscape changes may threaten bird populations is by shifting the spatiotemporal distribution of resources away from historical molting periods and regions. If a bird is deprived of resources during molt, genetic regulation of molting phenology may force it to invest in feather growth at the expense of body condition, a trade-off that in extreme cases can lead to death (Murphy et al., 1988; Saino et al., 2013). Resource-deprived birds may also grow poor quality feathers that function suboptimally and are likely to break, greatly elevating mortality risk until the next molting event (Holmgren and Hedenström, 1995). Even for populations in which molt phenology and intensity are flexible and strongly influenced by proximate environmental cues, deviations from historical patterns in resource availability may force individuals to delay molt or migrate farther in search of sufficient resources, incurring higher risks by retaining old, worn feathers for longer and reducing the amount of time available for feather growth (Terrill, 2018). Therefore, we predict that if populations are unable to shift molting strategies fast enough to track anthropogenic changes in resource distributions, individuals will struggle to supply molt, populations will suffer higher annual mortality rates, and species will decline (Marra et al., 2015).

Western Molt-Migrants and the North American Monsoon

North American birds exhibit tremendous variation in molting strategies (Pyle et al., 2018; Rohwer and Irwin, 2011), and therefore present ample opportunities to study how conditions in molting habitats influence population dynamics. Our study focuses on migratory passerine taxa that breed in the western half of the continent and exhibit a strategy known as molt-migration, in which they spatially isolate molt from other events in the annual cycle (Tonra and Reudink, 2018). After breeding, individuals migrate to distinct molting grounds in the Southwest, carry out a complete body and flight feather molt during an extended stopover, and then continue migrating to nonbreeding areas farther south in Central America (figure 1) (Rohwer and Irwin, 2011). This strategy evolved convergently across over 50% of western passerine species, likely as a means to avoid molting in their breeding territories, which become dry and unproductive in late summer (Pageau et al., 2020; Rohwer and Irwin, 2011; Rohwer et al., 2008). Additionally, molt-migration synchronizes the metabolic demands of feather growth with the North American monsoon (Pyle et al., 2009; Rohwer and Irwin, 2011), which brings abundant precipitation to the southwestern United States and western Central America in late summer (Cook and Seager, 2013). Monsoon precipitation, along with associated temperature suppression and increased soil nutrient availability, induces an annual productivity boom in otherwise dry, resource-poor habitats (Higgins et al., 1999). Specifically, monsoon rains precipitate a pulse in arthropod abundance, which in turn provides birds with sufficient nutrition for molt (Rohwer et al., 2005; Rowe et al., 2024).

A reliance on relatively predictable monsoonal productivity to supply nutrients necessary for prebasic molt likely renders western molt-migrants sensitive to variation in the timing and total precipitation of the North American monsoon. Therefore, spatiotemporal shifts in monsoon precipitation may be one of the most consequential manifestations of climate change for these populations. Historically, monsoon precipitation has fallen primarily from June through September, enabling molt-migrant passerines arriving in late summer to stopover during peak monsoon productivity (Bridge et al., 2016; Pillar et al., 2016). However, because monsoon precipitation originates through a discrepancy between sea surface and land temperatures, general circulation models have projected that warming in the Pacific Ocean will shift the North American Monsoon later in the fall (Cook and Seager, 2013) and Forecast-Oriented Low Ocean Resolution models project a significant reduction in overall monsoon precipitation (Pascale et al., 2017) (although there is some disagreement among different climate models (Munson et al., 2022)). Furthermore, rising temperatures may accelerate the rate at which soil dries following monsoon rains and agricultural landcover conversion may reduce the capacity of ecosystems in the Southwest to respond to monsoon precipitation (Peters et al., 2010; Qiu and Ben-Asher, 2010), reducing overall resource availability for molting birds. If avian populations are unable to track rapidly changing patterns in monsoon productivity through individual flexibility or evolutionary shifts in prebasic molt phenology, there may soon be a severe mismatch between monsoonal productivity and when individual birds initiate prebasic molt (figure **??**) (Zimova, 2016). In this study, we use long-term bird occurrence and climate datasets to estimate the extent to which ongoing shifts in precipitation volume and phenology of the North American monsoon threaten molt-migrant bird populations. Specifically, we explore interannual variation in species occurrence to estimate instraspecific variation in molting strategies, which we hypothesize to be a potential mechanism of resistance. We then investigate whether or not intraspecific variation can sufficiently buffer species against anthropogenic changes in monsoon precipitation regimes by testing for associations between interannual population abundance variation and deviations from historical monsoon conditions. By interpreting the strength of these associations as proxies for a population's sensitivity to ongoing shifts in monsoon phenology and volume, we then estimate the extent to which this sensitivity has already influenced molt-migrant population trends.

Methods

Monsoon precipitation data preparation

We performed all data preparation and analyses for this and all subsequent sections in Program R (version 4.3.1). First, we downloaded daily precipitation estimates from the Daymet climate database (Version 4, R1) using the "daymetr" package (Koen et al., 2018). While several aspects of the North American monsoon may facilitate molt (e.g., temperature suppression), monsoon precipitation has been associated with increases in arthropod abundance important for meeting the metabolic demands of molt (Rowe et al., 2024). The Daymet dataset includes daily climatic estimates for 1 x 1 km grids grouped by 2 x 2 degree tiles throughout North America. We imported daily precipitation data for tiles overlapping with potential molting areas in the Southwest from 1980 (the start of the Daymet dataset) through 2022 (Pyle et al., 2009; Young, 1991). We further subset Daymet tiles into four different regions (the Sonoran Desert, southern Baja California, the Central Mexican Pacific coast, and the southern Mexican Pacific coast), which represent potential areas where molt-migrants could stopover (figure **??**). Previous studies of banding station records and museum specimens have identified the Sonoran Desert and southern Baja California as molting locations for at least some molt-migrants (Pyle et al., 2009; Young, 1991), but recent evidence of intraspecific variation in molting location presents the possibility that individuals or populations could stopover in different areas throughout the monsoonal region (Pillar et al., 2015; Savides, 2022).

To describe interannual variation in monsoon precipitation characteristics at potential molting areas, we first estimated precipitation on each day of each year within each monsoonal subregion as the sum of predicted precipitation across all 1 x 1 km grids within the subregion. Unfortunately, Daymet does not include uncertainty associated with daily grid precipitation estimates. However, cross validation between daily precipitation recorded at weather stations and Daymet predictions at the same locations found predicted and observed values to be extremely close in the southwestern United States and western Mexico. Mean square error in many areas within the broader monsoonal region was found to be less than 0.23 mm per day (Thornton et al., 2021). Therefore, while in a perfect world we would be able to propagate uncertainty in the Daymet daily precipitation estimates throughout our transformations and analyses, we feel that generating monsoon metrics from the point estimates alone is sufficient. To estimate monsoon precipitation volume in each subregion in each year, we simply added the cumulative precipitation estimates for each day throughout the monsoonal period, which we defined as June through October (Cook and Seager, 2013; Pascale et al., 2017). We used the same method to estimate early season (June and July) and late season (September and October) monsoon precipitation for every year (Cook and Seager, 2013). We calculated several metrics to describe interannual variation in monsoon phenology. First, we estimated the monsoon halfway point within each subregion in each year as the number of days beginning on June 1st that it took to reach half the cumulative June - October precipitation. We also estimated monsoon start date and end date for each subregion in each year as the first and last instances when the subregion experienced three consecutive days with precipitation estimates above the median daily value for June through October (Ellis et al., 2004). Before analyses, we transformed all estimates of monsoon precipitation volume and phenology into anomalies centered on 0 by calculating differences between the estimates for each year and the mean value for each subregion across all years in the dataset.

Exploring intraspecific variation in molting strategies as a potential mechanism of resistance against shifting monsoon conditions

Intraspecific variation in molting strategies may reduce the toll of phenological mismatch between monsoonal productivity and individual molting effort on species abundance (Oney et al., 2013). This variation may result from either individual flexibility in molting phenology and location or genetic variation (Stager et al., 2024). Regardless of the underlying mechanism, however, intraspecific variation in molting strategies should be proportional to interannual variation in species occurrence during molt. For instance, if individual birds can flexibly alter prebasic molt phenology, location, and intensity in response to monsoon conditions, shared responses among individuals attempting to align feather growth with sufficient resource availability will manifest as species-level shifts in postbreeding distribution within a given year (Bock and Lepthien, 1976; Dougherty and Wilson, 2018). Alternatively, if molt phenotypes are regulated primarily by genetic variation, natural selection will result in heightened relative abundance of strategies that enable individuals to align feather growth with monsoonal productivity (Grant and Grant, 1995). Therefore, interannual variation in monsoon location and phenology will similarly manifest as spatial and temporal variation in species abundance (Campbell-Staton et al., 2017).

We used eBird data to quantify interannual variation in the arrival, stopover abundance, and stopover duration of molt-migrant taxa at monsoonal molting areas and then tested for species-level responses to monsoon conditions. eBird (http://www.ebird.org), a massive database of bird occurrence records submitted by volunteer amateur naturalists, has become an invaluable tool for estimating the distributions, abundances, population trends, and movements of bird species throughout the world (Dougherty and Carling, 2024; Minor et al., 2022; Sullivan et al., 2009; Walker and Taylor, 2017). Birders submit observations to eBird throughout the year, making the dataset useful for studying some aspects of migratory and molting strategies (Youngflesh et al., 2021). We downloaded all vetted records for each species as well as data for all eBird checklists submitted to the eBird basic dataset (Version ebd_relAug-2023) from Greenlee, Graham, Cochise, Santa Cruz, Pima, Pinal, Gila, Maricopa, La Paz, and Yuma counties in southern

Arizona. These counties comprise previously identified molting locations for many molt-migrant populations (Pyle et al., 2009; Young, 1991). Unfortunately, we were unable to analyze data from potential molting areas in western Mexico due to the paucity of eBird records in this region. We used the "auk" package in R to combine occurrence records with the full sampling event data to generate presence/absence datasets for each species. We then filtered these datasets to include only complete stationary and traveling checklists submitted between June 1st and October 31st (Strimas-Mackey et al., 2018). This date range includes the interval during which molt-migrant populations are expected to stopover in the monsoonal region, buffered by a month on either side to enable more accurate estimation of when most individuals arrive at and depart from molting habitats (Pillar et al., 2016, 2015; Pyle et al., 2009; Rohwer et al., 2005; Young, 1991). We also removed checklists started before 5:00 and after 19:00 local time to exclude nocturnal migrants. Lastly, we excluded checklists submitted before 2007 and after 2022. Although eBird was established in 2002, there are comparatively few records from the project's early years (Johnston et al., 2019; Minor et al., 2022).

We used the R package "rstanarm" to interface with Stan and fit generalized additive models (GAMs) in a Bayesian framework to illustrate molt stopover phenology for each species in each year in southern Arizona (Carpenter et al., 2017; Goodrich et al., 2020). Adapting the analysis pipeline established by Youngflesh et al. (2021) to predict species arrival date on breeding grounds, we modeled whether or not a species was detected on an eBird checklist as a Bernoulli-distributed random variable and the probability that the species would be detected as a logit-linear function of eBird checklist duration (in minutes) and day-of-year as a penalized thin-plate regression spline smoother with 30 knots. We assumed

$$\begin{gathered} y_i \sim \text{Bern}(p_i) \\ \text{logit}(p_i) = \alpha_{\text{GAM}} + \beta_{\text{GAM}}\text{T}_i + f(\text{Day}_i) \end{gathered} \tag{1}$$

where i is a given checklist, y is binary response of whether or not the focal species was recorded in the checklist, p is the probability that the species was detected, α_{GAM} is the intercept, $\beta_{GAM}T_i$ is the effect of checklist duration on detection probability, and $f(Day_i)$ is a smooth function for day-of-year. Although we considered including checklist distance and the number of observers as predictors, many checklists do not include these data. Modeling occurrence as a GAM flexibly accommodates potential interannual variation in presence over time (Pyle et al., 2009; Youngflesh et al., 2021). For each year, we ran the model with four chains, each for 1,500 iterations and a warmup of 750 iterations (Youngflesh et al., 2021). We examined Rhat and effective sample size to assess model convergence.

To estimate interannual variation in molting strategies for each species, we extracted a suite of values from each iteration of all models. First, we calculated the first date at which each model iteration predicts the species to have a probability of occurrence intermediate between the maximum and the minimum probabilities of occurrence prior to the date at which it reaches the maximum probability. We chose to represent arrival on molting grounds as the date when the species reached half its maximum, rather than the date of the maximum itself, as estimates for maximum date usually had much wider credible intervals. For each year, we calculated this half-maximum estimate for each posterior chain iteration to generate a probability distribution. We applied a similar approach to generate probability distributions for peak abundance in molting areas (the maximum probability of occurrence during the monsoonal period for the species) and molt stopover duration (the number of days after the half maximum date with predicted probability of occurrence greater than or equal to the occurrence probability at the half-maximum) for each species in each year (figure **??**).

Many focal molt-migrant species breed broadly throughout western North America, including in southern Arizona. Unfortunately, seasonal variation in the occurrence of local breeding populations may attenuate or completely overshadow signatures of migrants arriving in the region to molt, making it difficult to consistently distinguish and describe interannual variation in molt stopover characteristics. Other focal species are rarely recorded in southern Arizona, resulting in high uncertainty in our estimates. Therefore, we decided to analyze eBird records for only one molt-migrant species, the Lazuli Bunting (*Passerina amoena*), which does not breed in southern Arizona but is regularly abundant in the region during prebasic molt and migration (Dougherty, 2023; Young, 1991). Due to a shared molt-migration strategy, we interpret relationships between interannual variation in monsoon precipitation and postbreeding occurrence of *P. amoena* to be representative of molt-migrant taxa as a whole. Previous studies documenting similar interannual variation in molting habitat among molt-migrant species, including *P. amoena*, support this assumption (Pyle et al., 2009).

To estimate intraspecific variation in prebasic molt phenology, intensity, and location in response to monsoon conditions in *P. amoena*, we first calculated the median of the posterior distribution for each molt stopover parameter (arrival date, peak abundance, and stopover duration) in each year. We then modeled these parameters as a function of year, total monsoon precipitation for that year, monsoon halfway point, monsoon start date, and monsoon end date based on Daymet data from the Sonoran Desert subregion, which broadly overlaps with the counties in Southern Arizona from which we included eBird records (figure **??**). Because there were only sixteen observations in the final model dataset (2007-2022), we ran the models for each predictor independently to avoid overfitting. We ran each variant as a generalized linear model using the the "brms" package in R as an interface with STAN (Bürkner, 2017; Carpenter et al., 2017), assuming a Poisson distribution with a logarithmic link for models with the species' arrival date and stopover duration as response variables and a beta distribution with a logit link for models with maximum occurrence probability as the response (Zuur et al., 2009). We assumed weakly informative priors centered on beta coefficient estimates from frequentist models including the same predictors and with a variance of 10. We ran all models in three replicate chains of 3,000 iterations each and discarded the first 1,000 iterations from each chain as burn-in. We examined trace-plots to assess model convergence and plotted posterior predictions with observed data to assess model performance. To identify specific characteristics of monsoon precipitation that impart the strongest influence on molting behaviors, we compared WAIC values among models with different predictors (Watanabe, 2010).

Population selection

Population dynamics are influenced by many potential factors, such as conditions during breeding, migration, and nonbreeding (Garcia-Walther et al., 2024; Senner et al., 2019). Therefore, we predict that the effect size of conditions during molt on bird populations to be small (Pillar et al., 2015). To be able to potentially detect this effect, we employed a broad comparative approach testing whether monsoon conditions significantly influence molt-migrant population dynamics. Specifically, we tested for two different conditions, which if both met would signal a causal influence of molting conditions: (1) First, molt-migrant populations, which vary in natural history traits but share a reliance on monsoonal productivity during prebasic molt, will exhibit similar responses to interannual variation in monsoon precipitation (e.g., most populations will be more likely to decline in breeding abundance following a monsoon that is dryer than historical average). (2) Second, non-molt-migrant populations, which may be ecologically similar to molt-migrant populations but carry out prebasic molt in places other than the monsoonal region, will not show consistent responses to monsoonal variation.

We selected 14 taxa documented (or in two cases strongly inferred) to carry out prebasic molt in the monsoonal region (table **??**). For every molt-migrant taxon, we also selected a closely related taxon understood to carry out prebasic molt outside of the monsoonal region (either near breeding territories or in overwintering areas) (Table **??**). Current knowledge of a population's approximate molting location(s) comes from banding station records (Pyle et al., 2009, 2018), visual examination of museum specimens (Rohwer et al., 2005; Rohwer and Manning, 1990), year-round and range-wide genetic sampling (Battey et al., 2018), and deploying tracking devices, such as geolocators (Contina et al., 2013; Pillar et al., 2016). These datasets have thus far provided an incredibly valuable but incomplete understanding of molting strategies in North American birds. Doubtless, there are many populations that rely on monsoonal productivity to supply prebasic molt, but have not yet been documented molting in the monsoonal region and therefore are not included in our analyses.

Testing the influence of monsoon conditions on population breeding abundance

While intraspecific variation in molting strategies may confer some resilience against interannual variation in monsoon conditions, it may be insufficient to buffer populations against accelerating anthropogenic climate change (Beever et al., 2017). To more accurately predict the extent to which ongoing shifts in monsooon precipitation regimes threaten molt-migrant populations, we tested for associations between interannual variation in population breeding abundance and monsoon precipitation conditions over the past four decades. In years when monsoon precipitation volume and phenology deviate from historical means, elevated nonbreeding mortality rates resulting from resource deprivation during molt may be detectable as a decrease in breeding abundance the following summer. Therefore, describing how population abundance responds to monsoonal variation reveals the limits of individual flexibilty and genetic variation as mechanisms of species resilience. Specifically, we tested if exceptionally weak and late monsoons, which are predicted to become more common, are associated with population decreases.

For each focal molt-migrant and non-molt-migrant taxon, we used Breeding Bird Survey (BBS) data to generate estimates of breeding season abundance in all Bird Conservation Regions (BCRs) across North America for every year from 1966 to 2022 (figure **??**, Table **??**). The Breeding Bird Survey is a collaborative project overseen by the United States Geological Survey's Eastern Ecological Science Center and Environment Canada's Canadian Wildlife Service for which highly-skilled volunteers record birds along predetermined roadside routes throughout North America. Unlike other datasets generated by community scientists, such as eBird, volunteers recording birds for the Breeding Bird Survey follow a strict observation protocol and conduct surveys along identical routes within a restricted time window every year. Therefore, the Breeding Bird Survey is the most appropriate dataset for estimating interannual variation in breeding season abundance for North American bird populations (Sauer et al., 2003).

We used the "bbsBayes" package in R to generate indices of annual breeding abundance from raw BBS data. This packaged allowed us to download BBS data from the USGS database, stratify the data by BCR, and model population trend for each species over the time period as a hierarchical Bayesian log-linear regression (Edwards and Smith, 2021; Link and Sauer, 2002). This model assumes

$$\begin{gathered} y_{s,j,t} \sim \text{Poisson}(\lambda_{s,j,t-1}) \\ \log(\lambda_{s,j,t}) = \theta_s + \Delta_s(t) + \eta I[j,t] + \omega_j + \epsilon_{s,j,t} \\ \Delta_s(t) = \gamma_{t,s} \sim \text{Normal}(\gamma_{t-1,s}, \sigma_s^2) \end{gathered} \tag{2}$$

where y, the count of a species in a given BCR (s) by a given observer (j) in a given year (t), is modeled as an overdispersed Poisson distribution with mean $\lambda_{s,j,t-1}$. θ_s is a BCR-specific intercept, $\eta I[j,t]$ represents survey differences between an observer's first year and all subsequent years due to lack of experience, ω_j is a random effect for specific observer-route combinations, and $\epsilon_{s,j,t}$ is a random effect at the count-level for overdispersion (Edwards and Smith, 2021). The model assumes uninformative, normally distributed priors for θ and η with mean 0 and variance 10^6 (Smith et al., 2014). We chose to model count overdispersion (ϵ) as a heavy-tailed t-distribution, rather than a normal distribution, to prevent estimates of annual relative abundance from being skewed by extreme count events, which are regular in the BBS dataset (Link et al., 2020; Smith and Edwards, 2021). We modeled the change in abundance from one year to the next ($\Delta_s(t)$) as a normal distribution centered on the abundance estimate for the previous year (Link and Sauer, 2016). Although this approach may dampen interannual variation in breeding abundance by drawing the abundance estimate for a given year closer to that of the previous year, it enables annual abundance estimates in each BCR to vary without being drawn to an overarching slope or the trends in other BCRs (Edwards and Smith, 2021; Smith et al., 2014).

Before running the model for a given species, we removed BCRs with fewer than three survey routes on which the species has been observed, fewer than three years on which the species was recorded, and where the number of years with observations of the species averaged across all routes in the BCR is less than one (the "bbsBayes" default filters for modeling strata-specific trends) (Edwards and Smith, 2021). For every molt-migrant and non-molt-migrant species, we ran this model in three replicate chains of 40,000 iterations each. We discarded the first 20,000 steps as burn-in and recorded every 20th remaining posterior sample. We assessed model convergence based on potential scale reduction factor (Rhat) and visual examination of trace plots for each parameter. We also assessed the efficiency of each model in sampling from the posterior distributions based on the bulk effective sample size and tail effective sample size for each parameter. We then further subset the data to retain only BCRs in which at least two individuals of the focal species were predicted to occur every year between 1979 and 2019.

We used the "generate_trends" function in the "bbsBayes" to estimate proportion breeding population change for each species in each BCR from one year to the next. For each year from 1980 to 2019, we sampled 3,000 values from the posterior distribution estimating the species' breeding abundance in a given BCR for the year, divided each value by unique samples from the posterior distribution estimating the species abundance in that BCR in the previous year, then subtracted 1 from each quotient (Edwards and Smith, 2021). The resulting 3,000 values represent the probability distribution for the proportion population change for the species in the BCR between each year. We then took the median of each distribution to calculate point estimates.

To test for an influence of monsoon conditions on population size, we used linear regressions to model annual proportion change in breeding abundance as a function of anomaly in monsoon phenology and volume for the previous fall's monsoon. We assumed a global model:

$$y_i = \beta_0 + \beta \mathrm{T}_i + \beta \mathrm{H}_i + \beta \mathrm{T}_i \times \beta \mathrm{H}_i + \epsilon_i \tag{3}$$

where y_i is the proportion breeding population change in a given year (i) based on BBS estimates, β_0 is the intercept, T_i total precipitation in the monsoonal region in the previous June through October, H_i is the estimated monsoon halfway date from the previous monsoon season, β values are fixed-effect regression coefficients, and ϵ_i is the residual error. We considered using a generalized additive model to allow for potential nonlinear relationships between monsoon characteristics and breeding abundance change (e.g., threshold effects), but preliminary analyses found no support for more than one effective degrees of freedom for models fit to data for any population.

For each molt-migrant population (species-BCR combination), we ran separate global models for each monsoonal region. We then used the "dredge" function in the "MuMIn" package to run variants of each model with all possible combinations of predictors and selected the model with the lowest corrected AIC value (Barton, 2009). Comparing the best-fitting models from each monsoonal region, we then identified the model with the highest adjusted R^2. Because the estimates of monsoon phenology and volume from this region explain the most variance in abundance change in the focal population, the population is most likely to molt in this region. We then reran the top model in a Bayesian framework using "brms" to interface with Stan (Bürkner, 2017; Carpenter et al., 2017). We assumed weakly informative priors centered on beta coefficient estimates from the frequentist model and with a variance of 10. We ran the model in three replicate chains of 3,000 iterations each and discarded the first 1,000 iterations from each chain as burn-in. We examined trace-plots to assess model convergence and plotted posterior predictions with observed data to assess model performance. Based on these models exploring the relationships between a population's proportional breeding abundance change and monsoon precipitation anomalies, we interpret the β estimates for the influence of precipitation volume and phenology variation on abundance change as proxies for the population's sensitivity to monsoon conditions.

As a control, we ran all aforementioned analyses exploring the influence of monsoon conditions on interannual abundance variation with all non-molt-migrant populations. The Breeding Bird Survey dataset does not distinguish among subspecies. In the cases where only one subspecies or some populations within a species are known to be molt-migrants, we distinguished subspecies/populations based on their expected breeding distributions and selected only BCRs where we confidently believe only one of the two focal subspecies/population breeds.

How does sensitivity to monsoon conditions influence recent population trends?

Associations between variation in monsoon conditions and breeding abundance reveals the extent to which molt-migrant populations are sensitive to ongoing anthropogenic changes in precipitation regimes. We sought to determine if this sensitivity has already contributed to population declines by testing for associations between recent population trends and population responses to monsoon precipitation anomalies. Using the "bbsBayes" package in R, we estimated the average annual percent change for each molt-migrant population from 2010 to 2022 by fitting a log-linear slope to the posterior estimates of the population's annual breeding abundance indices (Edwards and Smith, 2021). We estimated population change since 2010 to encompass the most recent decade of accelerating climate change (Smith et al., 2015). We ran this regression 3,000 times, each with a different sample from the posterior distribution for the population's abundance index in each year, to propagate uncertainty in annual abundance estimates and generate a probability distribution, rather than a point estimate, for population trend. We then extracted 3,000 values from the posterior distributions representing each population's sensitivity to monsoon precipitation volume and phenology generated from our earlier models in the previous section. Drawing one value from the distributions representing each population's trend and sensitivity at a time, we ran 3,000 linear regressions modeling the overall relationship between population trend and sensitivity across all molt-migrant populations. We modeled the influences of sensitivity to monsoon volume and phenology on population trend separately. The resulting 3,000 estimates for β coefficients represent the overall influence of sensitivity to monsoon conditions on recent population trend as a distribution that preserves uncertainty associated with our estimates of these variables.

Results

Exploring intraspecific variation in molting strategies as a potential mechanism of resilience against shifting monsoon conditions

eBird records indicate substantial interannual variation in the phenology, density, and duration of *Passerina amoena* occurrence in southern Arizona during the molting period. Median posterior estimates for arrival date ranged from July 26th in 2007 to August 15th in 2010. Estimates for maximum probability of occurrence ranged from 0.106 in 2014 to 0.251 in 2020. Estimates for stopover duration ranged from 36 days in 2020 to 71 days in 2021. We observed a strong negative correlation between the posterior estimates for maximum occurrence probability and stopover duration (-0.582).

We found no evidence for monsoon precipitation volume or phenology influencing arrival date of *P. amoena* in southern Arizona, with intercept-only models being best supported. The absence of a significant association suggests that conditions in breeding areas, not monsoonal stopover locations, regulate post-breeding migration (and presumably prebasic molt) phenology. However, while variation in migration phenology appears decoupled from conditions in molting areas, our models indicate significant associations between monsoon conditions and prebasic molt location and behavior. *P. amoena* exhibits a negative linear relationship between maximum postbreeding occurrence probability and total monsoon precipitation in southern Arizona, such that the species occurs in lower densities during years with higher local monsoon precipitation than the historical average (95% credible interval for β: -0.333 - -0.0516). We also observed a negative linear relationship between *P. amoena* stopover duration and monsoon end date, such that more individuals occur in southern Arizona for longer in years when monsoon precipitation concludes earlier than the the historical average (95% credible interval for β: -0.195 - -0.0563) (figure 2)).

Molt-migrant sensitivity to variation in monsoonal precipitation

Despite this evidence of intraspecific variation in molting strategies, analyses of population-level responses to variation in monsoon phenology and volume indicate that many molt-migrant populations are still sensitive to conditions in molting areas. After filtering species/BCR combinations to include only those with sufficiently high breeding abundance, the final dataset included 155 molt-migrant and 268 non-molt-migrant populations. Of those, model selection of frequentist regressions exploring the influence of monsoon volume and phenology on interannual population changes identified intercept-only variants as best supported for 38 molt-migrant and 58 non-molt migrant populations. Because variation in monsoon conditions seemingly impart no significant influence on their breeding abundance, we infer these species to be resistant to the impacts of climate change in molting areas (at least up to the time of this study). Of the populations for which the best supported models included precipitation phenology and/or volume as predictor(s), we were able to compare adjusted R^2 among models to identify the monsoonal region in which precipitation conditions explain the most variance in interannual breeding abundance changes. Nine molt-migrant and 13 non-molt migrant populations were most sensitive to precipitation variation in the Sonoran Desert, 22 molt-migrant and 42 non-molt migrant populations were most sensitive to precipitation variation in central Mexico, 29 molt-migrant and 31 non-molt migrant populations were most sensitive to precipitation variation in the southern Baja California Peninsula, and ten molt-migrant and 25 non-molt migrant populations were most sensitive to precipitation variation in southern Mexico. Regardless of monsoonal subregion, top fitting models for 40 molt-migrants and 61 non-molt migrant populations included precipitation volume as a predictor, top fitting models for 35 molt-migrants and 63 non-molt migrant populations included monsoon halfway date as a predictor, and top fitting models for four molt-migrants and ten non-molt migrant populations included an interaction between precipitation volume and monsoon halfway date as a predictor.

The vast majority of molt-migrant populations for which the best-supported model included total monsoon precipitation as a predictor exhibited a positive relationship between breeding abundance change and precipitation volume, such that they were more likely to decline in breeding abundance following a monsoon dryer than the historical average (1.159 ± 2.223; mean ± SD of median β values, 31 out of 40 supported positive responses). Interestingly, all nine molt-migrant populations exhibiting a negative β estimate breed in BCRs in the southern United States. In contrast, non-molt-migrant populations for which the best-supported model included total monsoon precipitation as a predictor exhibited an approximately even split between positive and negative β estimates (0.593 ± 2.181; mean ± SD of median β values, 35 out of 61 supported positive responses) (figure 3).

Both molt-migrant and non-molt migrant populations for which the best fitting model included monsoon halfway date anomaly as a predictor exhibited more balanced ratios of positive and negative β estimates (molt migrants: -0.312 ± 1.779, mean ± SD of median β values, 23 out of 35 supported positive responses; non-molt-migrants: 0.471 ± 2.024, mean ± SD of median β values, 25 out of 63 supported positive responses) (figure 4). This consistency between the two groups initially suggests that molt-migrant populations are resistant to deviations in monsoon phenology. However, grouping populations by BCR reveals that a molt-migrant population's sensitivity to monsoon phenology depends on breeding latitude, with populations that breed farther north exhibiting more negative average β estimates for the relationship between interannual breeding abundance change and monsoon halfway date anomaly, such that they are more likely to decline following a monsoon that is later than historical average. Of the eleven molt-migrant populations that exhibit a positive β estimate, ten breed in BCRs in the southern United States (figure **??**).

Recent population trends

Our models identify 103 out of the focal 155 molt-migrant populations as having declined between 2010 and 2022 (i.e., have a negative median estimate for average annual percent change over these years). Populations previously found to exhibit a positive relationship between monsoon precipitation volume and interannual breeding abundance change (i.e., are more likely to decline following a monsoon dryer than historical average) are proportionately more likely to have declined in the past decade than resilient populations and populations found to exhibit a negative relationship between monsoon precipitation volume and interannual breeding abundance change (median proportions: 0.710, 0.619), although there is overlap in the estimated probability density functions for the two groups (figure **??**). Furthermore, populations identified as both declining and more likely to decline following a dry monsoon exhibit a significant negative linear relationship between estimated sensitivity to monsoon precipitation and average annual breeding abundance change (95% credible interval for β: -0.0201 - -0.000185), indicating that the populations most sensitive to monsoon volume are in the steepest decline (figure 5).

Populations previously classified as sensitive to interannual variation in monsoon phenology are proportionately more likely to have declined between 2010 and 2022 than resilient populations (median proportions: 0.743, 0.600) (figure **??**). A generalized linear model assuming a binomial error distribution and logit link supports a significant relationship between whether or not a population is sensitive to interannual variation in monsoon phenology and whether or not the population has declined (95% credible interval for β: 0.155 - 1.386). However, populations sensitive to variation in monsoon phenology have declined less rapidly than populations sensitive to variation in monsoon precipitation volume. That being said, populations identified as both declining and more likely to decline following a monsoon later than historical average exhibit a near-significant positive linear relationship between estimated sensitivity to monsoon phenology and recent population trend (95% credible interval for β: -0.000473 - 0.0147), indicating that the populations most sensitive to variation in monsoon phenology are in the steepest decline (figure 6).

Discussion

As anthropogenic climate change alters the spatiotemporal distribution of primary productivity, phenological mismatch between resource demand and availability will likely contribute to population declines across taxa (Aikens et al., 2020; Wilson, 2017; Zimova, 2016). Most literature exploring phenological mismatch in migratory birds focuses on shifts in spring green-up, which increasingly challenge birds to align breeding effort with annual pulses in arthropod and seed abundance required for provisioning young (Møller et al., 2008; Senner et al., 2017; Youngflesh et al., 2023). However, the persistence of migratory populations requires high adult survivorship between breeding events (Dokter et al., 2018; Winger and Pegan, 2021). Therefore, phenological mismatch challenging birds to access sufficient resources during molt, an annual life history event that functions to enhance individual survival throughout the year (Holmgren and Hedenström, 1995), may pose an overlooked and pervasive threat across birds.

The historic paucity of research on molt impedes our ability to predict how avian populations will respond to environmental change, presenting a major challenge in conservation. In this study, we employ a comparative approach to test the extent to which changing conditions in molting areas influence population dynamics in molt-migrant passerines that breed in western North America. First, analyzing eBird data for one molt-migrant species, *Passerina amoena*, as a model, we demonstrate that the occurrence of molt-migrants in monsoonal areas during prebasic molt varies in response to precipitation volume and duration. While these patterns suggest potential for intraspecific variation in molting strategies to buffer molt-migrant populations against deviations from historical monsoon conditions, analyses of Breeding Bird Survey records suggest that variation in resource availability during molt still influences the breeding abundance of many molt-migrant populations the following spring. Specifically, most molt-migrant populations found to be sensitive to variation in monsoon precipitation appear more likely to decline following monsoons that are dryer and later than historical averages. Although molt-migrant populations and non-molt-migrant populations included for comparison exhibited similar rates of sensitivity to interannual variation in monsoon precipiation (top models for 51% and 50% of populations included at least one monsoon characteristic as a predictor, respectively), concordance in effect direction among molt-migrants but not among non-molt-migrants support a causal influence of resource availability during prebasic molt on breeding abundance. Finally, because the dry and late monsoons that we observed to be detrimental to many molt-migrant populations are becoming more frequent with intensifying anthropogenic climate change, we tested the extent to which sensitivity to monsoonal variation is influencing recent population trends. We observed that populations sensitive to variation in monsoon precipitation are more likely to have declined in the past decade than populations that are not sensitive. Among declining molt-migrant populations found to be sensitive to monsoonal variation, we observed significant relationships between a population's sensitivity to variation in monsoon precipitation characteristics and the population's recent population trend, with the most sensitive populations declining the most rapidly. This result underscores both the potential for molting conditions to influence population dynamics and the importance of incorporating molt into conservation strategies. Overall, our study presents some of the first evidence that anthropogenic climate change negatively impacts bird populations during molt.

While we cannot definitively describe the exact mechanisms by which weak and late monsoons precipitate breeding abundance declines in molt-migrant populations based on community science data alone, we hypothesize that dry conditions during historical molting periods deprive individual birds of sufficient resources to supply molt. In this situation, birds may grow poor quality feathers, migrate longer distances with worn feathers in search of sufficient resources, and/or delay molt (Podlaszczuk et al., 2016). Reducing the resource and time investment in molt would increase individual mortality risk (Dawson et al., 2000), manifesting as a decline in population breeding abundance the following spring (Dawson et al., 2000). Because many climate models predict that the window of monsoonal resource availability is shrinking and shifting later into the fall (Cook and Seager, 2013; Hernandez and Chen, 2022; Pascale et al., 2017), we predict that individual birds stopping over in the monsoonal region to carry out prebasic molt increasingly suffer a phenological mismatch between resource demand and availability. Resource deprivation in their monsoonal molting areas may partially explain why migratory passerine populations that breed in western North America are overall declining more rapidly than those that breed in the east (Rosenberg et al., 2019). Comparison of estimated β coefficients from our analyses of BBS data suggests a latitudinal trend in population sensitivity to shifts in monsoon volume and phenology, with more sensitive populations breeding farther north. We speculate that the temporal constraints of migrating longer distances between breeding and molting areas reduce the potential for individual flexibility to mitigate phenological mismatch between feather growth and precipitation. Additionally, birds breeding closer to molting areas likely have access to information on molting habitats and precipitation conditions unavailable to individuals migrating to monsoonal areas from farther away. Describing nonbreeding locations more accurately using individual tracking data is necessary to robustly test this prediction and estimate the relative influences of primary productivity at different stages of the annual cycle on population dynamics.

The fact that we observed only approximately half of all molt-migrant populations in the study to be sensitive to variation in monsoon precipitation or phenology emphasizes that conditions during molt are just one of many potential factors that may influence avian population dynamics. Unfortunately, current gaps in our knowledge of migratory connectivity (individual fidelity to specific breeding and nonbreeding areas) prevent us from evaluating the relative influences of conditions during breeding, molt, migration, or nonbreeding on specific populations (Marra et al., 2011). Furthermore, it is worth noting that observed relationships between population trends and monsoon precipitation characteristics may result from processes other than resource deprivation during prebasic molt. For instance, monsoon precipitation influences winter seed availability in the southwest United States and western Mexico. For granivorous species that overwinter around the monsoonal region, such as *Spizella passerina*, monsoon precipitation may regulate populations primarily by defining nonbreeding food availability rather than supplying feather growth (Pulliam and Parker, 1979). However, because many species in our study occur only in monsoonal areas during prebasic molt and do not spend the entirety of the nonbreeding period in the monsoonal region, we still believe that resource deprivation during prebasic molt to be the dominant driver of widespread sensitivity to monsoon conditions among molt-migrant populations. Future comparisons of life history traits (e.g., distance between breeding and molting areas, overwintering location, diet) may reveal why conditions in monsoonal molting areas influence some molt-migrant populations more than others. Furthermore, it is possible that some populations appearing sensitive to variation in monsoon volume and phenology may actually be responding to different but correlated climatic conditions. While this reasoning may apply for some molt-migrant populations that breed close to monsoonal areas, weak spatial correlation in climate trends imply that shifts in resource availability during prebasic molt are unrelated to conditions in breeding and other nonbreeding areas (Senner et al., 2018). Overall, we believe that consistent responses to variation in monsoon precipitation volume and phenology among sensitive molt-migrant populations, which share a reliance on monsoonal productivity during prebasic molt but vary with respect to breeding locations, nonbreeding locations, and other aspects of natural history, and not sensitive non-molt-migrants support a causal influence of molting conditions on populations dynamics. Additionally, significant associations between monsoon conditions and interannual abundance variation in some populations that we assume to be non-molt-migrants may indicate an undescribed reliance on monsoon precipitation.

One likely predictor of a molt-migrant population's vulnerability to deviations from historical monsoon conditions may be the extent of intrapopulation variation in molting strategies. Previous research has identified intraspecific variation in migratory strategies as a potential mechanism of resistance to interannual climatic variation, and now helps some taxa cope with anthropogenic landscape and climate change (Gilroy et al., 2016). While the extent of intraspecific and intrapopulation variation in molting strategies remains unexplored, we hypothesize that this variation may similarly buffer avian populations against changing precipitation regimes. We observed associations between interannual variation in *Passerina amoena* occurrence in putative molting areas and monsoon conditions, indicating potential for intraspecific variation in molting strategies to buffer at least some populations of this species against interannual varation in monsoon precipitation. Specifically, we observed that *Passerina amoena* tends to stopover in southern Arizona in lower densities during years with high local monsoon precipitation and more individuals occur in the region for longer in years when monsoon precipitation concludes earlier. We attribute these negative associations to spatial precipitation patterns. In years with ample monsoon precipitation in southern Arizona, precipitation likely extends farther north into the western United States. Due to the temporal constraints of molt and migration, we expect that it is advantageous for individual birds to minimize migratory distance and time before prebasic molt. If individuals migrate only as far as they need to find sufficient resources, more birds likely stopover farther north in "good" monsoon years (Pillar et al., 2015). We assume that the interannual variation exhibited by *P. amoena* is representative of other molt-migrant taxa. Evidence for intraspecific variation in prebasic molt location is consistent with previous observations that molt-migrants occur in different habitat types in wet and dry monsoon years (Pyle et al., 2009). Future research focusing on individual birds (e.g., individual tracking or stable isotope data collected from the same individuals in different years) is necessary to estimate the extent to which variation in molting strategies results from individual flexibility versus population genetic variation. Importantly, individuals in some populations may be able to reduce phenological mismatch between resource demand and availability by flexibly suspending molt. It is understood that in some species, individuals are able to initiate prebasic molt, receive an exogenous cue that local resource availability is insufficient, then suspend molt until a later time when resource availability is greater (Scheiman and Dunning, 2004). The ability to suspend molt may buffer populations against increasing variability in resource availability (Thornton et al., 2014).

Across taxa, many populations appear capable of adapting to climate change, but it is unknown how many will respond fast enough to avoid extinction (Qvarnström et al., 2016). For molt-migrant passerines, the capacity for populations to respond to changing patterns in productivity during prebasic molt through individual flexibility or adaptive evolution in molting phenology depends on the genetic architecture of molting strategies (Schiffers et al., 2014). Although molt-migration evolved convergently across passerine populations breeding in western North America, the genetic architecture underlying this trait may vary among taxa (Pageau et al., 2020; Rosenblum et al., 2014). Importantly, different genetic architecture could enable different levels of flexibility in molt phenology. If monsoon phenology eventually deviates too far from historic conditions, many species may need to completely restructure fall migration programs. Future research mapping the genetic basis of intra- and interpopulation variation in molting strategies across birds is necessary to assess the potential for adaptation (Hoffmann and Merilä, 1999). It is also necessary to identify the environmental cues that regulate prebasic molt onset and the precise aspects of molt that are flexible. For most long-distance migratory passerines, changes in photoperiod are understood to exert the dominant influence on molt phenology (Dawson, 2013; Gwinner, 1989; Lesher and Kendeigh, 1941). However, evidence for flexibility in prebasic molt suggests that molt-migrant populations (as well as short-distance and facultative migrants) rely on additional cues, likely ones that more accurately signal resource availability (Dougherty, 2023; Savides, 2022). Alternatively, high interannual variability in precipitation in western North America may maintain balanced polymorphism of genetic variation that regulates molt. To comprehend the full extent to which human activity threatens bird populations during prebasic molt, we will need a more mechanistic understanding of the environmental and genomic regulation of molt, the potential for adaptive evolution in molting behavior, and the extent to which molt location, phenology, and intensity are flexible.

Acknowledgments

We would like to thank Ben Zuckerberg at the University of Wisonsin-Madison and members of the Stager and Senner labs at the University of Massachusetts Amherst for their invaluable feedback on the manuscript. We would also like to thank all birders, reviewers, and compilers who contribute to the eBird and the Breeding Bird Survey datasets. This research was made possible thanks to generous support from the University of Wyoming Department of Zoology and Physiology, the University of Wyoming Museum of Vertebrates, and the National Science Foundation (grants 2305971 to PJD and 1928870 to MDC).

Statement of Authorship

P.J.D., M.D.C., and R.S.T led the conceptualization. P.J.D. performed all analyses and wrote the original draft of the manuscript with input from M.D.C and R.S.T. P.J.D., M.D.C., and R.S.T. contributed to reviewing and editing the final manuscript.

Data and Code Availability

All Daymet, eBird, and Breeding Bird Survey Data are are available to download at `https://daymet.ornl.gov/getdata`, `https://ebird.org/data/download`, and `https://www.pwrc.usgs.gov/bbs/rawdata/`, respectively. We used the "bbsBayes" package in Program R to retrieve and process all Breeding Bird Survey data. All scripts are available and free to download at `https://zenodo.org/records/17561038` (Dougherty 2025) and `https://github.com/paul-dougherty/molt_migrant_conservation`.

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Figure legends

Figure 1: Breeding (red), prebasic molt (yellow), and overwintering (blue) distributions of *Passerina amoena*, a molt-migrant species, estimated from eBird data (`https://ebird.org`). In all periods, darker shading corresponds to higher predicted abundance. Distributions generated with the "ebirdst" package in R, which provides access to predictions from machine learning models estimating the relationships between species occurrence in eBird checklists and a suite of environmental and effort variables (Fink et al., 2023).
Alt text: a map showing the breeding, molting, and overwintering distirbutions of Lazuli Bunting (*Passerina amoena*).

Figure 2: (Upper) Maximum occurrence probability of *Passerina amoena* in southern Arizona during molting plotted as a function of total monsoon precipitation in the Sonoran Desert. (Lower) stopover duration of *Passerina amoena* in southern Arizona during prebasic molt plotted as a function of monsoon end date in the Sonoran Desert. In both, each point represents a different year centered on the median of the occurrence metric posterior distribution. Vertical bars represent 95% credible intervals. Blue lines represent posterior mean estimates from a Bayesian linear model fit to median point estimates of the occurrence metric, shaded areas represent model 95% credible intervals.
Alt text: Two regression plots. The first shows a negative relationship between total monsoon precipitation anomaly in the Sonoran Desert and Lazuli Bunting (*Passerina amoena*) maximum occurrence probability in southern Arizona. The second shows a negative relationship between monsoon precipitation end date anomaly in the Sonoran Desert and Lazuli Bunting stopover duration in southern Arizona.

Figure 3: β coefficients with 95% credible intervals for the linear relationship between total monsoon precipitation and annual population change for all molt-migrant populations (left) and non-molt-migrant populations (right) populations for which top models featured monsoon precipitation volume as a predictor variable.

Alt text: a comparison of the estimated beta coefficients for the relationship between total monsoon precipitation and breeding population change between molt-migrant and non-molt-migrant populations. Most molt-migrant populations show negative beta estimates.

Figure 4: β coefficients with 95% credible intervals for the linear relationship between monsoon halfway date and annual population change for all molt-migrant populations (left) and non-molt-migrant populations (right) for which top models featured monsoon halfway date as a predictor variable.

Alt text: a comparison of the estimated beta coefficients for the relationship between monsoon phenology and breeding population change between molt-migrant and non-molt-migrant populations. Both molt-migrants and non-molt-migrants exhibit relative even splits between negative and positive beta coefficients.

Figure 5: Average percent annual breeding abundance change 2010-2022 plotted as a function of sensitivity to variation in monsoon precipitation volume (the β coefficient previously identified for the linear relationship between breeding abundance change and total precipitation in the preceding monsoon) for molt-migrant populations estimated to have declined and previously found to exhibit a positive relationship between interannual abundance change and monsoon precipitation volume. Solid points represent median values from posterior distributions, with horizontal and vertical lines representing 95% credible intervals for sensitivity and average annual population change, respectively. The red line represents a linear regression fit to the median point estimates.

Alt text: Linear regression modeling the relationship between a population's estimated sensitivity to variation in monsoon precipitation volume and the population's estimated population trend between 2010 and 2022. The slope is negative.

Figure 6: Average percent annual breeding abundance change between 2010 and 2022 plotted as a function of sensitivity to variation in monsoon phenology (the β coefficient previously identified for the linear relationship between breeding abundance change and halfway date in the preceeding monsoon) for molt-migant populations estimated to have declined over these years. Solid points represent median values from posterior distributions, with horizontal and vertical lines around each point representing 95% credible intervals for sensitivity and average annual population change, respectively. The solid red line represents a linear regression fit to the median point estimates.

Alt text: Linear regression modeling the relationship between a population's estimated sensitivity to variation in monsoon phenology and the population's estimated population trend between 2010 and 2022. The slope is positive.

Figure 1

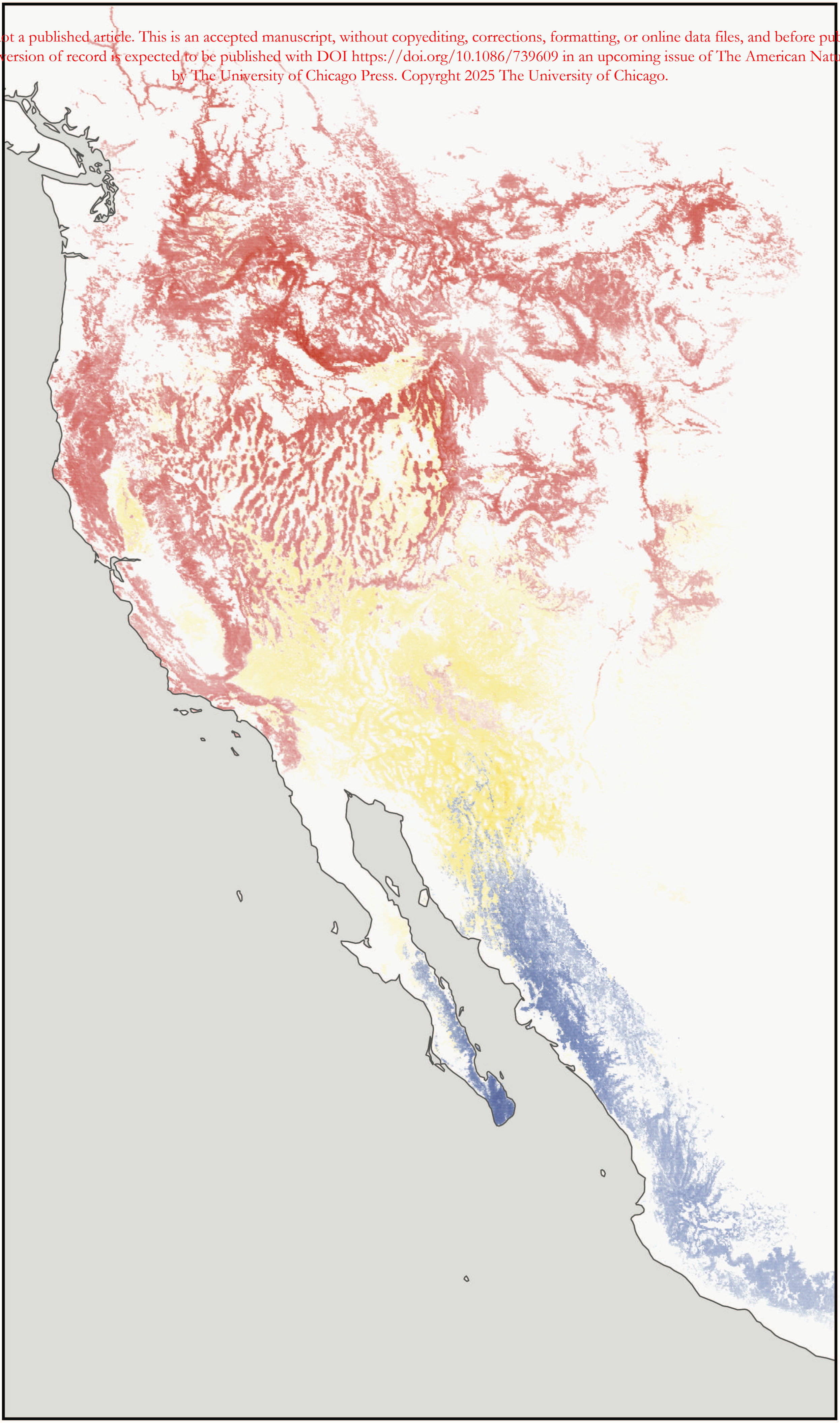
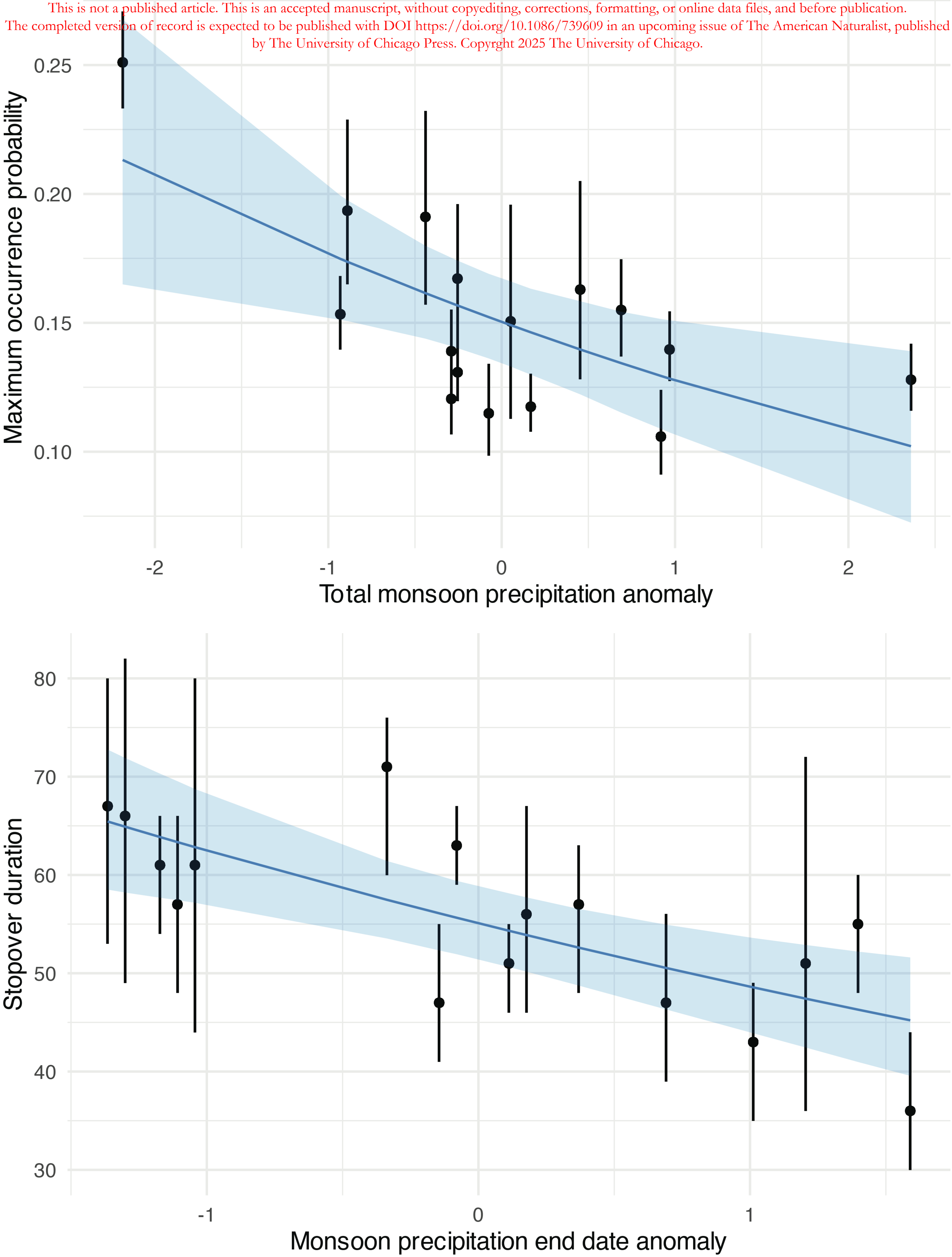


Figure 2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0.10
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60
50
40
30
Stopover duration
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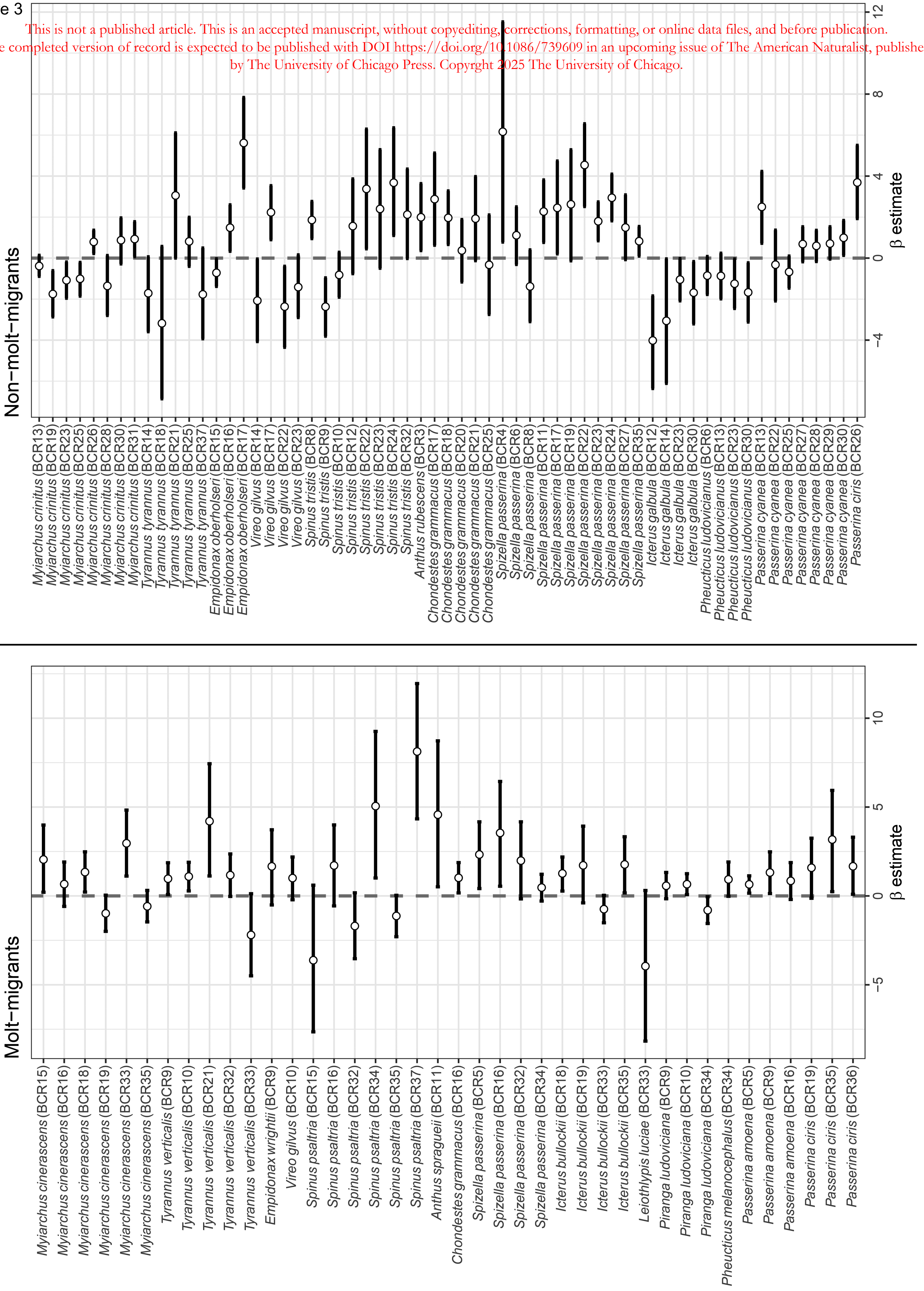
0
1
Monsoon precipitation end date anomaly

Figure 3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Myiarchus crinitus (BCR23)
Myiarchus crinitus (BCR25)
Myiarchus crinitus (BCR26)
Myiarchus crinitus (BCR28)
Myiarchus crinitus (BCR30)
Myiarchus crinitus (BCR31)
Tyrannus tyrannus (BCR14)
Tyrannus tyrannus (BCR18)
Tyrannus tyrannus (BCR21)
Tyrannus tyrannus (BCR25)
Tyrannus tyrannus (BCR37)
Empidonax oberholseri (BCR15)
Empidonax oberholseri (BCR16)
Empidonax oberholseri (BCR17)
Vireo gilvus (BCR14)
Vireo gilvus (BCR17)
Vireo gilvus (BCR22)
Vireo gilvus (BCR23)
Spinus tristis (BCR8)
Spinus tristis (BCR9)
Spinus tristis (BCR10)
Spinus tristis (BCR12)
Spinus tristis (BCR22)
Spinus tristis (BCR23)
Spinus tristis (BCR24)
Spinus tristis (BCR32)
Anthus rubescens (BCR3)
Chondestes grammacus (BCR17)
Chondestes grammacus (BCR18)
Chondestes grammacus (BCR20)
Chondestes grammacus (BCR21)
Chondestes grammacus (BCR25)
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Spizella passerina (BCR6)
Spizella passerina (BCR8)
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Spizella passerina (BCR19)
Spizella passerina (BCR22)
Spizella passerina (BCR23)
Spizella passerina (BCR24)
Spizella passerina (BCR27)
Spizella passerina (BCR35)
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Icterus galbula (BCR14)
Icterus galbula (BCR23)
Icterus galbula (BCR30)
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Passerina cyanea (BCR22)
Passerina cyanea (BCR25)
Passerina cyanea (BCR27)
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Passerina cyanea (BCR29)
Passerina cyanea (BCR30)
Passerina ciris (BCR26)
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4
8
12
β estimate
Molt−migrants
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Myiarchus cinerascens (BCR16)
Myiarchus cinerascens (BCR18)
Myiarchus cinerascens (BCR19)
Myiarchus cinerascens (BCR33)
Myiarchus cinerascens (BCR35)
Tyrannus verticalis (BCR9)
Tyrannus verticalis (BCR10)
Tyrannus verticalis (BCR21)
Tyrannus verticalis (BCR32)
Tyrannus verticalis (BCR33)
Empidonax wrightii (BCR9)
Vireo gilvus (BCR10)
Spinus psaltria (BCR15)
Spinus psaltria (BCR16)
Spinus psaltria (BCR32)
Spinus psaltria (BCR34)
Spinus psaltria (BCR35)
Spinus psaltria (BCR37)
Anthus spraguei (BCR11)
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Spizella passerina (BCR34)
Icterus bullockii (BCR18)
Icterus bullockii (BCR19)
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Icterus bullockii (BCR35)
Leiothlypis luciae (BCR33)
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Piranga ludoviciana (BCR10)
Piranga ludoviciana (BCR34)
Pheucticus melanocephalus (BCR34)
Passerina amoena (BCR5)
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Passerina amoena (BCR16)
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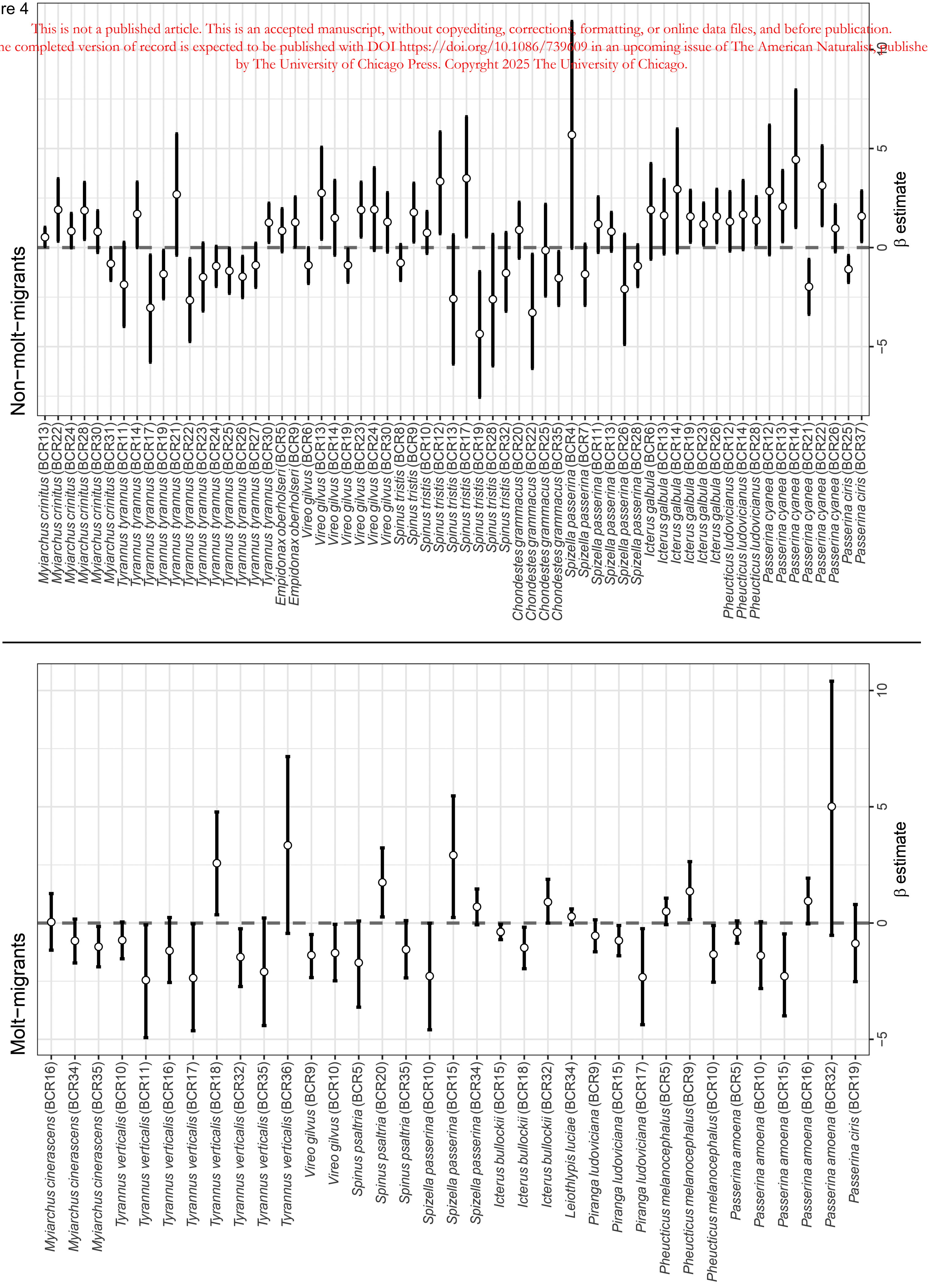
5
10
β estimate

Figure 4


Non−molt−migrants
β estimate
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Myiarchus crinitus (BCR28)
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Myiarchus crinitus (BCR31)
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Spizella passerina (BCR7)
Spizella passerina (BCR11)
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Pheucticus ludovicianus (BCR28)
Passerina cyanea (BCR12)
Passerina cyanea (BCR13)
Passerina cyanea (BCR14)
Passerina cyanea (BCR21)
Passerina cyanea (BCR22)
Passerina cyanea (BCR26)
Passerina ciris (BCR25)
Passerina ciris (BCR37)
Molt−migrants
β estimate
10
5
0
−5
Myiarchus cinerascens (BCR16)
Myiarchus cinerascens (BCR34)
Myiarchus cinerascens (BCR35)
Tyrannus verticalis (BCR10)
Tyrannus verticalis (BCR11)
Tyrannus verticalis (BCR16)
Tyrannus verticalis (BCR17)
Tyrannus verticalis (BCR18)
Tyrannus verticalis (BCR32)
Tyrannus verticalis (BCR35)
Tyrannus verticalis (BCR36)
Vireo gilvus (BCR9)
Vireo gilvus (BCR10)
Spinus psaltria (BCR5)
Spinus psaltria (BCR20)
Spinus psaltria (BCR35)
Spizella passerina (BCR10)
Spizella passerina (BCR15)
Spizella passerina (BCR34)
Icterus bullockii (BCR15)
Icterus bullockii (BCR18)
Icterus bullockii (BCR32)
Leiothlypis luciae (BCR34)
Piranga ludoviciana (BCR9)
Piranga ludoviciana (BCR15)
Piranga ludoviciana (BCR17)
Pheucticus melanocephalus (BCR5)
Pheucticus melanocephalus (BCR9)
Pheucticus melanocephalus (BCR10)
Passerina amoena (BCR5)
Passerina amoena (BCR10)
Passerina amoena (BCR15)
Passerina amoena (BCR16)
Passerina amoena (BCR32)
Passerina ciris (BCR19)

Figure 5

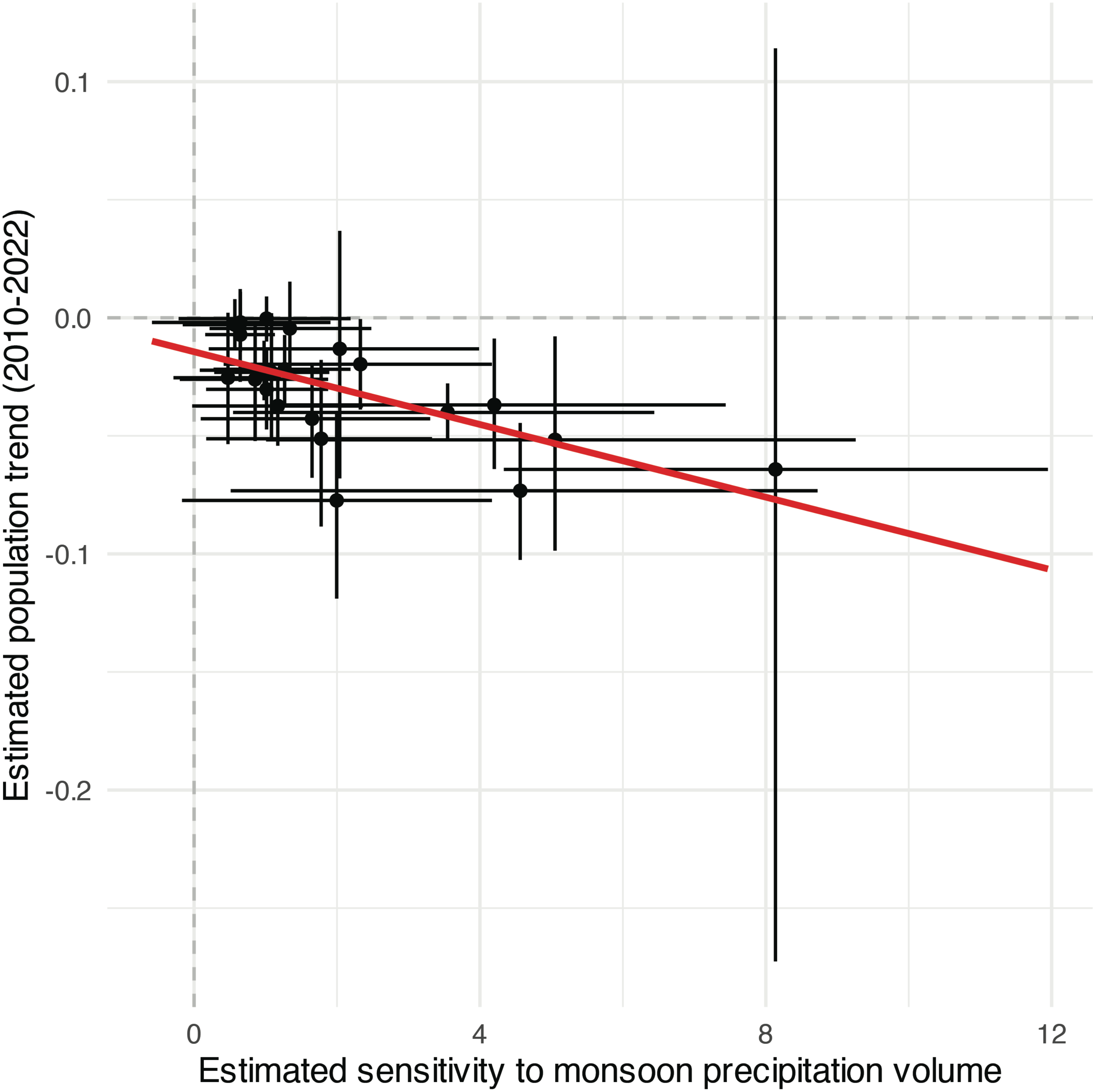
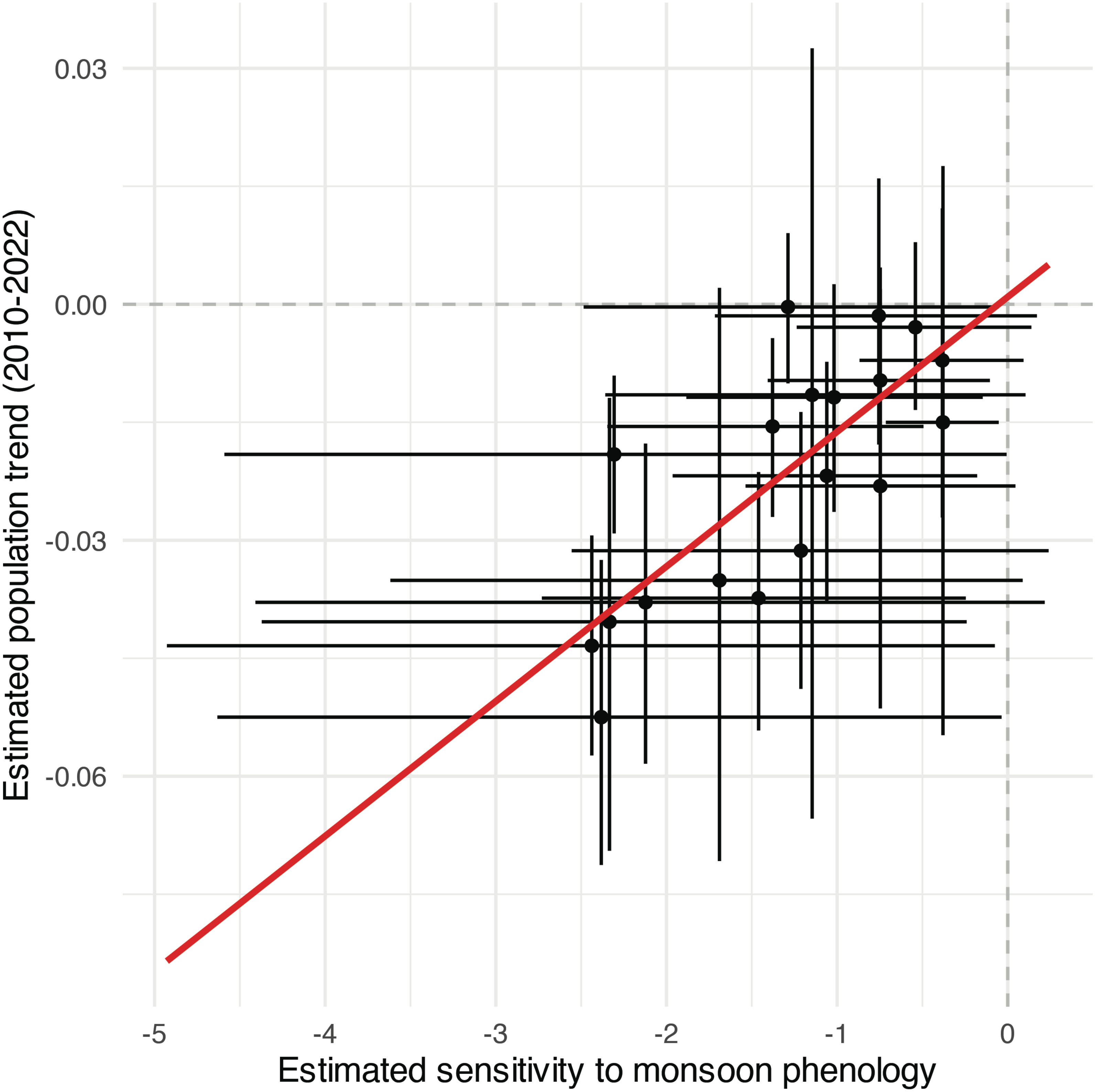

Estimated population trend (2010-2022)
0.1
0.0
-0.1
-0.2
0
4
8
12
Estimated sensitivity to monsoon precipitation volume

Figure 6


0.03
0.00
-0.03
-0.06
Estimated population trend (2010-2022)
-5
-4
-3
-2
-1
0
Estimated sensitivity to monsoon phenology

Molting strategy influences vulnerability to climate change in migratory birds

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Manuscript elements: Figure 1, figure 2, figure 3, figure 4, figure 5, figure 6, supplemental PDF. Figure 1 is to print in color.

Keywords: molt, migration, phenological mismatch, climate change, North American monsoon, community science.

Manuscript type: Major article.

Prepared using the suggested LATEX template for *Am. Nat.*

Supporting Information

Table S1: Molt-migrant and closely-related non-molt-migrant taxa examined in this study.

Molt-migrant	**Non-molt-migrant**
Myiarchus cinerascens	*Myiarchus crinitus*
Tyrannus verticalis	*Tyrannus tyrannus*
*Empidonax wrightii**	*Empidonax oberholseri*
Vireo gilvus (western ssp. group)	*Vireo gilvus* (eastern ssp. group)
Spinus psaltria	*Spinus tristis*
*Anthus spragueii**	*Anthus rubescens*
Chondestes grammacus strigatus	*Chondestes grammacus grammacus*
Spizella passerina arizonae	*Spizella passerina passerina*
Icterus bullockii	*Icterus galbula*
Leiothlypis luciae	*Leiothlypis virginiae*
Piranga ludoviciana	*Piranga olivacea*
Pheucticus melanocephalus	*Pheucticus ludovicianus*
Passerina amoena	*Passerina cyanea*
Passerina ciris (western interior)	*Passerina ciris* (eastern interior)

*indicates taxa suspected to carry out prebasic molt in monsoonal region but for which molt-migration has not yet been documented

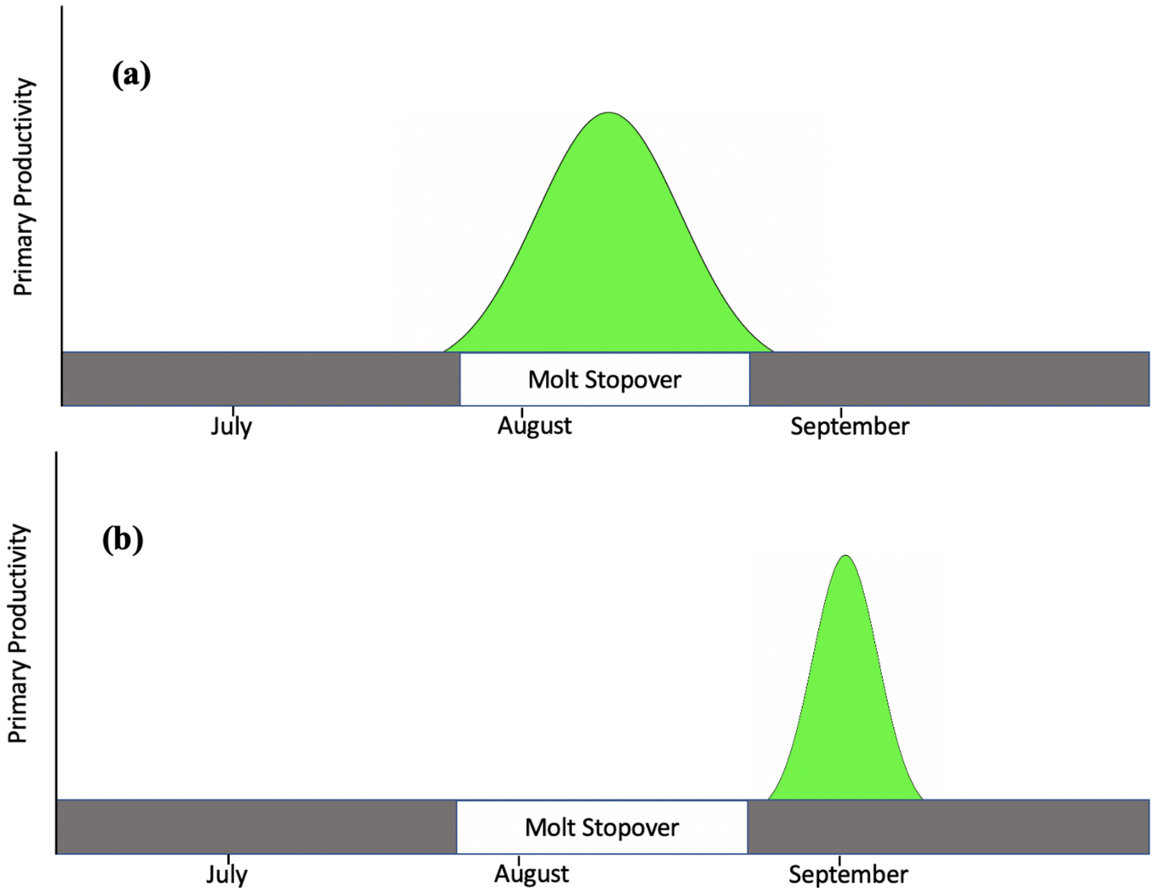

Figure S1: Conceptual figure illustrating potential phenological mismatch between prebasic molt and monsoon productivity. Western molt-migrant populations have evolved to align prebasic molt with relatively predictable pulses of monsoon productivity in late summer and early fall (A). Under ongoing anthropogenic climate change, models predict that the North American Monsoon will weaken and shift later into the fall (B). If western molt-migrant populations are unable to shift their prebasic molt phenology to track the changing precipitation regime, individual birds will experience discrepancy between the high metabolic demands of feather growth and sufficient resource availability.

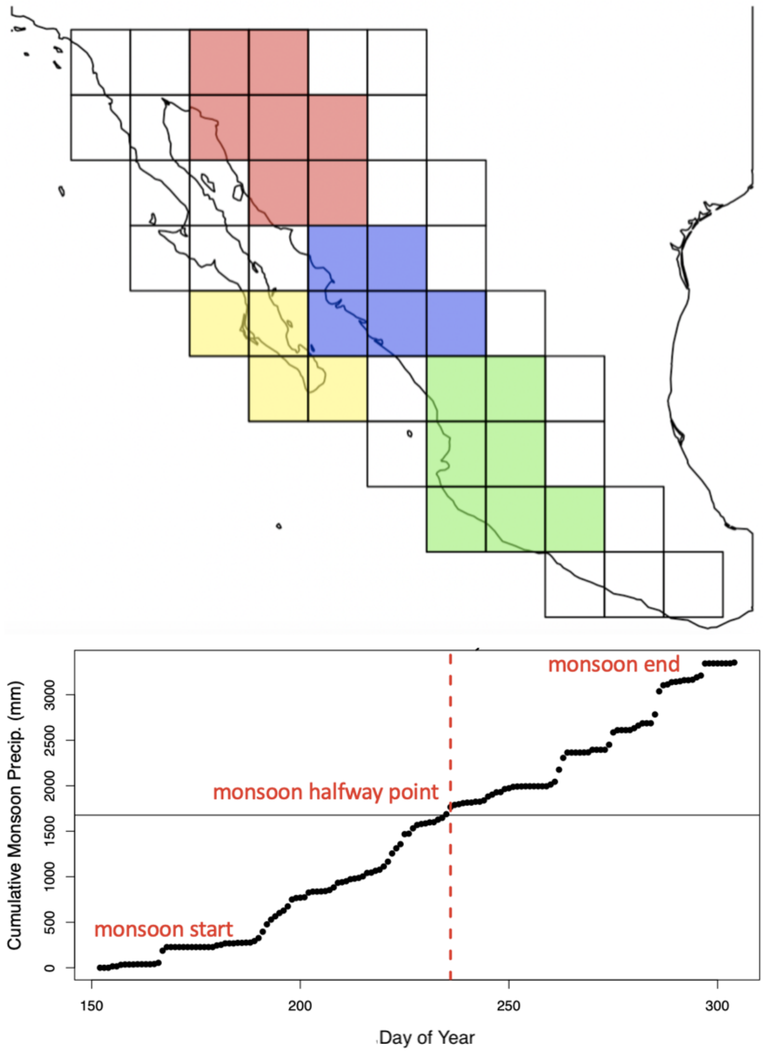

Figure S2: (Upper) Daymet tiles grouped by potential prebasic molt locations: Sonoran Desert (red), central Mexico (blue), southern Mexico (green), southern Baja California Peninsula (yellow). (Lower) Cumulative precipitation in the Sonoran Desert tiles during the monsoon period in 2018, which exemplifies our methods for estimating different metrics of monsoon phenology. For each subregion in each year, we estimated monsoon halfway point as the number of days beginning on June 1st that it took to reach half the cumulative June - October precipitation, monsoon start date as the first instance when the subregion experienced three consecutive days with precipitation estimates above the median daily value for June through October, and end date as the last instance when the subregion experienced three consecutive days with precipitation estimates above the median daily value for June through October.

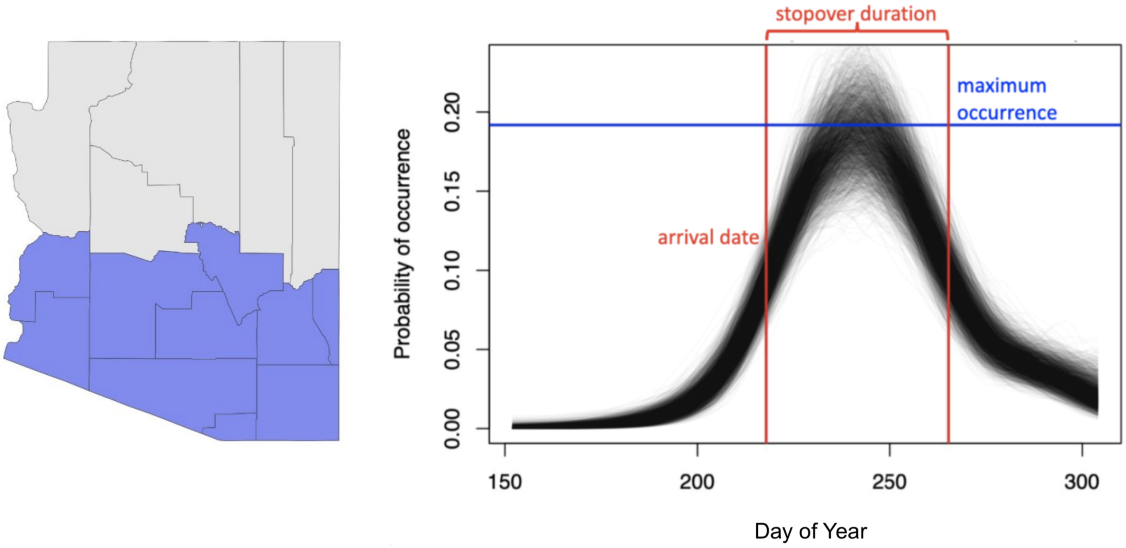

Figure S3: (Left) We analyzed eBird records from the shaded counties in southern Arizona to estimate stopover behaviors for each molt-migrant species. (Right) 3,000 posterior realizations of the generalized additive model representing the relationship between date and Lazuli Bunting (*Passerina amoena*) probabiity of detection on an eBird checklist in southern Arizona during the monsoonal period in 2022. For each iteration of the model, we estimated arrival date as the date at which the species reaches half its maximum occurrence probability in the region, stopover duration as the number of days after the half maximum date with predicted probability of occurrence greater than or equal to the half-maximum value, and maximum stopover abundance as the maximum probability of occurrence. Lines representing arrival date, stopover duration, and maximum occurrence probability represent median values from posterior draws.

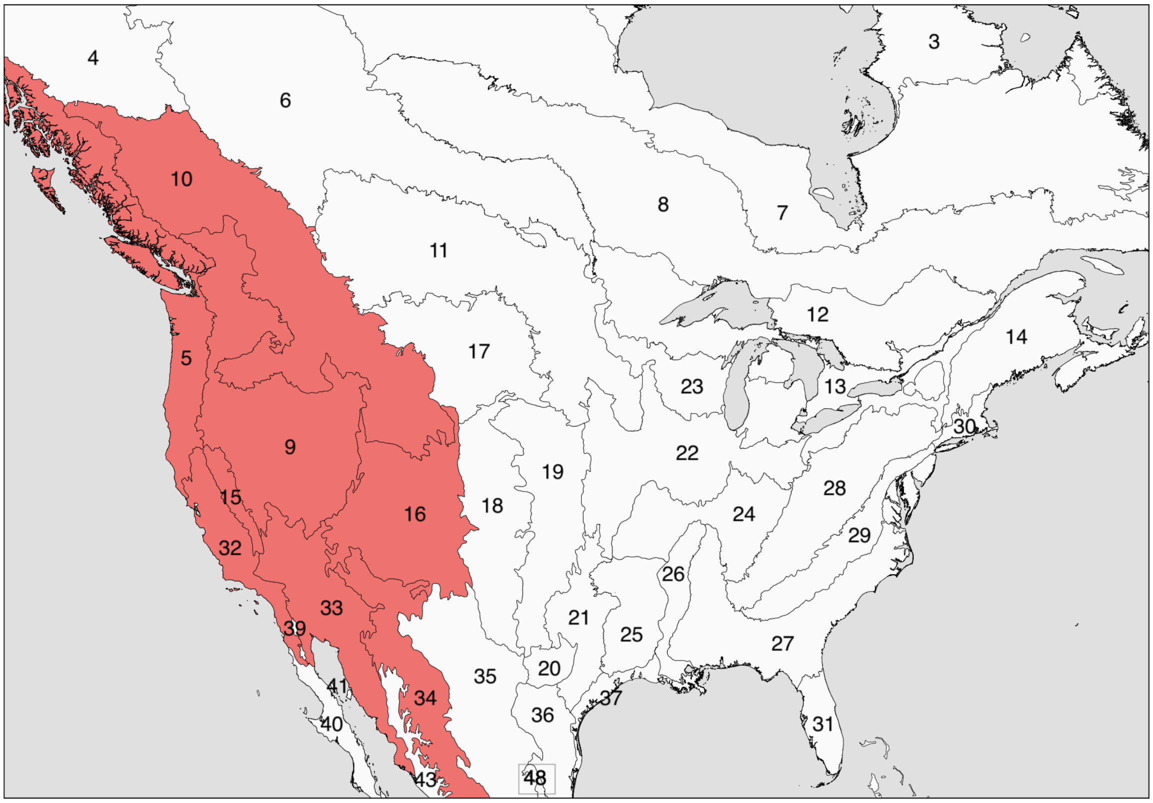

Figure S4: Bird Conservation Regions (BCRs) in North America. BCRs highlighted in red represent core molt-migrant breeding areas.

Table S2: Numbers used to represent Bird Conservation Regions (BCRs)

Number	**Description**
1	Aleutian/Bering Sea Islands
2	Western Alaska
3	Arctic Plains and Mountains
4	Northwestern Interior Forest
5	Northern Pacific Rainforest
6	Boreal Taiga Plains
7	Taiga Shield and Hudson Plain
8	Boreal Softwood Shield
9	Great Basin
10	Northern Rockies
11	Prairie Potholes
12	Boreal Hardwood Transition
13	Lower Great Lakes/St.Lawrence Plain
14	Atlantic Northern Forests
15	Sierra Nevada
16	Southern Rockies Colorado Plateau
17	Badlands and Prairies
18	Shortgrass Prairie
19	Central Mixed Grass Prairie
20	Edwards Plateau
21	Oaks and Prairies
22	Eastern Tallgrass Prairie
23	Prairie Hardwood Transition
24	Central Hardwoods
25	West Gulf Coastal Plain/Ouachitas
26	Mississippi Alluvial Valley
27	Southeastern Coastal Plain
28	Appalachian Mountains
29	Piedmont
30	New England/Mid-Atlantic Coasts
31	Peninsular Florida
32	Coastal California
33	Sonoran and Mojave Deserts
34	Sierra Madre Occidental
35	Chihuahuan Desert
36	Tamaulipan Brushlands
37	Gulf Coastal Prairie
38	Islas Marías
39	Sierras de Baja California
40	Desierto de Baja California
41	Islas del Golfo de California
42	Sierra y Planicies de El Cabo
43	Planicie Costera, Lomeríos y Cañones de Occidente
44	Marismas Nacionales
45	Planicie Costera y Lomeríos del Pacífico Sur
46	Sur del Altiplano Mexicano
47	Eje Neovolcánico Transversal
48	Sierra Madre Oriental

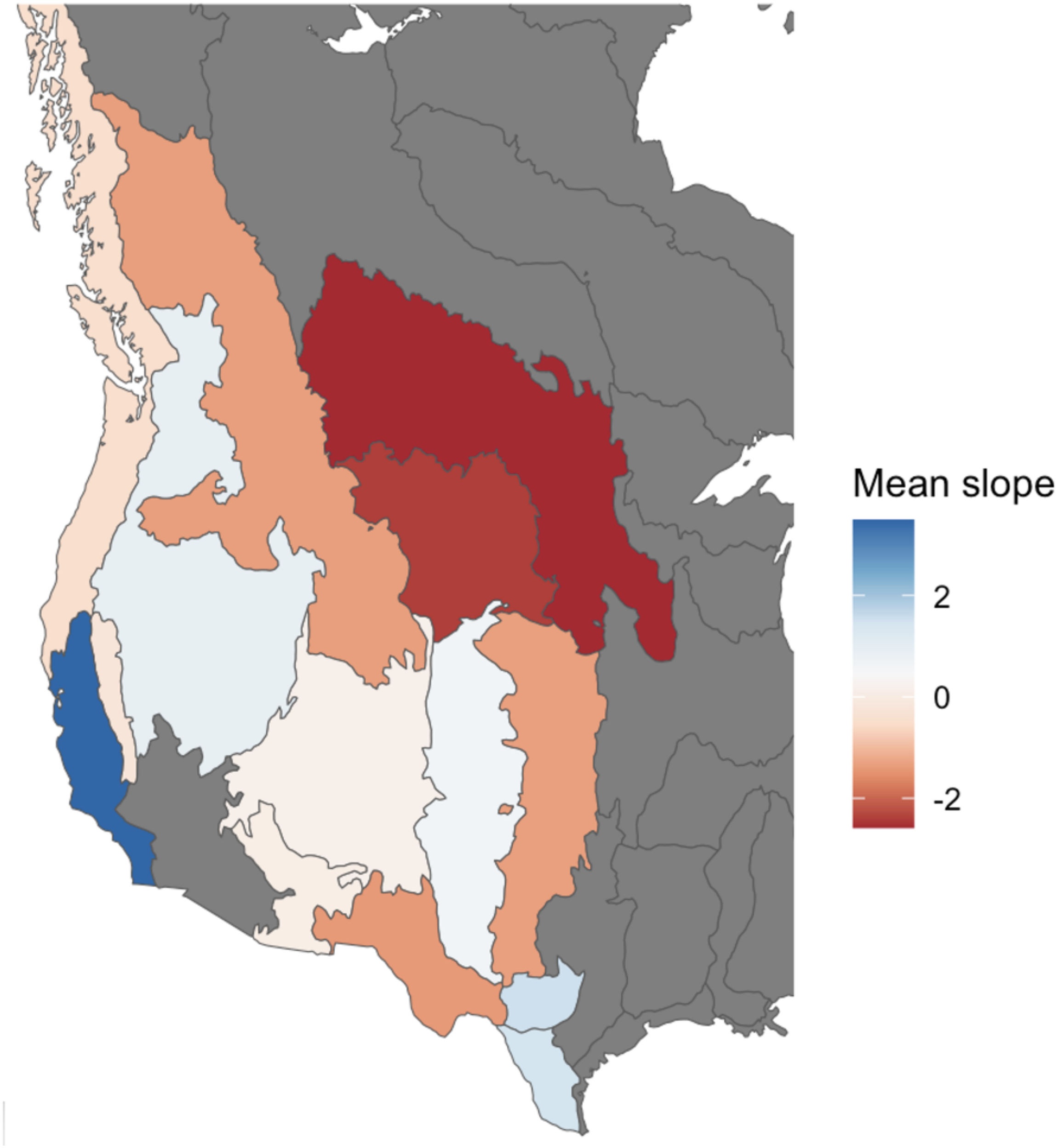

Figure S5: Mean slope for the linear relationship between monsoon halfway date and annual population change for all molt-migrant populations for which top models featured monsoon halfway date as a predictor variable grouped by Bird Conservation Region.

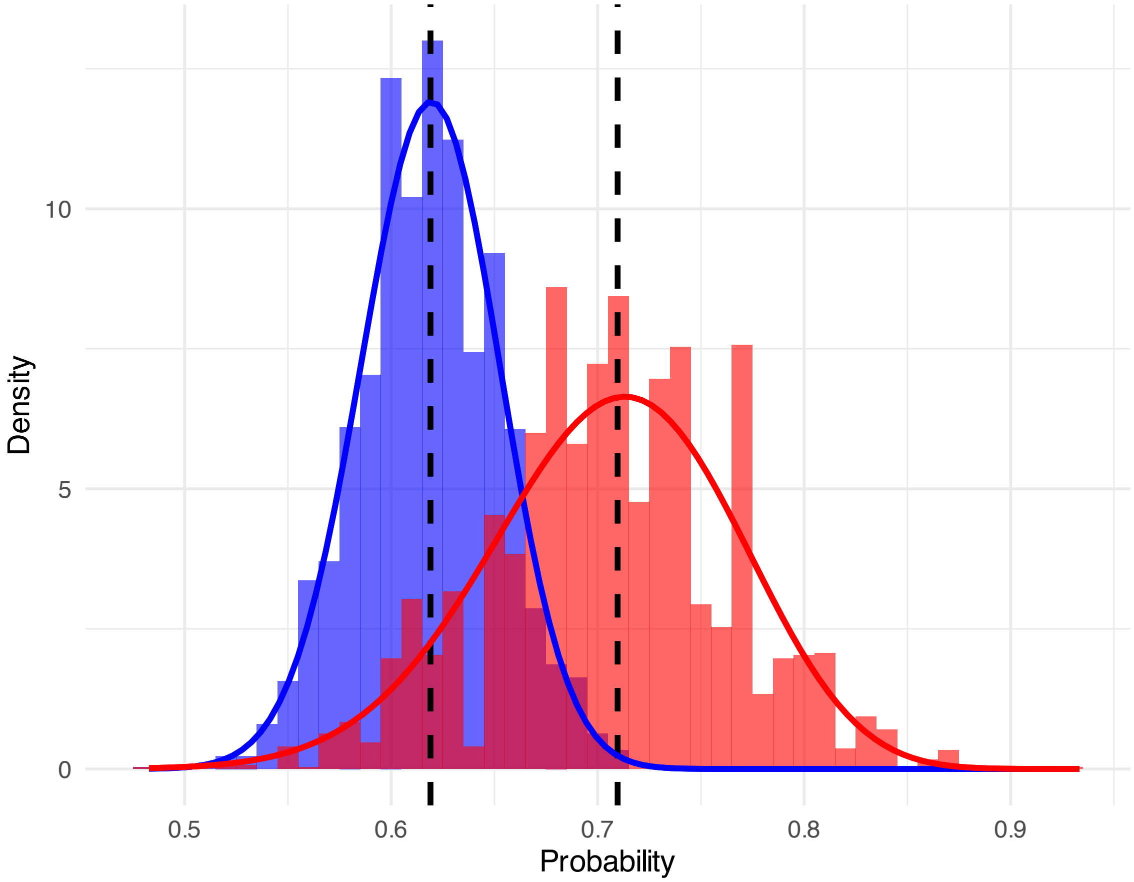

Figure S6: Probability densities for the proportion of molt-migrant populations previously found to exhibit a positive relationship between monsoon precipitation volume and interannual breeding abundance change that are declining (red) and the proportion of all other populations that are declining (blue). Histograms represent 3,000 transformed posterior draws. Dashed black lines represent the median of each set of 3,000 samples. Solid red and blue lines represent the probability density of the proportion of declining species in each group estimated as a beta distribution.

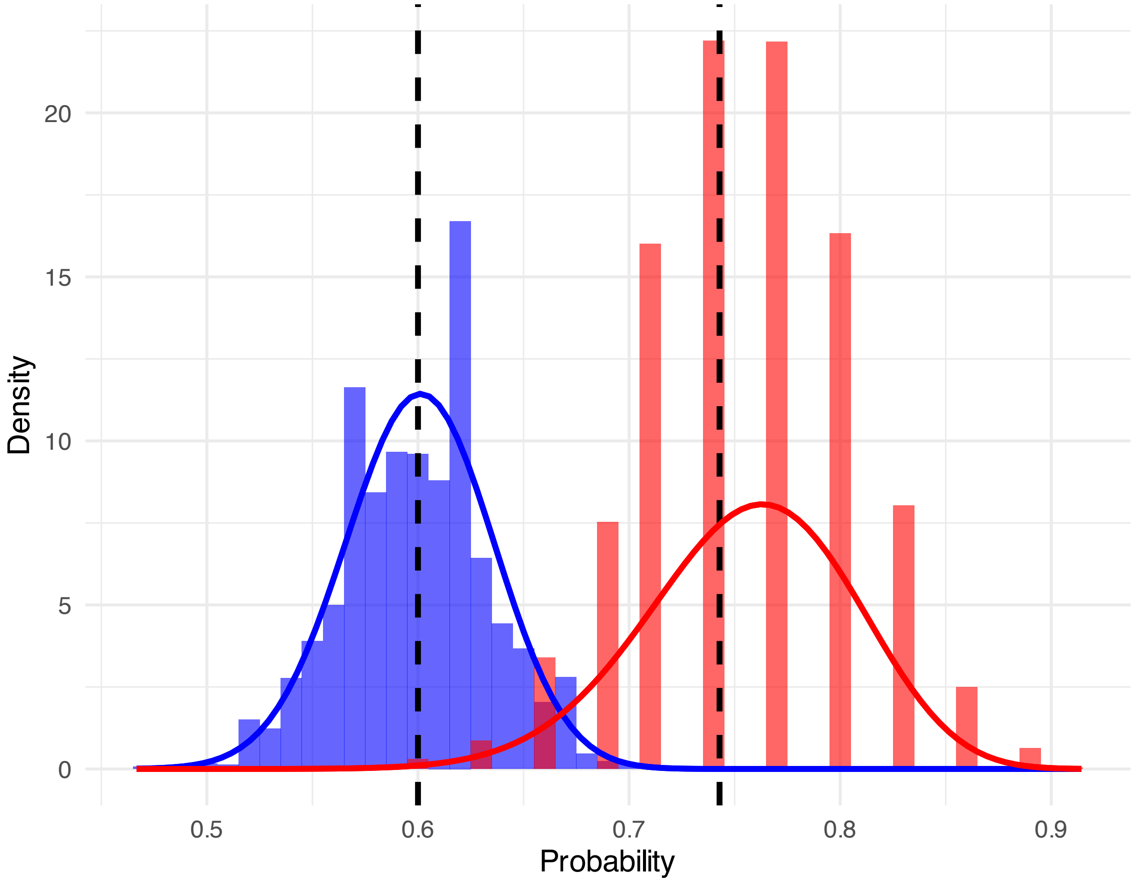

Figure S7: Probability densities for the proportion of molt-migrant populations previously found to be sensitive to interannual variation in monsoon phenology that are declining (red) and the proportion of all populations previously identified as resistant to variation in monsoon phenology that are declining (blue). Histograms represent 3,000 transformed posterior draws. Dashed black lines represent the median of each set of 3,000 samples. Solid red and blue lines represent the probability density of the proportion of declining species in each group estimated as a beta distribution.