



Shifts in breeding phenology for Cassin's Sparrow (*Peucaea cassinii*) over four decades

Cambios en la fenología reproductiva de *Peucaea cassinii* a lo largo de cuatro décadas

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ABSTRACT. Cassin's Sparrow (*Peucaea cassinii*) is an elusive resident of the southwestern United States, southern Great Plains, and northern Mexico. Despite long-standing interest, its breeding phenology is not well established. Using 40 years of eBird occurrence records, we quantified Cassin's Sparrow's breeding phenology and assessed how it has shifted over time. Our results demonstrate a complex east-to-west seasonal progression of breeding activity. We also identify a potential source of monitoring error in the North American Breeding Bird Survey that could lead to inaccurate population trend estimates and bring into question conservation status assessments for the species based on those estimates. Finally, we document regionally distinct shifts in phenology over the past four decades that suggest local populations may be responding differently to changing climatic conditions. These findings underscore the complexity of Cassin's Sparrow's breeding ecology and have broader implications for the monitoring and conservation of aridland birds.

RESUMEN. *Peucaea cassinii* es un esquivo residente del suroeste de Estados Unidos, las Grandes Llanuras del sur y el norte de México. A pesar del interés de larga data, su fenología reproductiva no está bien establecida. Utilizando 40 años de registros de presencia en eBird, cuantificamos la fenología reproductiva de la especie y evaluamos cómo ha cambiado a lo largo del tiempo. Nuestros resultados demuestran una compleja progresión estacional de la actividad reproductiva de este a oeste. También identificamos una posible fuente de error de monitoreo en el North American Breeding Bird Survey que podría llevar a estimaciones inexactas de las tendencias poblacionales y poner en duda las evaluaciones del estado de conservación de la especie basadas en estas estimaciones. Finalmente, documentamos cambios regionalmente distintos en la fenología durante las últimas cuatro décadas que sugieren que las poblaciones locales pueden estar respondiendo de manera diferente a las condiciones climáticas cambiantes. Estos hallazgos resaltan la complejidad de la ecología reproductiva de *Peucaea cassinii* y tienen implicancias más amplias para el monitoreo y la conservación de las aves de tierras áridas.

Key Words: climate change; conservation; eBird; opportunistic breeding; population trends; regional differences

INTRODUCTION

Cassin's Sparrow (*Peucaea cassinii* Woodhouse, 1852) is a native species of the arid shrub grasslands of the southwestern United States (U.S.), southern Great Plains, and northern Mexico. It is often a focal species in studies of grassland ecosystems (Gordon 2000, Roberts et al. 2017, Salas et al. 2017, Visser 2021, Forrest 2022) and has been used as an indicator species for long-term monitoring of grassland biodiversity (Ruth 2000, Lynn 2006, U. S. Fish and Wildlife Service 2012, 2016). Cassin's Sparrow's breeding phenology, however, is not well established. It is thought to be migratory in the northern part of its range, withdrawing into the southern part of its range and further south into Mexico for the winter, but the timing of these migratory movements and the onset of nesting vary greatly from year to year, apparently in response to the arrival of monsoon rainfall in some regions (Williams and LeSassier 1968, Ruth 2000, Dunning et al. 2020). There are reports that males in breeding condition can arrive early to some areas and wait for the onset of favorable environmental conditions and the appearance of females before becoming active (Phillips 1944, Williams and LeSassier 1968). Ohmart (1969) proposed a hypothesis of itinerant breeding wherein Cassin's Sparrows can maintain dual breeding ranges across the North American southwest and raise two broods per year, one in Texas and a second brood in Arizona (Phillips 1944, 1971, Ohmart 1969,

Hubbard 1977). It also has been suggested that only one population is involved in this itinerancy, moving east to west during the summer months, with the season beginning in southeastern Texas in early spring and ending in southeastern Arizona in late summer (Phillips 1944, Ohmart 1966, 1969, Ruth 2000).

This complicated picture likely reflects Cassin's Sparrow's ability to move and breed opportunistically (Phillips 1944, Ohmart 1966, 1969, Hubbard 1977, Ruth 2000), a trait that is found in many desert birds (Williams and Tieleman 2005, Duursma et al. 2017, Pascoe et al. 2021, Newton 2023). Such responsiveness is adaptive, given the highly variable and unpredictable nature of arid ecosystems and the physiological stresses placed on these birds (Davies 1984, Albright et al. 2017, Ma et al. 2023). Opportunistic breeding, however, makes understanding the breeding phenology and the phenological responses of a species to climate change more challenging, because these species are responding to seasonal changes in weather and local conditions that can influence resource availability, summertime movements, and breeding activity as well as decadal climate change that can shift seasonal conditions altogether and alter long-term migration patterns and ecosystem productivity (Visser et al. 2012, Renner and Zohner 2018, Pascoe et al. 2021, Robertson et al. 2024).

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Complicating things further, Cassin's Sparrows can be particularly difficult to observe in the field: they are rather plain, spend most of the time on the ground or hidden in shrubs, and they are generally quiet. As a result, few direct measures of breeding phenology exist for the species. A total of about 140 nesting records and egg dates can be found in the literature, dating from the mid-19th Century (Baird et al. 1858, Williams and LeSassier 1968, Hubbard 1977, Wolf 1977, Maurer et al. 1989, Schnase et al. 1991, Ruth 2000). The eBird database (<https://ebird.org/>), which is the source of most observational data on the species, largely overlaps with data available from the U.S. Geological Survey (USGS) North American Breeding Bird Survey (BBS, <https://www.pwrc.usgs.gov/BBS/>), iNaturalist (<https://www.inaturalist.org/>), and the Global Biodiversity Information Facility (GBIF, <https://gbif.org/>). The eBird database currently contains about 90,000 occurrence records for Cassin's Sparrow; however, only 200 records confirm evidence of breeding, and only 19 nests are noted. There are about 1800 banding records available for the species (<https://www.usgs.gov/labs/bird-banding-laboratory>), but only 12 of these are re-encounters, yielding little insight into the movements and reproductive ecology of the species. Because of this lack of data, efforts to quantify Cassin's Sparrow's breeding phenology have had to rely primarily on indirect estimates.

Fortunately, an exception to Cassin's Sparrow's elusiveness comes during the breeding season when males initiate flight song displays. This skylarking behavior is used to define and defend territories, attract females, and maintain pair bonds (Williams and LeSassier 1968, Schnase and Maxwell 1989, Schnase et al. 1991, Anderson and Conway 2000, Ruth 2000, Dunning et al. 2020). Cassin's Sparrow's flight displays are conspicuous, distinctive, and, importantly, can be used to delimit key phases of the breeding cycle of the species with high detection and identification confidence (Schnase et al. 1991, Anderson and Conway 2000). Natural history accounts consistently associate the onset and decline of male skylarking with the beginning and end of Cassin's Sparrow's breeding season (Williams and LeSassier 1968, Maxwell 1979, Schnase and Maxwell 1989, Dunning et al. 2020). Hormonal studies lend support to these observations. Testicular development and reproductive readiness, for example, are associated with the onset of skylarking at the start of the breeding season; cessation of skylarking and testicular regression mark the end of the season (Small et al. 2007, Deviche et al. 2008, 2012). The strongest evidence for a link between skylarking and breeding cycle events, however, comes from energetic studies. Schnase et al. (1991) have shown an association between the energy investment in male display activities (i.e., skylarking and singing rate) and three distinct phases of the breeding season: an early pre-incubation phase, during which males become detectable in the field, and flight displays and song production begins; a middle phase, during which skylarking continues, and incubation, nesting, and fledging occur; and an ending phase, during which fledglings disperse, skylarking and song weaken, and adult birds become quiescent or migrate away to overwintering grounds, sometimes after a second brooding attempt.

In this study, we draw on 40 years of citizen science observations to improve our understanding of Cassin's Sparrow's breeding phenology. We do this by taking advantage of Cassin's Sparrow's distinctive skylarking behavioral trait. We use eBird occurrence

record densities, the vast majority of which represent observations of skylarking males, as a proxy for major phases of Cassin's Sparrow's breeding season. We first determine the timing of key phases of the breeding cycle of the species, then look at how the timing of this cycle has changed over the past four decades and whether there is variability in the changes across the states and ecoregions where the species can be found. This multiscale approach provides a more complete view of Cassin's Sparrow's breeding phenology and phenological response to long-term climate change than was heretofore available.

METHODS

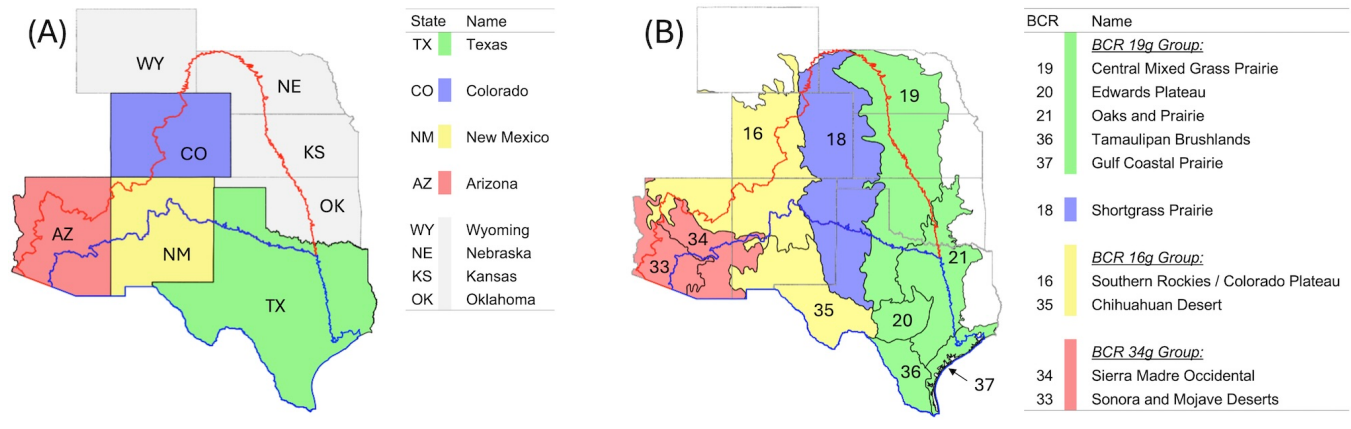
Obtaining observations and calculating state phenological trends

We obtained a total of 61,192 unique time-stamped Cassin's Sparrow point locations for the years 1985 to 2024 from the eBird database (Cornell Lab 2025). Of these, 59,251 records were from the continental U.S., and, of these, approximately 95% came from only four states: Texas, New Mexico, Colorado, and Arizona (Fig. 1A). To simplify our state-level analysis, we focused our study on these four states. We felt it was important to evaluate phenology at the state level given that much conservation assessment and action (e.g., development and implementation of State Wildlife Action Plans) is taken within state boundaries by state wildlife management agencies (<https://www.fishwildlife.org/afwa-informs/state-wildlife-action-plans>). These agencies increasingly try to work across state boundaries and regions at scales that are more ecologically relevant, but much project funding and decision making still occurs at the state level.

We first determined the timing and spatial location of seasonal peaks for each state. We did this by finding the overall day-of-the-year (DOY) maximum occurrence record count for each state and calculating the mean longitude and latitude coordinates for observations associated with these DOYs. We then tested for long-term trends in four breeding season metrics. We aggregated the occurrence records into eight, 5-year spans extending across the 40-year study period and used daily record counts grouped by DOY quantiles to characterize start, median, and end phases (9%, 50%, 93% quantiles, respectively) and duration (93% quantile - 9% quantile; Duursma et al. 2017, Mayor et al. 2017, Lehikoinen et al. 2019, Hällfors et al. 2020). We based our selection of start phase and end phase quantiles on the earliest and latest egg dates in the literature, which occur in Texas and Arizona, respectively. For Texas, the earliest reported egg date is 1 March (DOY 60, which corresponds to the 9% quantile in the Texas record distribution); in Arizona, the latest reported egg dates are from the first week of September (around DOY 250, which corresponds to the 93% quantile in the Arizona distribution; Ruth 2000, Dunning et al. 2020). Although the choice of quantiles is somewhat arbitrary, these broad phase boundaries provide a way of comparing long-term trends across states and regions, which was the major goal of the study.

We quantified trends by regressing each of the four phenological metrics against the eight 5-year spans of the 40-year study. We fitted linear regressions under a Bayesian framework using the *rstanarm* package in R (<https://mc-stan.org/rstanarm>). We ran three Markov chains with 100,000 iterations each, including a burn-in of 10,000 iterations and a thinning interval of two, using weakly informative priors for all parameters (Gelman et al. 2017). From the posterior distributions, we extracted mean estimates

Fig. 1. Maps show (A) the four U.S. states and (B) four Bird Conservation Region (BCR) groups that are the focus of this study. The different colors represent states and BCR groups that have similar occurrence record density patterns, as described in the accompanying text. The red and blue lines, respectively, show the northern extent of Cassin's Sparrow's (*Peucaea cassinii*) breeding and overwintering ranges.



and regression coefficients (β). We used the 95% credible interval (CI) to assess parameter uncertainty and Bayesian R^2 to evaluate the uncertainty in model fit (Gelman et al. 2019).

We used Probability of Direction (PD) to test for the existence of trends and to quantify the certainty with which trends go in a particular direction. PD represents the proportion of the posterior distribution that lies on the same side of zero as the mean, thereby indicating the probability that an effect is either positive or negative (Makowski et al. 2019a, 2019b). We interpreted PD values $> 95\%$ as very strong evidence for a directional effect, 90–94% as moderate to strong evidence for a trend, 80–89% as weak evidence, and 60–79% as very weak, inconclusive evidence for a trend (Makowski et al. 2019a, McElreath 2020). We used the Region of Practical Equivalence (ROPE), which defines an interval around zero representing negligible effects, to assess the practical significance of trends (Makowski et al. 2019b, Pan et al. 2025). ROPE percentages $> 95\%$ were taken to mean that the observed effects were possibly too small to be meaningful in real-world applications of the regression model results (Makowski et al. 2019b, Gelman et al. 2020, van de Schoot et al. 2021, Pan et al. 2025).

Calculating phenological trends for Bird Conservation Regions

In order to obtain a more meaningful ecological perspective on phenological trends, we also applied our analysis to the Bird Conservation Regions (BCRs) encompassed by Cassin's Sparrow's summer breeding range (Fig. 1B). BCRs are ecologically distinct areas in North America, each characterized by similar bird communities, habitats, and resource management challenges (<https://nabci-us.org/>). We used the USGS National Gap Analysis Program (GAP) (<https://doi.org/10.5066/F7Q81B3R>) range maps to select relevant BCRs, 10 of which extend across Cassin's Sparrow's range. In preparing these data, we observed similar occurrence record density patterns for BCR 34 (Sierra Madre Occidental) and BCR 33 (Sonoran and Mojave Deserts). We therefore aggregated these records into a single ecoregion group, which we refer to as BCR 34g. Likewise, BCR 16 (Southern Rockies / Colorado Plateau) and BCR 35

(Chihuahuan Desert) had similar record density patterns, as did BCRs 19–21, 36, and 37 (Central Mixed Grass Prairie, Edwards Plateau, Oaks and Prairie, Tamaulipan Bushlands, and Gulf Coastal Prairie, respectively). We aggregated these into BCR 16g and BCR 19g ecoregion groups. BCR 18 alone constituted the remaining, 10th group of records. These groupings allowed us to simplify our BCR analysis by focusing on four record clusters, each having a reasonably balanced representation of observations. These regions accounted for 97% of eBird's continental U.S. occurrence records for Cassin's Sparrow.

This two-tier, state/BCR stratification corresponds to the approach taken by the BBS, which is perhaps our most important, long-running source of population trend information for North American birds. The BBS computes species trends at the state level, providing data of particular value to the state conservation efforts referenced above; the BBS also reports trends across BCRs, which are particularly relevant to ecological studies.

RESULTS

East-to-west seasonal progression of breeding activity

Over the past 40 years, across the whole of Cassin's Sparrow's continental U.S. range, the breeding season has generally started in late March, peaked in early June, ended the first half of September, and lasted a little over five and one-half months (Table 1). The duration of the breeding season has varied from a high in Texas and BCR 19g of over seven months to a low of less than four months in Colorado and BCR 18. There is a trimodal distribution to the aggregate daily record count for U.S. occurrences that can be attributed to differences in the state and regional timing of events. The breeding season in Texas and BCR 19g generally peaks in early May and is responsible for the first mode in the overall distribution of U.S. records. In Colorado, New Mexico, BCR 18, and BCR 16g, the season peaks about one month later and contributes to the second mode. Arizona and BCR 34g peak two months later still and contribute to the third mode of the overall U.S. record distribution (Fig. 2). This pattern is consistent with an overall east-to-west seasonal progression of breeding activity across Cassin's Sparrow's U.S. range.

Table 1. Summary of Cassin's Sparrow (*Peucaea cassinii*) eBird occurrence record analysis for the study's focal states and Bird Conservation Regions (BCRs) as shown in Figure 1. The table shows the number of unique records; 40-year mean $\pm$ standard error (SE) of the breeding season start, median, and end phase day-of-the-year (DOY) and approximate calendar dates in parentheses; and the mean $\pm$ SE of the breeding season duration in days.

Region	Records	Start (DOY)	Median (DOY)	End (DOY)	Duration (days)
All	55,488	84.0 $\pm$ 1.5 (25 Mar)	159.3 $\pm$ 0.8 (08 June)	254.0 $\pm$ 2.6 (10 Sep)	170.0 $\pm$ 3.4
TX	28,044	68.0 $\pm$ 2.2 (09 Mar)	131.2 $\pm$ 1.4 (11 May)	282.8 $\pm$ 4.4 (09 Oct)	214.5 $\pm$ 5.9
CO	6,227	124.8 $\pm$ 2.3 (04 May)	160.0 $\pm$ 1.9 (09 Jun)	214.5 $\pm$ 3.1 (02 Aug)	89.8 $\pm$ 3.8
NM	9,720	110.5 $\pm$ 2.0 (20 Apr)	165.1 $\pm$ 1.4 (14 Jun)	243.8 $\pm$ 3.4 (31 Aug)	133.1 $\pm$ 5.2
AZ	11,497	114.8 $\pm$ 3.8 (24 Apr)	214.5 $\pm$ 0.5 (02 Aug)	249.1 $\pm$ 1.4 (06 Sep)	134.4 $\pm$ 4.6
BCR 19g	18,134	58.9 $\pm$ 2.4 (27 Feb)	122.9 $\pm$ 1.5 (02 May)	300.2 $\pm$ 4.2 (27 Oct)	241.3 $\pm$ 5.4
BCR 18	15,141	116.4 $\pm$ 1.1 (26 Apr)	159.0 $\pm$ 0.5 (08 Jun)	225.1 $\pm$ 0.6 (13 Aug)	108.8 $\pm$ 1.6
BCR 16g	10,088	85.3 $\pm$ 1.6 (26 Mar)	166.9 $\pm$ 1.0 (15 Jun)	268.9 $\pm$ 2.2 (25 Sep)	183.8 $\pm$ 2.8
BCR 34g	10,977	116.8 $\pm$ 3.2 (26 Apr)	214.3 $\pm$ 0.5 (02 Aug)	247.5 $\pm$ 1.8 (04 Sep)	130.8 $\pm$ 4.4

Shifts in breeding phenology across four decades

We found evidence for directional trends in 14 state-level regression models, with statistical support for the trends ranging from very weak to very strong (Fig. 3). In Texas, there is a 97% probability that the end phase has advanced over the past 40 years, accompanied by a contraction in the duration of the breeding season. Delayed start and median phases are also supported in the state (PD = 88% and PD = 87%, respectively). In New Mexico, there is evidence for an advancing end phase (PD = 90%) and for a shortening of the breeding season (PD = 81%); however, there is no directional evidence for a start phase trend in New Mexico (PD = 54%) or end phase trend in Colorado (PD = 58%). Although ROPE values for all state results exceeded 95%, indicating that the effect of time on phenology may not be ecologically important, the median phase of the breeding season in Arizona has almost certainly been delayed by approximately 10.9 days over the 40-year span of the study (PD = 100%; β = 0.31; CI = 0.14, 0.48; R^2 = 0.72). High PD with high percent in ROPE implies a consistent but small directional trend. Evidence for trends in the remaining phases was inconclusive (PDs = 65%–79%).

Phenological shifts are more apparent in the ecoregion groups, with all but one of the regressions showing evidence of directional trends (Fig. 4). Statistical support for these trends also ranged from very weak to very strong. In BCR 19g, there is a 93% probability that the breeding season end phase has advanced, accompanied by a decrease in duration over the past 40 years. We found very strong support for end phase advancements in BCR 18 (PD = 98%) and BCR 16g (PD = 96%). In BCR 18, the median phase has almost certainly advanced (PD = 99%), while in BCR 34g, it has almost certainly been delayed (PD = 100%). There also is evidence for a delayed median phase in 16g (PD = 91%). We found support for an earlier start to the breeding season in BCR 18 (PD = 88%) and for a contraction of the season in BCR 16g (PD = 87%). There is no evidence for a duration trend in BCR 18 (PD = 51%) and inconclusive evidence for trends in the remaining phases (PDs = 68%–79%). Although ROPE values for all ecoregion results also exceeded 95%, we estimate the median phase in BCR 34g has been delayed by approximately 9.2 days over the 40-year span of the study (β = 0.26; CI = 0.09, 0.43; R^2 = 0.64). Range-wide results ("All" in Figs. 3 and 4) suggest an overall 40-year advance in the end phase (PD = 84%) and a corresponding shortening of the breeding season (PD = 85%).

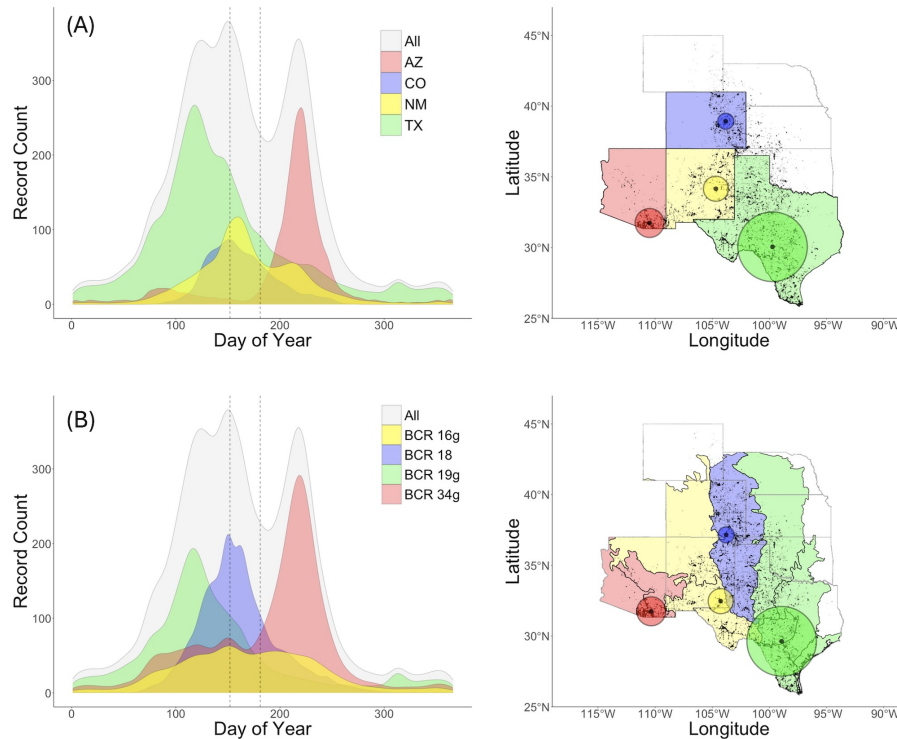
DISCUSSION

eBird record confirms east-to-west seasonal progression

We found confirmation of an east-to-west progression of breeding activity across the spring and summer months that begins in Texas and BCR 19g; moves through New Mexico, Colorado, BCR 18, and BCR 16g; then ends in Arizona and BCR 34g in early fall (Table 1, Fig. 2). Phenological descriptions from the historical literature are few, date back several decades, and come primarily from Texas and Arizona. In central Texas, the literature shows a migratory influx of birds, typically joining overwintering residents, in early March. Skylarking and competition for territories among males begins mid-March, with females appearing on territories later in the month. Most nesting reports and egg dates from Texas are in May, and the first-brood season has been estimated to end by early August (Williams and LeSassier 1968, Maxwell 1979, Schnase 1984, Schnase et al. 1991, Ruth 2000, Dunning et al. 2020). There are reports of reneesting after failed first attempts and of a resurgence of skylarking activity after first broods have fledged the nest (Schnase 1984, Dunning et al. 2020). Although there is no clear evidence for more than one brood, the long breeding season and the late-season resumption of skylarking in Texas and the BCR 19g ecoregion group suggests that double-brooding is possible (Williams and LeSassier 1968, Schnase 1984, Schnase et al. 1991, Dunning et al. 2020). We found evidence of this overall pattern in eBird's 40-year occurrence record and assumed that the long tail in the observation density distribution for Texas and BCR 19g and, to a lesser extent, New Mexico, Colorado, BCR 18, and BCR 16g, represents this late-season resumption of skylarking and may be an indicator of double-brooding attempts.

In southeastern Arizona, a 60-day breeding season starting in July has been reported (Monson and Phillips 1981, Dunning et al. 2020). We also observed late summer/early fall activity in Arizona and the BCR 34g group with the major start to the season occurring in July. The duration of the Arizona breeding season is shorter than in Texas and BCR 19g, presumably reducing opportunities for second broods. However, the observation density curves for Arizona and BCR 34g show a long head in contrast to the long tail seen in Texas and BCR 19g. Whether this is an indication of early nesting attempts by a resident population, an early migratory influx of a different population from Mexico, or some other phenomenon is an open question. Also unknown at this point is the extent to which monsoon rains in some parts

Fig. 2. Occurrence record summaries for Cassin's Sparrow (*Peucaea cassinii*) stratified by (A) states and by (B) Bird Conservation Regions (BCRs). Graphs on the left show the distribution of daily unique eBird record counts over the past 40 years. Maps on the right show the spatial distribution of the occurrence records. Colored circles indicate the average location of seasonal activity peaks within each focal state or BCR group. Circle size corresponds to the proportion of total records in that region at the seasonal peak. Vertical gray dashed lines mark the typical June survey window of the U.S. Geological Survey's North American Breeding Bird Survey.



of Arizona and New Mexico affect these patterns. However, the North American Monsoon, which typically occurs during the summer months from late June through mid-September, is known to strongly influence seasonal rainfall patterns across the southwestern U.S. and northwestern Mexico (Adams and Comrie 1997). Our results are consistent with what has been described as Cassin's Sparrow's opportunistic movements into these areas in response to precipitation.

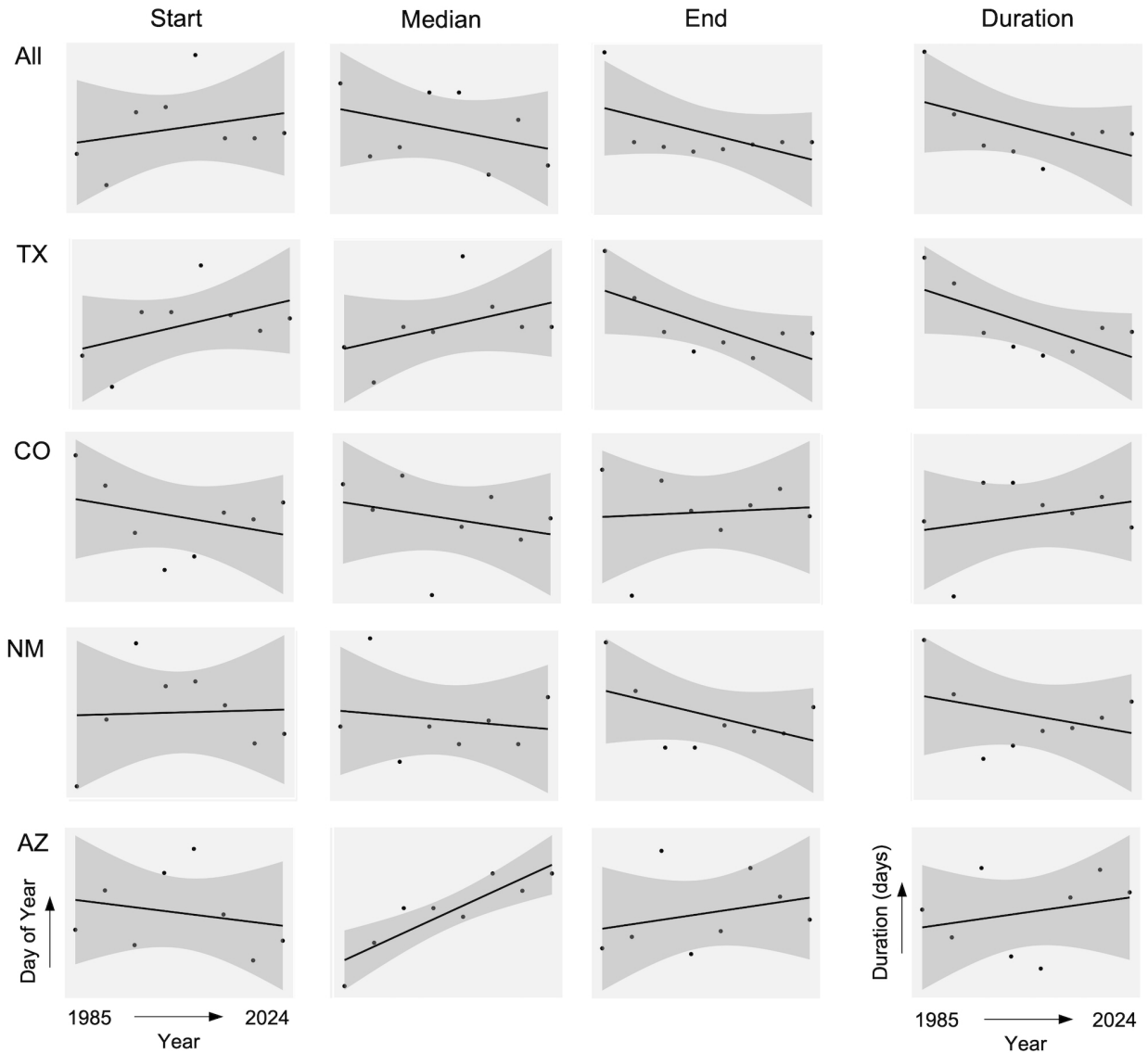
Regional differences in phenology a potential source of monitoring error

The median phase of Arizona's breeding season occurs fully three months later than the median phase in Texas, with timing of the seasonal peaks in New Mexico and Colorado intermediate between the Texas and Arizona peaks. Likewise, the median phase of BCR 34g occurs three months later than the median phase in BCR 19g, with timing of the seasonal peaks in BCR 18 and BCR 16g intermediate between the two. These patterns highlight one of the challenges to understanding the conservation status of a species like Cassin's Sparrow where assessments are based, in part, on state and BCR estimates of population trends (Lehikoinen et al. 2019, Anteau et al. 2023). The accuracy of such estimates is known to depend on survey timing (Dickie et al. 2014, Sauer et al. 2017, Lehikoinen et al. 2019). The BBS generally gathers data in June, which appears to roughly correspond to the height of the breeding season in New

Mexico, Colorado, BCR 18, and BCR 16g, but it apparently misses seasonal peaks in Texas, Arizona, BCR 19g, and BCR 34g (Fig. 2).

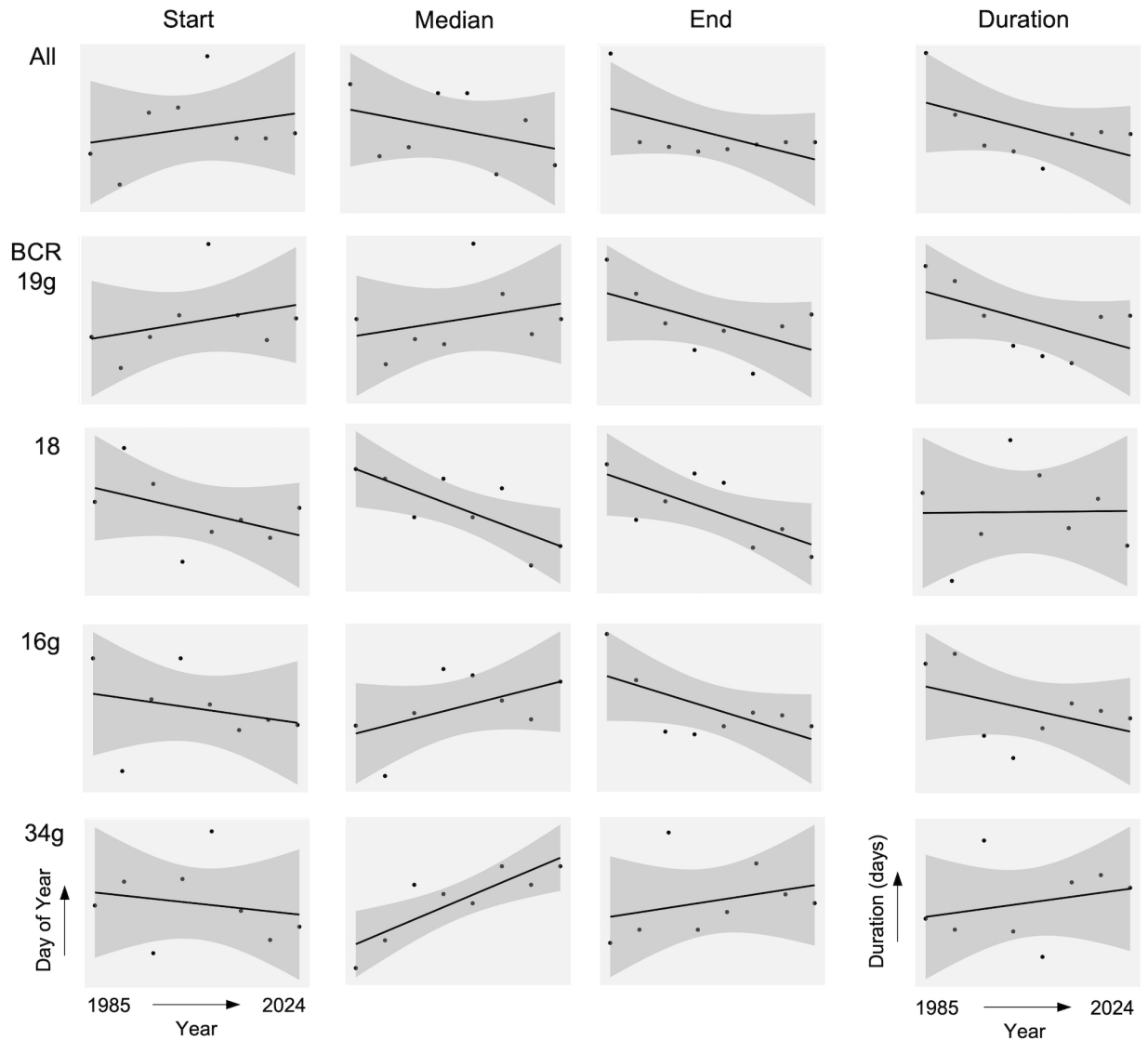
State BBS population trend estimates show a fairly uniform average decline across our focal states of $0.8\% \text{ yr}^{-1}$ over the past decade. BBS estimates positive population trends of $4.5\% \text{ yr}^{-1}$ for BCR 16 (Southern Rockies / Colorado Plateau) and $0.8\% \text{ yr}^{-1}$ for BCR 37 (Gulf Coastal Prairie). Population trends in the other BCRs within Cassin's Sparrow's range are all negative and range from $-2.2\% \text{ yr}^{-1}$ to $-0.8\% \text{ yr}^{-1}$. A consistent timing mismatch between survey period and breeding season peak, as appears to be the case with Cassin's Sparrow in some areas, raises the possibility that trend estimates are biased low in the mismatched areas (Sauer et al. 2017, 2020, Mahony et al. 2022). If that is the case, the population declines estimated for Texas and the grasslands, oaks and prairies, brushlands, and plateau regions along the eastern margin of Cassin's Sparrow's breeding range (all part of the BCR 19g group) may be exaggerated while the estimated increase along the Texas gulf coast (BCR 37, a small contributor to the BCR 19g group) may be underestimated (Fig. 1B). The western declines in Arizona and BCR 34g may be exaggerated as well. Given the timing of peak occurrences relative to BBS monitoring periods, we assume greater confidence can be placed in the New Mexico, Colorado, BCR 18, and BCR 16g estimates, while estimated trends in the other areas should be viewed with some caution.

Fig. 3. State phenology trends. Graphs show Cassin's Sparrow (*Peucaea cassinii*) breeding season day-of-the-year (DOY) start, median, and end phases (y-axis) regressed against the eight 5-year spans of the study period (x-axis) for the continental U.S. (ALL) and for the four states encompassing 95% of North American occurrence records: Texas (TX), New Mexico (NM), Colorado (CO), and Arizona (AZ; see Fig. 1A). Duration panels display breeding season length in days, also regressed against the 5-year intervals. Negative slopes for start, median, and end phases indicate earlier timing (advancement), while positive slopes indicate delays. For duration, negative slopes indicate shortening and positive slopes indicate lengthening of the breeding season. Trend lines represent predicted means from Bayesian regressions; shaded bands represent the 2.5th to 97.5th percentiles of those predictions. The accompanying table shows the regression coefficient (β), 95% credible interval (CI), Probability of Direction (PD), and Bayesian R^2 for each regression.



	β	CI	PD	R^2	β	CI	PD	R^2	β	CI	PD	R^2	β	CI	PD	R^2
ALL	0.16	-0.38, 0.69	0.75	0.10	-0.11	-0.38, 0.16	0.63	0.12	-0.61	-1.50, 0.30	0.84	0.25	-0.77	-1.92, 0.42	0.85	0.24
TX	0.43	-0.34, 1.20	0.88	0.19	0.26	-0.23, 0.73	0.87	0.17	-1.47	-2.99, 0.07	0.97	0.40	-1.91	-3.92, 0.15	0.97	0.39
CO	-0.29	-1.07, 0.50	0.79	0.11	-0.21	-0.85, 0.44	0.77	0.10	0.10	-0.97, 1.16	0.58	0.06	0.39	-0.92, 1.68	0.75	0.09
NM	0.03	-0.66, 0.72	0.54	0.06	-0.08	-0.56, 0.40	0.65	0.07	-0.68	-1.84, 0.48	0.90	0.20	-0.70	-2.47, 1.09	0.81	0.12
AZ	-0.33	-1.62, 0.96	0.71	0.08	0.31	0.14, 0.48	1.00	0.72	0.15	-0.33, 0.63	0.76	0.09	0.48	-1.13, 2.06	0.74	0.09

Fig. 4. Bird Conservation Region phenology trends. Graphs show Cassin's Sparrow (*Peucaea cassinii*) breeding season day-of-the-year (DOY) start, median, and end phases (y-axis) regressed against the eight 5-year spans of the study period (x-axis) for the continental U.S. (ALL) and for the Bird Conservation Regions (BCRs) encompassing 97% of North American occurrence records: the BCR 19g group (BCRs 19–21, 36, and 37), BCR 18, the BCR 16g group (BCRs 16 and 35), and the BCR 34g group (BCRs 34 and 33; see Fig. 1B). Duration panels display breeding season length in days, also regressed against the 5-year intervals. Negative slopes for start, median, and end phases indicate earlier timing (advancement), while positive slopes indicate delays. For duration, negative slopes indicate shortening and positive slopes indicate lengthening of the breeding season. Trend lines represent predicted means from Bayesian regressions; shaded bands represent the 2.5th to 97.5th percentiles of those predictions. The accompanying table shows the regression coefficient (β), 95% credible interval (CI), Probability of Direction (PD), and Bayesian R^2 for each regression.



	Δ	β	CI	R^2	Δ	β	CI	R^2	Δ	β	CI	R^2	Δ	β	CI	R^2
ALL	-5.5	0.16	-0.38, 0.69	0.01	3.9	-0.11	-0.38, 0.16	0.12	21.1	-0.61	-1.50, 0.30	0.25	-26.7	-0.77	-1.92, 0.42	0.24
19g	-10.6	0.30	-0.53, 1.13	0.11	-6.2	0.18	-0.36, 0.71	0.10	37.2	-1.07	-2.52, 0.43	0.27	-47.8	-1.37	-3.25, 0.54	0.27
18	7.7	-0.22	-0.61, 0.18	0.19	7.9	-0.23	-0.41, 0.04	0.52	7.4	-0.21	-0.42, 0.00	0.44	0.3	-0.01	-0.56, 0.58	0.06
16g	5.5	-0.16	-0.69, 0.38	0.09	-8.0	0.23	-0.13, 0.59	0.23	22.8	-0.65	-1.40, 0.12	0.35	-17.6	-0.51	-1.46, 0.47	0.17
34g	8.2	-0.23	-1.32, 0.86	0.07	-9.2	0.26	0.09, 0.43	0.64	-7.0	0.20	-0.41, 0.80	0.10	15.1	0.43	-1.09, 1.93	0.09

Regional differences in phenology reveal complex long-term changes

Recent work has demonstrated a northwesterly shift in suitable climate conditions for Cassin's Sparrow over the past four decades (Schnase et al. 2024), consistent with similar shifts in other North American bird species (Bateman et al. 2016, Huang et al. 2023). Phenological responses to such shifts can be complex (Thackeray et al. 2016, Cohen et al. 2018, Hällfors et al. 2020, Neate-Clegg et al. 2024). Multi-brooded species often extend their breeding season in response to warming, while single-brooded species tend to shorten them (Møller et al. 2010, Halupka and Halupka 2017, Hällfors et al. 2020). However, multi-brooded species may also shorten their seasons by reducing second clutches (Husby et al. 2009). Resident and short-distance migrants typically advance breeding onset, whereas long-distance migrants often show delays (Jenni and Kéry 2003, Davis et al. 2010, Møller et al. 2010, Lehtikoinen et al. 2019, Hällfors et al. 2020). Cassin's Sparrow is typically regarded as a multi-brooded, resident or short-distance migrant. Contrary to expectations, we found range-wide evidence of delayed onset and breeding season contraction, patterns typically associated with single-brooded, long-distance migrants. Notably, these trends vary regionally.

For example, in Texas and BCR 19g, which includes south and central Texas, delayed starts and advancing end phases appear to be contributing to substantial declines in breeding season duration, perhaps reflecting deteriorating conditions in the southeastern portions of Cassin's Sparrow's range (Figs. 3 and 4). In contrast, Colorado, Arizona, and BCR 34g, which encompasses the Sonoran Desert regions of southeastern Arizona and southwestern New Mexico, show trends toward earlier onset and increasing duration, more in line with expectations for the species. The start phase for the Colorado Plateau and Chihuahuan Desert regions of Colorado, New Mexico, and west Texas, encompassed by BCR 16g, is also advancing; however, in this case, the end phase is advancing as well, leading to an overall decrease in breeding season duration. Phenological advancement was most evident in BCR 18, where start, median, and end phases all advanced, effectively shifting the season earlier in the shortgrass prairie region of Cassin's Sparrow's central range. Notably, the median phase delays in Arizona and BCR 34g (10.9 and 9.2 days, respectively) were the strongest trends detected in the study.

These divergent patterns suggest shifting breeding strategies. In southeastern parts of the range, Cassin's Sparrow may increasingly rely on early-season single brooding followed by itinerant movement westward to exploit improved conditions. Alternatively, these trends may reflect population-specific responses to local environmental change, either through adaptive plasticity or evolutionary adjustment (Both and Visser 2005, Tingley et al. 2009, Charmantier and Gienapp 2014, Socolar et al. 2017, Radchuk et al. 2019, Rollinson et al. 2021, Neate-Clegg et al. 2024). Caution is warranted regarding these interpretations, however. Although the direction of most trends is statistically supported, one-third of the regressions are inconclusive, and effect sizes fall within ROPE thresholds, indicating they may be of little ecological significance. Collectively, however, the observed patterns generally align with broader understandings of phenological responses in grassland birds (Bateman et al. 2016, 2020, Huang et al. 2023). Whether these patterns for Cassin's

Sparrow reflect distinct population behaviors, itinerant breeding, or spatially differentiated responses within a single metapopulation remains unresolved. Still, our results underscore the complexity of the species' response to climate change and the need for continued investigation, particularly in the context of conservation planning that accounts for ecologically meaningful boundaries.

CONCLUSION

In this study, we used 40 years of eBird occurrence records to quantify the breeding phenology for Cassin's Sparrow. We determined the timing of key phases of the breeding cycle based on the distinctive skylarking behavior of male Cassin's Sparrows and examined how these phases have shifted over time, with particular attention to regional variation. Our results reveal a complex east-to-west seasonal progression of breeding activity across Cassin's Sparrow's U.S. range, consistent with patterns reported in the historical literature. We also identified a potential source of monitoring error in the North American Breeding Bird Survey that could lead to inaccurate population trend estimates for the species in areas where the timing of the survey differs from breeding season activity peaks. This could bring into question conservation status assessments for Cassin's Sparrow that are based on those estimates. Finally, we found regional differences in phenological trends over the past four decades. This is meaningful, because it suggests that local populations may be responding differently to changing climatic conditions. These findings enhance our understanding of Cassin's Sparrow's breeding ecology and may have broader implications for other aridland bird species.

Author Contributions:

JLS: conceptualization and design, data collection, and analysis, software development, manuscript writing (original draft); MLC, PMM, VAS: data analysis, manuscript writing (review and editing).

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Data Availability:

The data and code that support the findings of this study are openly available in GitHub at https://github.com/jschnase/MMX_Toolkit.

LITERATURE CITED

Adams, D. K., and A. C. Comrie. 1997. The North American monsoon. *Bulletin of the American Meteorological Society* 78:2197-2214. <https://doi.org/10.1175%2F1520-0477%281997%29078%3C2197%3ATNAM%3E2.0.CO%3B2>

- Albright, T. P., D. Mutibwa, A. R. Gerson, E. K. Smith, W. A. Talbot, J. J. O'Neill, A. E. McKechnie, and B. O. Wolf. 2017. Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences* 114:2283-2288. <https://doi.org/10.1073/pnas.1613625114>
- Anderson, J. T., and W. C. Conway. 2000. The flight song display of the Cassin's Sparrow (*Aimophila cassinii*): form and possible function. *Bulletin of the Texas Ornithological Society* 33:1-12.
- Anteau, M. J., K. S. Ellis, G. J. MacDonald, L. D. Igl, N. D. Niemuth, and J. L. Vest. 2023. Climate-induced shifts in grassland bird nesting phenology have implications for grassland management. *Global Ecology and Conservation* 48:e02700. <https://doi.org/10.1016/j.gecco.2023.e02700>
- Baird, S. F., J. Cassin, and G. N. Lawrence. 1858. General report upon the zoology of the several Pacific Railroad routes, Part II. Birds. *Annals and Magazine of Natural History* 2:466-468. <https://doi.org/10.1080/00222935808697066>
- Bateman, B. L., A. M. Pidgeon, V. C. Radeloff, J. VanDerWal, W. E. Thogmartin, S. J. Vavrus, and P. J. Heglund. 2016. The pace of past climate change vs. potential bird distributions and land use in the United States. *Global Change Biology* 22:1130-1144. <https://doi.org/10.1111/gcb.13154>
- Bateman, B. L., L. Taylor, C. Wilsey, J. Wu, G. S. LeBaron, and G. Langham. 2020. Risk to North American birds from climate change-related threats. *Conservation Science and Practice* 2:e243. <https://doi.org/10.1111/csp2.243>
- Both, C., and M. E. Visser. 2005. The effect of climate change on the correlation between avian life-history traits. *Global Change Biology* 11:1606-1613. <https://doi.org/10.1111/j.1365-2486.2005.01038.x>
- Charmantier, A., and P. Gienapp. 2014. Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evolutionary Applications* 7:15-28. <https://doi.org/10.1111/eva.12126>
- Cohen, J. M., M. J. Lajeunesse, and J. R. Rohr. 2018. A global synthesis of animal phenological responses to climate change. *Nature Climate Change* 8:224-228. <https://doi.org/10.1038/s41558-018-0067-3>
- Cornell Lab. 2025. eBird Basic Dataset Version: ebd_casspa_sm-p_relMar-2025. Cornell University, Ithaca, New York, USA.
- Davies, S. J. J. F. 1984. Nomadism as a response to desert conditions in Australia. *Journal of Arid Environments* 7:183-195. [https://doi.org/10.1016/S0140-1963\(18\)31382-X](https://doi.org/10.1016/S0140-1963(18)31382-X)
- Davis, C. C., C. G. Willis, R. B. Primack, and A. J. Miller-Rushing. 2010. The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3201-3213. <https://doi.org/10.1098/rstb.2010.0130>
- Deviche, P., J. Sabo, and P. J. Sharp. 2008. Glutamatergic stimulation of luteinising hormone secretion in relatively refractory male songbirds. *Journal of Neuroendocrinology* 20:1191-1202. <https://doi.org/10.1111/j.1365-2826.2008.01771.x>
- Deviche, P., P. J. Sharp, A. Dawson, J. Sabo, B. Fokidis, S. Davies, and L. Hurley. 2012. Up to the challenge? Hormonal and behavioral responses of free-ranging male Cassin's Sparrows, *Peucaea cassinii*, to conspecific song playback. *Hormones and Behavior* 61:741-749. <https://doi.org/10.1016/j.yhbeh.2012.03.012>
- Dickie, M., P. A. Smith, and H. G. Gilchrist. 2014. The importance of survey timing on shorebird density estimates at East Bay, Nunavut, Canada. *Waterbirds* 37:394-401. <https://doi.org/10.1675/063.037.0406>
- Dunning, J. B., Jr., R. K. Bowers Jr., S. J. Suter, and C. E. Bock. 2020. Cassin's Sparrow (*Peucaea cassinii*), version 1.0. In P. G. Rodewald, Editor. *Birds of the World*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.casspa.01>
- Duursma, D. E., R. V. Gallagher, and S. C. Griffith. 2017. Characterizing opportunistic breeding at a continental scale using all available sources of phenological data: an assessment of 337 species across the Australian continent. *Auk* 134:509-519. <https://doi.org/10.1642/AUK-16-243.1>
- Forrest, G. 2022. Habitat selection of the declining Cassin's Sparrow in an imperiled grassland biome. Thesis. Colorado State University Pueblo, Pueblo, Colorado, USA.
- Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2020. Bayesian data analysis. Third edition. Taylor & Francis, Boca Raton, Florida, USA.
- Gelman, A., B. Goodrich, J. Gabry, and A. Vehtari. 2019. R-squared for Bayesian regression models. *American Statistician* 73:307-309. <https://doi.org/10.1080/00031305.2018.1549100>
- Gelman, A., D. Simpson, and M. Betancourt. 2017. The prior can often only be understood in the context of the likelihood. *Entropy* 19:555. <https://doi.org/10.3390/e19100555>
- Gordon, C. E. 2000. Movement patterns of wintering grassland sparrows in Arizona. *Auk* 117:748-759. <https://doi.org/10.1093/auk/117.3.748>
- Hällfors, M. H., L. H. Antão, M. Itter, A. Lehtikainen, T. Lindholm, T. Roslin, and M. Saastamoinen. 2020. Shifts in timing and duration of breeding for 73 boreal bird species over four decades. *Proceedings of the National Academy of Sciences* 117:18557-18565. <https://doi.org/10.1073/pnas.1913579117>
- Halupka, L., and K. Halupka. 2017. The effect of climate change on the duration of avian breeding seasons: a meta-analysis. *Proceedings of the Royal Society B: Biological Sciences* 284:20171710. <https://doi.org/10.1098/rspb.2017.1710>
- Huang, Q., B. L. Bateman, N. L. Michel, A. M. Pidgeon, V. C. Radeloff, P. Heglund, A. J. Allstadt, A. J. Nowakowski, J. Wong, and J. R. Sauer. 2023. Modeled distribution shifts of North American birds over four decades based on suitable climate alone do not predict observed shifts. *Science of The Total Environment* 857:159603. <https://doi.org/10.1016/j.scitotenv.2022.159603>
- Hubbard, J. P. 1977. The status of Cassin's Sparrow in New Mexico and adjacent states. *American Birds* 31:933-941.
- Husby, A., L. E. B. Kruuk, and M. E. Visser. 2009. Decline in the frequency and benefits of multiple brooding in Great Tits as a

- consequence of a changing environment. *Proceedings of the Royal Society B: Biological Sciences* 276:1845-1854. <https://doi.org/10.1098/rspb.2008.1937>
- Jenni, L., and M. Kéry. 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society B: Biological Sciences* 270:1467-1471. <https://doi.org/10.1098/rspb.2003.2394>
- Lehikoinen, A., A. Lindén, M. Karlsson, A. Andersson, T. L. Crewe, E. H. Dunn, G. Gregory, L. Karlsson, V. Kristiansen, S. Mackenzie, et al. 2019. Phenology of the avian spring migratory passage in Europe and North America: asymmetric advancement in time and increase in duration. *Ecological Indicators* 101:985-991. <https://doi.org/10.1016/j.ecolind.2019.01.083>
- Lynn, J. 2006. Cassin's Sparrow (*Aimophila cassinii*): a technical conservation assessment. USDA Forest Service, Flagstaff, Arizona, USA.
- Ma, L., S. R. Conradie, C. L. Crawford, A. S. Gardner, M. R. Kearney, I. M. D. Maclean, A. E. McKechnie, C.-R. Mi, R. A. Senior, and D. S. Wilcove. 2023. Global patterns of climate change impacts on desert bird communities. *Nature Communications* 14:211. <https://doi.org/10.1038/s41467-023-35814-8>
- Mahony, N. A., B. C. Dale, and D. A. W. Miller. 2022. Grassland bird population declines at three Breeding Bird Survey spatial scales in contrast to a large native prairie. *Ecosphere* 13:e4309. <https://doi.org/10.1002/ecs2.4309>
- Makowski, D., M. S. Ben-Shachar, S. H. A. Chen, and D. Lüdtke. 2019b. Indices of effect existence and significance in the Bayesian framework. *Frontiers in Psychology* 10:2767. <https://doi.org/10.3389/fpsyg.2019.02767>
- Makowski, D., M. Ben-Shachar, and D. Lüdtke. 2019a. bayestestR: describing effects and their uncertainty, existence and significance within the Bayesian framework. *Journal of Open Source Software* 4:1541. <https://doi.org/10.21105/joss.01541>
- Maurer, B. A., E. A. Webb, and R. K. Bowers. 1989. Nest characteristics and nestling development of Cassin's and Botteri's Sparrows in southeastern Arizona. *Condor* 91:736-738. <https://doi.org/10.2307/1368132>
- Maxwell, T. C. 1979. Avifauna of the Concho Valley of west-central Texas with special reference to historical change. Texas A&M University, College Station, Texas, USA.
- Mayor, S. J., R. P. Guralnick, M. W. Tingley, J. Otegui, J. C. Withey, S. C. Elmendorf, M. E. Andrew, S. Leyk, I. S. Pearse, and D. C. Schneider. 2017. Increasing phenological asynchrony between spring green-up and arrival of migratory birds. *Scientific Reports* 7:1902. <https://doi.org/10.1038/s41598-017-02045-z>
- McElreath, R. 2020. Statistical rethinking: a Bayesian course with examples in R and Stan. Second edition. Chapman and Hall/CRC, New York, New York, USA. <https://doi.org/10.1201/9780429029608>
- Møller, A. P., E. Flensted-Jensen, K. Klarborg, W. Mardal, and J. T. Nielsen. 2010. Climate change affects the duration of the reproductive season in birds. *Journal of Animal Ecology* 79:777-784. <https://doi.org/10.1111/j.1365-2656.2010.01677.x>
- Monson, G., and A. R. Phillips. 1981. Annotated checklist of the birds of Arizona. Second edition. University of Arizona Press, Tucson, Arizona, USA.
- Neate-Clegg, M. H. C., B. A. Tonelli, and M. W. Tingley. 2024. Advances in breeding phenology outpace latitudinal and elevational shifts for North American birds tracking temperature. *Nature Ecology & Evolution* 8:2027-2036. <https://doi.org/10.1038/s41559-024-02536-z>
- Newton, I. 2023. The migration ecology of birds. Elsevier, Amsterdam, The Netherlands.
- Ohmart, R. D. 1966. Breeding record of the Cassin Sparrow (*Aimophila cassinii*) in Arizona. *Condor* 68:400. <https://doi.org/10.2307/1365460>
- Ohmart, R. D. 1969. Dual breeding ranges in Cassin's sparrow (*Aimophila cassinii*). Page 105 in C. C. Hoff and M. L. Riedesel, editors. *Physiological systems in semiarid environments*. University of New Mexico Press, Albuquerque, New Mexico, USA.
- Pan, J., R. Christoforou, L. N. Wiedermann, and M. Schweiker. 2025. The untapped potential of Bayesian region of practical equivalence for assessing null effects in multi-domain research. *Building and Environment* 283:113390. <https://doi.org/10.1016/j.buildenv.2025.113390>
- Pascoe, B. A., C. R. Pavey, S. R. Morton, and C. A. Schlesinger. 2021. Dynamics of bird assemblages in response to temporally and spatially variable resources in arid Australia. *Ecology and Evolution* 11:3977-3990. <https://doi.org/10.1002/ece3.7293>
- Phillips, A. R. 1944. Status of Cassin's Sparrow in Arizona. *Auk* 61:409-412. <https://doi.org/10.2307/4079512>
- Phillips, A. R. 1971. Avian breeding cycles: are they related to photoperiods? *Anales del Instituto de Biología, UNAM, Serie Zoológica*, Vol. 38-75 42:87-98.
- Radchuk, V., T. Reed, C. Teplitsky, M. van de Pol, A. Charmantier, C. Hassall, P. Adamik, F. Adriaensen, M. P. Ahola, P. Arcese, et al. 2019. Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications* 10:3109. <https://doi.org/10.1038/s41467-019-10924-4>
- Renner, S. S., and C. M. Zohner. 2018. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics* 49:165-182. <https://doi.org/10.1146/annurev-eolsys-110617-062535>
- Roberts, A. J., C. W. Boal, and H. A. Whitlaw. 2017. Nesting ecology of grassland birds following a wildfire in the southern Great Plains. *Southwestern Naturalist* 62:39-45. <https://doi.org/10.1894/0038-4909-62.1.39>
- Robertson, E. P., F. A. La Sorte, J. D. Mays, P. J. Taillie, O. J. Robinson, R. J. Ansley, T. J. O'Connell, C. A. Davis, and S. R. Loss. 2024. Decoupling of bird migration from the changing phenology of spring green-up. *Proceedings of the National Academy of Sciences* 121:e2308433121. <https://doi.org/10.1073/pnas.2308433121>
- Rollinson, C. R., A. O. Finley, M. R. Alexander, S. Banerjee, K.-A. Dixon Hamil, L. E. Koenig, D. H. Locke, M. L. DeMarche,

- M. W. Tingley, K. Wheeler, C. Youngflesh, and E. F. Zipkin. 2021. Working across space and time: nonstationarity in ecological research and application. *Frontiers in Ecology and the Environment* 19:66-72. <https://doi.org/10.1002/fee.2298>
- Ruth, J. M. 2000. Cassin's Sparrow (*Aimophila cassinii*) status assessment and conservation plan. U.S. Fish and Wildlife Service, Fort Collins, Colorado, USA.
- Salas, E. A. L., V. A. Seamster, K. G. Boykin, N. M. Harings, and K. W. Dixon. 2017. Modeling the impacts of climate change on species of concern (birds) in south central U.S. based on bioclimatic variables. *AIMS Environmental Science* 4:358-385. <https://doi.org/10.3934/environsci.2017.2.358>
- Sauer, J. R., W. A. Link, and J. E. Hines. 2020. The North American Breeding Bird Survey, analysis results 1966-2019. U.S. Geological Survey. <https://doi.org/10.5066/P96A7675>
- Sauer, J. R., K. L. Pardieck, D. J. Ziolkowski, A. C. Smith, M.-A. R. Hudson, V. Rodriguez, H. Berlanga, D. K. Niven, and W. A. Link. 2017. The first 50 years of the North American Breeding Bird Survey. *Condor* 119:576-593. <https://doi.org/10.1650/CONDOR-17-83.1>
- Schnase, J. L. 1984. The breeding biology of Cassin's Sparrow (*Aimophila cassinii*) in Tom Green County, Texas. Thesis. Angelo State University, San Angelo, Texas, USA.
- Schnase, J., M. Carroll, P. Montesano, and V. Seamster. 2024. Complex changes in climatic suitability for Cassin's Sparrow (*Peucaea cassinii*) revealed by retrospective ecological niche modeling. *Journal of Field Ornithology* 95(1):9. <https://doi.org/10.5751/JFO-00432-950109>
- Schnase, J. L., W. E. Grant, T. C. Maxwell, and J. J. Leggett. 1991. Time and energy budgets of Cassin's Sparrow (*Aimophila cassinii*) during the breeding season: evaluation through modelling. *Ecological Modelling* 55:285-319. [https://doi.org/10.1016/0304-3800\(91\)90091-E](https://doi.org/10.1016/0304-3800(91)90091-E)
- Schnase, J. L., and T. C. Maxwell. 1989. Use of song patterns to identify individual male Cassin's Sparrows. *Journal of Field Ornithology* 60:12-19. <https://sora.unm.edu/sites/default/files/journals/jfo/v060n01/p0012-p0019.pdf>
- Small, T. W., P. J. Sharp, and P. Deviche. 2007. Environmental regulation of the reproductive system in a flexibly breeding Sonoran Desert bird, the Rufous-winged Sparrow, *Aimophila carpalis*. *Hormones and Behavior* 51:483-495. <https://doi.org/10.1016/j.yhbeh.2007.01.004>
- Socular, J. B., P. N. Epanchin, S. R. Beissinger, and M. W. Tingley. 2017. Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts. *Proceedings of the National Academy of Sciences* 114:12976-12981. <https://doi.org/10.1073/pnas.1705897114>
- Thackeray, S. J., P. A. Henrys, D. Hemming, J. R. Bell, M. S. Botham, S. Burthe, P. Helaouet, D. G. Johns, I. D. Jones, D. I. Leech, et al. 2016. Phenological sensitivity to climate across taxa and trophic levels. *Nature* 535:241-245. <https://doi.org/10.1038/nature18608>
- Tingley, M. W., W. B. Monahan, S. R. Beissinger, and C. Moritz. 2009. Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences* 106:19637-19643. <https://doi.org/10.1073/pnas.0901562106>
- U.S. Fish and Wildlife Service. 2012. Guidance on selecting species for design of landscape-scale conservation. <https://digitalmedia.fws.gov/digital/collection/document/id/1789/>
- U.S. Fish and Wildlife Service. 2016. Comprehensive conservation plan: Rocky Mountain Arsenal National Wildlife Refuge. U.S. Department of the Interior, Lakewood, Colorado, USA.
- van de Schoot, R., S. Depaoli, R. King, B. Kramer, K. Märtens, M. G. Tadesse, M. Vannucci, A. Gelman, D. Veen, J. Willemsen, and C. Yau. 2021. Bayesian statistics and modelling. *Nature Reviews Methods Primers* 1:1. <https://doi.org/10.1038/s43586-020-00001-2>
- Visser, G. M. 2021. Paternity analysis of Cassin's Sparrows (*Peucaea cassinii*) in southern Colorado. Thesis. Colorado State University Pueblo, Pueblo, Colorado, USA.
- Visser, M. E., L. Te Marvelde, and M. E. Lof. 2012. Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology* 153:75-84. <https://doi.org/10.1007/s10336-011-0770-6>
- Williams, F. C., and A. L. LeSassier. 1968. Cassin's Sparrow. Pages 981-990 in O. L. Austin, editor. *Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies: order Passeriformes, family Fringillidae. Part 2, genera Pipilo through Spizella*. Dover, New York, New York, USA.
- Williams, J. B., and B. I. Tieleman. 2005. Physiological adaptation in desert birds. *BioScience* 55:416-425. [https://doi.org/10.1641/0006-3568\(2005\)055\[0416:PAIDBJ\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0416:PAIDBJ]2.0.CO;2)
- Wolf, L. L. 1977. Species relationships in the avian genus *Aimophila*. *Ornithological Monographs* 23:iii-viii, 1-220. <https://doi.org/10.2307/40166744>