

Direct and indirect drivers of grassland bird population declines and settlement decisions over  
broad spatial and temporal scales

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## Abstract

Many North American bird populations are declining, and of those, grassland bird populations are declining most rapidly, having been reduced by about half since 1970. Such declines are difficult to study, both because grasslands are characterized and maintained by disturbance, and because grassland birds have a high propensity for dispersal. The primary cause for population declines is habitat loss. For example, only ~14% of pre-European colonization eastern tallgrass prairie remains intact. Even where habitat remains, many species continue to decline, and these declines may be due to reductions in reproductive success. One potential cause of these local declines is the encroachment of woody vegetation on grasslands, which for grassland birds reduces the overall amount and degrades the quality of usable habitat. In addition, local demographic changes cause—and are caused by—regional- or continental-scale patterns. Thus, broad spatial approaches are needed to best understand the drivers of demographic change. In my first chapter, I sought to identify whether woody encroachment, via reductions in reproductive success, can explain changes in population abundance. I compiled and analyzed data on nest contents and nest success collected at Konza Prairie Biological station over nearly five decades. Nest success did not change since 1971, but the frequency of Brown-headed Cowbird (*Molothrus ater*) brood parasitism increased. In addition, grassland obligates were harder hit than species that prefer woodier habitat, supporting the idea that grassland degradation most strongly affects birds that rely on pristine prairie. In chapter 2, I tested alternative mechanisms linking the high degree of climatic variability in the Great Plains to inter-annual fluctuations breeding distribution and local abundance of a common grassland bird species, Grasshopper Sparrows (*Ammodramus savannarum perpallidus*). I used 11 years of citizen

science data from eBird spanning the entire Great Plains to determine whether overwinter mortality, temperature during migration, or precipitation during the preceding year's growing season and vegetation phenology best predicted local abundance. The start date of the growing season and the total precipitation in the preceding year's growing season correlated most strongly with sparrows' interannual settlement decisions. Local abundance was highest in areas where the growing season started before March and where the preceding year's growing season precipitation was low. The drivers of population declines and movement decisions in grassland birds are complex and often indirect or delayed. As grasslands face ongoing anthropogenic threats ranging from agricultural development to fire suppression and climate change, identifying the distributional and demographic responses of grassland birds will be crucial to conserving this declining group of species.

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# **Chapter 1 - Local grassland bird declines were not driven by long-term reductions in reproductive output**

## **Abstract**

Grassland bird populations have declined sharply, with current populations only about half the size of those 50 years ago. The most likely cause of such declines is habitat loss; there is less habitat available as native grasslands are co-opted for agriculture. However, locally, where the overall amount of natural habitat has remained relatively stable, changes in disturbance regime can reduce the quality of that habitat for grassland-obligate species. Habitat degradation could contribute to population declines via reduced reproductive success due to increased predation or Brown-headed Cowbird (*Molothrus ater*) brood parasitism. Both predation and parasitism can cause declines directly or indirectly through reduced parental investment resulting in reduced clutch size, hatching success, or fledging success, affecting reproductive success at the population level. To determine whether and how changes in reproductive success might contribute to declines, we compiled grassland bird nesting data collected at the Konza Prairie Biological Station from 1971–2020. Spanning nearly five decades and, comprising 6,355 nests of 48 species, this represents, to our knowledge, the longest-term bird nesting dataset ever compiled for a grassland site. We first identified temporal trends in each of the potential drivers, and tested whether species-specific trends match changes in abundance obtained from line-transect surveys collected over four decades. Finally, we tested several habitat and species-level covariates of changes in reproductive rates. Daily nest survival, clutch size, the number of eggs hatched, and the number of young fledged did not change from 1971–2020. However, the frequency of brood parasitism increased, and success at several nest stages correlated with habitat preference and/or

the number of years since a pasture was burned or grazed, which suggests a lack of disturbance can be detrimental. In addition, species-level responses differed based on habitat use with grassland specialists the hardest hit by woody encroachment, and shrub specialists' reproductive success remaining unchanged or increasing. Overall, our results suggest that woody encroachment and its influence on the risk of brood parasitism and predation may drive population declines as grassland specialists avoid shrubbier areas and move elsewhere.

## Introduction

North American bird populations have declined over the last fifty years, with a net loss of almost three billion birds since 1970 (Rosenberg 2019). Such declines can negatively affect ecosystems by removing food sources for predators and affecting multiple other types of ecosystem services such as seed dispersal or insect control (Şekercioğlu et al. 2004, Whelan et al. 2008). Not all bird species are declining at an equal rate; grassland-dependent species are declining most rapidly, having lost over 700 million or about half the individuals present fifty years ago (Brennan and Kuvlesky 2005, McCracken 2005, Rosenberg et al. 2019).

The largest causes of such declines are presumed to be habitat loss (Stanton et al 2018, Brennan and Kuvlesky 2005) and fragmentation (Herkert 1994, Herkert et al. 2003, Herse et al. 2020). As new technologies allow farmers to make use of previously non-commercially viable plots of land, most native grasslands of North America have been converted to cropland or managed intensively for cattle grazing (Gage et al. 2016, Stanton et al 2018, Ricklefs 1999). Today, only 36.3% of the grasslands present in the Great Plains when European colonizers arrived remains (Augustine et al. 2019). In addition to widespread habitat loss leading to declines on a large scale, there have also been local declines (Brennan and Kuvlesky 2005, With et al. 2008). However, grassland habitats are characterized and maintained by disturbances such as fire, grazing, and weather (Knapp et al. 1999), and the variability caused by such disturbances can make studying the drivers of local grassland bird declines difficult. At local scales, degradations in the *quality* of the remaining habitat could drive declines (Mac Nally et al. 2009, Ward et al. 2010). Anthropogenic suppression of disturbances such as fire allow encroachment of woody vegetation (Coppedge et al. 2001, Bond et al. 2005, O'Connor et al. 2020) resulting in the degradation of grasslands, and ultimately, conversion into shrublands and/or savannah (Van



Auken 2009, Ratajczak 2014). Although grazing can sometimes reduce the overall cover of woody vegetation (Collins and Calabrese 2012), in other cases grazing—especially of native bison, (*Bos bison*)—and fire interact in such a way to promote woody encroachment (Briggs et al. 2002). Thus, although lower fire frequencies generally lead to more woody encroachment, the consequences of grazing are more complex. If left unchecked, habitat degradation due to alteration of disturbance regimes can eventually lead to grassland loss (Archer et al. 2017, Fuhlendorf et al. 2017).

While habitat degradation may drive local declines, the proximate mechanisms are not well understood. One potential mechanism is via reductions in reproductive success. The early stages of a bird's life are its most vulnerable (Lima 2009), so understanding the drivers of changes in reproductive success is crucial to properly manage species. Habitat degradation could influence reproductive rates and, ultimately, population trends in several ways (Figure 1-1). Many nest predators (Klug et al. 2010, Atuo and O'Connell 2017) as well as brood parasitic Brown-headed Cowbirds (*Molothrus ater*, Wickard 2017, Andersen and Steidl 2019) prefer shrubby areas and are more common nearer the interface between grasslands and woody vegetation. Thus, woody encroachment can result in increases in nest predators (Klug et al. 2010) and cowbirds (Gates and Gysel 1978, Arnold and Higgings 1986), both of which could drive declines either directly or indirectly. Increases in complete nest failure due to predation or partial predation (i.e., some but not all of the eggs or young in a nest being depredated) reduce per capita reproductive success (Pease and Grzybowski 1995). A higher risk of nest predation can indirectly reduce reproductive success through its effects on nest parents (Zanette et al. 2011) as parents may respond by reducing their visitation rate and thus how often they are able to feed nestlings (Muchai and Du Plessis 2005, Fontaine et al. 2007). Alternatively, parents may

lay smaller clutches in the face of elevated risk (Eggers et al. 2006). An increase in brood parasitism can reduce reproductive success either directly because cowbirds often remove a host egg when laying one of their own in a nest (Pease and Grzybowski 1995, Peer et al. 2013, Lowther 2020), or indirectly by increasing stress in nest parents (Mark and Rubenstein 2013, Antonson et al. 2020). These direct and indirect factors can reduce success at multiple stages of the nest cycle, influencing clutch size (the number of eggs laid), hatching success (the number of eggs that hatch), and/or reduced fledging success (the number of young that survive to fledge). We sought to test whether reduced investment or success could mechanistically link habitat degradation and population declines.

Linking population declines and per capita reproductive success is uncommon, in part because nest data is difficult and time-consuming to collect, and most studies of reproductive behavior take place over only a few years (e.g., four years: Winter et al. 2006; three years: Byers et al. 2017 and Murphy et al. 2017). Such short-term studies are likely not long enough to see trends in reproduction that could be driving long-term population declines (Franklin 1989). The few long-term studies of avian reproduction primarily focus on species that use nest boxes (Lindenmayer et al. 2009, Wilkin et al. 2009), are large-bodied (Tourenq et al. 2000, Jiao et al. 2014), or nest colonially (Jehl, Jr. 1994), all traits which increase the ease of locating nests. While there have been long-term studies of grassland bird reproduction (e.g., Jones et al. 2010, Öberg et al. 2015), these are rarer than studies in species whose nests are easier to find. These studies of grassland bird reproduction did, however, find large interannual variation in reproductive success, further supporting the idea that long-term studies can more clearly elucidate patterns (Jones et al. 2010, Öberg et al. 2015). However, long-term research sites provide opportunities to address questions over longer temporal scales (Hobbie et al. 2003).

We collected and compiled nesting data spanning 49 years at a single site—the Konza Prairie Biological Station in northeast Kansas. We hypothesized that habitat degradation (i.e., loss of native grasslands in favor of woody plants) may be driving population declines among some of the species reproducing at this site, and that reduced reproductive success (number of eggs that survive to hatch or number of young that survive to fledge) and/or parental investment (clutch size) may be the mechanism by which those two factors are linked. If that were the case, we predicted that at least one of the following would be true: over the course of the study, (1) clutch size would decline, (2) fewer of the eggs laid would survive to hatch, (3) fewer of the nestlings that hatched would survive to fledge, (4) brood parasitism would become more frequent (more nests parasitized) or more intense (more parasites per nest), and/or (5) nest predation would become more common. We then tested the prediction that reductions in reproductive success are driving population declines by identifying whether changes in reproductive success match each species' trends in abundance over the same time period using complementary abundance data. Additionally, we sought to test whether reproductive trends can be explained by woody encroachment, i.e., if they were correlated with factors which influence vegetation composition and structure or with species-level habitat use. We included the day of year each nest was found to test whether vegetation growth over the course of a breeding season might exacerbate differences between areas where woody encroachment is more severe and pristine prairie. In addition, we tested whether this was correlated with reproduction by including the number of years since the pasture each nest was found in was burned/grazed. We did so because, over many years, areas with less frequent fire disturbance should experience more severe woody encroachment (Van Auken 2009, Ratajczak et al. 2014, O'Connor et al. 2020), and the effects of fire often interact with grazing treatments (Briggs et al. 2002, Collins and Calabrese

2012). Finally, although woody encroachment can result in a loss of grassland extent and quality, it also results in an increase in extent and quality of shrubland and/or savannah habitat.

Therefore, we tested whether the responses differed based on species-level preferred breeding habitat and nest substrate.

## **Methods**

### **Study site**

We conducted our study at Konza Prairie Biological Station (longitude: 39.106743, latitude: -96.609333) in the Flint Hills of Kansas. Our study included data collected over 49 years, from Konza's inception in 1971 to 2020. In 2020, the Konza Prairie was a 3,487 ha site co-owned and managed by Kansas State University and the Nature Conservancy. The site has been a Long-Term Ecological Research (LTER) site since 1980, experimentally managed as a mosaic of different burning and grazing regimes (Knapp et al. 1999). Each pasture is each either grazed by bison, cattle, or ungrazed, and burned every 1, 2, 3, 4, or 20 years (Knapp et al. 1999). Since its establishment, adjacent land has been purchased and added to the site. In 1977, 194 ha were added to the western side of Konza, and in 1979, 2,921 ha were added to the site. Burn treatments began on the original 371 ha in 1972. A herd of 200 bison was established on the site to study the effect of native grazers on the prairie ecosystem in 1987. In 1992, to compare the influence of native grazers and non-native grazers, cattle treatments were added initiated. Our study spans all of these additions of land and grazing treatments. We tested whether the number of years since a pasture was burned or grazed could explain trends in reproductive success, as reduced disturbance should exacerbate woody encroachment. Apart from occasional wildfires and the addition of new burning or grazing treatments in later years, most treatments have remained consistent since they were initiated. The resulting suppression of disturbance has

resulted in woody encroachment on much of Konza, especially in pastures where fire and grazing are reduced or absent (Briggs et al. 2002, Heisler et al. 2003, Van Auken 2009, Ratajczak et al. 2014). Specifically, rough-leaf dogwood (*Cornus drummondii*), smooth sumac (*Rhus glabra*), and eastern red cedar (*Juniperus virginiana*) have become increasingly common on Konza, especially in pastures which are ungrazed and/or burned infrequently (Briggs et al. 2002, Knapp et al. 2008, McKinley et al. 2008, Ratajczak et al. 2014). For our analysis, we identified the number of years since each pasture was grazed (by bison or cattle) and/or burned. As the land where Konza now sits was previously burned annually and heavily grazed by cattle, we categorized all pastures as having been burned and grazed in 1970 for the purposes of our analysis.

### **Data collection**

We located and monitored nests of a large proportion of the bird species nesting on the Konza Prairie. As these data were originally collected as part of separate studies, the species, nest-searching methods, and the frequency of nest visitation varied according to the goals of individual researchers. Collectively, nest searching methods included opportunistically flushing birds, systematically dragging a rope across the prairie to flush ground-nesting birds, and by observing birds' behavior. For cavity nesting species, researchers located nests by searching for holes in riparian trees or putting out nest boxes. All observers recorded each nest's contents at least once. For approximately 87% of nests, researchers marked nest locations and checked them one or more times after they were found, recording the number of eggs or young of hosts and brood parasites and inferring how many eggs hatched and on what date, and how many young fledged and on what date. In addition to the nests found by authors of this study, we incorporated data collected from the earliest days of research at the site available on the Konza Data Portal

(Sandercock 2019) and contacted every other researcher we could identify who had conducted avian studies at Konza Prairie. In addition to the authors, other researchers who contributed data to this study and associated dataset are listed in the acknowledgments.

To identify whether each species was increasing, decreasing, or stable at Konza, we used data from line-transect surveys spanning over 40 years (Boyle 2020) and modeled the sum total count for each species against a year by species interaction while accounting for effort by including the total transect distance covered per year. From these models, we obtained a beta estimate for each species' change in abundance. If the confidence intervals of the beta estimates for the interaction overlapped zero, we considered that species to be 'stable'. If the mean and upper and lower confidence intervals of the beta estimates were above or below zero, we considered that species to be increasing or declining, respectively.

To test whether trends in reproductive success were correlated with species-level variation in habitat use, we obtained data on each species' breeding habitat and nest substrate using the *Primary Breeding Habitat* categories defined by the Avian Conservation Assessment Database (Partners in Flight 2018). These categories were "aridlands" (at Konza, aridlands species breed in shrubby areas, so hereafter will be referred to as "shrublands" species), forests, generalist, grasslands, wetlands, and woodlands. We coded nest substrate for all species except Mourning Doves (*Zenaida macroura*) using categories listed in the All About Birds online bird identification resource (Cornell Lab of Ornithology 2019), which included building, burrow, cavity, ground, shrub, and tree nests. Mourning Doves were categorized as nesting in trees in the All About Birds resource, but often nest on the ground at Konza. Thus, we categorized this species as a ground nester in this study.

## Analyses

We conducted all analyses in R (R Core Development Team 2013). We constructed Generalized Linear Mixed Models using package '*glmmTMB*' (Brooks et al. 2017), as it provides a framework for fitting zero-inflated response variables. To identify trends across all species, rather than individual species-level responses, we included a random effect of species in all models. We also included a year term in all models, as we were primarily interested in trends across years. We constructed six model sets to test our predictions. First, we tested whether each response changed across years, using only a year term as our predictor. Second, we determined whether reproductive trends were associated with declines by including a year by population trend interaction. For our third and fourth model sets, we tested whether trends in our responses were correlated with species-level habitat use by including interactive terms between year and each species' primary breeding habitat (in the third model set) and nest substrate (in the fourth). Fifth, we related reproductive responses to habitat degradation by including additive effects of day of year, the number of years since each pasture was burned, and the number of years since the pasture was grazed. Although previous research suggested that grazing by bison and cattle can have different effects on woody encroachment, in preliminary models we found no difference between grazer identity on any of our responses, so lumped cattle and bison grazing treatments. In our sixth and final model set, we tested whether trends in responses were correlated with partial predation frequency by including only a year term and a binary term designating whether a nest experienced partial predation. For each model set, we ran separate models for each stage-specific metric of reproductive success as the response (i.e., clutch size, number of eggs hatched, and number of young fledged). We also included models with each of the potential mechanisms by which grassland degradation could drive declines as the response,

including parasitism frequency, parasitism intensity, and predation frequency. We list the full set of models in Tables S1 and S2.

From all analyses, we excluded records if they met any of the following conditions: experimentally manipulated nests, if we could not determine which pasture the nest was in, or the species of the nest was not recorded. For clutch size and hatching success models, we excluded nests where clutch size was not recorded. For fledging success models, we included data for all nests that survived to the nestling stage and where fate could be inferred. We included nests of precocial species (i.e., Greater Prairie-chickens (*Tympanuchus cupido*), Ring-necked Pheasants (*Phasianus colchicus*), Northern Bobwhites (*Colinus virginianus*), Killdeer (*Charadrius vociferus*), Upland Sandpiper (*Bartramia longicauda*), Wild Turkey (*Meleagris gallopavo*) that survived to hatch in models of fledging success, as precocial species leave the nest shortly after hatching. If we found a nest empty, but at the correct age for young to fledge or hatch (depending on species) and with no obvious damage from a predator, we presumed the nest was successful. For historical nest data, if fate or any information we could use to estimate fate was not recorded, we categorized the fate as “unknown” and excluded it from our predation models. For parasitism models, we excluded nests of any species which was parasitized by Brown-headed Cowbirds fewer than five times in our dataset. For parasitism intensity models, we restricted analyses to nests where the number of cowbird eggs was recorded. Finally, for our predation frequency models we excluded any nests for which fate was unknown.

For clutch size, we fit models with a zero-truncated Poisson distribution, as there could be no active nests with no clutch size. Because many of the nests failed before hatching or fledging, or were unparasitized, we fit models with a zero-inflated Poisson distribution as well as a Poisson distribution without a zero-inflation term for the number of eggs hatched, the number



of young fledged, and parasitism intensity, and compared the two models using Akaike's Information Criterion to determine which model better fit the data. For the models of clutch size, number of eggs hatched, the number of young fledged, and parasitism intensity, the zero-inflated model better fit the data. For parasitism and predation frequency, we fit zero-inflated and non-zero-inflated models with a binomial distribution and compared the fit of each model. For these models, the non-zero-inflated model fit the data better, so we used that model. We calculated effect sizes for all significant interactions and main effects using package '*effectsize*' (Ben-Shachar et al. 2020). Finally, we fit daily nest survival models using '*RMark*' (Laake 2013) and program MARK (White and Burnham 1999) to identify trends in overall nest survival over time.

## Results

We collected data for 6,355 nests total. Of those, 4,629 included adequate data on species, location, and nest contents to be included in our models. We excluded 32 nests without a recorded species, and removed 755 nests that were experimentally manipulated from our analyses. We excluded 7 nests of species that were not observed on the transect surveys we used to determine population trends. We further removed 33 nests with no location data recorded, and 211 nests collected on adjacent properties outside of the boundaries of Konza. These exclusions resulted in a total of 5,317 nests with adequate data on species and location to be included in our models, and each individual model set had further exclusions based on nest contents, resulting in our clutch size models (the models with the largest number of nests with adequate data) included data from 4,629 nests. Of the >60 bird species observed breeding on Konza, our dataset included 48 species, with 1–2,136 nests per species (mean = 115.9, SE = 2.6), and included species belonging to nine orders and 25 families (Figure 1-2). Of the 48 species in our nest data, most of the species' populations on Konza were stable ( $n = 28$ ), and more were decreasing ( $n = 11$ ) than

increasing ( $n = 9$ ) (Figure A-1). However, many of species with “stable” populations were rarer species for which trends in abundance were difficult or impossible to detect. Of the nine species that were increasing, six preferred breeding habitat was shrublands, forests, or woodlands, and only two preferred grasslands. Of the 11 species that were decreasing, five preferred breeding habitat was grasslands, while only three preferred forests. The three species increasing most sharply were Brown-headed Cowbirds ( $\beta = 1.957$ ,  $SE = 0.167$ ,  $P < 0.001$ ), Dickcissels (*Spiza americana*,  $\beta = 1.011$ ,  $SE = 0.167$ ,  $P < 0.001$ ), and Bell’s Vireo (*Vireo bellii*,  $\beta = 0.907$ ,  $SE = 0.167$ ,  $P < 0.001$ ), and the three species decreasing most sharply were Eastern Meadowlarks (*Sturnella magna*,  $\beta = -1.227$ ,  $SE = 0.167$ ,  $P < 0.001$ ), Grasshopper Sparrow (*Ammodramus savannarum*,  $\beta = -1.169$ ,  $SE = 0.167$ ,  $P < 0.001$ ), and Henslow’s Sparrow (*Centronyx henslowii*,  $\beta = -0.728$ ,  $SE = 0.167$ ,  $P < 0.001$ ) (Figure 1-3).

For each nest stage model, we summarize all significant interactions and additive main effects and their effect sizes in Table 1, and full model results are presented in Tables S1 and S2. Accounting for variation among species, clutch size did not change across years in 4,626 nests of 41 species ( $\beta = 0.002$ ,  $SE = 0.001$ ,  $z = 1.60$ ,  $P = 0.109$ , Table S1). However, clutch size decreased over the course of breeding seasons by 0.4 per month ( $X^2 = 64.50$ ,  $P < 0.001$ , Table 1). Declining species did not experience reductions in clutch size ( $\beta = 0.006$ ,  $SE = 0.007$ ,  $z = 0.004$ ,  $P = 0.362$ ). Grassland specialists’ clutch size did not reduce over the course of the study ( $\beta = 0.015$ ,  $SE = 0.014$ ,  $z = 1.03$ ,  $P = 0.303$ ) and nor did the clutch size of ground nesting species ( $\beta = 0.002$ ,  $SE = 0.003$ ,  $z = 0.75$ ,  $P = 0.452$ ). Finally, partial predation frequency did not affect clutch size ( $\beta = 0.003$ ,  $SE = 0.003$ ,  $z = 0.85$ ,  $P = 0.396$ , Tables S1, S2).

Accounting for variation among species, the number of eggs hatched per nest did not change across years in 3,682 nests of 34 species ( $\beta = 0.004$ ,  $SE = 0.003$ ,  $z = 1.33$ ,  $P = 0.182$ ,

Table S1). Relative to species with stable populations, the number of young per nest increased in species with increasing populations ( $\beta = 0.040$ , SE = 0.018,  $z = 2.21$ ,  $P = 0.027$ ), and in decreasing species ( $\beta = 0.040$ , SE = 0.018,  $z = 2.20$ ,  $P = 0.28$ , Table 1, Figure 1-4B). Nests contained more nestlings later in the breeding season than they did earlier, with 0.2 more nestlings per month ( $X^2 = 10.08$ ,  $P = 0.001$ ) and more young per nest in ungrazed pastures ( $X^2 = 8.27$ ,  $P = 0.004$ , Table 1). Species that prefer forests hatched fewer young than shrublands species ( $\beta = 0.128$ , SE = 0.073,  $z = 1.76$ ,  $P = 0.079$ ), as did species that prefer grasslands ( $\beta = 0.063$ , SE = 0.062,  $z = 1.01$ ,  $P = 0.313$ ) and generalist species ( $\beta = 0.047$ , SE = 0.067,  $z = 0.71$ ,  $P = 0.481$ , Table 1). Species that nest on the ground did not hatch fewer young ( $\beta = -0.002$ , SE = 0.007,  $z = -0.24$ ,  $P = 0.810$ ), and partial predation frequency did not affect the number of young that hatched ( $\beta = 0.003$ , SE = 0.008,  $z = 0.42$ ,  $P = 0.5674$ , Table S1).

Accounting for variation among species, the number of young fledged per nest did not change across years in 2,975 nests of 23 species ( $\beta = 0.007$ , SE = 0.006,  $z = 1.11$ ,  $P = 0.265$ , Table S1) but did increase over the course of breeding seasons, with 0.2 more young fledged per month ( $X^2 = 5.96$ ,  $P = 0.015$ , Table 1). Fewer young fledged per nest in forest species than in shrublands species ( $\beta = 0.376$ , SE = 0.174,  $z = 2.17$ ,  $P = 0.030$ , Table 1). Species whose populations were declining did not fledge fewer young ( $\beta = 0.044$ , SE = 0.047,  $z = 0.93$ ,  $P = 0.351$ ), and nor did species which nest on the ground ( $\beta = 0.014$ , SE = 0.014,  $z = 0.99$ ,  $P = 0.318$ ). Partial predation frequency did not affect the number of young fledged ( $\beta = 0.005$ , SE = 0.012,  $z = 0.42$ ,  $P = 0.674$ , Table S1).

After accounting for variation among species, more nests were parasitized across years in 4,376 nests of 11 species ( $\beta = 0.017$ , SE = 0.005,  $z = 3.08$ ,  $P = 0.002$ , Figure 1-5). Cowbirds parasitized ground nests more frequently than shrub nests initially ( $\beta = -0.043$ , SE = 0.012,  $z =$

-3.73,  $P < 0.001$ ), but over the years this reversed as ground nests were parasitized less often while shrub nests were parasitized more often (Table 1). Cowbirds parasitized the nests of declining species less often ( $\beta = -0.127$ ,  $SE = 0.062$ ,  $z = -2.04$ ,  $P = 0.041$ ) than species with stable populations (Table 1, Figure 1-4D). Parasitism frequency decreased over the course of the breeding season, with proportions decreasing by 0.08 per month ( $X^2 = 68.69$ ,  $P < 0.001$ ). Parasitism frequency was lower in ungrazed ( $X^2 = 14.20$ ,  $P < 0.001$ ) and/or infrequently burned ( $X^2 = 21.77$ ,  $P < 0.001$ ) pastures (Table 1). Parasitism frequency was not higher in nests of grassland specialists ( $\beta = 0.063$ ,  $SE = 0.062$ ,  $z = 1.01$ ,  $P = 0.313$ ), and partial predation frequency did not affect whether a nest was parasitized ( $\beta = 0.000$ ,  $SE = 0.007$ ,  $z = 0.05$ ,  $P = 0.961$ , Table S1).

After accounting for variation among species, the number of cowbird eggs per nest did not change in 3,926 nests of 11 species ( $\beta = -0.001$ ,  $SE = 0.002$ ,  $z = -0.59$ ,  $P = 0.553$ , Table 1). Cowbirds laid more eggs in ground nests than in shrub nests at the beginning of the study, but this reversed at the end of the study period ( $\beta = -0.013$ ,  $SE = 0.006$ ,  $z = -2.20$ ,  $P = 0.028$ , Table 1). Cowbirds laid more eggs per nest over the course of the breeding season, with 0.4 more eggs per month ( $X^2 = 35.83$ ,  $P < 0.001$ ), and more in infrequently grazed pastures ( $X^2 = 37.07$ ,  $P < 0.001$ ). Cowbirds did not lay more eggs in nests with declining populations ( $\beta = -0.038$ ,  $SE = 0.031$ ,  $z = -1.21$ ,  $P = 0.227$ ) or in nests of grassland specialists ( $\beta = 0.009$ ,  $SE = 0.029$ ,  $z = 0.33$ ,  $P = 0.739$ ), and partial predation frequency did not affect how many cowbird eggs were in a nest ( $\beta = 0.017$ ,  $SE = 0.018$ ,  $z = 0.96$ ,  $P = 0.336$ , Table S1).

After accounting for differences among species, predation frequency remained unchanged in 4,626 nests of 41 species ( $\beta = 0.006$ ,  $SE = 0.005$ ,  $z = 1.13$ ,  $P = 0.259$ , Table S1). Predation frequency decreased for forest species ( $\beta = -0.243$ ,  $SE = 0.097$ ,  $z = -2.50$ ,  $P = 0.012$ ),

generalists ( $\beta = -0.251$ , SE = 0.083,  $z = -3.04$ ,  $P = 0.002$ ), and grassland species ( $\beta = -0.270$ , SE = 0.82,  $z = -3.31$ ,  $P = 0.001$ ) relative to shrublands species (Table 1). Predation frequency decreased over the course of the breeding season ( $X^2 = 0.003$ ,  $P = 0.003$ ), with frequencies decreasing by a proportion of 0.02 per month, but increased the longer a pasture went without being grazed ( $X^2 = 7.05$ ,  $P = 0.008$ , Table 1). Predation frequency was not lower in species with declining populations ( $\beta = -0.039$ , SE = 0.025,  $z = -1.59$ ,  $P = 0.113$ ) or ground nesting species ( $\beta = -0.007$ , SE = 0.011,  $z = -0.67$ ,  $P = 0.506$ , Table S1). Daily nest survival did not change from 1971–2020 in 1,615 nests of six species (DSR =  $-0.003$ , 95% CI:  $-0.011$ , 0.006).

## Discussion

The hypothesis that reduced reproductive success is the mechanism by which habitat degradation is driving population declines does not appear to be true. Clutch size, the number of eggs hatched, the number of young fledged, brood parasitism intensity, and predation frequency did not change across species over the course of the study. Only the frequency of brood parasitism changed over the course of the study, with increasing rates of parasitism paralleling increases in the abundance of Brown-headed Cowbirds at the site. As cowbirds prefer areas with more woody vegetation, an increase in cowbird populations and a corresponding increase in parasitism frequency as woody vegetation spreads is consistent with previous research (Wickard 2017, Andersen and Steidl 2019). This is in direct contrast to previous work on Konza over shorter time scales which suggested that frequency of cowbird parasitism was declining across years (e.g., in Dickcissels, from ~85% in 1965–1979: Zimmerman 1983, to ~70% in 2002–2007: Rivers et al. 2010). Cowbird parasitism became more frequent overall, but this was driven by an increase in parasitism frequency for shrublands species and species that nest in shrubs. There are several potential explanations for the observed increase in cowbird parasitism of shrub-

associated hosts. First, as woody vegetation spreads on Konza and shrub-associated hosts become more frequent, cowbirds were more exposed to more individuals of the shrub-nesting species. This increased exposure might have increased the chances of parasitism in shrub nests through increased opportunities and via the formation of search images for increasingly common shrub-nesting species. Second, when grassland and woody vegetation are both present on the landscape, cowbirds prefer to parasitize nests in woody plants (Hovick and Miller 2013)), so with more woody vegetation, cowbirds are able to act on their preferences. However, despite this increase in parasitism, there was no corresponding decrease in reproductive success. This supports previous research that found nest parents in grassland species are able to cope with cowbird parasitism without reductions in immediate reproductive success (Winnicki 2019).

By identifying community-level patterns rather than species-level trends, we identified how habitat degradation affects the bird community as a whole at Konza. Differences in response to woody encroachment depend on species-level habitat association, with grassland specialists most negatively affected and shrub specialists most positively affected (Coppedge et al. 2001). We accounted for differences in response due to habitat preference by including a model set with habitat preference as a predictor. In addition, our dataset contains a diverse taxonomic range, including 24 families, and these families are quite split in their habitat preferences. For example, the two most common habitat preferences in our dataset—grasslands and forests—included species from 9 and 12 families, respectively. This suggests low niche conservatism and therefore a weak taxonomic signal in our results, so we did not account for phylogenetic relatedness in our models.

Although the overall amount of natural habitat on Konza was unchanged, the amount of *grassland* has declined as more and more prairie is overtaken by woody plants. At Konza, cover

of woody encroachment has steadily increased (reviewed in Briggs et al. 2005), with shrub cover in infrequently (every 4 years) to rarely (once in 18 years) burned pastures increasing by 28.6% and 23.7% from 1983–2000, respectively (Heisler et al. 2003). Even annual burning is not enough to stem the tide of woody vegetation; in annually burned pastures shrub cover increased by 3.7% from 1983–2000 (Heisler et al. 2003). In addition to the increase in shrub cover, gallery forests increased in coverage by 72% from 1939–2002 (Briggs et al. 2005), further reducing the amount of prairie remaining on Konza. These increases in woody plant cover on Konza parallel similar trends elsewhere in the Great Plains, with 1.1–2.3% change in percent cover of woody plants (*J. virginiana* from 1937–1969, 1956–2000; *Quercus spp.* and *Pinus spp.* from 1940–1988 and 1979–2002) in the Central Great Plains (reviewed in Barger et al. 2011). This is similar to the current rate of expansion of croplands in the Great Plains from 1961–1997 (4–5%/year, Gallant et al. 2007), suggesting that habitat loss due to woody encroachment may be one of the primary mechanisms by which grassland habitat is currently being lost.

Rather than reduced reproductive success, the mechanism by which habitat degradation drives population declines may be through habitat conversion driving reduced settlement and/or increased emigration. We observed decreases in the populations of grassland obligates, and increases in shrub-nesting species. Shrub-associated species increased despite an increase in brood parasitism frequency and intensity for shrub-nesting species, and an increase in predation in species that prefer shrubby shrublands. Shrub-associated species increasing while simultaneously experiencing higher predation may seem incongruent, but if shrubby habitat is increasing overall, one would expect an increase in abundance of bird species that nest in shrubs as well as an increase in predators and brood parasites searching for nests. However, although parasitism intensity and predation frequency did not increase for grassland specialists, their

populations still declined most severely. These findings corroborate similar results in previous studies (Bakker 2003, Brawn et al. 2001). A review of the effects of woody vegetation on grassland bird reproduction found that woody encroachment had a negative effect on occurrence, density, and/or reproductive success in all but two species (Bakker 2003). In addition, bird species that are adapted to disturbance-mediated habitats are declining overall (Brawn et al. 2001), suggesting that anthropogenic suppression of disturbance is resulting in population declines beyond just grasslands.

We found evidence consistent with habitat degradation in the form of woody encroachment operating as another means by which the effective area of grassland habitat is reduced. Although historically, agricultural development was the primary anthropogenic cause of habitat loss (Samson et al. 2004), in regions where much of the commercially viable land has already been converted to cropland such as the Great Plains of North America, woody encroachment is increasingly important as a driver of reductions in grassland habitat (Barger et al. 2011). Maintaining grassland habitat via the maintenance of site-specific disturbance regimes is crucial to ensure the persistence of grassland-dependent species on the landscape (Sherow et al. 1998).



## Tables

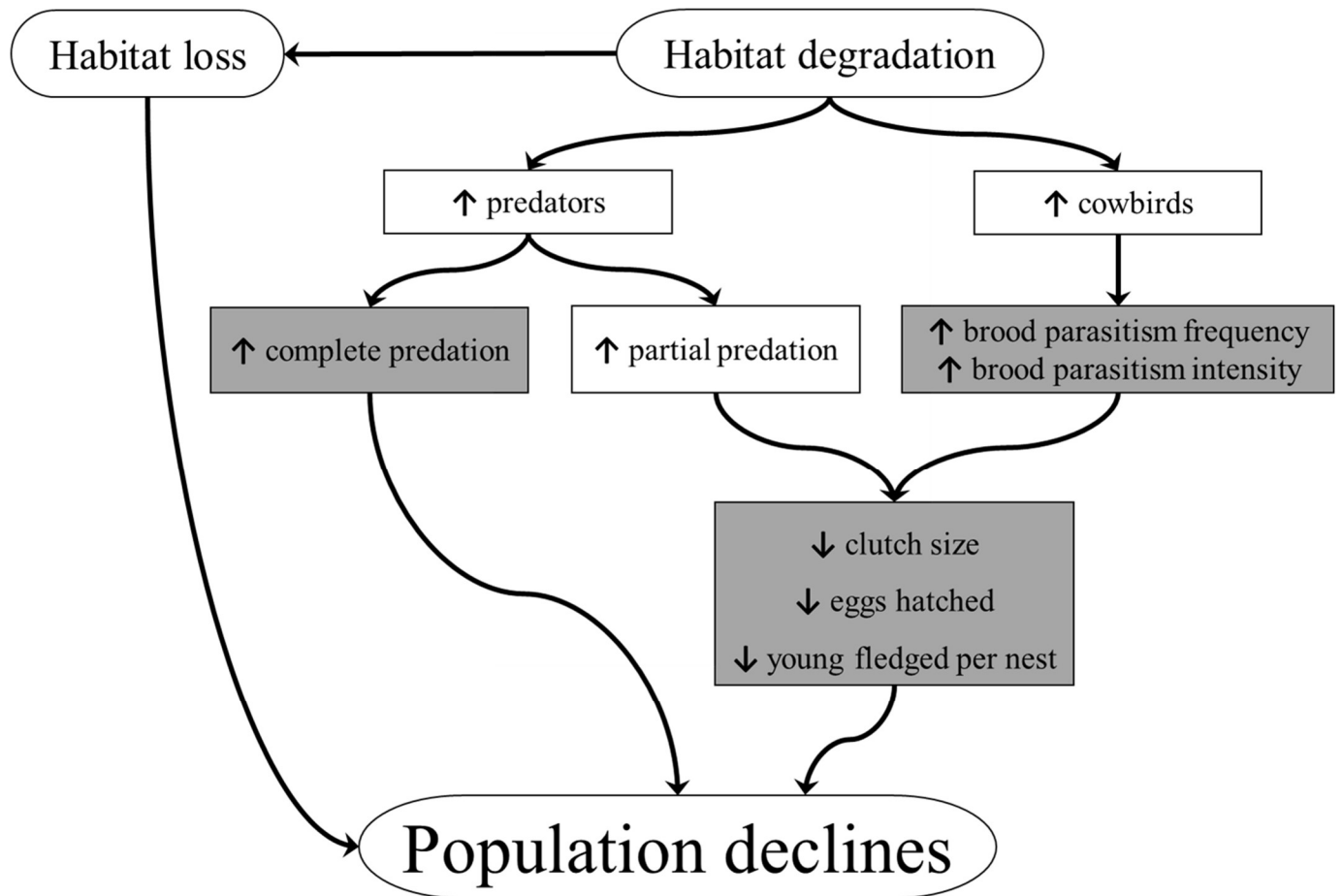
**Table 1-1. Results for each response variable across all models. Standardized coefficient and 95% confidence intervals represent effect size for the interactions where applicable, and for the main effect in additive models.**

Response	Predictor	Coefficient	95% CI	P-value
<b>Clutch size</b>				
	<i>year + day of year + years since grazed + years since burned</i>			
	<i>day of year</i>	-0.09	[-0.11, -0.07]	< 0.001
<b>N eggs hatched</b>				
	<i>year*population trend</i>			
	<i>decreasing</i>	0.24	[0.03, 0.45]	0.028
	<i>increasing</i>	0.24	[0.03, 0.45]	0.027
	<i>year*breeding habitat</i>			
	<i>forests</i>	0.49	[0.09, 0.88]	0.015
	<i>generalist</i>	0.42	[0.05, 0.79]	0.025
	<i>grasslands</i>	0.44	[0.09, 0.79]	0.015
	<i>year + day of year + years since grazed + years since burned</i>			
	<i>day of year</i>	0.07	[0.03, 0.12]	0.001
	<i>years since grazed</i>	0.06	[0.02, 0.10]	0.004
<b>N young fledged</b>				
	<i>year*habitat</i>			
	<i>forests</i>	2.27	[0.22, 4.32]	0.030
	<i>year + day of year + years since grazed + years since burned</i>			
	<i>day of year</i>	0.09	[0.02, 0.16]	0.015
<b>Parasitism frequency</b>				
	<i>year</i>			
	<i>year</i>	0.11	[0.04, 0.19]	0.002
	<i>year*population trend</i>			
	<i>decreasing</i>	-0.88	[-1.72, -0.04]	0.041
	<i>year*nest substrate</i>			
	<i>shrub</i>	0.30	[0.14, 0.46]	< 0.001

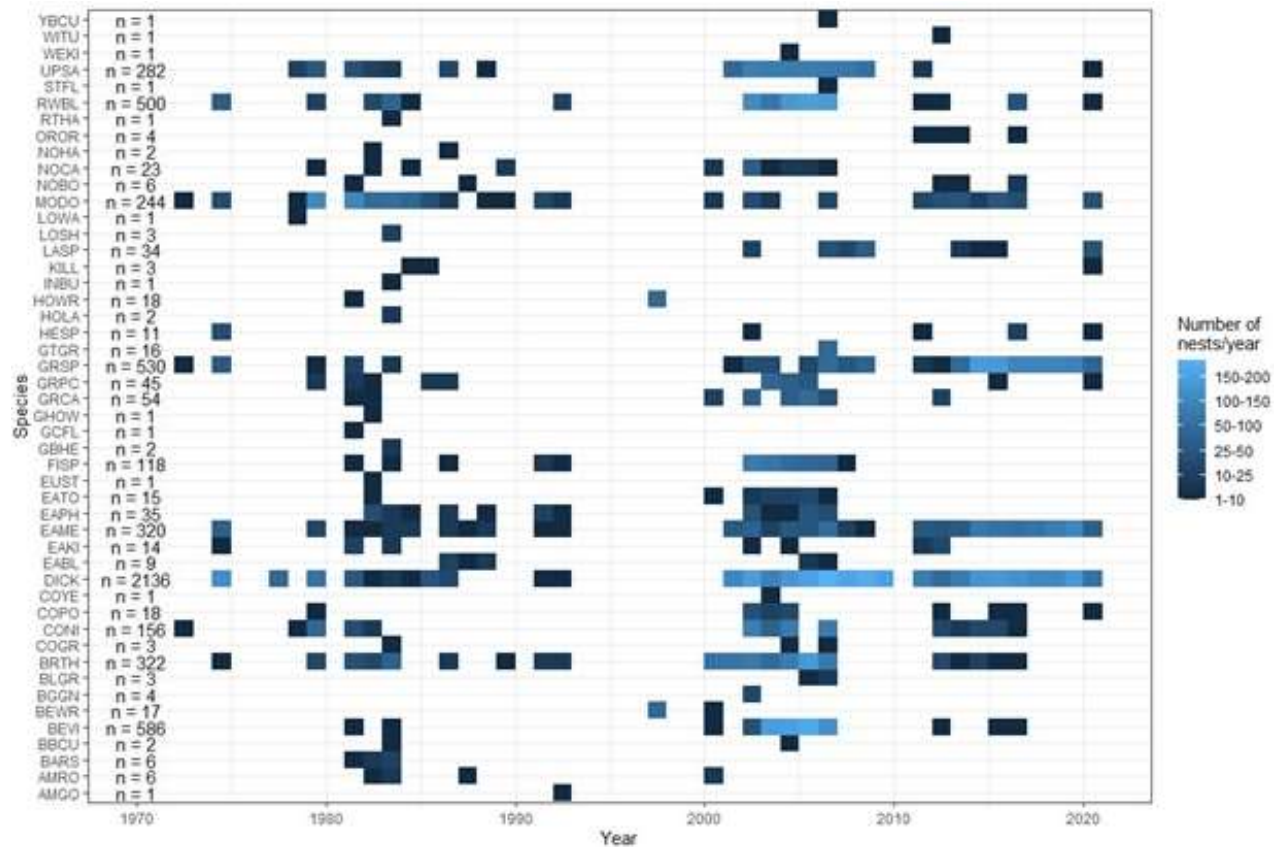
<i>year + day of year + years since grazed + years since burned</i>				
	<i>day of year</i>	-0.37	[-0.46, -0.28]	< 0.001
	<i>years since grazed</i>	-0.17	[-0.25, -0.08]	< 0.001
	<i>years since burned</i>	0.22	[0.13, 0.31]	< 0.001
<b>Parasitism intensity</b>				
	<i>year*nest substrate</i>			
	<i>shrub</i>	0.09	[0.01, 0.17]	0.028
<i>year + day of year + years since grazed + years since burned</i>				
	<i>day of year</i>	-0.11	[-0.14, -0.07]	< 0.001
	<i>years since grazed</i>	0.10	[0.07, 0.13]	< 0.001
<b>Predation frequency</b>				
	<i>year*habitat</i>			
	<i>forests</i>	-1.81	[-3.23, -0.39]	0.012
	<i>generalist</i>	-1.87	[-3.07, -0.66]	0.002
	<i>grasslands</i>	-2.01	[-3.20, -0.82]	0.001
<i>year + day of year + years since grazed + years since burned</i>				
	<i>day of year</i>	-0.13	[-0.22, -0.05]	0.003
	<i>years since grazed</i>	0.11	[0.03, 0.19]	0.008

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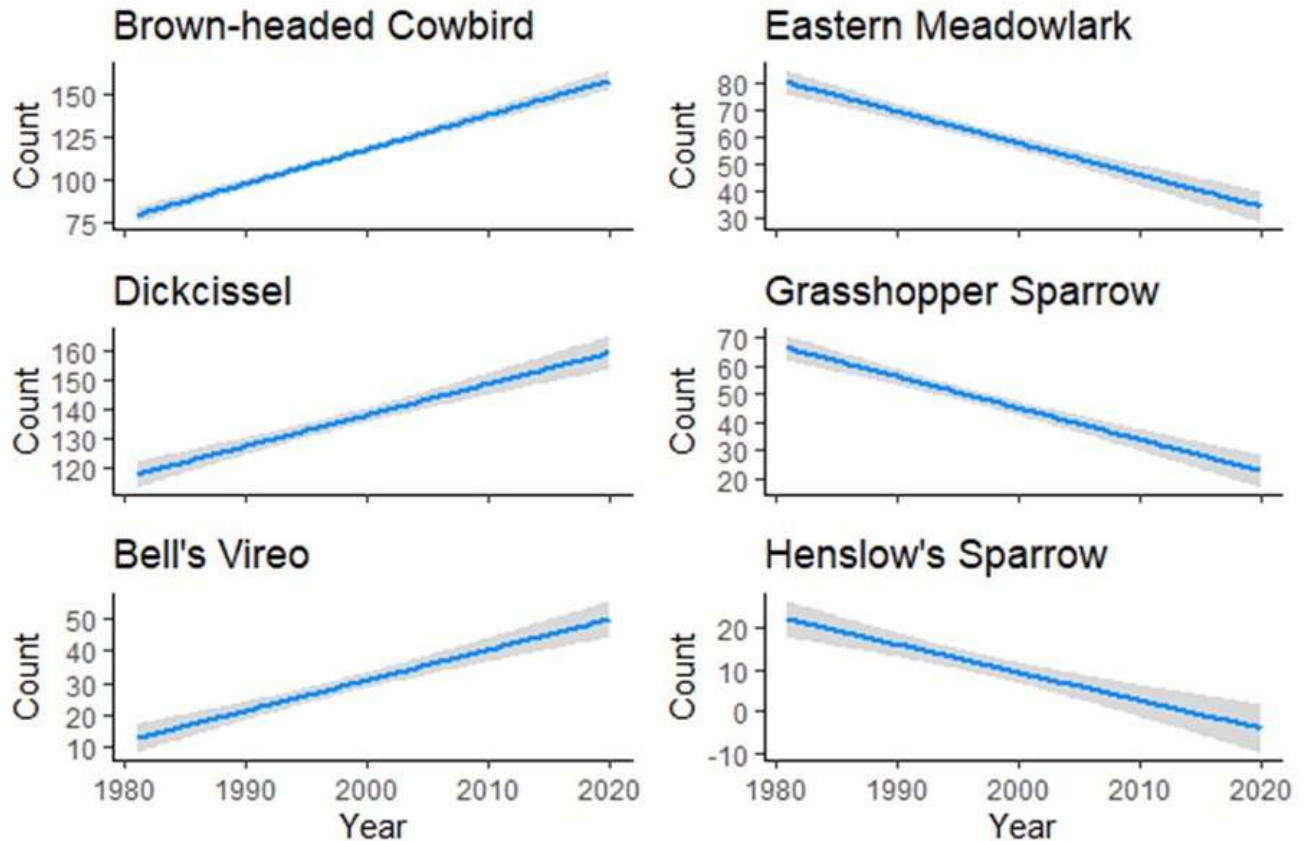
## Figures



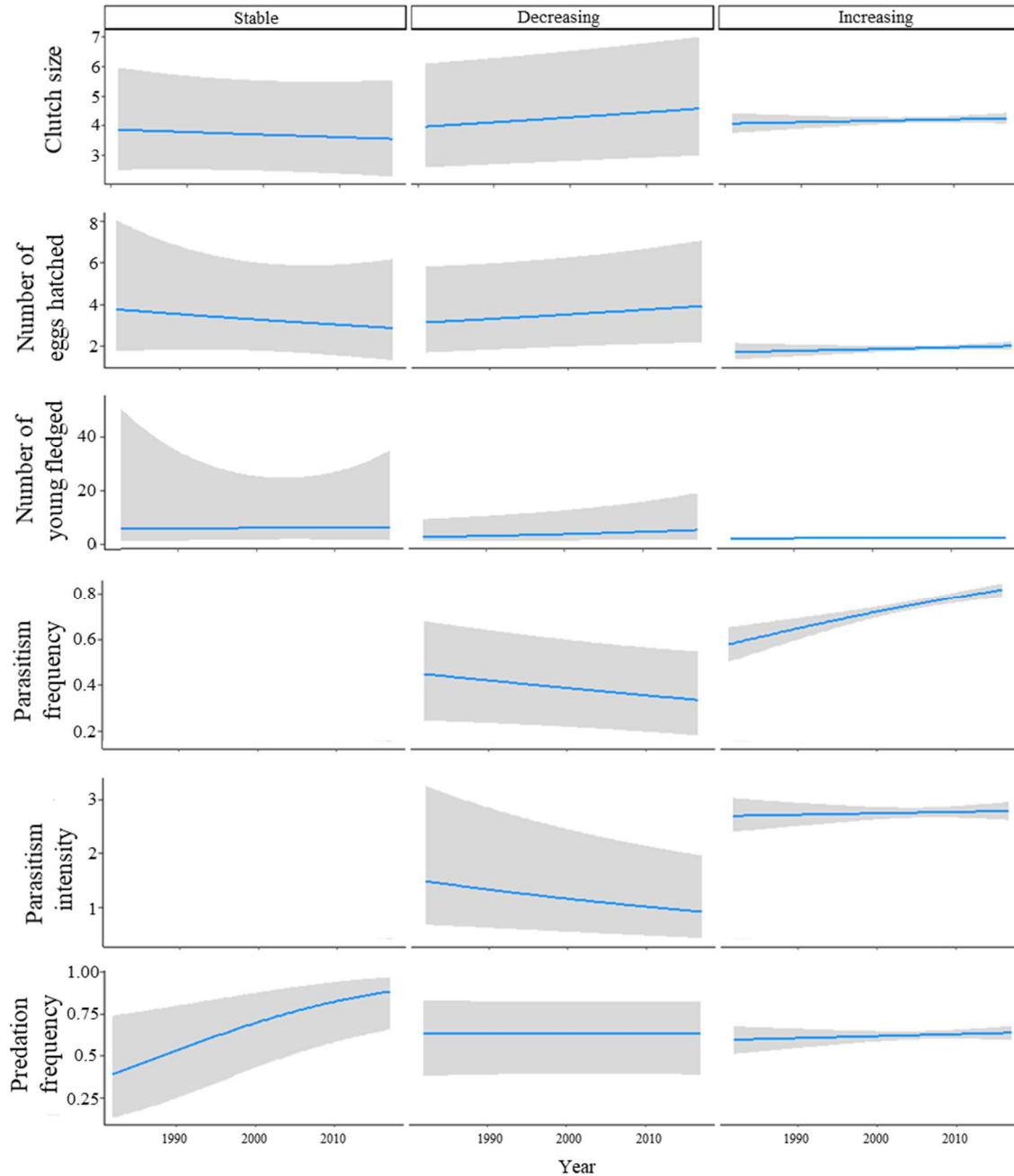
**Figure 1-1. Conceptual diagram showing the primary causes of population declines in grassland birds (habitat loss and degradation), as well as the hypothesized mechanisms by which habitat degradation can drive declines. In addition to driving declines via reductions in reproductive success as shown here, habitat degradation can result in a reduction of grassland habitat, and therefore, population declines through habitat loss. Shaded boxes represent the responses we measured in our study.**



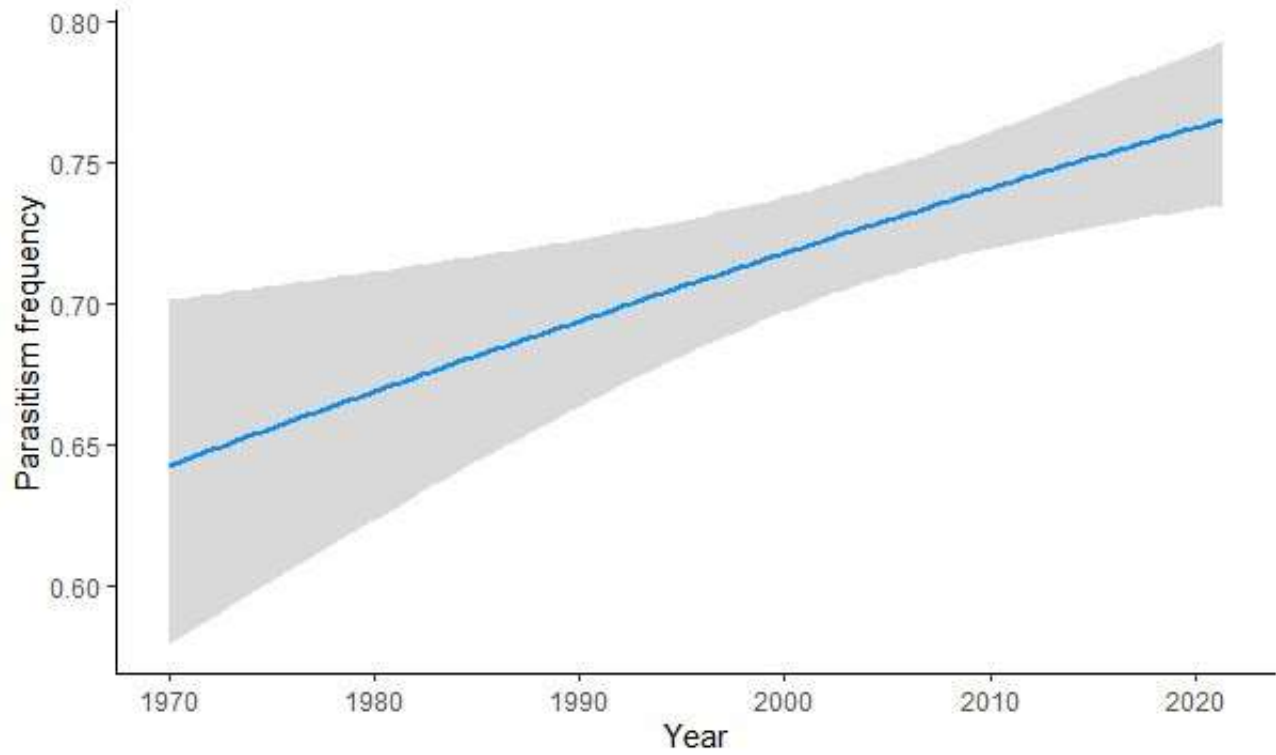
**Figure 1-2. Summary of species (designated by four-letter alpha codes; Pyle and DeSante 2009) included in our nest dataset, showing the presence and number of nests per year. Lighter shades designate years with more nests in our dataset for a given species, while darker blues designate years with fewer nests. The total number of nests for each species is listed across the left side of the figure (total n = 6,355).**



**Figure 1-3. Predicted change in abundance from 1981–2020 for the three species which had the sharpest inclines—Brown-headed Cowbird (*Molothrus ater*,  $\beta = 1.957$ , SE = 0.167,  $P < 0.001$ ), Dickcissel (*Spiza americana*,  $\beta = 1.011$ , SE = 0.167,  $P < 0.001$ ), and Bell’s Vireo (*Vireo bellii*,  $\beta = 0.907$ , SE = 0.167,  $P < 0.001$ ), and the three species that showed the sharpest declines—Eastern Meadowlark (*Sturnella magna*,  $\beta = -1.227$ , SE = 0.167,  $P < 0.001$ ), Grasshopper Sparrow (*Ammodramus savannarum*,  $\beta = -1.169$ , SE = 0.167,  $P < 0.001$ ) and Henslow’s Sparrow (*Centronyx henslowii*,  $\beta = -0.728$ , SE = 0.167,  $P < 0.001$ ). The top three increasing species (on the left) are all associated with shrubs, and the bottom three decreasing species (on the right) are all grassland obligates. Confidence bands represent 95% Wald confidence intervals. Y-axes are transformed to the scale of each response.**



**Figure 1-4. Predicted response by trend in populations for all reproductive success variables, obtained from our models. There are no “Stable” panels for either parasitism response because none of the stable species were parasitized by cowbirds. Parasitism frequency (panel D,  $\beta = 0.045$ ,  $SE = 0.011$ ,  $z = 4.14$ ,  $P < 0.001$ ), and parasitism intensity (panel E,  $\beta = 0.014$ ,  $SE = 0.006$ ,  $z = 2.47$ ,  $P = 0.014$ ) increased across years for increasing species relative to decreasing species, and predation frequency decreased across years for decreasing ( $\beta = -0.070$ ,  $SE = 0.027$ ,  $z = -2.60$ ,  $P = 0.014$ ) and increasing ( $\beta = -0.065$ ,  $SE = 0.027$ ,  $z = -2.45$ ,  $P = 0.014$ ) species, relative to stable species. Confidence bands represent 95% Wald confidence intervals. Y-axes are transformed to the scale of each response.**



**Figure 1-5. Predicted parasitism frequency by year, obtained from our model. Parasitism frequency increased from 1971–2020 ( $\beta = 0.017$ ,  $SE = 0.005$ ,  $z = 3.08$ ,  $P = 0.002$ ). Confidence bands represent 95% Wald confidence intervals. Y-axis is transformed to the scale of the response.**

## **Chapter 2 - Climatic variability explains interannual variation in breeding distributions of Grasshopper Sparrows**

### **Abstract**

For mobile animals, settlement decisions can have large consequences for survival and reproduction. In seasonal migrants, adults typically return to prior breeding locations, but in some species, differences in settlement decisions among years is common, resulting in interannual variation in how many and which individuals breed at any given site. We sought to determine the causes of interannual variation in breeding abundance of Grasshopper Sparrows (*Ammodramus savannarum perpallidus*), a highly mobile and common grassland songbird in the Great Plains of the United States and Canada. We tested predictions of hypotheses invoking interannual variation in climate resulting in winter mortality, conditions experienced during migration, or vegetation structure related to phenology. Local abundance of Grasshopper Sparrows was associated with precipitation in the preceding year's growing season and the timing of the current year's growing season. These results suggest that climatic variability influences settlement decisions and breeding distributions indirectly through effects on vegetation rather than via direct effects on individual survival and condition. Our results support the idea that grassland bird life history has evolved in response to a climatically variable ecosystem in ways that differ from most other migratory birds. As grassland birds are declining more rapidly than birds reliant on other habitats, this offers some hope that they will be able to cope with a changing climate.



## Introduction

Volant animals must make decisions about whether to move at any given time, and these decisions have wide-ranging consequences for fitness (Lidicker and Stenseth 1992). Moving to another location can result in an animal incurring numerous benefits or costs. Benefits of moving may include an increase in food resources or avoiding predation (Williams 2016). Costs of moving may include a decrease in food resources, an increase in predation risk (Yoder et al. 2004), difficulty in finding a mate (Danchin and Cam 2002), and/or increased disease prevalence (Spaan 2015). Movement can also affect scientists' ability to detect demographic changes, as it is difficult to tease apart mortality and emigration (Taylor et al. 2015). There are numerous factors that may influence animals' decisions to move, and different biotic or abiotic drivers may be important for different animals at different times. Large numbers of individuals making movement decisions can collectively result in temporal changes in patterns of relative abundance across distributions, and these changes in distributional patterns can mean that local changes in abundance may not be due to mortality or reproduction but rather due to settlement decisions (Paprocki et al. 2014). Consequently, understanding the drivers of settlement decisions will also help elucidate how best to conserve highly mobile species.

One way in which movement decisions manifest is through low site fidelity. Animals make dispersal decisions that lead to low site fidelity due to inter-annual variability from multiple factors (Switzer 1993) including food resources (Dean 1997, Woinarski 2006), risk of nest predation (Switzer 1997, Haas 1998), or habitat quality (Lanyon and Thompson 1986). Weather is another driver of unpredictability (Stenseth et al. 2002) that can affect organisms directly by changing thermoregulatory costs (Patil et al. 2013, Whitfield et al. 2015, Karvonen et al. 2018), and indirectly by affecting vegetation structure or phenology (Garcia and Ustin 2001,

Fatichi and Ivanov 2014). Mobile animals seek out particular temperatures (Huey 1991, Street et al. 2016), and very high or low temperatures can lead to mortality. Even in species with known genetic differences in dispersal tendency, temperature can outweigh the importance of those genetic differences (Edelsparre et al. 2021). However, the interaction between precipitation, vegetation, and movement decisions is more complex and less well understood than temperature (although see e.g., Holdo et al. 2009). Both temperature and rainfall influence habitat quality and can affect animals' movement and settlement decisions (Rushing et al. 2015, Shutt et al. 2021).

Weather influences settlement decisions and local abundance in several ways. First, severe weather can cause mortality (Gandiwa et al. 2016, Gorzo et al. 2016, Macías-Duarte et al. 2017) and dead animals cannot make any settlement decisions. Second, weather can influence settlement directly via increased metabolic costs. It may be energetically cheaper for an animal to go elsewhere rather than endure the conditions where they already are (Walls et al. 2005, Shepard et al. 2013). Third, weather can influence settlement indirectly via changes in vegetation structure or phenology (Orians and Wittenberger 1991, McGrath et al. 2009). Animals often select habitat based on the vegetation structure of a particular area (Morris 2003), and weather influences when and how much vegetation grows in a given year (Field et al. 1992). All else being equal, more precipitation in the preceding year's growing season will result in more vegetation growth, resulting in taller plants and more litter on the ground, both of which are important to grassland birds (Sala et al. 1988, Knapp et al. 1994). In addition, vegetation growth before animals arrive can provide them with information about what conditions will be like later in the season. Since dispersal is often tied to unpredictable resources (Newton 2012), and the more information an animal has the better their ability to predict where resources will be (Reed et al. 1999), an earlier growing season relative to the norm allows them to make more informed

decisions about where to go. Overlaid on external conditions, animals' settlement decisions are often mediated by past experience and social cues (Roche et al. 2011, Andrews et al. 2015). Species that undergo seasonal migration have ample opportunities to integrate these cues by prospecting for new breeding sites at the end of the preceding breeding season or during spring migration (Ward 2005).

We studied the direct and indirect effects of climatic variability on settlement of grassland songbirds during spring migration in the highly climatically variable Great Plains of central North America (Kunkel et al. 2013). There are substantial spatial differences in climatic conditions across the Great Plains. Due to the Great Plains' large latitudinal range, average temperatures are much higher in the south than in the north. The main source of moisture is the Gulf of Mexico, which leads to gradients of increasing dryness as one goes west or north (Kunkel et al. 2013). Additionally, the lack of mountains to the north results in polar winds that can bring very cold temperatures in the winter (Kunkel et al. 2013). The characteristically high winds on the Great Plains mean that weather systems move quickly across the landscape and precipitation can be erratic. Large storms are common, including blizzards, thunderstorms, and the highest incidence of tornadoes in the world (Kunkel et al. 2013). Weather in the Great Plains is also characterized by its temporal variability and unpredictability (Wishart 2004), and temperature and precipitation vary greatly between weeks and years. Grasslands and the grasses that dominate them are maintained by disturbances such as fire (Woodward et al. 2004). High climatic variation results in large within-year swings between high precipitation (when plants can grow rapidly) and long dry spells (when plants die back and become easy fuel for fires). In addition to climatic variability, grassland systems are co-dominated by herbaceous vegetation that often dies back each year (White et al. 2019), meaning that vegetation can change greatly

between years, unlike more long-lived vegetation such as that which dominates in shrublands or forests.

In relatively stable systems such as forests or shrublands, birds tend to be site faithful, and this is often driven by nest success (Schlossberg 2009, Chalfoun and Schmidt 2012). However, many grassland birds exhibit much lower site fidelity (Jones et al. 2007, Winger et al. 2019). In addition, in North America, grassland birds are declining more rapidly than birds in other habitat guilds (Rosenberg et al. 2019). Although habitat loss and fragmentation are almost certainly the primary cause of grassland bird declines (Norment 2002), low site fidelity complicates our ability to detect or accurately determine local or regional differences in population trends and results in high local variability in abundance. The influence of weather on settlement decisions can result in changes in site fidelity over time (Gorzo et al. 2016). Highly variable weather conditions are often a driver of low site fidelity in grassland birds (Price 1995, Niemuth et al. 2008). If climatic variability leads to low site fidelity, local interannual variation in relative abundance and range-wide shifts in relative abundance among years can reveal the drivers of dispersal over large spatial scales.

We studied the subspecies of Grasshopper Sparrows (*A. s. perpallidus*) living in the climatically variable grasslands of the Great Plains from the southern boundary of the boreal forests in the Canadian prairies to the Gulf Coast of Texas, and west to the Rocky Mountains (Vickery 2020). The breeding grounds of Grasshopper Sparrows in our study span five major grassland ecoregions, including tallgrass prairie, northern mixed-grass prairie, southern mixed-grass prairie, shortgrass steppe, and desert savannah (Augustine et al. 2019). Grasshopper Sparrows are a grassland songbird that habitually disperses locally within breeding seasons (Williams and Boyle 2018a), and often breeds in different areas in successive seasons (Boyle and

Sullins in review). *A. s. perpallidus* winters in the southern United States and central Mexico (Vickery 2020), and overwinter mortality is positively associated with low winter temperature (Macías-Duarte et al. 2017). Breeding Grasshopper Sparrows select grasslands where clumps of dead grasses are surrounded by short vegetation or bare ground to give them protection from predators, nesting sites, and foraging substrate (Vickery 2020), and they avoid areas with thick litter layers and more abundant vegetation (Whitmore 1981). At the Konza Prairie Biological Station in the Flint Hills of northeast Kansas, Grasshopper Sparrow return rates (from 18.4% to 39.2% per year, unpublished data), density (from 0 to 2.32 territories/ha; Winnicki et al. 2019), and abundance (20 to 100 sparrows per ~1.5km transect; Boyle 2019) varies between years, despite the fact that habitat area is consistent between years at that site. Weather conditions in the preceding year's growing season, as well as prescribed fire or grazing result in interannual variation in vegetation (Collins and Calabrese 2012). While burning and grazing are important in determining the amount and timing of vegetation growth (Knapp et al. 1999), these are largely local effects that will be evened out at the larger spatial scales ( $\geq 1000 \text{ km}^2$ ) at which weather acts.

It is difficult to study birds' large-scale movement decisions using traditional methods such as standardized surveys due to logistical constraints. Most studies take place over small enough scales that site-level characteristics can be the primary drivers (e.g., Williams and Boyle 2018), and even studies using large-scale surveys such as the Breeding Bird Survey (BBS, Sauer et al. 2013) are fairly coarse both spatially and temporally. Thus, we used citizen science data from eBird (Sullivan et al. 2009) to document the spatial patterns and scope of interannual variation in breeding distributions of Grasshopper Sparrows and relate that variation to factors associated with direct and indirect climatic drivers of settlement decisions.

We tested three hypotheses to explain how weather conditions might influence variability in local abundance of Grasshopper Sparrows during the breeding season in the Great Plains. Local abundance may be primarily driven by (1) *overwinter mortality*, as birds that die over the winter will not return to their previous breeding sites the following spring. Consequently, we predicted that as winter mean and minimum temperature decrease on the wintering grounds, so too will local abundance across the breeding range. Alternatively, local abundance could be shaped by (2) weather *during migration* affecting movement decisions, as birds may seek to minimize thermoregulatory costs. If so, we predicted that as mean and minimum temperature during spring migration decline over a given area, local abundance in that year would decline as well. Finally, local abundance could be driven by (3) the indirect effects of weather *before migration*, influencing movement decisions by affecting vegetation structure. As sparrows prefer sparse and low vegetation during the breeding season (Vickery 2020), we predicted that increased precipitation over the preceding growing season would result in lower local abundance, and that the later the start of the growing season, the lower local abundance would be.

## Methods

We studied interannual variation in breeding distribution and local abundance of Grasshopper Sparrows (*Ammodramus savannarum perpallidus*) breeding in the Great Plains of the central United States and Canada. We restricted our study to the *perpallidus* subspecies of Grasshopper Sparrows as they occur in the most climatically variable part of the breeding distribution. We selected prairie-associated Bird Conservation Regions defined by the North American Bird Conservation Initiative (NABCI 2020) encompassing the following Bird Conservation Regions:

11 (Prairie Potholes) and 17–22 (Badlands and Prairies, Shortgrass Prairie, Central Mixed Grass Prairie, Edwards Plateau, Oaks and Prairies, and Eastern Tallgrass Prairie, respectively). We restricted our study to only include *A. s. perpallidus* by excluding the eastern states of Illinois, Wisconsin, Indiana, Michigan, and Ohio, where *A. s. pratensis* breeds (Vickery 2020, Figure 2-1). We overlaid a grid of 100 km x 100 km cells on the study region. We chose this spatial extent because for precipitation, ~100 km is approximately the distance at which there is more difference between sites than within a site. Thus, minimizing the spatial autocorrelation of data aggregated at this spatial scale (Augustine 2010).

We obtained location-specific data on Grasshopper Sparrow abundance from eBird (<https://www.ebird.org>), a citizen science database of bird observations (Sullivan et al. 2009) launched in 2002. We limited our study to ‘complete’ checklists consisting of counts of all individual birds an observer could identify, submitted by observers from within the study region. We used data from within the sparrows’ primary breeding season (1 May–31 Jul) in 2008–2019, as data were too sparse prior to 2008 in the region. We accounted for potential spatial bias by including several effort covariates in our models (Hochachka et al. 2019, Johnston et al. 2020). First, we calculated the number of eBird hotspots (popular birding locations in an area) with 10 or more checklists in each cell, as birders may be drawn to popular hotspots, which we assume would increase the effort and number of sparrows reported. If sparrows were abundant at those hotspots, we may over-estimate sparrow abundance for that area or conversely, if birders were drawn to hotspots where sparrows were scarce. We included the total number of unique observers that reported sightings in each cell for each year, and the total number of checklists submitted within each cell for each year to account for the fact that each of these have increased as eBird has become more popular (Zhang 2020). Finally, we accounted for the proportion of

developed land (areas containing  $\geq 30\%$  human-constructed materials) within each cell using data from the NLCD (Yang et al. 2018) to account for the fact that eBird checklists are more commonly submitted near cities and roads.

We first sought to test the hypothesis that variation in local abundance is driven by overwinter mortality. We obtained temperature data from the Climate Prediction Center's (CPC) Global Daily Temperature dataset, from NOAA's Physical Sciences Laboratory, an interpolated dataset of temperature data from gauges across the world gridded using the Shepard Algorithm (Fan and van den Dool 2008). The winter distribution of *A. s. perpallidus* is not well known and made uncertain because of overlap with wintering *A. s. pratensis* and resident *A. s. ammolegus* in Mexico and the southwestern United States (Hill and Renfrew 2019, Vickery 2020). To minimize the inclusion of *A. s. pratensis* which is thought to predominantly winter farther east (Vickery 2020), we bounded the winter distribution to areas west of the Texas-Louisiana border. To minimize resident subspecies of southern Mexico, we only included potential wintering areas north of the central volcanic belt of central Mexico. To minimize resident subspecies to the western United States and Mexico, we bounded our study to areas east and south of the northwestern-most observation submitted to eBird over the winter (1 Dec–28 Feb). This resulted in a bounding box at (longitude:  $-14.7531$ ,  $-93.53536$ , latitude:  $23$ ,  $32.66821$ ). We extracted temperature data only from areas covered in grassland or shrublands corresponding to habitats used by sparrows in winter using data from the NLCD (Yang et al. 2018). The final wintering range we used for our calculations is displayed in Figure 2-1. We calculated the mean and minimum daily temperature across the winter range for each winter (1 Dec–28 Feb).

To test the hypothesis that weather influences sparrows' settlement decisions indirectly via changes in vegetation, we first tested the prediction that precipitation in the preceding year's



growing season would influence abundance. We obtained precipitation data from the Climate Prediction Center's Global Unified Gauge-Based Analysis of Daily Precipitation dataset from NOAA's Physical Sciences Laboratory (Higgins et al. 2000). We used the sum total precipitation from the preceding year's growing season (1 May–31 Sep) as one of our predictor variables in statistical models. We also predicted that an earlier start to the growing season in a given year would lead to an increase in local abundance. In temperate regions, the “climatological growing season”, or the period in between the last spring frost and the first fall frost, can vary in timing between years and is becoming longer in many parts of the world (Walther et al. 2002). Spring frosts, if they occur after aboveground growth begins, can kill buds and set back growth (Rigby and Porporato 2008). Therefore, we used the date of last frost as a proxy for the start date of the growing season as our other predictor.

If sparrows made settlement decisions based on minimizing thermoregulatory costs, we predicted that fewer birds would select local breeding sites when temperatures during migration were lower. While sparrows migrate from March–May, the peak of their spring migration is in April (Vickery 2020). We calculated mean and minimum temperature in each cell during April using the CPC's daily temperature dataset for each year of the study. We used both mean and minimum because the mean value best represents the conditions sparrows would need to endure for long periods of time, and the minimum value best represents more acute thermoregulatory stress.

We conducted all analyses in R (R Core Development Team 2013). We created raster layers for all data sources for each year using package '*raster*' (Etten et al. 2019). We rasterized the sum total count of sparrows observed within each cell in the 10000 km<sup>2</sup> grid using the function '*rasterize*'. We calculated the sum of the preceding year's precipitation, the mean of all

local mean daily temperatures, the mean start date of the growing season, and the minimum of all local minimum daily temperatures within each cell. We reprojected all data to the Albers Equal Area projection to ensure all cells had the same resolution across latitudes (Snyder 1988). To determine the extent of interannual variation in breeding distribution, we determined the centroid of the breeding distribution for each year by multiplying the centroid of each individual cell by a raster of weighted predicted values to obtain a single weighted centroid per year. We used the ‘*spDists*’ function from package ‘*sp*’ (Bivand et al. 2013) to calculate the distance the centroid moved from one year to the next. We evaluated the predicted relationships between weather and local abundance (at a 10000 km<sup>2</sup> resolution) using species distribution models. We fit Generalized Additive Models (GAMs) using package ‘*mgcv*’ (Wood 2017) with a negative binomial distribution, as GAMs can capture both linear and non-linear effects. As our goal was to determine which climatic variables most strongly influence local abundance, our response variable was the total count of Grasshopper Sparrows within each cell. We accounted for spatial autocorrelation by including latitude and longitude in models. The predictions of the three alternative hypotheses were embodied in three models. First, we tested whether overwinter mortality most influences local abundance by including (1) the mean and minimum temperatures on the wintering grounds in Dec–Feb of the preceding winter. Second, we tested whether climatic variability most influences local abundance directly by including (2) the mean and minimum temperatures in April (the peak of *A. s. perpallidus*’ migration). Third, we tested whether climatic variability influences local abundance indirectly via vegetation by including (3) total precipitation in the preceding growing season and the start date of the current year’s growing season. In each model, we included the covariates aimed at minimizing spatial variation in observer effort (proportion of developed land, number of observers, number of checklists,

number of hotspots). We included a categorical year term in all models and compared model fit using Akaike's Information Criterion (AIC).

## Results

We obtained 26,965 checklists submitted to eBird from 2008 to 2019 that included 85,229 individual Grasshopper Sparrows sightings within the Great Plains. The number of checklists that reported observations of Grasshopper Sparrows increased over the 11 years of the study from 413 checklists in 2008 to 4767 in 2018, corresponding to eBird becoming more widely adopted. On average, 7,748 (SE = 21) sparrows were observed per year. *A. s. perpallidus*' breeding distribution differed among years, with the general locations of high bird densities remaining consistent, but the densities within those areas varying among years (Figure 2-2). The net effect of that variation was that the centroid of the breeding distribution moved up to 87 km between years (Figure 2-3) in different directions.

The local abundance of breeding Grasshopper Sparrows was best explained by the preceding year's precipitation and the start date of the growing season (Table 1). This top model explained 49.1% of the deviance in the data, compared to ~48% for the other two models, and the  $\Delta$ AIC values for the other two models were 483 and 488. Within this model, the start date of the growing season better predicted local abundance than the preceding year's precipitation (growing season  $P$ -value = 0.002, precipitation  $P$ -value = 0.66). The more rain that fell the previous growing season, the fewer Grasshopper Sparrows counted by observers in that year (Figure 2-4). The start date of the growing season was associated with sparrow abundance nonlinearly; local abundance was depressed when the growing season began between day 60 and day 120 (early March–late April) and higher when the growing began before day 70 (Figure 2-4).

## Discussion

Sparrows made settlement decisions that resulted in an interannually variable breeding distribution. In addition, although the locations of the breeding hotspots (the 10000 km<sup>2</sup> cells with the highest density of sparrows during the breeding season) were similar each year, these were likely constrained by the very limited availability of extant grassland (Augustine et al. 2019). In addition, the predicted abundance of sparrows within these hotspots differed among years (Figure 2-3). Importantly, while both of these metrics of variation in breeding distribution differed among years, neither changed directionally, suggesting that sparrows' settlement decisions track habitat suitability from year to year. Sparrows' settlement decisions were correlated with weather, with the precipitation during the previous growing season and the start date of the growing season best explaining local abundance. Although the difference in the deviance explained by the top model and the other models was only 0.5%, we had a large dataset, meaning that small percentages translate into biologically meaningful differences in abundances between localities between years. Because both of these climatic variables operate at times when sparrows are not selecting habitat, both likely influence sparrows indirectly via vegetation growth. Therefore, birds' settlement decisions being driven primarily through vegetation (and, indirectly, weather) rather than prior nest success as in other systems (Schlossberg 2009).

Our results were not consistent with either of our other hypotheses, that settlement decisions would be driven by overwinter mortality or by climatic conditions during migration. First, sparrows' settlement decisions were not driven by overwinter mortality, and this is consistent with our observations at a local site, Konza Prairie, in northeastern Kansas. We have

observed birds which bred at Konza in a given year, were not present the following year, and bred at Konza again the year after that (unpublished data), which suggests that birds are choosing to breed elsewhere, rather than dying over the winter. Second, climatic conditions during migration did not drive settlement decisions. The mean April temperatures we observed (11.03 °C, SE = 0.05) was only slightly lower than that of the mean winter temperatures (14.68 °C, SE = 0.02), so it is possible that sparrows were already acclimated to these conditions before migration. It is also possible that the energetic costs of moving far enough to encounter warmer temperatures simply outweighs the cost of remaining where they already are.

By using data from eBird, we took advantage of an unprecedented dataset that allows researchers to answer questions on a larger and finer scale than was previously possible. Because these data can be collected anytime, anywhere, and by anyone, the spatial coverage is impressive and the dataset is larger than others available in North America (Callaghan et al. 2018). However, there are a few caveats important to consider when interpreting results using eBird data. Most importantly, eBird data are subject to spatial biases, e.g., birders tend to go birding more often nearer to cities or roads, and tend to go birding more often in popular birding locations. However, by controlling for these biases by limiting which data we used and by including effort covariates in our models (Johnston et al. 2020, Zhang 2020), our results are comparable to other sources such as the Breeding Bird Survey (Rosenberg et al. 2017) or satellite tracking (Munson et al. 2010, Walker and Taylor 2017, 2020). For studies like ours in which we are primarily interested in fine scale, interannual differences in the abundance of breeding birds, the spatial and temporal coverage of eBird data is critical.

Our results are consistent with grassland birds' settlement decisions and site fidelity being driven by vegetation structure and phenology, as in a highly variable system defaulting to a

previously successful breeding location is unreliable. The overall structure of a grassland can change substantially between years (White et al. 2019), much more so than in more stable systems such as forests, so the same strategies used in forests (e.g., high site fidelity) do not work in more variable grasslands. Because vegetation in a given year is largely determined by weather conditions in the preceding year in grasslands (Fischer et al. 2020), weather patterns in the preceding year have a stronger effect on settlement decisions than weather conditions during migration. The importance of the preceding year's weather means that there is a delay in the behavioral response to climatic variability, which complicates and can make more difficult observing the link between the two. At a minimum, to understand where birds such as *A. s. perpallidus* will breed in a given year, one must know what climatic conditions were like the year before and how this could influence vegetation growth.

One way in which grassland birds and likely other grassland animal taxa have adapted to living in a climatically variable environment is by responding behaviorally via flexible movement strategies (Bateman et al. 2015, Williams and Boyle 2018). Such behavioral flexibility will likely leave them well-equipped to cope with anthropogenic climate change. The Great Plains, along with many ecosystems worldwide, are projected to face several climatic changes over the next several decades (IPCC 2012). For example, the number of frost-free days is projected to increase in the Great Plains (especially in the northern Great Plains), lengthening the growing season (IPCC 2012). In addition, changes in precipitation are projected to vary across the Great Plains, with generally less rain in the southern regions and more in the north (IPCC 2012). Both of these changes could alter the structure and phenology of vegetation, and our results suggest that this may result in a corresponding change in where grassland birds decide to breed. Previous studies have suggested that some mobile grassland taxa (including birds) are

especially sensitive to climate change (Skagen and Adams 2012, Jarzyna et al. 2016, Wilsey et al. 2019). However, critically for many such studies the observed response was an increase in local extinctions or range shifts, which in mobile species could simply mean that they moved elsewhere. If dispersal is an adaptive response to climatic variability (Travis et al. 2013), local extinctions and range shifts do not necessarily indicate that grassland birds are more vulnerable to climate change, but rather the opposite. The alternative interpretation provides hope that these organisms will be able to adapt and overcome climate change as long as they have somewhere to go. Properly managing land by maintaining disturbances such as fire throughout these organisms' range will increase the likelihood that there are places that are available to these organisms as conditions continue to change.

## Tables

**Table 2-1. Model selection table.<sup>1</sup>**

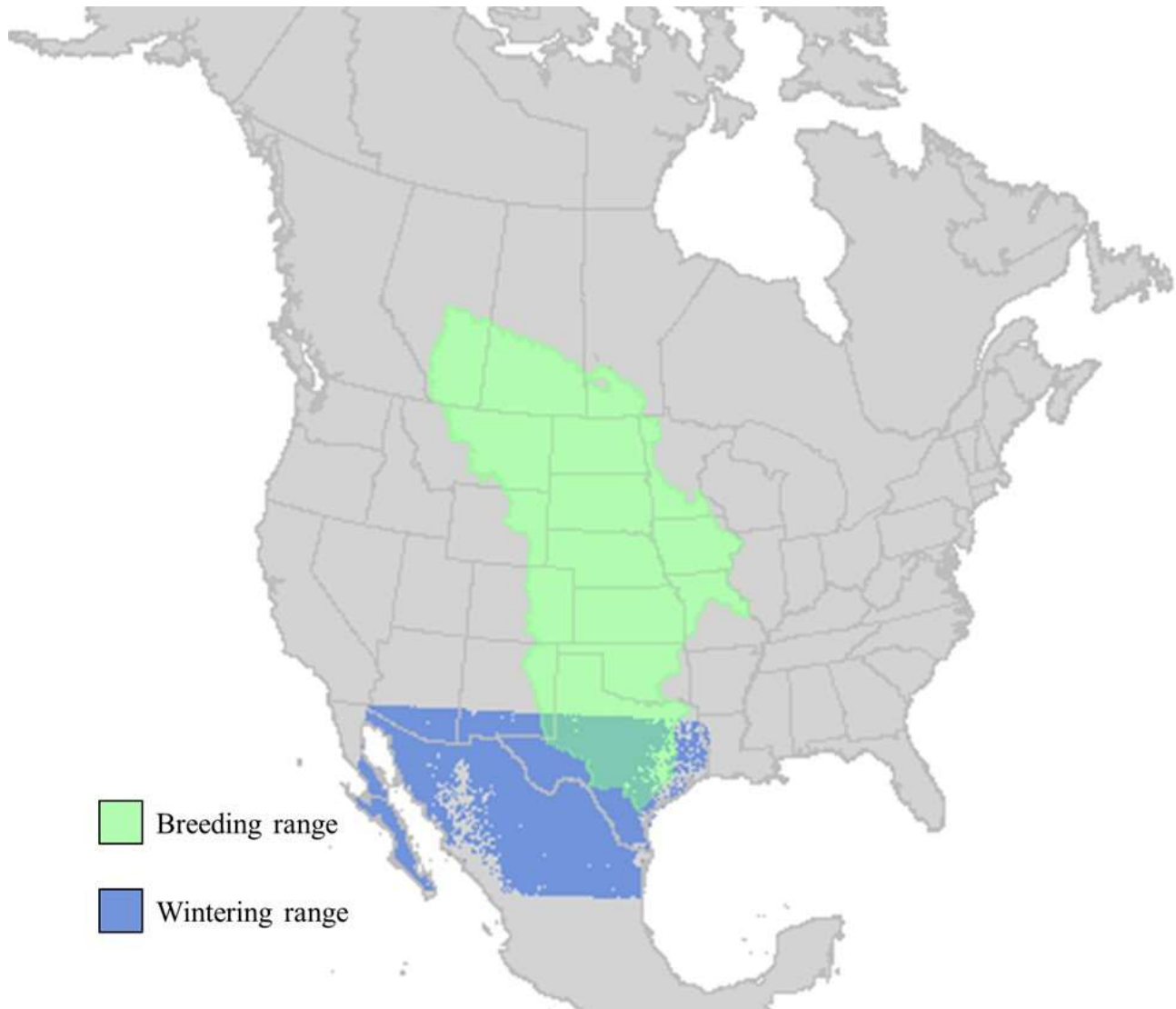
Predictor variables	df	Deviance explained	AIC	$\Delta$ AIC
f(precipitation) + f(start of growing season)	69	49.1%	14395	0
f(mean) + f(min) April temperature	67	48.6%	14878	483
f(mean) + f(min) winter temperature	58	48.0%	14883	488

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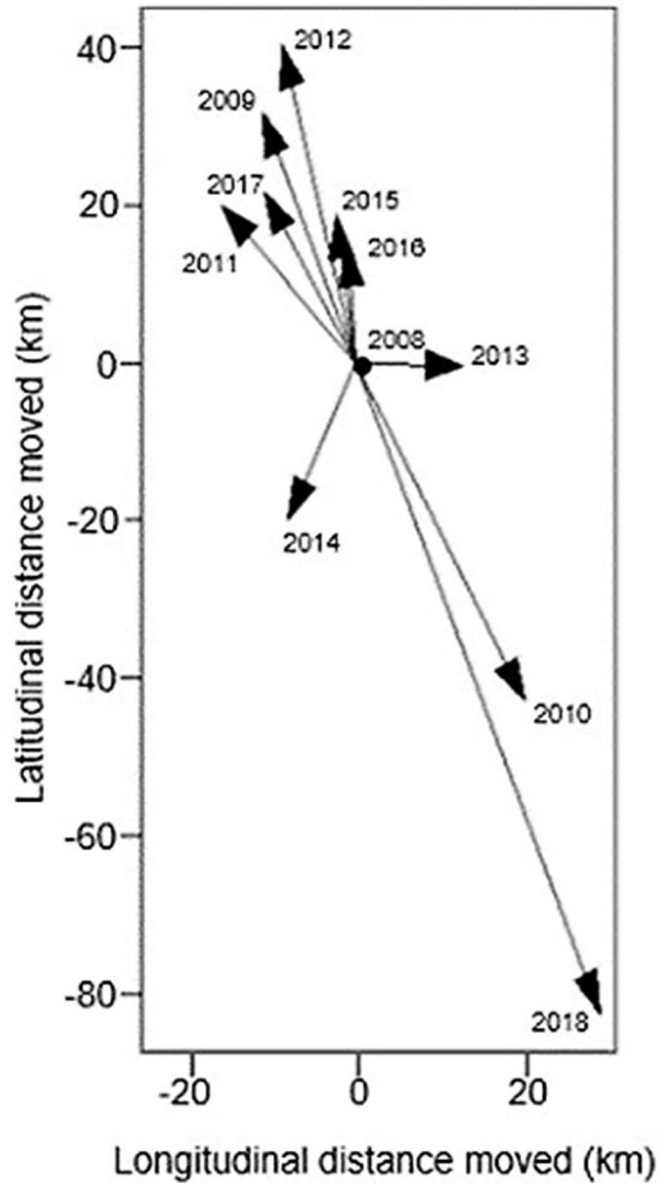
<sup>1</sup>Response variable for all models was count within each cell, and all models included several effort covariates: Year + Number of observers within cell + Number of checklists within cell + f(Proportion of developed land within cell) + Number of eBird hotspots within cell + f(Latitude and longitude of the cell). Several of the effort covariates, as well as the predictor variables of interest, were fit to splines to represent the full variability in the response; these are designated with an “f” before the variable name.



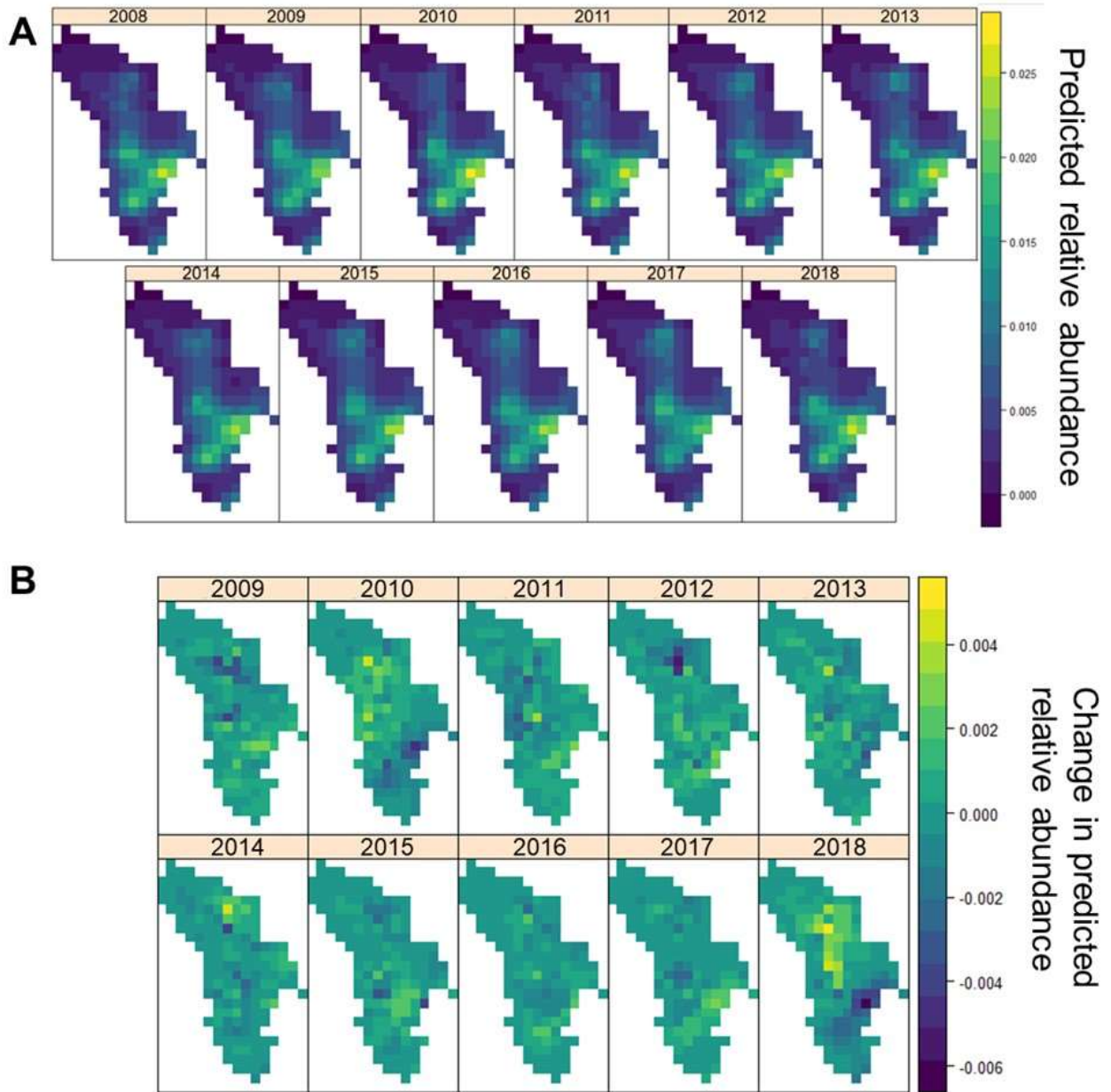
## Figures



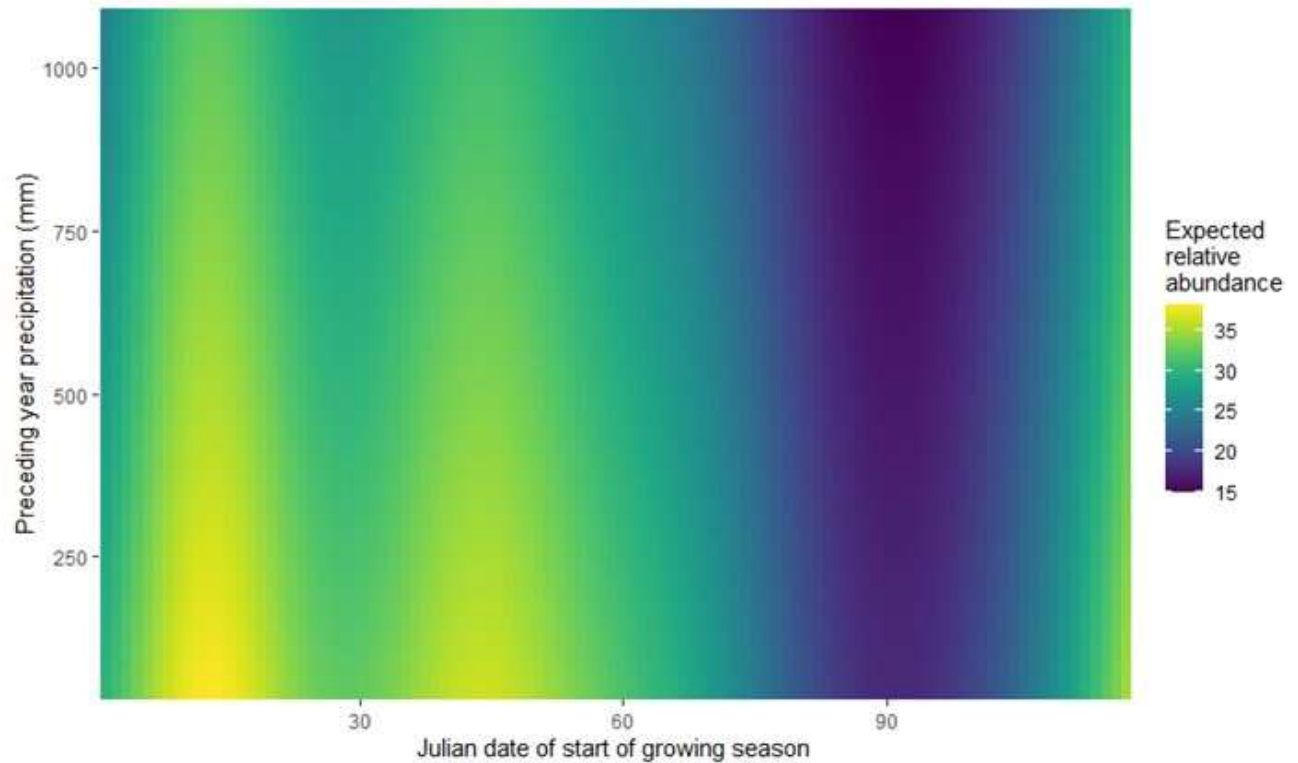
**Figure 2-1. Map of the study area within North America including the Great Plains portion of the breeding range (in green) and wintering range (blue). The breeding range represents portions of Bird Conservation Regions 11 and 17–22 (NABCI 2020) lying outside of Illinois, Wisconsin, Indiana, Michigan, and Ohio to limit to the *perpallidus* subspecies of Grasshopper Sparrow. The wintering range includes grasslands and shrublands (from National Landcover Database, Yang et al. 2018), limited to areas within the bounding box from longitude:  $-114.7531$ ,  $-93.53536$ , latitude:  $23$ ,  $32.66821$  to exclude migratory *pratensis* sparrows to the east, resident *ammolgeus* sparrows to the west and other resident subspecies to the south.**



**Figure 2-2. Distance and direction (indicated by the length and bearing of each arrow, respectively) moved by the centroid of the Grasshopper Sparrow breeding distribution from one year to the next. The centroid moved an average of 32.7 km (SE = 0.047) per year.**



**Figure 2-3. Maps showing predicted relative abundance (panel A) and change in relative abundance (panel B) within each of our 1000 km<sup>2</sup> cells. In panel A, darker blue colors represent lower predicted abundance, while brighter yellow colors represent higher predicted abundance. Notably, the predicted relative abundance varies among years, even within the hotspots of predicted abundance (the most yellow areas). This can be more clearly seen in panel B, where darker blue colors represent decreases in relative abundance from the year before, and brighter yellow colors represent increases. Note that there is no map for 2008 in panel B, as we cannot estimate change from the year before the first year in the study.**



**Figure 2-4. The correlation between start of growing season, the preceding year’s precipitation, and abundance in our top model. Bluer colors represent lower expected relative abundance, while more yellow colors represent higher expected relative abundance. Relative abundance was highest when the Julian start day of the growing season (date of last frost) came before day 60 (either 29 Feb or 1 Mar, depending on whether or not it was a leap year), and when the less rain fell during the preceding year’s growing season.**

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## Appendix A – Chapter 1 Supplementary Material

**Table A-1. Complete summaries for all models other than vegetation models. If there was not adequate data for a given category for a given response, that category is omitted. Asterisks denote  $P < 0.05$ .**

Model	Response	Category	$\beta$ -estimate	Std. Error	$z$ -value	$P$ -value
<b>Year</b>						
	<i>Clutch size</i>		0.002	0.001	1.60	0.109
	<i>N eggs hatched</i>		0.004	0.003	1.33	0.182
	<i>N young fledged</i>		0.007	0.006	1.11	0.265
	<i>Parasitism frequency</i>		0.017	0.005	3.08	0.002 *
	<i>Parasitism intensity</i>		-0.001	0.002	-0.59	0.553
	<i>Complete predation</i>		0.006	0.005	1.13	0.259
<b>Year * population trend</b>						
	<i>Clutch size</i>					
		<i>decreasing</i>	0.006	0.007	0.91	0.362
		<i>increasing</i>	0.004	0.007	0.58	0.560
	<i>N eggs hatched</i>					
		<i>decreasing</i>	0.040	0.018	2.20	0.028 *
		<i>increasing</i>	0.040	0.018	2.21	0.027 *
	<i>N young fledged</i>					
		<i>decreasing</i>	0.044	0.047	0.93	0.351
		<i>increasing</i>	0.021	0.046	0.47	0.640
	<i>Parasitism frequency</i>					
		<i>decreasing</i>	-0.127	0.062	-2.04	0.041 *
		<i>increasing</i>	-0.082	0.062	-1.34	0.182
	<i>Parasitism intensity</i>					
		<i>decreasing</i>	-0.038	0.031	-1.21	0.227
		<i>increasing</i>	-0.024	0.031	-0.77	0.442
	<i>Complete predation</i>					
		<i>decreasing</i>	-0.039	0.025	-1.59	0.113
		<i>increasing</i>	-0.033	0.024	0.18	0.179
<b>Year * breeding habitat</b>						
	<i>Clutch size</i>					

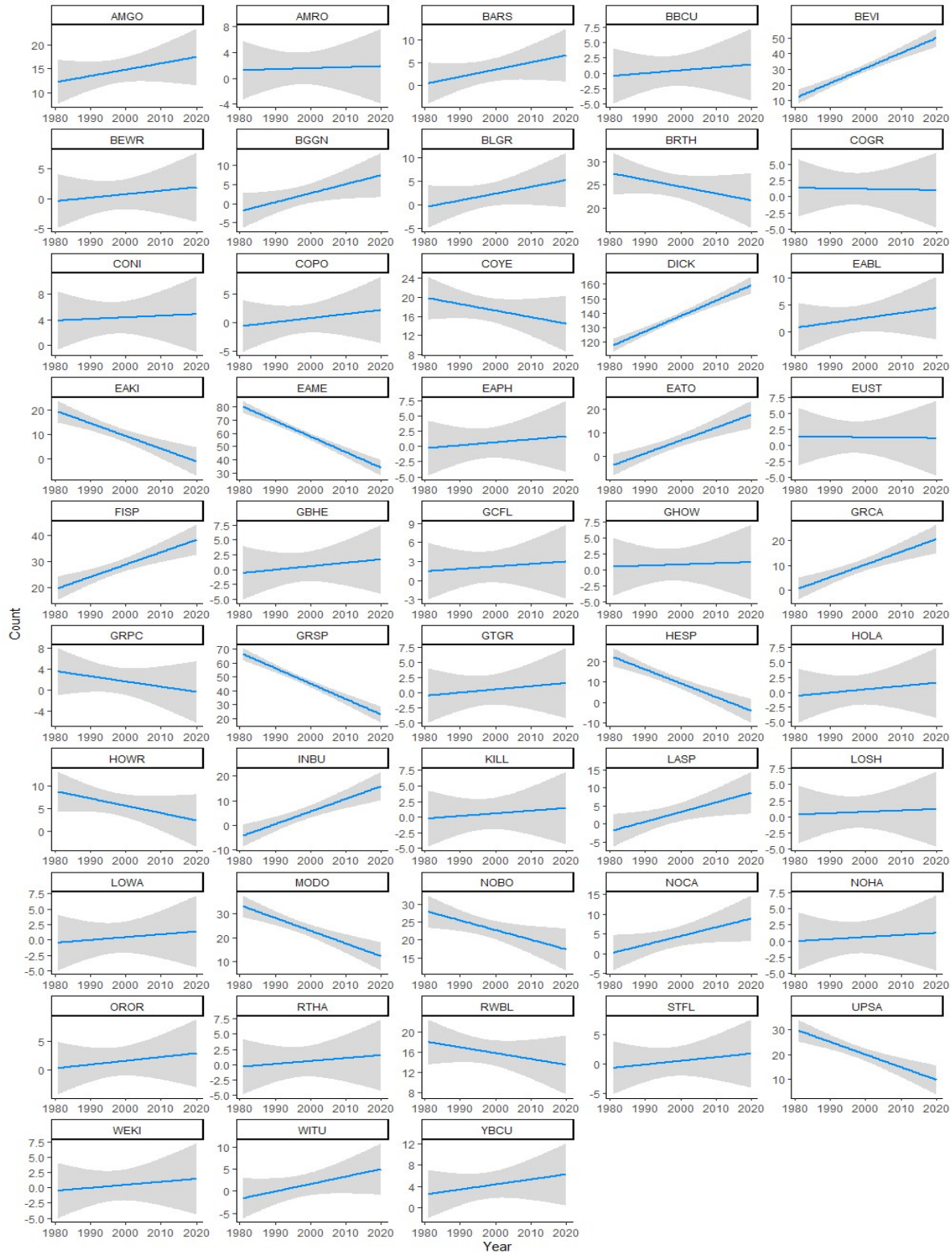
	<i>forests</i>	0.026	0.015	1.67	0.095
	<i>generalist</i>	0.017	0.015	1.10	0.273
	<i>grasslands</i>	0.015	0.014	1.03	0.303
<hr/>					
<i>N eggs hatched</i>					
	<i>forests</i>	0.082	0.034	2.43	0.015 *
	<i>generalist</i>	0.071	0.032	2.24	0.025 *
	<i>grasslands</i>	0.073	0.030	2.44	0.015 *
<hr/>					
<i>N young fledged</i>					
	<i>forests</i>	0.376	0.174	2.17	0.030 *
	<i>generalist</i>	0.241	0.168	1.43	0.153
	<i>grasslands</i>	0.248	0.167	1.48	0.139
<hr/>					
<i>Parasitism frequency</i>					
	<i>forests</i>	0.128	0.073	1.76	0.079
	<i>generalist</i>	0.047	0.067	0.71	0.481
	<i>grasslands</i>	0.063	0.062	1.01	0.313
<hr/>					
<i>Parasitism intensity</i>					
	<i>forests</i>	0.072	0.040	1.78	0.076
	<i>generalist</i>	-0.019	0.033	-0.57	0.571
	<i>grasslands</i>	0.009	0.029	0.33	0.739
<hr/>					
<i>Complete predation</i>					
	<i>forests</i>	-0.243	0.097	-2.50	0.012 *
	<i>generalist</i>	-0.251	0.083	-3.04	0.002 *
	<i>grasslands</i>	-0.270	0.082	-3.31	0.001 *
<hr/>					
Year * nest substrate					
<i>Clutch size</i>					
	<i>building</i>	-0.006	0.016	-0.39	0.698
	<i>cavity</i>	0.035	0.025	1.38	0.168
	<i>ground</i>	0.002	0.003	0.75	0.452
	<i>tree</i>	-0.026	0.015	-1.78	0.075
<hr/>					
<i>N eggs hatched</i>					
	<i>building</i>	0.009	0.068	0.14	0.889
	<i>cavity</i>	-2.245	0.021	-0.01	0.992
	<i>ground</i>	-0.002	0.007	-0.24	0.810



	<i>tree</i>	0.012	0.003	0.38	0.707	
<hr/>						
<i>N young fledged</i>						
	<i>ground</i>	0.014	0.014	0.99	0.318	
<hr/>						
<i>Parasitism frequency</i>						
	<i>ground</i>	-0.043	0.012	-3.73	< 0.001 *	
<hr/>						
<i>Parasitism intensity</i>						
	<i>ground</i>	-0.013	0.006	-2.20	0.028 *	
<hr/>						
<i>Complete predation</i>						
	<i>ground</i>	-0.007	0.011	-0.67	0.506	
	<i>tree</i>	-0.397	0.262	-1.52	0.129	
<hr/>						
Year * partial predation						
	<i>Clutch size</i>	<i>predation=TRUE</i>	0.003	0.003	0.85	0.396
<hr/>						
	<i>N eggs hatched</i>	<i>predation=TRUE</i>	0.003	0.008	0.42	0.675
<hr/>						
	<i>N young fledged</i>	<i>predation=TRUE</i>	0.005	0.012	0.42	0.674
<hr/>						
	<i>Parasitism frequency</i>	<i>predation=TRUE</i>	0.017	0.018	0.96	0.336
<hr/>						
	<i>Parasitism intensity</i>	<i>predation=TRUE</i>	0.000	0.007	0.05	0.961
<hr/>						

**Table A-2. Complete model summaries for vegetation models. Summaries obtained using ANOVAs with Type III Sums of Squares, as there are multiple explanatory variables in each model. Asterisks denote  $P < 0.05$ .**

Model	Response	Parameter	$X^2$	df	$P$ -value
Year + day of year + years since grazed + years since burned					
<i>Clutch size</i>					
		<i>day of year</i>	64.50	1	< 0.001 *
		<i>years since grazed</i>	3.82	1	0.051
		<i>years since burned</i>	1.46	1	0.227
<i>N eggs hatched</i>					
		<i>day of year</i>	10.08	1	0.001 *
		<i>years since grazed</i>	8.27	1	0.004 *
		<i>years since burned</i>	0.15	1	0.699
<i>N young fledged</i>					
		<i>day of year</i>	5.96	1	0.015 *
		<i>years since grazed</i>	0.74	1	0.389
		<i>years since burned</i>	0.67	1	0.412
<i>Parasitism frequency</i>					
		<i>day of year</i>	68.69	1	< 0.001 *
		<i>years since grazed</i>	14.20	1	< 0.001 *
		<i>years since burned</i>	21.77	1	< 0.001 *
<i>Parasitism intensity</i>					
		<i>day of year</i>	35.83	1	< 0.001 *
		<i>years since grazed</i>	37.07	1	< 0.001 *
		<i>years since burned</i>	1.81	1	0.178
<i>Complete predation</i>					
		<i>day of year</i>	0.003	1	0.003 *
		<i>years since grazed</i>	7.050	1	0.008 *
		<i>years since burned</i>	2.710	1	0.099



**Figure A-1. Predicted change in abundance from 1981–2020 for all 48 species in the study (designated by four-letter alpha codes, Pyle and DeSante 2009). Confidence bands represent 95% Wald confidence intervals. Y-axes are transformed to the scale of the response.**