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Emigration and survival correlate with different precipitation metrics throughout a grassland songbird's annual cycle

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Abstract

Many exogenous factors may influence demographic rates (i.e., births, deaths, immigration, emigration), particularly for migratory birds that must cope with variable weather and habitat throughout their range and annual cycle. In midcontinental grasslands, disturbance (e.g., fire and grazing) and precipitation influence variation in grassland structure and function, but we know little about when and why precipitation is associated with grassland species' vital rates. We related estimates of detection, survival, and emigration to *a priori* sets of precipitation metrics to test the putative alternative factors influencing movement and mortality in grasshopper sparrows (*Ammodramus savannarum*). This species is a migratory songbird that exhibits exceptionally high rates of within-season and between-season dispersal. Between 2013 and 2020, we captured and resighted grasshopper sparrows in northeastern Kansas, USA, compiling capture histories for 1,332 adult males. We tested predictions of climatic hypotheses explaining variation in survival and emigration throughout a grasshopper sparrow's annual cycle; both survival and emigration were associated with the El Niño-Southern Oscillation precipitation index (ESPI). Survival was positively related with ESPI during winter, and temporary emigration was curvilinearly related to breeding season ESPI lagged 2 years, with the highest site fidelity associated with intermediate rainfall values. The relationship between rainfall and temporary emigration likely reflects the influence of weather over multiple years on vegetation structure with consequent effects on local demography. This study provides compelling support for the idea that grassland species respond to high interannual variability by adopting dispersal strategies unlike those of many well-studied migrant birds. Furthermore, the results imply that the consequences of increasing climatic extremes may not be immediately apparent, with demographic consequences lasting for at least a few years.

KEYWORDS
breeding dispersal, Great Plains, Konza Prairie, rainfall, tallgrass prairie

Local abundance is determined by the relative contributions of births, deaths, immigration, and emigration, all of which are affected by biotic and abiotic factors. Density dependence may limit populations near thresholds (Schreiber 2003), but density-independent factors are a stronger influence on population dynamics and species interactions in many systems (Vucetich and Peterson 2003, Rêgo et al. 2013, Sudakov et al. 2017). Habitat loss, fragmentation, and weather are relatively well-documented factors influencing population change (Newton 1998, Addo-Bediako et al. 2000, Sahanatien et al. 2012, Albright et al. 2017). While temperature affects vital rates such as reproduction or survival via individual physiology influencing species ranges and life histories (Angilletta 2009, Forero-Medina et al. 2011, Day et al. 2018), less is known about when and why precipitation affects vital rates (Boyle et al. 2020).

In grassland systems, precipitation variability is a key feature of ecological function; precipitation mediates the effects of natural disturbances such as fire and grazing (Blair et al. 2014). The nature and magnitude of these interactions shape soil organic matter, primary productivity, and plant community composition (Briggs et al. 2002, Koerner and Collins 2014), making grasslands more sensitive to variation in precipitation than most systems (Blair et al. 2014). Vegetation can help buffer grassland consumer communities from weather variability by providing physical shelter during adverse conditions (Wiens 1973). Consequently, vegetation structure is closely intertwined with arthropods (Welti et al. 2020), mammals (Jones et al. 2017), and birds (Klug et al. 2010, Shew et al. 2019). Grassland animal populations are sensitive to variability in their environment, including precipitation regime (Reed et al. 2007, Skagen and Yackel Adams 2012, Wilson et al. 2018, Zuckerberg et al. 2018). That sensitivity is likely manifest as fluctuations in vital rates and local abundance; however, we lack a general understanding of how precipitation is related to demographic parameters and the underlying mechanisms that might lead to those relationships.

The influence of movement on local abundance is especially important in grassland systems (e.g., butterflies; Franzen et al. 2013). Many grassland species are highly mobile, which enables individuals to track changes in resources (e.g., bison [*Bison bison*], Plumb et al. 2009; amphibians, Searcy et al. 2012; birds, Wells et al. 2008). In particular, grassland birds exhibit lower rates of site fidelity than birds of most other biomes, which has been hypothesized to reflect adaptation to variability in their environment (Switzer et al. 1993). In migratory grassland birds, an individual may return to its previous breeding site, find the habitat unsuitable, and decide to settle elsewhere (Ahlering et al. 2009). Grassland songbirds exhibit both inter- and intraspecific variation in temporary emigration; some individuals will return to breed at the same site each year, while others will disperse elsewhere to breed (Jones et al. 2007, Ruth 2017). Additionally, individuals may settle in an area and find their home range has become unsuitable after a few weeks, leading to within-season dispersal (Gow and Stutchbury 2013). Dispersal can allow grassland birds to track rainfall-mediated fluxes in vegetation conditions and food availability conducive to survival and reproduction. But the ultimate factors influencing dispersal, the relationships between movement and rainfall (Wiens 1973), and the consequences of such mobility on demography remain unclear.

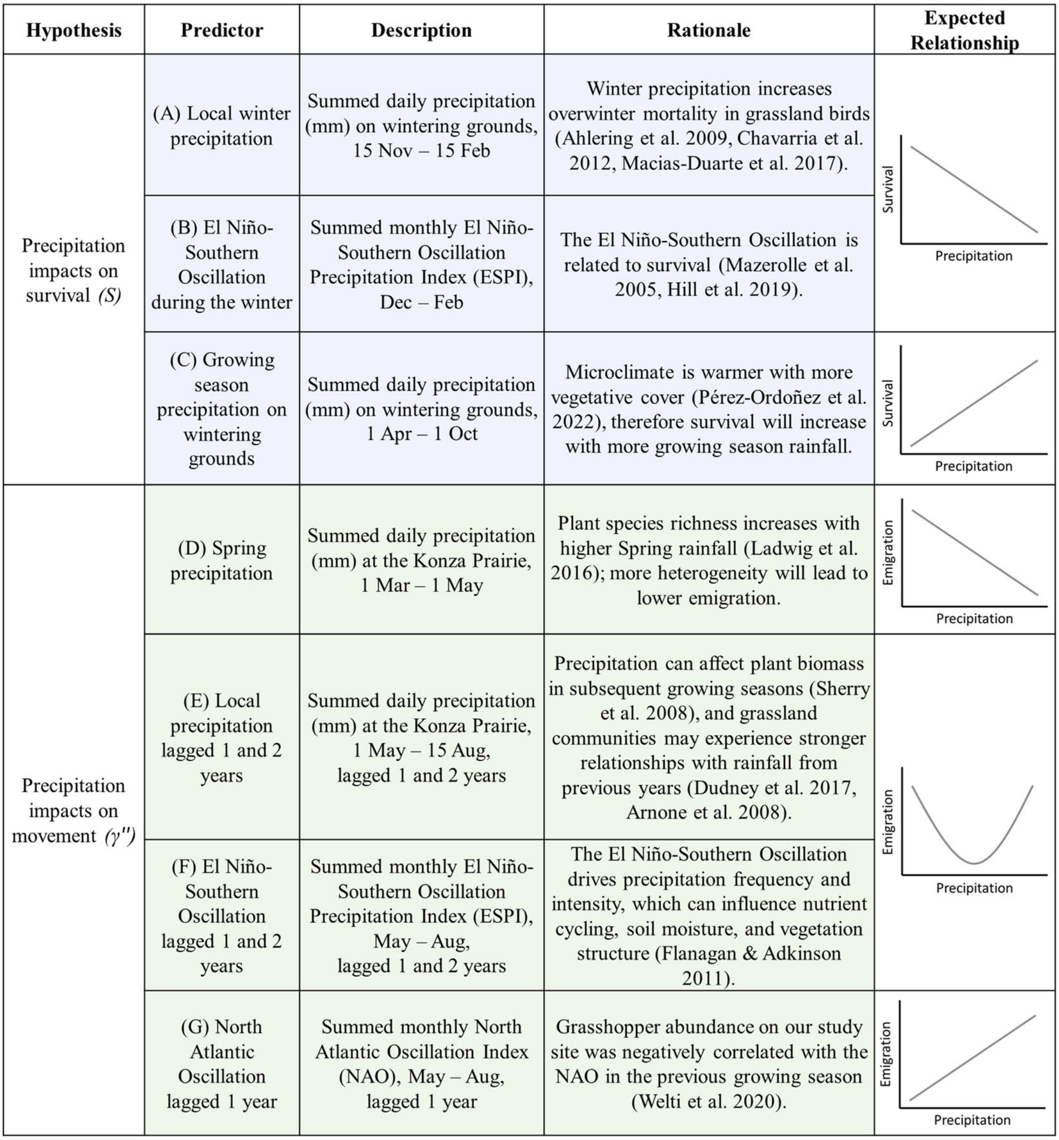
Given that many grassland songbirds move among sites within and among years, estimating vital rates can be challenging because researchers are often unable to collect sufficient data over large spatial scales to determine if individuals have dispersed from a study site. Therefore, true survival and site fidelity in mobile species are often combined into a single metric, apparent survival (Sandercock 2006). While apparent survival is assumed to be equivalent to (or at least, a good surrogate for) true survival by many authors, growing evidence suggests that in grassland birds, apparent survival estimates may largely be shaped by dispersal (Gilroy et al. 2012, Schaub and Royle 2014, Taylor et al. 2015, Becker et al. 2018). Thus, adopting modeling approaches that attempt to distinguish survival from emigration are required to elucidate the environmental factors that shape life-history traits and behaviors within and among species. Furthermore, because grassland birds are among the most imperiled groups of birds in North America with almost 75% of species declining since 1970 (Rosenberg et al. 2019), understanding the factors affecting grassland bird population dynamics can help guide effective conservation.

We studied the grasshopper sparrow (*Ammodramus savannarum*), a small (~17 g), migratory grassland songbird species that has declined by >70% since the 1960s (Sauer et al. 2020). They primarily breed in native and restored grasslands across the mid-continental and eastern United States and winter in grasslands and shrublands in the southern United States and northern Mexico, where they overlap with non-migratory sub-species whose ranges extend farther into Mesoamerica and the Caribbean (Vickery 2021). Their abundance and return rates vary geographically and interannually, with return rates as high as 88% in the eastern United States (Soha et al. 2009) and as low as 0% in the Midwest (Kaspari and O'Leary 1988). Breeding grasshopper sparrows select areas of substantial heterogeneity in vegetation structure (Powell 2008), which provides the disparate structure required for nesting, foraging, and shelter. They use overhanging litter and grasses to create woven nests, and nearby bare patches of ground to forage for arthropods, which comprise ≥70% of their breeding season diet (Kaspari and Joern 1993).

We related estimates of detection, survival, and temporary emigration from 2013–2020 to various precipitation metrics (Figure 1) to evaluate putative alternative factors influencing apparent survival throughout a grasshopper sparrow's annual cycle (Figure 2). We expected precipitation could influence interannual grasshopper sparrow return rates by directly affecting survival or indirectly influencing movement via vegetation structure or prey availability. We evaluated predictions of these alternative hypotheses to determine which precipitation metrics occurring during different portions of the annual cycle most strongly influenced estimates of survival and emigration.

STUDY AREA

We conducted our 8-year study (2013–2020) on the Konza Prairie Biological Station, a 3,487-ha native tallgrass prairie preserve in northeastern Kansas (39°05′N, 96°35′W) and the adjacent Rannells Preserve, a 1,175-ha site. These sites are composed of rolling hills with a mean elevation of approximately 390 m. Climate in the region is generally characterized by relatively cold, dry winters (Nov–Feb), mild springs (Mar–May), and hot summers with highly variable rainfall (Jun–Aug). Konza Prairie is a Long-Term Ecological Research site that has been managed experimentally for over 40 years. It is divided into 46 experimental units with replicated fire (1-, 2-, 4-, 20-yr burns) and grazing (bison-grazed or ungrazed) regimes. There are also 2 patch-burn units, grazed by cattle, each consisting of 3 pastures, 1 of which is burned annually in rotation. We worked on 16 experimental study units every year, representing replicated pastures managed with annual and biennial burn frequencies, all grazing regimes, and patch-burn grazing units. The Konza Prairie receives a mean annual precipitation of 835 mm, 75% of which occurs between May and September (Koerner and Collins 2014). The pastures on which we studied sparrows at the Rannells Preserve are annually burned and have intensive, early cattle stocking which is a common land management in the region (Owensby et al. 2008). Dominant grass species at our study sites include big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*), and dominant forb species include goldenrod (*Solidago canandensis*, *S. missouriensis*), ironweed



Hypothesis	Predictor	Description	Rationale	Expected Relationship
Precipitation impacts on survival *(S)*	(A) Local winter precipitation	Summed daily precipitation (mm) on wintering grounds, 15 Nov – 15 Feb	Winter precipitation increases overwinter mortality in grassland birds (Ahlering et al. 2009, Chavarria et al. 2012, Macias-Duarte et al. 2017).	Survival Precipitation
	(B) El Niño-Southern Oscillation during the winter	Summed monthly El Niño-Southern Oscillation Precipitation Index (ESPI), Dec – Feb	The El Niño-Southern Oscillation is related to survival (Mazerolle et al. 2005, Hill et al. 2019).	
	(C) Growing season precipitation on wintering grounds	Summed daily precipitation (mm) on wintering grounds, 1 Apr – 1 Oct	Microclimate is warmer with more vegetative cover (Pérez-Ordoñez et al. 2022), therefore survival will increase with more growing season rainfall.	Survival Precipitation
Precipitation impacts on movement (γ'')	(D) Spring precipitation	Summed daily precipitation (mm) at the Konza Prairie, 1 Mar – 1 May	Plant species richness increases with higher Spring rainfall (Ladwig et al. 2016); more heterogeneity will lead to lower emigration.	Emigration Precipitation
	(E) Local precipitation lagged 1 and 2 years	Summed daily precipitation (mm) at the Konza Prairie, 1 May – 15 Aug, lagged 1 and 2 years	Precipitation can affect plant biomass in subsequent growing seasons (Sherry et al. 2008), and grassland communities may experience stronger relationships with rainfall from previous years (Dudney et al. 2017, Arnone et al. 2008).	Emigration Precipitation
	(F) El Niño-Southern Oscillation lagged 1 and 2 years	Summed monthly El Niño-Southern Oscillation Precipitation Index (ESPI), May – Aug, lagged 1 and 2 years	The El Niño-Southern Oscillation drives precipitation frequency and intensity, which can influence nutrient cycling, soil moisture, and vegetation structure (Flanagan & Adkinson 2011).	
	(G) North Atlantic Oscillation lagged 1 year	Summed monthly North Atlantic Oscillation Index (NAO), May – Aug, lagged 1 year	Grasshopper abundance on our study site was negatively correlated with the NAO in the previous growing season (Welti et al. 2020).	Emigration Precipitation

FIGURE 1 Description of hypotheses, associated mechanisms, predictions, rationale, and expected relationships between grasshopper sparrow survival, movement, and precipitation in northeastern Kansas, USA, 2013–2020.

(*Vernonia baldwinii*), lead plant (*Amorpha canescens*), white heath aster (*Aster ericoides*), scurfpea (*Psoralidum tenuiflorum*), and ragweed (*Ambrosia psilotachya*). Dominant avifauna consist of eastern meadowlark (*Sturnella magna*), dickcissel (*Spiza americana*), brown-headed cowbird (*Molothrus ater*), northern bobwhite (*Colinus virginianus*), upland sandpiper (*Bartramia longicauda*), common nighthawk (*Chordeiles minor*), and greater prairie-chicken (*Tympanuchus cupido*). Other dominant fauna include white-tailed deer (*Odocoileus virginianus*), eastern cottontail (*Sylvilagus floridanus*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), deer mouse (*Peromyscus maniculatus*), eastern yellow-bellied racer (*Coluber constrictor flaviventris*), and gopher snake (*Pituophis catenifer sayi*), along with a variety of arthropods.

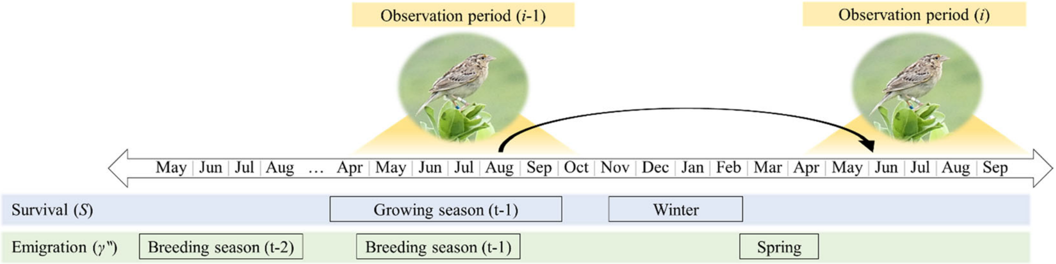


FIGURE 2 Temporal scale of precipitation variables in the grasshopper sparrow robust design model from northeastern Kansas, USA, 2013–2020. Boxes reflect the temporal extent over which precipitation variables are summarized. Precipitation may affect survival directly through mortality (blue box) or affect temporary emigration indirectly (green box) via habitat characteristics such as vegetation or prey abundance.

METHODS

Field data collection

We captured and marked territorial males within each of our 16 study units from 2013–2020. Each study unit contained a randomly located 10-ha plot on which we intensively captured birds and surveyed throughout the breeding season. Additionally, we captured and re-sighted birds opportunistically throughout the entirety of each unit. This resulted in about 50% spatial coverage of the whole of Konza and the Rannells Preserve. Between late April and early August, we captured territorial males by placing a 12 × 2.5-m mist net (Ecotone, Gdynia, Poland; 32-mm mesh size) adjacent to singing perches. At the base of each net, we placed a small audio player and speaker broadcasting conspecific song to attract territorial males. Each captured adult sparrow received a numbered United States Geological Survey leg band and a unique combination of 3 color bands (i.e., 2 bands/leg). We determined the age and sex of each bird using plumage, cloacal protuberances, and brood patches (only females incubate; Bent and Austin 1968, Pyle et al. 2008). We aged birds in the field as hatch year or after hatch year by plumage; all individuals undergo a complete pre-basic molt in late summer and early fall, so they cannot be aged as second years or older unless captured previously (Pyle et al. 2008). We measured tarsus length, wing length, and a structural measurement of skull morphology, and collected blood, feather samples, or both, for other portions of our project. We attempted to capture all unmarked territorial males and recapture individuals marked in previous years in every unit. Because of the frequency of within-season dispersal (Williams and Boyle 2018), we revisited each study unit repeatedly to capture birds throughout the whole season.

We surveyed each unit approximately once every 10 days (9.6 ± 4.5 [SD]) for an average of 9 times (range = 8–10 rounds) per season between late April and late July. Observers traversed the units via different routes each survey, attempting to pass within 100 m of all points within study units on each visit, or for the largest units, to ensure all areas were surveyed multiple times throughout the season. Observers recorded each individual as banded (with color band combination), unbanded (no silver or color bands), or unknown (banded but unable to discern combination). We determined the identity of each individual using 8 × 42 binoculars, 10× scopes, high zoom cameras, or a combination of optics to confirm color band combinations. We trained and tested all observers in color-band resighting skills, working in conjunction with a crew leader until survey methods and bird IDs were consistent with the crew leader. Each survey was generally conducted by 1 observer, but larger units were split between 2 observers to ensure the whole area was covered adequately. We did not survey in rainfall heavier than a mist because grasshopper sparrows are unlikely to perch and sing, making observations of band combinations difficult. We also occasionally spotted banded birds outside our focal units and included these opportunistic detections in resighting histories.

Weather covariates

If apparent survival estimates primarily reflect true survival, we predicted precipitation would affect sparrows over winter when they are most vulnerable. Grasshopper sparrows experience high rates of mortality on their wintering grounds, particularly during winter storms (Macias-Duarte et al. 2017, Pérez-Ordoñez et al. 2022). Because precipitation increases thermoregulatory costs (Wilson et al. 2004, Boyle et al. 2020), individuals may be less likely to survive during periods of high winter precipitation. To test the relationship between survival and local winter precipitation (Figure 1A), we first estimated the wintering range for the subspecies of grasshopper sparrow that occurs in northeastern Kansas (*A. s. perpadillus*). We limited their estimated wintering range to west of the Texas-Louisiana border to minimize overlap with another overwintering subspecies, *A. s. pratensis*, and north of the central volcanic belt of central Mexico to minimize overlap with a resident subspecies, *A. s. ammolegus* (longitude: −14.7531, −93.53536, latitude: 23, 32.66821; Ruth 2017, Vickery 2021). We obtained winter precipitation data from the National Oceanic and Atmospheric Association Physical Sciences Laboratory (NOAA PSL 2020) from grasslands and shrublands cover (Dewitz 2020) across the estimated wintering range for our breeding population, calculated the mean daily precipitation across all pixels, and summed the daily precipitation from 15 November–15 March.

Overwinter survival may also be influenced by large-scale climate indices, such as the El Niño-Southern Oscillation (ENSO), that reflect multiple aspects of climate variability. Local precipitation and ENSO are often correlated (Davey et al. 2014), but ENSO events affect multiple axes of weather including precipitation frequency, intensity, total breeding season precipitation, and temperature regime (Cai et al. 2018). To test the relationship between survival and ENSO over the winter, we obtained monthly values for the ENSO precipitation index (ESPI) from the University of Maryland Global Precipitation Climatology Project (2020). We then summed these monthly values for December, January, and February. If survival on the wintering grounds influences the number of individuals that return each year, then we expected survival to be negatively affected by local winter precipitation on overwintering sites or ENSO (Figure 1A, B).

Alternatively, vegetation on overwintering sites may provide important refugia for overwintering grassland sparrows during inclement weather. Vegetation growth is correlated with rainfall, particularly in arid grasslands, so we expected survival may increase with growing season precipitation on wintering grounds (Figure 1C). To test the relationship between survival and precipitation on the wintering grounds during the previous growing season (i.e., *t* – 1), we summed daily precipitation across the previous 1 April–1 October in the wintering range.

Given the putative importance of movement to sparrow life history, movement propensity (i.e., temporary emigration) may instead have a stronger effect on local abundance than survival. If so, we expected weather to affect grasshopper sparrow emigration via vegetation structure or arthropod abundance. Grasshopper sparrows prefer grasslands with a mosaic of cover types (Shaffer et al. 2021). In tallgrass prairies, these heterogenous landscapes are created through variation in vegetation structure and plant species richness over the growing season, which is positively correlated with spring precipitation (Ladwig et al. 2016). Therefore, if vegetation structure influences temporary emigration estimates via settlement decisions, we expected temporary emigration to decrease with more spring precipitation (Figure 1D). To test the relationship between temporary emigration and breeding range spring precipitation, we obtained daily local precipitation data from the Konza Prairie Data Portal (Nippert 2021) and summed the daily precipitation from 1 March–1 May.

Vegetation productivity is also correlated with fluctuations in precipitation between May–August, mediated by ENSO (Ferris 1999). Because precipitation can influence growth and recruitment of even small perennial herbaceous plants for 2 years (Tenhumberg et al. 2018), we considered local breeding season precipitation and ENSO, and both at 1- and 2-year lags. If intermediate growing (i.e., breeding) season precipitation supports heterogenous vegetation structure and intermediate vegetation density, then we would expect lower rates of emigration (i.e., higher site fidelity) following years with intermediate precipitation. Conversely, we would expect higher rates of emigration in extreme dry or wet years. We therefore expected a curvilinear relationship between temporary emigration and summer breeding season precipitation and the ESPI (Figure 1E). To assess local breeding season precipitation at a 1- and 2-year lag (i.e., $t - 1$, $t - 2$), we summed daily local precipitation data from the Konza Prairie Data Portal (Nippert 2021) data from 1 May–15 August. To test relationships between temporary emigration and broad-scale climatic indices (Figure 1F), we summed the monthly ESPI May–August and delayed the index for 1- and 2-year lags (i.e., $t - 1$, $t - 2$).

Arthropods, particularly grasshoppers, are grasshopper sparrows' primary food sources (Kaspari and Joern 1993), and intake rates are positively associated with fledging success (Kaspari 1991). Insect abundances have been linked to the North Atlantic Oscillation (NAO) cycle in many biomes (Halkka et al. 2006, Westgarth-Smith et al. 2007). Grasshopper abundance on our study site was negatively correlated with the NAO in the previous growing season (Welti et al. 2020). This affects prey abundance through vegetation composition; higher rainfall increases plant biomass resulting in higher carbon and lower nutrient concentrations, ultimately decreasing grasshopper abundance. Therefore, if precipitation negatively affects prey availability, we expected a positive relationship between summer NAO lagged 1 year and temporary emigration (Figure 1G). We obtained NAO values from the University of Maryland Global Precipitation Climatology Project (2020) and summed the monthly values for May–August at a 1-year lag (i.e., $t - 1$). For all precipitation variables, we summed instead of averaging, as averages do not always reflect extremes in the dataset (Gaines and Denny 1993).

Analytical methods

We compiled capture and re-sighting histories for each individual male. We split each breeding season into 3 observation periods: early-season (9 Apr–31 May), mid-season (1 Jun–10 Jul), and late-season (11 Jul–3 Sep). Individuals that were captured or re-sighted at least once within each observation period were assigned a 1 in their capture histories for that period. If an individual was not captured or re-sighted within that period, it was assigned a 0. We did not include age or sex in our analyses because in most cases, adults cannot be aged more precisely than after hatch year and females are extremely secretive, leading to low resighting and recapture probabilities. Therefore, we excluded females from our analyses and our inferences are limited to adult males.

Using the individual capture histories, we fit Pollock's robust design models (Pollock 1982) in RMark (Laake 2013) to assess correlations between effort and precipitation metrics to estimates of survival, emigration, and detection. These models allow for temporary and permanent emigration between primary observation periods (i.e., yrs), while assuming the population remains closed to mortality and emigration between secondary sampling periods (i.e., within the breeding season; Pollock 1982). The robust design model allows estimation of the probability of survival between each primary observation period (S), the probability of surviving and not permanently emigrating from the study site between primary observation periods (F), the probability of being off the study site between primary observation periods given the individual was not present in the previous observation period (γ'), the probability of temporary emigration between primary observation periods given the individual was present in the previous observation period (γ''), the probability of encountering an individual (p), and the probability of recapturing or resighting an individual (c).

We fit 3 sets of models to our data: detection (p), survival (S), and movement (i.e., temporary emigration [γ'']). In the first set of models, we determined the variables most closely associated with detection while keeping survival and movement constant. We fit 3 models to assess detection as a function of the summed time that all observers spent surveying each year (i.e., effort), the number of surveys completed by experienced observers (i.e., experience), and year. We ranked models using second-order Akaike's Information Criterion (AIC_c) to adjust for small sample size and considered models with a $\Delta AIC_c > 2$ to be uncompetitive (Burnham and Anderson 2002). If multiple models were within $\Delta AIC_c < 2$, we considered the most parsimonious model (i.e., the model with the fewest parameters with $\Delta\text{AIC}_c < 2$) to be the most competitive (Arnold 2010). We used AIC_c instead of the quasi-Akaike's Information Criterion (QAIC_c) because the data were not overdispersed (i.e., $\hat{c} < 1$ for our dataset); therefore, an overdispersion parameter was unnecessary (Burnham and Anderson 2002).

In the second step, we retained the top detection model and evaluated factors potentially explaining variation in true survival (Figure 1). While our survival estimates may be influenced to some degree by permanent emigration, we limited our predictions to those we expect to be related to true survival (S) instead of the probability of surviving and not permanently emigrating from the study site between primary observation periods (F). We therefore interpret our estimates as true survival. We fit 3 models to assess survival as a function of the summed precipitation on the wintering grounds during the winter, the summed winter ESPI, and the summed precipitation on the wintering grounds during the previous growing season. Again, we ranked models using AIC_c and retained the top ranked model within the final modeling step.

In the final step, we used the top detection and survival models and evaluated factors potentially explaining variation in temporary emigration (Figure 1). We fit 6 models to assess temporary emigration as a function of 1) the summed precipitation on the breeding grounds during spring, 2) the summed precipitation on the breeding grounds during the breeding season lagged 1 year (quadratic), 3) the summed precipitation on the breeding grounds during the breeding season lagged 2 years (quadratic), 4) the summed ESPI on the breeding grounds during the breeding season lagged 1 year (quadratic), 5) the summed ESPI on the breeding grounds during the breeding season lagged 2 years (quadratic), and 6) the summed NAO on the breeding grounds during the breeding season lagged 1 year. We transformed all covariates hypothesized to be quadratic into orthogonal polynomials to reduce collinearity. We then ranked models using AIC_c and considered models with a $\Delta\text{AIC}_c > 2$ to be uncompetitive (Burnham and Anderson 2002). Finally, we used parameter estimates and detection probabilities from the top model to estimate the number of territorial males present within our study units each year.

RESULTS

Between late April to early August from 2013 to 2020, we color-banded 1,332 adult male grasshopper sparrows, 26% of which were resighted or recaptured in later years, for 3,821 observations. Of these individuals, 248 were resighted in 2 years, 69 were sighted in 3 years, 20 were resighted in 4 years, 3 were resighted in 5 years, and 1 was resighted in 6 consecutive years. Many individuals apparently skipped breeding seasons and were undetected at any time during an entire breeding season but then returned to breed in another year, often in almost the same location. Approximately 9.5% of individuals were absent for ≥1 breeding season at our site, and some individuals skipped up to 5 breeding seasons at our site before returning to breed. Six individuals lived to be ≥6 years old. The oldest adult male recorded within our study was banded as an adult in 2014 and was detected in all 6 subsequent years, which means the individual was ≥7 years old in 2020.

We spent, on average, 347.1 ± 2.12 (SE) hours (range = 182.2–424.6 hr) surveying each year. Precipitation fell on 24–42 days (mean = 33 days) during the breeding season, and rain throughout the previous biological year ranged from 706 mm in 2014 to 1,003 mm in 2015 (mean = 842 mm). This is consistent with local long-term average annual precipitation of 834 mm (Knapp and Smith 2001). Precipitation on the wintering grounds ranged from 39 mm in 2013 to 72 mm in 2015 (mean = 50 mm). Local breeding season precipitation varied from 191 mm in 2012 to 430 mm in 2015 (mean = 328 mm), and the ESPI ranged from −4.4 in 2013 to 10.7 in 2015 (mean = 0.66).

In the first modeling step, year best explained annual detection probability. The next most competitive model included effort and year and was 2.02 ΔAIC_c from the top model (Table 1). The detection probability over the entire study period was 0.34 ± 0.04 (range = 0.29 − 0.40). In the next modeling step, winter ESPI best explained survival ($\hat{\beta} = 0.15$, 95% CI = −0.06 − 0.35). The next most competitive model was growing season precipitation on the wintering grounds and was 2.70 ΔAIC_c from the top model (Table 2). The probability of survival ($\hat{S}$) was 0.77 ± 0.06

TABLE 1 Models fit to describe variation in grasshopper sparrow detection estimates as a function of effort (summed amount of time spent surveying each year), proportion of surveys conducted by observers with ≥2 years of experience, and year in northeastern Kansas, USA, 2013–2020. Detection models were fit while holding all other parameters constant.

Detection model	K[a]	ΔAIC$_c$[b]	w_i[c]	Deviance
Year	13	0.00	0.54	−3,337.40
Effort + year	14	2.02	0.20	−6,785.89
Year + experience	14	2.02	0.20	−6,785.89
Effort + year + experience	15	4.05	0.07	−6,785.89
Experience	7	12.82	0.00	−6,760.96
~1 (constant model)	6	13.93	0.00	−3,309.35
Effort	7	13.95	0.00	−6,759.83
Effort + experience	8	14.42	0.00	−6,761.38

[a] Number of parameters used in each model. Each covariate has 1 value/year.

[b] The difference in Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$) between the model and the best-fitting model.

[c] Model weight = exp(−0.5 × ΔAIC$_c$ for that model), divided by the sum of these values for all models.

TABLE 2 Models fit to describe variation in grasshopper sparrow survival estimates as a function of precipitation in northeastern Kansas, USA, 2013–2020. All models were fit with detection varying by year, which was the top detection model.

Survival model	K[a]	ΔAIC$_c$[b]	w_i[c]	Deviance
Winter ESPI[d]	14	0.00	0.69	−6,789.44
Growing season precipitation on wintering grounds	14	2.70	0.18	−6,786.74
Local winter precipitation	14	3.30	0.13	−6,786.14
~1 (constant model)	6	15.46	0.00	−3,309.35

[a] Number of parameters used in each model. Each covariate has 1 value/year.

[b] The difference in Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$) between the model and the best-fitting model.

[c] Model weight = exp(−0.5 × ΔAIC$_c$ for that model), divided by the sum of these values for all models.

[d] El Niño-Southern Oscillation precipitation index.

(range = 0.71–0.84). Survival was lowest in years when birds experienced dry and warm conditions on the wintering grounds, and highest in years with wet and cold winter weather (Figure 3A). In the final modeling step, the top ranked model included temporary emigration as a function of ESPI lagged 2 years (Table 3). The relationship between temporary emigration and ESPI lagged 2 years was curvilinear (ESPI lagged 2 years: $\hat{\beta} = -0.11$, 95% CI = −0.59–0.38; ESPI lagged 2 years^2: $\hat{\beta} = 0.62$, 95% CI = 0.16–1.08). The probability of temporary emigration ($\widehat{\gamma''}$) each year was 0.63 ± 0.05 (range = 0.53–0.70), with the lowest estimates of emigration occurring in years of average precipitation (Figure 3B). The ESPI lagged 1 year was 0.87 AIC$_c$ from the top model, but the model weight was much lower than that of ESPI lagged 2 years and the 95% confidence interval of the beta estimate overlapped

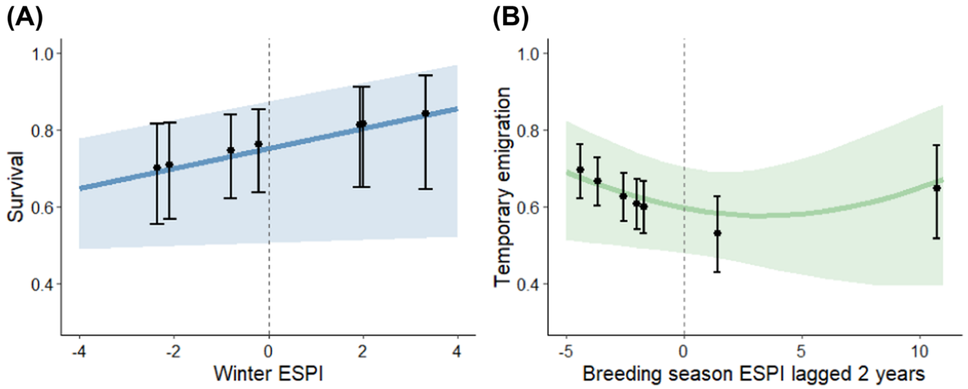


FIGURE 3 A) Grasshopper sparrow survival in northeastern Kansas, USA, 2013–2020, is positively correlated with the El Niño-Southern Oscillation precipitation index (ESPI) on their winter range. Positive ESPI values are associated with wetter, cooler conditions, and negative ESPI values indicate dryer, warmer conditions. Survival is highest in years with slightly wetter winters; however, the estimates of the slope of this relationship overlap zero. The blue line represents model predictions with 95% prediction intervals highlighted in light blue. Black points are survival estimates with 95% confidence intervals. B) Grasshopper sparrow temporary emigration exhibits a quadratic relationship with the ESPI cycle lagged 2 years in northeastern Kansas, USA, 2013–2020. Temporary emigration is highest in years with average or slightly lower precipitation and decreases towards extreme ESPI values. The dark green line represents model predictions with 95% prediction intervals highlighted in light green. Black points are temporary emigration estimates with 95% confidence intervals.

TABLE 3 Models fit to describe variation in grasshopper sparrow emigration estimates as a function of precipitation in northeastern Kansas, USA, 2013–2020. All models were fit with detection varying by year and survival varying by winter El Niño-Southern Oscillation precipitation index (ESPI), which were retained from the previous modeling steps.

Temporary emigration model	K[a]	ΔAIC_c[b]	w_i[c]	Deviance
ESPI lagged 2 yr^2	16	0.00	0.43	−6,797.44
ESPI lagged 1 yr^2	16	0.87	0.28	−6,796.57
Local breeding season precipitation lagged 1 yr^2	16	2.93	0.10	−6,794.51
~1 (constant model)	14	3.94	0.06	−6,789.44
Local spring precipitation	15	4.01	0.06	−6,791.40
NAO[d] lagged 1 yr	15	4.02	0.06	−6,791.39
Local breeding season precipitation lagged 2 yr^2	16	6.47	0.02	−6,790.96
0 (i.e., no temporary emigration)	12	149.39	0.00	−6,639.95

[a] Number of parameters used in each model. Each covariate has 1 value/year.

[b] The difference in Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$) between the model and the best-fitting model.

[c] Model weight = exp(−0.5 × ΔAIC_c for that model), divided by the sum of these values for all models.

[d] North Atlantic Oscillation index.

zero. Estimates for the number of territorial males in our study units varied between 250 and 393 in different years of the study: 285 (95% CI = 265 −310) in 2013, 346 (95% CI = 326–371) in 2014, 393 (95% CI = 373–418) in 2015, 328 (95% CI = 308–353) in 2016, 292 (95% CI = 272–317) in 2017, 264 (95% CI = 244–289) in 2018, 317 (95% CI = 297 −342) in 2019, and 250 individuals (95% CI = 230–275) in 2020.

DISCUSSION

Grasshopper sparrow emigration and survival were related to precipitation in different periods of their annual cycle and exhibited delayed effects, suggesting rainfall can affect grassland birds over relatively long time scales. While about a quarter of the male grasshopper sparrows likely did not return for the breeding season because they did not survive, >50% did not return because they had temporarily emigrated to another site. We highlight these high emigration rates, which provides compelling support for the idea that grassland species respond to high interannual variability by routinely engaging in breeding dispersal, unlike many well-studied migrant birds (Winger et al. 2018). Local abundance is determined in large part by the indirect effects of precipitation on adult vital rates, particularly movement, a relationship likely mediated by vegetation structure. These results suggest the effects of more variable weather under future climate conditions may not be evident for several years, which may confound attempts to detect the effects of conservation actions via population responses.

The ESPI throughout the winter was positively correlated with survival estimates, which was opposite to the relationship we expected; under wet and cold conditions, sparrows were more likely to survive the winter. Part of the uncertainty regarding mechanisms linking weather and winter mortality may also result from the fact that we estimated winter conditions over large geographic scales that may poorly reflect conditions that individual sparrows in this study experienced. More precise estimates of grasshopper sparrow wintering ranges may yield stronger relationships between winter weather and survival. Alternatively, the positive relationship between winter ESPI and survival may manifest from more food availability (Hill et al. 2019), another axis of winter weather captured by ESPI (e.g., temp; Macias-Duarte et al. 2017), or precipitation increasing the amount of vegetative cover (i.e., refugia) during inclement weather (Pérez-Ordoñez et al. 2022). While our survival estimates may be slightly affected by permanent emigration, the relationship between winter weather and survival suggests most individuals that never returned to our study site to breed likely died.

Survival models often assume that when individuals move away from a study site, they are permanently emigrating (Schaub and Royle 2014), but individuals within our study frequently appeared to skip years at our site to breed elsewhere then return to our site in later years. We have multiple lines of evidence that individuals within our breeding population often disperse within and among breeding seasons; this study provides yet another. This result is borne out by the high estimates for temporary emigration and is consistent with preliminary geolocator data and feather stable isotope data; feathers collected in 2014 and 2015 indicated about 75% of individuals bred ≥100 km away the previous year (W. A. Boyle, Kansas State University, unpublished data). Over larger scales within the Great Plains, local abundances change each year, shifting the centroid of the grasshopper sparrow breeding distribution by up to 87 km, consistent with high mobility and low breeding site fidelity (Smith 2021). If grasshopper sparrows exhibited high side fidelity, we would expect their behavior and demography to be more strongly correlated with local weather than regional climatic indices because they would be subject to conditions at 1 breeding site. But the relationship between temporary emigration and broad-scale weather metrics affirms their propensity for regional breeding dispersal and responses to conditions at multiple sites over larger spatial scales.

Grassland birds likely respond to habitat characteristics at multiple spatial scales (Shahan et al. 2017); grasshopper sparrow behavior is correlated with large-scale weather patterns, which likely act via local, site-, and territory-level habitat features. Once grasshopper sparrows establish their breeding territories each year, they spend most of their time within their territories, making territory selection important for their survival and reproduction (Wiens 1969, Ruth and Skagen 2017). Grasshopper sparrows nest on the ground, and their reproductive success is dependent on with vegetation structure (Ruth and Skagen 2018). We present a new line of evidence the relationships between precipitation, vegetation, and grasshopper sparrows may be influenced by weather conditions multiple years prior. Given that grasshopper sparrows have limited time in the year to breed (Vickery 2021), it is possible that individuals take cues from their nest success in previous years to indicate whether they should return to breed. Individuals entering the breeding season with information about where to settle will be able to select higher quality territories at the start of the breeding season, increasing the likelihood they could successfully fledge multiple broods. If patchy vegetation conditions, shaped at our site by average values of precipitation in combination with management (e.g., fire return interval), lead to higher nest success, then individuals may be more likely to return to nest in subsequent years. These hypotheses reflect patterns observed for within-season dispersal; individuals are more likely to disperse following nest failure, adopting a win-stay, lose-switch strategy (Williams and Boyle 2019). Approximately 75% of males disperse at some point within the breeding season (Williams and Boyle 2018). This value is roughly congruous with our average detection probability because Pollock's robust design model assumes no death or dispersal occurs within the breeding season (Pollock 1982). If males on average are detected in only 1 period during the breeding season (because of within-season dispersal), the 34% detection in this study suggests we detect the majority of individuals present at some point during each year.

Our annual survival estimates averaged 77%, which is considerably higher than prior estimates from 2 sites in Florida, averaging 51% annual apparent survival over a 3-year study (Perkins and Vickery 2001). The Florida grasshopper sparrow (*A. s. floridanus*) is endangered and this difference may reflect real differences in risks to these different populations, but it could also highlight the importance of explicitly incorporating movement into apparent survival models. With mobile species, estimates of apparent survival likely would increase with study length. This is particularly true when short-term studies span less time than the species' longevity because individuals may emigrate to another study area for several breeding seasons before returning. If the study period does not overlap the individual's return, then the individual will be considered deceased instead of dispersed.

The relationship between grassland songbird demography, climatic cycles, and lagged precipitation suggests ecological processes may extend beyond the spatial or temporal extent of most studies, potentially missing lagged effects. Studies of mobile species in dynamic systems should be conducted at broad spatial and temporal scales to capture climatic and landscape-level factors and ensure correct conservation assessments (Webb et al. 2017). Long-term studies in species with high dispersal rates are essential to increase the likelihood that individuals will be re-observed and delayed effects can be detected (Igl and Johnson 1999). Furthermore, future analyses should include consideration of habitat at multiple sites to assess if emigration is a function of habitat at 1 site or a tradeoff of relative habitat quality at multiple sites.

Many grassland taxa have exhibited declines over the past decades (With et al. 2008, Rosenberg et al. 2019, birds; Sang et al. 2010, insects; Bruggeman and Licht 2020, mammals), several of which have delayed responses to environmental change (Thompson et al. 2015, Welti et al. 2020). While grassland species live in areas characterized by periodic weather disturbances, climate change is expected to increase the frequency and intensity of severe weather events across all ecosystems (Prein and Mearns 2021). These extremes in weather variability will affect population dynamics in many systems (Frederiksen et al. 2008, Latimer and Zuckerberg 2021, Neilson et al. 2020), the results of which may not be evident for years. Movement may be one of many strategies to cope with changing conditions, and temporary emigration may help bolster small or declining populations. Temperature regulates changes in vital rates across many taxa (Savage et al. 2004, Giovanni et al. 2015, Wingler and Hennessey 2016), but precipitation is an often-overlooked factor influencing population dynamics (Boyle et al. 2020). Precipitation may be particularly influential during important periods in an organism's life cycle and during periods of extreme precipitation, ultimately dictating species persistence. We can gain insights about how other systems may respond to a changing climate by studying systems, like grasslands, that already experience weather variability.

MANAGEMENT IMPLICATIONS

Grassland bird demography is largely shaped by land managers because of the ways by which precipitation interacts with fire and grazing to determine vegetation structure. While methods like patch-burn grazing are promising for creating vegetation heterogeneity to which grassland species respond positively, the relationships between precipitation and management may change under future climate conditions. Because management outcomes are heavily influenced by climate, these relationships may be further complicated by multi-year effects of weather on ecological relationships in grassland systems, challenging assessments of current management practices. By revealing the mechanistic links between weather and local demography, we gain a greater understanding of how to support declining species, time scales over which local demography responds to management decisions, and potential methods to slow range-wide declines in a variety of grassland taxa.

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CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available at https://doi.org/10.5061/dryad.dv41ns22w.

ETHICS STATEMENT

All aspects of this study were approved through the Kansas State University Institutional Animal Care and Use Committee (protocols 3260, 3733, and 4250) and the North American Bird Banding Laboratory (permit 23836).

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REFERENCES

Addo-Bediako, A., S. L. Chown, and K. J. Gaston. 2000. Thermal tolerance, climatic variability and latitude. Proceedings of the Royal Society B: Biological Sciences 267:739–745.

Ahlering, M. A., D. H. Johnson, and J. Faaborg. 2009. Factors associated with arrival densities of grasshopper sparrow (*Ammodramus savannarum*) and Baird's sparrow (*A. bairdii*) in the Upper Great Plains. Auk 126:799–808.

Albright, T. P., D. Mutiibwa, 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 114:2283–88.

Allen, M. C., J. L. Lockwood, and J. Burger. 2021. Finding clarity in ecological outcomes using empirical integrated social–ecological systems: a case study of agriculture-dependent grassland birds. Journal of Applied Ecology 58:528–538.

Angilletta, M. 2009. Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford, United Kingdom.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Becker, A., D. Roeder, M. S. Husak, and M. T. Murphy. 2018. Annual survival and breeding dispersal of a migratory passerine, the scissor-tailed flycatcher. Journal of Field Ornithology 89:22–36.

Bent, A. C., and O. L. Austin. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Bulletin of the United States National Museum, Washington, D.C., USA.

Blair, J., J. Nippert, and J. Briggs. 2014. Grassland ecology. Pages 389–423 *in* R. J. Monson, editor. Ecology and the environment, the plant sciences 8. Springer Science+Business Media, New York, New York, USA.

Boyle, W. A., E. H. Shogren, and J. D. Brawn. 2020. Hygric niches for tropical endotherms. Trends in Ecology and Evolution 35:938–952.

Briggs, J. M., A. K. Knapp, and B. L. Brock. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. American Midland Naturalist 147:287–294.

Brommer, J. E., H. Pietiäinen, and H. Kolunen. 2002. Reproduction and survival in a variable environment: Ural owls (*Strix uralensis*) and the three-year vole cycle. Auk 119:544–550.

Bruggeman, J. E., and D. S. Licht. 2020. Drought-mediated changes in black-tailed prairie dog colonies in the Northern Great Plains. Journal of Mammalogy 101:1189–1204.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Cai, W., G. Wang, B. Dewitte, L. Wu, A. Santoso, K. Takahashi, Y. Yang, A. Carréric, and M. J. McPhaden. 2018. Increased variability of eastern Pacific El Niño under greenhouse warming. Nature 564:201–206.

Churchwell, R. T., C. A. Davis, S. D. Fuhlendorf, and D. M. Engle. 2008. Effects of patch-burn management on dickcissel nest success in a tallgrass prairie. Journal of Wildlife Management 72:1596–1604.

Davey, M. K., A. Brookshaw, and S. Ineson. 2014. The probability of the impact of ENSO on precipitation and near-surface temperature. Climate Risk Management 1:5–24.

Day, P. B., R. D. Stuart-Smith, G. J. Edgar, and A. E. Bates. 2018. Species' thermal ranges predict changes in reef fish community structure during 8 years of extreme temperature variation. Diversity and Distributions 24:1036–1046.

Dewitz, J. 2020. National Land Cover Database (NLCD) 2016 Products: U.S. Geological Survey Data Release. <https://doi.org/10.5066/P96HHBIE>. Accessed 25 Jul 2020.

Elliott, L. H., and D. H. Johnson. 2018. The grasshopper sparrow as an indicator species in tallgrass prairies. Journal of Wildlife Management 82:1074–1081.

Ferris, J. N. 1999. An analysis of the impact of ENSO (El Niño/Southern Oscillation) on global crop yields. Proceedings of American Agricultural Economics Association, Nashville, Tennessee, USA.

Flanagan, L. B., and A. C. Adkinson. 2011. Interacting controls on productivity in a northern Great Plains grassland and implications for response to ENSO events. Global Change Biology 17:3293–3311.

Forero-Medina, G., L. Joppa, and S. L. Pimm. 2011. Constraints to species' elevational range shifts as climate changes. Conservation Biology 25:163–171.

Franzén, M., S. G. Nilsson, V. Johansson, and T. Ranius. 2013. Population fluctuations and synchrony of grassland butterflies in relation to species traits. PLoS One 8:1–7.

Frederiksen, M., F. Daunt, M. P. Harris, and S. Wanless. 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. Journal of Animal Ecology 77:1020–1029.

Gaines, S. D., and M. W. Denny. 1993. The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. Ecology 74:1677–1692.

Gilroy, J. T., T. Virzi, R. L. Boulton, and J. L. Lockwood. 2012. A new approach to the "apparent survival" problem: estimating true survival rates from mark-recapture studies. Ecology 93:1509–1516.

Giovanni, M. D., L. A. Powell, and W. H. Schacht. 2015. Habitat preference and survival for western meadowlark (*Sturnella neglecta*) fledglings in a contiguous prairie system. Wilson Journal of Ornithology 127:200–211.

Gow, E. A., and B. J. M. Stutchbury. 2013. Within-season nesting dispersal and molt dispersal are linked to habitat shifts in a Neotropical migratory songbird. Wilson Journal of Ornithology 125:696–708.

Halkka, A., L. Halkka, O. Halkka, K. Roukka, and J. Pokki. 2006. Lagged effects of North Atlantic Oscillation on spittlebug *Philaenus spumarius* (Homoptera) abundance and survival. Global Change Biology 12:2250–2262.

Hill, J. M., J. D. Lloyd, K. P. McFarland, and C. C. Rimmer. 2019. Apparent survival of a range-restricted montane forest bird species is influenced by weather throughout the annual cycle. Avian Conservation and Ecology 14:16.

Holcomb, E. D., C. A. Davis, and S. D. Fuhlendorf. 2014. Patch-burn management: implications for conservation of avian communities in fire-dependent sagebrush ecosystems. Journal of Wildlife Management 78:848–856.

Hovick, T. J., J. R. Miller, S. J. Dinsmore, D. M. Engle, D. M. Debinski, and S. D. Fuhlendorf. 2012. Effects of fire and grazing on grasshopper sparrow nest survival. Journal of Wildlife Management 76:19–27.

Huang, A. C., C. A. Bishop, R. McKibbin, A. Drake, and D. J. Green. 2017. Wind conditions on migration influence the annual survival of a neotropical migrant, the western yellow-breasted chat (*Icteria virens auricollis*). BMC Ecology 17: 1–10.

Igl, L. D., and D. H. Johnson. 1999. Le Conte's sparrows breeding in conservation reserve program fields: precipitation and patterns of population change. Studies in Avian Biology 80:1189–1204.

Jones, S. K., J. Ripplinger, and S. L. Collins. 2017. Species reordering, not changes in richness, drives long-term dynamics in grassland communities. Ecology Letters 20:1556–1565.

Jones, S. L., J. S. Dieni, M. T. Green, and P. J. Gouse. 2007. Annual return rates of breeding grassland songbirds. Wilson Journal of Ornithology 119:89–94.

Kaspari, M. 1991. Central place foraging in grasshopper sparrows: opportunism or optimal foraging in a variable environment? Oikos 60:307–312.

Kaspari, M., and A. Joern. 1993. Prey choice by three insectivorous grassland birds: reevaluating opportunism. Oikos 68: 414–430.

Kaspari, M., and H. O'Leary. 1988. Nonparental attendants in a north-temperate migrant. Auk 105:792–793.

Klug, P. E., S. L. Jackrel, and K. A. With. 2010. Linking snake habitat use to nest predation risk in grassland birds: the dangers of shrub cover. Oecologia 162:803–813.

Knapp, A. K., P. A. Fay, J. M. Blair, S. L. Collins, M. D. Smith, J. D. Carlisle, C. W. Harper, B. T. Danner, M. S. Lett, and J. K. McCarron. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298: 2202–2205.

Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291:481–484.

Koerner, S. E., and S. L. Collins. 2014. Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. Ecology 95:98–109.

Laake, J. L. 2013. R Mark: An R Interface for analysis of capture-recapture datawith MARK. AFSC Processed Report 2013-01. Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Seattle, Washington, USA.

Ladwig, L. M., Z. R. Ratajczak, T. W. Ocheltree, K. A. Hafich, A. C. Churchill, S. J. K. Frey, C. B. Fuss, C. E. Kazanski, J. D. Muñoz, M. D. Petrie, et al. 2016. Beyond arctic and alpine: the influence of winter climate on temperate ecosystems. Ecology 97:372–382.

Latimer, C. E., and B. Zuckerberg. 2021. Habitat loss and thermal tolerances influence the sensitivity of resident bird populations to winter weather at regional scales. Journal of Animal Ecology 90:317–329.

Lindenmayer, D. B., P. Lane, C. N. Foster, M. J. Westgate, C. Sato, K. Ikin, M. Crane, M. D. Florance, and B. C. Scheele. 2019. Do migratory and resident birds differ in their responses to interacting effects of climate, weather and vegetation? Diversity and Distributions 25:449–461.

Macías-Duarte, A., A. O. Panjabi, E. H. Strasser, G. J. Levandoski, I. Ruvalcaba-Ortega, P. F. Doherty, and C. I. Ortega-Rosas. 2017. Winter survival of North American grassland birds is driven by weather and grassland condition in the Chihuahuan Desert. Journal of Field Ornithology 88:374–386

National Oceanic and Atmospheric Association Physical Sciences Laboratory [NOAA PSL]. 2020. Climate Prediction Center global unified gauge-based analysis of daily precipitation. https://psl.noaa.gov/data/gridded/data.cpc.globalprecip.html. Accessed 7 Oct 2020.

Neilson, E. W., C. T. Lamb, S. M. Konkolics, M. J. L. Peers, Y. N. Majchrzak, D. Doran-Myers, L. Garland, A. R. Martinig, and S. Boutin. 2020. There's a storm a-coming: ecological resilience and resistance to extreme weather. Ecology and Evolution 10:12147–12156.

Newton, I. 1998. Population limitation in birds. Academic Press, Cambridge, Massachusetts, USA.

Nippert, J. B. 2021. APT01 Daily precipitation amounts measured at multiple sites across Konza Prairie. http://lter.konza.ksu.edu/content/apt01-daily-precipitation-amounts-measured-multiple-sites-across-konza-prairie. Accessed 7 Oct 2020.

Nott, M. P., D. F. Desante, R. B. Siegel, and P. Pyle. 2002. Influences of the El Niño/Southern oscillation and the North Atlantic oscillation on avian productivity in forests of the Pacific Northwest of North America. Global Ecology and Biogeography 11:333–342.

Owensby, C. E., L. M. Auen, H. F. Berns, and K. C. Dhuyvetter. 2008. Grazing systems for yearling cattle on tallgrass prairie. Rangeland Ecology and Management 61:204–210.

Pérez-Ordoñez, D. J., M. Titulaer, M. D. Correll, E. H. Strasser, F. Baeza-Tarin, R. L. Martin, and L. A. Harveson. 2022. The role of temperature and microclimate in the survival of wintering grassland birds. Avian Conservation and Ecology 17:1.

Perkins, D. W., and P. D. Vickery. 2001. Annual survival of an endangered passerine, the Florida grasshopper sparrow. Wilson Bulletin 113:211–216.

Plumb, G. E., P. J. White, M. B. Coughenour, and R. L. Wallen. 2009. Carrying capacity, migration, and dispersal in Yellowstone bison. Biological Conservation 142:2377–2387.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:752–757.

Powell, A. F. L. A. 2008. Responses of breeding birds in tallgrass prairie to fire and cattle grazing. Journal of Field Ornithology 79:41–52.

Prein, A. F., and L. O. Mearns. 2021. U.S. extreme precipitation weather types increased in frequency during the 20th Century. Journal of Geophysical Research: Atmospheres 126:1–18.

Pyle, P., S. L. Jones, and J. M. Ruth. 2008. Molt and aging criteria for four North American grassland passerines. Biological Technical Publication. U.S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication, FWS/BTP-R6011-2008, Washington, D.C., USA.

Reed, A. W., G. A. Kaufman, and B. K. Sandercock. 2007. Demographic response of a grassland rodent to environmental variability. Journal of Mammalogy 88:982–988.

Rêgo, A. S., V. A. Teodoro, G. S. A. Maciel, and R. A. Sarmento. 2013. Relative contribution of biotic and abiotic factors to the population density of the cassava green mite, *Mononychellus tanajoa* (Acari: Tetranychidae). Experimental and Applied Acarology 60:479–484.

Reichmann, L. G., O. E. Sala, and D. P. C. Peters. 2013. Precipitation legacies in desert grassland primary production occur through previous-year tiller density. Ecology 94:435–443.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. O. Panjabi, L. Helft, M. Parr et al. 2019. Decline of the North American avifauna. Science 366:120–124.

Ruth, J. M. 2017. Life history attributes of Arizona grasshopper sparrow (*Ammodramus savannarum ammolegus*) and comparisons with other North American subspecies. American Midland Naturalist 178:64–81.

Ruth, J. M., and S. K. Skagen. 2017. Territory and nest site selection patterns by grasshopper sparrows in southeastern Arizona. Condor 119:469–483.

Ruth, J. M., and S. K. Skagen. 2018. Reproductive response of Arizona grasshopper sparrows to weather patterns and habitat structure. Condor 120:596–616.

Sahanatien, V., A. E. Derocher, and M. Gompper. 2012. Monitoring sea ice habitat fragmentation for polar bear conservation. Animal Conservation 15:397–406.

Sandercock, B. K. 2006. Estimation of demographic parameters from live-encounter data: a summary review. Journal of Wildlife Management 70:1504–1520.

Sang, A., T. Teder, A. Helm, and M. Pärtel. 2010. Indirect evidence for an extinction debt of grassland butterflies half century after habitat loss. Biological Conservation 143:1405–1413.

Santisteban, L., C. W. Benkman, T. Fetz, and J. W. Smith. 2012. Survival and population size of a resident bird species are declining as temperature increases. Journal of Animal Ecology 81:352–363.

Sauer, J. R., J. E. Hines, and J. Fallon. 2020. The North American Breeding Bird Survey Dataset, 1955–2019. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Savage, V. M., J. F. Gillooly, J. H. Brown, G. B. West, and E. L. Charnov. 2004. Effects of body size and temperature on population growth. American Naturalist 163:429–441.

Schaub, M., and J. A. Royle. 2014. Estimating true instead of apparent survival using spatial Cormack-Jolly-Seber models. Methods in Ecology and Evolution 5:1316–1326.

Schreiber, S. J. 2003. Allee effects, extinctions, and chaotic transients in simple population models. Theoretical Population Biology 64:201–209.

Searcy, C. A., E. Gabbai-Saldate, and H. B. Shaffer. 2012. Microhabitat use and migration distance of an endangered grassland amphibian. Biological Conservation 158:80–87.

Shaffer, J. A., L. D. Igl, D. H. Johnson, M. L. Sondreal, C. M. Goldade, M. P. Nenneman, T. L. Wooten, and B. R. Euliss. 2021. The effects of management practices on grassland birds–grasshopper sparrow (*Ammodramus savannarum*). Chapter GG *in* D. H. Johnson, L. D. Igl, J. A. Shaffer, and J. P. DeLong, editors. The effects of management practices on grassland birds. U.S. Geological Survey Professional Paper 1842, Reston, Virginia, USA.

Shahan, J. L., B. J. Goodwin, and B. C. Rundquist. 2017. Grassland songbird occurrence on remnant prairie patches is primarily determined by landscape characteristics. Landscape Ecology 32:971–988.

Shew, J. J., B. J. Nielsen, and D. W. Sparling. 2017. Finer-scale habitat predicts nest survival in grassland birds more than management and landscape: a multi-scale perspective. Journal of Applied Ecology 56:929–945.

Sinclair, A. R. E., and C. J. Krebs. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. Philosophical Transactions of the Royal Society B: Biological Sciences 357:1221–1231.

Skagen, S. K., and A. A. Yackel Adams. 2012. Weather effects on avian breeding performance and implications of climate change. Ecological Applications 22:1131–1145.

Smith, D. J. 2021. Direct and indirect drivers of grassland bird population declines and settlement decisions over broad spatial and temporal scales. Thesis, Kansas State University, Manhattan, USA.

Soha, J. A., B. Lohr, and D. E. Gill. 2009. Song development in the grasshopper sparrow, *Ammodramus savannarum*. Animal Behaviour 77:1479–1489.

Stutchbury, B. J. M., J. R. Hill, III, P. M. Kramer, S. A. Rush, and S. A. Tarof. 2009. Sex and age-specific annual survival in a Neotropical migratory songbird, the purple martin (*Progne subis*). Auk 126:278–287.

Sudakov, I., S. A. Vakulenko, D. Kirievskaya, and K. M. Golden. 2017. Large ecosystems in transition: bifurcations and mass extinction. Ecological Complexity 32:209–216.

Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7:533–555.

Taylor, C. M., D. B. Lank, and B. K. Sandercock. 2015. Using local dispersal data to reduce bias in annual apparent survival and mate fidelity. Condor 117:598–608.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336–347.

Tenhumberg, B., E. E. Crone, S. Ramula, and A. J. Tyre. 2018. Time-lagged effects of weather on plant demography: drought and *Astragalus scaphoides*. Ecology 99:915–925.

Thompson, S. J., T. W. Arnold, J. Fieberg, D. A. Granfors, S. Vacek, and N. Palaia. 2015. Grassland birds demonstrate delayed response to large-scale tree removal in central North America. Journal of Applied Ecology 53:284–294.

University of Maryland Global Precipitation Climatology Project. 2020. El Nino-Southern Oscillation Precipitation Index, 1979-present. http://gpcp.umd.edu/espi.htm. Accessed 17 Sep 2020.

Verheijen, B. H. F. 2017. Demographic responses of grassland songbirds to rangeland management in the tallgrass prairie. Dissertation, Kansas State University, Manhattan, USA.

Vickery, P. D. 2021. Grasshopper sparrow (*Ammodramus savannarum*), version 1.0. https://birdsoftheworld.org/bow/species/graspa/cur/introduction. Accessed 5 Jan 2022.

Vucetich, J. A., and R. O. Peterson. 2003. The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. Proceedings of the Royal Society B: Biological Sciences 271:183–189.

Webb, M. H., A. Terauds, A. Tulloch, P. Bell, D. Stojanovic, and R. Heinsohn. 2017. The importance of incorporating functional habitats into conservation planning for highly mobile species in dynamic systems. Conservation Biology 31:1018–1028.

Wells, K. M. S., J. J. Millspaugh, M. R. Ryan, and M. W. Hubbard. 2008. Factors affecting home range size and movements of post-fledging grassland birds. Wilson Journal of Ornithology 120:120–130.

Welti, E. A. R., K. A. Roeder, K. M. De Beurs, A. Joern, and M. Kaspari. 2020. Nutrient dilution and climate cycles underlie declines in a dominant insect herbivore. Proceedings of the National Academy of Sciences 117:7271–7275.

Westgarth-Smith, A. R., S. A. G. Leroy, P. E. F. Collins, and R. Harrington. 2007. Temporal variations in English populations of a forest insect pest, the green spruce aphid (*Elatobium abietinum*), associated with the North Atlantic Oscillation and global warming. Quaternary International 173–174, 153–160.

Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monographs 8:1–93.

Wiens, J. A. 1973. Pattern and process in grassland bird communities. Ecological Monographs 43:237–270.

Williams, E. J., and W. A. Boyle. 2018. Patterns and correlates of within-season breeding dispersal: a common strategy in a declining grassland songbird. Auk 135:1–14.

Williams, E. J., and W. A. Boyle. 2019. Causes and consequences of avian within-season dispersal decisions in a dynamic grassland environment. Animal Behaviour 155:77–87.

Wilson, G. R., S. J. Cooper, and J. A. Gessaman. 2004. The effects of temperature and artificial rain on the metabolism of American kestrels (*Falco sparverius*). Comparative Biochemistry and Physiology 139:389–394.

Wilson, S., A. C. Smith, and I. Naujokaitis-Lewis. 2018. Opposing responses to drought shape spatial population dynamics of declining grassland birds. Diversity and Distributions 24:1687–1698.

Winger, B. M., G. A. Giorgia, T. M. Pegan, and B. C. Weeks. 2018. A long winter for the Red Queen: rethinking the evolution of seasonal migration. Biological Reviews 94:737–752.

Wingler, A., and D. Hennessy. 2016. Limitation of grassland productivity by low temperature and seasonality of growth. Frontiers in Plant Science 7:1–6.

With, K. A., A. W. King, and W. E. Jensen. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. Biological Conservation 141:3152–3167.

Wu, D., X. Zhao, S. Liang, T. Zhou, K. Huang, B. Tang, and W. Zhao. 2015. Time-lag effects of global vegetation responses to climate change. Global Change Biology 21:3520–3531.

Zuckerberg, B., C. A. Ribic, and L. A. McCauley. 2018. Effects of temperature and precipitation on grassland bird nesting success as mediated by patch size. Conservation Biology 32:872–882.

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