Under the weather: mechanisms underlying avian responses to precipitation

by

Katherine MM Silber

B.S., University of Vermont, 2015

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

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Abstract

The goal of this dissertation is to understand how and why bird populations respond to precipitation. Bird responses to precipitation have been reported from most biomes, but the nature of those responses and vital rates affected differ among studies, hindering mechanistic understanding of links between demography and the environment. I combined intensive field studies in the mid-continental grasslands of the USA with a meta-analysis of responses to precipitation globally to elucidate mechanisms underlying responses. I first synthesized published evidence to test if life history traits or habitat characteristics mediate relationships between precipitation and reproductive success. Birds living at high elevations or having young requiring substantial parental care respond more negatively to precipitation than birds with other distributions or life histories, implicating both life history traits and habitat characteristics in mediating avian responses to precipitation. I then focused on a broader suite of vital rates in Grasshopper Sparrows, a grassland songbird in steep decline, that exhibits altricial development and experiences high variability in annual precipitation. Using a 10-year field-collected dataset of mark-resight and nesting data from the Konza Prairie in NE Kansas, I found that population growth rate was most sensitive to fluctuations in adult apparent survival (i.e. true survival and site fidelity) than other life stages. Under future precipitation regimes, my projections predict the population will likely be extirpated in the next 100 years. Given the importance of precipitation, survival, and movement in the dynamics of this population, I used mark-resight data of 1,332 territorial male Grasshopper Sparrows between 2013-2020 at the Konza Prairie to test the alternative drivers of inter-annual variability in survival and emigration. While survival was shaped by winter precipitation, emigration was shaped by 2-year lagged breeding season precipitation, and changes in the number of territorial males at a breeding site each year could be more strongly attributed to movement than mortality. Lagged responses suggested that relationships between precipitation and emigration are likely mediated by vegetation structure. Finally, I tested alternative explanations for the relationship between emigration and precipitation by determining the factors that drive settlement decisions. I paired mark-resight data from three grassland songbirds at the Konza Prairie with vegetation and topography data. Vegetation varied with land management and precipitation up to two years prior, consistent with links between precipitation and movement decisions. Birds selected territories on flat areas based on species-specific vegetation attributes, but all avoided woody vegetation cover. The simulated removal of isolated trees improved grassland songbird habitat by over 14 hectares. These results provide specific and achievable conservation recommendations with substantial impacts on declining grassland songbirds. At a local level, this dissertation provides a comprehensive explanation for how and why local variation in abundance of grassland bird occurs, and on a global scale, it helps explain why rain leads to divergent responses in species living in different regions and with different life histories.

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Approved by:

Major Professor
Dr. W. Alice Boyle

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Dedication

This work is dedicated to my grandmother, Margaret Cutler, who exudes unparalleled wit, intelligence, curiosity, and kindness.

Chapter 1 - Introduction

Precipitation and temperature are the primary drivers of climatic variation. They define biomes (Holdridge 1967, Jiang et al. 2017), dictate seasonality (Knoben et al. 2019), and generate regional climate (Nadeau et al. 2017), ultimately driving community changes via interspecific interactions (Louthan et al. 2013), relative abundance (Stampfli and Zeiter 2004), and range limits (Smith 2013). However, the impacts of weather on animal populations can be difficult to determine given the nonlinear responses to climatic variables on populations across their ranges (Boyle et al. 2020, Louthan and Morris 2021) and divergent effects of weather on specific vital rates (Kanno et al. 2015) or life stages (Burant et al. 2022).

The range of conditions under which an organism can persist defines its abiotic niche, but near the edge of that niche, negative individual consequences are thought to scale up to reduce vital rates and limit populations (Anigletta 2009, Boyle et al. 2020). In endotherms, relationships between temperature and populations are relatively well studied; temperature physiologically limits individuals near critical thresholds, which ultimately shapes population persistence and species distributions (Smith 2013, McKechnie and Wolf 2019). However, we know less about how and why precipitation affects endotherm populations. Birds are ideal systems for studying the effects and mechanisms underlying responses to precipitation because they have external development, inherently linking their reproduction to environmental conditions, and they are mobile, allowing researchers to study the effects of precipitation on dispersal as well as survival and reproduction. This dissertation tackles existing gaps in knowledge via four mechanistic studies that collectively illustrate the nature of bird responses to precipitation across species and biomes and identify mechanisms underlying these responses.

Many plausible explanations exist for the direct and indirect effects precipitation may have on bird populations, with different implications for individual life stages or vital rates. Eggs and nestlings must be within a species-specific spectrum of environmental conditions to properly develop (Martin et al. 2007) and are stationary throughout development, making them prone to depredation, parasites, and flooding. Precipitation may have a myriad of effects on one nest (e.g., Scholl and Hille 2020) given the potential direct and indirect mechanisms, making it difficult to predict precipitation's net effect. Birds exhibit many strategies to mitigate the effects of environmental conditions on their young; nest parents may select specific nest locations or orientations (With and Webb 1993, Lockwood et al. 2001), construct concealed nests to protect their young (Grant et al. 2017), or actively defend their nest (Gottfried et al. 1979). Once young leave the nest, post-fledge movements are often associated with rainfall-mediated vegetation structure (Suedkamp Wells et al. 2008) and prey availability (Wiens et al. 2006).

Precipitation may indirectly affect adult or young survival through changes in food availability, predation risk, and vegetation structure (Ockendon et al. 2014, Deguines et al. 2017) with varying responses across biomes (Renton et al. 2004, Cox et al. 2020) and elevational gradients (Boyle et al. 2020). Changes in prey abundance, mediated by precipitation, can have consequent effects on adult survival (Frederiksen et al. 2008) and fecundity (Illera and Diaz 2006, Fisher et al. 2015). These changes can track through trophic levels, affecting predation risk (Rodewald and Yahner 2001), brood parasitism (Colon et al. 2017), or ectoparasites (Dudaniec et al. 2007). Simultaneously, precipitation can shape aboveground plant biomass and structure, therefore providing refugia (Lewis Najev et al. 2019), altering prey availability (Wade et al. 2017), or reducing predation risk (Klug et al. 2010). Indirect relationships between precipitation and animal populations may become increasingly complex with higher trophic level species and operate over longer time scales than direct effects (Deguines et al. 2017).

Alternatively, precipitation can also lead to thermoregulatory challenges or other direct consequences for birds. Rainier conditions can decrease survival in adults and young by increasing the costs of thermoregulation and homeothermy (McKechnie and Wolf 2019). Endotherms may be more susceptible to precipitation during energy-intensive activities, like migration (Halupka et al. 2017) or reproduction (Conrey et al. 2016), or periods of extreme weather (e.g., storms; Martin et al. 2017), ultimately leading to severe energy deficits and lower survival. Young birds may incur high thermogenic costs when wet if they have not developed enough body mass (Lomas and Bender 2007, Mikkelsen et al. 2021) or feathers (Butler et al. 2008).

Birds use environmental cues to track weather-mediated resources, like food (Both et al. 2010), and evade areas with high risk of predation (Hakkarainen et al. 2001). In migratory species, individuals make seasonal movements based on the phenology or quality of these resources, while sometimes incurring extreme physiological costs (William et al. 1983, Battley et al. 2000). Because migrants spend time in different locations throughout their annual cycles, specific vital rates may be sensitive to conditions at certain periods or locations (Wilson et al. 2011). For example, adult apparent survival may decrease in response to winter weather but not summer weather (Hill et al. 2019). Although most migrants are highly site-faithful (Winger et al. 2018), some birds also make one-way dispersal movements within or between seasons, commonly thought to function in seeking prey or avoiding predators (Powell and Frasch 2000, Steenhof et al. 2005).

Bird populations exhibit multiple, divergent responses to precipitation across taxa, biomes, temporal scales, and levels of biological organization. There is a lack of consensus on the relative importance of precipitation and the mechanisms underlying such relationships. Some studies report variation in community responses to precipitation at a given site (Rotenberry and Wiens 1991, Eeva et al. 2020, McGowan et al. 2021, Wheelwright et al. 2022), or within-species responses across sites (Peery et al. 2012) or at different times throughout the annual or nesting cycle (Moynahan et al. 2007, Skagen and Adams 2012, Beck et al. 2015, Descamps et al. 2015, Eggers et al. 2015, Zuckerberg et al. 2018, Murphy et al. 2020, Capilla-Lasheras et al. 2021).

Understanding the nature and mechanistic basis of responses in grasslands is critical from both basic and applied perspectives. Grassland weather is highly variable (Augustine 2010), which interacts with management (e.g., fire and grazing) to create patchy landscapes (Blair et al. 2014). Plant composition changes over relatively fine scales (Koerner & Collins 2013), and at least some birds can respond by altering their dispersal and settlement decisions to track conditions that presumably increase their survival and reproduction (Kentie et al 2014). Grassland birds apparently exhibit a higher propensity for breeding dispersal than most migratory birds, likely in response to the high degree of variability in grassland systems (Switzer 1993); 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). Site fidelity may not be advantageous in grassland systems that have frequent weather-mediated changes in vegetation structure, in combination with habitat loss that may eliminate previously viable breeding grounds. About 90% of Great Plains tallgrass prairie has been converted to urban or agricultural areas (White et al. 2000), leading to declines in almost 75% of North American grassland bird species since 1970 (Rosenberg et al. 2020). These declines present an urgent need to understand the mechanisms underlying fluctuations in grassland bird populations in the context of current and future precipitation variability to direct effective conservation actions. It also provides an opportunity to identify the behavioral and life history constraints underlying responses to precipitation.

The goal of this dissertation is to understand why and how bird populations respond to precipitation. In my second chapter, I synthesized literature on bird responses to precipitation globally and conducted a meta-analysis to distinguish between alternative mechanisms underlying bird responses to precipitation. I then focused on a broader suite of vital rates in Grasshopper Sparrows, a grassland songbird in steep decline, using a 10-year field-collected dataset of mark-resight and nesting data from the Konza Prairie in NE Kansas. In my third chapter, I tested alternative explanations for mechanisms underlying fluctuations in vital rates and interannual abundance, and projected Grasshopper Sparrow population size under future precipitation scenarios. In my fourth chapter, I focused on a set of adult vital rates to evaluate how environmental variability drives survival and movement. In my fifth chapter, I paired mark-resight data at the Konza Prairie with vegetation and topography data to elucidate the drivers of territory selection in three grassland songbirds. At a local level, this dissertation provides a comprehensive explanation for how and why local variation in abundance of grassland bird occurs, and on a global scale, it helps explain why rain leads to divergent responses in species living in different regions and with different life histories.

Chapter 2 - Precipitation timing, elevation, and life history traits mediate relationship between precipitation and avian reproductive success: A global meta-analysis

Silber, K. M. and W. A. Boyle

Abstract

Mechanisms underlying animal responses to temperature are relatively well studied, but we know less about how and why precipitation affects animal populations. Responses to precipitation may be influenced by physiology, ecology, or behavior, resulting in a myriad of potential mechanisms that may operate at specific points or times throughout a species' distribution, annual cycle, or life cycle. We synthesized published literature in a formal meta-analysis accounting for shared evolutionary history to (a) understand the nature of relationships between precipitation and avian reproductive success, globally, and (b) test alternative hypotheses regarding the causes of variation in those relationships based on species-level attributes or environmental characteristics. Precipitation timing, life history traits, and elevation mediated the nature and magnitude of responses to precipitation. Birds responded negatively to precipitation during nesting, while lagged precipitation (i.e. precipitation before the start of the breeding season) was associated with more positive responses to precipitation. Species with altricial nestling development and those that live at higher elevations responded negatively to precipitation, likely due to thermogenic consequences of wet conditions. Positive responses to precipitation over longer time scales were unrelated to diet or predator abundance, suggesting vegetation likely mediates indirect responses to precipitation. This study elucidates why rain leads to divergent responses in species living in different regions and with different life histories and provides a framework for understanding environmental mechanisms underlying bird population change under current and future precipitation regimes.

Introduction

Precipitation and temperature are the primary sources of climatic variation across the globe. The timing of hot and cold, wet and dry, and the absolute values of temperature and precipitation define biomes (Holdridge 1967, Jiang et al. 2017), set species range limits (Smith 2013), and shape seasonality in animal populations (Polo and Colmenares 2006). Consequently, animal distributions and phenology are often shaped by both local and large-scale temperature and precipitation regimes (e.g., Ficetola and Maiorano 2016, Grunig et al. 2017). The mechanisms underlying relationships between temperature and animals are well studied; temperature increases energetic costs of thermoregulation and sometimes leads to mortality near critical thresholds, which ultimately affects population growth rates and species distributions (Sunday et al. 2012, Smith 2013, McKechnie and Wolf 2019). However, we know less about how and why precipitation affects animal population growth rates. Precipitation may drive changes in animal population growth rates via species physiology, ecology, or behavior, presenting a myriad of potential mechanisms that may operate throughout a species' distribution, annual cycle, or life cycle (Boyle et al. 2020). These complex processes often produce ambiguous, and sometimes contradictory, evidence for responses to precipitation, making it difficult to disentangle the mechanisms underlying direct and indirect responses.

Relationships between animal population growth rates and the timing of precipitation timing can indicate whether responses manifest via direct or indirect mechanisms. Precipitation over the course of a season, a year, or multiple years can produce a variety of indirect effects on animal populations, including changes in food availability, predation risk, and vegetation structure (Ockendon et al. 2014, Deguines et al. 2017). As plant communities and structure change in response to precipitation, associated animal communities may experience changes in their prey items or refugia (Jirinec et al. 2022). Changes in prey abundance, mediated by precipitation, can have consequent effects on survival (Sandvik et al. 2005) and fecundity (Illera and Diaz 2006). Furthermore, variation in precipitation may also affect the risk of predation (Loveridge et al. 2006) brood parasitism (Colon et al. 2017), or ectoparasite infection (Dudaniec et al. 2007). Indirect relationships between precipitation and animal populations may operate over longer time scales than direct effects and become increasingly complex with higher trophic level interactions (Desguines et al. 2017).

Early life stages may be particularly susceptible to precipitation for endotherms with external embryonic development, such as birds. Eggs must be maintained within a species-specific spectrum of environmental conditions to properly develop (Martin et al. 2007), and eggs remain stationary throughout development, exposing them to a higher risk of predation and unfavorable environmental conditions. For species with altricial development, young hatch early in their development and are relatively helpless. They are blind, featherless, and immobile upon hatching, and remain in the nest for one to several weeks. While these challenges can reduce the incubation period, they may hinder a chick’s ability to cope with environmental variation. When precocial young hatch, they have structures (e.g., feathers, developed legs) that help them cope with environmental variation. Nest parents exhibit many behavioral strategies to mitigate the effects of environmental conditions on their young; they may select specific nest locations or orientations (With and Webb 1993, Lockwood et al. 2001), construct concealed nests to protect their young (Grant et al. 2017), or actively defend their nest (Gottfried et al. 1979). The capacity for behavioral strategies to protect the nest may increase with more individuals caring for a nest. Birds exhibit a variety of parental care, from uniparental care to biparental or cooperative care, which may affect the degree to which nestlings suffer adverse consequences of environmental variation.

Precipitation is associated with bird reproduction in species exhibiting many life history strategies and living in different biomes, but those responses vary between positive and negative even within similar geographic and temporal scales. For example, some studies report divergent species-level responses to precipitation at a given site (Rotenberry and Wiens 1991, Eeva et al. 2020, McGowan et al. 2021, Wheelwright et al. 2022). Even variation in within-species responses to precipitation exists; species may exhibit positive or negative relationships with precipitation at different sites (Peery et al. 2012) or at different times throughout the annual or nesting cycle (Moynahan et al. 2007, Skagen and Adams 2012, Beck et al. 2015, Descamps et al. 2015, Eggers et al. 2015, Zuckerberg et al. 2018, Murphy et al. 2020, Capilla-Lasheras et al. 2021).

Many plausible explanations exist for the variation in bird reproductive success following precipitation. (*i*) The period over which precipitation occurs in relation to the nesting period (i.e. *precipitation timing*) may shape whether responses will be mediated by direct or indirect mechanisms. If thermoregulation or physical nest destruction lead to nest failures (i.e. direct mechanisms), we would expect reproductive success to decline within 24-48 hours of the precipitation event. If indirect mechanisms, such as prey availability, predator abundance, or vegetation structure mediate nest success responses, we would expect lagged precipitation, summarized over seasonal or annual periods, or occurring prior to the nesting season, to be more strongly associated with nest success, and potentially generate positive or curvilinear responses to precipitation.

The direct effects of precipitation on avian reproductive success may vary depending on species-specific or site characteristics. If thermoregulation of nestlings underlies negative responses to precipitation, then we would expect species that exhibit altricial (*ii*) *nestling development* will incur higher thermoregulatory costs than those that exhibit precocial nestling development. Altricial chicks are relatively helpless upon hatching; they are featherless and immobile and require substantial parental care. Conversely, precocial chicks down feathers upon hatching and may be mobile within 24 hours, allowing them to better cope with environmental variation. Because larger animals thermoregulate more efficiently than smaller animals (Angilletta 2009), we would also expect nest success in response to precipitation to increase with (*iii*) *body size*. If thermoregulation of nestlings or nest parents underlies associations between nest success and precipitation, we would expect smaller-bodied species to exhibit more negative responses to precipitation than larger-bodied species. Species often experience thermoregulatory constraints and lower nest success at higher (*iv*) *elevations* (Evans Ogden et al. 2012, Boyle et al. 2016, Pierce et al. 2019). These relationships likely result from the colder temperatures at higher elevations that shape biotic and abiotic constraints for populations at higher elevations (Boyle et al. 2020). Thus, we expected young birds and nest parents would incur higher thermoregulatory costs at higher elevations, therefore reducing nest success.

Avian nest success may vary in response to precipitation via a combination of direct and indirect mechanisms. Species that adopt biparental or cooperative (*v*) *parental care* strategies may be better able to cope with variation in precipitation than those with uniparental care. If nest parents incur thermoregulatory costs during or after bouts of precipitation, having more individuals to assist with parental care will increase the likelihood of the nest succeeding. If predator or prey abundance mediate the relationship between precipitation and nest success, greater nest attendance (i.e. more nest helpers) may also help defend nests against increased risk of predation or variation in prey activity or abundance following precipitation. Conversely, species with uniparental care will likely exhibit more negative responses to precipitation because reproductive success relies on one individual. If nestling thermoregulation, physical destruction of nests, or predator abundance mediate the effects of precipitation on nest success, we expect nest success to vary by (*vi*) *nest structure* or (*vii*) *nest height*. Species that nest in structured nests without cover (e.g., cup nests) or nests with little to no cover (e.g., platform nests) may incur more thermoregulatory costs and higher risk of flooding or predation than those that nest in more protected nests (e.g., cavity nests). Species that build *ground nests* would likely be more susceptible to flooding (i.e. greater likelihood of nestlings getting wet and nests getting washed away) and predation than those that build elevated nests. If physical nest destruction or vegetation structure mediate the effects of precipitation on nest success, we would expect responses to precipitation would vary by (*viii*) *biome*. Populations that inhabit aquatic biomes might be more susceptible to nest flooding or physical nest destruction because precipitation may contribute to water already at the site. Alternatively, populations in biomes with vegetation structure that rapidly grows in response to precipitation (e.g., grasslands) may have higher nest success following precipitation because more aboveground biomass may provide more nest concealment. Finally, if prey availability mediates the effects of precipitation on nest success, we expect species that have a wider (*ix*) *diet breadth* (i.e. generalists) to have higher nest success following precipitation than those that rely on one prey item (i.e. specialists).

We tested these predictions of alternative explanations for how and why bird reproductive success varies in responses to precipitation by synthesizing literature on precipitation and avian reproductive success and determining the species-specific or environmental characteristics associated with variation in those relationships. We conducted both simple vote-counting and formal meta-analyses that accounted for phylogenetic relatedness of taxa using published data from birds, worldwide.

Methods

Literature search and inclusion criteria

We searched three databases for published studies relating precipitation and reproductive success. We searched the Web of Science and Scopus databases using the following search criteria: [bird* AND (nest*) NEAR (succe* OR surviv*) AND (precipit* OR rain OR rainfall)] and the Wildlife & Ecology Studies database using the following search criteria: [SU bird* AND SU nest* AND (succe* OR surviv*) AND (precipit* OR rain OR rainfall)] on July 14, 2022. We read the abstracts for all journal articles, dissertations, conference papers, and books obtained from these searches and excluded sources that did not mention any metrics for weather and reproductive success within the abstract and sources not in English. For remaining sources, we screened the entire article, dissertation chapter, or book chapter and excluded those that did not mention precipitation anywhere within the article and/or did not include a metric for reproductive success as a response variable in an original analysis.

We included sources that referenced precipitation in any form (e.g., rainfall or snowfall), but excluded sources that assessed only humidity rather than precipitation because relationships between humidity and reproductive success would involve a different set of mechanisms than those we considered. We also excluded sources that assessed river/lake levels, as these depend on factors outside the scope of this study (e.g., snowmelt). We excluded sources that used year as a proxy for precipitation, as multiple environmental variables vary annually. We excluded sources that pooled estimates across sites or species and those that did not describe the nature (i.e. positive or negative) of the relationship between precipitation and reproductive success.

We included sources that reported metrics related to nest success (e.g., daily nest survival, hatching success, fledging success), but excluded sources that reported only counts of clutch size or brood size. Some studies included analyses of both nest-level and annual population-level summaries of nest success. In such cases, we included nest-level results rather than annual estimates (i.e. average annual productivity), as individual responses likely more directly reflect the mechanistic drivers of response to climate. We excluded sources that reported only climatic correlates of reproductive phenology, vital rates of young birds following fledging, and vital rates of adults. If sources referenced reproductive success estimates from another study, we obtained the original study to include in our analysis. We made a list of all citations within our included sources and repeated the review process on those referenced articles to obtain as large a sample of studies as possible.

Data collection

We collected site-level data from the source articles for the following predictors: precipitation variable included in original study, biome, and mean elevation. We recorded the precipitation variables used in the original study, coding them by the temporal scale at which they would affect nest success: "direct" precipitation metrics were those measured on the same day or the day before the nest was checked; "seasonal" metrics were those measured at the temporal scale of the breeding season (e.g., breeding season total, or precipitation throughout nesting period but not within 1-2 days of the nest check), or "lagged" if precipitation occurred prior to the breeding season (e.g., winter, annual, or previous breeding season's precipitation).

We coded the biome in which the study took place, based on descriptions in the source articles. We then coded biomes into four groups: “aquatic” for coastal and wetland habitats, “wooded” for forested and shrubby habitats, “developed” for urban and zoo habitats, and “open” for grasslands, agricultural, tundra, and desert habitats. These groupings reflect similar vegetation heights and structure. We recorded the study site elevation as reported by the source authors. If the elevation was not included in the paper, we estimated the latitude, longitude, and average elevation across the study site in Google Earth (earth.google.com/web/) based on the site description.

For each source included in our dataset, we coded information about the species, study site, and results (Table 2.1). We recorded the scientific name of the species in the study, according to Jetz et al. (2012), and coded species-level data from Birds of the World (Birds of the World 2022) for the following variables: diet, nest type, nest location, nestling development, parental care, and average body size. We grouped prey types into the following categories and noted the presence or absence of each in the diet of each species: vegetation (including seeds and leaves), fruit, invertebrates, or vertebrates (i.e. birds, reptiles, mammals, fish, or carrion). To capture each species’ *diet breadth*, we then coded each species as a “specialist” if, according to Birds of the World (Birds of the World 2022), they typically consumed one prey type or a “generalist” if they take two or more types of prey. Based on descriptions and photos of nests, we coded three categories for nest types: “minimal” for scrape and platform nests, “structured” for cup, bowl, and adherent nests, and “protected” for cavity, burrow, domed, and pendulous nests. We considered these groupings reflective of the amount of protection provided by the *nest structure*. We coded if species typically nests on the ground or more than 1 m off the ground because we expected *ground nests* would be more susceptible to flooding. For species that nest both on and above the ground, we coded it according to what authors of Birds of the World species accounts (Birds of the World 2022) considered the most common nesting location (i.e. on or above the ground). We coded a species as being "altricial" if they exhibit altricial or semi-altricial nestling development, or "precocial" if they exhibit precocial or semi-precocial nestling development, as we expected *nestling development* would relate to the thermoregulatory costs of precipitation on young birds. To characterize the amount of *parental care*, we coded "uniparental" for species in which one parent primarily raises the brood, "biparental" if two individuals share roughly equally in raising the brood, or "cooperative" if three or more individuals raise the brood. If species typically exhibit both biparental and cooperative care, we coded them as "biparental/cooperative". When species were documented to rarely exhibit cooperative care, we did not consider their typical parental care to be cooperative. We calculated the mean *body size* for adult males and females because we expected smaller species to incur higher thermoregulatory costs. For vote counting analyses, we kept body size as a continuous, numeric variable, and for the phylogenetic meta-analyses, we categorized the species into four categories: "<20 g", "20-45 g", "46-400 g" and ">400 g". We expected these groupings would reflect thermoregulatory thresholds over which responses to precipitation would change.

We recorded the nature of the relationship between precipitation and reproductive success (i.e. positive or negative) for the given study. We recorded the effect size (i.e. parameter estimate, model-averaged parameter estimate, or median of the posterior distribution) of the relationship between precipitation and the nest-related metric, along with the associated standard error, if reported. We recorded sample size, response variable (e.g., daily nest success, nest survival), and metric of precipitation (e.g., annual rainfall). We then split our dataset into three groups based on the temporal extent of response variables: 1) daily metrics of reproductive success (hereafter: “daily nest survival”), 2) metrics of reproductive success throughout the nesting period (hereafter: “nest success”), and 3) annual metrics of population-level productivity (hereafter: “annual nest success”). We excluded any metrics of reproductive success that did not fall into one of these categories (e.g., lifetime reproductive success). We analyzed these three groups separately because they each have different units of replication (i.e. nest versus population level), and we expected precipitation might have different effects over distinct time periods reflecting different mechanistic links.

Vote-counting analyses

Given that species may exhibit variation in their responses to precipitation across their range and many studies did not report effect sizes, we first conducted vote-counting analyses to maximize sample size in this synthesis of relationships between precipitation and reproductive success. We included all studies for which we could obtain information about the precipitation variable tested and nature of the response (i.e. positive, negative, or no response). We assigned a “1” to all studies that reported a positive relationship between precipitation and reproductive success, a “0” to all studies that reported no relationship, and a “-1” to all studies that reported a negative relationship between precipitation and reproductive success. We excluded studies that reported quadratic effects. We fit three multiple linear regression models; one for each response variable group (i.e. daily nest survival, nest success, and annual nest success). Each model included all predictors (i.e. precipitation timing, nestling development, body size, elevation, parental care, nest structure, nest height, biome, and diet breadth).

Formal meta-analyses

To test the direct and indirect mechanisms that may mediate the relationship between precipitation and reproductive success accounting for the magnitude of the response, the sample size of the original dataset, and in a way that incorporates the non-independence of species, we included any studies for which we could obtain an effect size (i.e. parameter estimate) and associated SE. We converted each predictor into categorical variables with three or fewer groupings (Table 2.1). If our dataset included multiple studies for a given species, we calculated a weighted mean and variance of each species' effect size using the effect size and sample size of each study.

We downloaded 1,000 phylogenetic trees for the species represented in our dataset from vertlife.org (Jetz et al. 2012). We calculated Blomberg's *k* (Blomberg 2003) to assess the strength of the phylogenetic signal across the phylogenetic trees. We fit formal meta-analyses using the software phyloMeta, version 1.3 (LaJeunesse 2011). To avoid potential phylogenetic bias due to the non-independence of effect sizes for closely-related species in our dataset (Lajeunesse 2009), we conducted both traditional and phylogenetically-independent analyses. We used phyloMeta to fit univariate Phylogenetic Generalized Least Squares (PGLS) regressions for each phylogenetic tree, response variable group (i.e. daily nest survival, nest success, and annual success), and species-specific predictor (i.e. diet, nest type, nest location, nestling development, parental care, and average body size). We fit individual regressions for each predictor because of low sample sizes and because we wanted to quantify the effects of individual predictors on responses to precipitation. The PGLS regressions pooled effect sizes and weighted them according to sampling error, which is a modification of the methods from Hedges and Olkin (1985) and Hedges (1992) that accounts for relatedness among taxa. We fit formal meta-analyses for all predictors except precipitation timing and elevation, as these varied by study and could not be easily summarized to make species-level inferences. We considered a variable to be a satisfactory predictor for responses to precipitation if any groups within that variable had non-overlapping 95% CIs.

Results

The Web of Science search yielded 320 sources, the Scopus search yielded 303 sources, and the Wildlife & Ecology Studies search yielded 196 sources. After removing duplicates 523 sources remained. We then compiled all citations from included sources and repeated our exclusion process, which yielded an additional 30 articles. We screened the abstracts of these 553 sources and retained 299 sources that included mention of weather and a nest-related metric within the abstract. We then reviewed the entire source and retained 148 sources for our vote counting analyses and 57 sources for our phylogenetic meta-analyses, reflecting each of our reproductive response variables and precipitation variables (Figure 2.1).

Studies spanned all seven continents, with approximately 50% of studies coming from North America, 29% from Europe, 9% from Africa, 6% from Asia, 5% from Oceania, 1% from South America, and <1% from Antarctica. Studies also occurred in a variety of biomes; 19% in aquatic biomes, 4% in developed biomes (i.e. cities or zoos), 33% in open biomes, and 44% in wooded biomes. Elevation at the study sites ranged from 0 m to 2500 m, with an average elevation across all studies of 670 m. The dataset included 117 species (Table 2.2) from 53 families (Figure 2.2). Species' average body mass ranged from 5 g to 9,750 g, with 50% of the species between 24 g and 775 g. Species used a fairly balanced range of nest constructions; 30% used minimal nests (e.g., platform or scrape), 34% used structured nests (e.g., constructed cup or bowls), and 36% used protected nests (e.g., cavity or burrow). Ground-nesting species represented 38% of the species in the dataset. Over 84% of species exhibit biparental care, and 80% of species exhibit altricial nestling development. Species consumed a variety of food types, from seeds to carrion, with over 85% of the species relying on invertebrates for part of or all of their diet. We excluded six studies that reported quadratic relationships between precipitation and reproductive success. The dataset for annual variables of reproductive success only included 20 studies (Figure 2.3), therefore the sample size was too small to fit the model to this dataset.

Birds responded both positively and negatively to precipitation (Table 2.3), but responses differed by response variable (i.e., daily nest survival (Table 2.4) and overall nest success (Table 2.5). The generalized linear model of daily nest survival included 64 studies and explained 41.2% of the deviance in the dataset (Table 2.4). Daily nest survival decreased in response to precipitation for species that construct protected nests ($\hat{\beta}$ = -1.568, SE = 0.5252) and those that exhibit cooperative parental care ($\hat{\beta}$ = -2.2191, SE = 0.9177).

The generalized linear model for nest success included 131 studies and explained 31.9% of the deviance in the dataset (Table 2.5). Precipitation timing influenced responses to precipitation (Figure 2.5); lagged precipitation resulted in more positive relationships between precipitation and reproductive success ($\hat{\beta}$ = 1.7910, SE = 0.4793) than direct precipitation ($\hat{\beta}$ = -0.7713, SE = 0.8174). Structured nests had more positive relationships with precipitation ($\hat{\beta}$ = -0.7539, SE = 0.2463). Daily nest survival and overall nest success both declined at higher elevations (daily nest survival: $\hat{\beta}$ = -0.0006, SE = 0.0002; nest success: $\hat{\beta}$ = -0.0002, SE = 0.0001; Figure 2.6).

The formal meta-analyses included 64 species from 57 sources. The daily nest survival dataset included 29 species and the nest success dataset included 36 species. The annual success dataset included only 4 species, thus, we were unable to fit any models to this dataset. Although we detected minimal phylogenetic signal within our predictors (Blomberg's *k* = 0.15, calculated across 1,000 phylogenetic trees), we interpreted results from the phylogenetically-independent analyses (Figure 2.7) instead of the traditional meta-analyses (Figure 2.8) to ensure our conclusions were not biased by evolutionary histories (Lajeunesse 2009).

Parameter estimates for all phylogenetic meta-analyses are in Tables 2.5 and 2.6. Species from aquatic biomes had negative responses to precipitation ($\hat{\beta}$ = -1.200, 95% CI = -1.224, -1.167), while those from wooded biomes had positive responses to precipitation ($\hat{\beta}$ = 0.294, 95% CI = 0.266, 0.323). Species that exhibited biparental or cooperative care had lower daily nest survival ($\hat{\beta}$ = -0.001, 95% CI: -0.003, 0.000) and overall nest success ($\hat{\beta}$ = -0.001, 95% CI: -0.001, -0.001) in response to precipitation, while species that exhibit uniparental care had higher daily nest survival ($\hat{\beta}$ = 0.019, 95% CI: 0.018, 0.020) and overall nest success ($\hat{\beta}$ = 0.021, 95% CI: -0.113, 0.156) in response to precipitation. Altricial species had lower daily nest survival ($\hat{\beta}$ = -0.186, 95% CI: -0.199, -0.172) and overall nest success following precipitation ($\hat{\beta}$ = -0.035, 95% CI: -0.048, -0.023), while precocial species had positive daily nest survival ($\hat{\beta}$ = 0.019, 95% CI: 0.006, 0.032) and overall nest success following precipitation ($\hat{\beta}$ = 0.742, 95% CI: 0.602, 0.882). Smaller species (i.e. <20 g) had lower daily nest survival in response to precipitation ($\hat{\beta}$ = -0.389, 95% CI: -0.530, -0.248) than larger species (i.e. >400 g; $\hat{\beta}$ = 0.019, 95% CI: -0.049, 0.088), while body size exhibited a curvilinear relationship with overall nest success following precipitation (i.e. birds with intermediate body sizes [20-45 g] had higher overall nest success than those with smaller or larger body sizes). No consistent patterns emerged for nest location or diet.

Discussion

Precipitation influences avian reproductive success both directly and indirectly, and the nature of the response depends on precipitation timing and ecological context. As we anticipated, precipitation during the nesting period tends to reduce nest success, while precipitation occurring prior to nesting often positively affects nest success. Negative responses to precipitation are likely explained by direct, thermogenic costs on young and adult birds, and positive responses are likely mediated by indirect relationships between lagged precipitation, vegetation structure, and nest success. These relationships probably reflect a combination of physiological and behavioral individual-level responses that scale up to the population-level. This study provides evidence for a concrete framework for understanding bird responses to precipitation across biomes and taxa, under current and future precipitation regimes.

Contrary to many studies, we did not find support for prey availability affecting the relationship between nest success and precipitation (i.e. no consistent difference among dietary classes in the magnitude or nature of responses), but these responses may be elevation-, biome-, or region-dependent. Diet may play a larger role in areas where prey items are seasonally limited or have higher interannual fluctuations in abundance (Zárybnická et al. 2015). Prey populations may also exhibit contrasting responses to precipitation among vital rates, years, and regions, masking food-mediated responses at higher trophic levels. These responses may also vary throughout a species range because species can exhibit nonlinear responses to climate across gradients (Boyle et al. 2020, Louthan and Morris 2021), suggesting that the location in a species' range where the study is conducted may impact the observed relationships.

We also did not find support for predator abundance mediating relationships between precipitation and avian nest success. We expected species with more nest attendants would be able to better defend the nest from predators, but contrary to our prediction, species with uniparental care had higher nest success in response to precipitation than those with biparental or cooperative care. This phenomenon could result from three mechanisms. First, uniparental care could be conflated with precocial nestling development, given these two reproductive strategies are often linked. Alternatively, parental investment may vary at the individual level, not species level, and parental investment may not decrease with the addition of nest parents or helpers (Mumme et al. 1990). For example, biparental care may not involve two highly-invested nest parents, but two nest parents that invest just enough to prevent abandonment by their mate (Jones et al. 2002), the product of which may be equal to or less than the investment of one fully invested nest parent. Another potential explanation for more positive responses in uniparental care systems is that one nest parent attending to the nest may draw less predator attention to a nest than two or more nest attendants (Meyer et al. 2020). If nest parents forage following bouts of precipitation, then having two or more nest parents provisioning at a nest may allow nests to become more easily detected by predators than nests with only one attendant.

We found conflicting evidence for the effects of precipitation on avian nest success via physical nest destruction. Nest failures and flooding were more common in aquatic biomes following precipitation, but nest height and structure were not associated with precipitation. Ground nests did not have a greater risk of failure than elevated nests, and more structured nests (e.g., cavity nests) did not exhibit any clear, directional relationship with avian nest success following precipitation compared to minimal nests (e.g., scrapes). These ambiguous relationships may result from the diverse factors that could affect thermal and physical properties of nests. For example, nest substrate may have a greater impact on protection from environmental variability than nest height or structure.

Avian nest success declined in response to precipitation due to thermogenic costs of nestling and nest parents. Responses to the direct, thermogenic costs of precipitation varies by nestling development and elevation. Species with precocial young had more positive responses to temporal variation in precipitation than those with altricial young, which likely reflects physiological and behavioral constraints for altricial chicks because they are often blind, featherless, and immobile upon hatching. Precocial chicks, however, are usually feathered and mobile within 24 hours of hatching and are therefore better able to cope with environmental variability. Precocial chicks, in general, also require less parental care than altricial chicks. Along with species-level developmental characteristics, the thermogenic costs of precipitation may vary by elevation. Birds living at higher elevations had more negative responses to precipitation than those at lower elevations, which was apparent through both daily nest survival and overall nest success. Birds at higher elevations have smaller clutches and fewer reproductive attempts than those at lower elevations (Boyle et al. 2015), implying reproductive constraints that may manifest from the direct and indirect consequences of weather. Higher elevations can lead to greater thermogenic and homeothermic costs (McKechnie and Wolf 2019) on both young and adult birds. Indirectly, reduced evapotranspiration rates at cooler, higher, elevations may reduce vegetation biomass, therefore limiting populations via prey availability or refugia (Boyle et al. 2020, Jirinec et al. 2022). Many bird species are moving to higher elevations to track the changing climate (Freeman et al. 2018, Neate-Clegg et al. 2021), which may increase the likelihood of extinction (Sekercioglu et al. 2008). This suggests species will exhibit more negative responses to precipitation as climate continues to change as they move upslope.

Precipitation over different time scales define predictions about whether processes are bottom-up or top-down (e.g., lagged vs direct precipitation). In general, lagged, indirect relationships with precipitation were positive and concurrent, direct relationships were negative. Precipitation metrics summarized throughout the breeding season were not associated with nest success, likely because climatic predictors at coarse resolutions have low predictive accuracy in areas where weather is temporally variable (Nadeau et al. 2017). Testing precipitation variables over multiple time periods was critical to elucidate relationships between weather and reproductive success, and the ways in which precipitation is summarized may affect interpretations. For example, extreme precipitation may better predict changes in reproductive vital rates than averages (Marcelino et al. 2020), and deviations from averages, as opposed to raw precipitation values, allow for ease of cross-site comparisons.

Birds are declining across most guilds and biomes (e.g., Rosenberg et al. 2019), and understanding the relationships between weather, environmental characteristics, and life history traits is essential to effectively halt these declines. Species living at high elevations or in biomes with heavy breeding season precipitation will be more affected by future changes in precipitation regimes than those living at lower elevations or in areas with less breeding season precipitation. Furthermore, smaller species with altricial chick development will incur greater thermoregulatory costs in response to rainfall than larger species with precocial chick development, ultimately leading to lower nest success. While weather often has direct and indirect effects on animal populations around the world, these responses become more exaggerated under climate change (Ockendon et al. 2014). Species responses to climate change can be difficult to predict because species distributions change in response to climatic and non-climatic factors (Mustin et al. 2007), however understanding responses to climate is the basis to many projection models and conservation initiatives for animal populations. A better understanding of the mechanisms underlying animal responses to weather variability provides context for ecological relationships, population declines, and species distributions.

Tables

Table 2.1. Descriptions of variables included in dataset. All variables were included in vote counting analyses, and all variables except elevation and precipitation timing were included in the phylogenetic meta-analyses to assess factors that mediate the relationship between precipitation and reproductive success.

Predictor	**Coded terms**
(*i*) Precipitation	Direct = precipitation within two days of estimated nest survival Nesting period = precipitation within the breeding season Lagged = precipitation before breeding season or throughout entire year
(*ii*) Biome	Aquatic = coastal and wetland habitats Wooded = forested and shrubby habitats Developed = urban and zoo habitats Open = grasslands, tundra, and desert habitats
(*iii*) Elevation	Mean elevation (m) at study site
(*iv*) Diet	Specialist = relies on 1 prey type (i.e. vegetation, fruit, invertebrates, or vertebrates) Generalist = relies on 2+ prey types
(*v*) Nest type	Minimal = scrape, platform Structured = cup, bowl Protected = cavity, burrow, pendulous, domed
(*vi*) Ground nest	Yes = species typically nests in/on ground No = species typically nests above ground
(*vii*) Nestling development	Altricial = nestlings are altricial or semi-altricial in development Precocial = nestlings are precocial or semi-precocial in development
(*viii*) Parental care	Uniparental = one parent raises chicks Biparental or cooperative = 2 or more individuals raise chicks
(*ix*) Average body size	<20 = avg. adult body mass less than 20 g 20-45 = avg. adult body mass is 20-45 g 46-400 = avg. body mass is 45-400 g >400 g = avg. adult body mass is greater than 400 g

Table 2.2. Table of all species and coded species-specific variables included in quantitative analyses.

Family	**Genus**	**Species**	**Common Name**	**Ground Nest**	**Nest Code**	**Nestling Development**	**Parental Care**	**Average Body Size (g)**	**Diet**
Accipitridae	*Accipiter*	*gentilis*	Northern Goshawk	No	Minimal	Altricial	Biparental	998	Specialist
Accipitridae	*Aegypius*	*monachus*	Cinereous vulture	No	Minimal	Altricial	Biparental	9750	Specialist
Accipitridae	*Buteo*	*lagopus*	Rough-legged Hawk	No	Minimal	Altricial	Biparental	1130	Specialist
Accipitridae	*Buteo*	*lineatus*	Red-shouldered Hawk	No	Minimal	Altricial	Biparental	625	Generalist
Accipitridae	*Clanga*	*pomarina*	Lesser Spotted Eagle	No	Minimal	Altricial	Biparental	1600	Generalist
Accipitridae	*Gyps*	*fulvus*	Eurasian Griffon	No	Minimal	Altricial	Biparental	8700	Specialist
Accipitridae	*Haliaeetus*	*leucocephalus*	Bald Eagle	No	Minimal	Altricial	Biparental	4650	Specialist
Accipitridae	*Rostrhamus*	*sociabilis*	Snail Kite	No	Minimal	Altricial	Biparental	460	Specialist
Acrocephalidae	*Acrocephalus*	*arundinaceus*	Great Reed-warbler	No	Structured	Altricial	Biparental	27	Generalist
Alaudidae	*Calandrella*	*cinerea*	Red-capped larks	Yes	Structured	Altricial	Biparental	23	Generalist
Alaudidae	*Eremophila*	*alpestris*	Horned Lark	Yes	Structured	Altricial	Biparental	34	Generalist
Alcidae	*Fratercula*	*cirrhata*	Tufted Puffin	Yes	Protected	Precocial	Biparental	775	Specialist
Anatidae	*Anser*	*caerulescens*	Snow Goose	Yes	Minimal	Precocial	Biparental	2333	Specialist
Anatidae	*Branta*	*canadensis*	Canada Goose	Yes	Minimal	Precocial	Uniparental	5700	Specialist
Apodidae	*Apus*	*pallidus*	Pallid Swift	No	Protected	Altricial	Biparental	42	Specialist
Apodidae	*Cypseloides*	*niger*	Black Swift	No	Protected	Altricial	Biparental	45	Specialist
Ardeidae	*Ardea*	*alba*	Great Egret	No	Minimal	Altricial	Biparental	1000	Generalist
Ardeidae	*Ardea*	*intermedia*	Intermediate Egret	No	Minimal	Altricial	Biparental	450	Generalist
Ardeidae	*Botaurus*	*stellaris*	Great Bittern	Yes	Minimal	Altricial	Uniparental	1355	Generalist
Ardeidae	*Egretta*	*garzetta*	Little Egret	Yes	Minimal	Altricial	Biparental	495	Generalist
Ardeidae	*Nycticorax*	*nycticorax*	Black-crowned Night-heron	No	Structured	Altricial	Biparental	883	Generalist
Bucorvidae	*Bucorvus*	*leadbeateri*	Southern Ground-Hornbill	No	Protected	Altricial	Cooperative	4205	Generalist
Cacatuidae	*Lophochroa*	*leadbeateri*	Pink Cockatoo	No	Protected	Altricial	Biparental	420	Specialist
Calcariidae	*Plectrophenax*	*nivalis*	Snow Bunting	No	Protected	Altricial	Biparental	35	Generalist
Charadriidae	*Charadrius*	*dubius*	Little Ringed Plover	Yes	Minimal	Precocial	Biparental/Cooperative	40	Specialist

Charadriidae	*Charadrius*	*montanus*	Mountain Plover	Yes	Minimal	Precocial	Uniparental	101	Specialist
Charadriidae	*Charadrius*	*nivosus*	Snowy Plover	Yes	Minimal	Precocial	Biparental	46	Specialist
Charadriidae	*Charadrius*	*vociferus*	Killdeer	Yes	Minimal	Precocial	Biparental	88	Generalist
Ciconiidae	*Ciconia*	*ciconia*	White Stork	No	Minimal	Altricial	Biparental	3338	Generalist
Ciconiidae	*Ephippiorhynchus*	*asiaticus*	Black-necked Stork	No	Minimal	Altricial	Biparental	4000	Generalist
Ciconiidae	*Leptoptilos*	*crumenifer*	Marabou Stork	No	Minimal	Altricial	Biparental	7500	Specialist
Coraciidae	*Coracias*	*garrulus*	European Roller	No	Protected	Altricial	Biparental	144	Generalist
Corvidae	*Aphelocoma*	*coerulescens*	Florida Scrub-Jays	No	Structured	Altricial	Biparental/Cooperative	80	Generalist
Corvidae	*Corvus*	*corone*	Carrion Crow	No	Structured	Altricial	Biparental/Cooperative	499	Generalist
Corvidae	*Pica*	*hudsonia*	Black-billed Magpie	No	Protected	Altricial	Biparental	178	Generalist
Cuculidae	*Crotophaga*	*major*	Greater Ani	Yes	Structured	Altricial	Cooperative	175	Generalist
Falconidae	*Falco*	*peregrinus*	Peregrine Falcon	No	Minimal	Altricial	Biparental	1005	Generalist
Falconidae	*Falco*	*punctatus*	Mauritius Kestrel	No	Protected	Altricial	Biparental	177	Generalist
Falconidae	*Falco*	*tinnunculus*	Eurasian Kestrel	No	Protected	Altricial	Biparental	225	Generalist
Fringillidae	*Palmeria*	*dolei*	Akohekohe	No	Structured	Altricial	Biparental	29	Generalist
Furnariidae	*Phacellodomus*	*rufifrons*	Rufous-fronted Thornbird	No	Protected	Altricial	Biparental	25	Specialist
Gruidae	*Antigone*	*antigone*	Sarus Crane	Yes	Minimal	Precocial	Biparental	8820	Generalist
Gruidae	*Grus*	*americana*	Whooping Crane	Yes	Minimal	Precocial	Biparental	6850	Generalist
Hirundinidae	*Hirundo*	*atrocaerulea*	Montane Blue Swallow	No	Structured	Altricial	Biparental	13	Specialist
Hirundinidae	*Hirundo*	*neoxena*	Welcome Swallow	No	Protected	Altricial	Biparental	15	Specialist
Hirundinidae	*Tachycineta*	*bicolor*	Tree Swallow	No	Protected	Altricial	Biparental	20	Specialist
Icteridae	*Dolichonyx*	*oryzivorus*	Bobolink	Yes	Structured	Altricial	Biparental	43	Generalist
Icteridae	*Icterus*	*oberi*	Montserrat Oriole	No	Protected	Altricial	Biparental	37	Generalist
Laniidae	*Lanius*	*bucephalus*	Bull-headed Shrike	No	Structured	Altricial	Biparental	43	Generalist
Laniidae	*Lanius*	*collurio*	Red-backed Shrike	No	Structured	Altricial	Biparental	28	Specialist
Laniidae	*Lanius*	*ludovicianus*	Loggerhead Shrike	No	Structured	Altricial	Biparental	48	Specialist
Laridae	*Sternula*	*antillarum*	Least Tern	Yes	Minimal	Precocial	Biparental	46	Generalist
Monarchidae	*Chasiempis*	*ibidis*	Oahu Elepaio	No	Structured	Altricial	Biparental	13	Specialist

Motacillidae	*Anthus*	*berthelotii*	Berthelot's Pipit	Yes	Structured	Altricial	Biparental	18	Generalist
Motacillidae	*Anthus*	*pratensis*	Meadow Pipit	Yes	Structured	Altricial	Biparental	19	Generalist
Motacillidae	*Anthus*	*rubescens*	American Pipit	No	Structured	Altricial	Biparental	21	Generalist
Motacillidae	*Anthus*	*spragueii*	Sprague's Pipit	Yes	Protected	Altricial	Biparental	24	Generalist
Muscicapidae	*Luscinia*	*svecica*	Bluethroat	Yes	Structured	Altricial	Biparental	19	Generalist
Muscicapidae	*Phoenicurus*	*phoenicurus*	Common Redstart	No	Protected	Altricial	Biparental	17	Generalist
Muscisapidae	*Ficedula*	*albicollis*	Collared Flycatcher	No	Protected	Altricial	Biparental	12	Specialist
Muscisapidae	*Ficedula*	*hypoleuca*	European Pied-Flycatcher	No	Protected	Altricial	Biparental	16	Generalist
Numididae	*Numida*	*meleagris*	Helmeted Guineafowl	Yes	Minimal	Precocial	Biparental	1475	Generalist
Odontophoridae	*Callipepla*	*squamata*	Scaled Quail	Yes	Structured	Precocial	Biparental	184	Generalist
Odontophoridae	*Colinus*	*virginianus*	Northern Bobwhite	Yes	Minimal	Precocial	Biparental	155	Generalist
Otididae	*Chlamydotis*	*undulata*	Houbara Bustard	Yes	Minimal	Precocial	Uniparental	2200	Generalist
Paridae	*Parus*	*major*	Great Tit	No	Protected	Altricial	Biparental	17	Specialist
Parulidae	*Cardellina*	*rubrifrons*	Red-faced Warbler	Yes	Structured	Altricial	Biparental	10	Specialist
Parulidae	*Leiothlypis*	*celata*	Orange-crowned Warbler	Yes	Structured	Altricial	Biparental	9	Generalist
Parulidae	*Parkesia*	*motacilla*	Louisiana Waterthrush	Yes	Structured	Altricial	Biparental	20	Specialist
Parulidae	*Parus*	*monticolus*	Green-backed Tit	No	Protected	Altricial	Biparental	15	Generalist
Parulidae	*Setophaga*	*ruticilla*	American Redstart	No	Structured	Altricial	Biparental	8	Generalist
Passerellidae	*Ammodramus*	*savannarum*	Grasshopper Sparrow	Yes	Protected	Altricial	Biparental	17	Generalist
Passerellidae	*Ammospiza*	*maritima*	Seaside Sparrow	No	Structured	Altricial	Biparental	24	Generalist
Passerellidae	*Artemisiospiza*	*nevadensis*	Sagebrush Sparrow	No	Structured	Altricial	Biparental	19	Generalist
Passerellidae	*Calamospiza*	*melanocorys*	Lark Bunting	Yes	Structured	Altricial	Biparental	40	Generalist
Passerellidae	*Centronyx*	*bairdii*	Baird's Sparrow	Yes	Structured	Altricial	Biparental	19	Generalist
Passerellidae	*Melospiza*	*melodia*	Song Sparrow	No	Structured	Altricial	Biparental	19	Generalist
Passerellidae	*Passerculus*	*sandwichensis*	Savannah Sparrow	Yes	Structured	Altricial	Biparental	16	Generalist
Passerellidae	*Spizella*	*breweri*	Brewer's Sparrow	No	Structured	Altricial	Biparental	11	Generalist
Passeridae	*Passer*	*domesticus*	House Sparrow	No	Protected	Altricial	Biparental	28	Generalist
Passeridae	*Passer*	*montanus*	Eurasian Tree Sparrow	No	Protected	Altricial	Biparental	23	Generalist
Phalacrocoracidae	*Gulosus*	*aristotelis*	European Shag	No	Structured	Altricial	Biparental	1781	Specialist

Phasianidae	*Centrocercus*	*urophasianus*	Greater Sage-grouse	Yes	Minimal	Precocial	Uniparental	1950	Generalist
Phasianidae	*Meleagris*	*gallopavo*	Wild Turkey	Yes	Minimal	Precocial	Uniparental	6800	Generalist
Phasianidae	*Phasianus*	*colchicus*	Ring-necked Pheasant	Yes	Structured	Precocial	Uniparental	1750	Generalist
Phasianidae	*Tympanuchus*	*cupido*	Greater Prairie-Chicken	Yes	Structured	Precocial	Uniparental	860	Generalist
Phasianidae	*Tympanuchus*	*pallidicinctus*	Lesser Prairie-chicken	Yes	Structured	Precocial	Uniparental	707	Generalist
Phasianidae	*Tympanuchus*	*phasianellus*	Sharp-tailed Grouse	Yes	Structured	Precocial	Uniparental	813	Generalist
Phoeniculidae	*Phoeniculus*	*purpureus*	Green Woodhoopoe	No	Protected	Altricial	Cooperative	75	Generalist
Picidae	*Dendrocopos*	*major*	Great Spotted Woodpecker	No	Protected	Altricial	Biparental	75	Generalist
Picidae	*Dendrocoptes*	*medius*	Middle Spotted Woodpecker	No	Protected	Altricial	Biparental	68	Specialist
Picidae	*Dryobates*	*minor*	Lesser Spotted Woodpecker	No	Protected	Altricial	Biparental	23	Specialist
Picidae	*Jynx*	*torquilla*	Wrynecks	No	Protected	Altricial	Biparental	40	Specialist
Picidae	*Leuconotopicus*	*borealis*	Red-cockaded Woodpecker	No	Protected	Altricial	Biparental	46	Generalist
Ploceidae	*Philetairus*	*socius*	Sociable Weaver	No	Protected	Altricial	Biparental/Cooperative	29	Generalist
Procellariidae	*Ardenna*	*tenuirostris*	Short-tailed Shearwater	Yes	Protected	Altricial	Biparental	705	Generalist
Procellariidae	*Thalassoica*	*antarctica*	Antarctic Petrel	Yes	Minimal	Altricial	Biparental	638	Generalist
Psittacidae	*Amazona*	*finschi*	Lilac-crowned Parrots	No	Protected	Altricial	Biparental	304	Generalist
Psittaculidae	*Eclectus*	*roratus*	Eclectus Parrot	No	Protected	Altricial	Biparental/Cooperative	485	Specialist
Rallidae	*Porphyrio*	*hochstetteri*	South Island Takahe	Yes	Protected	Precocial	Biparental	2673	Generalist
Recurvirostridae	*Himantopus*	*mexicanus*	Black-necked Stilt	Yes	Minimal	Precocial	Biparental	178	Generalist
Recurvirostridae	*Recurvirostra*	*americana*	American Avocet	Yes	Minimal	Precocial	Biparental	313	Generalist
Scotocercidae	*Abroscopus*	*albogularis*	Rufous-faced Warbler	No	Structured	Altricial	Biparental	5	Specialist
Spheniscidae	*Eudyptula*	*minor*	Little Penguin	Yes	Protected	Altricial	Biparental	1300	Specialist
Strigidae	*Athene*	*cunicularia*	Burrowing Owl	Yes	Protected	Altricial	Biparental	160	Generalist
Strigidae	*Ninox*	*novaeseelandiae*	Morepork	No	Protected	Altricial	Biparental	190	Generalist
Strigidae	*Strix*	*occidentalis*	Spotted Owl	No	Protected	Altricial	Biparental	623	Specialist
Thraupidae	*Melopyrrha*	*portoricensis*	Puerto Rican Bullfinch	No	Structured	Altricial	Biparental	33	Generalist

Threskiornithidae	*Eudocimus*	*albus*	White Ibis	No	Minimal	Altricial	Biparental	900	Specialist
Troglodytidae	*Cistothorus*	*palustris*	Marsh Wren	No	Protected	Altricial	Biparental	12	Specialist
Turdidae	*Sialia*	*currucoides*	Mountain Bluebird	No	Protected	Altricial	Biparental	30	Specialist
Turdidae	*Sialia*	*mexicana*	Western Bluebird	No	Protected	Altricial	Biparental	28	Generalist
Turdidae	*Turdus*	*merula*	Eurasian Blackbird	No	Structured	Altricial	Biparental	95	Generalist
Tyrannidae	*Myiarchus*	*cinerascens*	Ash-throated Flycatcher	No	Protected	Altricial	Biparental	28	Generalist
Tyrannidae	*Pyrocephalus*	*nanus*	Brujo Flycatcher	No	Structured	Altricial	Biparental	13	Specialist
Tyrannidae	*Tyrannus*	*tyrannus*	Eastern Kingbird	Yes	Structured	Altricial	Biparental	40	Specialist
Upupidae	*Upupa*	*epops*	Hoopoe	No	Protected	Altricial	Biparental	68	Specialist

Table 2.3. Observed relationships between environmental characteristics and species-specific characteristics and bird responses to precipitation. Predictors with P-values less than 0.05 percent include a minus sign to indicate a negative relationship and a plus sign to indicate a positive relationship. Predictors from the phylogenetic meta-analyses with non-overlapping 95% CIs include a minus sign to indicate a negative relationship and a plus sign to indicate a positive relationship. If the cell is blank, no relationship was observed. Asterisks (*) indicate the relationship was contrary to the expected relationship, and the tilde (~) indicates a curvilinear relationship. "." indicates variable was not included in that analyses.

	Vote counting		Phylogenetic meta-analyses	
	Daily nest survival	Overall nest success	Daily nest survival	Overall nest success
Direct precipitation		—	.	.
Seasonal precipitation			.	.
Lagged precipitation		+	.	.
Elevation	—	—	.	.
Biome: aquatic			—	
Biome: wooded			+	
Biome: developed				
Biome: open				
Specialist diet			+*	
Generalist diet			—*	
Ground nest				
Elevated nest				
Nest structure: protected	—*			+
Nest structure: structured		+		+
Nest structure: minimal				—
Altricial nestling development			—	—
Precocial nestling development			+	+
Biparental/cooperative parental care	—*		—*	
Uniparental care			+*	
Average body size			+	~ *

Table 2.4. Parameter estimates from generalized linear models assessing the relationship between species-specific and study site characteristics and *daily* responses of reproductive success (n = 64). Precipitation type is a categorical variable with daily precipitation as the reference level. Biome is a categorical variable with aquatic biomes as the reference level. Nest structure is a categorical variable with minimal nests as the reference level. Parental care is a categorical variable with biparental as the reference level.

	Parameter estimate	**Std. error**	***P*-value**
(Intercept)	1.5731304	0.5966663	0.01187
Direct precipitation	-0.0557663	0.2659003	0.83495
Lagged precipitation	0.3966952	0.3954706	0.32184
Biome: aquatic	-0.7959658	0.4786392	0.10413
Biome: developed	1.4688216	0.8931699	0.10791
Biome: open	-0.6002806	0.4209981	0.16167
Elevation	-0.0006326	0.0001851	0.00146
Specialist diet	-0.3882007	0.3222483	0.23541
Ground nest	0.1795911	0.4123794	0.66554
Nest structure: protected	-1.5681899	0.5252429	0.00481
Nest structure: structured	-0.7315087	0.4098540	0.08188
Precocial nestling development	-0.9234033	0.5501524	0.10106
Cooperative parental care	-2.2191335	0.9176906	0.02024
Uniparental care	0.5216636	0.5882440	0.38048
Average body size	-0.0002161	0.0001238	0.08850

Table 2.5. Parameter estimates from generalized linear models assessing the relationship between environmental characteristics of study sites and *nesting period* responses of reproductive success (n = 131). Precipitation type is a categorical variable with nesting period precipitation as the reference level. Biome is a categorical variable with wooded biomes as the reference level. Nest structure is a categorical variable with minimal nests as the reference level. Parental care is a categorical variable with biparental as the reference level.

	Parameter estimate	**Std. error**	**P-value**
(Intercept)	-0.29835267	0.25788825	0.249687
Direct precipitation	-0.76120429	0.23156434	0.001339
Lagged precipitation	0.62640080	0.16641614	0.000264
Biome: aquatic	-0.59840577	0.21713729	0.006800
Biome: developed	0.08939634	0.33009513	0.787011
Biome: open	-0.12183705	0.17779982	0.494554
Elevation	-0.00024606	0.00011461	0.033882
Specialist diet	-0.05364101	0.15800844	0.734861
Ground nest	0.33769794	0.25051162	0.180274
Nest structure: protected	0.10040932	0.21675814	0.644066
Nest structure: structured	0.75390237	0.24629542	0.002742
Precocial nestling development	0.54695270	0.31775146	0.087858
Parental care: cooperative	-0.19693983	0.30525391	0.520093
Parental care: uniparental	0.16172093	0.51225544	0.752795
Average body size	0.00004588	0.00004225	0.279744

Table 2.6. Parameter estimates from phylogenetically-independent Generalized Least Squares regressions assessing the relationship between species-specific characteristics and *daily* responses of reproductive success. Parameter estimates and confidence intervals are averaged (mean) across all 1,000 phylogenetic trees. Predictors with asterisks have at least one group with non-overlapping 95% CIs and differing directional effects.

Group	**# of species**	**Parameter estimate**	**95% CI**
Biome *			
Aquatic	7	-1.20	-1.224, -1.167
Wooded	8	0.294	0.266, 0.323
Open/developed	22	-0.770	-0.799, -0.742
*Diet**			
Specialist	10	0.422	0.252, 0.592
Generalist	19	-3.265	-3.400, -3.132
Nest location			
Elevated	11	0.584	0.569, 0.599
Ground	18	0.353	0.338, 0.368
Nest type			
Minimal	10	-0.154	-0.180, -0.128
Structured	15	-0.640	-0.666, -0.614
Protected	4	-0.136	-0.163, -0.110
Nestling development *			
Altricial	19	-0.186	-0.199, -0.172
Precocial	10	0.019	0.006, 0.032
Parental care *			
Uniparental	8	0.019	0.018, 0.020
Biparental/cooperative	21	-0.001	-0.003, 0.000
Average body size *			
<20 g	6	-0.389	-0.530, -0.248
20-45 g	8	-.909	-0.978, -0.840
46-400 g	5	-0.007	-0.080, 0.066
>400 g	10	0.019	-0.049, 0.088

Table 2.7. Parameter estimates from phylogenetically-independent Generalized Least Squares regressions assessing the relationship between species-specific characteristics and responses of reproductive success throughout *nesting period*. Parameter estimates and confidence intervals are averaged (mean) across all 1,000 phylogenetic trees. Predictors with asterisks have at least one group with non-overlapping 95% CIs and differing directional effect sizes.

Group	**# of species**	**Parameter estimate**	**95% CI**
Biome			
Aquatic	6	0.319	0.290, 0.347
Wooded	16	0.0594	0.03, 0.088
Open/developed	15	0.125	0.096, 0.153
Diet			
Specialist	11	0.130	-0.010, 0.269
Generalist	25	0.319	0.186, 0.451
Nest location			
Elevated	28	0.350	0.335, 0.365
Ground	8	0.987	0.972, 1.002
Nest type *			
Minimal	11	-0.896	-0.922, -0.870
Structured	8	0.374	0.348, 0.400
Protected	17	0.430	0.404, 0.456
Nestling development *			
Altricial	32	-0.035	-0.048, -0.023
Precocial	4	0.742	0.602, 0.882
Parental care			
Uniparental	2	0.021	-0.113, 0.156
Biparental/cooperative	34	-0.001	-0.001, -0.001
Average body size *			
<20 g	4	-0.150	-0.218, -0.082
20-45 g	12	-0.034	-0.103, 0.035
46-400 g	8	0.070	-0.006, 0.147
>400 g	12	-0.352	-0.436, -0.268

Figures

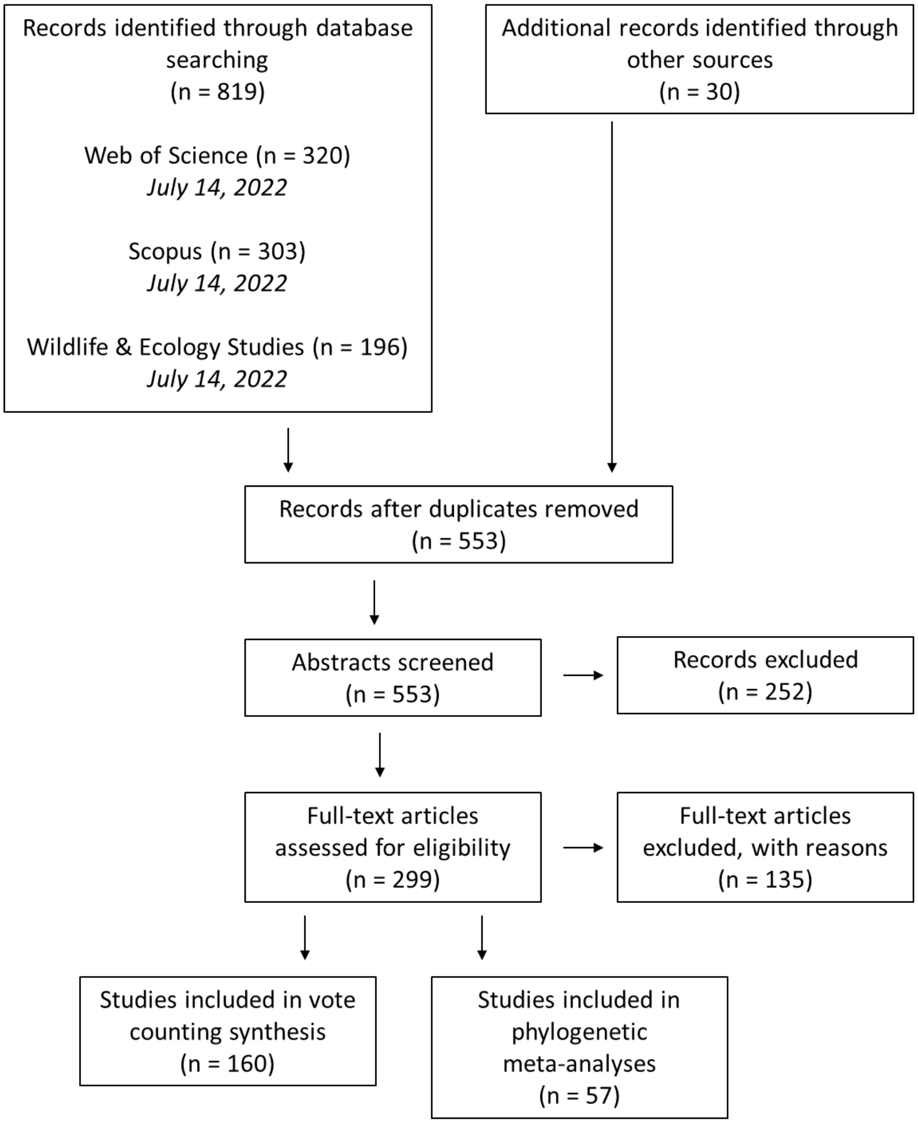

Figure 2.1. Flowchart adapted from Transparent Reporting of Systematic Reviews and Meta-analyses (PRISMA) methods of sources included in vote counting synthesis and meta-analyses to test alternative explanations for how and why bird reproductive success varies in response to precipitation.

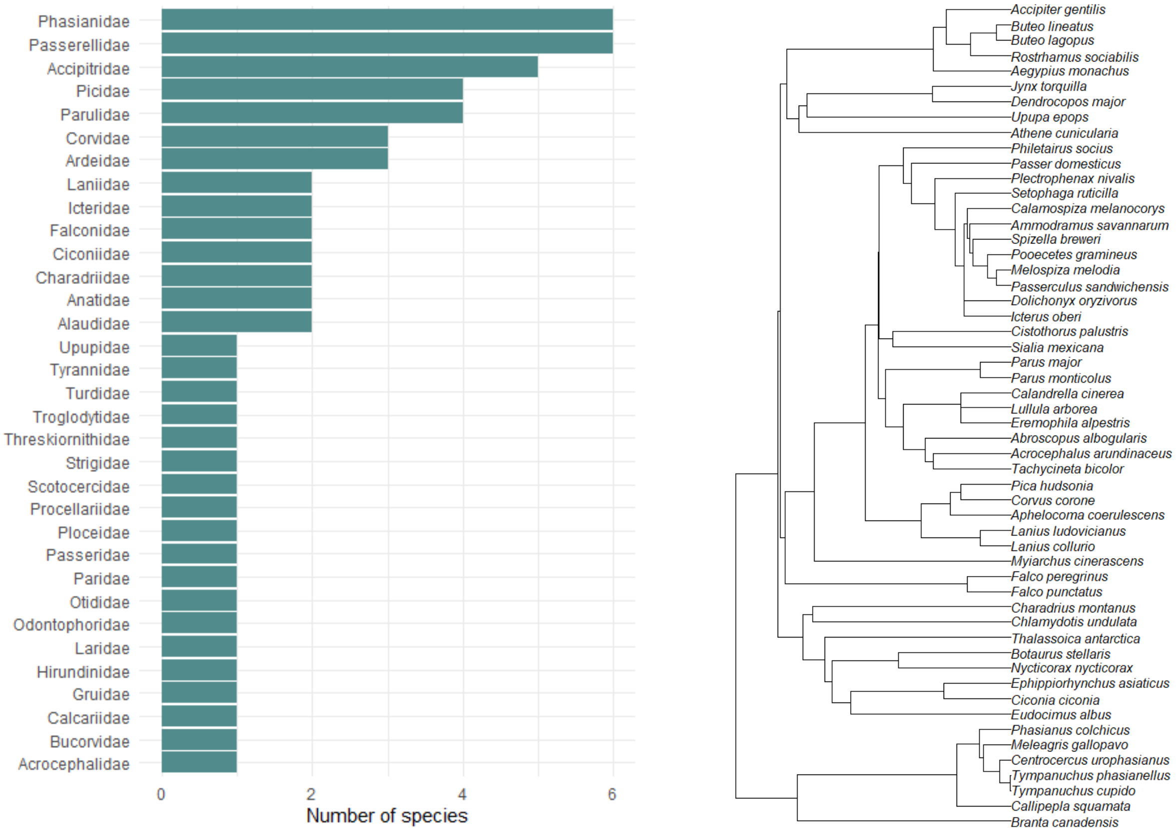

Figure 2.2. Histogram (left) and representative phylogenetic tree (right) for all species included in species-level analyses. The phylogenetic tree is one of the 1,000 trees used in the phylogenetic meta-analyses.

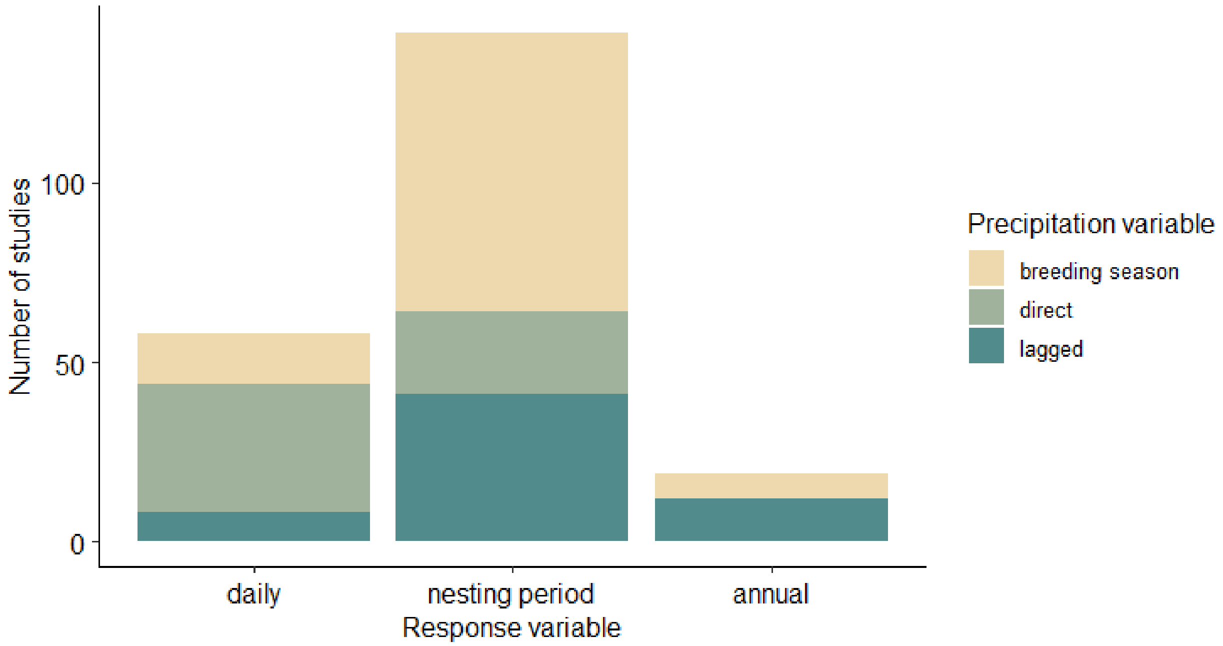

Figure 2.3. Bar plot of response and precipitation variables represented in each study of the vote counting analyses. A "daily" response variable indicates the original study estimated daily nest success, "nesting period" indicates the original study estimated nest success across the entire nesting period, and "annual" indicates the original study estimated an annual metric of nest success across multiple nesting pairs. Precipitation variables in the original studies varied from "direct" precipitation (i.e. precipitation within 48 hours), to "breeding season" precipitation (i.e. precipitation aggregated throughout the nesting period or breeding season) or "lagged" (i.e. precipitation that occurred anytime before the start of the breeding season or aggregated at an annual extent). Most studies included in the analysis summarized reproductive success at the nest level and used a precipitation metric across the breeding season. Some studies included multiple response and/or precipitation variables for the same species.

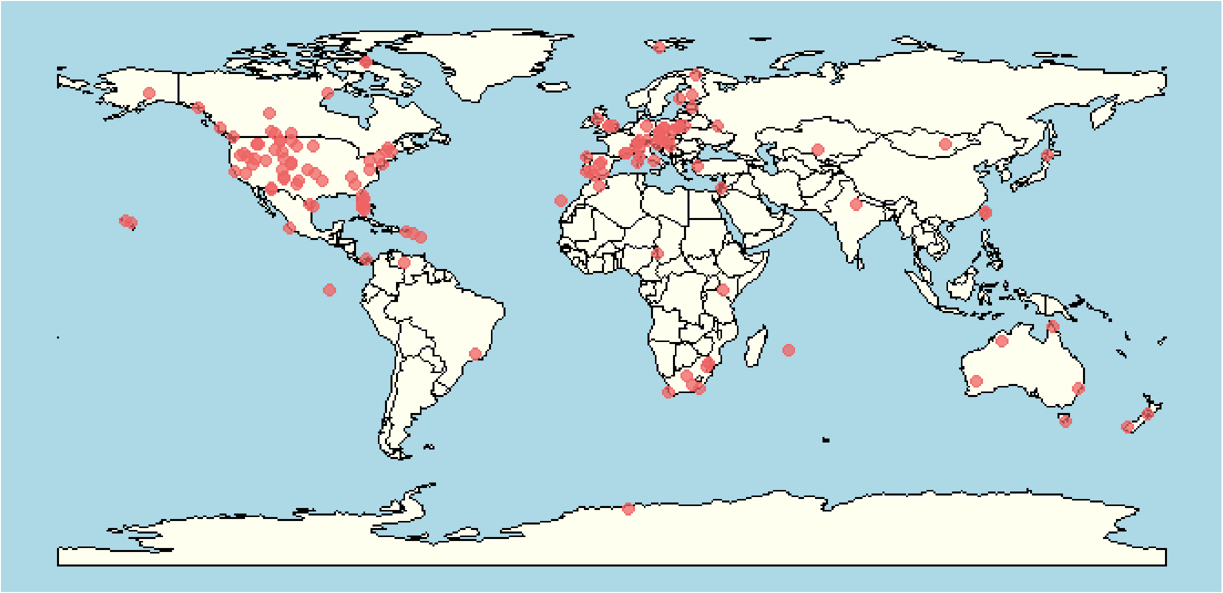

Figure 2.4. Map of study locations included in quantitative analyses (i.e. vote-counting analyses and meta-analyses). Each point represents a study.

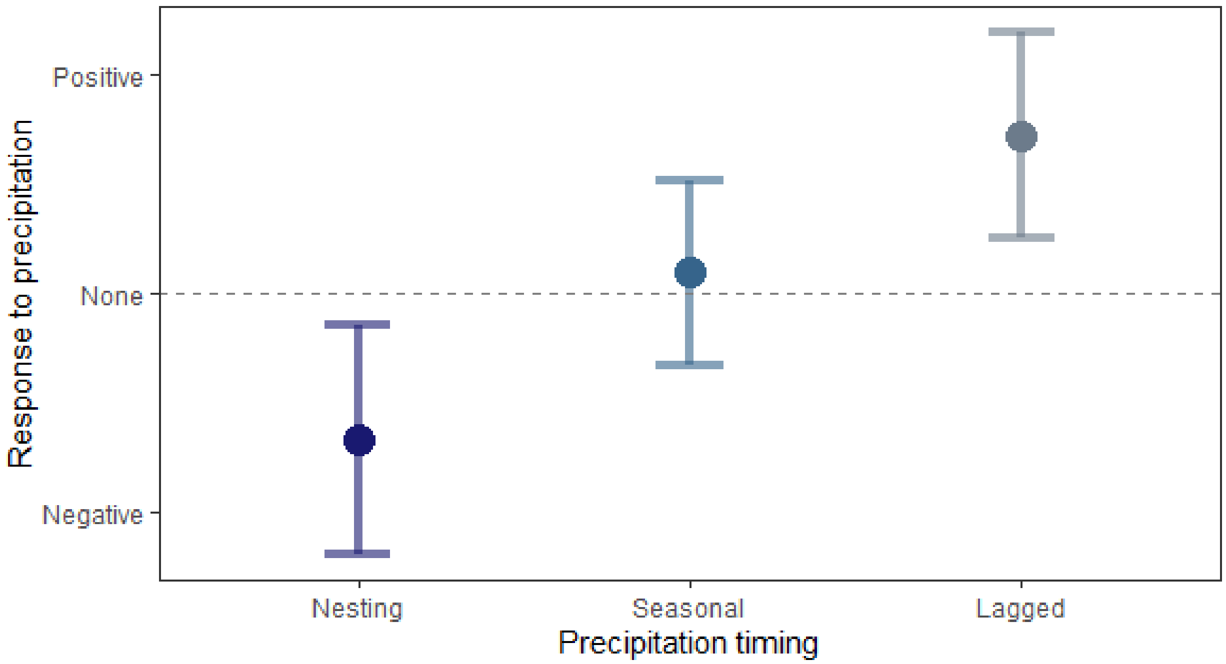

Figure 2.5. Effect of precipitation on nest success. Reproductive success declines in response to direct precipitation but increases in response to precipitation prior to the breeding season. Points are parameter estimates from vote-counting analyses and error bars are 95% confidence intervals.

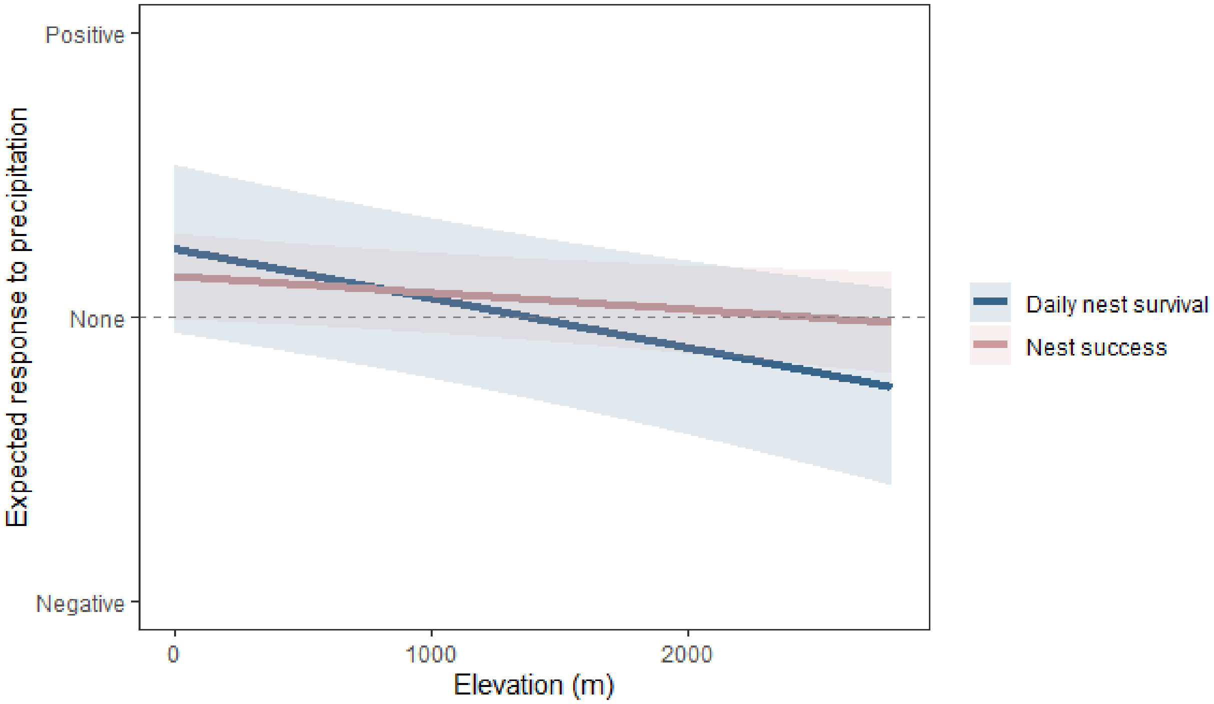

Figure 2.6. Expected response to precipitation for daily reproductive metrics (blue) and nest-level reproductive metrics (pink) across an elevational gradient. Reproductive success declines at higher elevations, with a more notable response in daily nest survival than nest success. Transparent areas indicate 95% confidence intervals.

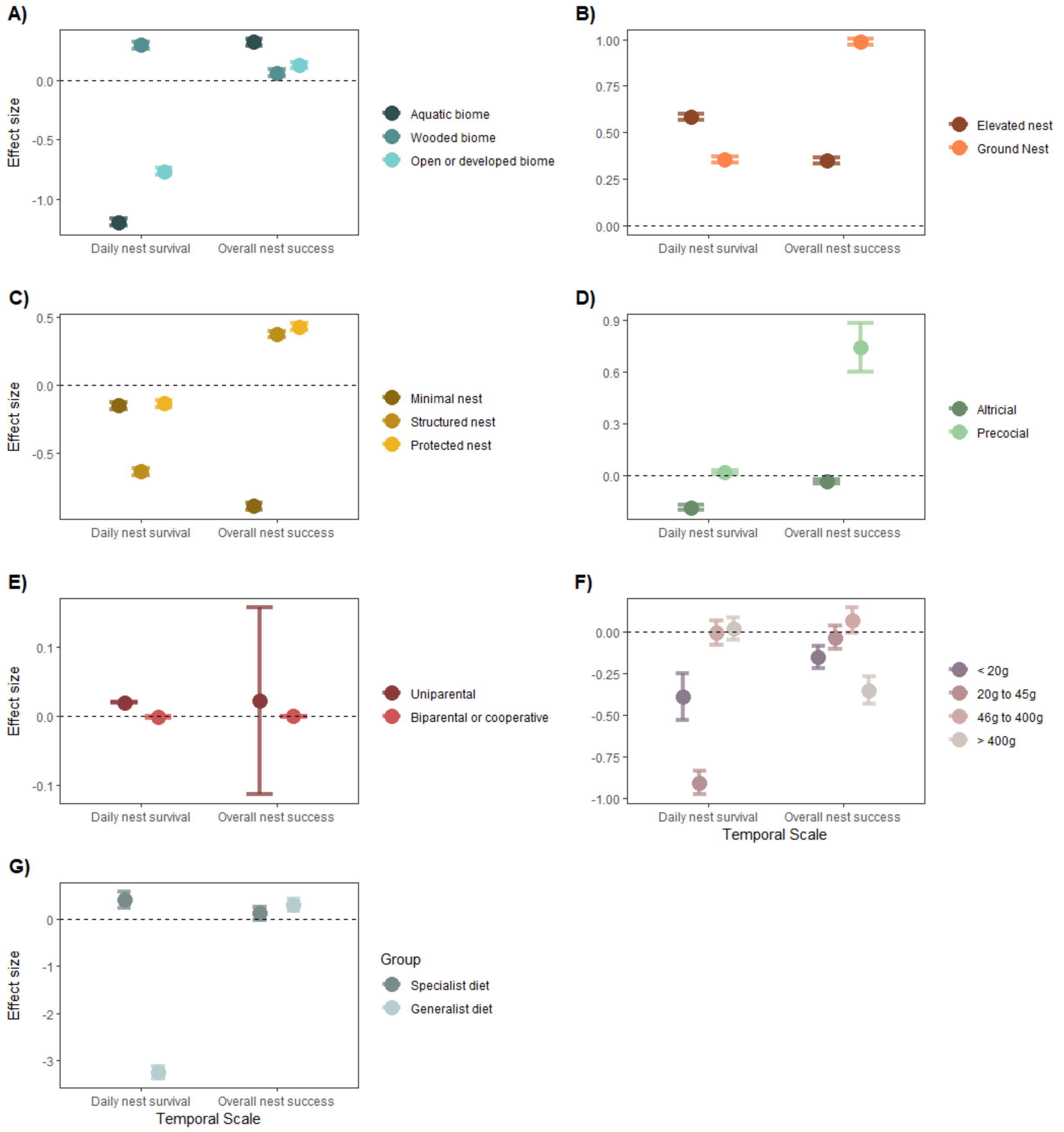

Figure 2.7. Results from phylogenetic meta-analyses for the effects of precipitation on species by biome (A), nest location (B) nest structure (C), nestling development (D), parental care (E), average body size (F), and diet breadth (G). Points are the mean of effect sizes estimated across 1,000 phylogenetic trees, and error bars are 95% CI estimated using univariate generalized least squares models. Note: y-axes differ between panels.

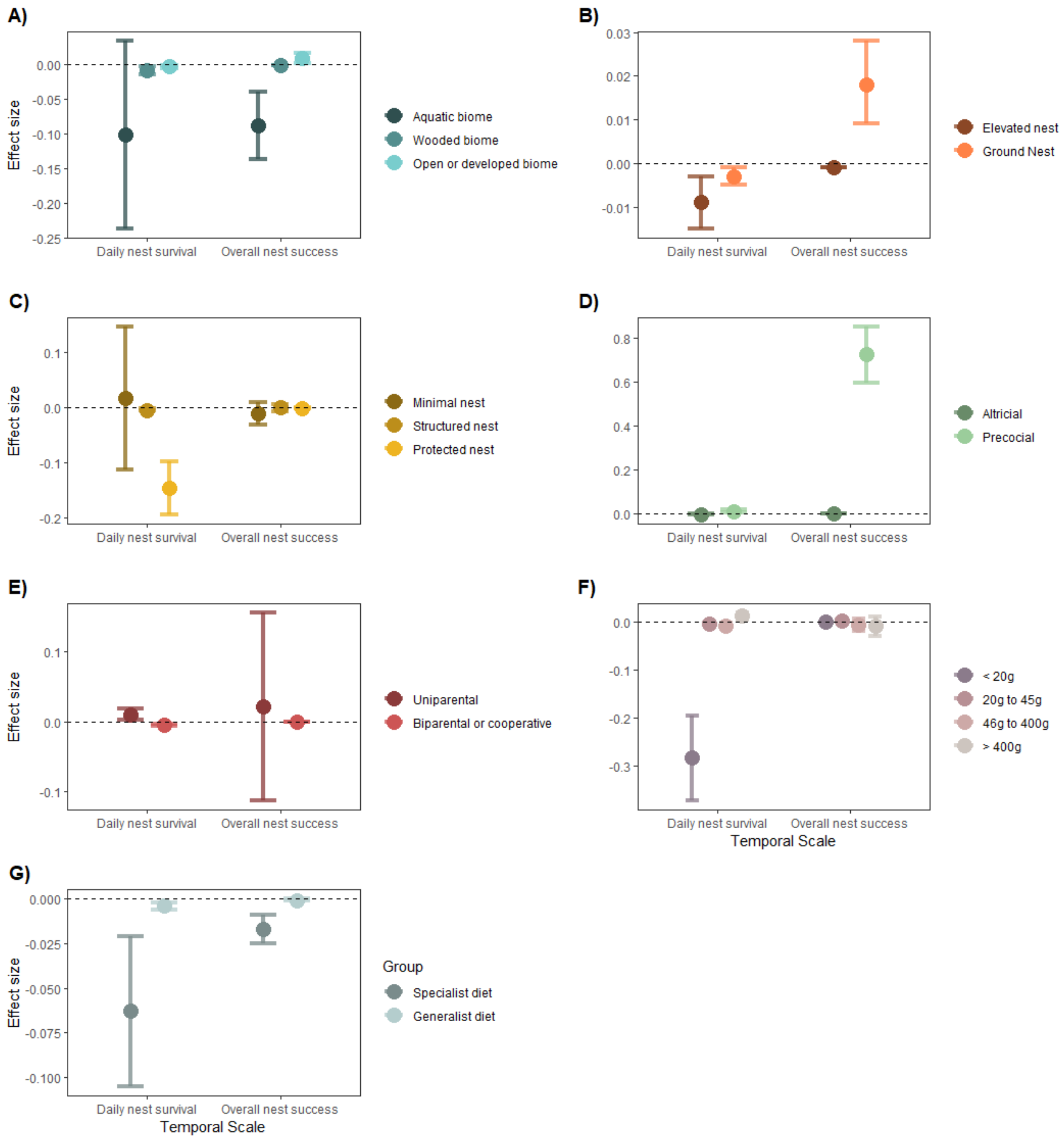

Figure 2.8. Results from traditional meta-analyses for the effects of precipitation on species by biome (A), nest location (B) nest structure (C), nestling development (D), parental care (E), average body size (F), and diet breadth (G). Points are the mean of effect sizes estimated across 1,000 phylogenetic trees, and error bars are 95% CI estimated using univariate generalized least squares models. Note: y-axes differ between panels.

Chapter 3 - Population growth rate is most sensitive to apparent survival in a mobile grassland songbird

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Abstract

In mobile species, population growth is determined by births, deaths, immigration, and emigration. Each of these vital rates may vary in response to environmental conditions, such as weather variability and land management, which affect processes from primary production up through animal communities. The Central Great Plains of North America is a highly dynamic biome and is subject to variable weather and land management across space and time. Grassland species are thought to have evolved plasticity in their life history traits and behavior in response to this variability. For example, grassland birds often disperse during or in between breeding seasons, which ultimately may influence population growth in the following years. However, we know little about how weather variability impacts population dynamics and the importance of movement for population growth relative to variation in other vital rates such as births and deaths. We estimated changes in Grasshopper Sparrow (*Ammodramus savannarum*) population growth rate using vital rate estimates from an integrated population model based on data from 2013-2021 at the Konza Prairie Biological Station in NE Kansas. Population growth rate was more sensitive to adult apparent survival (i.e., the summation of true survival and emigration) than to fecundity, juvenile survival, or immigration. Because adult apparent survival in this system is shaped more by movement (i.e. emigration) than mortality, these results suggest population declines are largely mediated by adults dispersing from the study site. Projections of population size using these vital rate estimates indicate Grasshopper Sparrows may be locally extirpated in the next under future climate scenarios. Our study suggests quantifying emigration within mobile species will be critical for predicting trends in population growth and guiding regional conservation, particularly in declining species.

Introduction

Populations change over time in response to intrinsic and extrinsic factors. These changes manifest as fluctuations in population size (e.g., Hopkins and Kennedy 2004, Oparina et al. 2016, Hammond et al. 2021), but estimates of population size may not detect extinction debts (Lehtilä et al. 2016), demographic bottlenecks (Giménez-Benavides et al. 2008), and interactions between individual vital rates (Coulson et al. 2005, Doak et al. 2005). Population size may oscillate or exhibit directional growth (either positive or negative); however, frequent fluctuations in population size, a product of changes in individual vital rates, are more likely to lead to local or broad scale extinctions than stable population trajectories (Morris and Doak 2002). Variation in individual vital rates regulate the nature and magnitude of population change over time, ultimately determining population persistence. Therefore, understanding the mechanisms underlying relative contributions of individual vital rates to population change is essential for prioritizing conservation initiatives.

Estimating vital rates can be particularly challenging in mobile species because more vital rates are needed within analyses and individuals frequently leave the study area, making it difficult to track individuals to obtain vital rate estimates (Lebreton et al. 1992). In migratory species, vital rates may be sensitive to factors affecting them at certain times or locations throughout their annual cycles (e.g., in areas of degraded habitat or during energy-intensive activities such migration or reproduction; Flockhart et al. 2015). These processes may reduce accuracy of vital rate estimates or obscure mechanisms underlying responses of vital rates to environmental factors like precipitation.

Estimates of the impacts of precipitation variability are easier to detect in dynamic systems, such as grasslands, due to their inherent precipitation variability allowing for observations of populations under a range of hygric conditions. Grassland birds exhibit variation in survival (Wellicome et al. 2014), reproduction (Londe et al. 2020), and dispersal (Smith 2021) in response to precipitation. Grasshopper Sparrows are grassland-obligate songbirds that respond to precipitation throughout their life cycles. Nests are more likely to fail following heavy storms (Freeman and Boyle, unpublished data). Adult males, however, incur lower survival in years of lower winter precipitation on their wintering grounds and make facultative movements in response to broad scale climate lagged two years, likely mediated by vegetation structure (Silber et al. 2023). These changes in individual vital rates likely drive interannual variation in local abundance, but we know little about how weather and variation in individual vital rates impact local Grasshopper Sparrow abundance. Furthermore, North American Grasshopper Sparrow populations have declined by 72% in the last 50 years and continue to decline by 3.1% each year (Road to Recovery 2022), presenting an urgent need to understand the dynamics behind these declines and project local abundances under future climate scenarios.

We estimated vital rates using an integrated population model for Grasshopper Sparrows in NE Kansas from 2014-2021. We quantified relationships between estimated vital rates and three weather variables, used these weather-dependent vital rates to build a population model, and perturbed individual vital rates to assess the relative contribution of each vital rate on overall population growth. We then projected population growth rate under several future climate models over the next 80 years to estimate the population trajectory.

Methods

Study site

We studied Grasshopper Sparrows on the Konza Prairie Biological Station and Rannell's

Pasture in Northeastern Kansas. Konza Prairie is a 3,487 hectare native tallgrass prairie preserve in The Flint Hills Ecoregion (39°05’ N, 96°35’ W) and has been managed as an experimental Long Term Ecological Research (LTER) site for >40 years. The site is divided into 46 experimental units with replicated fire (1-, 2-, 4-, or 20-year burns) and grazing (bison-, cattle-, or ungrazed) regimes, as well as two patch-burn grazing units. Each patch-burn grazing unit consists of three pastures, one of which is burned annually in rotation. Rannell’s Pasture, a 1175 ha site adjacent to Konza, is annually burned and intensively, early cattle stocked (Owensby et al. 2008).

Study species

Grasshopper Sparrows (*Ammodramus savannarum*) are small (~17g), grassland-obligate, migratory songbirds. They 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 further into Mesoamerica and the Caribbean (Vickery 2021). The exact wintering sites for Kansas breeding population are unknown, but preliminary evidence from geolocators suggests that they overwinter in Texas and Northern Mexico. They are present in Northeastern Kansas from mid-April to September. Populations of migratory Grasshopper Sparrows vary considerably in their dispersal behavior, 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). Approximately 30-47% of the breeding males from our site that survived the winter dispersed to new breeding sites (Silber et al. 2023), with some individuals breeding at sites at least 80 km away (Boyle & Sullins, *in review*).

Grasshopper Sparrows nest between early May and late July, using litter and grasses to create domed, woven nests (Ruth and Skagen 2018). Males and females differ in their breeding behavior; territorial males perch and sing from tall forbs and fences, and females primarily remain on the ground among dense grasses (Vickery 2021). Females incubate eggs and brood young, and both parents are responsible for feeding young (Vickery 2021). The nesting period lasts for up to 19 days, with 11 days for incubation and young fledging within 5-10 days (Ruth 2017, Winnicki 2019). Grasshopper Sparrows at our site have remarkably low nest success; less than 14% of nests successfully fledge at least one host nestling (Winnicki 2019). The post-fledge period is often characterized by high rates of mortality as young are not fully developed and are therefore at risk of predation and inclement weather (Kaspari & O'Leary 1988). Juveniles reach sexual maturity the following breeding season (Vickery 2021).

Field methods

We captured and banded Grasshopper Sparrows within 12 study units: 2 patch-burn cattle-grazed units; 2 cattle-grazed, annually burned units; 2 bison-grazed, annually burned units; 2 bison-grazed, biennially burned units; 2 ungrazed, annually burned units; and 2 ungrazed, biennially burned units. Each unit contained a randomly-located 10 ha plot. We intensively captured and surveyed within these plots at least every ten days and sampled opportunistically throughout the entirety of each unit throughout each breeding season. To capture birds, we placed a 12 x 2.5m mist net (Ecotone, Gdynia, Poland; 32mm mesh size) adjacent to perches where we had observed territorial males sometime between late April and early August from 2013-2021. At the base of each net, we placed a small audio player and speaker broadcasting conspecific song to attract territorial males. We fitted each individual with a numbered United

States Geological Survey band and a unique combination of 3 color bands (i.e., total of two bands per leg). We determined age and sex of each bird using plumage, cloacal protuberances, and brood patches (only females incubate; Bent & Austin 1968). We aged newly captured birds in the field as HY (hatch year) or AHY (after hatch year); all individuals undergo a complete pre-basic molt in late summer and early fall, so they cannot be aged as second years or older without previous records (Pyle et al. 2008). We attempted to capture all unmarked territory holders and recapture site-faithful individuals marked in previous years in every study unit. Due to the frequency of within-season dispersal (Williams & Boyle 2018), we revisited each pasture unit repeatedly to capture birds throughout the whole season. We determined the identity of each individual using 8 x 42 binoculars, 10x scopes, and/or high zoom cameras to confirm color band combinations. Each survey was conducted by one observer, but larger units were split between two observers to ensure the whole area was adequately surveyed within earshot. Each observer worked in conjunction with a crew leader until survey methods and bird IDs were consistent with the crew leader. Observers walked different routes each survey 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 searched for nests between early May and late July 2013-2021. Given the secretive nature of nests and breeding behavior, we used a combination of rope-dragging (Higgins et al. 1969), behavioral observation, and opportunistic foot flushing to detect nests. We then marked nests with using GPS units (GPSmap 60CSx, Garmin, Olathe, KS, U.S.A.) and painted rocks and flagging 5 m from the nest opening and 5 m perpendicular to the nest opening for ease of relocation. We counted number of eggs and/or nestlings present, and candled eggs to estimate lay date (Lokemoen & Koford 1996). We returned to each nest every 2-3 days to monitor partial egg or brood loss, fledged young, and nest failures. We coded a nest as having successfully fledged young if a juvenile was observed near the recently fledged nest or if parents were observed making alarm calls or carrying food near the nest once it was empty. A subset of nests also contained nest cameras, which we cross-referenced with our fledge estimates and found we correctly estimated successful fledging success ~97% of the time (Williams & Boyle 2019).

Estimating vital rates: integrated population model

We fit an integrated population model (IPM), similar that of Woodworth et al. (2017), to estimate annual grasshopper sparrow vital rates and population growth. We used a state-space model to generate annual, sex-specific estimates for the number of recruits, surviving adults, and immigrants. Recruits (R) were individuals born in the study area in the previous year, surviving adults (S) were two or more years old and had bred at the study site in the previous year, and immigrants (I) were adults two or more years old that were not observed at the study site in the previous year. We estimated stage-specific counts using binomial and Poisson distributions (Woodworth et al. 2017).

We fit Cormack-Jolly-Seber models to estimate sex-specific juvenile apparent survival (ϕ_j) and adult apparent survival (ϕ_a). We estimated juvenile survival (ϕ_j) as the probability of a juvenile surviving from fledge in one breeding season (t) until returning to the study site as an adult the following breeding season ($t + 1$). We estimated adult survival (ϕ_a) as the probability of an individual two or more years old surviving from one breeding season (t) to the next ($t + 1$) and returning to the study site. In adult male Grasshopper Sparrows, approximately 25% of apparent survival is attributed to mortality and over 50% to emigration (i.e. individuals surviving but moving out of the study site; Silber et al. 2023).

To estimate productivity, we fit a regression model with a Poisson distribution. Because females may have multiple nest attempts per season and often disperse between re-nesting attempts, we did not track the fate of every nest for a female and could not estimate individual fecundity at the population level. Thus, we estimated fecundity (F), as the total number of fledglings produced over the total number of females surveyed each year.

We used these count and vital rate estimates to predict annual population growth rates. We used Markov chain Monte Carlo (MCMC) to fit the IPM in a Bayesian framework in R version 4.1.1 (R Core Team 2023) using the package jagsUI (Kellner 2016). We used three independent chains for 1,500,000 iterations (burn in = 750,000 and thin =100). We fit the IPM using informative priors with uniform distributions, informed by preliminary data at our study site and published literature. Initial population size limits were 80 to 350 individuals. Fecundity was set to 0 to 14 because Grasshopper Sparrows may produce two or more broods per breeding season (Wray et al. 1992, Vickery et al. 1992). Immigration was constrained to 0 to 150. Juvenile survival was limited to 0.1-0.5, and adult survival was limited to 0.3-0.9. Recapture rates were constrained to 0 to 0.3 for juveniles, 0 to 0.5 for adult females, and 0 to 1 for adult males.

Weather variables

We calculated three weather variables previously shown to be associated with Grasshopper Sparrow physiology and vital rates to quantify the relationship between weather, vital rates, and population growth. We downloaded daily precipitation data from the 4-km Gridded Surface Meterological (gridMET) dataset (Abatzoglou 2013) to calculate storms throughout each breeding season. We expected storms might reduce nest success via flooding.

We classified precipitation as a storm event if more than 18.21 mm of precipitation fell within a day (i.e. one standard deviation above the mean, Freeman et al. 2023), and summed the number of storms per breeding season (May 1 – August 31). The El Niño-Southern Oscillation Precipitation Index across the breeding season and lagged two years ($ESPI_{t-2}$) exhibits a curvilinear relationship with Grasshopper Sparrow emigration rates (Silber et al. 2023), therefore we expected it might influence the population growth rate. We downloaded monthly ESPI data from the University of Maryland Global Precipitation Climatology Project (2020) and summed the ESPI across the breeding season (May – Aug) and lagged it by two years. Because metrics of temperature that take into account humidity (i.e. wet bulb temperature) more accurately reflect thermoregulatory costs than temperature under dry conditions (Gerson et al. 2014, Freeman et al. 2023), we predicted that higher wet bulb temperatures would be associated with mortality of young and adult birds, influencing the population growth rate. We downloaded daily maximum temperature data from gridMET and calculated daily high wet bulb temperature using the equation from Stull (2011). We then calculated the average high wet bulb temperature for each breeding season.

Path analysis

We used a path analysis similar to that of Woodworth et al. (2017) and Sutton et al. (2021) to assess the relative contributions of weather variables to variation in vital rates and the population growth rate. We scaled all weather variables by subtracting the mean and dividing by the standard deviation. We used multiple linear regression to estimate the correlations between the weather variables (presence of storms, lagged breeding season precipitation, and wet bulb temperature) on each vital rate, and the consequent effects of each vital rate on the population growth rate. We fit each regression to the sample of the posterior distribution for each vital rate generated by the IPM. We ran each path (i.e. regression) for 225,000 iterations, then calculated the direct effects of each weather variable on each vital rate and the effects of each vital rate on the population growth rate. We considered the product of these two direct pathways to be indirect effects of weather on the population growth rate. To obtain the indirect effect of each weather variable on the population growth rate, we summed the effects across all vital rates.

Climate projections

We used the weather variable with the greatest effect size from the path model to estimate the population size under future climate scenarios. We used climate data from gridMET for weather conditions during our study period and Multivariate Adaptive Constructed Analogs (MACA) global climate models from the Climatology Lab (Abatsoglou and Brown 2012) to project future climate conditions. Because ESPI is estimated from a source other than gridMET, we extracted daily precipitation from the gridMET dataset across our study site and summed these data from May 1 – August 31, then lagged these estimates by two years. We downloaded monthly, projected precipitation data from 18 MACA models, summed precipitation across the breeding season (May – August), then lagged these estimates by two years.

We selected these datasets, as opposed to using the ESPI values, because the underlying climate models of gridMET and MACA are analogous, allowing us to pair current and projected climate data. Using the weather metric from the path model with the greatest effect on population growth, we fit a regression to predict weather-mediated changes in the population growth rate. We projected the population growth rate from our regression under each of the 18 MACA model-predicted climate scenarios from 2021-2100. Using the projected population growth rate estimates, we estimated future abundance from 2021-2100.

Sensitivity analyses

We used the annual vital rates derived from the integrated population model to construct a simple stage-based population model. We estimated population size in a given year (t) as $N_t = I_t + \left(N_{t-1} * \phi_{a,t}\right) + (N_{t-1} * F_t) * \phi_{j,t}$, using male estimates of juvenile apparent survival (ϕ_j) and adult apparent survival (ϕ_a), male immigration estimates (I_t), and fecundity estimates (F_t). We estimated stochastic lambda as the geometric mean of annual lambdas over the 7 transitions (Morris and Doak 2002).

We then used a perturbation approach to estimate sensitivity and elasticity to each of our four vital rates (fecundity, juvenile apparent survival, adult apparent survival, and immigration). To estimate the sensitivity to one vital rate, we perturbed the vital rate values for all years by 5% and then recalculated stochastic lambda. We estimated the change in vital rate values resulting from these perturbations by averaging changes in the vital rate across years.

Results

Between 2013-2021, we surveyed each pasture approximately once every 10 days throughout the breeding season to resight color-banded individuals. We surveyed each study unit an average of 9 times (range: 8-10 rounds) between late April and late July each year. We captured and banded 277 adult females, 1,640 adult males, 20 juvenile females, and 36 juvenile males. We also banded 925 juveniles of unknown sex. We found 498 Grasshopper Sparrow nests, with an average of 3.32 eggs (range = 0-7), 1.67 nestlings, and 0.85 fledglings per nest. The mean fecundity estimate was 0.92 (range = 0.64-1.13), the mean juvenile survival estimate was 0.21 (range = 0.13-0.28), the mean adult survival estimate was 0.55 (range = 0.31-0.83), and the mean immigration estimate was 84 (range = 35-100). The average lambda for this population was 1.09 (range = 0.88 to 1.69).

Weather was highly variable throughout the study period. During the breeding season, the number of storms ranged from 4 to 10, the breeding season ESPI_{t-2} ranged from -4.4 to 10.7, and the daily high wet bulb temperature ranged from 8.33° to 30.38° C. Breeding season ESPI_{t-2} had the most pronounced effect on the population growth rate (mean = -0.19, 90% CI = -0.57, 0.21). However, the 90% credible intervals for all weather variables (storms: mean = -0.04, 90% CI: -0.18, 0.08; wet bulb temperature: mean = -0.01, 90% CI: -0.68, 0.65) overlapped zero.

Because the breeding season ESPI_{t-2} had the greatest effect on the population growth rate, we used breeding season precipitation lagged two years to project the population growth rate from 2021 to 2100. The gridMET breeding season precipitation data lagged two years was highly correlated with the breeding season ESPI_{t-2} (r = 0.73), and the population growth rate declined following wetter years ($\hat{\beta}$ = -0.0004, SE = 0.0003; Figure 3.2). The projected population growth rate across years and the 18 MACA models we evaluated was 0.98 (SE = 0.06; Figure 3.3), and the projected population size declined under all 18 MACA climate scenarios (Figure 3.4). Across all models, the median population estimate was expected to decrease to 87 individuals by 2100. One model projected the population size to drop below 100 individuals as early as 2050, and another model projected the population size to drop below 50 individuals as early as 2076.

Population growth rate was most sensitive to changes adult apparent survival (Figure 3.1). Sensitivity was highest for adult apparent survival (0.11), moderate for juvenile survival (0.10), and lowest for fecundity (0.03) and immigration (~0). The elasticity (i.e. proportional change in population growth rate) was also higher for adult apparent survival (0.08) than for fecundity (0.02), juvenile survival (0.02), and immigration (0.01).

Discussion

Grasshopper Sparrows are expected to decline under future precipitation scenarios and may be locally extirpated in the next 100 years. Declines in population size were most closely linked with declines in adult apparent survival, which is largely the product of emigration (Silber et al. 2023). The overall population growth rate was not strongly associated with weather variables previously documented to relate to specific vital rates in this population (Silber et al. 2023, Freeman et al 2023), which may result from divergent responses in each vital rate to weather, masking relationships between weather variables and demography. The high propensity of dispersal within this system and parallel declines at both local and regional scales (Road to Recovery 2022) imply the need for large scale, regional conservation initiatives.

The average population growth rate in this population across all years was positive, but the population growth rate exhibited high interannual variation. Variability in population growth rates and individual vital rates often leads to declines more than relatively stable population growth rates (Morris and Doak 2002). Interannual variation in the population growth rate was most sensitive to changes in adult apparent survival (i.e. the product of true survival and movement), which were highly variable each year. Although apparent survival is often equated with true survival, apparent survival in this population is shaped more by emigration than true survival (Silber et al. 2023).

Relationships between Grasshopper Sparrow vital rates and environmental variation are often mediated by vegetation structure. At our study site, 53-70% of adult males disperse to new breeding sites each year, likely reflecting changes in vegetation structure (Silber et al. 2023). Approximately 75% of territorial males disperse within the breeding season, usually in response to land management and nest failure (Williams and Boyle 2018, Williams and Boyle 2019). Nest success in Grasshopper Sparrows is associated with vegetation structure, mediated, in part, by precipitation in previous years (Ruth and Skagen 2018), and juveniles move to areas with higher vegetation cover (Small et al. 2015, Guido 2020). Because vegetation structure is associated with multiple vital rates in this species and other grassland birds (e.g., Anderson et al. 2015, Giovanni et al. 2015), population dynamics in grassland bird communities are likely intertwined with changes in vegetation structure.

Vegetation structure in grasslands is shaped by weather variability in combination with land management. Vegetation structure changes over relatively fine scales in grasslands systems in response to disturbances (Koerner and Collins 2013), and grassland birds exhibit preferences for specific vegetation structure and cover types (e.g., Rader et al. 2007, Hansen et al. 2016, Ruth and Skagen 2017). Grassland birds likely use vegetation cues to make inferences about risk of predation and vulnerability to environmental variation (e.g., storms), ultimately driving movement and settlement decisions. Given the propensity for movement in grassland birds (Jones et al. 2007), and the ultimate effects on local population persistence, management at a regional scale is imperative. Pastures with heterogenous vegetation and best support diverse communities of grassland-dependent species (Wiens 1969, Bakker 2003), but specific relationships between grassland birds vary by species (Wiens 1969) and time of season (Gehrt et al. 2020).

This study supports a growing body of evidence that population change is sensitive to vital rates of reproductive adults (e.g., Saether et al. 2000). Assessments that incorporate movement and long-term datasets are essential to fully understand the mechanisms underlying population change in response to environmental variation. Weather may have detectable effects on individual vital rates at certain periods throughout an animal's annual cycle. However, if responses within other vital rates or during other periods of an annual cycle have minimal or contradictory responses to the same weather, the net effect on population growth may be undetectable. Furthermore, animals may exhibit lagged responses to precipitation, the effects of which may not be detectable for several years. Reliable estimates of vital rates, their responses to weather, and their effects on population growth are essential for targeted conservation.

Figures

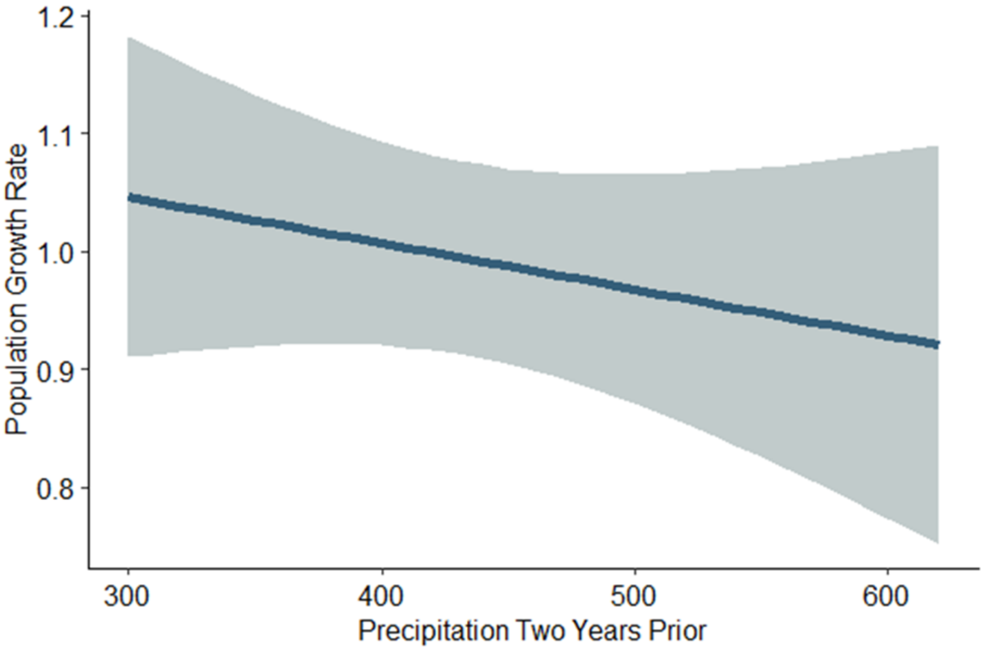

Figure 3.1. Relationship between breeding season precipitation two years prior and the population growth rate for Grasshopper Sparrows at the Konza Prairie, 2014-2021. The population is expected to decrease following wetter conditions. The line represents the expected population growth rate and the shaded region represents the 95% confidence intervals.

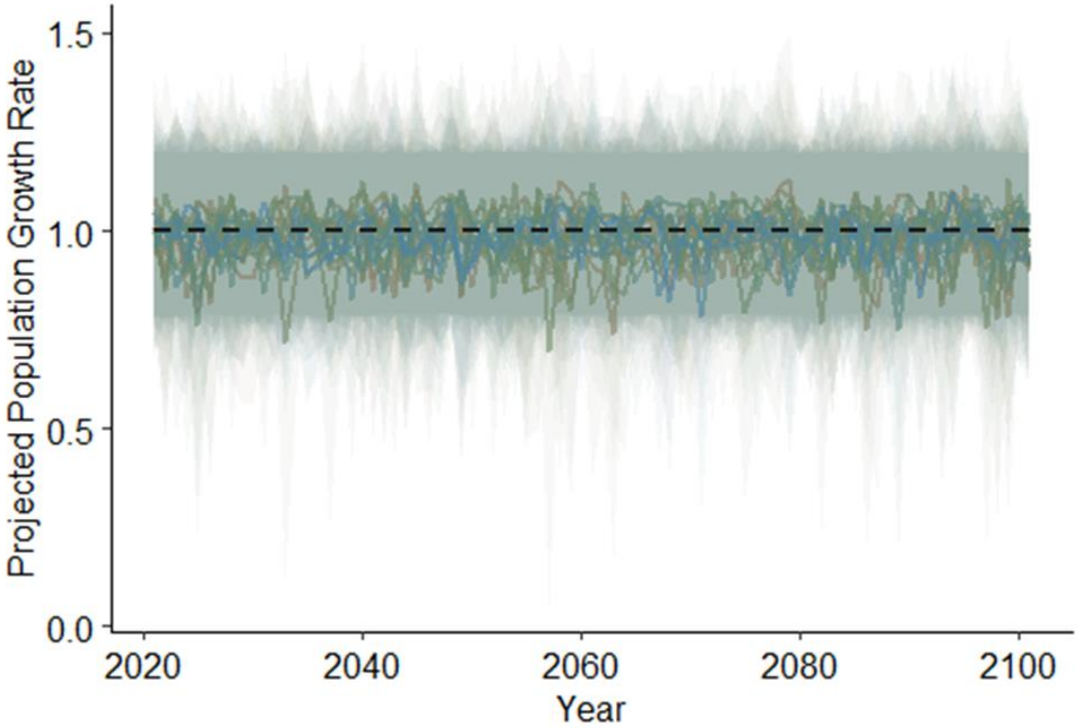

Figure 3.2. Projected population growth rates for Grasshopper Sparrows at the Konza Prairie, 2021-2100. Future population growth rates were calculated using projected breeding season precipitation lagged two years, derived from Multivariate Adaptive Constructed Analogs (MACA) global climate models. Each line represents projections derived from a different MACA global climate model and shaded areas are 95% confidence intervals around the projected population growth rate.

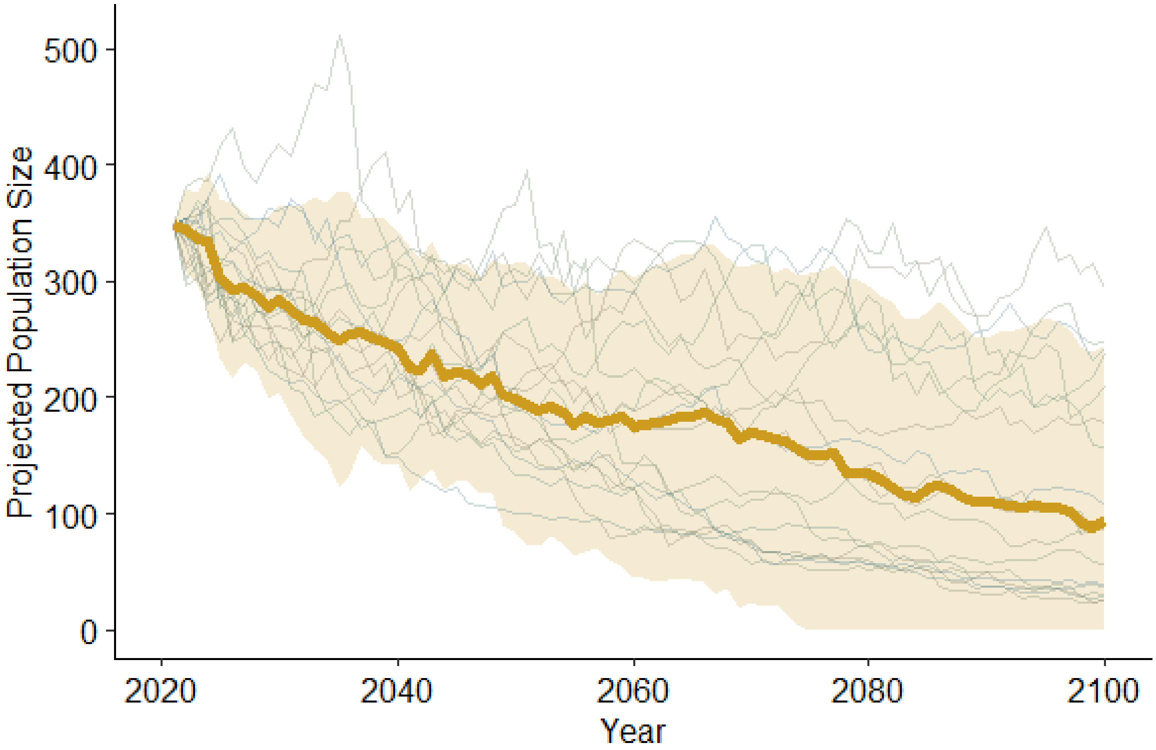

Figure 3.3. Projected population size for Grasshopper Sparrows at the Konza Prairie, 2021-2100. Future population sizes were calculated using projected breeding season precipitation lagged two years, derived from Multivariate Adaptive Constructed Analogs (MACA) global climate models. Each line represents a different MACA model. The yellow line and shaded region represent mean population size and 95% prediction interval for projected population size, respectively.

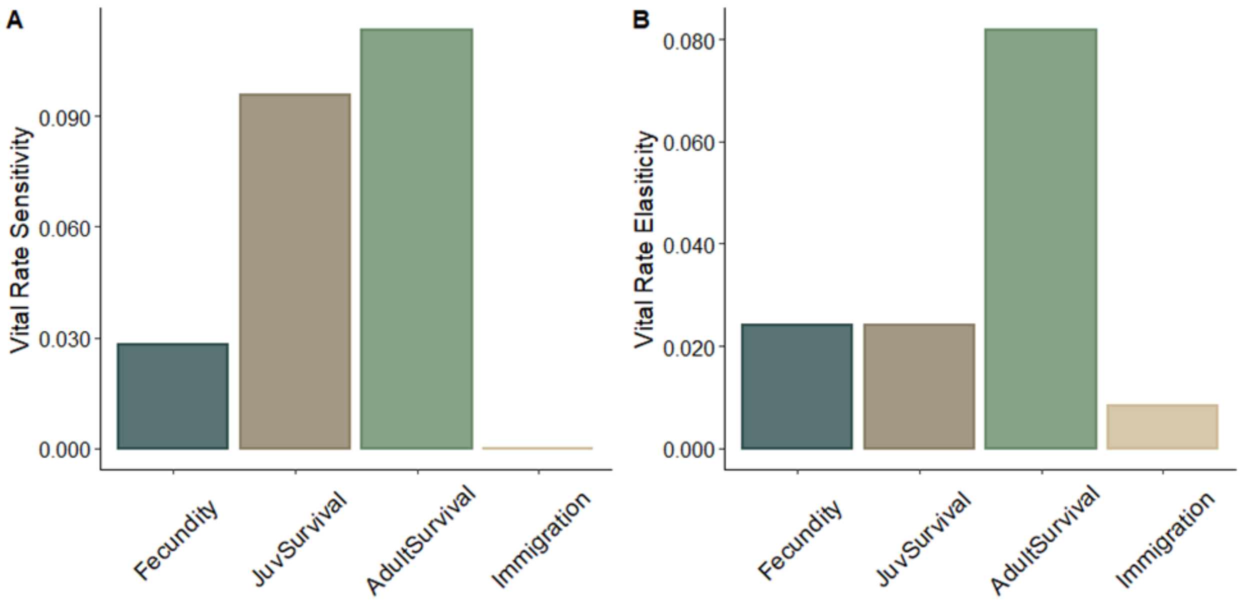

Figure 3.4. Percent change in the population growth rate (λ) given a 5% change in each vital rate each year (i.e. sensitivity; A). The proportional contribution, or percent change scaled for vital rate units, in the population growth rate (B). The population growth rate changes more in response to adult survival than in response to changes in juvenile survival, fecundity, or immigration.

Chapter 4 - 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 precipitation values. The relationship between precipitation 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.

Introduction

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. 2010, 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, Zuckerberg et al. 2018, Wilson 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 4.1) to evaluate putative alternative factors influencing apparent survival throughout a grasshopper sparrow's annual cycle (Figure 4.2). 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 influence estimates of survival and emigration.

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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 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 (*Vernonia baldwinii*), lead plant (*Amorpha canescens*), white heath aster (*Aster ericoides*), scurfpea (*Psoralidum tenuiflorum*), and ragweed (*Ambrosia psilotachya*). Dominant fauna include white-tailed deer (*Odocoileus virginianus*), eastern cottontail (*Sylvilagus floridanus*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), deer mouse (*Peromyscus maniculatus*), eastern racer (*Coluber constrictor*), and gopher snake (*Pituophis catenifer*), along with a variety of arthropods. 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*).

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 philopatric 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 (mean = 9.6, sd = 4.5) 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 4.1A), 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*a*, 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 4.1A, 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 4.1C). 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 4.1D). 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 4.1E). 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 4.1F), 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 4.1G). 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., $t-1$, $t-2$). 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 $\Delta AIC_c < 2$) 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 4.1). 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 4.1). 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 $\Delta AIC_c > 2$ 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 4.1). 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 4.2). The probability of survival ($\hat{S}$) was 0.77 ± 0.06 (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 4.3A). In the final modeling step, the top ranked model included temporary emigration as a function of ESPI lagged 2 years (Table 4.3). 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 4.3B). 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 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. 2019). 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 site 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.

Tables

Table 4.1. 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 4.2. 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	$\Delta AIC_c{}^b$	$w_i{}^c$	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.

Table 4.3. 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]	$\Delta \mathrm{AIC}_c$[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 × $\Delta \mathrm{AIC}_c$ for that model), divided by the sum of these values for all models.

[d] North Atlantic Oscillation index.

Figures

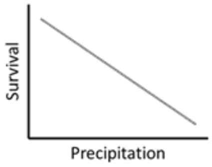
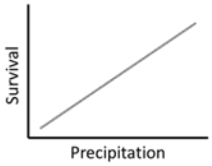
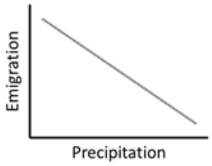
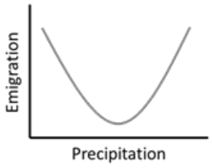
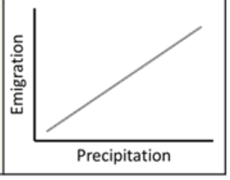
Hypothesis	Predictor	Description	Rationale	Expected Relationship
Precipitation impacts on survival *(S)*	(A) Local winter precipitation	Summed daily precipitation (mm) on wintering grounds, 15 Nov – 15 Feb	Winter precipitation increases overwinter mortality in grassland birds (Ahlering et al. 2009, Chavarria et al. 2012, Macias-Duarte et al. 2017).	
	(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.	
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.	
	(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).	
	(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).	

Figure 4.1. Description of hypotheses, associated mechanisms, predictions, rationale, and expected relationships between grasshopper sparrow survival, movement, and precipitation in northeastern Kansas, USA, 2013–2020.

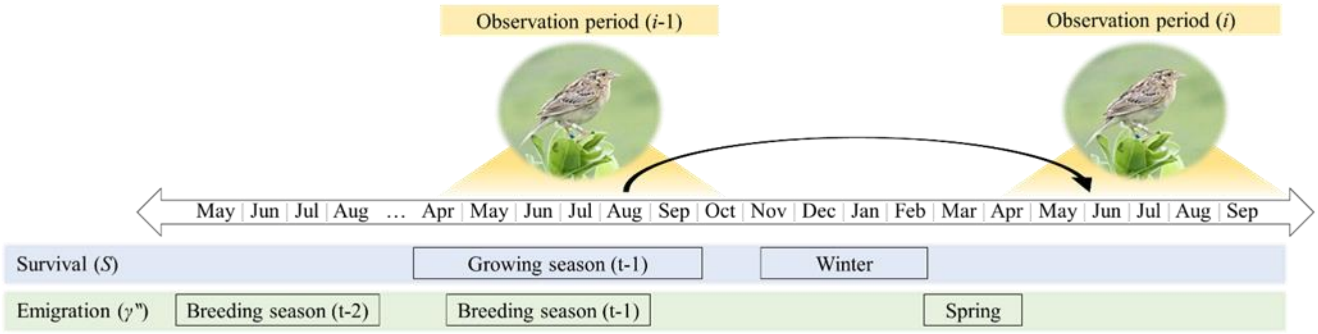


Figure 4.2. Temporal scale of precipitation variables in the grasshopper sparrow robust design model from northeastern Kansas, USA, 2013–2020. Boxes reflect the temporal extent over which precipitation variables are summarized. Precipitation may affect survival directly through mortality (blue box) or affect temporary emigration indirectly (green box) via habitat characteristics such as vegetation or prey abundance.

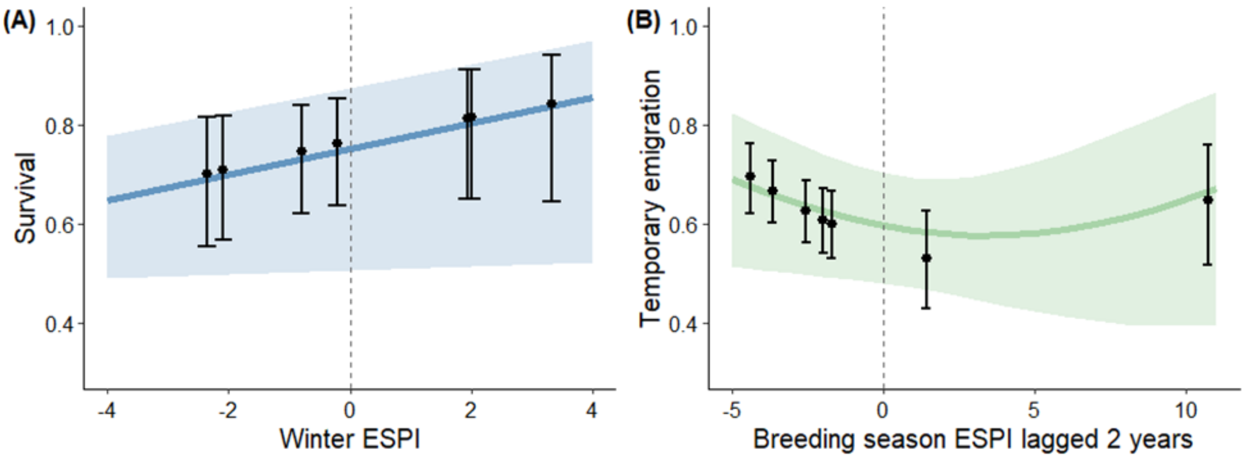


Figure 4.3. A) Grasshopper sparrow survival in northeastern Kansas, USA, 2013–2020, is positively correlated with the El Niño-Southern Oscillation precipitation index (ESPI) on their winter range. Positive ESPI values are associated with wetter, cooler conditions, and negative ESPI values indicate dryer, 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.

Chapter 5 - The long shadow of woody encroachment: an integrated approach to modeling grassland songbird habitat

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Abstract

Quantifying animal resource selection provides important information that underlie many conservation actions. Animals must track resources over relatively fine spatial and temporal scales, particularly in disturbance-mediated systems like grasslands. Grasslands are highly variable systems in both space and time; fire, grazing, and weather variability create heterogeneity in grassland landscapes and populations. Mobile taxa like grassland birds respond to this heterogeneity by dispersing among sites within and between years, yet we know little about how they make post-dispersal settlement decisions. A variety of methods exist to quantify bird resource selection, but the habitat data used in these models are frequently not collected at the same location or time an individual was present. This spatio-temporal misalignment may lead to incorrect interpretations and adverse conservation outcomes, particularly in dynamic systems. To investigate the extent to which spatially- and temporally dynamic vegetation conditions superimposed on a topographically complex landscape drive grassland bird settlement decisions, we integrated multiple data sources from our study site to predict slope, vegetation height, and multiple metrics of vegetation cover at any point in space and time within the temporal and spatial scope of our study. We paired these predictions with avian mark-resight data for eight years at the Konza Prairie Biological Station in NE Kansas to evaluate territory selection for Grasshopper Sparrows (*Ammodramus savannarum*), Dickcissels (*Spiza americana*), and Eastern Meadowlarks (*Sturnella magna*). Each species selected different types and amounts of herbaceous vegetation cover, but all three species preferred relatively flat areas with less than 5% shrub cover and less than 1% tree cover. We evaluated several scenarios of woody vegetation removal and found that with a targeted approach, simulated removal of just one isolated tree in the uplands created up to 14 hectares of grassland bird habitat. This study supports growing

evidence that even small amounts of woody encroachment can fragment landscapes and pose a conservation threat across the southern Great Plains. On the other hand, these results demonstrate that drastic increases in bird habit area could be achieved through relatively economical and rapid management interventions. It also provides a framework for assessing species-habitat relationships via leveraging multiple datasets within integrated models to reduce spatio-temporal misalignment. These methods and inferences help determine conservation initiatives to support declining species across many taxa and systems.

Introduction

Identifying species-habitat relationships and resource selection are critical tools for directing conservation and land management. Relationships between animal distributions and landscape attributes shed light on factors shaping current distributions, characterize use within those distributions, and better predict changes in future distributions (Matthiopolos et al. 2020). Biotic and abiotic factors may affect habitat use, but these relationships can be difficult to detect in dynamic systems because of high environmental variability across space and time can conceal relationships (Ribic et al. 1997, Gonzalez-Gajardo et al. 2009).

Grasslands are dynamic systems with highly variable weather (Augustine 2010) which interacts with similarly variable management (e.g., fire and grazing) to create patchy landscapes (Blair et al. 2014). Grassland plant composition changes over relatively fine scales in response to these disturbances (Koerner & Collins 2013), and the vast majority of global circulation models project that this variability will increase (Cook et al. 2015). Measuring drivers of ecological processes can be challenging in grasslands because of the dynamic nature of these systems, particularly given that vegetation can be influenced by lagged or legacy effects of prior events (Sherry et al. 2008, Dudney et al. 2017, Broderick et al. 2022). Human development has created additional spatial variability by increasing habitat fragmentation. This is particularly true in North America’s Central Great Plains (Fuhlendorf & Engle 2004) where about 90% of Great Plains tallgrass prairie has been converted to human development or agriculture (White et al. 2000). An understanding of grassland species-habitat relationships is essential to help conserve species living in these dynamic and endangered systems.

In response to this variability, organisms in the Central Great Plains exhibit phenotypic plasticity in their phenology (Wagle et al. 2019), physiology (Bachle & Nippert 2022), and behavior (McNew et al. 2013, McMillan et al. 2021). Mobile species, like grassland birds, may also alter their dispersal and settlement decisions to track conditions that presumably increase their survival and reproduction (Kentie et al 2014). However, "favorable" conditions is a species-specific (Wiens 1969), location (Verheijen et al. 2021) and time-dependent concept (Gehrt et al. 2020). Many grassland bird species rely on a variety of vegetation cover types for successful nesting and foraging, but the specific attributes of vegetation height and composition selected differs among species (e.g., Wiens 1969, Chapman et al. 2004, Conover 2009, Duchardt et al. 2020). Through interactions with fire, large grazers (e.g. cattle, bison) can alter the availability of these habitat types, often favoring less litter cover and a higher abundance of forbs at the expense of tall grasses (Collins and Calabrese 2012). The presence and proportion of these vegetation cover types drive nest and territory selection in many species (e.g., Rader et al. 2007, Hansen et al. 2016, Ruth and Skagen 2017). While grassland birds exhibit species-specific responses to various aspects of herbaceous vegetation, responses to woody vegetation tend to be negative across grassland bird communities (Bakker 2003). Trees and shrubs are expanding in many grasslands and that encroachment has been implicated in the declines of grassland-dependent birds (Coppedge 2001, Lautenbach et al. 2020). Woody vegetation in grasslands is associated with lower occurrence, abundance, nest densities, and nest survival (Coppedge 2001, Bakker et al. 2003, Graves et al. 2010, Ellison et al. 2013, Lautenbach et al. 2020). Territory selection may also relate to topography, although few have analyzed this relationship (Renfrew and Ribic 2002). Grassland birds may choose to avoid flatter territories to avoid predators having better vantage points or optimize nest microclimate.

Despite the ability of mobile grassland birds to cope with changing conditions via their high mobility (Herkert 2007), almost 75% of North American grassland bird species have declined since 1970 (Rosenberg et al. 2019). Although these declines are often attributed to habitat loss, many grassland species are declining even in some protected areas, suggesting an important role of management within these areas (With et al. 2008) and regional connections between multiple sites. Habitat selection studies are essential to understand which management actions result in the most positive population-level responses, but it is often challenging to collect auxiliary data, such as vegetation measurements, over space and time that are co-located with animal observations. This can lead to misalignment between animal observations and environmental covariates (i.e. spatio-temporal misalignment), as it is uncommon that environmental data collected at the exact same time and place as an animal is observed (Gotway and Young 2002). Spatio-temoral misalignment can produce inaccurate inferences about species distributions and resource selection (Pacific et al. 2019), which can lead to misguided conservation actions.

We aimed to determine the extent to which vegetation and topography drive grassland bird settlement decisions and characterize the attributes associated with territory occupancy at the Konza Prairie Biological Station in NE Kansas between 2014-2021. We combined multiple data sources including ground surveys, weather, and remotely sensed data to predict vegetation height, vegetation cover, and slope at any point in space and time within our study site and over the temporal duration of our study. We then integrated these predictions with avian mark-resight data collected from May-July in all years of the study for three of the most common grassland species in the Central Great Plains: Grasshopper Sparrows (*Ammodramus savannarum*), Dickcissels (*Spiza americana*), and Eastern Meadowlarks (*Sturnella magna*). Based on prior studies, we expected that each species would select for different territory attributes, but all would avoid sloped topography and woody vegetation. This study lends insights into habitat selection in multiple species, across multiple management regimes, and over a relatively long time period, which will contribute to a more comprehensive understanding of why grassland birds decided to settle at some sites and not others and shed light on how to slow and potentially reverse grassland bird declines.

Methods

Study Site

We conducted our study on the Konza Prairie Biological Station, located within the Flint Hills ecoregion near Manhattan, Kansas (39°05' N, 96°33' W). The Konza Prairie encompasses 3,487 hectares of native tallgrass prairie divided into 46 experimental study units; each study unit is either patch-burn grazed or reflects a grazing regime of bison-, cattle-, or ungrazed and a fire return interval of one, two, four, or twenty years. We collected vegetation and bird data on nine of these study units that were burned every one, two, or three years, grazed by bison or cattle, or ungrazed (Figure 1). Cattle treatments with a three-year fire frequency were managed under a patch-burn graze management regime. Burns were conducted in March and April before the nesting season began. Cattle grazed from March or April through until August or September, and bison graze year-round, with greater bison densities (per unit weight) during the growing season. These treatments created varied plant communities in each study unit, depending on grazing regime and fire return interval (Koerner & Collins 2013). Dominant grasses included big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), buffalo grass (*Bouteloua dactyloides*) blue grama (*B. gracilis*), hairy grama (*B. hirsuta*) and sideoats grama (*B. curtipendula*). Dominant forbs included goldenrod (*Solidago canandensis, S. missouriensis*), ironweed

(*Vernonia baldwinii*), lead plant (*Amorpha canescens*), white heath aster (*Aster ericoides*), scurfpea (*Psoralidum tenuiflorum*), and ragweed (*Ambrosia psilotachya*). Shrub and tree cover have increased at the site over the last four decades (Ratajczak et al. 2014), particularly in the less frequently burned treatments. Woody species that have increased include rough-leafed dogwood (*Cornus drummondii*), smooth sumac (*Rhus glabra*), Eastern red cedar (*Juniperus virginiana*), and a diverse set of deciduous trees such as Honeylocust (*Gleditsia triacanthos*), Redbud (*Cercsis canadensis*), and several elm species. The terrain of the site is characteristic of the Flint Hills region being dominated by steeply rolling hills ranging in elevation from 320 m to 444 m, punctuated by flat lowlands, mid-elevation benches, and uplands (Brunsell et al. 2008).

Study Species

Grasshopper Sparrows (*Ammodramus savannarum*) are small (~17 g), ground nesting grassland sparrows that breed in grasslands across North America. Their breeding range spans from the grasslands of the Pacific Northwest across to the Northeast, with the core of their breeding range in the Great Plains. They spend the non-breeding season in the southern United States and most of Mexico (Vickery 2021). Throughout much of the year, Grasshopper Sparrows are elusive, foraging on the ground and remaining hidden within grassland vegetation. However, during the breeding season, territorial males sing from the tops of forbs and other prominent perches. Grasshopper Sparrows are present at our study site from mid-April to September. They exhibit high rates of inter- and intra-annual dispersal (Silber et al. 2023, Williams & Boyle 2018), apparently spurred by nest failures or changes in their environment such as vegetation structure. Sparrows construct domed nests on the ground using both gathered and intact dry grasses from previous growing seasons. Areas of bare ground allow for easier foraging for insect prey. At our study site, male territories are on average 43 ± 2 m in diameter (Williams & Boyle 2018). Across North America, Grasshopper Sparrow populations have declined by 72% in the last 50 years and continue to decline by 3.1% each year (Road to Recovery 2022).

Eastern Meadowlarks (*Sturnella magna*) are relatively large (~120 g), grassland-dependent songbirds of central and eastern North America. Their annual movements are poorly understood, as some individuals are non-migratory and others migrate >1000 km (Jaster et al. 2022). Eastern Meadowlarks are present at our study site year-round, although interannual site fidelity is low and wintering individuals may differ from breeding individuals. They require intact dead grass grown in previous breeding seasons to construct domed nests on the ground and tall perches from which males to sing and defend territories. Territory size is not well understood and varies across the species' range from 1.2 to 4.8 ha (Wiens 1969, Francq 1972). Across North America, Eastern Meadowlark populations have declined by 76% in the last 50 years and continue to decline by 2% each year (Road to Recovery 2022).

Dickcissels (*Spiza americana*) are ubiquitous, medium-sized (~32 g) grassland songbirds of Great Plains prairies. They are long-distance migrants, wintering in Venezuela and breeding throughout most of the central United States (Fretwell 1986). They are well known for exhibiting low site fidelity, leading to fluctuations in breeding densities and distributions across their range (Gross 1968). Males arrive at our site in early- to mid-May to establish a breeding territory and attract a mate by singing from nearby perches on tall shrubs, trees, or fence lines. Following pair formation, the male and female will build an open cup nest in dense forbs or small shrubs, on or near the ground, or up to 4 m (Gross 1968). Territory sizes range from 0.22 to over 0.95 hectares (Schartz & Zimmerman 1967, Harmeson 1974), with a decrease in territory size later in the breeding season and in patch-burn grazed units (Veheijen et al. 2022). Dickcissel populations declined by 12% in the last 50 years, but have recently increased at an average of 2.4% each year since 2009 (Road to Recovery 2022).

Bird data

We captured and monitored Grasshopper Sparrows from 2014 to 2021, and Dickcissels and Eastern Meadowlarks from 2019 to 2021. Throughout each breeding season (late-April to early-August), we intensively captured and surveyed on randomly-located 10 ha plots within each study unit. We prioritized efforts on these plots to ensure we thoroughly sampled a consistent area, but also sampled the remainder of the study units several times per season. To capture breeding males, we placed a 12 x 2.5m mist net (Ecotone, Gdynia, Poland; 32mm mesh size) adjacent to preferred perches of territorial males. At the base of each net, we placed a small audio player and speaker broadcasting conspecific song to lure males into nets. We equipped each bird with a uniquely numbered aluminum band from the United States Geological Survey and unique combinations of three plastic color bands (total of two bands on each leg). We determined sex by looking for brood patches (female) or cloacal protuberances (male). Adult birds can only be assigned the age of After Hatch Year since the study species all undergo a complete pre-basic molt in late summer prior to migration making it impossible to age as second year or older (Pyle et al. 2008). Before releasing, we collected morphometric measurements, feather samples, and blood samples for other long-term projects. We aimed to capture and mark all territorial male Grasshopper Sparrows within our 7 study units (Figure 5.1). Due to the high abundance of Eastern Meadowlarks and Dickcissels, we focused our sampling for those species within four study units: one (three pasture) patch-burn grazed unit; one annually-burned, ungrazed unit; one biennially burned, ungrazed unit; and one annually-burned, bison-grazed unit.

Due to high frequencies of within-season dispersal, we returned to each study unit multiple times throughout the season to capture, band, and re-sight adults. By marking individuals with unique combinations of color bands, we identified independent territories and reduced the likelihood of double-counting the same territories within a given season. All aspects of this study were approved through the Kansas State University IACUC (protocols 3260, 3733, and 4250) and the North American Bird Banding Laboratory (permit 23836).

We surveyed all units to resight color banded adults approximately every 10 days from late April to the beginning of August 2014-2021, for a total of 8-10 survey rounds per breeding season. Starting 30 minutes before sunrise, technicians chose a haphazard route throughout the study unit, walking within at least 300m of every point, looking and listening for the focal species. Observers used 8 x 42 binoculars and 10x spotting scopes to record the color band combination of each bird they detected and took GPS waypoints at all observed perches. If birds were unbanded, observers marked their location on a map and returned later to band the individual. Observers did not conduct surveys during precipitation or in wind exceeding 35 kph because the focal species are unlikely to sing in these conditions, reducing bird detection.

Vegetation height and composition data

We conducted vegetation surveys within each study units once per month in May, June, and July. Within each study unit, we collected repeated vegetation measurements at three (2014-2017) or 10 randomly-located points (2018-2021). We measured visual obstruction by placing a Robel Pole at each point and measuring the vegetation height from all four cardinal directions from a distance of 4 m (Robel et al. 1970). We then placed the Robel Pole 5 m distant from the central point in each of the cardinal directions and measured visual obstruction at a further 4 m distance from the central point for a total of eight visual obstruction measurements per point. We placed a 20 x 50 cm quadrat (i.e. Daubenmire frame) at the center point to estimate percent cover to the nearest 5% of standing dead grass, live grass (green, not brown/dry), other dead veg (standing dead forbs and shrubs), forbs/herbaceous veg, bare ground (bare soil or rocks), litter (horizontal dead plant material and animal droppings), and shrubs/woody veg >0.5 m. We repeated this measurement at four additional locations, 5 m distant from the central point in each cardinal direction, collecting a total of five measurements of vegetation cover per point.

Vegetation height and composition models

We fit generalized additive models (GAMs) to predict vegetation height (dm) and % cover for live grass, live forbs, bare ground, and dead grass/litter across our study units. We included the following variables as linear predictors for vegetation height and composition: precipitation, fire, grazing, month, elevation, and slope. We included three metrics of local precipitation as predictors for vegetation height and cover: spring (Mar 1 – May 1) precipitation, breeding season (i.e., May 1 – Aug 15) precipitation lagged one year, and breeding season precipitation lagged two years. We included multiple metrics for precipitation because they each relate to different metrics of vegetation height and composition. Spring precipitation at the beginning of the growing season increases plant biomass (Darenova et al. 2017) and species richness (Ladwig et al. 2016), and precipitation can have a legacy effect of at least two years on vegetation (Tenhumberg et al. 2018). Fire and grazing determine plant composition and aboveground biomass, so we included a binary variable for whether or not the unit was burned that breeding season and a variable for the management regime. We included management regimes (e.g., bison-grazed, annual burn) as one variable instead of separately including fire return interval and grazer identity because not all combinations of fire and grazing are reflected in our study units. We sampled two replicates per management regime (Figure 1) previously shown to provide suitable grassland bird habitat (Powell 2008, Powell and Busby 2013), except annually burned, ungrazed units, where we ceased sampling in all but one of these units by 2020 due to extremely low bird densities. We included month as a predictor because vegetation is taller later in the growing season and the prevalence of vegetation cover types can change over time due to plant phenology. We included elevation and slope, as they can predict soil types and where grazing lawns and paths occur. We included smooth terms for space (i.e. UTM easting and northing) and time, as we expected there to be some degree of spatial and temporal autocorrelation (Hefley et al 2017). We also included observer as a random effect to account for variation attributed to differences in observer. We used these models to predict vegetation height and composition in our study area, with at a daily, 4 m^2 resolution.

Remote sensing woody vegetation

We calculated slope from a dataset of gridded elevation across the Konza Prairie (Blackmore 2019). We obtained elevation from a 2 m^2 resolution digital elevation model, which was produced using a 2010 LiDAR digital elevation model collected according to United States Geological Survey protocols. We then calculated a matrix containing the derivative of elevation (i.e. slope) for each grid cell. We also used a classification map of our study site that combined high-resolution aerial data and machine learning to estimate land cover at a 2 m^2 resolution, with land cover classes of grassland, shrub-dominated, deciduous tree dominated, evergreen tree dominated, or other (mostly a mix of roads and open water; Noble et al. in *review*). We used this classification map to calculate proportion of shrub and tree cover in each territory and create two additional rasters: the distance of each 2 m^2 pixel to the closest shrub and the distance of each 2 m^2 pixel to the closest tree.

Territory selection modelling

We established territories for each territorial male based on GPS waypoints collected during surveys and banding efforts and average species territory sizes. If the Euclidean distance between two GPS waypoints for an individual in a given year was equal to or less than the average territory size, we calculated the centroid between the two points and repeated this procedure with all points for an individual in that year until centroids were farther apart than we would expect to consider them the same territory (i.e. 40 m for Grasshopper Sparrows, 60 m for Dickcissels, and 100 m for Eastern Meadowlarks). If the centroid between each waypoint was farther the expected territory size, we considered the points to be part of different territories. We did not calculate the centroid for all waypoints for an individual within an entire breeding season because ~52% of male Grasshopper Sparrows disperse each month (Williams & Boyle 2018). We then created a buffer (20 m for Grasshopper Sparrows, 30 m for Dickcissels, and 50 m for Eastern Meadowlarks) around the centroid of their territory, reflecting each species' average territory size. If an individual was observed in a territory on several days, we assigned the earliest date the individual was observed there to represent the date it was selected. These buffered areas (i.e. territories) were then considered the "use" locations for our resource selection analysis.

To create "available", or pseudo-absence, locations for our resource selection analysis, we randomly sampled coordinates throughout our study units between May-July, 2014-2020. This period reflects peak breeding season at our site throughout the extent of our study. For each "available" point, we created a buffer to reflect average territory sizes around the randomly sampled point to establish an "available" territory. The randomly selected pseudo-absences represent all available locations in the study units for a comparison with "used" (i.e. observed) territories. For each species, we created the same number of pseudo-absences as observed territories.

To integrate the predictions from our habitat variables (i.e. vegetation height and composition, topography, and woody plant cover) into the resource selection model, we predicted vegetation height, % live grass, % live forbs, % bare ground, % dead grass and litter, slope, proportion of territory with shrub cover, proportion of territory with shrub cover, distance to the closest shrub, and distance to the closest tree for each territory (observed and pseudo-absence). We then fit a GAM, modeling our response variable (i.e. present or absent) with a Bernoulli distribution to predict probability of territory selection for each bird species (Pearce and Boyce 2006, Fithian and Hastie 2013). We included a smoothed effect for UTM easting and northing to account for spatial autocorrelation in territory locations (Winnicki et al. 2020) and a separable smoothed effect for time (i.e. numeric day since onset of the project) to account for temporal autocorrelation (Hefley et al. 2017).

Model validation

We evaluated the predictive accuracy of our territory selection model using a dataset of observed Grasshopper Sparrow territories in 2021. We predicted our habitat variables (i.e. vegetation height and composition, topography, and woody plant cover) for every observed Grasshopper Sparrow territory (i.e. "use" territories) in 2021 and an equal number of randomly sampled (i.e. "available") territories. We used these predictions to predict the probability of territory selection for every “use” and “available” territory. To quantify the concordance between observed Grasshopper Sparrow territories and the integrated resource selection model’s predicted probability of a territory, we calculated the Brier score (Brier 1950, Harrell et al. 1996).

Woody cover removal scenarios

We simulated several scenarios of shrub and tree removal to assess management strategies that may increase territory availability for Grasshopper Sparrows. Using our vegetation model, we predicted the probability of Grasshopper Sparrow territory selection for every 4 m^2 pixel in four study units (patch-burn grazed [C3A/C3B/C3C], annually burned and bison grazed [N1B], annually burned and ungrazed [K1B], and biennially burned and ungrazed [2D]) for the middle of the 2020 breeding season (June 15). We used those probabilities as baseline spatial predictions of where Grasshopper Sparrows were likely to select territories. We chose these study units because they are geographically near to each other and represent both two units with substantial woody encroachment and two units with minimal woody encroachment. We then simulated four scenarios of woody vegetation removal: 1) removal of one small, contiguous shrub patch, less than 10 m diameter, isolated from other woody cover; 2) removal of one tree, isolated from other woody cover; 3) removal of all shrubs in the upland portions of unit (areas with less than 10% slope and >400 m in elevation); and 4) removal of all trees in upland areas. We selected areas we suspected would otherwise be preferred Grasshopper Sparrow habitat (i.e. upland prairies instead of woody riparian areas). We then calculated the area over which territory selection probability increased over the baseline predictions if the woody vegetation we “removed” were not there, and estimated 95% confidence intervals around that prediction using 1,000 bootstrap samples.

Results

We captured 1,200 male Grasshopper Sparrows in our study units between 2014 and 2020, and 97 male Eastern Meadowlarks and 180 male Dickcissels between 2019 and 2021. We surveyed each study unit approximately once every 10 days (mean = 9.6, sd =4.5) for an average of 9 times (range: 8-10 rounds) per season. We observed each Grasshopper Sparrow at up to 57 locations (mean = 3.34, sd = 4.68) over up to six years. We observed Eastern Meadowlarks up to sixteen times (mean = 2.29, sd = 2.35) and Dickcissels up to 21 times (mean = 2.58, sd= 2.81) over the course of the three years they were sampled. After calculating territory centroids and distinguishing unique territories over space and time, our dataset contained 2,057 Grasshopper Sparrow territories, 72 Eastern Meadowlark territories, and 111 Dickcissel territories. Within each month in which an individual was observed, we collected up to 26 waypoints for each Grasshopper Sparrow (mean = 2.6, sd = 2.8), up to five waypoints for each Eastern Meadowlark (mean = 1.4, sd = 1.0), and up to four waypoints for each Dickcissel (mean = 1.3, sd = 0.8).

Vegetation height and composition

We measured vegetation height and composition at 1,812 points between 2014-2021. Vegetation height ranged from 0-30 dm (mean = 3.15, sd = 2.70), live grass ranged from 0-100% cover (mean = 25%, sd = 18%), live forbs ranged from 0-100% cover (mean = 19%, sd = 17%), bare ground ranged from 0-99% cover (mean = 32%, sd = 28%), and dead grass and litter ranged from 0-96% cover (mean = 19%, sd = 21%). Vegetation height and composition had differing responses to precipitation and management (Table 5.1).

Remote sensing data

Elevation at Konza ranges from 318 to 445 m asl. (mean = 397 am asl.), and slope ranges from 0 to 2.5 meters rise per meter run (mean = 0.15, sd = 0.11). In 2020, only about ~76% of Konza consisted of grassland, while the remainder was covered by shrubs (~12%), trees (~10%), and less than 1% in roads, rivers, or buildings. The average distance to shrubs was 18 m (sd = 20, range = 0-191 m), and the average distance to trees was 45 m (sd = 44, range = 0-320) across all of Konza.

Territory selection

Each bird species preferred different vegetation conditions and slopes than the means for “available” (i.e. pseudo-absence) territories (Table 5.2). However, Grasshopper Sparrows, Eastern Meadowlarks, and Dickcissels all selected territories having different vegetation characteristics from each other (Table 5.3, Figure 5.3, Figure 5.4). Grasshopper Sparrows selected territories in areas with higher forb and dead grass cover than live grass and bare ground, while Eastern Meadowlarks and Dickcissels preferred areas with live grass cover. In some ways, the three species’ territory selection was alike; they all primarily occupied flatter areas with less than 6% shrub cover and less than 1% tree cover (Figure 5.5). The average shrub cover in the “available” territories was 10% and the average tree cover was 9% (Table 5.2). There was more bare ground in the “available” territories (mean = 34%) than in each of the species’ territories (Grasshopper Sparrows: 16%; Eastern Meadowlarks: 12%; Dickcissels: 21%).

Model validation

In 2021, we observed 194 Grasshopper Sparrows which occupied 289 territories. The integrated resource selection model successfully predicted where Grasshopper Sparrows would select territories. The average probability of a GRSP selecting territory calculated over all 20212 pixels in the study area in 2021 was 35% (se = 30%). By contrast, the mean estimated probability of territory selection at locations where we actually observed territories in 2021 was 93% (se = 8%). The model exhibited high concordance (i.e. predictive accuracy) with observed territories (Brier score = 0.11).

Simulated woody cover removal

The amount of grassland bird habitat increased under each of the four woody vegetation removal scenarios we tested (Figures 8-11). Simulated removal of an isolated shrub island increased the likelihood of Grasshopper Sparrow territory selection from 0.19 hectares (95% CI = 0.18, 0.21) in the annually burned, ungrazed unit (K1B) to 0.76 hectares (95% CI = 0.72, 0.79) in the patch-burn grazed unit (C3A/C3B/C3C). Simulated removal of one isolated tree increased the probability of territory selection from 2.12 hectares (95% CI = 2.07, 2.17) in the patch-burn grazed unit (C3A/C3B/C3C) to up to 14.64 hectares (95% CI = 14.50, 14.78) in the annually burned, ungrazed unit (K1B). Simulated removal of all shrubs in flat, high elevation areas increased the probability of territory selection by 11.46 hectares (95% CI = 11.36, 11.60) in the biennially burned, ungrazed unit (2D) to 97.78 hectares (95% CI = 97.48, 98.02) in the patch-burn grazed unit (C3A/C3B/C3C). Simulated removal all trees in the flat, high elevation areas resulted in a 22.38 hectare (95% CI = 22.27, 22.55) increase in the biennially burned, ungrazed unit (2D), where only about 0.02 uplands hectares were encroached. In the patch-burn grazed unit (C3A/C3B/C3C), where approximately 1.01 hectares of the uplands were encroached by trees, removing all trees in the flat, high elevation areas resulted in improved habitat across 103.24 hectares (95% CI = 102.91, 103.50).

Discussion

Grasshopper Sparrows, Eastern Meadowlarks, and Dickcissels made settlement decisions based on topography and vegetation structure, particularly woody plant cover. All three species primarily selected territories with less than 5% shrub cover and less than 1% tree cover, presenting an immediate need to limit woody encroachment in the Central Great Plains. While all three species avoided woody vegetation, they each selected for different herbaceous vegetation cover types (i.e. grasses and forbs). Therefore, fire and grazing regimes that support heterogenous vegetation and suppress woody encroachment will more likely support diverse communities of grassland birds. Furthermore, our integrated resource selection model combined multiple environmental datasets to predict grassland bird territory selection with remarkably high accuracy. Models such as the one presented in this study are powerful tools to leverage multiple datasets, assess species-habitat relationships, and simulate conservation initiatives to evaluate the results of potential support declining species across many systems (Royle et al. 2013, Linden et al. 2018).

Grasshopper Sparrows, Eastern Meadowlarks, and Dickcissels all tended to select territories in relatively flat areas. These findings contradict previous reports that Eastern Meadowlarks prefer slopes as opposed to tops of hills or flat valleys (Roseberry & Klimstra 1970). One potential explanation is that selection may vary geographically based on grazing intensity, as many flat areas can be intensively grazed leaving slopes with more preferable vegetation cover. Although our study described factors associated with territory selection and not nest site selection, territory selection constrains nest selection, therefore territory characteristics are often similar to nest site characteristics (e.g., Jones and Robertson 2001, Ruth and Skagen 2017). Slope may affect nest success through nest microclimate or risk of predation. In water pipits, a ground nesting bird of alpine grasslands, slope affected nestling survival; nests on east-by-north-east slopes, where the maximum temperature occurred in the morning, had higher nestling survival than nests on west-by-southwest slopes, where the maximum temperature was in the afternoon (Rauter et al. 2002). Slope may also indirectly impact territory selection by driving vegetation structure, as different slopes may have different plant biomass and community composition (Collins and Calabrese 2012, Liu et al. 2019). Sloped areas may provide more sunning spots for reptiles or crevices for mammal burrows, which increase predation threat for bird nests and sometimes adults. Finally, grassland birds may avoid slope for the same reason they avoid tall structures and trees; high perches may increase risk of predation (Pitman et al. 2005). The limited number of studies published on the relationships between territory selection and slope warrants further investigation.

Although Grasshopper Sparrows, Eastern Meadowlarks, and Dickcissels all breed in grasslands, they have different preferences for vegetation cover within their breeding territories. Grasshopper Sparrows selected territories composed primarily of dead grass and forbs, supporting previous studies noting higher abundance in grazed pastures with a 2-3 year fire return interval, but not during the year that pastures burn (Powell 2008, Augustine and Derner 2015). Eastern Meadowlarks did not exhibit strong preferences for any one cover type except an aversion to areas with predominantly dead grass cover, supporting previous findings that they occupy both burned and unburned pastures (Powell 2008). Dickcissels are considered grassland-facultative (Gross 1968), and our findings support the conclusion that they are generalists when it comes to vegetation selection and preferred management (Powell 2008, Verheijen et al. 2019). Although Dickcissels preferred areas with ample grass cover, they had no other strong associations with herbaceous vegetation cover. Furthermore, unlike the sparrows and meadowlarks, they did not avoid territories near shrubs. These differences in territory selection likely reflect differences in life histories and nesting strategies, as Grasshopper Sparrows and Eastern Meadowlarks are ground-nesting birds that primarily construct nests from grasses (Roseberry and Klimstra 1970, Wiens 1969), and Dickcissels use a variety of nest construction materials, and sometimes place nests up to 126 cm above the ground in shrubs or small trees (Overmire 1962, Gross 1968). While each species had different preferences for cover types, all three species preferred intermediate vegetation height (~25 cm). Given some common grass species in tallgrass prairies can reach over 75 cm by July (Nippert et al. 2011), grazing is essential to keep vegetation at heights preferable for grassland birds throughout the breeding season.

Grassland vegetation structure and composition is largely mediated by the interaction between land management (e.g., fire and grazing) and weather (Collins and Calabrese 2012). The effects of land management vary in response to concurrent and lagged weather (Blair et al. 2014, Dudney et al. 2017), thereby affecting the amount of cover for functional plant groups. For example, live grass cover increases following concurrent precipitation, leading to greater dead grass cover in the following years until a pasture is burned. Because grassland birds select areas territories and nesting sites based on vegetation characteristics, they exhibit preferences for land management types (e.g., Wiens 1973). Interannual variation in their return rates and densities within their preferred land management regime can therefore largely be attributed to weather variability. For example, while Grasshopper Sparrows living in tallgrass prairies occur in high densities in grazed pastures a year or two years after a burn, they were more likely to select territories having more dead grass cover within those management constraints. Because the amount of dead grass is primarily shaped by precipitation in prior years, the inter-annual variation in abundance within this management regime is associated with lagged precipitation. These indirect relationships between precipitation, vegetation, and grassland birds manifest as variation in grassland bird survival and emigration (Silber et al. 2023). Thus, management in combination with delayed consequences of precipitation acting via vegetation structure ultimately regulate local abundances and play a role in population declines.

While agriculture and human development are the commonly-cited drivers of grassland bird declines (Samson and Knopf 1994, With et al. 2008), our results reinforce the importance of controlling woody encroachment to conserve grassland bird habitat. Woody vegetation is increasing across the Great Plains and in grassland around the world (Archer 1995, Roques et al. 2001, Briggs et al. 2005) with dire consequences for grassland-obligate birds. Variation in aversion to woody vegetation may depend on species-specific behavior and natural history. Grassland-obligate birds, including Grasshopper Sparrows and Eastern Meadowlarks, nest on the ground and need herbaceous vegetation to form nest structures (Wiens 1969). Dickcissels, on the other hand, form cup nests in vegetation above the ground, and may therefore be more tolerant of shrubs. While Dickcissel territory selection did not decline near shrubs, as the two other species did, all three species declined as the proportion of trees and shrubs increased. Grass at our study site decreased by 29% between 2000-2013, primarily due to an increase in woody vegetation (Ratacjzak et al. 2017). Because woody vegetation increases the likelihood of nest predation (With 1994, Ellison et al. 2013) and lowers nest survival (Graves et al. 2010), this lack of preferred habitat may mean these birds incur lower fitness, contributing to population declines. Therefore, the encroachment of woody plants in grassland systems undoubtedly contributes to the staggering declines in grassland-obligate and grassland-facultative species.

Fortunately, removal of woody vegetation has potential for substantial, economically-efficient conservation gains. As this study shows, multiple scenarios of woody vegetation removal increased grassland bird habitat. The impacts of removing a single shrub or tree were greatest in areas with minimal woody encroachment; removing one isolated tree added over 14 hectares of grassland bird habitat. This supports the idea that effective grassland bird conservation defends “core” grassland areas by prioritizing removing isolated woody plants (Roberts et al. 2022). However, in areas with severe woody encroachment, removing several woody plants was necessary to improve grassland bird habitat. These results suggest woody vegetation suppression and targeted removal should be a conservation priority.

Frequent fires may limit the expansion of woody vegetation (Briggs et al. 2005) but is less successful in removing woody vegetation once it has become established (Collins et al. 2021). Extreme fire can sometimes reverse woody encroachment (Twidwell et al. 2016) but may reduce grass abundance for years (Ratajczak et al. 2019). If woody encroachment is severe, a combination of fire, mechanical removal, and chemical removal will likely be necessary to suppress woody vegetation (Briggs et al. 2005). Fortunately, targeted removal of upland woody vegetation will remove seed sources from the landscape and increase grassland bird territory availability (Wilcox et al. 2022). Furthermore, management that leads to suppression and removal of woody vegetation is a common interest for many stakeholders, given woody plants pose a threat to both conservation and ranching.This common threat could be the basis for future research into cost-effective solutions for eliminating woody encroachment and meaningful partnerships between ranchers and researchers.

While many North American birds have experienced devastating declines since 1970, grassland birds are the most imperiled (Rosenberg et al. 2019). They inhabit largely human-dominated systems, privately-owned land, and areas of intensive agriculture (White et al. 2000, Ahlering et al. 2018), and exhibit sharp declines in response to habitat loss, habitat degradation, and habitat fragmentation (Herkert 1998, Stanton et al. 2018). Furthermore, the losses are likely to continue given that public perception of grasslands is still that they are “empty” and there for the exploitation. Compared to most other remaining grassland taxa, such as insects and small mammals, they likely require much larger areas. Mid-continental grasslands in North America are among the most endangered ecosystems globally (Hoekstra et al. 2005, Scholtz and Twidwell 2022), putting native grassland organisms at risk. Understanding grassland bird habitat requirements will help us prioritize conservation initiatives, such as woody plant removal, to slow grassland bird declines. Restoration projects that prioritize grassland bird populations may ultimately benefit grassland organisms across multiple levels of ecological organization and humans that depend on grassland landscapes.

Tables

Table 5.1. Estimates and model fit for vegetation height and composition predicted from a Generalized Additive Model. Data were collected at Konza Prairie Biological Station between 2014-2021. All models also include smooth terms for observer, time, and location (i.e. x and y coordinates). The reference level for management is annually burned and bison-grazed.

	Vegetation Height		**Live Grass**		**Live Forbs**		**Bare Ground**		**Dead Grass & Litter**	
Covariates	*Estimate*	*SE*	*Estimate*	*SE*	*Estimate*	*SE*	*Estimate*	*SE*	*Estimate*	*SE*
Intercept	9.7489	0.8998	1.9922	1.2856	0.5353	1.2614	-1.0657	1.6045	-8.2080	1.7148
Spring precip	-0.0241	0.0032	0.0006	0.0035	-0.0093	0.0024	0.0129	0.0037	-0.0083	0.0060
Breeding season precip, 1-year lag	-0.0021	0.0010	-0.0094	0.0013	-0.0042	0.0013	0.0010	0.0016	0.0160	0.0019
Breeding season precip, 2-year lag	-0.0049	0.0009	-0.0039	0.0014	-0.0016	0.0013	-0.0017	0.0018	0.0034	0.0021
Month	0.2053	0.0087	0.1278	0.0143	0.0721	0.0156	-0.2726	0.0176	0.1093	0.0176
Elevation	-0.0088	0.0009	0.0019	0.0012	0.0042	0.0014	-0.0019	0.0016	-0.0006	0.0014
Slope	0.1538	0.0699	-0.3590	0.1027	-0.8916	0.1197	0.6271	0.1319	0.1364	0.1271
Burn year (yes/no)	-0.3375	0.0131	0.0252	0.0193	0.1508	0.222	0.9415	0.0243	-0.8521	0.0234
Bison-grazed, 2-year fire return	0.2394	0.690	0.2897	0.0808	0.1997	0.088	-0.4558	0.1130	-0.1766	0.0937
Patch-burn grazed	0.5901	0.1385	0.6551	0.1446	-0.2803	0.1644	-0.0214	0.1999	-0.3713	0.1716
Ungrazed, 1-year fire return	0.9086	0.1469	1.4025	0.1462	-0.4062	0.1645	-0.2945	0.2088	-0.8969	0.1720
Ungrazed, 2-year fire return	0.7849	0.1349	0.8235	0.1297	-0.4869	0.3425	-0.3843	0.1882	-0.2034	0.1528
Deviance explained	29.4%		37.3%		24.4%		69.4%		61.5%	

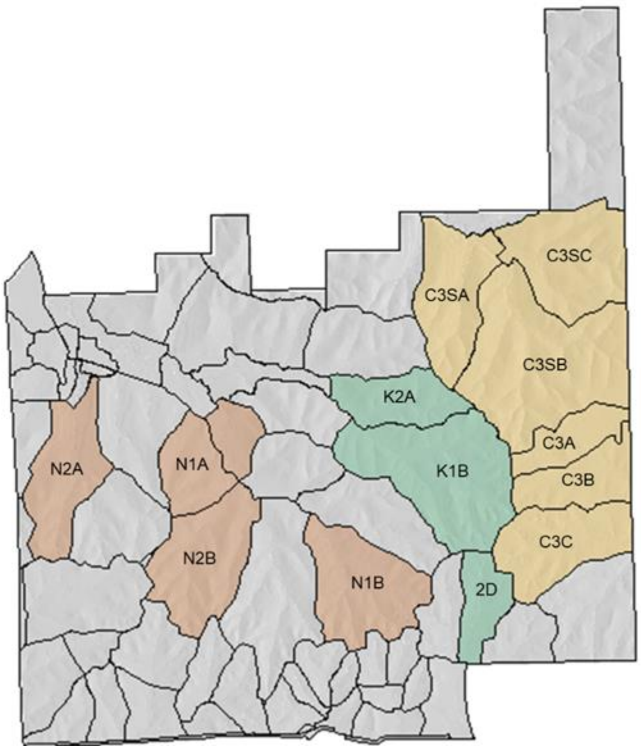
Table 5.2. Model-predicted averages for habitat variables in Grasshopper Sparrow territories (n = 2057; 2014-2020), Eastern Meadowlark territories (n = 72; 2019-2021), and Dickcissel territories (n = 111; 2019-2021) at the Konza Prairie Biological Station.

	Random territories		**Grasshopper Sparrows**		**Eastern Meadowlarks**		**Dickcissels**	
Covariates	*Mean*	*SE*	*Mean*	*SE*	*Mean*	*SE*	*Mean*	*SE*
Slope (%)	16	8	9	6	8	5	10	6
Vegetation height (dm)	2.80	1.10	2.71	0.85	2.68	0.86	2.78	0.97
Live grass (%)	24%	11%	22%	9%	36%	10%	36%	10%
Live forbs (%)	16%	5%	16%	5%	22%	4%	23%	5%
Bare ground (%)	34%	15%	25%	12%	20%	9%	21%	10%
Dead grass and litter (%)	24%	17%	33%	18%	11%	5%	10%	4%
Proportion of shrubs (%)	10%	14%	3%	7%	3%	6%	6%	9%
Proportion of trees (%)	9%	23%	<1%	4%	<1%	<1%	<1%	<1%
Distance to shrubs (m)	16.98	16.60	27.24	17.29	32.59	18.99	23.37	19.13
Distance to trees (m)	47.98	41.31	75.52	43.78	92.21	48.12	76.92	48.12

Table 5.3. Summary of Resource Selection Model for Grasshopper Sparrows, Eastern Meadowlarks, and Dickcissels at the Konza Prairie Biological Station, 2014-2020.

	Grasshopper Sparrows		**Eastern Meadowlarks**		**Dickcissels**	
Covariates	*Estimate*	*SE*	*Estimate*	*SE*	*Estimate*	*SE*
Intercept	4.9030	0.6622	1.3597	8.9835	-16.5296	10.8829
Slope	-9.6930	0.7108	-23.6055	6.9073	-8.0069	4.2055
Vegetation Height	-0.5563	0.0689	-0.0088	0.5799	-0.5216	0.3387
Live Grass	-5.7332	0.7279	0.3364	4.6023	7.5286	3.1952
Live Forbs	2.7541	1.6316	-3.3171	11.2709	15.0135	7.3952
Bare Ground	-7.2063	0.7413	-5.9682	7.1500	2.3251	5.3099
Dead Grass and Litter	2.6862	0.7357	-0.9662	16.7078	29.1168	13.2225
Distance to Shrubs	2.4570	3.3784	1.8005	26.7817	-2.6811	16.3980
Distance to Trees	3.8485	1.2534	7.3861	10.2108	4.9421	7.9259
Proportion of Shrubs	-4.1662	0.5304	-4.4675	4.2483	-0.5749	3.0959
Proportion of Trees	-3.5792	0.6546	-15.5416	16.8562	-42.0740	19.8125
Deviance explained	31.4%		78.2%		76.6%	

Figures



Unit	Fire return interval	Grazing regime
2D	2 years	Ungrazed
C3A/C3B/C3C	3 years	Patch-burn grazing
C3SA/C3SB/C3SC	3 years	Patch-burn grazing
K1B	1 year	Ungrazed
K2A	2 years	Ungrazed
N1A	1 year	Bison-grazed
N1B	1 year	Bison-grazed
N2A	2 years	Bison-grazed
N2B	2 years	Bison-grazed

Figure 5.1. Experimental fire and grazing regimes in sampled units at the Konza Prairie Biological Station in NE Kansas. Vegetation and bird data were collected on units reflecting 1-3 year fire return intervals and ungrazed, bison-grazed, and cattle-grazed (i.e. patch-burn grazed) pastures. Units filled in gray were unsampled.

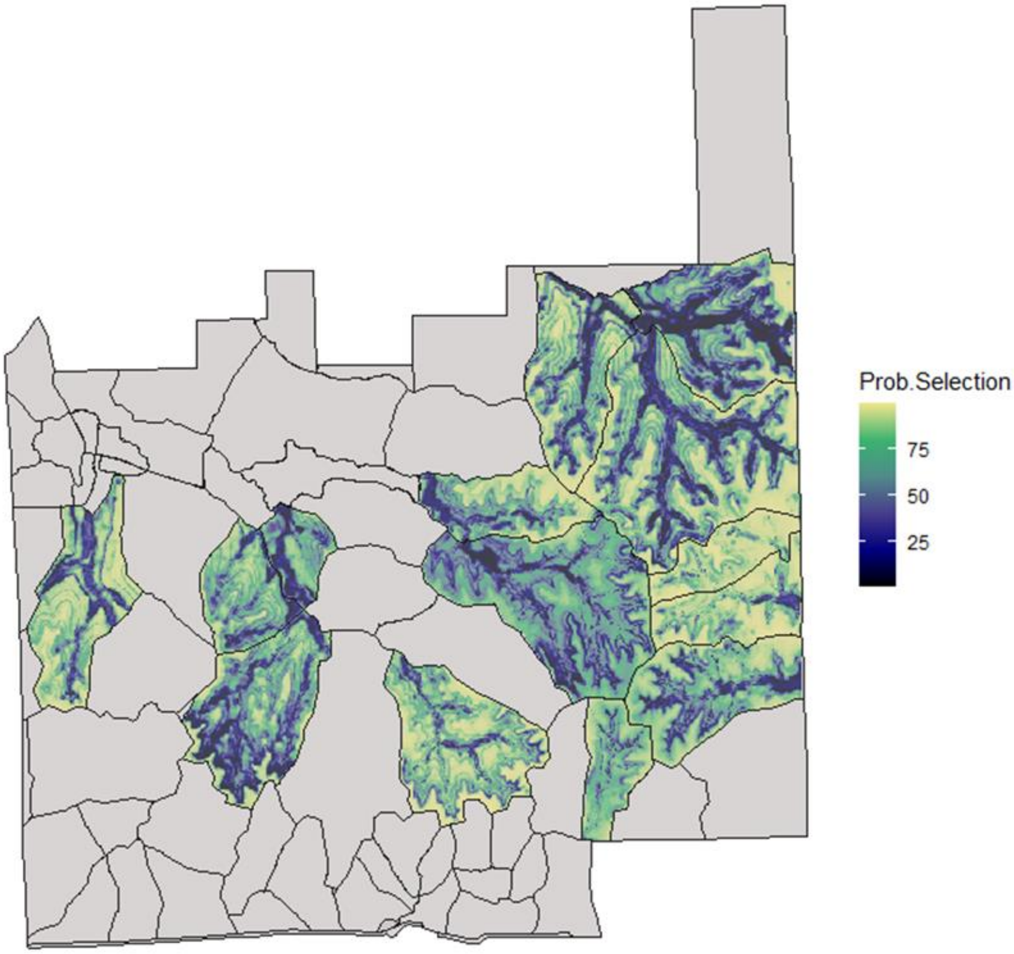


Figure 5.2. Probability of territory selection for the Grasshopper Sparrow at the Konza Prairie Biological Station on June 15, 2020. Units filled in gray were unsampled.

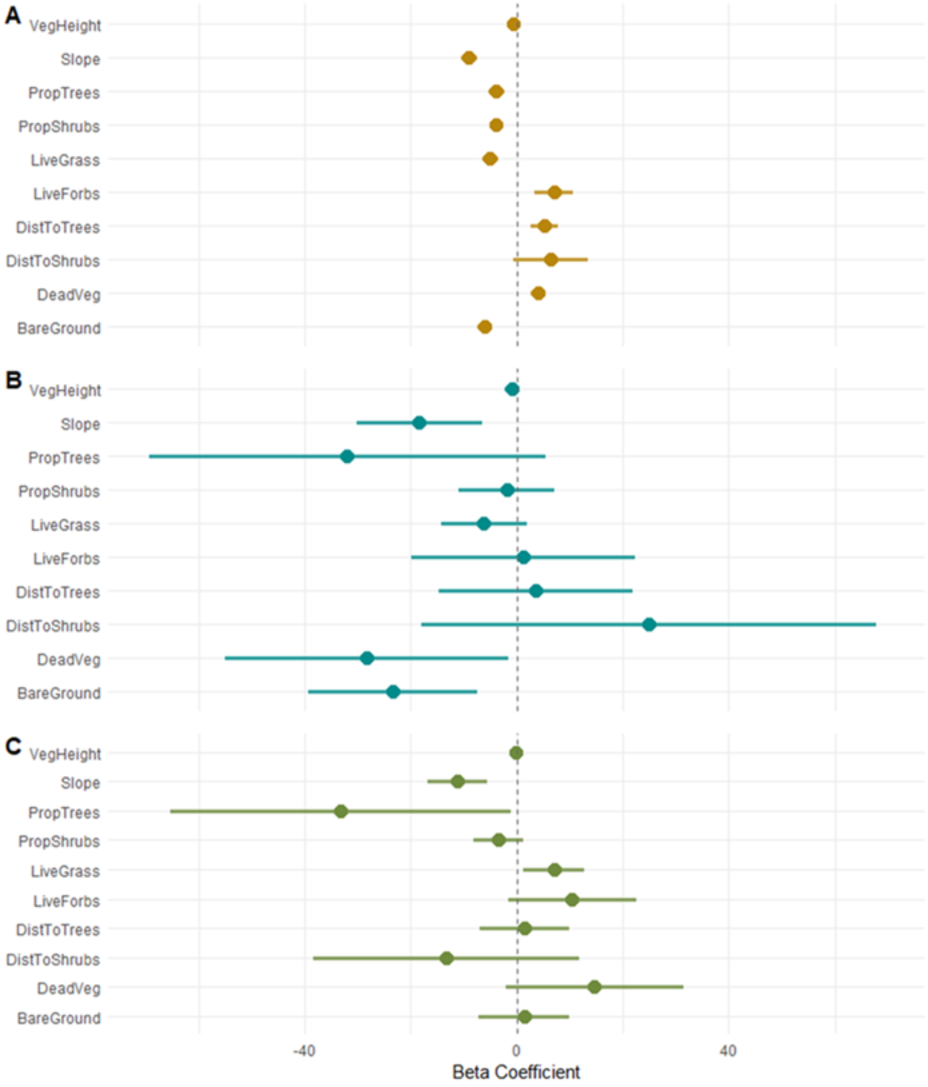


Figure 5.3. Resource selection coefficients for Grasshopper Sparrows (A; yellow; n = 2,346; 2014-2020), Eastern Meadowlarks (B; blue; n = 132; 2019-2021), and Dickcissels (C; green; n = 241; 2019-2021) at the Konza Prairie Biological Station.

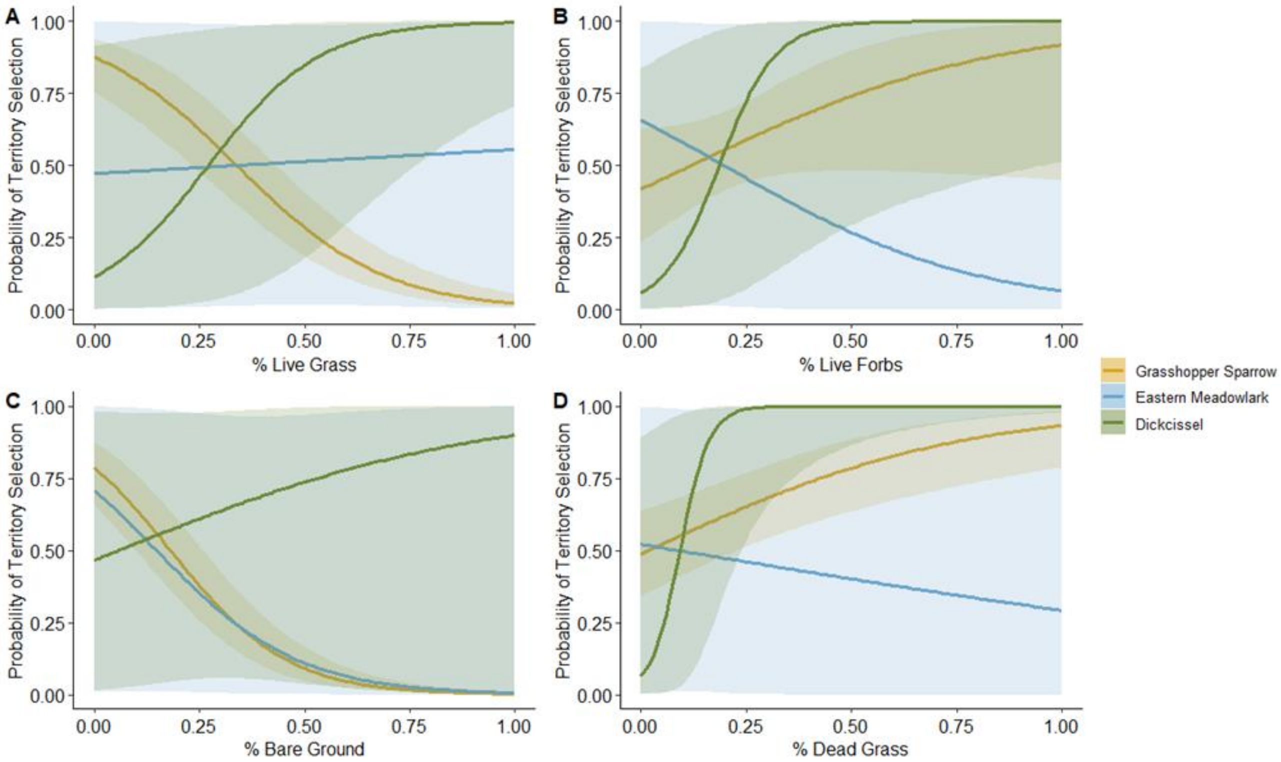


Figure 5.4. Probability of territory selection as a function of plant cover in Grasshopper Sparrows (yellow), 2014-2020, and Eastern Meadowlarks (blue) and Dickcissels (green), 2019-2021, at the Konza Prairie Biological Station. Solid lines are model predicted responses and shading indicates 95% confidence intervals. Each species prefers different amounts of live grass (A), live forbs (B), bare ground (C), and dead grass (D).

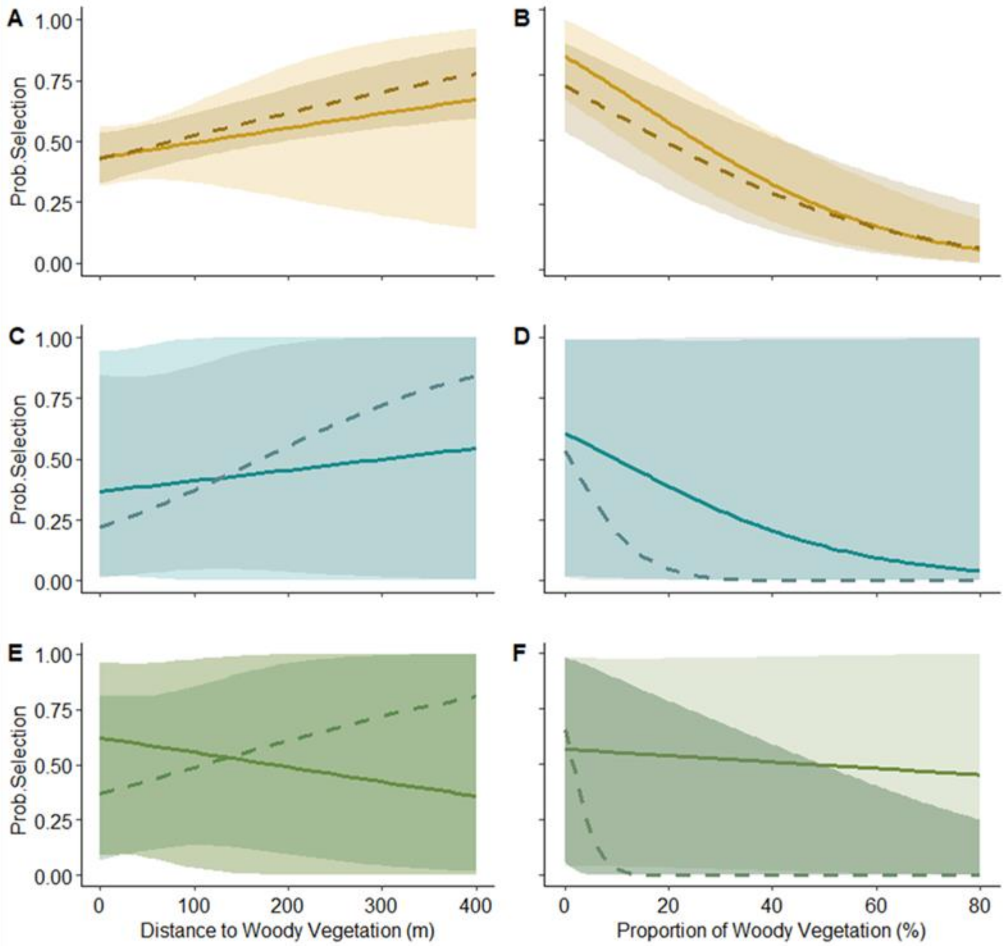


Figure 5.5. Probability of territory selection as a function of distance to shrubs (solid line) and trees (dashed line) in Grasshopper Sparrows (Panel A) and proportion of shrubs (solid line) and trees (dashed line) in Grasshopper Sparrows (Panel B) at the Konza Prairie Biological Station, 2014-2020. Probability of territory selection as a function of distance to shrubs (solid line) and trees (dashed line) in Eastern Meadowlarks (Panel C) and proportion of shrubs (solid line) and trees (dashed line) in Eastern Meadowlarks (Panel D), 2019-2021. Probability of territory selection as a function of distance to shrubs (solid line) and trees (dashed line) in Dickcissels (Panel E) and proportion of shrubs (solid line) and trees (dashed line) in Dickcissels (Panel F), 2019-2021. Grasshopper Sparrows and Eastern Meadowlarks are more likely to select territories far from woody vegetation, but Dickcissels are more likely to select territories within 150m of shrubs.

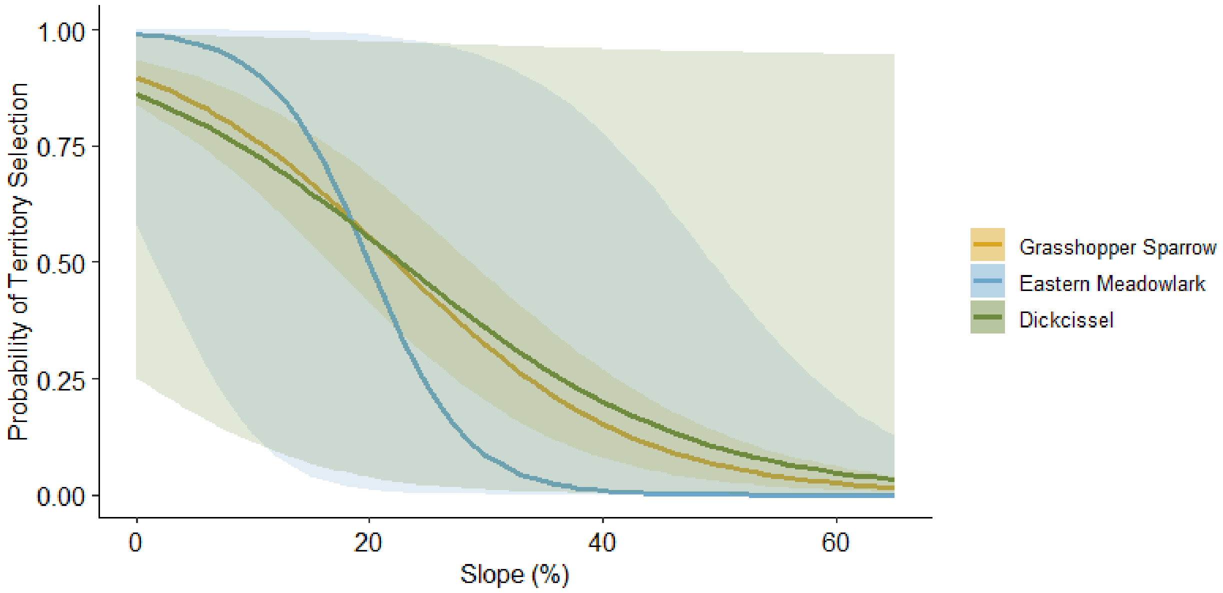


Figure 5.6. Probability of territory selection as a function of slope in Grasshopper Sparrows (yellow), 2014-2020, and Eastern Meadowlarks (blue) and Dickcissels (green), 2019-2021, at the Konza Prairie Biological Station. All three species prefer flat areas.

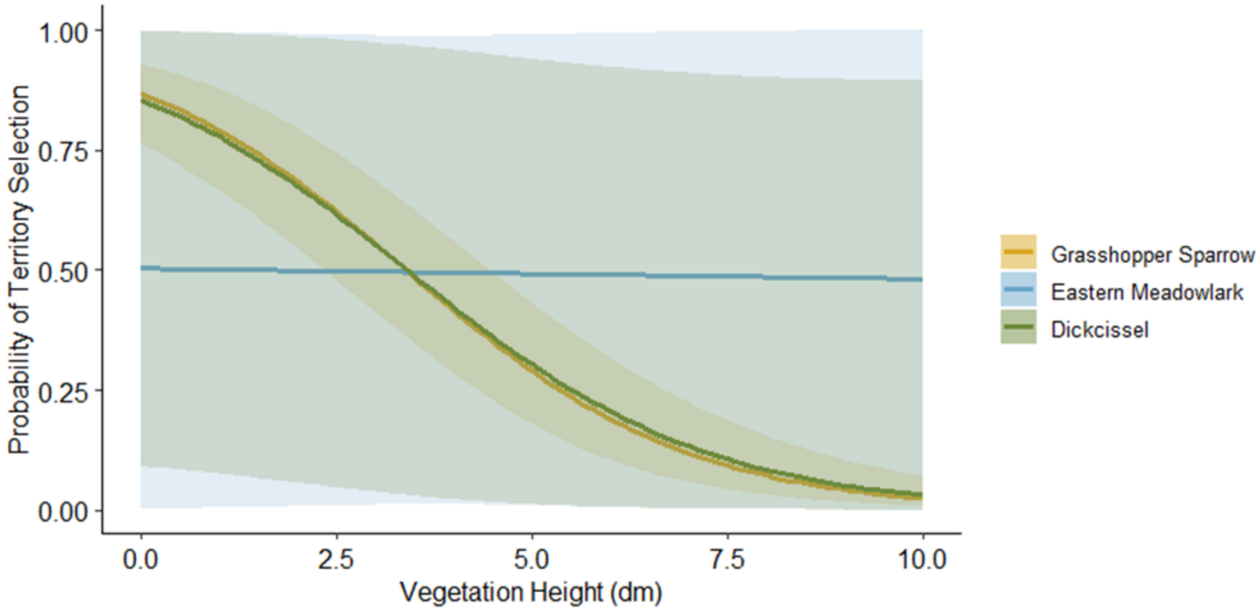


Figure 5.7. Probability of territory selection as a function of vegetation height in Grasshopper Sparrows (yellow) Eastern Meadowlarks (blue) and Dickcissels (green) at the Konza Prairie Biological Station, 2014-2020. Grasshopper Sparrows and Dickcissels prefer areas with shorter vegetation, while Eastern Meadowlarks do not exhibit a preference.

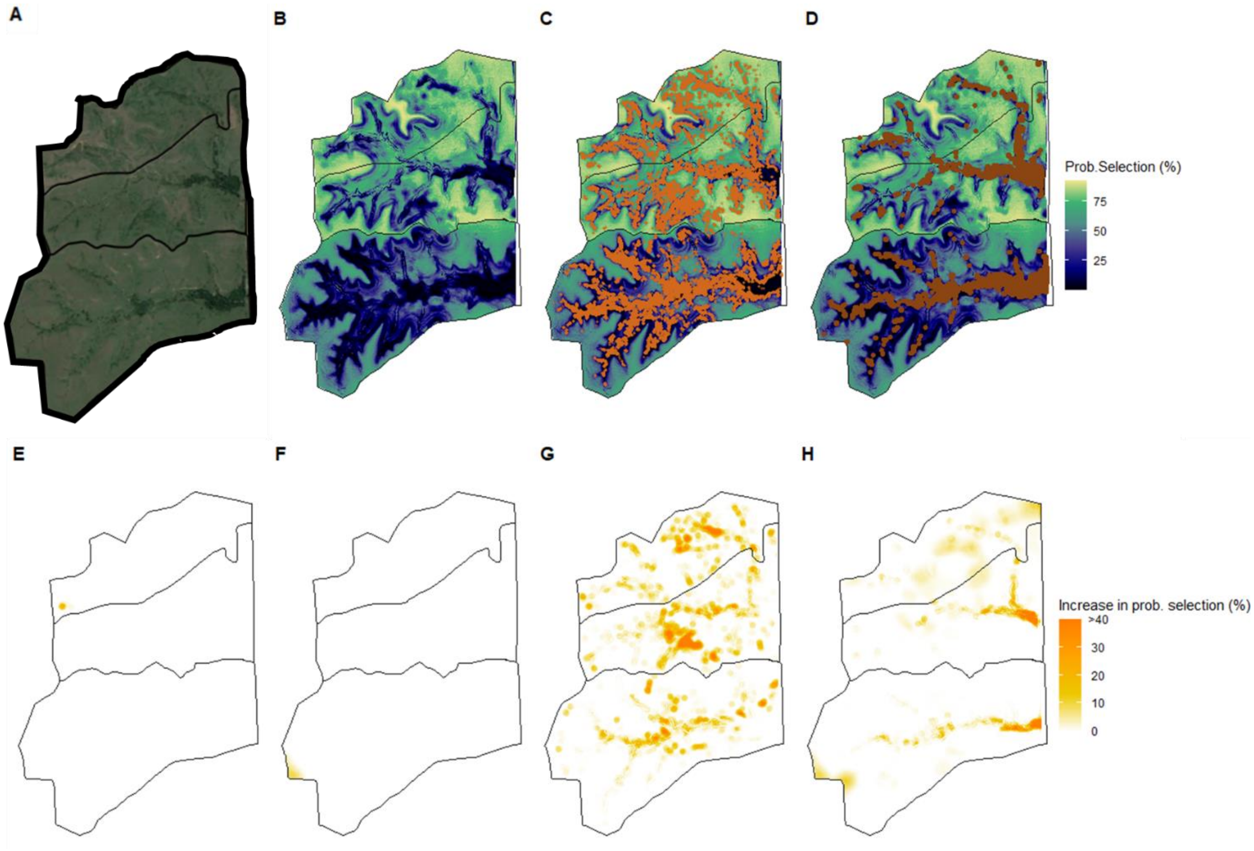


Figure 5.8. Aerial map (A) of patch-burn grazed unit (C3A/C3B/C3C) at the Konza Prairie Biological Station. Map of predicted probability of Grasshopper Sparrow territory selection (B) on June 15, 2020. This unit has substantial shrub (C) and tree (D) cover. The probability of Grasshopper Sparrow territory selection improves under four woody vegetation removal scenarios: (E) removal of one upland shrub; (F) removal of one upland tree; (G) removal of all shrubs in areas with less than 10% slope and above 400 m asl.; and (H) removal of all trees in areas with less than 10% slope and above 400 m asl.

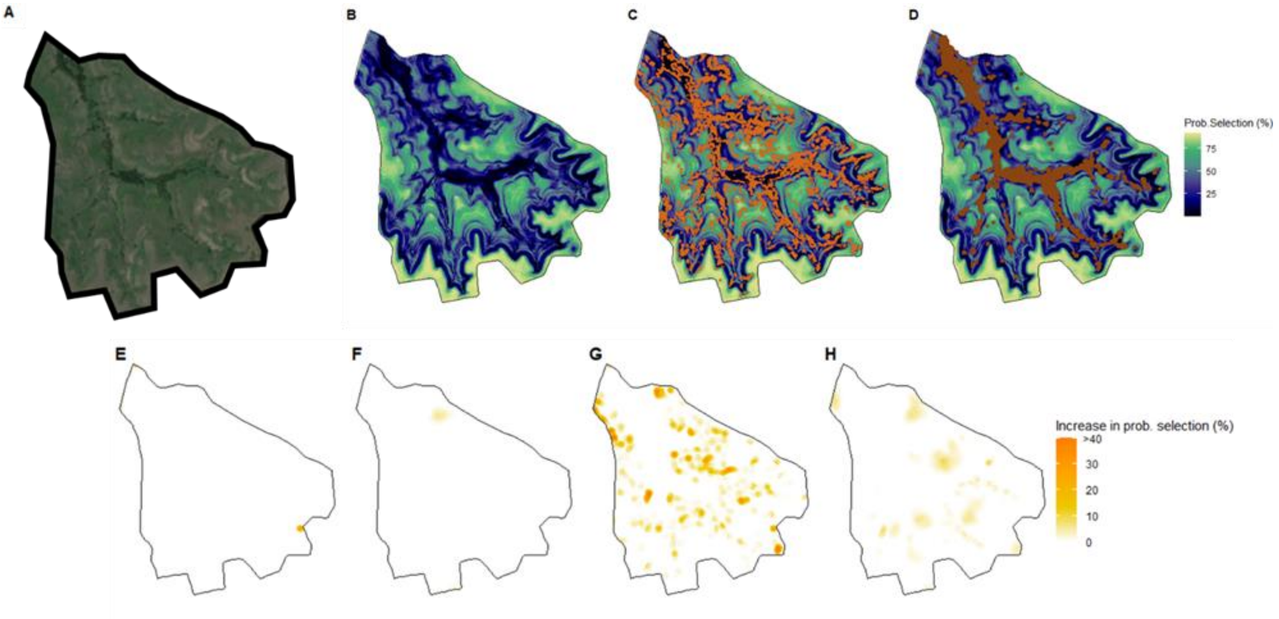


Figure 5.9. Aerial map (A) of an annually burned, bison-grazed unit (N1B) at the Konza Prairie Biological Station. Map of predicted probability of Grasshopper Sparrow territory selection (B) on June 15, 2020. This unit has substantial shrub (C) and tree (D) cover. The probability of Grasshopper Sparrow territory selection improves under four woody vegetation removal scenarios: (E) removal of one upland shrub; (F) removal of one upland tree; (G) removal of all shrubs in areas with less than 10% slope and above 400 m asl.; and (H) removal of all trees in areas with less than 10% slope and above 400 m asl.

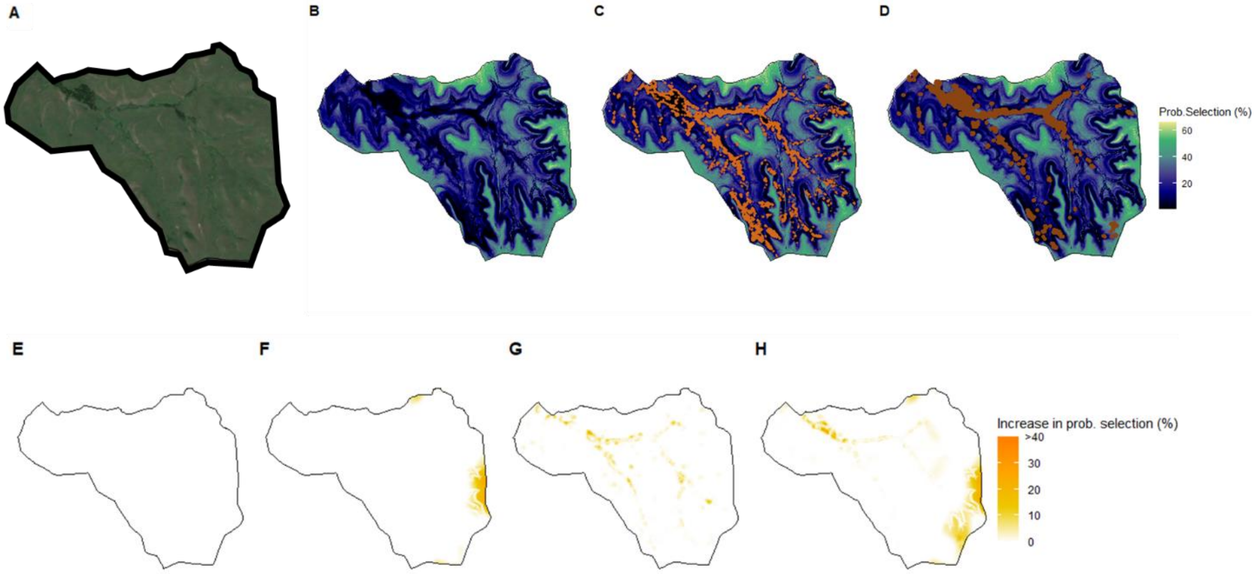


Figure 5.10. Aerial map (A) of an annually burned, ungrazed unit (K1B) at the Konza Prairie Biological Station. Map of predicted probability of Grasshopper Sparrow territory selection (B) on June 15, 2020. This unit has minimal shrub (C) and tree (D) cover. The probability of Grasshopper Sparrow territory selection improves under four woody vegetation removal scenarios: (E) removal of one upland shrub; (F) removal of one upland tree; (G) removal of all shrubs in areas with less than 10% slope and above 400 m asl.; and (H) removal of all trees in areas with less than 10% slope and above 400 m asl.

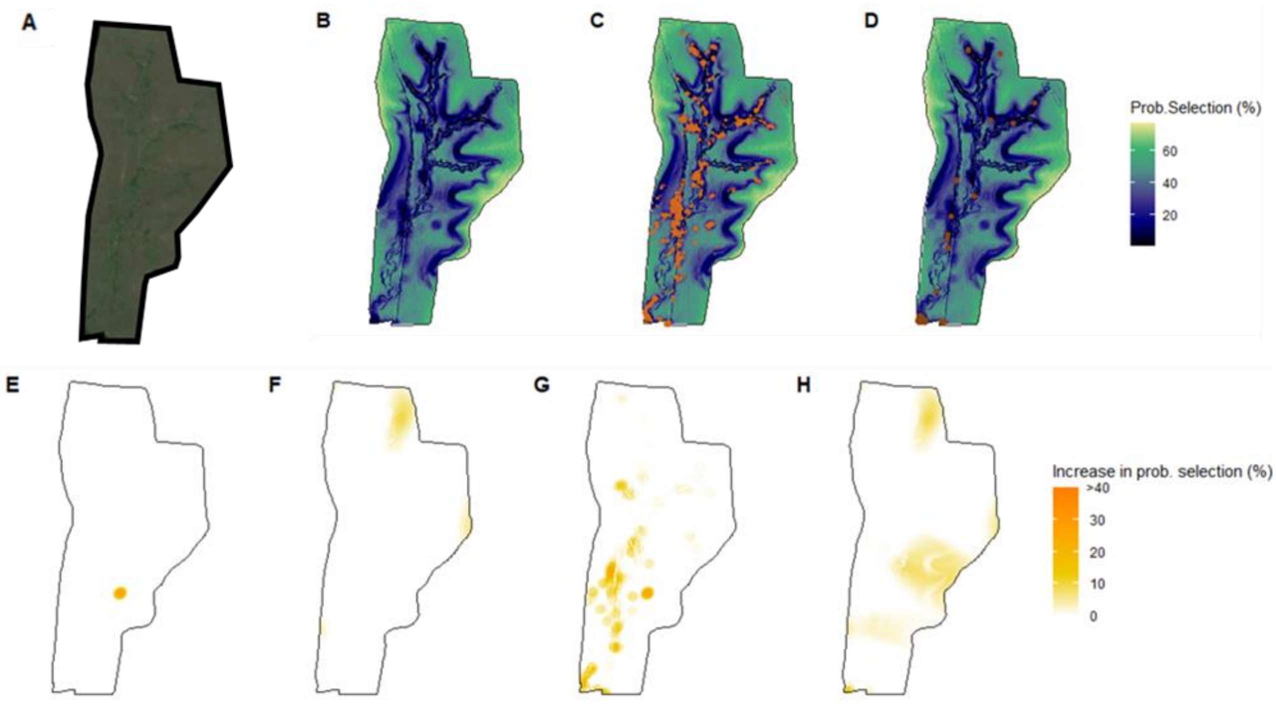


Figure 5.11. Aerial map of a biennially burned, ungrazed unit (2D) at the Konza Prairie Biological Station. Map of predicted probability of Grasshopper Sparrow territory selection (B) on June 15, 2020. This unit has minimal shrub (C) and tree (D) cover. The probability of Grasshopper Sparrow territory selection improves under four woody vegetation removal scenarios: (E) removal of one upland shrub; (F) removal of one upland tree; (G) removal of all shrubs in areas with less than 10% slope and above 400 m asl.; and (H) removal of all trees in areas with less than 10% slope and above 400 m asl.

Chapter 6 - Conclusions and Implications

This dissertation contributes to our understanding of the ways in which precipitation affect bird populations and the mechanisms underlying these relationships. Each chapter tested a different set of hypothesized mechanisms, but the results from each chapter present a cohesive understanding of how precipitation affects avian ecology from the level of a single species up to global patterns, and at life stages from the nest to adult survival. A combination of field-based research and literature synthesis provided support for the direct, thermogenic costs of precipitation on young and adult birds, and the indirect, vegetation-mediated link between precipitation and bird populations. However, these findings challenge a large body of existing work that considers food the primary link between rainfall and avian populations.

At a local level, this dissertation provides a comprehensive explanation for how and why local variation in abundance of grassland bird occurs. I provided several lines of evidence that local abundance is primarily determined by variation in adult vital rates, particularly movement, via rainfall-mediated effects on vegetation structure. These mechanisms result from lagged precipitation, suggesting ecological processes may extend beyond the spatial or temporal extent of most 2-3 year studies. Under future climate conditions, the effects of more variable weather on populations may not be evident for several years, which may confound attempts to detect the effects of conservation actions via population responses.

I provided additional support for the growing body of evidence that grassland songbirds exhibit unusually high rates of dispersal (Williams and Boyle 2018, Boyle and Sullins *in review*, Smith 2021) compared to other migratory songbirds (Winger et al. 2018). This result highlights the importance of incorporating movement into analyses of survival in mobile species. 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).

On a global scale, this dissertation helps explain why rain leads to divergent responses in species living in different regions and with different life histories. I found support among my chapters for the following patterns. First, precipitation timing affects the nature of the population's response to precipitation, and this response may vary across a species' range or life stage. In many species, direct precipitation negatively affected reproductive success and lagged precipitation often positively affected reproductive success (e.g., Descamps et al. 2015, Skagen et al. 2012). However, the nature and magnitude of these responses vary for other vital rates (e.g., survival or emigration). Grasshopper Sparrows exhibited higher rates of nest failure in response to storms (Freeman et al. 2023), reduced survival in response to winter precipitation, and a curvilinear relationship with lagged precipitation. Remarkably, these birds exhibited more variation in responses to precipitation across vital rates in one species than within one vital rate across species.

Second, behavior can help alleviate detrimental effects of precipitation. In my second chapter, I found that parental care was a mediating factor for the relationship between precipitation and reproductive success. Thus, parental investment and behavior may determine reproductive outcomes more than the amount or timing of precipitation by altering provisioning, nest off bouts, or nest defense. Breeding adults may also emigrate to areas that they perceive would increase their probability of reproductive success, which may drive the relationship between precipitation, vegetation structure, and emigration.

Third, responses to precipitation likely interact with temperature. Birds at higher elevation, where temperatures are lower than at low elevations, responded to precipitation negatively. Precipitation at higher elevations can lead to higher costs of thermoregulation and homeothermy (McKechnie and Wolf 2019) and reduced prey availability or refugia (Jirinec et al. 2022). Temperature may also be the basis for divergent responses to precipitation throughout a bird's annual cycle. Birds may respond negatively to precipitation during colder periods (e.g., winter) and positively during warmer periods (e.g., summer), responses which may be shaped by both direct and indirect mechanisms.

We did not find support for food limitation underlying the relationship between any vital rates and precipitation at a local or global scale. Food-mediated mechanisms may be elevation-, biome-, or region-dependent, suggesting that the location in a species' range where the study is conducted may affect observed relationships. For example, food may play a larger role in areas where prey items are seasonally limited or have higher interannual fluctuations in abundance (Zárybnická et al. 2015). However, evidence from this body of work demonstrates that relationships between precipitation and avian vital rates tended to be mediated by vegetation structure more than food.

Understanding the relationships between precipitation, vegetation, and bird populations is essential to effectively manage for vegetation structure that supports bird populations, particularly in systems in which vegetation structure is highly responsive to precipitation variability like grasslands. Birds may select vegetation that they perceive will increase their survival and reproduction, and these choices may be specific to their biome or life history traits. Measuring species-specific responses to precipitation within a site, along with the vegetation that mediates these relationships, is essential to determine management for vegetation structure that supports bird populations.

This dissertation provided a framework for understanding why and how precipitation affects bird populations, resulting in several inferences transferable to other endotherms. By revealing the mechanistic links between weather and demography, we gain a greater understanding of how to support declining species, the time scales over which local demography responds to environmental conditions, and how to halt range-wide declines in a variety of taxa.

References

Abatzoglou, J. T. (2013). Development of gridded surface meteorological data for ecological applications and modelling. *International Journal of Climatology*, *131*, 121–131. https://doi.org/10.1002/joc.3413

Abatzoglou, J. T., & Brown, T. J. (2012). A comparison of statistical downscaling methods suited for wildfire applications. *International Journal of Climatology*, *780*, 772–780. https://doi.org/10.1002/joc.2312

Addo-Bediako, A., Chown, S. L., & Gaston, K. J. (2000). Thermal tolerance, climatic variability and latitude. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1445), 739–745. https://doi.org/10.1098/rspb.2000.1065

Ahlering, M. A., Johnson, D. H., & Faaborg, J. (2009). Factors Associated with Arrival Densities of Grasshopper Sparrow (*Ammodramus savannarum*) and Baird's Sparrow (*A. bairdii*) in the Upper Great Plains. *The Auk*, *126*(4), 799–808. https://doi.org/10.1525/auk.2009.08154

Ahlering, M. A., Johnson, D. H., & Elliott, L. H. (2019). Land Ownership and Use Influence Grassland Bird Abundance. *The Journal of Wildlife Management*, *83*(2), 343–355. https://doi.org/10.1002/jwmg.21590

Albright, T. P., Mutiibwa, D., Gerson, A. R., Smith, E. K., Talbot, W. A., O'Neill, J. J., McKechnie, A. E., & Wolf, B. O. (2017). Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences*, *114*, 2283–2288. https://doi.org/10.1073/pnas.1613625114

Allen, M. C., Lockwood, J. L., & Burger, J. (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*(3), 528–538. https://doi.org/10.1111/1365-2664.13776

Anderson, L. C., Powell, L. A., Schacht, W. H., Lusk, J. J., & Vodehnal, W. L. (2015). Greater Prairie-Chicken Brood-Site Selection and Survival in the Nebraska Sandhills. *The Journal of Wildlife Management*, *79*(4), 559–569. https://doi.org/10.1002/jwmg.876

Angilletta, M. (2009). *Thermal adaptation: a theoretical and empirical synthesis. Oxford University press, Oxford*.

Archer, S. (1995). Tree-grass dynamics in a Prosopis-thornscrub savanna parkland: Reconstructing the Past and Predicting the Future. *Ecoscience*, *2*(1), 83–89.

Arnold, T. W. (2010). Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *Journal of Wildlife Management*, *74*(6), 1175–1178. https://doi.org/10.2193/2009-367

Augustine, D. J. (2010). Spatial versus temporal variation in precipitation in a semiarid ecosystem. *Landscape Ecology*. https://doi.org/10.1007/s10980-010-9469-y

Augustine, D. J., & Derner, J. D. (2015). Patch-Burn Grazing Management, Vegetation Heterogeneity, and Avian Responses in a Semi-Arid Grassland. *The Journal of Wildlife Management, 79*(6), 927–936. https://doi.org/10.1002/jwmg.909

Bachle, S., & Nippert, J. B. (2022). Climate variability supersedes grazing to determine the anatomy and physiology of a dominant grassland species. *Oecologia*, *198*(2), 345–355. https://doi.org/10.1007/s00442-022-05106-x

Balent, K. L., & Norment, C. J. (2003). Demographic Characteristics of a Grasshopper Sparrow Population in a Highly Fragmented Landscape of Western New York State. *Journal of Field Ornithology, 74*(4), 341–348.

Battley, P. F., Piersma, T., Dietz, M. W., Tang, S., Dekinga, A., & Hulsman, K. (2000). Empirical evidence for differential organ reductions during trans-oceanic bird flight. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1439), 191–195. https://doi.org/10.1098/rspb.2000.0986

Baudier, K. M., D'Amelio, C. L., Malhotra, R., O'Connor, M. P., & O'Donnell, S. (2018). Extreme insolation: Climatic variation shapes the evolution of thermal tolerance at multiple scales. *American Naturalist*, *192*(3), 347–359. https://doi.org/10.1086/698656

Becker, A., Roeder, D., Husak, M., & Murphy, M. (2018). Annual survival and breeding dispersal of a migratory passerine, the Scissor-tailed Flycatcher. *Wiley Online Library, 89*(1), 22–36.

Bent, A. A. C., & Austin, O. L. (1968). Life Histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and Allies. In *Bulletin of the United States National Museum* (Vol. 237). https://doi.org/10.5479/si.03629236.237.1

Blair, J., Nippert, J., & Briggs, J. (2014). Grassland ecology. In *Ecology and the Environment, The Plant Sciences 8* (pp. 389–423). https://doi.org/10.1007/978-1-4614-7501-9_14

Both, C., Turnhout, C. A. M. Van, Bijlsma, R. G., Foppen, B., Siepel, H., Strien, A. J. Van, & Ruud, P. (2010). Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B: Biological Sciences, 277*, 1259–1266. https://doi.org/10.1098/rspb.2009.1525

Boyle, W. A., Shogren, E. H., & Brawn, J. D. (2020). Hygric Niches for Tropical Endotherms. *Trends in Ecology and Evolution, 35*(10), 938–952. https://doi.org/10.1016/j.tree.2020.06.011

Boyle, W. A., & Sullins, D. S. (*in review*). *Long-distance breeding dispersal in a grassland bird; patterns and climatic drivers*.

Brier, G. (1950). Verification of forecasts expressed in terms of probability. *Monthly Weather Review*, *75*, 1–3.

Briggs, J. M., Knapp, A. K., Blair, J. M., Heisler, J. L., Hoch, G. A., Lett, M. S., & McCarron, J. K. (2005). An ecosystem in transition: Causes and consequences of the conversion of mesic grassland to shrubland. *BioScience*, *55*(3), 243–254. https://doi.org/10.1641/0006-3568(2005)055[0243:AEITCA]2.0.CO;2

Briggs, J. M., Knapp, A. K., & Brock, B. L. (2002). Expansion of Woody Plants in Tallgrass Prairie: A Fifteen-year Study of Fire and Fire-grazing Interactions. *The American Midland Naturalist*, *147*(2), 287–294. https://doi.org/10.1674/0003-0031(2002)147[0287:eowpit]2.0.co;2

Broderick, C. M., Wilkins, K., Smith, M. D., & Blair, J. M. (2022). Climate legacies determine grassland responses to future rainfall regimes. *Global Change Biology, 28*(8), 2639–2656. https://doi.org/10.1111/gcb.16084

Brommer, J. E., Pietiäinen, H., & Kolunen, H. (2002). Reproduction and Survival in a Variable Environment : Ural Owls (*Strix uralensis*) and the Three-Year Vole Cycle. *The Auk*, *119*(2), 544–550.

Bruggeman, J. E., & Licht, D. S. (2020). Drought-mediated changes in black-tailed prairie dog colonies in the Northern Great Plains. *Journal of Mammalogy*, *101*(4), 1189–1204. https://doi.org/10.1093/jmammal/gyaa070

Brunsell, N. A., Ham, J. M., & Owensby, C. E. (2008). Assessing the multi-resolution information content of remotely sensed variables and elevation for evapotranspiration in a tall-grass prairie environment. *Remote Sensing of Environment*, *112*(6), 2977–2987. https://doi.org/10.1016/j.rse.2008.02.002

Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Second edition*. 2nd Edition, Springer-Verlag, New York. http://dx.doi.org/10.1007/b97636

Butler, L. K., Rohwer, S., Speidel, M. G., Butler, L. K., Rohwer, S., & Speidel, M. G. (2008). Quantifying Structural Variation in Contour Feathers to Address Functional Variation and Life History Trade-Offs. *Journal of Avian Biology, 39*(6), 629–639. https://doi.org/10.1111/j.1600-048X.2008.04432.x

Cahill, A., Aiello-Lammens, M., Fisher-Reid, M., Hua, X., Karanewsky, C., Ryu, H. Y., Sbeglia, G. C., Spagnolo, F., Waldron, J. B., & Wiens, J. (2014). Causes of warm-edge range limits: systematic review, proximate factors, and implications for climate change. *Journal of Biogeography*, *41*, 429–442.

Cai, W., Wang, G., Dewitte, B., Wu, L., Santoso, A., Takahashi, K., Yang, Y., Carreric, A, & McPhaden, M. J. (2018). Increased variability of eastern Pacific El Niño under greenhouse warming. *Nature*, *564*(7735), 201–206. https://doi.org/10.1038/s41586-018-0776-9

Center, N. O. and A. A. N. W. S. C. P. (2020). *North Atlantic Oscillation Observations and Forecasts*. Retrieved from https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml#publication

Chapman, R. N., Engle, D. M., Masters, R. E., & Leslie, D. M. (2004). Grassland vegetation and bird communities in the southern Great Plains of North America. *Agriculture, Ecosystems and Environment*, *104*(3), 577–585. https://doi.org/10.1016/j.agee.2004.01.026

Churchwell, R. T., Davis, C. A., Fuhlendorf, S. D., & Engle, D. M. (2008). Effects of Patch-Burn Management on Dickcissel Nest Success in a Tallgrass Prairie. *The Journal of Wildlife Management*, *72*(7), 1596–1604.

Collins, S. L., & Calabrese, L. B. (2012). Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *Journal of Vegetation Science*, *23*(3), 563–575. https://doi.org/10.1111/j.1654-1103.2011.01369.x

Collins, S. L., Nippert, J. B., Blair, J. M., & Briggs, J. M. (2021). Fire frequency, state change and hysteresis in tallgrass prairie. *Ecology Letters*, *24*, 636–647. https://doi.org/10.1111/ele.13676

Conover, R. R. (2009). *Grassland bird associations in a managed agricultural matrix*. Thesis. Iowa State University.

Cook, B. I., Ault, T. R., & Smerdon, J. E. (2015). Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances*, *1*(1), 1–8. https://doi.org/10.1126/sciadv.1400082

Coppedge, B. R., Engle, D. M., Masters, R. E., & Gregory, M. S. (2001). Avian response to landscape change in fragmented southern great plains grasslands. *Ecological Applications*. https://doi.org/10.1890/1051-0761(2001)011[0047:ARTLCI]2.0.CO;2

Coulson, T., Gaillard, J. M., & Festa-Bianchet, M. (2005). Decomposing the variation in population growth into contributions from multiple demographic rates. *Journal of Animal Ecology*, *74*(4), 789–801. https://doi.org/10.1111/j.1365-2656.2005.00975.x

Cox, W. A., Schwarzer, Y. C., Tornwall, B., & Chicalo, R. (2020). Tide and habitat features affect salt marsh songbird nest survival in northeast Florida, USA. *ENDANGERED SPECIES RESEARCH*, *41*, 119–129. https://doi.org/10.3354/esr01021

Curtis, S., & Adler, R. (2000). ENSO indices based on patterns of satellite-derived precipitation. *Journal of Climate*, *13*(15), 2786–2793. https://doi.org/10.1175/1520-0442(2000)013<2786:EIBOPO>2.0.CO;2

Darenova, E., Holub, P., Krupkova, L., & Pavelka, M. (2017). Effect of repeated spring drought and summer heavy rain on managed grassland biomass production and CO2 efflux. *Journal of Plant Ecology*, *10*(3), 476–485. https://doi.org/10.1093/jpe/rtw058

Davey, M. K., Brookshaw, A., & Ineson, S. (2014). The probability of the impact of ENSO on precipitation and near-surface temperature. *Climate Risk Management*, *1*, 5–24. https://doi.org/10.1016/j.crm.2013.12.002

Dawson, W. R., & Yacoe, M. E. (1983). Metabolic adjustments of small passerine birds for migration and cold. *American Journal of Physiology - Regulatory Integrative and Comparative Physiology*, *14*(6). https://doi.org/10.1152/ajpregu.1983.245.6.r755

Day, P. B., Stuart-Smith, R. D., Edgar, G. J., & Bates, A. E. (2018). Species' thermal ranges predict changes in reef fish community structure during 8 years of extreme temperature variation. *Diversity and Distributions*, *24*(8), 1036–1046. https://doi.org/10.1111/ddi.12753

Descamps, S., Tarroux, A., Varpe, Ø., Yoccoz, N. G., Tveraa, T., & Lorentsen, S. H. (2015). Demographic effects of extreme weather events: Snow storms, breeding success, and population growth rate in a long-lived Antarctic seabird. Ecology and Evolution, 5(2), 314–325. https://doi.org/10.1002/ece3.1357

Dewitz, J. (2019). *National Land Cover Database (NLCD) 2016 Products (ver 2.0, July 2020): U.S. Geological Survey data release*. https://doi.org/https://doi.org/10.5066/P96HHBIE

Doak, D. F., Morris, W. F., Pfister, C., Kendall, B. E., & Bruna, E. M. (2005). Influences Fitness and Population Growth. *American Naturalist*, *166*(1), E14–E21. https://doi.org/10.1086/430642

Duchardt, C. J., Beck, J. L., & Augustine, D. J. (2020). Mountain Plover habitat selection and nest survival in relation to weather variability and spatial attributes of black-tailed prairie dog disturbance. *The Condor*, *122*(1). https://doi.org/10.1093/condor/duz059

Dudaniec, R., Fessl, B., & Kleindorfer, S. (2007). Interannual and interspecific variation in intensity of the parasitic fly, *Philornis downsi*, in Darwin's finches. *Biological Conservation*, *139*(3), 325–332.

Dudney, J., Hallett, L. M., Larios, L., Farrer, E. C., Spotswood, E. N., Stein, C., & Suding, K. N. (2017). Lagging behind: have we overlooked previous-year rainfall effects in annual grasslands? *Journal of Ecology*, *105*, 484–495. https://doi.org/10.1111/1365-2745.12671

Gow, E. A., & Stutchbury, B. (2013). Within-season nesting dispersal and molt dispersal are linked to habitat shifts in a neotropical migratory songbird. *The Wilson Journal of Ornithology*, *125*(4), 696–708.

Elliott, L. H., & Johnson, D. H. (2018). The grasshopper sparrow as an indicator species in tallgrass prairies. *Journal of Wildlife Management*, *82*(5), 1074–1081. https://doi.org/10.1002/jwmg.21447

Ellison, K. S., Ribic, C. A., Sample, D. W., Fawcett, M. J., & Dadisman, J. D. (2013). Impacts of Tree Rows on Grassland Birds and Potential Nest Predators: A Removal Experiment. *PLoS ONE*, *8*(4). https://doi.org/10.1371/journal.pone.0059151

Ferris, J. N. (1999). An Analysis of the Impact of ENSO (El Niño/Southern Oscillation) on Global Crop Yields. *American Agricultural Economics Association*.

Fithian, W., & Hastie, T. (2013). Finite-sample equivalence in statistical models for presence-only data. *The Annals of Applied Statistics*, *7*(4), 1917–1939. https://doi.org/10.1214/13-AOAS667

Flanagan, L. B., & Adkinson, A. C. (2011). Interacting controls on productivity in a northern Great Plains grassland and implications for response to ENSO events. *Global Change Biology*, *17*, 3293–3311. https://doi.org/10.1111/j.1365-2486.2011.02461.x

Flockhart, D., Pichancourt, J., Norris, D., & Martin, T. (2015). Unravelling the annual cycle in a migratory animal: breeding-season habitat loss drives population declines of monarch butterflies. *Journal of Animal Ecology*, *84*, 155–165.

Forero-Medina, G., Joppa, L., & Pimm, S. L. (2011). Constraints to Species' Elevational Range Shifts as Climate Changes. *Conservation Biology*, *25*(1), 163–171. https://doi.org/10.1111/j.1523-1739.2010.01572.x

Francq, G. E. (1972). *Parental Care of the Eastern Meadowlark (Sturnella Magna)*. Thesis. Emporia State University.

Franzén, M., Nilsson, S. G., Johansson, V., & Ranius, T. (2013). Population Fluctuations and Synchrony of Grassland Butterflies in Relation to Species Traits. *PLoS ONE*, *8*(10), 1–7. https://doi.org/10.1371/journal.pone.0078233

Frederiksen, M., Daunt, F., Harris, M. P., & Wanless, S. (2008). The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology*, *77*(5), 1020–1029. https://doi.org/10.1111/j.1365-2656.2008.01422.x

Freeman, N. E., Gustafson, M., Hefley, T. J., & Boyle, W. A. (*in review*). *Riding out the storm: depleted fat stores and elevated hematocrit in a small bodied endotherm exposed to severe weather*. Conservation Physiology.

Fretwell, S. (1986). Distribution and abundance of the Dickcissel. *Current Ornithology*, *4*, 211:242.

Fuhlendorf, S. D., & Engle, D. M. (2004). Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology*, *41*(4), 604–614. https://doi.org/10.1111/j.0021-8901.2004.00937.x

Fung, Y. L., Newman, K., King, R., & de Valpine, P. (2022). Building integral projection models with nonindependent vital rates. *Ecology and Evolution*, *12*(3), 1–15. https://doi.org/10.1002/ece3.8682

Gaines, S. D., & Denny, M. W. (1993). The Largest, Smallest, Highest, Lowest, Longest, and Shortest: Extremes in Ecology. *Ecology*, *74*(6), 1677–1692.

Gehrt, J. M., Sullins, D. S., & Haukos, D. A. (2020). Looking at the Bigger Picture: How Abundance of Nesting and Brooding Habitat Influences Lek-Site Selection by Lesser Prairie-Chickens. *American Midland Naturalist*, *183*(1), 52–77. https://doi.org/10.1637/19-020

Gilroy, J. J., Virzi, T., Boulton, R. L., & Lockwood, J. L. (2012). A new approach to the “apparent survival” problem: estimating true survival rates from mark-recapture studies. *Ecology*, *93*(7), 1509–1516.

Giménez-Benavides, L., Escudero, A., & Iriondo, J. (2008). What shapes the altitudinal range of a high mountain Mediterranean plant? Recruitment probabilities from ovule to seedling stage. *Ecography*, *31*, 731–740.

Giovanni, M. D., Powell, L. A., & Schacht, W. H. (2015). Habitat preference and survival for western meadowlark (Sturnella Neglecta) fledglings in a contiguous prairie system. *Wilson Journal of Ornithology*, *127*(2), 200–211. https://doi.org/10.1676/wils-127-02-200-211.1

González-Gajardo, A., Sepúlveda, P. V., & Schlatter, R. (2009). Waterbird Assemblages and Habitat Characteristics in Wetlands : Influence of Temporal Variability on Species-Habitat Relationships. *Waterbird Society*, *32*(2), 225–233.

Gottfried, B. M. (1979). Anti-Predator Aggression in Birds Nesting in Old Field Habitats : An Experimental Analysis. *The Condor*, *81*(3), 251–257.

Gotway, C. A., & Young, L. J. (2002). Combining incompatible spatial data. *Journal of the American Statistical Association*, *97*(458), 632–648. https://doi.org/10.1198/016214502760047140

Gow, E. A., & Stutchbury, B. J. M. (2013). Within-season nesting dispersal and molt dispersal are linked to habitat shifts in a Neotropical migratory songbird. *The Wilson Journal of Ornithology*, *125*(4), 696–708. https://doi.org/10.1676/13-015.1

Grant, T. A., Shaffer, T. L., Madden, E. M., & Nenneman, M. P. (2017). Contrasting nest survival patterns for ducks and songbirds in northern mixed-grass prairie. *The Journal of Wildlife Management*, *81*(4), 641–651. https://doi.org/10.1002/jwmg.21224

Graves, B. M., Rodewald, A. D., & Hull, S. D. (2010). Influence of woody vegetation on grassland birds within reclaimed surface mines. *The Wilson Journal of Ornithology*, *122*(4), 646–654. Retrieved from http://www.jstor.org/stable/40962333

Griffin, K. A., Hebblewhite, M., Robinson, H. S., Zager, P., Barber-Meyer, S. M., Christianson, D., Creel, S., Harris, N. C., Hurley, M. A., Jackson, D. H., Johnson, B. K., Myers, W. L., Raithel, J. D., Schlegel, M., Smith, B. L., White, C., & White, P. J. (2011). Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *Journal of Animal Ecology*, *80*(6), 1246–1257. https://doi.org/10.1111/j.1365-2656.2011.01856.x

Gross, A. (1968). Dickcissel. In O. L. Austin (Ed.), *Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and their allies* (pp. 158–191). Part 1. Bulletin of the United States National Museum.

Gubler, S., Fiddes, J., Keller, M., & Gruber, S. (2011). Scale-dependent measurement and analysis of ground surface temperature variability in alpine terrain. *Cryosphere*, *5*(2), 431–443. https://doi.org/10.5194/tc-5-431-2011

Guido, N. A. (2020). *Habitat Selection Across the Reproductive Cycles of Grassland Songbirds in the Northern Great Plains*. Thesis. University of Maine.

Hakkarainen, H., Ilmonen, P., Koivunen, V., & Korpim, E. (2001). Experimental increase of predation risk induces breeding dispersal of Tengmalm's owl. *Oecologia*, (126), 355–359. https://doi.org/10.1007/s004420000525

Halkka, A., Halkka, L., Halkka, O., Roukka, K., & Pokki, J. (2006). Lagged effects of North Atlantic Oscillation on spittlebug *Philaenus spumarius* (Homoptera) abundance and survival. *Global Change Biology*, *12*, 2250–2262. https://doi.org/10.1111/j.1365-2486.2006.01266.x

Halupka, L., Wierucka, K., Sztwiertnia, H., & Klimczuk, E. (2017). Conditions at autumn stopover sites affect survival of a migratory passerine. *Journal of Ornithology*, *158*(4), 979–988. https://doi.org/10.1007/s10336-017-1472-5

Hammond, P. S., Francis, T. B., Heinemann, D., Long, K. J., Moore, J. E., Punt, A. E., Reeves, R. R., Sepulveda, M., Sigurosson, G. M., Siple, M. C., Vikingsson, G., Wade, P. R., Williams, R., & Zerbini, A. N. (2021). Estimating the Abundance of Marine Mammal Populations. *Frontiers in Marine Science*, *8*(September). https://doi.org/10.3389/fmars.2021.735770

Hansen, C. P., Schreiber, L. A., Rumble, M. A., Millspaugh, J. L., Gamo, R. C., Kehmeier, J. W., & Wojcik, N. (2016). Microsite Selection and Survival of Greater Sage-Grouse Nests in South-Central Wyoming. *The Journal of Wildlife Management*, *80*(5), 862–876. Retrieved from http://www.jstor.org/stable/24765225

Harmeson, J. P. (1974). Breeding Ecology of the Dickcissel. *The Auk*, *91*(2), 348–359.

Harrell, F., Lee, K. L., & Mark, D. B. (1996). Multivariable prognostic models: issues in developing models, evaluating assumptions and adequacy, and measuring and reducing errors. *Statistics in Medicine*, *15*, 361–387.

Hefley, T. J., Broms, K. M., Brost, B. M., Buderman, F. E., Kay, S. L., Scharf, H. R., Tipton, J. r., Williams, P. J., & Hooten, M. B. (2017). The basis function approach for modeling autocorrelation in ecological data. *Ecology*, *98*(3), 632–646. https://doi.org/10.1002/ecy.1674

Herkert, J. R. (1998). The influence of the CRP on Grasshopper Sparrow population trends in the Mid-continental United States. *Wildlife Society Bulletin*, *26*(2), 227–231.

Herkert, J. R. (2007). Evidence for a Recent Henslow's Sparrow Population Increase in Illinois. *Journal of Wildlife Management*, *71*(4), 1229–1233. https://doi.org/10.2193/2006-029

Higgins, K. F., Kirsch, L. M., & Ball, I. J. (1969). A Cable-Chain Device for Locating Duck Nests. *Journal of Wildlife Management*, *33*(4), 1009–1011.

Hill, J. M., Lloyd, J. D., McFarland, K. P., & Rimmer, C. C. (2019). Apparent survival of a range-restricted montane forest bird species is influenced by weather throughout the annual cycle. *Avian Conservation and Ecology*, *14*(2). https://doi.org/10.5751/ACE-01462-140216

Hoekstra, J. M., Boucher, T. M., Ricketts, T. H., & Roberts, C. (2005). Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecology Letters*, *8*(1), 23–29. https://doi.org/10.1111/j.1461-0248.2004.00686.x

Holcomb, E. D., Davis, C. A., & Fuhlendorf, S. D. (2014). Patch-Burn Management: Implications for Conservation of Avian Communities in Fire-Dependent Sagebrush Ecosystems. *The Journal of Wildlife Management*, *78*(5), 848–856. Retrieved from http://www.jstor.org/stable/43188214

Hopkins, H. L., & Kennedy, M. L. (2004). An assessment of indices of relative and absolute abundance for monitoring populations of small mammals. *Wildlife Society Bulletin*, *32*(4), 1289–1296. https://doi.org/10.2193/0091-7648(2004)032[1289:aaoior]2.0.co;2

Hovick, T. J., Miller, J. R., Dinsmore, S. J., Engle, D. M., Debinski, D. M., & Fuhlendorf, S. D. (2012). Effects of Fire and Grazing on Grasshopper Sparrow Nest Survival. *The Journal of Wildlife Management*, *76*(1), 19–27. Retrieved from https://about.jstor.org/terms

Huang, A. C., Bishop, C. A., McKibbin, R., Drake, A., & Green, D. J. (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), 1–10. https://doi.org/10.1186/s12898-017-0139-7

Igl, L. D., & Johnson, D. H. (1999). Le Conte's Sparrows breeding in conservation reserve program fields: Precipitation and patterns of population change. *Studies in Avian Biology*, *80*(7), 1189–1204.

Illera, J. C., & Díaz, M. (2006). Reproduction in an endemic bird of a semiarid island: A food-mediated process. *Journal of Avian Biology*, *37*, 447-456.

Jones, J., & Robertson, R. J. (2001). Territory and Nest-Site Selection of Cerulean Warblers in Eastern Ontario. *The Auk*, *118*(3), 727–735.

Jones, S. L., Dieni, J. S., Green, M. T., & Gouse, P. J. (2007). Annual Return Rates of Breeding Grassland Songbirds. *The Wilson Journal of Ornithology*, *119*(1), 89–94. Retrieved from https://about.jstor.org/terms

Jones, S. K., Ripplinger, J., & Collins, S. L. (2017). Species reordering, not changes in richness, drives long-term dynamics in grassland communities. *Ecology Letters*, *20*(12), 1556–1565. https://doi.org/10.1111/ele.12864

Kanno, Y., Letcher, B. H., Hitt, N. P., Boughton, D. A., Wofford, J. E. B., & Zipkin, E. F. (2015). Seasonal weather patterns drive population vital rates and persistence in a stream fish. *Global Change Biology*, *21*(5), 1856–1870. https://doi.org/10.1111/gcb.12837

Kaspari, M. (1991). Central Place Foraging in Grasshopper Sparrows: Opportunism or Optimal Foraging in a Variable Environment? *Oikos*, *60*(3), 307–312.

Kaspari, M., & Joern, A. (1993). Prey Choice by Three Insectivorous Grassland Birds: Reevaluating Opportunism. *Oikos*, *68*(3), 414–430.

Kaspari, M., & O'Leary, H. (1988). Nonparental Attendants in a North-temperate Migrant. *The Auk*, *105*(4), 792–793.

Kendall, W., Nichols, J., & Hines, J. (1997). Estimating Temporary Emigration Using Capture-Recapture Data with Pollock's Robust Design. *Ecology*, *78*(2), 563–578.

Kentie, R., Both, C.,Hooijmeijer, J. C. E. W., & Piersma, T. (2014). Age-dependent dispersal and habitat choice in black-tailed godwits *Limosa limosa limosa* across a mosaic of traditional and modern grassland habitats. *Journal of Avian Biology*, *45*, 396–405.

Klug, P. E., Jackrel, S. L., & With, K. A. (2010). Linking snake habitat use to nest predation risk in grassland birds: The dangers of shrub cover. *Oecologia*, *162*(3), 803–813. https://doi.org/10.1007/s00442-009-1549-9

Knapp, A. K., Fay, P. A., Blair, J. M., Collins, S. L., Smith, M. D., Carlisle, J. D., … McCarron, J. K. (2002). Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science*, *298*(5601), 2202–2205. https://doi.org/10.1126/science.1076347

Knapp, A. K., & Smith, M. D. (2001). Variation among Biomes in Temporal Dynamics of Aboveground Primary Production. *Science*, *291*(5503), 481–484. https://doi.org/10.1126/science.291.5503.481

Koerner, S. E., & Collins, S. L. (2013). Small-scale patch structure in North American and South African grasslands responds differently to fire and grazing. *Landscape Ecology*, *28*(7), 1293–1306. https://doi.org/10.1007/s10980-013-9866-0

Koerner, S. E., & Collins, S. L. (2014). Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. *Ecology*, *95*(1), 98–109. https://doi.org/10.1890/13-0526.1

Laake, J. (2013). RMark: An R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep. 2013-01, 25 p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

Ladwig, L. M., Ratajczak, Z. R., Ocheltree, T. W., Hafich, K. A., Churchill, A. C., Frey, S. J. K., Fuss, C. B., Kazanski, C. E., Munoz, J. D., Petrie, M. D., Reinmann, A. B., & Smith, J. G. (2016). Beyond arctic and alpine: The influence of winter climate on temperate ecosystems. *Ecology*, *97*(2), 372–382. https://doi.org/10.1890/15-0153.1

LaManna, J. A., George, T. L., Saracco, J. F., Nott, M. P., & DeSante, D. F. (2012). El Niño–Southern Oscillation influences annual survival of a migratory songbird at a regional scale. *The Auk*, *129*(4), 1–10. https://doi.org/10.1525/auk.2012.12017

Latimer, C. E., & Zuckerberg, B. (2021). Habitat loss and thermal tolerances influence the sensitivity of resident bird populations to winter weather at regional scales. *Journal of Animal Ecology*, *90*(2), 317–329. https://doi.org/10.1111/1365-2656.13332

Lautenbach, J. M., Stricker, N., Ervin, M., Hershner, A., Harris, R., & Smith, C. (2020). Woody vegetation removal benefits Grassland birds on reclaimed surface mines. *Journal of Fish and Wildlife Management*, *11*(1), 89–98. https://doi.org/10.3996/062019-JFWM-053

Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, *62*(1), 67–118. https://doi.org/10.2307/2937171

Lehtilä, K., Dahlgren, J. P., Garcia, M. B., Leimu, R., Syrjänen, K., & Ehrlén, J. (2016). Forest succession and population viability of grassland plants: long repayment of extinction debt in Primula veris. *Oecologia*, *181*(1), 125–135. https://doi.org/10.1007/s00442-016-3569-6

Lewis Najev, B. S., Schofield, A., Flores, R. I., Hutchins, B. T., Andrew McDonald, J., & Perez, K. E. (2019). Terrestrial snail communities of the lower Rio Grande valley are affected by human disturbance and correlate with vegetation community composition. *Southwestern Naturalist*, *64*(3–4), 216–227. https://doi.org/10.1894/0038-4909-64.3-4.216

Lindell, T., Ehrlén, J., & Dahlgren, J. (2021). Weather-driven demography and population dynamics of an endemic perennial plant. *Ecology*, *110*, 582–592.

Linden, D., Siren, A., & Pekins, P. (2018). Integrating telemetry data into spatial capture recapture modifies inferences on multi-scale. *Ecosphere*, *9*(8).

Lindenmayer, D. B., Lane, P., Foster, C. N., Westgate, M. J., Sato, C., Ikin, K., Crane, M., Michael, D., Florance, D., & Scheele, B. C. (2019). Do migratory and resident birds differ in their responses to interacting effects of climate, weather and vegetation? *Diversity and Distributions*, *25*(3), 449–461. https://doi.org/10.1111/ddi.12874

"The Road to Recovery Species Urgency List." (2022).

Liu, J., Qiu, L., Chen, J., Zheng, B., Wei, X., Gao, H., Zhang, Y., Cheng, J. (2019). Responses of plant biomass and nutrients to fire vary with functional group and slope aspect in a semiarid restored grassland on the Loess Plateau. *Journal of Arid Environments*, *171*(May), 104008. https://doi.org/10.1016/j.jaridenv.2019.104008

Lokemoen, J. T., & Koford, R. R. (2011). Using Candlers to Determine the Incubation Stage of Passerine Eggs. *Journal of Field Ornithology*, *67*(4), 660–668.

Lomas, L., & Bender, L. (2007). Survival and Cause-Specific Mortality of Neonatal Mule Deer Fawns North-Central New Mexico. *The Journal of Wildlife Management*, *71*(3), 884–894.

Louthan, A. M., Doak, D. F., Goheen, J. R., Palmer, T. M., & Pringle, R. M. (2013). Climatic stress mediates the impacts of herbivory on plant population structure and components of individual fitness. *Journal of Ecology*, *101*(4), 1074–1083. https://doi.org/10.1111/1365-2745.12090

Louthan, A. M., & Morris, W. (2021). Climate change impacts on population growth across a species' range differ due to nonlinear responses of populations to climate and variation in rates of climate change. *PLoS ONE*, *16*(3 March), 1–20. https://doi.org/10.1371/journal.pone.0247290

Louthan, A. M., Walters, J. R., Terando, A. J., Garcia, V., & Morris, W. F. (2021). Shifting correlations among multiple aspects of weather complicate predicting future demography of a threatened species. *Ecosphere*, *12*(9). https://doi.org/10.1002/ecs2.3740

Macías-Duarte, A., Panjabi, A. O., Strasser, E. H., Levandoski, G. J., Ruvalcaba-Ortega, I., Doherty, P. F., & Ortega-Rosas, C. I. (2017). Winter survival of North American grassland birds is driven by weather and grassland condition in the Chihuahuan Desert. *Journal of Field Ornithology*, *88*(4), 374–386. https://doi.org/10.1111/jofo.12226

Martin, K., Wilson, S., MacDonald, E. C., Camfield, A. F., Martin, M., & Trefry, S. A. (2017). Effects of severe weather on reproduction for sympatric songbirds in an alpine environment:

Interactions of climate extremes influence nesting success. *AUK*, *134*(3), 696–709. https://doi.org/10.1642/AUK-16-271.1

Martin, T. E., Auer, S. K., Bassar, R. D., Niklison, A. M., & Lloyd, P. (2007). Geographic variation in avian incubation periods and parental influences on embryonic temperature. *Evolution*, *61*(11), 2558–2569. https://doi.org/10.1111/j.1558-5646.2007.00204.x

Matthiopoulos, J., Fieberg, J., & Aarts, G. (2020). *Species-Habitat Associations: Spatial data, predictive models, and ecological insights*.

McDermott, M. E., & DeGroote, L. W. (2016). Long-term climate impacts on breeding bird phenology in Pennsylvania, USA. *Global Change Biology*, *22*(10), 3304–3319. https://doi.org/10.1111/gcb.13363

McMillan, N. A., Fuhlendorf, S. D., Luttbeg, B., Goodman, L. E., Davis, C. A., Allred, B. W., & Hamilton, R. G. (2021). Are bison movements dependent on season and time of day? Investigating movement across two complex grasslands. *Ecosphere*, *12*(1). https://doi.org/10.1002/ecs2.3317

Mcnew, L. B., Gregory, A. J., & Sandercock, B. K. (2013). Spatial heterogeneity in habitat selection: Nest site selection by greater prairie-chickens. *Journal of Wildlife Management*, *77*(4), 791–801. https://doi.org/10.1002/jwmg.493

McNew, L. B., Gregory, A. J., Wisely, S. M., & Sandercock, B. K. (2012). Demography of greater prairie-chickens: Regional variation in vital rates, sensitivity values, and population dynamics. *Journal of Wildlife Management*, *76*(5), 987–1000. https://doi.org/10.1002/jwmg.369

Mikkelsen, A., Lesmeister, D., O’Reilly, K., & Dugger, K. (2022). Feather corticosterone reveals developmental challenges in a long-term study of juvenile northern spotted owls. *Functional Ecology*, *36*, 51–63.

Mitchell, M. S., Pacific, L. B., Grand, J. B., & Powell, R. A. (2009). Contributions of vital rates to growth of a protected population of American black bears. *International Association for Bear Research and Management*, *20*(2), 77–84.

Morris, W. F., & Doak, D. F. (2002). *Quantitative conservation biology: theory and practice of population viability analysis*.

National Oceanic and Atmospheric Association Physical Sciences Laboratory (2020). *Climate Prediction Center Global Unified Gauge-Based Analysis of Daily Precipitation*.

Neilson, E. W., Lamb, C. T., Konkolics, S. M., Peers, M. J. L., Majchrzak, Y. N., Doran-Myers, D., Garland, L., Martinig, A. R., & Boutin, S. (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*. Retrieved from http://lter.konza.ksu.edu/content/apt01-daily-precipitation-amounts-measured-multiple-sites-across-konza-prairie

Nippert, J. B., Ocheltree, T. W., Skibbe, A. M., Kangas, L. C., Ham, J. M., Arnold, K. B. S., & Brunsell, N. A. (2011). Linking plant growth responses across topographic gradients in tallgrass prairie. *Oecologia, 166*(4), 1131–1142. https://doi.org/10.1007/s00442-011-1948-6

Noble, B., & Ratajczak, Z. R. (*in review*). NEON's LiDAR increases woody plant detection in a grassland using machine learning.

Nott, M. P., Desante, D. F., Siegel, R. B., & Pyle, P. (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*(4), 333–342. https://doi.org/10.1046/j.1466-822X.2002.00296.x

Oparina, O. S., Kondratenkov, I. A., Oparin, M. L., Mamaev, A. B., & Trofimova, L. S. (2016). Abundance dynamics of the Trans-Volga great bustard (Otididae, Aves) population. *Biology Bulletin, 43*(10), 1428–1433. https://doi.org/10.1134/S1062359016100125

Overmire, T. (1962). Nesting of the Dickcissel in Oklahoma. *Auk, 79*, 115–116.

Owensby, C. E., Auen, L. M., Berns, H. F., & Dhuyvetter, K. C. (2008). Grazing systems for yearling cattle on tallgrass prairie. *Rangeland Ecology and Management, 61*(2), 204–210. https://doi.org/10.2111/07-034.1

Pacifici, K., Reich, B. J., Miller, D. A. W. W., & Pease, B. S. (2019). Resolving misaligned spatial data with integrated species distribution models. *Ecology, 100*(6), 1–15. https://doi.org/10.1002/ecy.2709

Pearce, J., & Boyce, M. (2006). Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology, 43*, 405–412.

Pérez-Ordoñez, D. J., Titulaer, M., Correll, M. D., Strasser, E. H., Baeza-Tarin, F., Martin, R. L., & Harveson, L. A. (2022). The role of temperature and microclimate in the survival of wintering grassland birds. *Avian Conservation and Ecology, 17*(1). https://doi.org/10.5751/ACE-02010-170101

Perkins, D. W., & Vickery, P. D. (2001). Annual survival of an endangered passerine, the Florida Grasshopper Sparrow. *Wilson Bulletin, 113*(2), 211–216. https://doi.org/10.1676/0043-5643(2001)113[0211:ASOAEP]2.0.CO;2

Pitman, J. C., Hagen, C. A., Robel, R. J., Loughin, T. M., & Applegate, R. D. (2005). Location and Success of Lesser Prairie-Chicken Nests in Relation to Vegetation and Human Disturbance. *The Journal of Wildlife Management*, *69*(3), 1259–1269. https://doi.org/10.2193/0022-541x(2005)069[1259:lasolp]2.0.co;2

Plumb, G. E., White, P. J., Coughenour, M. B., & Wallen, R. L. (2009). Carrying capacity, migration, and dispersal in Yellowstone bison. *Biological Conservation*, *142,* 2377–2387. https://doi.org/10.1016/j.biocon.2009.05.019

Pollock, K. H. (1982). A Capture-Recapture Design Robust to Unequal Probability of Capture. *The Journal of Wildlife Management*, *46*(3), 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. https://doi.org/10.1111/j.1557-9263.2008.00144.x

Powell, A., Alexis, F. L. A., & William, H. (2013). Effects of Grassland Management on Breeding Birds at the Western Edge of the Tallgrass Prairie Ecosystem in Kansas Effects of Grassland Management on Breeding Birds at the Western Edge of the Tallgrass Prairie Ecosystem in Kansas. *Natural Areas Journal*, *33*(2), 130–138.

Powell, L. A., & Frasch, L. L. (2000). Can nest predation and predator type explain variation in dispersal of adult birds during the breeding season? *Behavioral Ecology*. https://doi.org/10.1093/beheco/11.4.437

Prein, A. F., & Mearns, L. O. (2021). U.S. Extreme Precipitation Weather Types Increased in Frequency During the 20th Century. *Journal of Geophysical Research: Atmospheres*, *126*(7), 1–18. https://doi.org/10.1029/2020JD034287

Previtali, A. M., Lehmer, E. M., Pearce-Duvet, J. M. C., Jones, J. D., Clay, C. A., Wood, B. A., Ely, P. W., Laverty, S. M., Dearing, M. D. (2010). Roles of human disturbance, precipitation, and a pathogen on the survival and reproductive probabilities of deer mice. *Ecology, 91*(2), 582–592. https://doi.org/10.1890/08-2308.1

Pyle, P., L., J. S., & Ruth, J. M. (2008). *Molt and Aging Criteria for Four North American Grassland Passerines. U.S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication, FWS/BTP-R6011-2008, Washington, D.C.*

Rader, M. J., Brennan, L. A., Hernandez, F., Silvy, N. J., & Wu, B. (2007). Nest-site selection and nest survival of Northern Bobwhite in Southern Texas. *Wilson Journal of Ornithology, 119*(3), 392–399. https://doi.org/10.1676/06-069.1

Ratajczak, Z., Churchill, A. C., Ladwig, L. M., Taylor, J. H., & Collins, S. L. (2019). The combined effects of an extreme heatwave and wildfire on tallgrass prairie vegetation. *Journal of Vegetation Science*, 30. https://doi.org/10.1111/jvs.12750

Ratajczak, Z., D'odorico, P., Collins, S. L., Bestelmeyer, B. T., Isbell, F. I., & Nippert, J. B. (2017). The interactive effects of press/pulse intensity and duration on regime shifts at multiple scales. *Ecological Monographs*, *87*(2), 198–218.

Ratajczak, Z., Nippert, J. B., & Ocheltree, T. W. (2014). Abrupt transition of mesic grassland to shrubland: Evidence for thresholds, alternative attractors, and regime shifts. *Ecology*, *95*(9), 2633–2645. https://doi.org/10.1890/13-1369.1

Ratajczak, Z. (2023). *GIS20 GIS Coverages defining Konza elevations. Environmental Data Initiative.* Retrieved from http://dx.doi.org/10.6073/pasta/cf734ae0fb6e013415a990a1f15aa6d3

Rauter, C. M., Reyer, H. U., & Bollmann, K. (2002). Selection through predation, snowfall and microclimate on nest-site preferences in the Water Pipit Anthus spinoletta. *Ibis*, *144*(3), 433–444. https://doi.org/10.1046/j.1474-919X.2002.00013.x

Reed, A. W., Kaufman, G. A., & Sandercock, B. K. (2007). Demographic response of a grassland rodent to environmental variability. *Journal of Mammalogy*, *88*(4), 982–988. https://doi.org/10.1644/06-MAMM-A-109R.1

Rêgo, A. S., Teodoro, V. A., Maciel, G. S. A., & Sarmento, R. A. (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. https://doi.org/10.1007/s10493-013-9667-9

Reichmann, L. G., Sala, O. E., & Peters, D. P. C. (2013). Precipitation legacies in desert grassland primary production occur through previous-year tiller density. *Ecology*, *94*(2), 435–443.

Renton, K., & Salinas-Melgoza, A. (2004). Climatic Variability, Nest Predation, and Reproductive Output of Lilac-Crowned Parrots (*Amazona finschi*) in Tropical Dry Forest of Western Mexico. *The Auk*, *121*(4), 1214–1225. https://doi.org/10.2307/4090489

Reynolds, J. F., Virginia, R. A., Kemp, P. R., De Soyza, A. G., & Tremmel, D. C. (1999). Impact of drought on desert shrubs: Effects of seasonality and degree of resource island development. *Ecological Monographs*, *69*(1), 69–106. https://doi.org/10.1890/0012-9615(1999)069[0069:IODODS]2.0.CO;2

Ribic, C., Ainley, D., & Spear, L. (1997). Scale-related seabird-environmental relationships in Pacific equatorial waters , with reference to El Nino-Southern Oscillation events. *Marine Ecology Progress Series*, *156*, 183–203.

Robel, R. J., Briggs, J. N., Dayton, A. D., & Hulbert, L. C. (1970). Relationships between Visual Obstruction Measurements and Weight of Grassland Vegetation. *Journal of Range Management*, *23*(4), 295. https://doi.org/10.2307/3896225

Roberts, C. P., Uden, D. R., Cady, S. M., Allred, B., Fuhlendorf, S., Jones, M. O., Maestas, J. D., Naugle, D., Olsen, A. C., Smith, J., Tack, J., & Twidwell, D. (2022). Tracking spatial regimes as an early warning for a species of conservation concern. Ecological Applications, 32(1), 1–10. https://doi.org/10.1002/eap.2480

Rodewald, A. D., & Yahner, R. H. (2001). Avian Nesting Success in Forested Landscapes: Influence of Landscape Composition, Stand and Nest-Patch Microhabitat, and Biotic Interactions. *The Auk*, *118*(4), 1018–1028. https://doi.org/10.2307/4089850

Roques, K. G., O'Connor, T. G., & Watkinson, A. R. (2001). Dynamics of shrub encroachment in an African savanna: Relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, *38*(2), 268–280. https://doi.org/10.1046/j.1365-2664.2001.00567.x

Roseberry, J., & Klimstra, W. (1970). The Nesting Ecology and Reproductive Performance of the Eastern Meadowlark. *The Wilson Bulletin*, *82*(3), 243–267.

Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., Stanton, J. C., Panjabi, A., Helft, L., Parr, M., & Marra, P. P. (2019). Decline of the North American avifauna. *Science*, *366*(6461), 120–124. https://doi.org/10.1126/science.aaw1313

Royle, J. A., Chandler, R. B., Sun, C. C., & Fuller, A. K. (2013). *Integrating resource selection information with spatial capture – recapture*. 520–530. https://doi.org/10.1111/2041-210X.12039

Ruth, J. M. (2017). Life History Attributes of Arizona Grasshopper Sparrow (*Ammodramus savannarum ammolegus*) and Comparisons with Other North American Subspecies. *The American Midland Naturalist*, *178*(1), 64–81. https://doi.org/10.1674/0003-0031-178.1.64

Ruth, J. M., & Skagen, S. K. (2017). Territory and nest site selection patterns by Grasshopper Sparrows in southeastern Arizona. *Condor*, *119*(3), 469–483. https://doi.org/10.1650/CONDOR-16-210.1

Ruth, J. M., & Skagen, S. K. (2018). Reproductive response of Arizona Grasshopper Sparrows to weather patterns and habitat structure. *The Condor*, *120*(3), 596–616. https://doi.org/10.1650/CONDOR-17-128.1

Sæther, B. E., & Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. Ecology, 81(3), 642–653. https://doi.org/10.1890/0012-9658(2000)081[0642:alhvac]2.0.co;2

Sahanatien, V., Derocher, A. E., & Gompper, M. (2012). Monitoring sea ice habitat fragmentation for polar bear conservation. *Animal Conservation*, *15*, 397–406. https://doi.org/10.1111/j.1469-1795.2012.00529.x

Samson, F., & Knopf, F. (1994). Prairie conservation in North America. *BioScience, 44*(6), 418–421.

Sandel, B., Goldstein, L. J., Kraft, N. J. B., Okie, J. G., Shuldman, M. I., Ackerly, D. D., … Suding, K. N. (2010). Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. *New Phytologist, 188*(2), 565–575. https://doi.org/10.1111/j.1469-8137.2010.03382.x

Sandercock, B. K. (2006). Estimation of Demographic Parameters from Live-Encounter Data: a Summary Review. *Journal of Wildlife Management*, *70*(6), 1504–1520. https://doi.org/10.2193/0022-541x(2006)70[1504:eodpfl]2.0.co;2

Sang, A., Teder, T., Helm, A., & Pärtel, M. (2010). Indirect evidence for an extinction debt of grassland butterflies half century after habitat loss. *Biological Conservation*, *143*(6), 1405–1413.

Santisteban, L., Benkman, C. W., Fetz, T., & Smith, J. W. (2012). Survival and population size of a resident bird species are declining as temperature increases. *Journal of Animal Ecology*, *81*(2), 352–363. https://doi.org/10.1111/j.1365-2656.2011.01918.x

Sauer, J. R., Hines, J. E., & Fallon, J. (2020). The North American Breeding Bird Survey Dataset, 1955-2019*, USGS Patuxent Wildlife Research Center, Laurel, Md.*

Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B., & Charnov, E. L. (2004). Effects of body size and temperature on population growth. *American Naturalist*, *163*(3), 429–441. https://doi.org/10.1086/381872

Schartz, R. L., & Zimmerman, J. L. (1971). The Time and Energy Budget of the Male Dickcissel (*Spiza americana*). *The Condor*, *73*(1), 65–76. https://doi.org/10.2307/1366125

Schaub, M., & Royle, J. A. (2014). Estimating true instead of apparent survival using spatial Cormack-Jolly-Seber models. *Methods in Ecology and Evolution*, *5*(12), 1316–1326. https://doi.org/10.1111/2041-210X.12134

Scholtz, R., & Twidwell, D. (2022). The last continuous grasslands on Earth: Identification and conservation importance. *Conservation Science and Practice*, *4*(3), 1–21. https://doi.org/10.1111/csp2.626

Schreiber, S. J. (2003). Allee effects, extinctions, and chaotic transients in simple population models. *Theoretical Population Biology*, *64*, 201–209. https://doi.org/10.1016/S0040-5809(03)00072-8

Schwarzwald, K., Poppick, A., Rugenstein, M., Bloch-Johnson, J., Wang, J., McInerney, D., & Moyer, E. J. (2021). Changes in future precipitation mean and variability across scales. *Journal of Climate*, *34*(7), 2741–2758. https://doi.org/10.1175/JCLI-D-20-0001.1

Searcy, C. A., Gabbai-Saldate, E., & Shaffer, H. B. (2012). Microhabitat use and migration distance of an endangered grassland amphibian. *Biological Conservation*, *158*, 80–87. https://doi.org/10.1016/j.biocon.2012.08.033

Shaffer, J. A., Igl, L. D., Johnson, D. H., Sondreal, M. L., Goldade, C. M., Nenneman, M. P., Wooten, T. L., & Euliss, B. R. (2021). *The Effects of Management Practices on Grassland Birds -- Grasshopper Sparrow (Ammodramus savannarum)*. USGS.

Shahan, J. L., Goodwin, B. J., & Rundquist, B. C. (2017). Grassland songbird occurrence on remnant prairie patches is primarily determined by landscape characteristics. *Landscape Ecology*, *32*, 971–988. https://doi.org/10.1007/s10980-017-0500-4

Sherry, R. A., Weng, E., Arnone, J. A., Johnson, D. W., Schimel, D. S., Verburg, P. S., Wallace, L. L., & Luo, Y. (2008). Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie. *Global Change Biology*, *14*(12), 2923–2936. https://doi.org/10.1111/j.1365-2486.2008.01703.x

Shew, J., Nielsen, C., & Sparling, D. (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.

Silber, K. M., Mohankumar, N. M., Hefley, T. J., & Boyle, W. A. (2023). Emigration and survival correlate with different precipitation metrics throughout a grassland songbird's annual cycle. *Journal of Wildlife Management*, 87(3) 1–17. https://doi.org/10.1002/jwmg.22371

Sinclair, A. R. E., & Krebs, C. J. (2002). Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*(1425), 1221–1231. https://doi.org/10.1098/rstb.2002.1123

Skagen, S. K., & Adams, A. A. Y. Y. (2012). Weather effects on avian breeding performance and implications of climate change. *Ecological Applications*, *22*(4), 1131–1145. https://doi.org/10.1890/11-0291.1

Small, D. M., Blank, P. J., Lohr, B., Journal, S., March, N., Small, D. M., … Lohr, B. (2015). Habitat use and movement patterns by dependent and independent juvenile Grasshopper Sparrows during the post-fledging period. *Journal of Field Ornithology*. *86*(1), 17–26. https://doi.org/10.1111/jofo.

Smith, A. B. (2013). The relative influence of temperature, moisture and their interaction on range limits of mammals over the past century. *Global Ecology and Biogeography*, *22*(3), 334–343. https://doi.org/10.1111/j.1466-8238.2012.00785.x

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.

Soha, J. A., Lohr, B., & Gill, D. E. (2009). Song development in the grasshopper sparrow, *Ammodramus savannarum*. *Animal Behaviour*, *77*(6), 1479–1489. https://doi.org/10.1016/j.anbehav.2009.02.021

Stampfli, A., & Zeiter, M. (2004). Plant regeneration directs changes in grassland composition after extreme drought: A 13-year study in southern Switzerland. *Journal of Ecology*, *92*(4), 568–576. https://doi.org/10.1111/j.0022-0477.2004.00900.x

Stanton, R. L., Morrissey, C. A., & Clark, R. G. (2018). Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. *Agriculture, Ecosystems and Environment*, *254*(November 2017), 244–254. https://doi.org/10.1016/j.agee.2017.11.028

Steenhof, K., Fuller, M., Kochert, M., & Bate, K. (2005). Long-Range Movements and Breeding Dispersal of Prairie Falcons from Southwest Idaho. *The Condor*, *107*(3), 481–496.

Stutchbury, B. J. M., Hill III, J. R., Kramer, P. M., Rush, S. A., & Tarof, S. A. (2009). Sex and Age-specific Annual Survival in a Neotropical Migratory Songbird, the Purple Martin (*Progne subis*). *The Auk*, *126*(2), 278–287. https://doi.org/10.1525/auk.2009.08038

Sudakov, I., Vakulenko, S. A., Kirievskaya, D., & Golden, K. M. (2017). Large ecosystems in transition: Bifurcations and mass extinction. *Ecological Complexity*, *32*, 209–216. https://doi.org/10.1016/j.ecocom.2017.01.002

Suedkamp Wells, K. M., Millspaugh, J. J., Ryan, M. R., & Hubbard, M. W. (2008). Factors Affecting Home Range Size and Movements of Post-Fledging Grassland Birds. *The Wilson Journal of Ornithology*, *120*(1), 120–130. https://doi.org/10.1676/06-117.1

Sutton, A. O., Strickland, D., Freeman, N. E., & Norris, D. R. (2021). Climate-driven carry-over effects negatively influence population growth rate in a food-caching boreal passerine. *Global Change Biology*, *27*, 983–992.

Switzer, P. V. (1993). Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, *7*(6), 533–555. https://doi.org/10.1007/BF01237820

Taylor, C. M., Lank, D. B., & Sandercock, B. K. (2015). Using local dispersal data to reduce bias in annual apparent survival and mate fidelity. *Condor*, *117*(4), 598–608. https://doi.org/10.1650/CONDOR-14-184.1

Taylor, R. L., Walker, B. L., Naugle, D. E., & Mills, L. S. (2012, February). Managing multiple vital rates to maximize greater sage-grouse population growth. *Journal of Wildlife Management*, Vol. 76, pp. 336–347. https://doi.org/10.1002/jwmg.267

Team, R. C. (n.d.). *(2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.*

Tenhumberg, B., Crone, E. E., Ramula, S., & Tyre, A. J. (2018). Time-lagged effects of weather on plant demography: drought and Astragalus scaphoides. *Ecology*, *99*(4), 915–925. https://doi.org/10.1002/ecy.2163

Thompson, S. J., Arnold, T. W., Fieberg, J., Granfors, D. A., Vacek, S., & Palaia, N. (2015). Grassland birds demonstrate delayed response to large-scale tree removal in central North America. *Journal of Applied Ecology*, *53*(1), 284–294. https://doi.org/10.1111/1365-2664.12554

Twidwell, D., Rogers, W. E., Wonkka, C. L., Taylor Jr, C. A., & Kreuter, U. P. (2016). Extreme prescribed fire during drought reduces survival and density of woody resprouters. *Journal of Applied Ecology*, *53*, 1585–1596. https://doi.org/10.1111/1365-2664.12674

University of Maryland Global Climate Project. (2020). *El Nino-Southern Oscillation Precipitation Index, 1979-present*. Retrieved from http://gpcp.umd.edu/espi.htm

Verheijen, B. H. F., Clipp, H. L., Bartolo, A. J., Jensen, W. E., & Sandercock, B. K. (2019). Effects of patch-burn grazing on breeding density and territory size of dickcissels. *Avian Conservation and Ecology*, *14*(1). https://doi.org/10.5751/ACE-01343-140107

Verheijen, B. H. F., Plumb, R. T., Gulick, C. K. J., Hagen, C. A., Robinson, S. G., Sullins, D. S., & Haukos, D. A. (2021). Breeding Season Space Use by Lesser Prairie-Chickens (*Tympanuchus Pallidicinctus*) Varies among Ecoregions and Breeding Stages. *American Midland Naturalist*, *185*(2), 149–174. https://doi.org/10.1674/0003-0031-185.2.149

Verheijen, B. H. F., Hendrik, B., & Verheijen, F. (2017). *Demographic responses of grassland songbirds to rangeland management in the tallgrass prairie*. Thesis. Kansas State University.

Vickery, P. D. (2021). Grasshopper Sparrow (*Ammodramus savannarum*), version 1.0. Retrieved from Birds of the World website: https://birdsoftheworld.org/bow/species/graspa/cur/introduction

Vickery, P. D., Hunter, M. L., & Wells, J. V. (1992). Evidence of Incidental Nest Predation and Its Effects on Nests of Threatened Grassland Birds. *Oikos*. *63*(2), 281–288.

Vucetich, J. A., & Peterson, R. O. (2004). 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. https://doi.org/10.1098/rspb.2003.2589

Wade, R. N., Karley, A. J., Johnson, S. N., & Hartley, S. E. (2017). Impact of predicted precipitation scenarios on multitrophic interactions. *Functional Ecology*, *31*(8), 1647–1658. https://doi.org/10.1111/1365-2435.12858

Wagle, P., Gowda, P. H., Northup, B. K., Starks, P. J., & Neel, J. P. S. (2019). Response of tallgrass prairie to management in the U.S. Southern great plains: Site descriptions, management practices, and eddy covariance instrumentation for a Long-Term Experiment. *Remote Sensing*, *11*(17). https://doi.org/10.3390/rs11171988

Webb, M. H., Terauds, A., Tulloch, A., Bell, P., Stojanovic, D., & Heinsohn, R. (2017). The importance of incorporating functional habitats into conservation planning for highly mobile species in dynamic systems. *Conservation Biology*, *31*(5), 1018–1028. https://doi.org/10.1111/cobi.12899

Wellicome, T., Fisher, R., … R. P.-T. C., & 2014, U. (2014). Apparent survival of adult Burrowing Owls that breed in Canada is influenced by weather during migration and on their wintering grounds. *Condor*, *116*, 446–458. Retrieved from https://academic.oup.com/condor/article-abstract/116/3/446/5153130

Welti, E. A. R., Roeder, K. A., De Beurs, K. M., Joern, A., & Kaspari, M. (2020). Nutrient dilution and climate cycles underlie declines in a dominant insect herbivore. *Proceedings of the National Academy of Sciences*, *117*(13), 7271–7275. https://doi.org/10.6084/m9.figshare.11862459

Westgarth-Smith, A. R., Leroy, S. A. G., Collins, P. E. F., & Harrington, R. (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. https://doi.org/10.1016/j.quaint.2007.05.001

White, R. P., Murray, S., & Rohweder, M. (2000). Grassland ecosystems. In *Biogeography*. https://doi.org/10.4324/9781315845227-11

Wiens, J. A. (1973). Pattern and Process in Grassland Bird Communities. *Ecological Monographs*, *43*(2), 237–270.

Wiens, J. A. (1969). An Approach to the Study of Ecological Relationships among Grassland Birds. *Ornithological Monographs*, *8*, 1–93. https://doi.org/10.2307/40166677

Wilcox, B. P., Fuhlendorf, S. D., Walker, J. W., Twidwell, D., Wu, X. Ben, Goodman, L. E., Treadwell, M., & Birt, A. (2022). Saving imperiled grassland biomes by recoupling fire and grazing : a case study from the Great Plains. *Frontiers in Ecology and Environment*, *20*(3), 179–186. https://doi.org/10.1002/fee.2448

Williams, E. J., & Boyle, W. A. (2018). Patterns and correlates of within-season breeding dispersal: A common strategy in a declining grassland songbird. *The Auk*, *135*(1), 1–14. https://doi.org/10.1642/AUK-17-69.1

Williams, E. J., & Boyle, W. A. (2019). Causes and consequences of avian within-season dispersal decisions in a dynamic grassland environment. *Animal Behaviour*, *155*, 77–87. https://doi.org/10.1016/j.anbehav.2019.06.009

Wilson, G. R., Cooper, S. J., & Gessaman, J. A. (2004). The effects of temperature and artificial rain on the metabolism of American kestrels (Falco sparverius). *Comparative Biochemistry and Physiology*, *139*(3), 389–394. https://doi.org/10.1016/j.cbpb.2004.10.009

Wilson, S., Smith, A. C., & Naujokaitis-Lewis, I. (2018). Opposing responses to drought shape spatial population dynamics of declining grassland birds. *Diversity and Distributions*, *24*(11), 1687–1698. https://doi.org/10.1111/ddi.12811

Winger, B. M., Auteri, G. G., Pegan, T. M., & Weeks, B. C. (2018). A long winter for the Red Queen: rethinking the evolution of seasonal migration. *Biological Reviews*, *94*(3), 737–752. https://doi.org/10.1111/brv.12476

Wingler, A., & Hennessy, D. (2016). Limitation of grassland productivity by low temperature and seasonality of growth. *Frontiers in Plant Science*, *7*, 1–6. https://doi.org/10.3389/fpls.2016.01130

Winnicki, S. K., Munguía, S. M., Williams, E. J., & Boyle, W. A. (2020). Social interactions do not drive territory aggregation in a grassland songbird. *Ecology*, *101*(2). https://doi.org/10.1002/ecy.2927

With, K. A., King, A. W., & Jensen, W. E. (2008). Remaining large grasslands may not be sufficient to prevent grassland bird declines. *Biological Conservation*, *141*(3152–3167). https://doi.org/10.1016/j.biocon.2008.09.025

Woodworth, B. K., Wheelwright, N. T., Newman, A. E., Schaub, M., & Norris, D. R. (2017). Winter temperatures limit population growth rate of a migratory songbird. *Nature Communications*, *8*(1). https://doi.org/10.1038/ncomms14812

Wray, T., Strait, K. A., Whitmore, R. C., & Sparrow, F. (1982). Reproductive success of grassland sparrows on a reclaimed surface mine in West Virginia. *The Auk*, *99*(1702), 157–164.

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

Zuckerberg, B., Ribic, C. A., & McCauley, L. A. (2018). Effects of temperature and precipitation on grassland bird nesting success as mediated by patch size. *Conservation Biology*, *32*(4), 872–882. https://doi.org/10.1111/cobi.13089

Zuidema, P. A., & Franco, M. (2001). Integrating vital rate variability into perturbation analysis: An evaluation for matrix population models of six plant species. *Journal of Ecology*, *89*(6), 995–1005. https://doi.org/10.1046/j.0022-0477.2001.00621.x