

SPATIAL AND TEMPORAL VARIABILITY IN
ENVIRONMENTAL CONDITIONS AND ITS
INFLUENCE ON THE HABITAT SELECTION AND
REPRODUCTION OF THE GREATER PRAIRIE-
CHICKEN

By

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Abstract: Spatial and temporal heterogeneity in resource availability and environmental conditions are key determinants of the distribution of many organisms and in-part shapes ecosystem function. As a result, understanding how species respond to this heterogeneity will be critical to effectively conserving wildlife into the future. Among the most important conditions influencing organisms is the thermal environment. In grassland landscapes that varied in their degree of structural and compositional heterogeneity we observed a pattern towards increasing thermal variability with increasing compositional variation at the landscape scale, but only a moderate connection between thermal variation and structural variation at this scale. However, at the level of individual sample locations, thermal patterns were primarily driven by vegetation structure. Further, when we evaluated how female Greater Prairie-Chickens (*Tympanuchus cupido*) made trade-off decisions between food resources and the thermal environment, at the patch level it appeared the prairie-chickens were prioritizing food availability by selecting invertebrate rich patches that were among the hottest parts of the landscape. Despite this, prairie-chickens were able to modify their space use at relatively fine spatial and temporal scales to select for cooler conditions during the hottest part of the day. These results suggest that the scale of observation has an important influence on perceived patterns in the thermal environment. Finally, we used a nine-year data set of nest records to evaluate the influence of weather conditions on prairie-chicken reproductive behaviors. Daily nest survival was negatively influenced by higher levels of precipitation and high temperatures. Additionally, warmer spring temperatures resulted in earlier start dates for nest incubation and smaller clutch sizes. This work provides important information about how structural and compositional vegetation heterogeneity influences resource availability in grasslands, and how a species of conservation concern responds to environmental variability.

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CHAPTER I

STRUCTURAL AND COMPOSITIONAL HETEROGENEITY INFLUENCES THE THERMAL ENVIRONMENT ACROSS MULTIPLE SCALES

Abstract:

Heterogeneity has a critical influence on biodiversity and ecosystem processes. While the influence of heterogeneity on species diversity and abundance is well documented, how heterogeneity influences the distribution and arrangement of necessary resources across a landscape is still unclear. Heterogeneity in vegetation structure and composition is often cited as an important factor in the near-ground thermal environment. However, due to a paucity of comparative studies across landscapes that differ in their degree of vegetation heterogeneity, researchers lack knowledge of the underlying mechanisms that influence variation in the thermal environment. Particularly, we do not have a clear understanding of the relative contribution of structural and compositional vegetation heterogeneity to thermal patterns. Therefore, we assessed the thermal environment in nine grasslands that differed in their degree of structural and compositional heterogeneity. At the landscape level, we used a variance partitioning approach with linear mixed models to assess the link between four different metrics of vegetation heterogeneity and temperature variability. At the microsite level, we used piecewise Structural Equations Models to assess the fine-scale drivers of temperature in these landscapes and develop a causal model describing the relationship between vegetation variables and temperature. We found that landscape temperature variance was strongly related to the diversity of plant functional group, heterogeneity in plant species composition, and variation in vegetation height. At finer scales, species richness, vegetation height, and overhead obstruction were the best predictors of temperature once weather was accounted for. Additionally, vegetation composition variables primarily had an indirect influence on fine-scale temperature variation. These results suggest that scale has a strong influence on the observed relationship between temperature variance and different metrics of vegetation heterogeneity. Our results provide support for the role of landscape heterogeneity in shaping the thermal landscape and offer insights into the possible impacts of habitat homogenization on the thermal environment.

Introduction

A foundational concept in ecology is that landscape heterogeneity is a primary determinant of biodiversity (Lack 1969, McArthur and McArthur 1961, Tews et al. 2004). Heterogeneity is defined as the variation in biotic and abiotic conditions across space and through time (Wiens 1997). Heterogeneous landscapes offer organisms a greater variety and abundance of critical resources (Gould and Walker 1997, Halaj et al. 2000), and physical refugia from adverse abiotic conditions (Suggett et al. 2011) or predators (Huffacker et al. 1963). As a result, heterogeneity is recognized as a critical component of conservation efforts (Christensen 1997). A relatively unexplored mechanism that potentially underpins biodiversity in highly variable systems is the link between vegetation heterogeneity and the thermal environment. The recognition of temperature as a critical component of ecosystems and the fundamental niche for many species suggests that developing a clearer understanding of how landscape heterogeneity shapes the thermal environment may be an important step towards effective conservation of biodiversity.

Temperature is among the most important environmental conditions that shape ecological patterns and processes (Begon et al. 2006). The thermal environment influences a variety of ecosystem processes such as nutrient cycling by regulating microbial activity in soils (Mielnick and Dugas 2000, Tscherko et al. 2001), and water cycles by altering rates of evaporation or transpiration (Gates 1968, Schlesinger and Jasechko 2014). Temperature also shapes the distribution and abundance of many plant and animal species (Magnuson et al. 1979, Woodward 1988), as well as growth and survival rates of these species (Berry and

Bjorkman 1980, Cunningham et al. 2013). For these reasons, variation in thermal conditions across a landscape may have profound impacts on the spatial structure of populations and ecosystem processes (Rosenberg et al. 1983). This has led researchers to posit that more thermally heterogeneous systems may have higher biodiversity because these areas provide wider ranges of temperatures offering a greater diversity of thermal niches (Elmore et al. 2017).

Many organisms require a specific range of temperatures at which physiological and metabolic processes are able to operate optimally (Angilletta and Angilletta 2009). Ambient weather conditions frequently exceed these tolerance ranges for many species, so behavioral modifications or access to sites with thermally buffered microclimates are important strategies for minimizing exposure to deleterious thermal conditions (Carroll et al. 2015, Tanner et al. 2017, Rakowski et al. 2019). Vegetation structure and composition is particularly important for shaping the near-ground thermal environment in many landscapes, which in turn influences what temperatures are available for many organisms (Saunders et al. 1998, Jenerette et al. 2007, Carroll et al. 2016). Selection for certain vegetation patches or structure by a number of animals has been linked to differences in temperature among vegetation patches (Hovick et al. 2014, Carroll et al. 2015, Rakowski et al. 2019). Further, use of cooler areas has been linked to improved survival or fitness outcomes in several species (Warner and Andrews 2002, Hovick et al. 2014, Grisham et al. 2016, Raynor et al. 2018). Given the importance of the thermal environment to survival and habitat selection for many species, understanding the factors that influence temperature variability across the landscape may be essential for managing and conserving biodiversity.

Much of our understanding of how vegetation heterogeneity shapes the thermal environment has come from studies in heterogeneous landscapes that have focused on the role of specific patch types in shaping the thermal environment (Saunders et al. 1998, van Beest et al. 2012, Krause et al. 2013, Carroll et al. 2015, Rakowski et al. 2019). At present, there are relatively few comparative studies evaluating the thermal environment across multiple landscapes that differ in their degree of structural and compositional heterogeneity (Elmore et al. 2017), and this lack of comparative data limits our ability to understand the underlying mechanisms that shape temperature variation in a landscape. Though it is often helpful to understand variation in temperature according to broad patch types in the context of specific organisms, this approach can also obscure the drivers of temperature variation or the scales at which variation occurs. This is because broadly classifying areas by vegetation patches or plant type may hide small-scale variation in vegetation structure and composition within patches that can influence temperature indirectly by changing exposure to solar radiation or altering airflow, or directly through physiological processes such as transpiration or reflective heating (Cook and Leopold 1964, Stuntz et al. 2002). By considering how temperature varies within and between patches, ecologists can potentially gain a better understanding of the factors that shape ecosystem processes and the distribution of organisms across landscapes.

While the influence of temperature on organisms and ecosystem processes is well established in the literature, the precise mechanisms that determine temperature variation across a landscape are not well understood. In this study, our primary objective was to develop a clearer understanding of how vegetation heterogeneity influences the thermal environment at multiple scales. In particular, we focused on how variation in plant

communities shaped the thermal environment by comparing thermal patterns from nine landscapes that varied in their overall structural and compositional complexity. As part of our investigation, we assessed the thermal environment at two scales. At the landscape scale, we tested for a relationship between landscape-level measures of vegetation heterogeneity and variance in temperature to assess the relative importance of vegetation structure versus composition of vegetation patches in shaping broad-scale patterns of thermal variation. At the microsite scale, we developed a causal model describing the relative contribution of various vegetation composition and structure measures to fine-scale temperature variation within and between patches.

Site Selection and Study Site

We choose grasslands of the Southern Great Plains of North America as a case study to explore how vegetation heterogeneity influences temperature. Historically, grasslands in this region were highly dynamic systems with diverse plant communities and variable disturbance regimes. Similar to grasslands across the globe, grasslands in the Southern Great Plains have undergone widespread homogenization, primarily as a result of intensive agronomic practices (Hoekstra et al. 2005, Fuhlendorf et al. 2012). Intensive use of herbicides or highly altered fire and grazing patterns have greatly simplified vegetation communities and reduced structural diversity in many grasslands (New 1997, Fuhlendorf et al. 2012). In extreme cases, entire vegetation communities have been replaced by introduced forage species to promote production of domestic grazers (*Bos taurus*; Franklin et al. 2006, Gabbard and Fowler 2007). As a result, grasslands in this region form a gradient from heavily altered and simplified landscapes often dominated by few introduced grass species to areas where the vegetation community is still relatively intact and diverse with both

monocots and dicots. This gradient of structural and compositional heterogeneity creates a natural opportunity for investigating the effects of vegetation heterogeneity on the thermal environment.

We sampled the thermal environment and vegetation data from nine grassland landscapes chosen from three grassland heterogeneity types (three grassland landscapes in each type). We ranked grassland landscapes from low to high heterogeneity based on their broadly defined plant communities to represent a gradient of structural and compositional vegetation complexity (Figure 1.1, Table 1.1). In the subsequent analysis, we refer to the nine grassland sites as separate landscapes for clarity purposes. For low heterogeneity grassland landscapes, we used areas that were dominated by a non-native grass species that was introduced as a forage species (Bermuda grass; *Cynodon dactylon*; Table 1.1). These sites are representative of highly modified grasslands that have been converted from their historical plant community and have relatively low species richness and uniform vegetation structure. This type of dramatic conversion is typical of many grassland systems globally (Hoekstra et al. 2005). For the medium heterogeneity landscapes, we used grasslands dominated by native graminoids (monocots), but with limited broad-leaved (dicots) plant composition which could represent moderate levels of human grassland modification (Table 1.1) where long-term management practices such as herbicide or grazing may have simplified the plant community. Finally, for the grassland landscapes with the highest levels of heterogeneity, we selected areas where the broad-leaved plant component of the community was still intact with limited agronomic modification (Table 1.1). This grassland type would have a variety of monocots and dicots (both herbaceous and low growing woody).

We selected our study sites from research properties managed by Oklahoma State University (OSU) in Payne County, Oklahoma, USA. We collected data for the moderate and high heterogeneity sites (native grass and grass/shrub communities) on the OSU Research Range and the Cross Timbers Experimental Range Station located approximately 20 kilometers southwest of Stillwater, Oklahoma, USA. Vegetation was composed primarily of tallgrass prairie species such as big bluestem (*Andropogon gerardi*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), Indian grass (*Sorghastrum nutans*), and a variety of broad-leaved herbaceous plants including western ragweed (*Ambrosia psilostachya*), various asters including white heath aster (*Symphyotrichum ericoides*), and the invasive legume sericea lespedeza (*Lespedeza cuneata*). The high heterogeneity sites differed from the moderate heterogeneity sites as these areas were also interspersed with patches of native shrubs, including Oklahoma blackberry (*Rubus oklahomus*), Chickasaw Plum (*Prunus angustifolia*), winged sumac (*Rhus copallinum*), and smooth sumac (*Rhus glabra*). The low heterogeneity sites (introduced grass pastures) were located on the OSU Cimarron River Valley Research Station located north of Perkins, OK, USA. Vegetation in these grasslands was dominated by Bermuda grass. To control for confounding effects, we choose to focus on heterogeneity in species composition and structure and thus attempted to control for the immediate effects of disturbance processes such as fire and grazing. For these reasons, we selected grasslands that received only moderate and similar grazing pressure, and that had been unburned for at least two years as previous research in this region indicates that biomass accumulation drastically declines after two growing seasons (Fuhlendorf et al. 2006). Landscapes ranged in size from 2.5 to 8.5 hectares (mean 6.8 ha).

Methods

Throughout this study we define three levels of organization, the landscape, patch and microsite level. We defined landscapes as areas composed of one or more patch types, with patches being areas within a landscape composed of distinct vegetation from the surrounding area (Turner and Gardner 2001). We defined microsites throughout the study as specific locations within patches that may differ in their microclimates due to fine-scale variation in vegetation structure or composition (Rosenberg et al. 1983). We acknowledge there is considerable overlap between these levels that are dependent on the scale of observation; however, we choose these definitions to represent what may be perceived by a small ground-dwelling animal that would be influenced by the near-ground temperature in our study landscape. We do not attempt to compare the specific thermal conditions among specific patch types (ex. shrubs versus herbaceous), as our focus was on how differences in number and variation of patches influences thermal variability at the landscape-level and to assess how specific structural and compositional characteristics at the microsite-level influences thermal variability within and between patches.

Data collection

We sampled the thermal environment and vegetation in September of 2019. This month was selected for sampling as September is characterized by stable weather, high temperatures (15-year average 22°C; average minimum and maximum temperatures: 16°C - 33°C) and dry conditions (15-year average rainfall: 7.1 cm), meaning patterns of thermal heterogeneity would likely be the most pronounced and easily detected during this period if they existed. Additionally, September is at the peak of annual biomass accumulation, and

most perennial plants are identifiable and available to sample during this time. To sample thermal conditions, we generated 30 random locations (hereafter referred to as microsites) within each of the nine grassland landscapes. We constrained sample locations so that each point had to be greater than 50 meters from woodland borders to minimize the effect of shading, and at least 10 meters from the next closest sample point. We used Maxim Integrated Thermochron iButton data loggers (Model Number: DS1921G; Maxim Integrates Products, Sunnyvale, California, USA; hereafter, I-button) to collect thermal data. We secured each I-button to a steel spike using double-sided mounting tape, and we drove the spikes into the ground such that each I-button was approximately 5-10 centimeters above the ground surface. We did this to avoid insulation of the I-buttons by grass litter at ground level, which allowed us to better characterize the effects of surrounding vegetation structure. Field tests were performed before data collection to ensure that the steel spikes had minimal effect on I-button temperature readings. Each I-button was programmed to record temperature every 15 minutes. We selected days that had minimal to low cloud cover, no precipitation, and near average ambient temperatures to collect thermal data. Each thermal sample period was 48 hours in length so that we could capture a range of weather conditions within and between sample days at a microsite. We randomly assigned one landscape from each grassland type (one landscape with low, moderate, and high heterogeneity) to one of three sample groups, and we collected thermal data at all three landscapes in each sample group simultaneously. We did this to minimize variation in weather conditions among the three grassland heterogeneity types. We used onsite weather stations that recorded weather conditions every 5-minutes at both the Stillwater and Perkins sites to compare the ambient temperature to the I-button temperatures (Oklahoma Mesonet Stations; Brock et al. 1995).

After collection of the temperature data was complete, we revisited each site to collect vegetation structure, species composition and functional group composition measurements. At each microsite, we centered a standard 20 x 50 cm Daubenmire frame over the I-button location and recorded the percent cover of plant functional group (grass, litter, forb, and shrub) and bare ground (Daubenmire 1959). Forbs are defined as herbaceous (non-woody) broad-leaved plants. We then identified and recorded every plant species observed within the frame. To measure vegetation structure, we recorded plant height directly over the I-button site and four angle of obstruction measurements. Angle of obstruction provides an index of the amount of cover directly above a point, which would influence the amount of solar radiation and airflow at a site (Kopp et al. 1998). We measured the angle of obstruction by attaching a digital level to a meter stick and tilting the digital level at an angle until it came into contact with the vegetation layer (Carroll et al. 2016). We recorded an angle of obstruction measurement in each of four cardinal directions at each site, and we averaged the four obstruction measurements to obtain a single overhead obstruction metric per site (Carroll et al. 2016). We did not consider height thresholds for the angle of obstruction measurements as the majority of vegetation encountered was less than 2 meters tall, and we placed I-buttons 50 meters away from forested areas.

Data analysis

Landscape level vegetation and thermal heterogeneity—We used four metrics to characterize vegetation heterogeneity at the landscape-level based on the vegetation data collected at microsites. Below, we describe how each landscape-level heterogeneity metrics were calculated prior to final data analyses.

To estimate structural heterogeneity for each landscape, we calculated the standard deviation of vegetation height and overhead obstruction across all sites within each of the nine grasslands. To estimate compositional heterogeneity based on the percent cover of plant functional groups, we used an ordination-based approach similar to McGranahan et al. (2016). Specifically, we used a polar coordinate analysis to plot each site in ordination space based on its composition of functional group cover estimates. We then estimated the centroid (weighted mean value of the cover data in a group) for each grassland landscape. To assess functional group heterogeneity, we then calculated the mean distance from each site in a landscape to the centroid from that landscape using Gower distance values (Anderson et al. 2006). This measure assumes that grasslands with higher functional group diversity will have more points that are farther from the average conditions (centroid) in a landscape resulting in a higher mean distance for more heterogeneous landscapes (McGranahan et al. 2016, Anderson et al. 2006). We used the function *vegdist* and *betadisper* in the R package "vegan" for this analysis (Oksanen et al. 2013). To estimate heterogeneity of species composition at the landscape level, we calculated the average Bray-Curtis dissimilarity values between all sites in a grassland. Landscapes with greater variation in species across microsites should have, on average, higher dissimilarity values than grasslands where species composition is similar across sites. We used different distance measures for the functional group and species-level data as the Gower distances allowed us to use the percent cover data for functional groups while the Bray-Curtis distances are better suited for our presence/absence species-level data (Anderson et al. 2006).

To estimate the amount of thermal variability that could be attributed to site-level differences in each grassland landscape, we used a variance partitioning approach with

mixed-effects models (McGranahan et al. 2016, McGranahan et al. 2018). Using the “lme4” package in program R (Bates et al. 2019), we calculated separate mixed-effect model for each grassland landscape with I-button temperatures as the response variable and a random effect variable for I-button site in a grassland landscape. We assigned each I-button temperature reading to the closest air temperature and solar radiation reading from the onsite weather stations and included ambient temperature and solar radiation as well as the time of day as fixed effects in the model to account for known sources of temperature variation. We used the variance estimate (σ^2) for the I-button site random effect in each landscape as an index of thermal variance resulting from site level differences after accounting for weather and time of day. These variance estimates were used in the subsequent analysis to link thermal variance to vegetation heterogeneity.

We used simple linear regression to describe the relationship between our four measures of heterogeneity and the temperature variance estimates from the mixed-effects models. For each regression, we used the variance estimates from the linear mixed-effects models as the response variable, and a single measure of heterogeneity as a predictor variable resulting in four regression models. We deemed a vegetation heterogeneity variable as influencing thermal variance if the p-value associated with the slope parameter was ≤ 0.05 , and we further measured the strength of the relationship using the R^2 value from each of the regression models.

Microsite-level path analysis— To describe the relationships between vegetation variables and infer the relative contribution of vegetation composition, vegetation structure, species richness, and weather on I-button temperature at the microsite level we fit a piecewise Structural Equation Model (piecewise SEM) to the data. This analysis allowed us to evaluate

multivariate relationships as well as describe causal pathways in a system by allowing explanatory variables to influence a response variable directly or indirectly through other predictor variables. Standard SEMs assume independence of observations, but piecewise SEMs allow for the modeling of hierarchical relationships in separate generalized linear mixed models, which are then combined into a single causal network. Shipley (2009) provides a simple metric to assess the completeness of a causal network developed with piecewise SEMs using directional separation (d-separation) tests and Fischer's *C* statistic. As this is primarily an exploratory analysis meant to improve our understanding of the relationships between our variables, we constructed a single piecewise SEM. We built our model based on previous research on drivers of the thermal environment in grasslands, and to test whether vegetation composition and richness directly or indirectly (through their effects on structure variables such as overhead obstruction and vegetation height) influenced I-button temperature. We constructed the components of the SEM using separate linear mixed models with a random effect for the I-button site nested in grassland. The separate linear mixed models were combined into a single causal network, and we assessed model fit using d-separation tests and Fisher's *C* using the R package *piecewiseSEM* (Lefcheck 2016).

Results

We observed a wide range of I-button temperatures relative to ambient temperatures throughout the study in all three landscape types (Figure 2A). However, the three landscape types differed in their range and average temperatures throughout the study. Low heterogeneity grassland landscapes had a narrower range of temperatures during midday hours, which corresponded to the hottest part of the day (11:00-17:00; Figure 2B), and were on average cooler throughout the day compared to the medium and high heterogeneity

landscapes (Figure 3A). The medium and high heterogeneity grassland landscapes showed similar ranges in midday temperatures and similar average hourly temperatures (Figure 2B; Figure 3A). Despite the similarity in the mean and range of I-button temperatures, the medium and high heterogeneity landscapes showed distinct differences in hourly temperature variability as measured by the standard deviation of temperatures, especially during the midday (Figure 3B). Specifically, the high heterogeneity landscapes had the largest standard deviations in temperature during the midday period. The low heterogeneity landscapes showed the least temperature variability throughout the day (Figure 1.3B).

Landscape-level temperature variance

Variance in the thermal environment at the landscape-level as estimated by the linear mixed-effects models, showed a general trend towards higher variance estimates for the landscapes that were predicted to have greater heterogeneity (Figure 1.4). The three landscape types also differed in their degree of between landscape variability, with low heterogeneity landscapes having a small range for their variance estimates and high heterogeneity sites showing the greatest range in landscape-level variance estimates. When we considered specific measures of vegetation heterogeneity, we found temperature variability was strongly related to both functional group composition and diversity of plant species at the landscape-level (Figure 1.4A, B). Landscapes with greater diversity in species composition, as measured by the average Bray-Curtis dissimilarity among sites, had a strong positive relationship with estimates of temperature variability ($\beta = 1.45$, $p\text{-value} = 0.005$, $R^2 = 0.69$; Figure 1.4A). We observed a similar pattern for functional group composition, where grassland landscapes that had greater heterogeneity in functional groups showed greater levels temperature variability ($\beta = 4.64$, $p\text{-value} = 0.037$, $R^2 = 0.49$; Figure 1.4B). Temperature variability at the landscape-

level was significantly related to only one of the two structure variables we considered.

Temperature variability in a landscape was positively related to the standard deviation of vegetation height ($\beta = 0.016$, $p\text{-value} = 0.04$, $R^2 = 0.46$; Figure 1.4C), but standard deviation in overhead obstruction was not significantly related to temperature variance at the $\alpha = 0.05$ level ($\beta = 0.07$, $p\text{-value} = 0.09$, $R^2 = 0.35$; Figure 1.4D). However, the R^2 -value and p -value for the relationship between variability in overhead obstruction and thermal variability still suggest moderate support for a positive relationship between these variables.

Microsite-level temperature

Our structural equation model describing the direct and indirect relationships between vegetation variables and I-button temperature at the microsite level fit the data well (Fisher's $C = 4.354$, $p = 0.824$; high p -values indicate that the proposed model likely did not occur by chance and that it is unlikely that paths that were not included contained important information). The standardized coefficients for air temperature and solar radiation indicate these variables had the strongest influence on I-button temperature at the microsite, with I-button temperature increasing as both variables increased (air temperature: $\beta = 0.71$, standardized $\beta = 0.46$, $p\text{-value} < 0.001$; solar radiation: $\beta = 0.01$, standardized $\beta = 0.55$, $p\text{-value} < 0.001$, Table 1.2, Figure 1.5). Vegetation structure and species richness had the next greatest influence on I-button microsite temperature. At microsites with greater overhead obstruction and vegetation height, I-button temperatures were on average cooler compared to microsites with lower values for these variables (overhead obstruction: $\beta = -0.04$, standardized $\beta = -0.04$, $p\text{-value} < 0.001$; vegetation height: $\beta = -0.01$, standardized $\beta = -0.04$, $p\text{-value} = 0.003$, Table 1.2, Figure 1.5). I-button temperature was positively related to species richness, resulting in higher average temperatures at sites with greater species richness ($\beta =$

0.89, standardized $\beta = 0.032$, p-value = 0.0075). Percent cover of bare ground at a microsite was the only composition variable that directly influenced temperature, resulting in warmer temperatures at sites with greater amounts of bare ground ($\beta = 0.02$, standardized $\beta = 0.04$, p-value < 0.001). Percent cover of grass, forbs, shrubs, or litter did not have a significant direct influence on I-button temperature at the microsite level (Table 1.2, Figure 1.5).

While vegetation structure (height and overhead obstruction) had the strongest direct influence on I-button temperature, vegetation composition variables indirectly influenced I-button temperatures through their interactions with the structure variables (Table 1.2, Figure 1.5). As bare ground at a site increased, overhead obstruction decreased ($\beta = -0.12$, standardized $\beta = -0.19$, p-value < 0.001) and vegetation was on average shorter ($\beta = -0.4$, standardized $\beta = -0.14$, p-value = 0.007). Sites with greater shrub cover tended to have greater overhead obstruction ($\beta = 0.15$, standardized $\beta = 0.41$, p-value < 0.001), and greater vegetation height ($\beta = 1.06$, standardized $\beta = 0.64$, p-value < 0.001). In addition to its direct effect on I-button temperature, species richness also influenced temperature indirectly through its negative effect on overhead obstruction ($\beta = -0.73$, standardized $\beta = -0.27$, p-value = 0.0004). Species richness did not influence vegetation height. Percent cover of grass, forbs and litter had minimal influence on vegetation structure (Table 1.2, Figure 1.5).

Discussion

Heterogeneity is considered the foundation of biodiversity and a critical for shaping spatial patterns of ecosystem processes (McArthur and McArthur 1961, Lack 1969, Tews et al. 2004). Our results provide support for variation in the thermal environment as being a potential mechanism for increased biodiversity in heterogeneous landscapes, as landscapes

with more variable vegetation structure and composition likely contain a broader array of thermal niches for organisms to select from (Elmore et al. 2017). However, the relative importance of vegetation composition versus structure in influencing the thermal environment differed depending on the scale of observation. For example, landscapes that were more compositionally diverse, at both the plant functional group and species levels, had higher variation in temperature at broad-scales compared to grasslands that were compositionally homogeneous. Alternatively, at the microsite-level, we found that vegetation structure was a better predictor of fine-scale temperature than vegetation composition. As our study is among the first to compare the thermal environment across multiple landscapes that vary in their degree of heterogeneity, our findings provide insights into the factors that influence of thermal patterns across diverse landscapes. Further, this study indicates that the simplification of ecosystems resulting from human activity can have important implications for the thermal environment, which could in turn affect ecological processes and landscape biodiversity.

Vegetation composition and structure are inherently linked, yet their relative influence on the thermal environment varied depending on the scale of observation. Our findings at the landscape-level are similar to previous studies that attributed thermal patterns to specific patch or vegetation types in different landscapes (van Beest et al. 2012, Carroll et al. 2016, Rakowski et al. 2019). However, when we assessed causal relationships at the microsite-level, vegetation composition had minimal direct effects on variability in microsite temperatures. At the microsite-level, temperature was more strongly associated with variation in overhead obstruction and vegetation height than vegetation composition variables. Despite this, vegetation composition variables still indirectly influenced temperature at the microsite-

level through their direct effects on vegetation structure. Specifically, bare ground was associated with shorter vegetation and lower overhead cover, resulting in warmer I-button temperatures at the microsite. In contrast, increased shrub cover was related to increased vegetation height and overhead cover, resulting in cooler I-button temperatures. Based on these results and results of previous studies, careful consideration of scale is imperative when conducting studies of the thermal environment, as the scale of observation affects the relative importance of vegetation structure and composition on temperature patterns (Saunders et al. 1998, Sears et al. 2011, Elmore et al. 2017). Though there is likely no single “appropriate” scale for all studies of ecological processes (Wiens 1997), a clear understanding of how scale influences the observed relationship between vegetation and temperature is needed for accurately predicting availability of different microclimate temperature and how this can in turn influence different organism’s spatial distribution in a landscape. Further, it is important to consider that the relationship between scale, vegetation, and thermal patterns may differ among landscapes with different vegetation communities. Therefore, an important area for future research will be to test the how transferable the relationships described in our study are to other systems that differ in their vegetation communities and their sources of heterogeneity.

Temperature variability at the landscape level was positively related to three of the four measures of heterogeneity considered, and showed a moderate relationship to the fourth measure. These findings provide evidence for the hypothesis that more heterogeneous landscapes provide a broader diversity of thermal niches for organisms (Elmore et al. 2017), potentially supporting the role of the thermal environment as one causal mechanism for the link between biodiversity and landscape heterogeneity (Retana and Cerdá 2000, Scheffers et

al. 2013, Suggitt et al. 2018). Organisms often have a narrow range of temperatures at which metabolic performance is maximized, and energy inputs into thermoregulation are at a minimum (Gilchrist 1995, Angilletta and Angilletta 2009). Landscapes with more diverse thermal environments provide organisms greater opportunities to select sites with specific microsite conditions that allow them to maintain their body temperatures within these thermal preferences (Tieleman et al. 2002, Angilletta and Angilletta 2009, Gifford et al. 2012). Temperature is a foundational component of many species fundamental niches and likely influences patterns of biodiversity over large spatial scales. Our research adds to this by emphasizing that the consideration of fine-scale heterogeneity on temperature should be an important consideration when assessing patterns of biodiversity.

At the microsite-level species richness acted on temperature both directly and indirectly through its effects on overhead obstruction. Areas with low species richness had greater overhead cover and was associated with lower temperatures. In our study, these patterns were the result of patches of native shrubs or landscapes dominated by exotic Bermuda Grass, further emphasizing the importance of considering scale when evaluating the thermal environment. Despite the common features of low species diversity and high overhead obstruction, these vegetation types likely influenced the thermal environment in different ways. The dominance of one or a few species over large areas, such as in our low heterogeneity landscapes that were dominated by Bermuda grass, result in narrow or shortened environmental gradients reducing resources availability for other species (Hickman et al. 2006, McKinley et al. 2008, Ratajczak et al. 2012). In our study these highly homogenous landscapes were characterized by relatively low thermal variability, potentially reducing the number of species able to use these areas due to limited thermal conditions (Bell

et al. 1991). Alternatively, areas with low species diversity associated with shrub patches in high heterogeneity landscapes tended to be small in area, and likely represented keystone structures in our landscapes. Keystone structures are features whose structure or composition differ from the surrounding matrix, and whose features offer important “goods or services” for other species (Tews et al. 2004). Patches of shrubs embedded in a larger matrix of herbaceous vegetation at our high heterogeneity sites likely provide distinct structural conditions resulting in cooler microclimates for organisms (Manning et al. 2006, Martin et al. 2015, Carroll et al. 2016). Several gallinaceous bird species found in the Southern Great Plains are known to use shrub patches similar to the ones observed in our study for refuge during thermally stressful periods of the day (Carrol et al. 2015, Raynor et al. 2018, Rakowski et al. 2019). The presence of keystone structures may extend the thermal gradient in these landscapes allowing more species to inhabit these areas (Carroll et al. 2015).

Anthropogenic activities have resulted in widespread landscape and habitat homogenization across all parts of the globe. This homogenization has contributed to widespread declines in biodiversity and loss of ecosystem function (McKinney and Lockwood 1999, Western 2001, Thrush et al. 2006). Previous research in grassland systems, similar to the ones considered in this study have demonstrated that agronomic practices, such as altering disturbance regimes and intensive use of herbicides, can result in a variety negative impacts to biodiversity and ecosystem function (Hickman et al. 2006, Fuhlendorf et al. 2006). The simplification of the thermal environment may be an additional and understudied consequence of these intensive agronomic activities. The low heterogeneity landscapes in our study, which were characteristic of highly modified grasslands, had the lowest overall thermal variability when compared to the medium and high heterogeneity

landscapes that likely approximated vegetation communities prior to European settlement. While our study was not designed to evaluate the specific impact of different anthropogenic activities or agronomic practices on the thermal environment, our results provide a mechanistic understanding of which components of vegetation heterogeneity are most important in determining temperature variability, and offer insight into the possible outcomes of intensive agronomic practices that reduce heterogeneity. These results should provide future researchers with a foundation for making predictions and developing hypotheses about the impacts of human activities on landscapes and the thermal environment.

Conclusions

Many researchers have suggested that heterogeneity should be considered as the foundation of conservation efforts (Christenson 1997, Fuhlendorf et al. 2006). Landscape heterogeneity is an integral driver of ecosystem processes and biodiversity (Wiens 1997), and in this study we provide evidence linking heterogeneity in vegetation structure and composition to the thermal environment. However, vegetation heterogeneity and temperature variability showed a complex relationship that was, in part, determined by the scale of observation. For this reason, conservation actions that aim to maintain the full range of potential thermal niches in a landscape will need to consider both compositional and structural heterogeneity and how they interact to shape the thermal environment across multiple spatial scales. Importantly, our results also suggest that the effects of compositional and structural heterogeneity are linked, as landscapes with a greater diversity of patches contained a greater diversity of structural conditions at microsites resulting in high thermal variability. As many ecosystems face threats from a wide variety of sources including homogenization from anthropogenic activities and climate change (Parmesan and Yohe

2003, Tilman et al. 2017), effective conservation will require careful consideration of the thermal environment and thermal niches of organisms as well as the factors that determine the distribution of fine-scale temperatures across landscapes (Sinervo et al. 2010, Suggitt et al. 2018).

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Table 1.1. Mean, standard deviation (in parenthesis), and range of vegetation variables for three grassland landscape types that were selected to represent a gradient of structural and compositional complexity in Payne County, Oklahoma, USA in 2019. Measurements include the percent cover of plant functional groups, vegetation height in centimeters, overhead obstruction (average angle of obstruction), and microsite-level species richness.

Measurement	Low heterogeneity (n=90)		Medium heterogeneity (n=84)		High heterogeneity (n=87)	
	Mean	Range	Mean	Range	Mean	Range
% Grass	94.7 (8.5)	38 - 98	45.8 (19.5)	3 - 85.5	47.5 (26.8)	0 - 85.5
% Forb	1 (4.6)	0 - 38	17 (11.5)	3 - 38	14.3 (12.5)	0 - 63
% Litter	2.9 (2.2)	0 - 15.5	18.1 (13.0)	3 - 63	15.2 (16.8)	3 - 98
% Shrub	0.1 (0.5)	0 - 3	0.8 (3.3)	0 - 15.5	22.9 (31.3)	0 - 98
% Bare ground	3.4 (4.0)	0 - 15.5	12.1 (14.0)	0 - 63	12.1 (14.5)	0 - 63
Vegetation height (cm)	43.1 (12.8)	22 - 79	58.4 (23.1)	3 - 110	81.5 (46.9)	24 - 300
Overhead obstruction	0.5 (1.6)	0 - 7.75	10.7 (7.1)	0 - 45	9 (7.6)	0 - 36.75
Species richness	1.6	1 - 4	6.5	3 - 12	6.1	1 - 11

Table 1.2. Structural equation model coefficients describing the relationships among vegetation composition (percent cover), species richness, vegetation structure, air temperature, solar radiation, and I-button temperature in grassland landscapes that form a gradient of structural and compositional heterogeneity located in Payne County, Oklahoma, USA in 2019.

Response variable	Predictor variable	Estimate	Standard error	p-value	Standardized coefficients
I-button temperature	Air temperature	0.71	0.01	0.00	0.46
I-button temperature	Solar radiation	0.01	0.00	0.00	0.55
I-button temperature	% Grass	0.00	0.00	0.87	0.00
I-button temperature	% Forb	0.00	0.01	0.92	0.00
I-button temperature	% Bare	0.02	0.01	0.00	0.04
I-button temperature	% Litter	0.01	0.01	0.16	0.02
I-button temperature	% Shrub	-0.01	0.00	0.21	-0.02
I-button temperature	Height	-0.01	0.00	0.00	-0.04
I-button temperature	Overhead obstruction	-0.04	0.01	0.00	-0.05
I-button temperature	Species richness	0.09	0.03	0.01	0.04
Vegetation height	% Grass	-0.09	0.11	0.38	-0.08
Vegetation height	% Forb	0.03	0.17	0.83	0.01
Vegetation height	% Bare	-0.39	0.15	0.01	-0.14
Vegetation height	% Litter	0.10	0.15	0.51	0.04
Vegetation height	% Shrub	1.06	0.10	0.00	0.64
Vegetation height	Species Richness	-0.27	0.82	0.74	-0.02
Overhead obstruction	% Grass	0.00	0.02	0.89	0.01
Overhead obstruction	% Forb	0.02	0.04	0.54	0.04
Overhead obstruction	% Bare	-0.12	0.03	0.00	-0.19
Overhead obstruction	% Litter	-0.05	0.03	0.12	-0.10
Overhead obstruction	% Shrub	0.15	0.03	0.00	0.41
Overhead obstruction	Species richness	-0.73	0.20	0.00	-0.27
Overhead obstruction	Vegetation height	-0.01	0.01	0.52	-0.04

Figure 1.1. Example grasslands representing landscapes characterized by A) low, B) medium, and C) high vegetation heterogeneity in Payne County, Oklahoma, 2019. Low heterogeneity landscapes were characterized by low species richness and uniform vegetation. Medium heterogeneity landscapes were characterized by high species diversity with variable structure. High heterogeneity landscapes had similar vegetation communities to medium heterogeneity landscapes but also contained a number of woody plant species.

Figure 1.2. A) Scatter plot showing the distribution of I-button temperatures over the range of observed ambient temperatures and B) plots showing range and distribution of midday I-button temperatures in nine landscapes grouped into three types that differ in predicted amount of vegetation heterogeneity (Low, Medium, High) located in Payne County, Oklahoma 2019. The red dashed line in panel A shows where I-button temperature equals ambient temperature and each curve in panel B represents a separate landscape.

Figure 1.3. Mean (A) and standard deviation (B) of hourly I-button temperatures in three grassland types that differ in the amount of vegetation structural and compositional heterogeneity based on vegetation characteristics in Payne County Oklahoma, 2019.

Figure 1.4. Linear regressions showing the relationship between temperature variability at the landscape level as estimated using linear mixed-effects models and four metrics representing different sources of vegetation heterogeneity. The data was collected from nine grasslands into three levels of predicted heterogeneity located in Payne County, Oklahoma, 2019. Thermal variance estimates were regressed on A) variation in plant species composition among sites measured using Bray-Curtis dissimilarity B) variation in the composition of plant functional groups across sites C) variation in vegetation height and D) variation in overhead obstruction.

Figure 1.5. Path diagram describing the relationships between vegetation composition (green box), vegetation structure (yellow box), vegetation diversity (blue box), and I-button temperature at the microsite. Significant paths ($p < 0.05$) are represented by solid arrows, and non-significant paths are represented by dashed arrows. Red and Blue arrows are used to describe negative and positive relationships, respectively. Standardized coefficients and p-values are given for significant paths only. Widths of the significant paths are scaled to the size of the standardized coefficients.

Figure 1.1

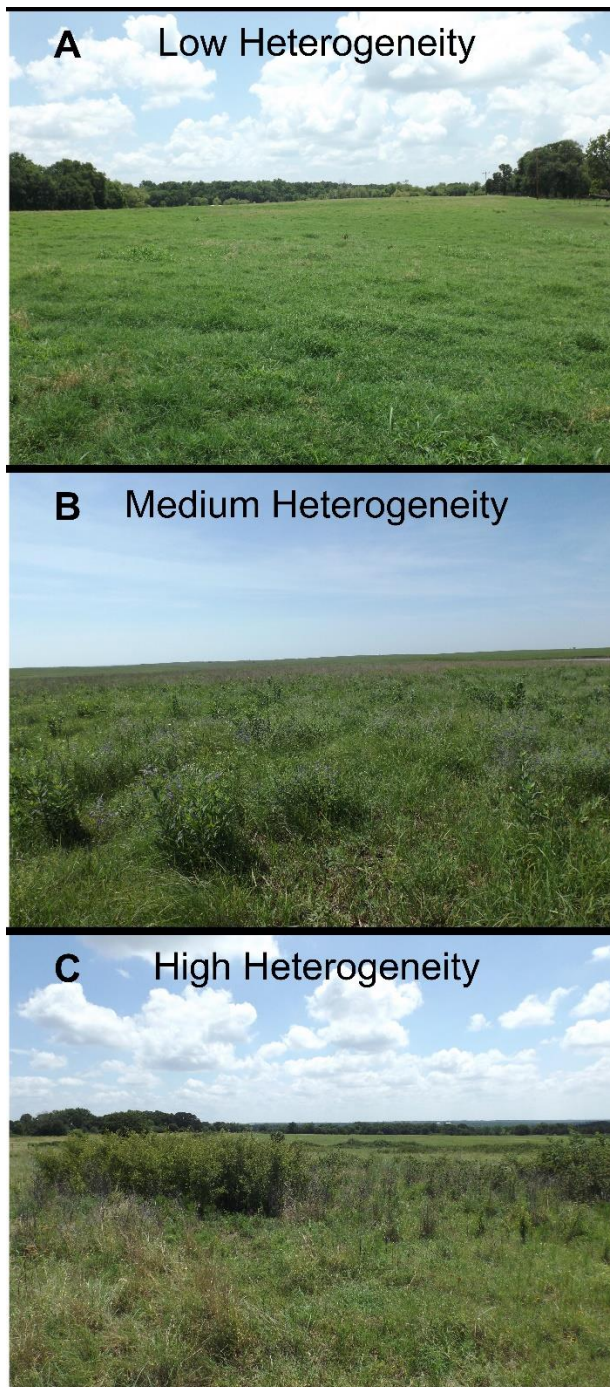


Figure 1.2

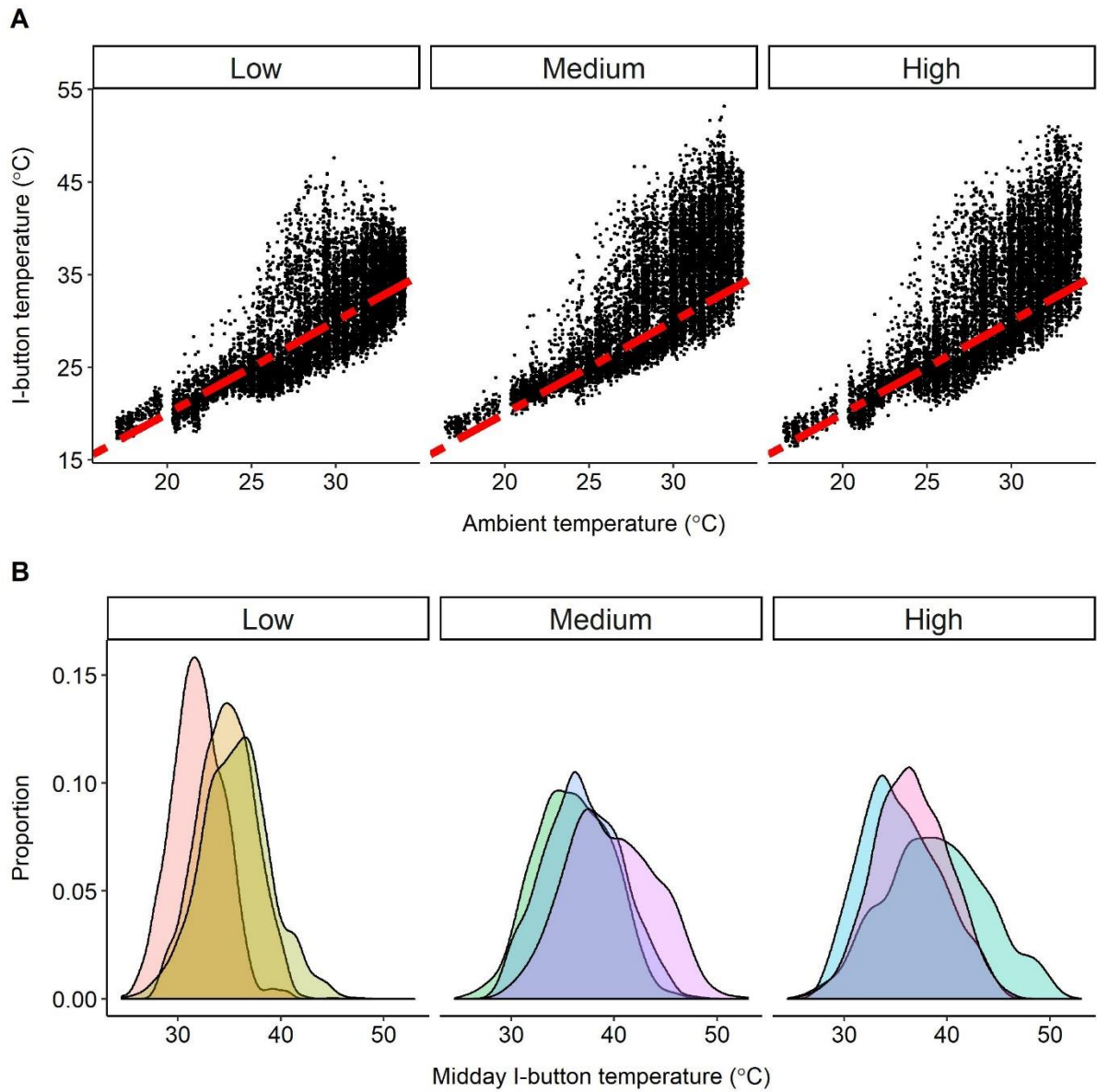


Figure 1.3

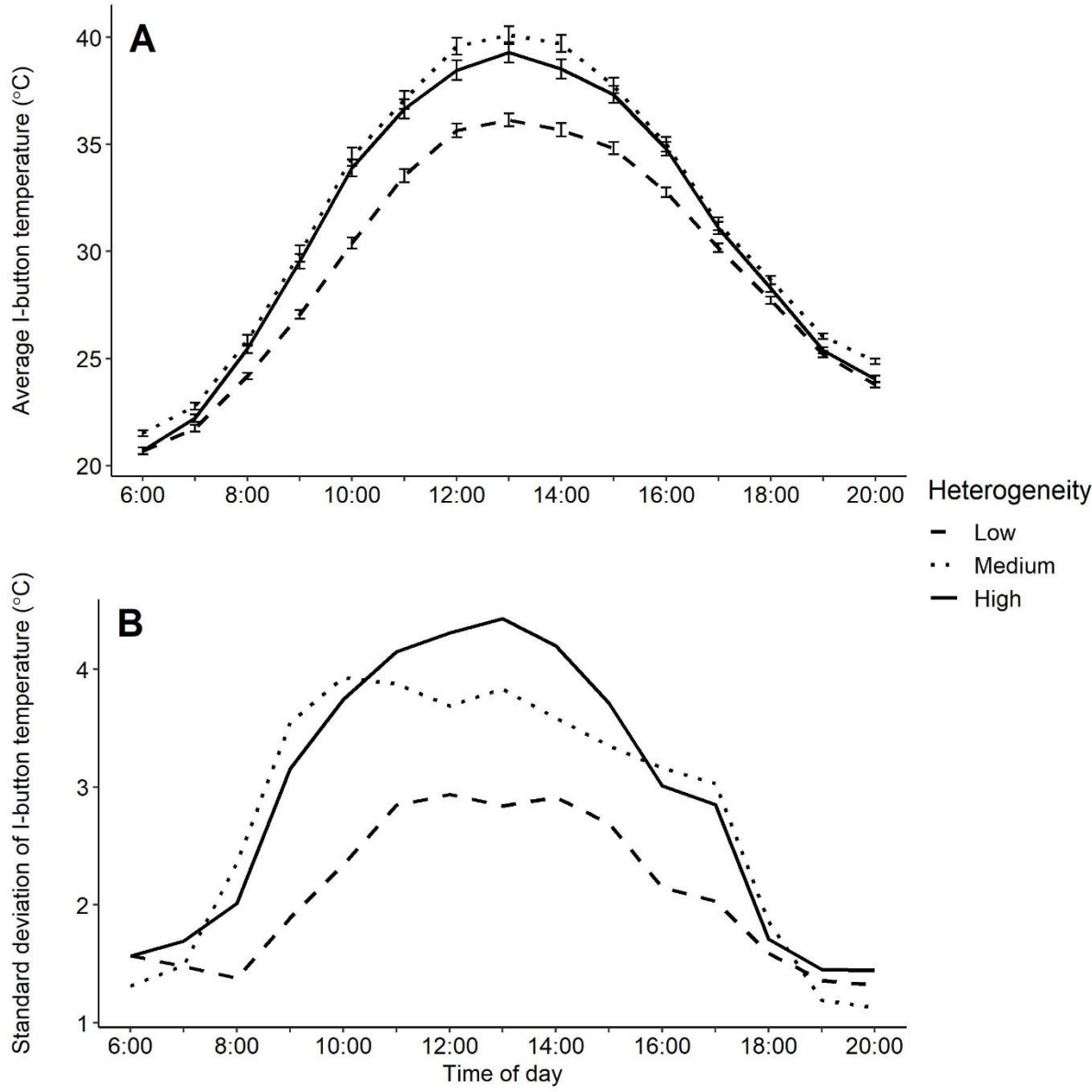


Figure 1.4

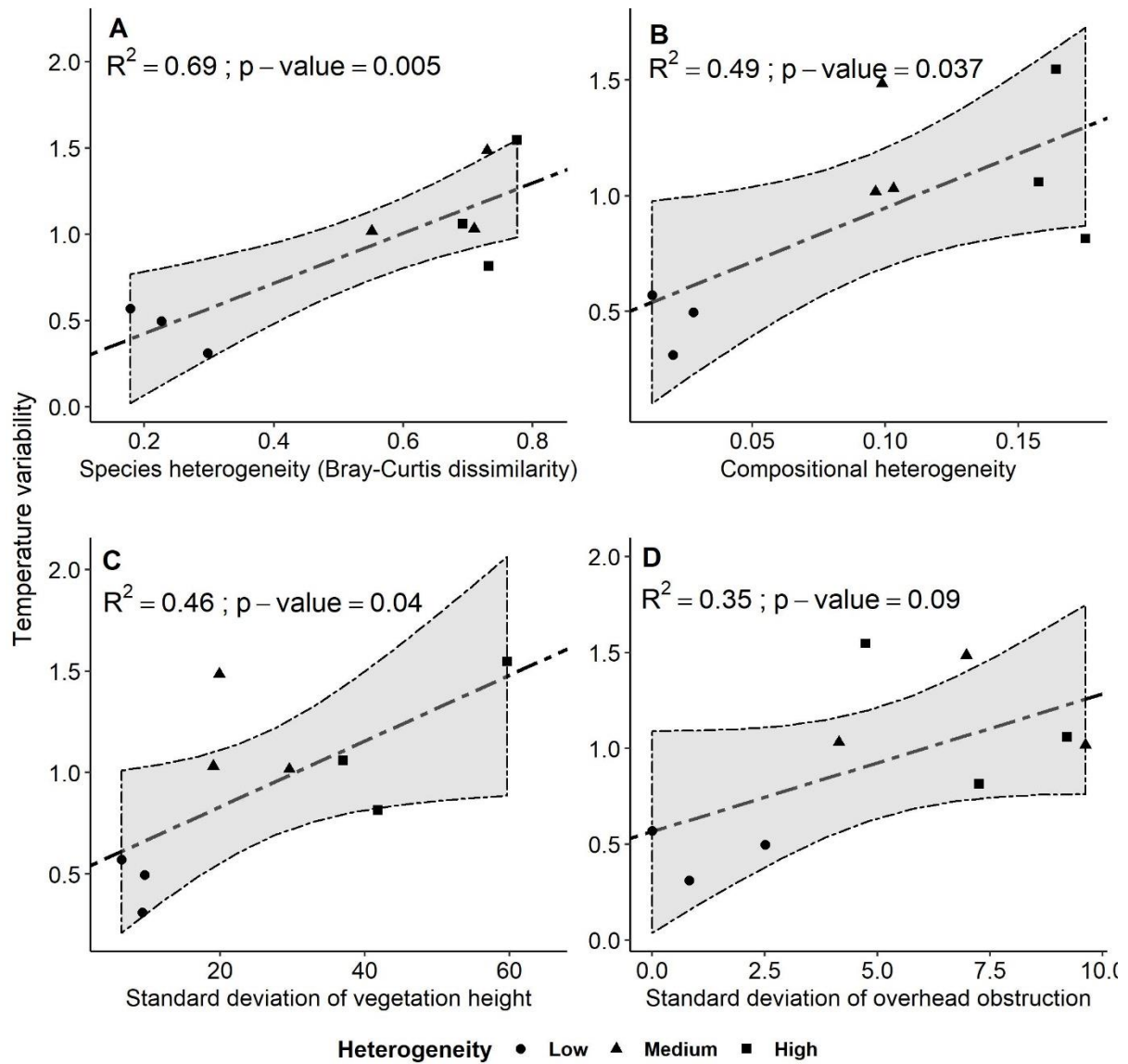
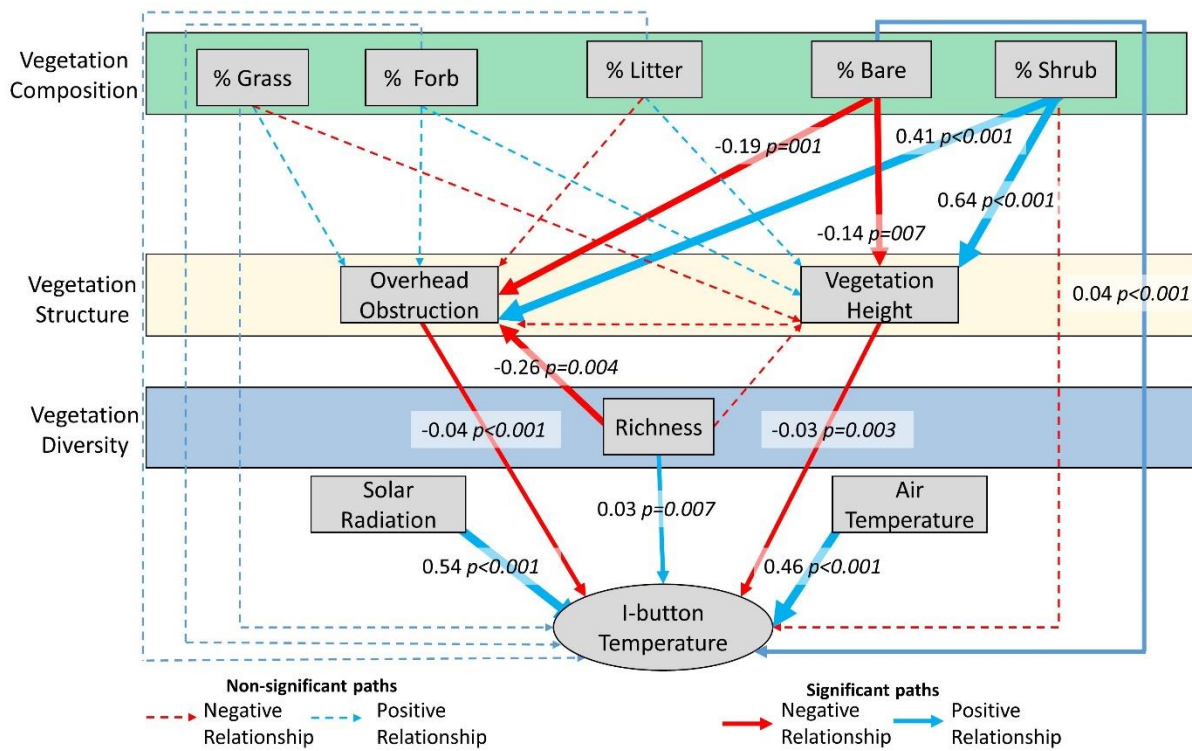


Figure 1.5



CHAPTER II

FINE-SCALE HABITAT SELECTION MODERATES TRADE-OFFS BETWEEN FOOD AVAILABILITY AND TEMPERATURE IN A GROUND-DWELLING GROUSE

Abstract:

Many species are frequently faced with the decision about how to balance the use of thermal refuge against access to food resources. We evaluated the habitat use of female greater prairie-chickens (*Tympanuchus cupido*) to assess the potential for trade-offs between thermal conditions and food resources during the habitat selection process in a heterogeneous grassland. Our objectives were to 1) compare near-ground temperatures, invertebrate availability, and vegetation characteristics at sites used by greater prairie-chickens to conditions at random landscape locations in various time since fire patches and 2) assess changes in conditions at sites used throughout the day to determine if selection for resources changes relative to ambient conditions resulting in trade-offs between foraging sites and thermal refuge. We found that greater prairie-chickens primarily used patches 0-12 months post fire that had relatively high abundances and biomasses of invertebrates compared to the landscape. Greater prairie-chickens further modified their selection at relatively fine spatial scales within these food-rich patches to select for areas with cooler temperatures during the hottest part of the day. The use of thermal refuge did not appear to influence access to food resources as invertebrate abundance at used sites were consistent throughout the day. Our results show that both food resources and thermal cover influence habitat selection for prairie-chickens, but there was little evidence for trade-offs during the habitat selection process. Consideration of spatial and temporal scales is critical for evaluating trade-offs in habitat selection in animals and this research provides insights into the decision-making process of animals.

Introduction

Environmental heterogeneity shapes ecosystem processes and functions (Wiens 1997, Turner and Chapin 2005), as well as the abundance and distribution of many animals (MacArthur and MacArthur 1961, Lack 1969, Tews et al. 2004). Variation in abiotic and biotic factors often results in a patchy distribution of resources, which can result in the spatial or temporal separation of important resources needed for animals to survive or maintain fitness (Godvick et al. 2009, Cunningham et al. 2013, Pigeon et al. 2016). To meet all of their survival needs, mobile animals require access to a variety of different patches that provide food and optimal thermal environments, protection from predators, and avoidance of inter or intra-species competition (Fletcher et al. 2007, Hebblewhite et al. 2008, Godvick et al. 2009). As a result, animals frequently make trade-offs between different resource needs based on environmental conditions and their internal state - selecting patches on the landscapes based on these needs (Ricklefs and Hainsworth 1968, Werner et al. 1983, Rettie and Messier 2000, Verdolin 2006, Tanner et al. 2017). However, without a clear understanding of the factors that determine habitat selection by an animal, it is difficult to assess the presence of these trade-offs and how they may influence a population's vulnerability to changing environments.

Temperature is an important component of a species' fundamental niches (Magnuson et al. 1979). Temperature determines the daily and annual cycles of many animals (Sims et al. 2004, Rakowski et al. 2019), as well as their distribution across a landscape (Martin et al. 2015, Tanner et al. 2017). Animals use a wide array of strategies for maintaining internal body temperatures (Boyles et al. 2011), including behaviors such as panting or gular fluttering, altered activity levels (Stelzner 1988, Broders et al. 2012), or altered

space use to select for areas that are thermally buffered compared to ambient conditions (Carroll et al. 2015, Martin et al. 2015, Pigeon et al. 2016, Rakowski et al. 2019). As animals allocate more time to thermoregulatory behaviors this can impose trade-offs with other essential activities such as foraging or predator avoidance (Amo et al. 2004, Beever et al. 2017, Veldhuis et al. 2020). Numerous studies have found that animals will change or limit foraging behaviors under extreme temperatures conditions (Wildhaber 2001, Tieleman and Williams 2002, Aublet et al. 2009, Cunningham et al. 2015, Edwards et al. 2015). Many thermoregulatory behaviors can be energetically expensive, and reductions in food intake due to altered behaviors associated with thermoregulation can result in a loss of body condition and reduced energy stores (Scheucher et al. 1991, Burton and Weathers 2003), potentially leading to reduced survival or fitness (du Plessis et al. 2012, Edwards et al. 2015, Van de Van et al. 2019). It is widely hypothesized that use of thermal cover negatively impacts individuals by limiting access to food or reducing foraging efficiency (Aublet et al. 2009, Pigeon et al. 2016, Street et al. 2016), though few studies have measured microclimate and food availability simultaneously, or at fine enough scales, to assess the presence of habitat selection trade-offs in animals from non-captive populations. As temperatures are predicted to continue to rise and become more extreme, researchers will need to develop a clearer understanding of the implications of changing animal behavior and habitat selection to assess the impacts of extreme weather on animals.

In addition to extreme weather, many landscapes are undergoing widespread homogenization as a result of anthropogenic activities (Western 2001). Grasslands, in particular, are among the most heavily altered ecosystems in the world (Hoekstra et al.

2005), with the simplification of disturbance regimes being among the leading causes of declines in grassland biodiversity (Samson and Knopf 1994, Fuhlendorf et al. 2006).

Grasslands were historically maintained by variable patterns of fire and grazing resulting in a spatial and temporal mosaic of successional patches that differ in both time since disturbance and vegetation structure (Fuhlendorf and Engle 2001). A variety of grassland species have evolved to rely on the different successional stages that result from variable disturbance patterns in grasslands to meet life-history requirements (Hovick et al. 2014a, McNew et al. 2015, Sandercock et al. 2015, Hovick et al. 2017, Sandercock et al. 2015). Changes in management practices in many North American grasslands have resulted in the simplification or removal of historic disturbance processes in grasslands, particularly with regards to fire, resulting in highly homogenized ecosystems (Fuhlendorf and Engle 2001). The resulting homogenization of vegetation structure can potentially limit an animal's ability to access critical resources, thereby placing greater stress on populations in landscapes where resources are limited. In order to fully understand the potential impacts of grassland homogenization on wildlife species, it is necessary to understand how animals select resources and balance resource needs regarding multiple habitat components in a heterogeneous environment.

The Greater Prairie-Chicken (hereafter, prairie-chicken; *Tympanuchus cupido*) is a species of conservation concern that has experienced significant population and distribution declines over the last half century (Svedarsky et al. 2000), in part due to homogenization of grassland vegetation (Robbins et al. 2002, McNew et al. 2015, Winder et al. 2017a). This species requires a diversity of vegetation structure to meet their habitat needs (Johnson et al. 2011, Fuhlendorf et al. 2017), potentially making prairie-chickens

an important model for understanding how animals make decisions about resource selection in heterogeneous landscapes. As a ground-dwelling species, prairie-chickens are highly sensitive to changes in near ground temperatures that result from variation in plant structure (Hovick et al. 2014b), and habitat selection by prairie-chickens is likely constrained by the availability of suitable thermal microsites. Further, similar to other gallinaceous birds, prairie-chickens likely have relatively high energetic demands, especially during the breeding season (Case et al. 1972, Theberge and West 1973), which necessitates access to abundant food resources (Savory 1989). Despite the known importance of food and thermal conditions for this species, little is known about how prairie-chickens respond to environmental heterogeneity when making decisions between food and thermal resources. These decisions may have especially important implications for survival during stressful periods such as the summer months when prairie-chickens are exposed to high temperatures while being engaged in energetically demanding activities such as nesting and brood-rearing. Developing a better understanding how prairie-chickens balance resource needs will be especially important as current management practices in parts of the prairie-chicken's distribution, that rely on extensive annual prescribed fires and intensive grazing, result in highly homogeneous landscapes, which may lack important patch types needed by prairie-chickens to persist (Robbins et al. 2002, Hovick et al. 2014b, McNew et al. 2015).

As grasslands are expected to continue to undergo changes from anthropogenic activity and increasing weather variability, developing a better understanding of how grassland species make decisions about competing resources needs will be essential for guiding future conservation efforts. In this study, we monitored brooding and non-brooding

female prairie-chickens in May-July, a period expected to be thermally stressful and energetically demanding, in a landscape that is managed to promote structural and compositional heterogeneity in vegetation through the use of fire and grazing. Our primary objectives were to 1) determine if prairie-chickens make resource trade-offs when making habitat selection decisions by assessing differences in vegetation characteristics, thermal conditions and food availability (specifically invertebrates as these are the main food source for prairie-chickens during this period; Rumble et al. 1988) at sites used by prairie-chickens during two behaviorally distinct portions of the prairie-chickens daily cycle, and 2) collect the same suite of variables across a heterogeneous landscape managed with prescribed fire and grazing to assess availability of resources across the landscape. While habitat selection is only one potential means by which an animal may make trade-off decisions, understanding how species prioritize resources during the selection process may offer important insights about how animals make trade-off decisions. By evaluating habitat selection at multiple spatial scales (different patches and sites used throughout the day), gain a better understanding of how this species makes decisions regarding multiple habitat needs.

Study Site

We conducted our research in Osage County, Oklahoma on a private cattle ranch and The Nature Conservancy's Tallgrass Prairie Preserve. The ecoregion occurs in the southernmost extent of the Flint Hills and is dominated by tallgrass prairie vegetation. The dominant grass species include little bluestem (*Shizachyrium scoparium*), big bluestem (*Andropogon gerardii*), and indian grass (*Sorghastrum nutans*). Common forbs include western ragweed (*Ambrosia psilostachya*), ironweed (*Vernonia baldwinii*), and

the invasive legume *Serecia lespedeza* (*Lespedeza cuneata*)(Hamilton 2007). The climate in the region is temperate with dry summers (10-year average June-July rainfall totals = 20.4 cm SD = 7.94), average daytime temperatures of 25.5° C (SD = 2.95), and an average daytime high temperature of 31.5° C (SD = 3.6). Areas where prairie-chickens were captured and monitored were primarily managed for cattle production using management strategies intended to promote vegetation heterogeneity. This management was important for our study objectives as it provided a gradient of vegetation structure from short stature to tall, dense vegetation. In general, prescribed fire was implemented on a rotational basis across the landscape, where after a patch or pasture was burned and grazed the pasture was then allowed to rest without fire for several years before being burned again (Fuhlendorf and Engle 2001). Grazers were allowed to preferentially forage in recently burned patches, resulting in minimal or no grazing pressure in unburned patches in a given year. Prescribed burns were conducted in such a way as to result in a mosaic of burned and unburned patches intermixed across the landscape. Approximately a third of the landscape was burned each year of the study (2018 = 35.09%; 2019 = 33.7%), with the average burn size of 289 ha (SE = 47.52; range=1 – 3078 ha). Areas where prairie-chickens were monitored were primarily grazed seasonally by domestic cattle, however, a portion of The Nature Conservancy's property was grazed by bison (*Bison bison*; Hovick et al. 2015, Hamilton 2007)

Methods

We trapped greater prairie-chickens using standard walk-in funnel traps at lek sites (communal display areas) during March-April of each from 2018-2019 (Schroeder and Braun 1991). We determined the age and sex of all individuals captured based on

plumage and the presence of secondary sex characteristics (eye combs and air sacs in males; Henderson et al. 1967). We marked both males and females using metal leg bands with a unique identifier number, and we attached rump-mounted 22-gram ARGOS/PPT GPS transmitters (Microwave Telemetry, Columbia MD) to all captured females. The transmitters were programmed to collect one GPS location every two hours from 7:00 to 21:00 during the breeding season, and the GPS transmitters had an error of approximately 18-20 meters. Additionally, GPS transmitters were equipped with UHF ground-track capabilities that facilitated tracking greater prairie-chicken hens in the field. Each spring, we located prairie-chicken nests via UHF telemetry using a handheld Yagi antenna and a radio receiver, and subsequently monitored nesting activity via remote GPS data downloads from the ARGOS server. After a female was determined to have left the nest based on GPS locations, we relocated nests and visually inspected nest bowls and eggshell fragments to determine if the nest was successful (≥ 1 egg hatched). Following nest hatch, we then located brooding hens once per week via radio-telemetry and flushed the attending hen to count chicks and to monitor brood survival. Non-brooding hens were monitored remotely via GPS satellite data.

To evaluate potential trade-offs during different parts of the days, we classified prairie-chicken GPS locations into two predicted behavior classes based on movement rates and previous literature from other gallinaceous birds (Patten et al. 2011, Carroll et al. 2015, Rakowski et al. 2019; Figure 2.1). Specifically, we classified GPS locations recorded between 7:00 and 10:00 as active locations due to the relatively high movement rates and the cooler ambient temperatures during this period, while GPS locations recorded between 12:00 and 16:00 were classified as refuge locations due to the prairie-chicken's

low rates of movement and the high ambient temperatures during this time of day (Carroll et al. 2015; Figure 2.1). These two activity classes likely correspond to foraging and loafing behaviors, where prairie-chickens are actively moving and seeking out food (invertebrates) during the active period and seeking cover from the heat or predators during the refuge period.

Thermal, Invertebrate and Vegetation Sampling

Prairie-chicken locations- On every day with stable weather conditions (sunny and no rain), we randomly selected either a brooding or non-brooding prairie-chicken to evaluate habitat use. For the selected prairie-chicken, we selected four GPS locations from that day (Figure 2.1). Locations were selected such that two GPS locations occurred during the morning active period (6:30 – 10:30) and two GPS locations were recorded during the afternoon refuge period (12:30 – 16:30). To account for the fact that changing weather conditions throughout the day could influence invertebrate activity and thermal conditions at a site, we divided our thermal and invertebrate data collection efforts into two sampling periods that matched the two activity periods (Figure 2.1). We then randomly assigned one telemetry location from the active period and one telemetry location from the refuge period to be sampled during the morning sample period (6:30-10:30). The remaining two points from that day (one from the active period and one from the refuge period) were assigned to be sampled during the afternoon sample period (12:30-16:30; Figure 2.1). The actual sampling of vegetation, thermal environment, and food resources (insects) took place within 3-4 days of the telemetry location (mean = 3.74 days). This sampling methodology allowed us to assess thermal conditions and invertebrate resources under ambient weather conditions similar to when the individual

was actually at the location as well as the period of the day that the prairie-chicken was not present at a location.

To account for error associated with the transmitters (up to 18 meters), we established sampling arrays consisting of nine sample points around each of the used GPS locations where vegetation and thermal measurements would occur. The use of multiple sampling points per site allowed us to characterize the average vegetation and thermal conditions available at a given location. We delineated the area around each telemetry location into four quadrants using two perpendicular 36-meter transects (2x the error of the transmitters) that intersected at the telemetry location and were aligned with the cardinal directions. In addition to a sample point at the telemetry location (center of the plot), we established two sample points that were located at a random distance (1-6 meters) and cardinal direction from the center of the quadrant in each of the four quadrants resulting in a total of 9 sample points per telemetry point. All subsequent vegetation and temperature measurements occurred at all nine sample points for each plot, allowing us to characterize the average vegetation and thermal conditions available at a given location.

We estimated thermal conditions at prairie-chicken locations using black-bulb temperature probes. Black-bulb temperature incorporates information about ambient temperature, solar radiation, wind, and convective heating into a single temperature measurement providing a more accurate approximation of what an organism experiences compared to ambient conditions alone (Bakken 1992). The black-bulb temperature probes consisted of a temperature sensor placed in the center of a 101.6mm diameter, 20-gauge steel spheres painted matte black that was connected to a HOBO data logger (U12-008, Onset Corporation, Bourn, Massachusetts, USA; Guthery et al. 2005). We deployed

black-bulb sensors at all nine sample locations at each telemetry location assigned to a sampling period and programmed the data loggers to record a temperature reading every minute for the duration of the four-hour sample period. Black-bulb sensors were placed on the ground or the surface of the litter layer at the base of any vegetation structure directly above the sample point. If no plants were above the sample point, the black-bulb was placed in the open.

While the thermal sensors were recording at each prairie-chicken location, we used sweep-net transects to sample the invertebrate community along the two perpendicular transects used to delineate the plots. While sweep-net samples may underestimate certain orders of insects, we choose this method as we felt it provided an adequate index of the overall availability of invertebrates for prairie-chickens, particularly insect orders that are known to be important for prairie-chickens (Orthoptera and Lepidoptera). To account for changing invertebrate activity throughout the day, we timed our sweep net samples based on the timestamps from the used prairie-chicken telemetry locations. For example, at locations where the sampling period matched the telemetry location time (ex. an active location sampled during the morning sampling period), we conducted sweep net samples within 30 minutes of the approximate time the prairie-chicken had previously been at the location. At locations where the prairie-chicken activity period did not match the sampling period (ex. an afternoon refuge location sampled in the morning sampling period), we conducted the sweep-net samples two hours before or after the other sweep-net sample for a given sampling period. To perform sweep-net samples, we walked each transect at a moderate pace, taking one sweep of the sweep-net with each step (Doxon et al. 2011). We transferred sweep-net samples to plastic bags and stored them in a freezer

until they could be sorted. We sorted invertebrate specimens to the level of order and size class (eg., 0-5 mm, 6-10 mm, etc.) for each sample and we recorded the total number of insects and mass (grams) to estimate abundance and biomass for each order and size class combination at a location.

After the thermal sensors had been removed from a site, we collected vegetation data at each of the nine sample points. We centered a 0.5 m² vegetation sampling frame over each point where the black-bulb temperature sensor was located, and in each frame, we estimated the percent cover of grass, sericea lespedeza (an introduced invasive forb), forbs (excluding sericea), shrub, litter, and bare ground using standard Daubenmire cover classes (Daubenmire 1959). Additionally, we recorded the height of the tallest vegetation in the frame (cm), litter depth (cm, taken 10 cm west of the black-bulb location) and visual obstruction using a Nudd's profile board (Nudds 1977).

Random Landscape Locations- To assess vegetation, thermal conditions and invertebrate availability across the landscape, we collected the same suite of data collected at prairie-chicken locations at random sampling locations that were stratified over the three time since fire categories (0-12 months post fire, 13-24 months post fire, and >24 month post fire). Each random site was composed of a cluster of four locations. We generated clusters by generating a single starting location, followed by three additional points that were a random direction and distance from the previous location, with the restriction that random points must be >36 meters apart and within the same time since fire patch as the first random point. Distances between sample locations were based on distributions of observed distances between sequential prairie-chicken telemetry locations. Within each cluster of 4 random locations, we randomly assigned two of the locations to be sampled

during the morning sampling period and two locations were assigned to the afternoon sampling period. Sampling at each of the random locations followed the same sampling designs as the used prairie-chicken locations.

Data Analysis

A preliminary analysis indicated that brooding and non-brooding females selected for similar habitat, so we combined these two groups for the final analysis for the site level vegetation, thermal and invertebrate analysis reported in this manuscript (Appendix A Table A1; contains brooding and non-brooding data comparisons).

Patch-scale selection- To assess selection for time since fire by prairie-chickens, we first calculated the frequency of prairie-chicken GPS locations recorded in each patch type (i.e. the three time since fire categories) and compared this to the percent of the landscape composed of those patch types. We overlaid brooding and non-brooding adult GPS locations on GIS (Geographic Information Systems) maps showing the different time since fire patches during each year of the study, and extracted the time since fire values to each location. To provide an index of selection by individuals for each of the patch types we then calculated Ivlev's electivity ratio for each prairie-chicken (Ivlev 1961, Jacobs 1974). Ivlev's selection ratio provides an index of the strength of selection by comparing the relative difference between the proportion of a resource used and its availability. A values of -1 and 1 indicate strong avoidance and preference for a resource respectively.

Invertebrates and Vegetation- We used linear mixed models to assess differences in vegetation conditions and food availability at sites used by prairie-chickens versus randomly selected sites that were not used by prairie-chickens. For all models, we used

sample location (four GPS telemetry locations for prairie-chicken locations or four sample locations associated with a random site) nested in sample site (cluster of four telemetry or random sample locations) for our random effects structure (Figure 2.1). We used the eight vegetation metrics and the abundance and biomass as separate response variables and constructed separate univariate models for each with location type (active, refuge or random location) and year as predictor variables. In the invertebrate models we also included sampling period (morning vs afternoon period) as a predictor variable to test if abundance or biomass changed at sites as environmental conditions change throughout the day. Additionally, we constructed models with orthopteran (grasshoppers, crickets and katydids) biomass and abundance as response variables, as this order of invertebrates are an especially important food source for prairie-chickens (Rumble et al. 1988, Hagen et al. 2007). To meet assumptions of uniform variance in the model residuals, biomass and abundance were log-transformed in all models. In cases where the LMM models indicated a significant difference in location types, we used Post-Hoc Tukey Honesty Test to perform multiple comparisons among active, refuge and random locations to determine how the groups differed from each other with the package *emmeans* in Program R (Lenth et al. 2020). Pairwise differences were deemed to be significant at the $p < 0.05$ level.

For the invertebrate data, we considered differences among all location types (prairie-chicken active and refuge locations, and random locations in each time since fire category). However, we only compared vegetation conditions at the two prairie-chicken location types to random locations in patches 0-12 month post fire. We choose to only compare prairie-chicken locations to random locations in patches 0-12 month as

differences in the vegetation characteristics among different time since fire patches at our study site have been well established in other studies (Fuhlendorf et al. 2006). Further, previous research from our study site (Londe et al. 2019), and preliminary analysis of our data shows that prairie-chickens primarily select for recently burned patches and use of patches that are 13-24 months post fire and >24 months is limited during the summer months. We felt it was appropriate to restrict our analysis to only the patch types used by prairie-chickens to minimize our risk of Type I error by limiting the number of multiple comparisons made between patches. However, as invertebrate communities and thermal patterns are not as well established in these landscapes we felt justified in considering comparisons among patches for these analyses.

Thermal Data- To evaluate differences in temperature between location types: active, refuge, and random locations (associated with the three time since fire categories), we used linear mixed models where black-bulb temperatures (T_{bb}) was modeled as a function of ambient air temperature ($^{\circ}\text{C}$; T_{air}) and solar radiation (watts per m^2) (Hovick et al. 2014a, Carroll et al. 2015, Anthony et al. 2020). Before analysis, we calculated hourly averages for each black-bulb sensor and paired these averages with measurements of T_{air} and solar radiation measurements obtained from an onsite weather station that was located within approximately 10 km of most sample sites (Oklahoma Mesonet Stations; Brock et al. 1995). Our model of T_{bb} included the additive effects of T_{air} , and solar radiation, and location type, as well as the two-way interaction of T_{air} with location/patch type to account for different location types warming or cooling at different rates relative to ambient conditions. To account for repeated temperature measurements from individual black-bulb sensors through time, we included each black-bulb sensor nested

within a sample location and sample site as the random effect in our models. Confidence intervals for model predictions were based on percentile-based bootstrapping method.

The use of the hierarchical bootstrapping approach allowed us to incorporate information about the uncertainty associated with residual variability and between-group variability in our accuracy estimates (Thai et al. 2013). We used 1000 bootstrap iterations to generate estimates and selected the upper and lower confidence limits based on the distribution of the bootstrap estimates. We compared slopes and 95% confidence intervals to determine if there was an effect for location types, and we assessed differences in thermal patterns between location types based on effect size (Steidl et al. 1997, Anthony et al. 2020).

Invertebrate Availability Relative to Microsite Temperature- Finally, to determine if the specific thermal conditions at a site influenced invertebrate availability for prairie-chickens, we developed models to assess the relationship between invertebrate abundance and biomass relative to black-bulb temperatures at a site. For this analysis, we paired each sweep-net sample with the average black-bulb temperature for the hour prior to the sweep-net sample. We only considered prairie-chicken locations in this analysis as we wanted to determine if use of areas with cooler microclimates restricted access to food resources. In this model, we included the interaction between location type (active vs refuge) to allow for the possibility that invertebrate availability responded to black-bulb temperatures differently across sites. We used the same random effect structure as in previous analysis and log transformed the response variables.

Results

We monitored 13 brooding and 21 non-brooding female greater prairie-chickens between 2018 and 2019 (Table 2.1). Both brooding and non-brooding females

preferentially selected for patches that were between 0 and 12 months post fire during the breeding season. Approximately 66% and 79% of telemetry locations from brooding and non-brooding adults, respectively, occurred in this patch type, even though it only represented 36.7% of the landscape (Figure 2.2). Results from Ivlev's selection index indicated the majority of female prairie-chickens selected for patches 0-12 months post fire, and showed increasing levels of avoidance with greater times since fire (Figure 2.3).

Vegetation

Vegetation conditions among the three patch types conformed to expectations from previous studies. Specifically, the cover of bare ground decreased with increasing time since fire, while the cover of grass and litter generally increased through time (Table 2.2). These compositional changes with time since fire resulted in structural changes including increasing visual obstruction, vegetation height, and litter depth in patches 13-24 months and > 24 months post fire when compared to patches 0-12 months post fire (Table 2.2).

The vegetation characteristics selected for by prairie-chickens in patches 0-12 months post fire differed between the active and refuge periods (Figure 2.4; Supplemental Appendix B Table B1). Prairie-chickens used sites with higher amounts of grass cover during the refuge period, compared to the locations recorded during the active period; (F-statistic = 6.30, p-value = 0.002; Figure 4a), however, both active and refuge locations had similar amounts of grass cover when compared to random locations in patches 0-12 months post fire. Prairie-chickens also selected for sites with less bare ground during the refuge period compared to the active period (F-statistic = 10.45, p-value < 0.001), and both active and refuge locations had less bare ground than random

locations in 0-12 month post fire patches (Figure 2.4a). Finally, active sites and refuge sites had greater visual obstruction compared to random locations in patches 0-12 months post fire (F-statistic = 7.24, p-value < 0.001; Figure 2.4b).

Invertebrates

Seven invertebrate orders comprised 98% of individuals in sweep net samples. These orders included Orthoptera, Araneae, Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera. Orthoptera was the most commonly captured invertebrate order comprising approximately 42% of captured individuals. The majority (~70%) of invertebrates captured were < 15mm in length and were likely available for consumption by both adults and chicks (Appendix C Figure C1).

Abundance of all invertebrates and Orthoptera varied among the five location types (All Invertebrates: F-statistic = 7.6, p-value = <0.001; Orthoptera Only: F-statistic = 7.6, p-value = <0.001). Locations used by prairie-chickens during the active and refuge periods had higher abundances of invertebrates when compared to random landscape locations in all three time since fire patches (Figure 2.5a). Further, the three time since fire patches did not differ from each other in their total abundance of invertebrates (Figure 2.5a). Similar to total invertebrate abundance, both active and refuge prairie-chicken locations had the highest average abundance of Orthoptera, however, the abundance of this order appeared to decline with increasing time since fire (Figure 2.5B). Orthoptera abundance at prairie-chicken locations was significantly greater than abundance in patches both 13-24 months post fire and patches > 24 months post fire but did not differ from random locations in patches 0-12 months post fire (Figure 2.5B). Neither the abundance of all invertebrates or abundance of only orthopterans differed

between the two sampling periods (All Invertebrates: F-statistic = 0.31, p-value = 0.57; Orthoptera Only: F-statistic = 0.5, p-value = 0.51).

Similar to abundance, biomass of all invertebrate orders and Orthoptera varied among the location types, but was generally the highest at sites used by prairie-chickens (All Invertebrates: F-statistic = 8.9, p-value <0.001; Orthoptera Only: F-statistic = 10.4, p-value <0.001). Average biomass of all invertebrates showed a declining trend with increasing time since fire, with patches 13-24 months and > 24 months post fire having on average the lowest biomass of invertebrate (Figure 2.5C). Sites used by prairie-chickens had greater biomass of all invertebrates compared to unburned patches (12-13 month post fire and > 24 month post fire) but did not differ from random locations that were 0-12 months post fire (Figure 2.5C). The average biomass of Orthoptera showed a similar pattern across sites, with biomass declining with greater time since fire (Figure 2.5D). Locations used by prairie-chickens during the active period had greater biomass of grasshoppers compared to random locations in patches both 13-24 months post fire and >24 months post fire but did not differ from random locations in patches 0-12 months post fire. Additionally, the biomass of Orthoptera was significantly higher at sites used by prairie-chickens during the refuge period compared to all other location types (Figure 2.5D). Neither the abundance of all invertebrates or abundance of orthopteran only differed between the two sampling periods (All Invertebrates: F-statistic = 2.6, p-value = 0.11; Orthoptera Only: F-statistic = 0.45, p-value = 0.50).

Thermal Patterns

The landscape showed highly variable temperature patterns. T_{bb} had a positive linear relationship with T_{air} ($\beta = 1.34$; CI = 1.26, 1.42) and solar radiation ($\beta = 0.01$; CI =

0.011, 0.012). However, the interaction between T_{air} and location type was significant indicating the relationship between T_{bb} and T_{air} differed among the three patch types. At the patch level, random locations 0-12 months post fire were on average the hottest sites on the landscape (Figure 2.6, Table 2.3). The interaction between location type and T_{air} showed that the slope between T_{bb} and T_{air} was lower in patches 13-24 months post fire ($\beta = -0.19$; CI = -0.29, -0.09) and patches >24 months post fire ($\beta = -0.21$; CI = -0.31, -0.1), compared to patches 0-12 months post fire (Figure 2.6). This difference resulted in an average of a 5° Celsius difference between recently burned patches and unburned patches during periods of high temperature (Figure 2.6). The overlap in the 95% confidence intervals of the 13-24 month post fire patches and >24 month post fire patches suggest there may be no significant difference in temperatures between these patch types.

T_{bb} measured at prairie-chicken active locations had similar thermal patterns to patches 0-12 months post fire. The 95% confidence intervals for the interaction between active locations and T_{air} overlapped zero suggesting these locations may not differ significantly from random sites in 0-12 month post fire patches ($\beta = 0.02$; CI = -0.08, 0.11; Table 2.3). However, prairie-chicken refuge locations were cooler than what was available at both the random 0-12 month post fire locations and prairie-chicken active locations ($\beta = -0.13$; CI = -0.22, -0.03; Figure 2.6 and Table 2.3). Specifically, at high temperatures prairie-chicken refuge locations averaged 2-3° Celsius cooler than prairie-chicken active locations (Figure 2.6). Models predicting T_{bb} at the different location types over hourly averages of T_{air} and solar radiation showed considerable variation throughout the day between the various location types (Figure 2.7). All location types overlapped during the morning sampling period, whereas the differences among location types were most

pronounced throughout the entirety of the afternoon sampling period as ambient air temperatures and solar radiation increased.

Invertebrate Availability and Temperature

There was no detectable relationship between black-bulb temperatures at prairie-chicken locations and invertebrate abundance (F-statistic= 0.45, p-value=0.5) or biomass (F-statistic= 0.004, p-value=0.95). The confidence intervals for the interaction terms and the main effect for black-bulb temperature in both the abundance (Interaction: $\beta = 0.01$, CI= -0.01, 0.03; T_{bb} ; $\beta = -0.005$; CI= -0.01, 0.002) and biomass models (Interaction: $\beta = 0.01$, CI= -0.01, 0.03; T_{bb} ; $\beta = -0.003$; CI= -0.01, 0.004) included zero indicating there was likely little difference in invertebrates at sites with different thermal conditions (Figure 2.8).

Discussion

It has been hypothesized that use of thermal refuge may negatively impact animals by limiting their access to other critical resources such as food (Beever et al. 2017), however, our data suggest that prairie-chickens are able to modify their habitat use at multiple scales to meet these competing resource needs in a heterogeneous grassland without making apparent trade-offs in resource availability throughout the day. Structural heterogeneity of vegetation resulted in a broad array of conditions in-terms of food availability and near-ground temperatures at the patch level, and female prairie-chickens primarily selected for food rich (high abundance and biomass of invertebrates) areas that were in patches 0-12 months post fire. Within these food rich time since fire patches prairie-chickens further selected for locations with even higher amounts of invertebrates,

showing that food may drive habitat selection at multiple scales - both between and within patches. However, female prairie-chickens were capable of modifying their habitat use during the hottest parts of the day by selecting for sites with greater grass cover and denser vegetation that provided cooler microsite temperatures compared to what was available at random in these patches. These refuge sites had similar invertebrate resources as compared to locations used during cooler periods of the day suggesting that temperature may be influencing space use during thermally stressful periods, but may not limit availability of food resources. understanding how animals make decisions about trade-offs between thermoregulation and other activities such as foraging will be essential for predicting an animal's vulnerability to changing weather conditions. Our results show that in a heterogeneous landscape, some species, such as the prairie-chicken, may be able to meet resource needs by altering patterns of selection across spatial and temporal scales without making trade-offs among critical resources.

For many species, the use of alternative locations with thermally buffered conditions is an important strategy for maintaining internal body temperatures during periods of extreme heat (Carroll et al. 2015, Martin et al. 2015, Pigeon et al. 2016, Rakowski et al. 2019). However, increased use of these sites may have indirect fitness or survival consequences for individuals (Beever et al. 2017), as spending more time in thermal refuge may limit the access to resources such as food, water, and potential mates (Sinervo et al. 2010, Murray and Smith 2012, Cunningham et al. 2015), or it may increase predation risk (Amo et al. 2004). Prairie-chickens adjusted their habitat use to select for areas with cooler temperatures during the midday refuge period, however, these changes in habitat use did not appear to influence access to food resources as abundance

and biomass of invertebrates at afternoon refuge sites were similar to invertebrate numbers at sites used during the active period. The lack of differences in invertebrate numbers at locations used by prairie-chickens throughout the day and at sites with different microsite temperatures indicate that it is unlikely that prairie-chickens are faced with trade-offs between thermoregulation and food availability when making decisions about habitat use.

Despite the lack of difference in invertebrate availability at sites used throughout the day, temperature can modify prairie-chicken behavior in a variety of ways that can potentially still limit access to food resources resulting in negative consequences for individuals. The denser vegetation cover at refuge sites may make movement more difficult, especially for young chicks (Doxon and Carroll 2010). This can potentially reduce a prairie-chicken's ability to detect and capture invertebrates, reducing foraging efficiency at refuge sites compared to the more sparsely vegetated active sites. Previous research has shown that even small modifications in habitat use, such as moving from open areas to shaded areas at the same site, can impact foraging and hunting efficiency in birds (Cunningham et al. 2015). Further, thermoregulatory behaviors are energetically demanding (Schoener 1971, Scheucher et al. 1991, Burton and Weathers 2003, Van de Ven et al. 2019). As thermoregulatory costs increase throughout the day, animals are likely to reduce allocation of time and energy to other activities to minimize energetic costs during this period (Schoener 1971, Tieleman and Williams 2002, Du Plessis et al. 2012, Edwards et al. 2015). This can result in a situation where even though individuals have access to adequate food resources they may not be able to maintain body condition due to changes in behavior that reduce consumption of food resources (Edwards et al. 2015). While our

results do not support the hypothesis that prairie-chickens make trade-offs when selecting habitat, further work is needed to understand how temperature influences foraging behaviors of prairie-chickens and determine the potential negative consequences at high temperatures due to changes in feeding behavior.

In addition to thermal cover and food resources, concealment from predators is likely an important driver of space use that we did not consider. Predation is one of the most important sources of mortality for prairie-chickens (McNew et al. 2012, Winder et al. 2017a), making selection for sites that offer greater concealment an important survival strategy for this species. We attributed the use of sites with greater vegetation cover to selection for thermal cover, the cooler temperatures at these sites may actually be confounded with selection for sites that offer greater concealment from predators. Despite this, there are several lines of evidence that suggest temperature is still likely an important factor. A wide variety of animals display bimodal activity patterns similar to prairie-chickens (Tieleman and Williams 2002, Aublet et al. 2009, Carroll et al. 2015, Rakowski et al. 2019) where movement and activity is at its lowest when temperatures are highest, and peaks at the beginning and end of the days when temperatures decline. For many of these species, including prairie-chickens (Patten et al. 2011), these patterns are influenced by daily maximum temperature, with individuals moving less on days with higher temperatures (Carroll et al. 2015, Rakowski et al. 2019). Even if temperature is not the immediate cause of habitat selection, previous work has shown that use of sites with hotter temperatures by prairie-chickens can have demographic consequences, as nest sites with higher microsite temperatures had lower rates of survival compared to cooler nests (Hovick et al. 2014a). While it will be difficult to fully disentangle the role of predator

concealment and temperature on habitat selection, as temperature modifies other behaviors and an animal's fitness it should be considered an important component of a prairie-chicken's environment.

By considering multiple spatial scales, we were able to develop a much clearer understanding of the factors that influenced habitat use of prairie-chickens and how they make selection decisions and the scale at which they are likely making selection decisions. Animals perceive their environment across a range of spatial and temporal scales (Kolasa and Waltho 1998, McGarigal et al. 2016), and respond to this variation by modifying their behaviors at different scales to meet their most pressing resource needs (Rettie and Messier 2000, McMahon et al. 2017). At the patch level, female prairie-chickens appeared to prioritize food resources over the thermal environment as females selected patches that were recently burned (0-12 months post fire), which had high concentrations of invertebrates, particularly Orthoptera, but were also the hottest parts of the landscapes. Despite this apparent trade-off at the patch level, by considering conditions at sites used by prairie-chickens throughout the day we found that areas used by prairie-chickens during the afternoon refuge period in 0-12 months post fire patches had cooler temperatures compared to overall patch level conditions. The fine-scale selection for both higher invertebrate abundance and cooler microsites in the recently burned 0-12 month post fire patches suggest that prairie-chickens are making decisions about these factors at small spatial and temporal scales. While broad patch level heterogeneity is important for structuring a number of ecological processes and biotic communities in grasslands, our results show the importance of fine scale heterogeneity

and the need measure behavior at multiple scales when studying behavior and decision making process.

In our study, we combined brooding and non-brooding females and considered their habitat selection patterns together. However, reproductive status has been shown to influence habitat selection patterns in animals, even within sexes (Panzacchi et al. 2010, Smith et al. 2018, Tanner et al. 2019). While preliminary analysis of the data supported the decision to combine reproductive groups, the small sample size of brooding adults may have precluded detecting subtle differences in selection patterns between the two groups. Additionally, by using GPS locations from transmitters on the attending adults rather than chick locations, our methods may have biased our measurements towards conditions used by the adults rather than the chicks although they are highly associated with each other. While this error is likely small when the chicks are young and highly dependent on the adult for foraging and thermoregulation, this bias may become increasingly important as the chicks develop and gain independence from the attending female. Further, even if selection is the same between hens of differing reproductive status, selection decisions may have different fitness and survival consequences for adults and chicks (Blomberg et al. 2013, Tanner et al. 2019). While the small sample size of broods and our study methodology (monitoring only adults and not identifying individual chicks) prevented us performing a detailed comparison of chick and adult habitat selection and survival, this is an area for future research as chick survival and juvenile recruitment are believed to be among the most limiting demographic parameters for prairie-chickens and other grouse (Bergerud 1988, Hagen et al. 2007, McNew et al. 2012).

Conclusions

Our results show that in a heterogeneous grassland, prairie-chicken habitat selection is influenced by availability of food resources and the need for thermal cover during the summer period following nesting. At the patch level, prairie-chickens appeared to make a trade-off between food availability and the thermal environment, however, prairie-chickens were able to balance competing resource needs at fine scales by responding to fine-scale heterogeneity in vegetation structure, food availability, and the thermal environment. However, while prairie-chickens do not appear to be faced with trade-offs between food availability and thermal refuge when making habitat selection decisions in a heterogeneous grassland, habitat selection is only one component of an animal's behavior that can be influenced by thermal conditions. Our research offers an important first step in understanding potential trade-offs by animals as course-scale habitat selection influences what resources are available to individuals, and thus, any subsequent decisions about how to use those resources. Further studies on the impacts of temperature on foraging behaviors, foraging efficiency, and the duration of different behaviors over a range of thermal conditions will be urgently needed to predict the vulnerability of this species to potentially increasing climate variability. As grasslands are under pressure from a variety of threats including increasing homogenization and more extreme temperatures, understanding the factors underpinning selection and how organisms respond to their environment will be essential for effective conservation.

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Table 2.1. Total number of sample locations (n) where vegetation, temperature and invertebrate data was collected for brooding and non-brooding female greater prairie-chickens and random landscape locations in Osage County, Oklahoma, USA in 2018 and 2019. Sample locations consisted of four sample sites where data was collected either in the morning sample period (6:30-10:30) or afternoon sample period (12:30-16:30). Greater prairie-chicken sites were further divided into active locations and refuge locations based on observed prairie-chicken behavior and movement rates. Random landscape locations were stratified over three time since fire categories.

Location Type	Morning Sample Period	Afternoon Sample Period
<i>Non-brooding (n=30)</i>		
Active	30	30
Refuge	30	30
<i>Brooding (n=32)</i>		
Active	32	32
Refuge	32	32
<i>Random Landscape</i>		
0-12 months post fire (n=23)	46	46
13-24 months post fire (n=23)	46	46
>24 months post fire (n=21)	42	42

Table 2.2. Means and standard errors (in parentheses) for vegetation metrics measured at random landscape locations in patches that were 0-12, 13-24, and >24 months post fire in Osage County, Oklahoma USA in 2018-2019.

	0-12 Months Post Fire	13-24 Months Post Fire	>24 Months Post Fire
% Grass	34.4 (2.95)	53.3 (3.78)	42.3 (3.74)
% Forb	15.5 (1.96)	11.6 (1.92)	11.6 (2.17)
% Litter	6.7 (1.07)	24.1 (2.86)	37.4 (3.81)
% Serecia	4.6 (1.93)	5.9 (2.55)	5 (2.33)
% Shrub	0.7 (0.51)	0.5 (0.41)	1.1 (0.74)
% Bare	38.7 (3.53)	3.9 (1.29)	2.7 (1.29)
Litter Depth (cm)	0.5 (0.17)	7.4 (0.73)	10.4 (1)
Tallest Vegetation (cm)	50.4 (2.29)	77.2 (2.87)	76.7 (3)
Visual Obstruction	33 (1.62)	52.5 (2.06)	52.6 (2.17)

Table 2.3. Beta coefficients for the top model describing predicted T_{bb} at greater prairie-chicken active and refuge location and random landscape locations stratified over three time since fire categories in Osage County, Oklahoma, USA in 2018 and 2019.

Coefficient	Estimate	Standard Error	95% Confidence Intervals	
			Lower	Upper
<i>Main Effects</i>				
(Intercept)	-7.41	1.36	-9.64	-5.18
T _{air}	1.34	0.05	1.26	1.42
Solar Radiation	0.01	0.00	0.01	0.01
Random 13-24 months	2.56	1.85	-0.47	5.60
Random >24 months	4.23	1.89	1.12	7.34
GRPC Active	-0.72	1.69	-3.49	2.06
GRPC Refuge	2.25	1.69	-0.52	5.02
<i>Interaction Effects</i>				
T _{air} *Random 13-24 months	-0.19	0.06	-0.29	-0.09
T _{air} *Random >24 months	-0.21	0.06	-0.31	-0.10
T _{air} *GRPC Active	0.02	0.06	-0.08	0.11
T _{air} *GRPC Refuge	-0.13	0.06	-0.22	-0.03

Figure 2.1. A) Graphical depiction (grey boxes) of activity periods and sampling periods used to investigate habitat selection of brooding and non-brooding female greater prairie-chickens relative to vegetation structure, thermal conditions and invertebrate availability in Osage County, Oklahoma, USA in 2018 and 2019. Hourly average step lengths are plotted to illustrate differences in activity by greater prairie-chickens throughout the day. B) Example of Greater Prairie-Chicken sample site composed of two GPS locations recorded in the active period (dot) and two GPS locations recorded during the refuge period (triangle). One of each location type was assigned to be sampled in either the morning (blue circle) or afternoon sampling period (grey circle).

Figure 2.2. Proportion of telemetry locations from brooding (n=13) and non-brooding (n=21) female greater prairie-chickens recorded in three time since fire categories compared to the proportion of the landscape in each time since fire in Osage County Oklahoma, USA in 2018 and 2019.

Figure 2.3. Ivlev's electivity ratio of brooding (n=13) and non-brooding (n=21) female greater prairie-chickens for three time since fire categories in Osage County Oklahoma, USA between 2018 and 2019. Electivity ratios of 0 indicate no selection while positive values indicate selection for a patch type, and negative values indicate avoidance of a patch type.

Figure 2.4. A) Percent cover of plant functional groups and B) vegetation structure measurements (cm) at greater prairie-chicken active and refuge locations and random locations in patches that are 0-12 months post fire in Osage County, Oklahoma, USA 2018-2019. Error bars equal ± 1 standard error. VOR represents visual obstruction measurements. Asterisks next to measurement names indicate significant differences among location types, and pairwise differences among means Tukey Post Hoc Honesty tests are denoted by different letters above bars.

Figure 2.5. Abundance and biomass (grams) of invertebrates captured on sweep-net transects at greater prairie-chicken active and refuge locations and random landscape locations in patches that are 0-12, 13-24, and > 24 months post fire in Osage County, Oklahoma, USA in 2018 and 2019. The left column shows abundance (A) and biomass (C) for all invertebrate orders identified at a site. The right column shows abundance (B) and biomass (D) for orthoptera (grasshoppers and crickets) only. Abundance and biomass estimates are log-transformed. Error bars equal ± 1 standard error. Letters indicate significant differences based on post-hoc pairwise comparisons.

Figure 2.6. Predicted black-bulb temperatures (T_{bb}) over a range of ambient temperatures (T_{air}) at greater prairie-chicken active and refuge locations and random landscape

locations stratified over three time since fire categories in Osage County, Oklahoma, USA between 2018 and 2019. Grey bands represent 95% confidence intervals.

Figure 2.7. Predicted black-bulb temperatures (T_{bb}) throughout the morning (06:30-10:30) and afternoon (12:30-16:30) sampling periods at greater prairie-chicken active and refuge locations and random landscape locations stratified over three time since in Osage County, Oklahoma, USA between 2018 and 2019. Confidence intervals were omitted for clarity.

Figure 2.8. The abundance (A) and biomass (B) of invertebrates captured on sweep-net transects at greater prairie-chicken active (solid lines) and refuge (dashed lines) locations relative to black-bulb temperatures (T_{bb}) at the site when the sample was collected in Osage County, Oklahoma USA in 2018 and 2019. Both abundance and biomass are log transformed.

Figure 2.1

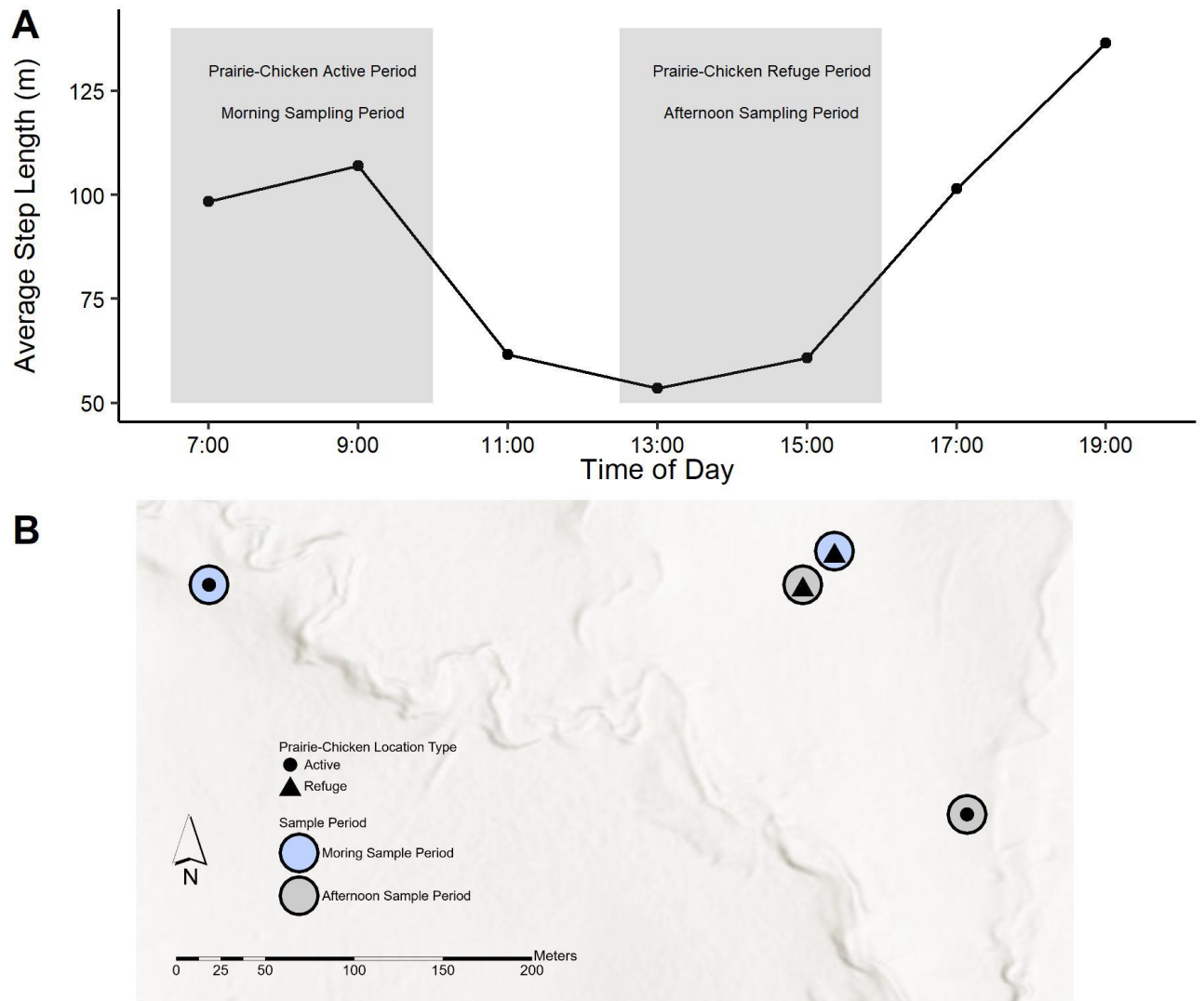


Figure 2.2

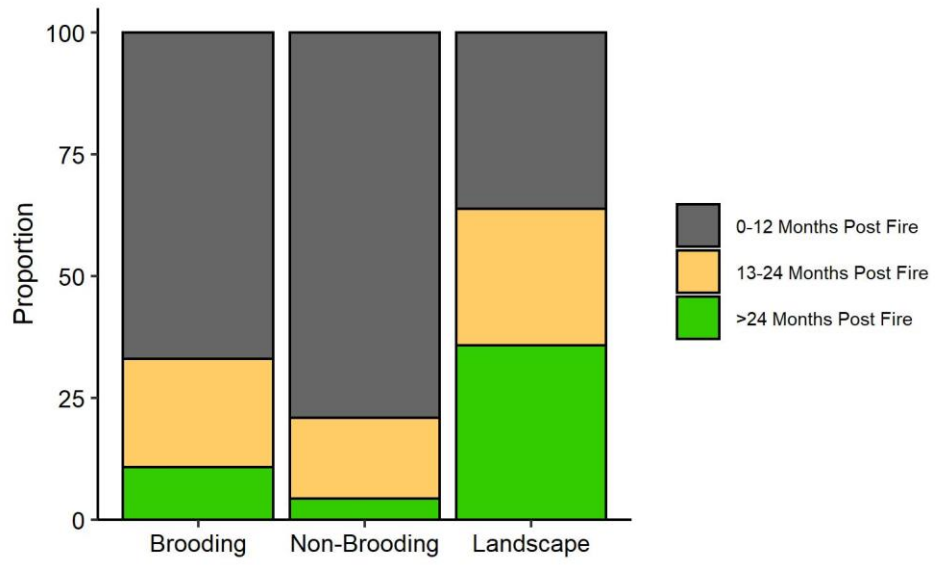


Figure 2.3

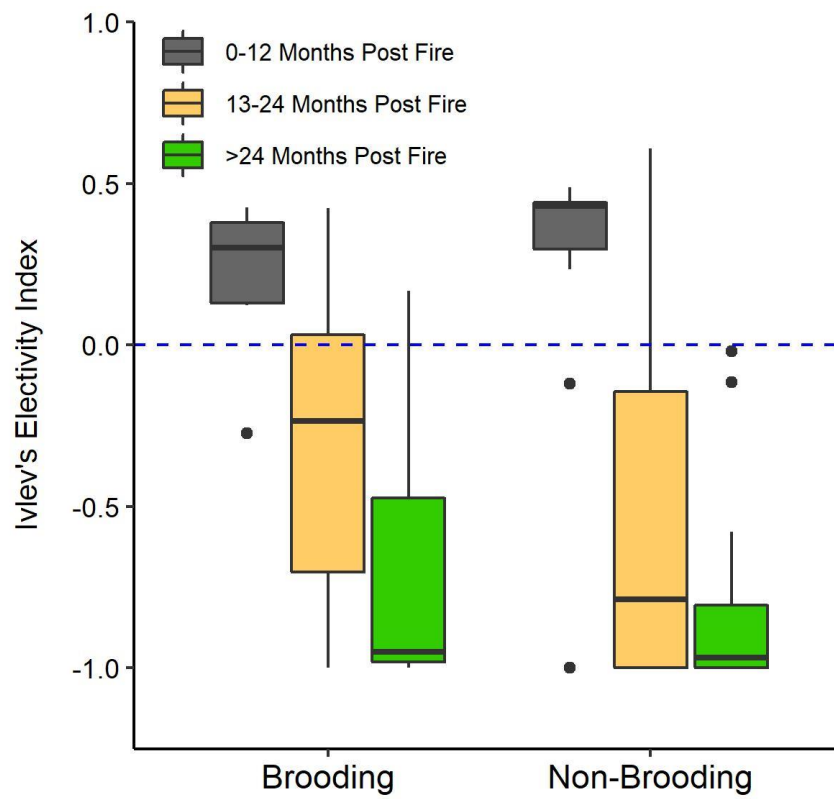


Figure 2.4

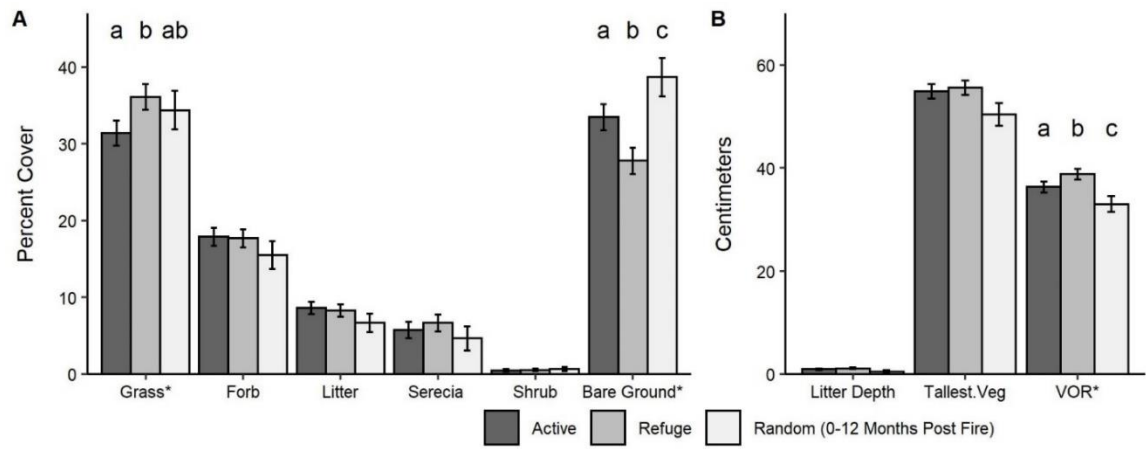


Figure 2.5

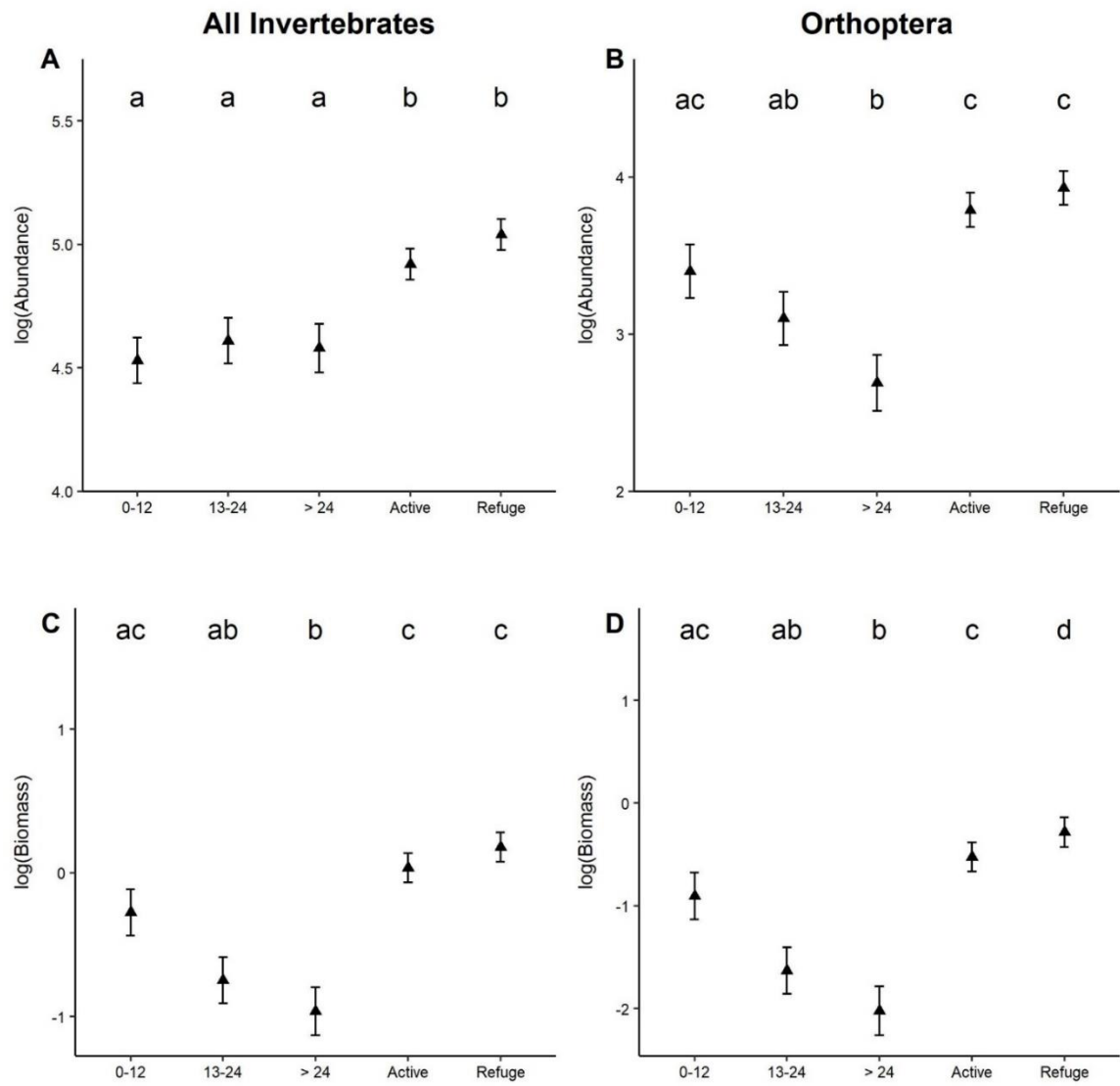


Figure 2.6

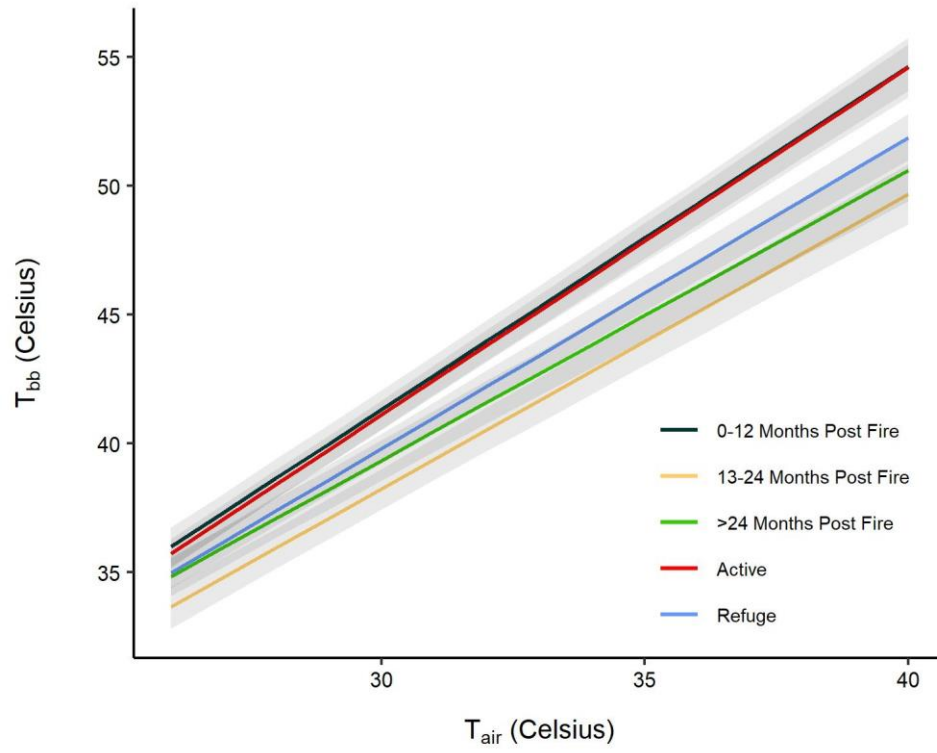


Figure 2.7

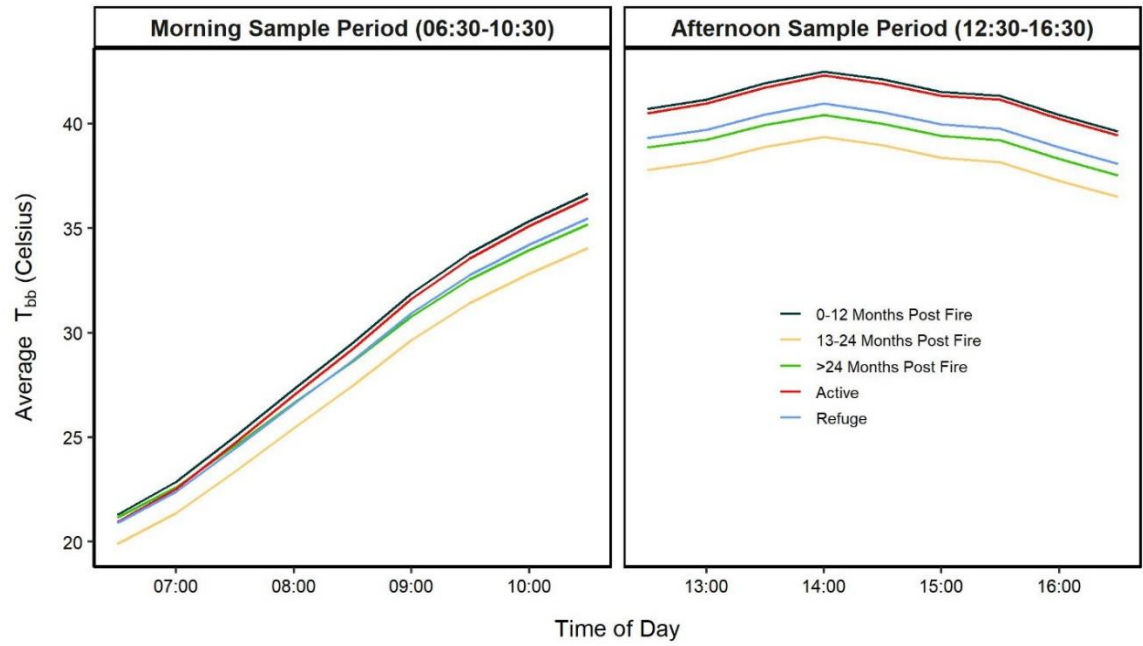
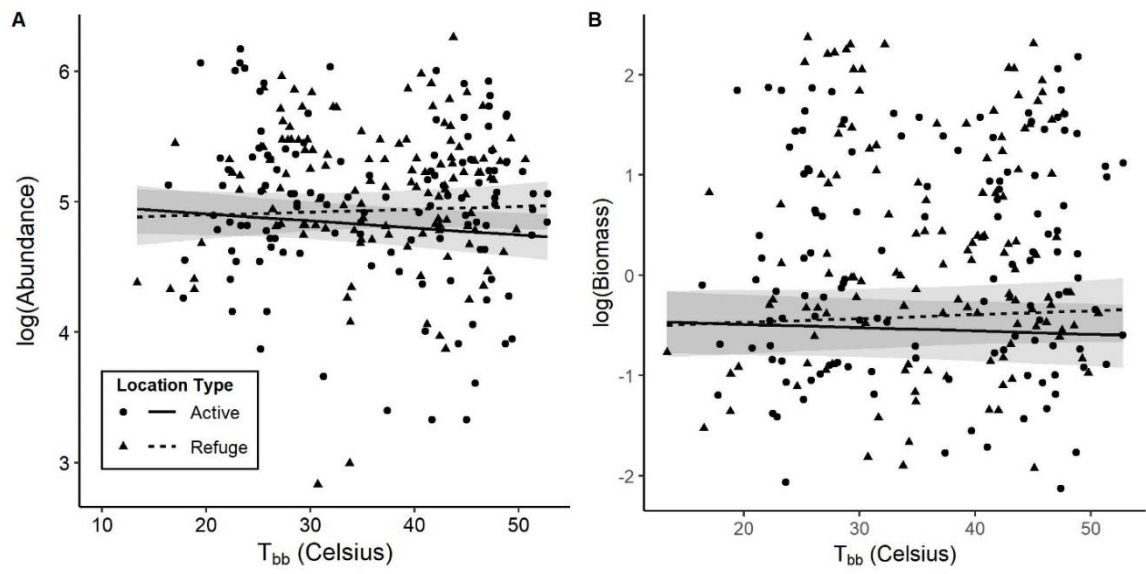


Figure 2.8.



CHAPTER III

WEATHER INFLUENCES MULTIPLE COMPONENTS OF GREATER PRAIRIE-CHICKEN REPRODUCTION

Abstract:

The influence of weather on wildlife populations has been well documented for many species. However, much of the current literature has focused on the impacts of weather within a season and consists of short-term studies. The use of datasets that cover a variety of environmental conditions will be essential for assessing possible carry-over effects of weather experienced in one season on behavior and fitness in subsequent seasons. In this study, we evaluated the effects of weather variables measured over multiple temporal scales on the reproductive performance and behavior of a declining grassland grouse species, the Greater Prairie-Chicken (*Tympanuchus cupido*) in Osage County, Oklahoma from 2011-2019. By considering weather over a range of temporal extents, this allowed us to determine the relative importance of short-term weather events, such as daily temperature and precipitation, versus more chronic shifts in weather such as persistent drought on the reproductive performance of Greater Prairie-Chickens. Specifically, we assessed the effects of daily weather variables and drought conditions on daily nest survival, nest incubation start dates, and clutch size. We found that daily nest survival was primarily influenced by conditions experienced during incubation with daily nest success declining in years with wetter than average springs and during extreme precipitation events. Daily nest survival also declined under higher maximum daily temperatures, especially in years with below-average rainfall. Greater Prairie-Chickens began nesting earlier and had smaller clutch sizes for both initial nests and re-nests in years with warmer temperatures prior to the nesting season. Additionally, incubation of nests started later in the spring in drought years, indicating carry-over effects in Greater Prairie-Chicken reproductive behaviors. Our work shows that if weather in the Great Plains becomes more variable, with increasing frequency of drought and extreme precipitation events, wildlife species that inhabit these grassland landscapes are expected to experience changes in reproduction, potentially influencing future populations.

Introduction

Climate (long-term weather averages in an area) is considered an important component in the fundamental niches of many species (Grinnell et al. 1917, Begon et al. 2006, Jackson et al. 2009). Predictive climate models suggest that many regions across the globe are likely to experience an increase in the range of variation in weather events (short-term measures of variables such as temperature or precipitation) and an increase in the frequency of extreme weather in the future (Intergovernmental Panel on Climate Change 2007, Smith et al. 2011). This increase in variation in weather patterns can affect wildlife populations through several pathways (Parmesan and Yohe et al. 2003, Root et al. 2003) including changes in habitat selection and survival at the individual level, potentially resulting in population declines (Tanner et al. 2017, Skagen et al. 2018). Additionally, although extreme events are by nature rare, when they do occur they can have important effects on population numbers and viability of wildlife species (e.g., mass die-offs associated with heatwaves; Ratnayake et al. 2019). Because of the stochastic nature and increasing variability of weather patterns, relatively few studies have focused on the long-term effects of weather on wildlife populations. For this reason, the use of data that captures the effects of a wide range of weather conditions will be important for making accurate predictions about species' responses to increasing variability in weather and potentially longer-term shifts in climate.

For many species, conditions experienced in a given life stage can have persistent effects, shaping their fitness or survival for a significant time into the future (Harrison et al. 2011, Rockwell et al. 2012, Finch et al. 2014, O'Connor et al. 2015). Despite this, much of the current literature has focused on the immediate direct effects of weather

events on survival and behavior of animals (Simmons et al. 2004, Marra et al. 2015). Because different periods of an animal's life cycle are closely linked, the lack of studies that consider the influence of conditions and weather across periods can potentially limit our ability to fully understand factors that shape population dynamics and how wildlife populations may respond to changing weather patterns. Recently, increasing attention has begun to shift toward understanding the carry-over effects of weather conditions experienced during 1 season or life stage and how these shape behavior and fitness in subsequent periods (Finch et al. 2014, Rushing et al. 2016, Franks et al. 2017). Incorporating weather variables measured over periods outside of the life stage of interest may be important for understanding the potential effects of changing weather patterns on a species.

Climate models predict that the Great Plains of North America will experience more frequent and intense droughts, rising temperatures, and a greater frequency of extreme precipitation events in the future (Melillo et al. 2014). Although it is unclear what the exact outcomes of these changes will be, they are expected to affect many wildlife species that inhabit grassland landscapes, including grassland birds (Peterson 2003, Skagen and Adams 2012, Jarzyna et al. 2016). In particular, drought conditions have been associated with changes in species distribution and abundance for several grassland bird species (Peterson 2003, Wilson et al. 2018, Cady et al. 2019), and reduced productivity and annual survival of individuals (George et al. 1992). Extremes in daily or seasonal conditions such as high rainfall totals or periods of extreme heat have been associated with reduced reproductive success for several species (George et al. 1992, Dreitz et al. 2012, Skagen and Adams 2012, Conrey et al. 2016, Zuckerberg et al. 2018).

The Great Plains is characterized by highly variable inter- and intra-annual weather conditions, and many grassland bird species have evolved to cope with such conditions (Lovett et al. 2005); however, grassland birds, particularly those that are non-migratory or possess limited dispersal abilities, may not have the ability to adequately cope with increasingly variable weather patterns as grasslands become more fragmented (Ross et al. 2016, Zuckerberg et al. 2018).

One species that may be at particular risk to increased weather variability is the greater prairie-chicken (*Tympanuchus cupido*; prairie-chicken). The prairie-chicken is a non-migratory, resident grassland grouse that was historically found in much of the tallgrass prairies and parts of the mixed-grass prairies of North America (Johnson et al. 2011). Over the last half-century, prairie-chickens have experienced substantial population and distribution declines primarily as a result of the loss of habitat, and they are considered vulnerable throughout most of their distribution (Svedarsky et al. 2000). The effects of extreme weather events on prairie-chicken populations are unclear. Researchers reported that prairie-chicken nest success is negatively affected by solar radiation, potentially caused by heat stress for females incubating nests (Hovick et al. 2014, 2015), and that higher temperatures reduce the duration of incubation off-bouts, potentially restricting a female's ability to take in sufficient amounts of food (Hoppe et al. 2019). Long-term data on demographic parameters over a wide variety of environmental conditions for this species is limited, which hinders the ability to assess risk associated with changing weather patterns. Because many parts of the prairie-chicken's distribution are predicted to experience increasingly variable and unpredictable weather patterns (including rising temperatures, more frequent and intense droughts, and changing rainfall

patterns) understanding the effects of these events on this species will be necessary for effective conservation.

In this study, we used a 9-year dataset of prairie-chicken nests to evaluate the effects of weather on the reproductive parameters for this species at the southernmost extent of its distribution. The long-term nature of our dataset provides us with a unique opportunity to assess the effects of weather variability on a species of conservation concern by linking our detailed records of productivity to weather data for our study site (Simmons et al. 2004). Our objective was to investigate the relative importance of daily and seasonal weather variables, and drought conditions on daily nest survival, nest initiation date, and clutch size. Additionally, we investigated the potential for carry-over effects by evaluating how the timing and duration of drought relative to a nesting season influenced reproductive parameters.

STUDY AREA

We conducted our research on a private cattle ranch and The Nature Conservancy's Tallgrass Prairie Preserve from 2011 to 2019 in Osage County, Oklahoma, USA. The focal area of our study covered approximately 40,000 ha and was composed of rolling topography with elevations ranging from 320–400 m. Our study area occurred in the southernmost portion of the Flint Hills Ecoregion and was dominated by tallgrass prairie vegetation. Dominant plant species included little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), and a mixture of forbs. The climate for the region was temperate with an average annual rainfall of 104 cm and relatively hot summers (Jun-Sep; mean daily high 31.4°C) and cold winters (Oct-Mar; mean daily low –5°C). This region also experienced considerable inter-annual

rainfall conditions resulting in periodic drought conditions at multiple temporal scales (Appendix D, Figure D1). Weather conditions during the study period were similar to long term weather patterns recorded for the region (Appendix D, Figure D1). Potential prairie-chicken nest predators in the region include coyote (*Canis latrans*), striped skunk (*Mephitis mephitis*), American badger (*Taxidea taxus*), and bullsnake (*Pituophis catenifer*; Winder et al. 2016)

The dominant land use at our site was cattle production, and properties where prairie-chickens were monitored were managed primarily with prescribed fire and grazing. In general, properties used prescribed fire to create structural and compositional vegetation heterogeneity by burning portions of the landscape, allowed grazers to preferentially forage in the recently burned patches, while leaving the rest of the landscape unburned and either lightly grazed or ungrazed for ≥ 1 year (Fuhlendorf and Engle 2001). This method of deferring fire for several years resulted in a landscape composed of a variety of successional stages, including patches that had been unburned and ungrazed for several years with thick, dense vegetation that was ideal for prairie-chicken nesting cover (Hovick et al. 2015, McNew et al. 2015). Prescribed burns primarily occurred in the spring (Mar–Apr) prior to prairie-chicken nesting activity, with a small number of burns taking place in late summer (Aug–Sep) and winter (Nov–Dec). As a result, relatively few nests were lost to prescribed fire activity. Grazing pressure was moderate across properties throughout the study (2.5 animal unit months [AUM]/ha; Hamilton et al. 2007, Hovick et al. 2015).

METHODS

Prairie-Chicken Capture and Monitoring

All methods relevant to the capturing and handling of prairie-chickens were reviewed and approved by the Oklahoma State University Institutional Animal Care and Use Committee (protocol AG1724). We captured female greater prairie-chickens at communal breeding sites (i.e., leks) using walk-in funnel traps from 2011 to 2019 (Schroeder and Braun et al. 1991). We aged and determined sex of every individual captured based on plumage and secondary sex characteristics (presence of air sacs and size of eye combs in males; Henderson et al. 1967). We marked males and females with an aluminum leg band with unique identifier numbers, and we outfitted females with transmitters, which allowed us to locate the nests. Throughout the study, we used 2 types of telemetry units to track and monitor nesting activity by female prairie-chickens. From 2011–2013, we outfitted females with 16-g necklace style very high frequency (VHF) radio-transmitters (Advanced Telemetry Systems, Isanti, MN, USA), and from 2014 to 2019, we fitted females with rump-mounted 22-g solar-powered ARGOS global positioning system (GPS) transmitters (Microwave Telemetry; Columbia, MD, USA). We programmed the GPS transmitters to record 1 GPS fix every 2 hours from 0600 to 1800 during the nesting season (1 Apr–31 Jun). We monitored females with VHF collars every 1–3 days using a handheld receiver and a directional Yagi antenna. Once we recorded a female with a VHF collar as being in the same location for ≥ 3 days, we approached the bird on foot and flushed the female from the nest (Hovick et al. 2015). We monitored females with GPS transmitters daily via remote data downloads from the ARGOS server, and we identified nests when a female's GPS locations localized to a single site. We then searched the area until the female flushed from the nest. To reduce the potential for abandonment, we only approached nests after telemetry data suggested

the female had begun incubating. Once a nest was identified, we recorded the time since fire of for the patch where the nest was located.

For all nests, after we flushed the female, we recorded the Universal Transverse Mercator (UTM) coordinates using a handheld GPS unit, and we recorded the number of eggs in the nest to determine the clutch size. We did not disturb nests for the remainder of the incubation period (25–28 days), and we only approached the nest if we determined the female had left the nest. After the departure of the female, we approached the nest and determined nest fate by examining the contents remaining in the nest bowl. We estimated nest initiation date as the first date that we recorded females with VHF transmitters at the nest, and as the first day where the majority of GPS fixes occurred at the nest for females with GPS transmitters. For the majority of failed nests, we were unable to directly determine a cause of failure. This was because of the lag between nest failure and discovery that made it unclear if a destroyed nest was first abandoned because of factors such as weather, disturbance, or female choice and then scavenged before nest contents could be checked, or if the nest failed as a direct result of nest predation. Researchers have suggested nest predation as the primary cause of nest loss for the Flint Hills Ecoregion (Winder et al. 2016). We excluded nests lost because of prescribed fire ($n = 1$), researcher interference ($n = 2$), or those lost prior to incubation ($n = 3$) from further analysis.

Daily Weather and Drought Data

In this study, we used 2 separate sources of weather data in our analysis. To assess daily weather patterns, we used measurements from an on-site weather station (Oklahoma Mesonet; Brock et al. 1995). For calculation of drought indices, we used PRISM climate

data (Prism Climate Group 2017). We used 2 sources because local weather station data likely provided better estimates of the conditions the birds incubating nests were likely experiencing, whereas PRISM allowed for more accurate estimation of drought indices because ≥ 30 years of monthly weather data are needed to produce valid drought estimates (Vincente-Serrano et al. 2010).

For the nest survival analysis, for each day we monitored a nest, we included several daily weather variables that influence grassland bird reproduction including daily precipitation totals (cm), daily average temperature ($^{\circ}\text{C}$), daily maximum temperature ($^{\circ}\text{C}$), and daily minimum temperature ($^{\circ}\text{C}$; Dreitz et al. 2012, Skagen and Adams 2012, Hovick et al. 2015, Conrey et al. 2016). To characterize the effects of extreme weather events on daily nest survival, we included binary variables for days when daily precipitation and maximum temperature was ≥ 2 standard deviations above the seasonal average for the entire period that daily records were available from the weather station (1997–2019). To summarize local weather conditions before nest initiation, we included the mean average temperature ($^{\circ}\text{C}$), mean minimum temperature ($^{\circ}\text{C}$), mean maximum temperature ($^{\circ}\text{C}$), and total precipitation (cm) from 15 February to 15 April. This period corresponds approximately to 2 months prior to nesting and egg-laying activities for the majority of nests.

To characterize drought conditions, we calculated standardized precipitation evapotranspiration indices (SPEI) for specific periods of interest (Vincente-Serrano et al. 2010). These values are used to characterize drought conditions because they describe the balance between precipitation and potential evapotranspiration based on time of year, average temperatures, and latitude for a site. We used SPEI because it offers greater

flexibility in the temporal windows and extents over which the index can be calculated compared to other drought indices, such as Palmer drought severity indices, while incorporating information about observed precipitation and temperatures. This is ideal for our study because our objective was to assess drought conditions during specific periods relevant to prairie-chicken biology that differ in their temporal extents (Vincente-Serrano et al. 2010). We made all calculations using package SPEI in Program R (Beguería et al. 2017). For each year of the study, we calculated 4 period-specific drought indices: early spring (Mar–Apr preceding nesting), nesting season (Apr–Jun), summer drought (Jun–Sep preceding nesting), and winter (Oct–Feb preceding nesting). Additionally, we included 2 long-term drought indices to capture the cumulative effects of droughts occurring over multiple seasons prior to nest initiation. These included a 6-month drought index (Oct–Mar preceding nesting) and a year-long drought index (entire year preceding nesting). We chose to use only drought variables to represent long-term weather patterns because the SPEI variables were highly correlated with precipitation measured over the same period ($r > 0.9$), and at least moderately correlated with temperature variables ($r > 0.6$).

Data Analysis

Nest site selection. — We calculated the number of nests that occurred in each time since fire category to provide a coarse index of habitat selection during our study. Additional details about nest site selection at our study site can be found in Hovick et al. (2014, 2015) and Londe et al. (2019).

Nest detection.—To determine if nest detection probability differed between females marked with VHF and GPS transmitters, we calculated the number of nests

initiated per female that survived to the start of the nesting season of each year (1 Apr). We then used a student's *t*-test to determine if nest initiation rates differed between the 2 groups. We tested for a significant difference in mean nest initiation rates at $\alpha = 0.05$.

Daily nest survival.— We used daily nest survival models in Program MARK (White and Burnham 1999) to estimate the influence of weather on daily nest success. These models estimate daily survival probabilities for a nest using generalized linear modeling and a binomial likelihood distribution for the response variable (White and Burnham 1999, Dinsmore et al. 2002). Because we were considering a large number of covariates, we used a multi-step model-building approach based on an information-theoretic analysis to select the models that were most influential for nest survival (Table 3.1; Skagen et al. 2012, Webb et al. 2012, Hovick et al. 2015). Prior to assessing the influence of weather variables, we developed a base model from variables that have been documented to influence nest survival in avian species. To develop the base model, we first selected the best expression of the temporal variables (linear or quadratic forms of nest age and time of season) using Akaike's Information Criterion corrected for sample size (AIC_c). After selecting the top ranked models describing temporal variables, we generated a new set of models each of which contained the temporal variable expressions selected in the previous step and one of the variables describing nest or female characteristics (Table 3.1, Appendix Table E1). We then selected the top ranked model from this step for use as the base model in subsequent steps (Webb et al. 2012).

In the second step of the model-building process, we compared separate models that included each drought variable in addition to the variables from the base model. We considered a drought variable as supported if it improved model fit by $>2 AIC_c$ over the

base model, and we added supported drought variables to the base model for subsequent modeling steps. For the third step in the model-building analysis, we repeated this process with the temperature and precipitation variable sets. We retained supported temperature and precipitation variables (>2 AIC_c change) for the final model set. In addition to examining the main effects of precipitation and temperature, we considered the interaction of drought conditions and daily weather in this step. We considered this interaction because daily weather's influence on nest survival may be contingent on the overall drought conditions (e.g., if drought influenced nesting cover or adult body conditions). Additionally, at each step, we evaluated Pearson's correlation among supported variables, and from each pair of variables with a Pearson's $|r| \geq 0.7$, we retained only the variable with the lowest AIC_c value within model groups. In the final step of the model-building process, we then created models representing all possible combinations of supported weather variables or supported interactions (drought and daily weather interactions) for our final set of candidate models. From this model set, we selected the model with the lowest AIC_c as the top model describing daily nest survival. In cases where there were multiple competitive models (<2 AIC_c), we chose not to perform model averaging because this procedure can result in erroneous parameter estimates when interaction terms are present in the model set (Grueber et al. 2011).

Clutch size and nest initiation date.—We used generalized linear models (GLM) with a Gaussian link function to estimate the effects of weather on clutch size and the start date of nest incubation. We used a similar model-building approach to construct the top model describing the effects of weather and drought on clutch size and incubation start date. Similar to the nest survival models and tested if weather influenced either of

these 2 groups. We could not directly assess the effects of weather on individual days for these response variables, so we used averages calculated during 2 months before nest initiation to capture the effects of short-term weather dynamics on clutch size and incubation start dates. The incubation start date for each nest was the number of days after 1 April because we did not find any females incubating earlier than 3 April. Unlike the daily nest survival analysis, we did not generate a final model set for these analyses because the models would have largely been redundant with previous steps in the model-building process. The resulting model-building steps for the clutch size and initiation date analysis first considered nest and female characteristics, then drought variables, and finally combinations of early spring weather variables and the supported drought, nest, and female characteristics variables. We considered the top model from the final step to be the best model describing clutch size and nest initiation date. We did not consider combinations of early spring variables because many of these variables were highly correlated. Further, for the clutch size analysis, we did not consider early spring drought because it was correlated with 6-month drought, which was included and had a lower AIC_c score. Similar to daily nest survival analysis, when multiple competitive models were present in the final step, we did not perform model averaging (Grueber et al. 2011).

RESULTS

We monitored 156 prairie-chicken nests (125 initial nest attempts, 31 reneest attempts) from 93 females. Nest survival varied between years ranging from 12% nest success in 2019 to 60% nest success in 2014. The estimated daily nest survival for our study was 0.965, which corresponds to a 36% chance of survival when extrapolated over the entire 28-day incubation period. Over the 9-year study period, we recorded 90% (140 nests) of

monitored nests in patches that were considered unburned (>12 months post-fire). Nest detection did not differ between females marked with VHF transmitters and females marked with GPS transmitters ($t = 3.48$, $P = 0.47$). Specifically, we detected on average 1.31 ± 0.07 (SE) nests/female with VHF transmitters (2011–2013), and 1.24 ± 0.08 nests/female with GPS transmitters (2014–2019). Additionally, transmitter type was not among the supported variables included in the final model, suggesting similar nest survival rates between nests incubated by females marked with GPS and VHF transmitters (Table 3.2).

The best model describing daily nest survival indicated that nest survival decreased with nest age and time of season (days since 1 Apr), and extreme precipitation events (24-hr rainfall >2 SD above the seasonal average). Additionally, the relationship of daily survival with maximum daily temperature was dependent on drought during the nesting season (Apr–Jun of the current year; Tables 3.2 and 3.3; Appendix Table E1). Daily nest survival decreased for nests initiated later in the season and with increasing nest age (Table 3.3). Daily nest survival showed a marked decline on days with extreme precipitation events (Table 3.3). The main effect for drought during the nesting period indicated lower average daily nest success for nests initiated in wet years (SPEI > 0) compared to nests initiated in years with low rainfall during the nesting period (Fig. 3.1A; Table 3.3). The main effect for maximum daily nest temperature indicated a negative relationship between daily nest survival and daily maximum temperature; however, the confidence intervals for the main effect of daily maximum temperature overlapped zero (Table 3.3). The interaction of drought conditions during the nesting season and maximum temperature indicated contrasting responses to maximum temperature in dry

versus wet years. In dry years (SPEI during the nesting season < 0), daily nest survival decreased with higher maximum temperatures, whereas in wet years (SPEI during the nesting season > 0), daily nest survival increased with greater daily maximum temperatures (Fig. 3.1B). Although the age of the incubating female (second year vs. after second year) was included in the final model, the confidence intervals for this variable overlapped zero suggesting this variable may have limited influence on nest survival (Table 3.3). The model with the variables for nest age, time of season, female age, nest drought (drought during Apr and May of the current year), and extreme rain events was competitive ($\Delta AIC_c = 0.51$) with the top model (Table 3.2).

The top model for greater prairie-chicken nest incubation start date included nest attempt, year-long drought, and average temperature during the early spring period (Table 3.2; Appendix Table E2). We estimated the average incubation start date for first nest attempts under average conditions to be approximately 1 May with the average nest incubation start date for renests occurring on average 30 days later (30 May; Table 3.3). Nest incubation start date had a negative relationship with drought measured over the 12 months preceding nesting (year-long drought) with nest incubation starting later following drought years (Fig. 3.2A). Similarly, the start date for nest incubation had a negative relationship with the average temperature during the early spring period (Feb–Apr preceding nesting season), with nest incubation starting earlier in the season with warmer spring temperatures (Fig. 3.2B). Models containing the main effects for average daily maximum temperature ($\Delta AIC_c = 0.41$) and average daily minimum temperature ($\Delta AIC_c = 1.24$) were competitive, and similar to the top model; they indicated that as

early spring season maximum and minimum temperatures increased, nest initiation occurred earlier in the season (Table 3.2).

Greater prairie-chicken clutch size was similarly influenced by nest attempt, year-long drought, and the average maximum daily temperature during the early spring period (Feb–Apr; Tables 3.2 and 3.3; Appendix Table E3). Clutch size in years with moderate spring temperatures and average drought conditions over the previous year (previous year SPEI = 0) was 12.32 for first nests, whereas renests on average contained 2.50 fewer eggs. Clutch size had a negative relationship with the average daily maximum temperature during the early spring (Fig. 3.3). Previous year drought had a negative relationship to clutch size, but the confidence intervals for this variable included zero, suggesting this variable may not influence clutch size (Table 3.3). There was considerable model uncertainty for clutch size; 3 additional models were competitive (Table 3.2). Competitive models also contained combinations of variables related to drought and temperatures prior to the nesting season (Table 3.2).

DISCUSSION

Greater prairie-chicken reproduction was influenced by weather over multiple time scales, and no single variable or time period completely explained the relationship. Clutch size and daily nest survival were most strongly influenced by conditions during the nesting season or just prior to nest initiation, whereas long-term drought influenced incubation start date, providing evidence for carry-over effects. Specifically, nest survival was affected by short-term changes in precipitation patterns in the spring, with nest success decreasing in years with wetter than average springs and during extreme rainfall events. Temperature also influenced nest survival, but the effect varied depending on

precipitation. Nest survival had a negative relationship with daily maximum temperatures in years with low precipitation, and a positive relationship with daily maximum temperature during years with high precipitation. Additionally, warmer temperatures before nest initiation resulted in earlier incubation start dates and smaller clutch sizes. Although persistent drought conditions the year prior to nesting resulted in later incubation start dates, nest survival and clutch size were unaffected by conditions in previous seasons, suggesting there may be limited carry-over effects on prairie-chicken demographics. Our results emphasize the importance of considering weather measured over multiple temporal scales, ranging from daily to annual conditions because this can provide a more complete picture of how weather variation can influence reproduction. High temperatures and increasingly variable rainfall patterns, including extreme rainfall events, are predicted to become more common throughout the Great Plains (Groisman et al. 1999, Melillo et al. 2014); therefore, our research suggests prairie-chickens in the Southern Great Plains may experience reduced reproductive output in the future. These results add to a growing body of literature highlighting the importance of considering the effects of weather on grassland bird demographics and reproduction (Dreitz et al. 2012, Skagen and Adams 2012, Conrey et al. 2016, Skagen et al. 2018).

By accounting for the scalar nature of weather, we were better able to assess potential resource and energetic factors that influence nesting success and behavior for greater prairie-chickens. Drought indices calculated over different temporal extents reflect different information about the environment (McKee et al. 1993). Short-term drought indices are indicative of fine-scale variation in precipitation patterns (McKee et al. 1993). Alternatively, drought calculated over longer periods correspond to more

chronic changes in precipitation (Lorenzo-Lacruz et al. 2010) that can potentially result in reduced soil moisture and decreased plant primary production (Knapp et al. 2015). The only drought variable that directly influenced nest survival in our study was drought conditions while the female was incubating. We found that nest survival increased in years with drier springs, and nest survival was suppressed in years with above-average rainfall. This suggests nest success may be highly influenced by changes in adult incubation behavior or energy input into thermoregulatory behaviors associated with rainfall events (Jovani and Tella 2004, Öberg et al. 2015). Alternatively, short-term variation in rainfall may alter predator activity resulting in higher risk for incubating females (Vickery and Bider 1981). Extended drought prior to the nesting season resulted in later start dates for nest incubation, which may reflect reduced body condition of females going into the breeding season due to limited food resources prior to nesting (Pietiainen and Kolunen 1993, Nooker et al. 2005, Robinson et al. 2005). These changes in nest incubation start dates due to long-term drought can potentially influence prairie-chicken demographics if they result in subsequent changes in survival of nests or chicks that hatch later in the season (Fields et al. 2006, Fletcher et al. 2013). As energy and resource needs vary across species and life-history stages, the inclusion of weather measured over multiple time scales into survival models offers a possible means of assessing the factors that control different demographic parameters, and ultimately population structure and viability.

Temperature can influence nest success in several grassland bird species (George et al. 1992, Dreitz et al. 2012, Skagen and Adams 2012, Conrey et al. 2016), and our results suggest that greater prairie-chickens may be negatively influenced by higher

maximum daily temperatures in some contexts. In years with wet springs, nest survival was positively related to maximum daily temperatures, whereas in dry years, the relationship was negative. Increasing variability in weather will likely result in wildlife populations being exposed to multiple extremes in weather, such as temperature and precipitation, over a given time period (Groisman et al. 1999, Easterling et al. 2000, Katz et al. 2005). As a result of this environmental stochasticity, the relative importance of different weather conditions for a species' fitness will likely differ between years depending on the context of additional environmental variables experienced (Anthony et al. 2009, Albright et al. 2010). But female prairie-chickens may be able to mitigate the negative effects of high daily temperatures through selection of nest sites. Over 90% of nest monitored in our study occurred in patches >12 months post fire, with these patches being characterized by tall dense vegetation. Prairie-chicken nests with taller vegetation and greater amounts of cover have on average higher nest survival (Hovick et al 2015, McNew et al. 2015). This observed increase in nest survival with taller vegetation at the nest site has been linked to cooler operative temperatures in the nest (Hovick et al. 2014). This suggests that management practices, such as reduced stocking rates or deferred burning, that maintain nesting cover may offer an important strategy for limiting the effects of high temperatures on incubating females, in the context of more frequent droughts.

We also found evidence that temperature prior to the nesting season influenced reproduction; incubation start dates were earlier in the year and clutch size was smaller when daily temperatures were higher in the months preceding nest initiation. Warmer temperatures prior to the nesting season have been associated with earlier nesting activity

in several avian species (Both et al. 2004, Ardia et al. 2006, Visser et al. 2009), and are often attributed to greater food resources as plant and invertebrate phenology shift earlier to match spring temperatures. Clutch size is also positively associated with food abundance in many avian species (Dijkstra et al. 1982, Hussell et al. 1987, Murphy 1983, Perrins and McCleery 1989). The disconnect between the onset of nesting and clutch size for prairie-chickens in years with higher spring temperatures suggests that prairie-chickens may be relying on external cues such as daily temperature to make decisions about nest initiation, rather than actual food abundance or internal state (Perrins et al. 1966, Rowe et al. 1994, Visser et al. 2006). Prairie-chickens rely on energy resources acquired during reproduction to fuel egg production and incubation (Thomas et al. 1988, Jönsson et al. 1997). If a mismatch among the cues females use to make nesting decisions and actual food abundance occurs, females may begin nesting activities before adequate food resources are available, resulting in smaller clutch sizes (Klomp 1970, Perrins and McCleery 1989).

Although many researchers have demonstrated the link between weather and nest survival in grassland birds, few have investigated the mechanisms that cause nest loss under adverse conditions (Carver et al. 2017). Weather events can directly cause nest failure through destruction of the nest (e.g., flooding, hail) or through abandonment of the nest by the adult under extreme conditions (Skagen and Adams 2012, Conrey et al. 2016, Carver et al. 2017). Alternatively, extreme weather can influence the behavior of the attending adult and potential nest predators making the nest more vulnerable to depredation. Warmer temperatures and increased winds influence the number and timing of off-bouts taken by incubating adult prairie-chickens (Hoppe et al. 2019), potentially

making nests more visible to predators because of the increased activity by the female at nests sites (Muchai and du Plessis 2005). Additionally, predator activity or foraging behavior may vary with the weather (Vickery and Bider 1981, Fogarty et al. 2017), and predation may increase following certain weather events such as heavy rains or high temperatures as predators increase their foraging activities. Predation is considered to be among the most important sources of nest failure for many grassland birds (Johnson et al. 1990, Vickery et al. 1992, Roos et al. 2018), so developing a clear understanding of how weather and predation interact to influence nest fate is important. Although our study was not designed to investigate the interacting effects of predators and weather on nest survival, this will likely be an important avenue for future research because understanding the causes of nest losses under increasing weather variability will be important for developing effective management strategies for grassland birds.

MANAGEMENT IMPLICATIONS

Our results suggest that management practices that maintain nesting cover will be essential for ensuring population viability for this species because greater prairie-chickens are expected to experience reduced reproduction under increasingly variable weather patterns. Taller vegetation structure and cooler nest site temperatures are related to prairie-chicken nest survival, and managing for patches with adequate nesting cover may help potentially buffer prairie-chicken populations against weather events such as high temperature and precipitation. This has important implications to the scale of prescribed fire and the intensity of grazing because they both alter the structural composition of potential nesting cover. However, the context-dependent nature of prairie-chicken response to temperature that we observed suggests that managers should use

caution when making predictions about demographic responses to weather in other parts of their distribution. Finally, even in our study area, which contains relatively continuous grasslands that are specifically managed for prairie-chickens, we still observed a wide range of nest success values under differing weather conditions. This highlights that weather variability and projected shifts in climate should be an essential consideration when managing for prairie-chickens, and that failure to do so may result in inadequate conservation measures.

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Table 3.1. Variables used to evaluate the effects of weather on reproductive parameters of Greater Prairie-Chickens monitored in Osage County, Oklahoma between 2011 and 2019. Columns marked with an X indicate if a variable was included in the analysis for incubation start date, clutch size, or daily nest survival.

Variable	Description	Nest initiation	Clutch size	Nest survival
Temporal variables				
Age, age2	Linear or quadratic trend for nest age			X
Time, time2	Linear or quadratic trend for time of season (days past 1 Apr)			X
Female characteristics				
Female age	Age of female (subadult vs. adult)	X	X	X
Nest attempt	Initial nest or renest	X	X	X
Clutch size	Clutch size of current nest attempt	X		X
Time since fire	Indicator variable for if the nest is located in a patch that was burned in previous 12 months	X	X	X
Transmitter type	Very high frequency vs. global positioning system transmitter			X
Daily precipitation				
Daily precipitation	Daily rainfall			X
Extreme precipitation ^a	Indicator variable for an extreme rainfall event			X
Daily temperature				
Average temperature	Average temperature for each day during nesting			X
Maximum temperature	Maximum temperature for each day during nesting			X
Minimum temperature	Minimum temperature for each day during nesting			X
Extreme heat ^a	Indicator variable for extreme heat event			X
Early spring season weather				
Average early spring temperature	Average of daily mean temperature for a 2-month period before nesting.	X	X	
Average early spring maximum temperature ^b	Average of daily maximum temperature for a 2-month period before nesting.	X	X	
Average early spring minimum temperature ^b	Average of daily minimum temperature for a 2-month period before nesting.	X	X	
Total precipitation ^b	Total precipitation for a 2-month period before nesting	X	X	
Drought conditions ^c				
Nesting season drought	SPEI for the period when females are on the nest	X	X	X
Early spring drought	SPEI for Mar–Apr preceding nesting season (2 months)	X	X	X
Winter drought	SPEI for Oct–Feb preceding nesting season (4 months)	X	X	X
Summer drought	SPEI for Jun–Sep preceding nesting season (4 months)	X	X	X
6-month drought	SPEI of entire 6 months preceding nesting (Oct–Mar; 6 months)	X	X	X

Year-long drought	SPEI of entire year preceding current nesting season (10 months)	X	X	X
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^aWe defined extreme events as >2 standard deviations above the seasonal average.

^bWe calculated the early spring season averages over the period from 15 February to 15 April.

^cWe calculated drought conditions using standardized precipitation evapotranspiration indices

Table 3.2. Top ranked competitive models showing the effects of weather on daily nest survival, incubation start date, and clutch size for Greater Prairie-Chicken nests in Osage County, Oklahoma 2011- 2019. Six-month modelling steps can be found in Appendix Tables E1-E3.

	Model	k	AIC _c	ΔAIC_c	w
Nest Survival	Age + Time + Hen Age + Nesting Season Drought \times Maximum Temperature + Extreme Rainfall	9	885.9	0	0.5
	Age + Time + Hen Age + Nesting Season Drought + Extreme Rainfall	7	886.4	0.5	0.4
Incubation Start Date	Nest Attempt + Year-Long Drought + Average Daily Mean Temperature	5	1154.3	0	0.26
	Nest Attempt + Year-Long Drought + Average Daily Maximum Temperature	5	1154.7	0.41	0.21
	Nest Attempt + Year-Long Drought + Average Daily Minimum Temperature	5	1155.5	1.24	0.14
Clutch Size	Nest Attempt + Year-Long Drought + Mean Daily Maximum Temperature	5	605.59	0	0.25
	Nest Attempt + Year-Long Drought + Mean Daily Average Temperature	5	606.81	1.22	0.14
	Nest Attempt + Six-month Drought \times Mean Daily Maximum Temperature	6	607.11	1.52	0.12
	Nest Attempt + Six-month Drought + Mean Daily Maximum Temperature	5	607.56	1.97	0.09

Table 3.3. Coefficient estimates, standard errors, and 95% confidence intervals for weather variables influencing daily nest survival, incubation start date, and clutch size for Greater Prairie-Chicken nests monitored between 2011 and 2019 in Osage County, Oklahoma.

Variable	Estimate	Standard Error	LCI	UCI
Daily nest survival				
Intercept	6.25	0.88	4.50	7.98
Nest age	-0.04	0.01	-0.06	-0.02
Time	-0.02	0.01	-0.35	-0.01
Female age	-0.31	0.23	-0.77	0.14
Nesting season drought	-1.39	0.58	-2.54	-0.25
Maximum temperature	-0.03	0.03	-0.09	0.04
Extreme rainfall	-0.98	0.39	-1.75	-0.22
Nesting season drought \times maximum temperature	0.04	0.02	0.01	0.08
Incubation start date				
Intercept	42.75	4.47	33.81	51.69
Nest attempt	30.67	1.93	26.80	34.54
Year-long drought	-3.21	0.93	-5.06	-1.36
Average early spring temperature	-1.06	0.39	-1.85	-0.28
Clutch size				
Intercept	15.67	1.28	13.12	18.23
Nest attempt	-2.49	0.34	-3.17	-1.80
Average early spring maximum temperature	-0.18	0.07	-0.32	-0.05
Year-long drought	-0.25	0.16	-0.56	0.07

Figure 3.1. Estimated daily survival rates A) nesting season drought (April- June) when daily maximum temperature is held at its average (28° Celcius) and B) daily maximum temperature in dry years (solid line) and wet years (dotted line) for Greater Prairie-Chicken nests monitored in Osage County, Oklahoma, USA between 2011 and 2019. Gray bands indicate 95% confidence intervals for regressions lines. Drought conditions were calculated using SPEI (Standardized Precipitation-Evapotranspiration Index) indices, where positive values indicate wet periods, and negative values indicate dry periods.

Figure 3.2. Predicted effects of A) year Long drought (June-April) conditions and B) average daily temperature (°C) on the incubation start date for initial nests (solid line) and renests (dotted line) for Greater Prairie-Chicken nests monitored in Osage County, Oklahoma, USA between 2011- 2019. Gray bands indicate 95% confidence intervals for regression lines. Drought conditions were calculated using SPEI (Standardized Precipitation-Evapotranspiration Index) indices, where positive values indicate wet periods, and negative values indicate dry periods.

Figure 3.3. Predicted effects of average maximum daily temperatures (°Celcius) during the two months prior to the nesting season on clutch size for Greater Prairie-Chicken initial nests (solid line) and renests (dashed lines) in Osage County Oklahoma between 2011 and 2019. Grey bands represent 95% confidence intervals.

Figure 3.1

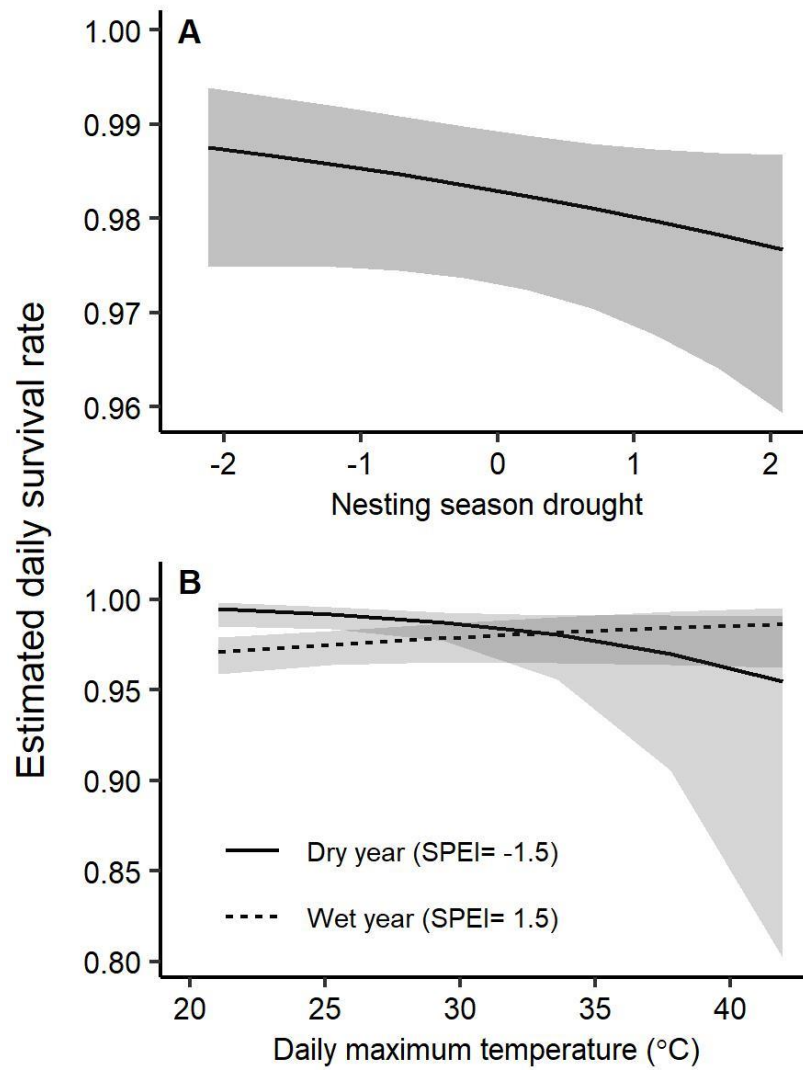


Figure 3.2

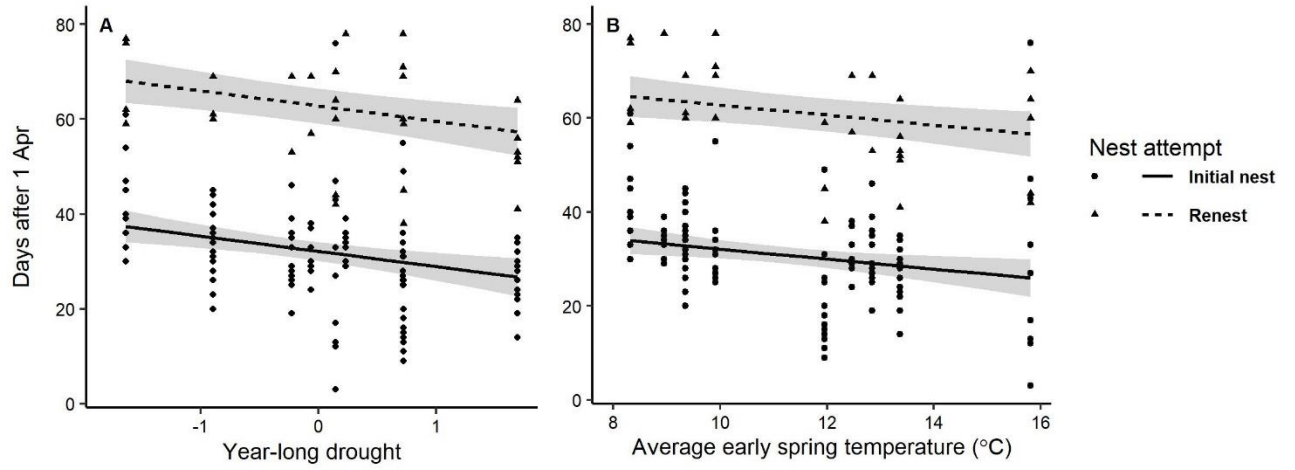
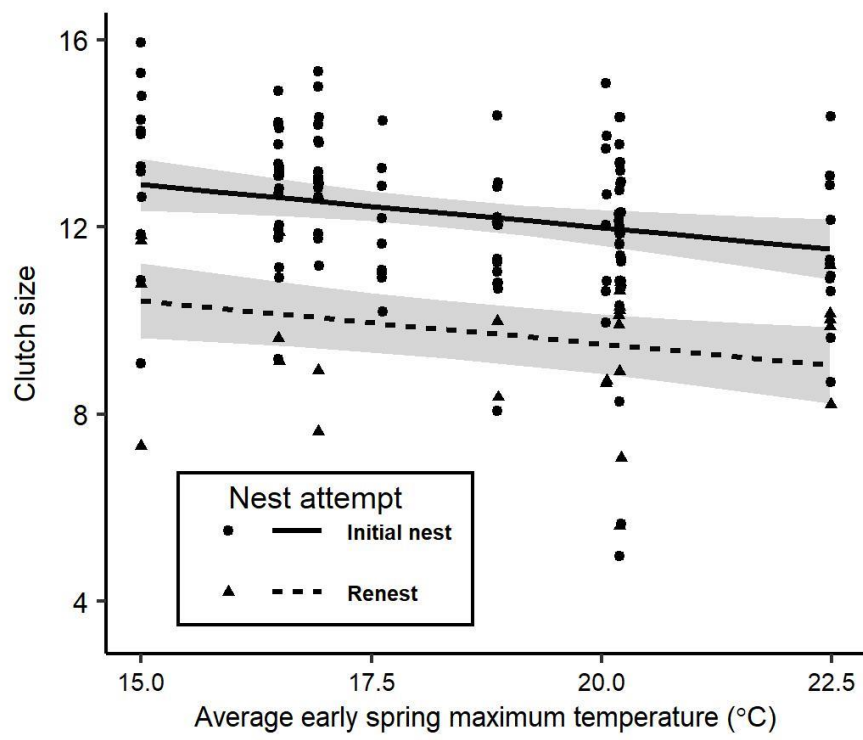


Figure 3.3



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APPENDICES

APPENDIX A

Table A1. AICc table comparing models assessing the influence of activity period and reproductive status (brooding vs nonbrooding) on vegetation characteristics at locations used by greater prairie-chickens throughout the day in Osage County, Oklahoma in 2018 and 2019.

GRASS

	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Sample Period+Year	6	19218.05	0	0.71	0.71	-9603.01
Sample Period*Reproductive Status+year	8	19219.94	1.88	0.28	0.98	-9601.94
Reproductive Status+Year	6	19227.31	9.25	0.01	0.99	-9607.63
Sample Period*Year	7	19227.68	9.63	0.01	0.99	-9606.82
Sample Period	5	19228.03	9.97	0	1	-9609
Reproductive Status	5	19235.06	17	0	1	-9612.51
Null	4	19237.41	19.36	0	1	-9614.7

FORB

Null	4	17762.52	0	0.3	0.3	-8877.25
Reproductive Status+year	6	17762.64	0.12	0.28	0.58	-8875.3
Reproductive Status	5	17763.34	0.82	0.2	0.78	-8876.66
Sample Period	5	17764.48	1.96	0.11	0.89	-8877.23
Sample Period+year	6	17766.49	3.97	0.04	0.93	-8877.23
Sample Period*Reproductive Status+year	8	17766.52	4	0.04	0.97	-8875.23
Sample Period*Reproductive Status	7	17767.23	4.71	0.03	1	-8876.59

LITTER

Sample Period+year	6	15560.67	0	0.44	0.44	-7774.32
Reproductive Status+year	6	15560.87	0.2	0.4	0.84	-7774.42
Sample Period*Reproductive Status+year	8	15564	3.32	0.08	0.92	-7773.97
Reproductive Status	5	15564.6	3.93	0.06	0.98	-7777.29
Sample Period*Reproductive Status	7	15567.72	7.05	0.01	1	-7776.83
Null	4	15570.57	9.9	0	1	-7781.28
Sample Period	5	15572.23	11.55	0	1	-7781.1

Table A.1 Continued

SERICIA

Sample Period+year	6	17233.75	0	0.44	0.44	-8610.85
Reproductive Status+year	6	17234.51	0.76	0.3	0.74	-8611.24
Sample Period*Reproductive Status+year	8	17236.13	2.39	0.13	0.88	-8610.03
Reproductive Status	5	17237.07	3.32	0.08	0.96	-8613.52
Sample Period*Reproductive Status	7	17238.69	4.94	0.04	1	-8612.32
Null	4	17247.86	14.11	0	1	-8619.92
Sample Period	5	17249.02	15.27	0	1	-8619.5

SHRUB

Null	4	11233.31	0	0.31	0.31	-5612.65
Reproductive Status	5	11233.92	0.61	0.23	0.53	-5611.95
Sample Period*Reproductive Status	7	11235.05	1.74	0.13	0.66	-5610.5
Sample Period	5	11235.14	1.83	0.12	0.79	-5612.56
Reproductive Status+year	6	11235.9	2.59	0.08	0.87	-5611.93
Sample Period+year	6	11235.98	2.67	0.08	0.95	-5611.97
Sample Period*Reproductive Status+year	8	11237.03	3.72	0.05	1	-5610.48

BARE GROUND

Sample Period+year	6	19477.17	0	0.76	0.76	-9732.57
Sample Period*Reproductive Status+year	8	19480.95	3.78	0.11	0.87	-9732.44
Sample Period*Reproductive Status	7	19480.99	3.82	0.11	0.99	-9733.47
Sample Period	5	19485.52	8.34	0.01	1	-9737.75
Reproductive Status+year	6	19489.88	12.7	0	1	-9738.92
Reproductive Status	5	19489.92	12.75	0	1	-9739.95
Null	4	19496.42	19.25	0	1	-9744.2

LITTER DEPTH

Null	4	8680.57	0	0.28	0.28	-4336.28
Sample Period	5	8681.02	0.45	0.22	0.51	-4335.5
Sample Period+year	6	8681.78	1.21	0.15	0.66	-4334.87
Reproductive Status	5	8682.35	1.78	0.12	0.77	-4336.16
Reproductive Status+year	6	8682.64	2.06	0.1	0.87	-4335.3
Sample Period*Reproductive Status	7	8683.42	2.85	0.07	0.94	-4334.69
Sample Period*Reproductive Status+year	8	8683.72	3.14	0.06	1	-4333.83

VEGETATION HEIGHT

Null	4	18067.18	0	0.37	0.37	-9029.58
Sample Period	5	18068.51	1.33	0.19	0.56	-9029.24
Reproductive Status	5	18068.76	1.59	0.17	0.72	-9029.37
Reproductive Status+year	6	18069.34	2.16	0.12	0.85	-9028.65
Sample Period+year	6	18070.51	3.33	0.07	0.92	-9029.24
Sample Period*Reproductive Status+only	7	18071.26	4.08	0.05	0.96	-9028.6

Sample Period*Reproductive Status+year	8	18071.84	4.66	0.04	1	-9027.89
VOR						
Sample Period	5	16105.63	0	0.45	0.45	-8047.8
interaction	7	16107.14	1.52	0.21	0.66	-8046.55
Sample Period+year	6	16107.32	1.69	0.19	0.86	-8047.64
Sample Period*Reproductive Status+year	8	16108.8	3.18	0.09	0.95	-8046.37
Null	4	16111.43	5.8	0.02	0.98	-8051.71
Reproductive Status	5	16112.31	6.68	0.02	0.99	-8051.14
Reproductive Status+year	6	16113.96	8.34	0.01	1	-8050.96

APPENDIX B

Table B1. Summary of all linear mixed effects models tested to investigate vegetation at active and refuge prairie-chicken locations and random landscape locations in patches 0-12 months post fire in Osage County, Oklahoma in 2018 and 2019.

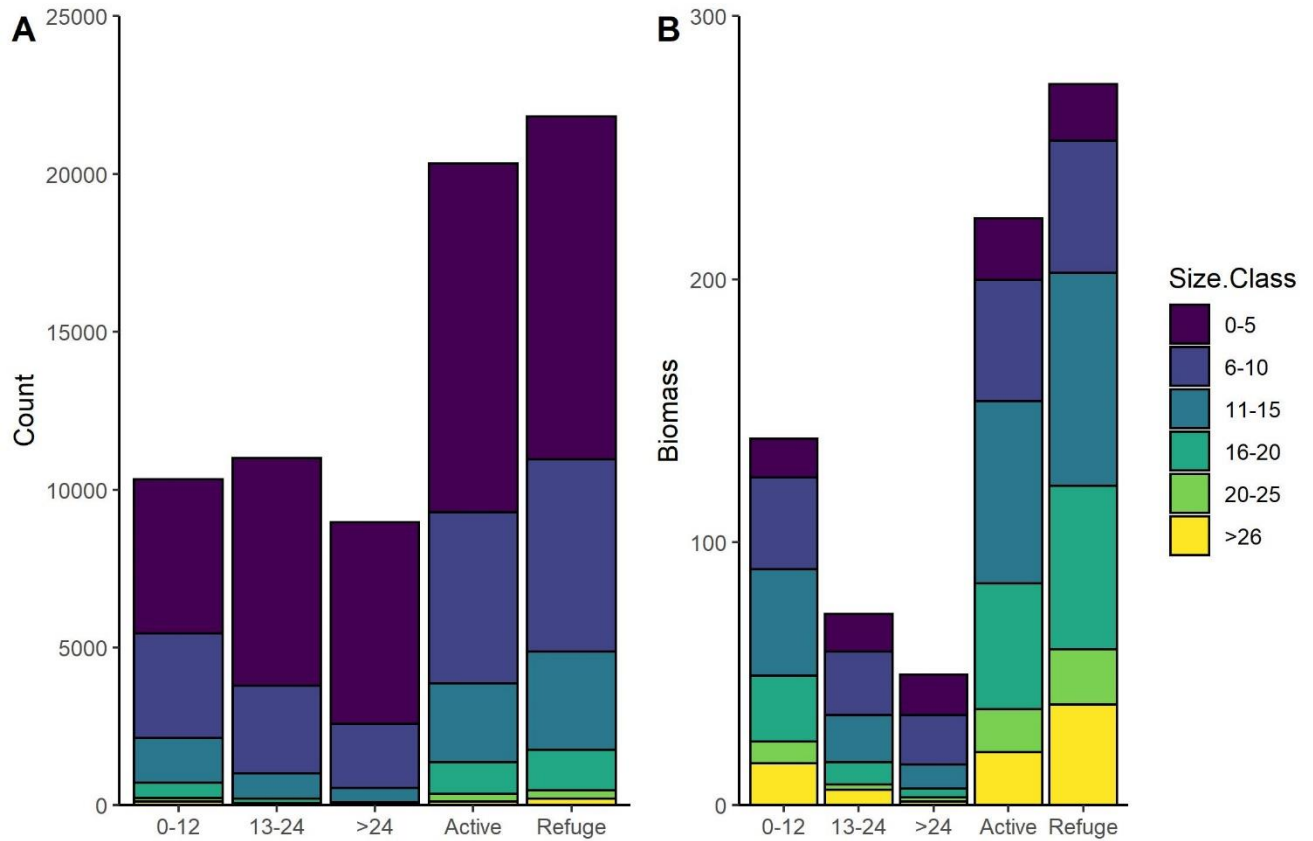
Vegetation Measurement	Variable	df	F-statistic	p-value
Grass	(Intercept)	2719	753.3	<.0001
	Location Type	253	6.305	0.0021
	year	83	12.1	0.0008
Forb	(Intercept)	2719	337.5	<.0001
	Location Type	253	0.61	0.5394
	year	83	0.40	0.5276
Litter	(Intercept)	2719	181.0	<.0001
	Location Type	253	1.1	0.3337
	year	83	14.1	0.0003
Serecia	(Intercept)	2719	59.9	<.0001
	Location Type	253	0.85	0.4271
	year	83	20.5	<.0001
Shrub	(Intercept)	2719	13.08	0.0003
	Location Type	253	0.14	0.8632
	year	83	0.31	0.5743
Bare Ground	(Intercept)	2719	733.1	<.0001
	Location Type	253	11.02	<.0001
	year	83	13.51	4.00E-04
Litter Depth	(Intercept)	2719	50.9	<.0001
	Location Type	253	2.6	0.076
	year	83	1.74	0.1896
Vegetation Height	(Intercept)	2719	2194	<.0001
	Location Type	253	2.1	0.1255
	year	83	0.03	0.8599
VOR	(Intercept)	2719	2032.1	<.0001
	Location Type	253	7.23	0.0009
	year	83	0.79	0.3742

Table B2. Summary of all linear mixed effects models tested to investigate abundance and biomass of invertebrates at active and refuge prairie-chicken locations and random landscape locations in patches 0-12 month, 13-24 months and >24 months post fire in Osage County, Oklahoma in 2018 and 2019.

Response Variable	Predictor Variable	Estimate	SE	df	F-statistic	p-value
Abundance (All Invertebrates Orders)	Location Type			379	7.6	<.0001
	0-12 months post fire	4.59	0.10			
	13-24 months post fire	0.07	0.13			
	> 24 months post fire	0.04	0.13			
	Active	0.39	0.11			
	Refuge	0.51	0.11			
	Year	-0.11	0.08	127	1.8	0.18
	Sample Period	0.02	0.07	379	0.31	0.57
Abundance (Orthoptera Only)	Location Type			379	7.6	<0.0001
	0-12 months post fire	4.59	0.10			
	13-24 months post fire	0.07	0.13			
	> 24 months post fire	0.04	0.13			
	Active	0.39	0.11			
	Refuge	0.51	0.11			
	Year	-0.11	0.08	127	104.7	<0.0001
	Sample Period	-0.23	0.12	379	0.5	0.51
Biomass (All Invertebrates Orders)	Location Type			379	8.9	<0.0001
	0-12 months post fire	0.34	0.17			
	13-24 months post fire	-0.47	0.23			
	> 24 months post fire	-0.69	0.23			
	Active	0.31	0.19			
	Refuge	0.45	0.19			
	Year	-1.22	0.14	127	80.8	<0.0001
	Sample Period	0.06	0.04	379	2.6	0.11
Biomass (Orthoptera Only)	Location Type			379	10.49	<0.0001
	0-12 months post fire	0.34	0.17			
	13-24 months post fire	-0.47	0.23			
	> 24 months post fire	-0.69	0.23			
	Active	0.31	0.19			
	Refuge	0.45	0.19			
	Year	-1.22	0.14	127	90.29	<0.0001
	Sample Period	-0.12	0.13	379	0.45	0.50

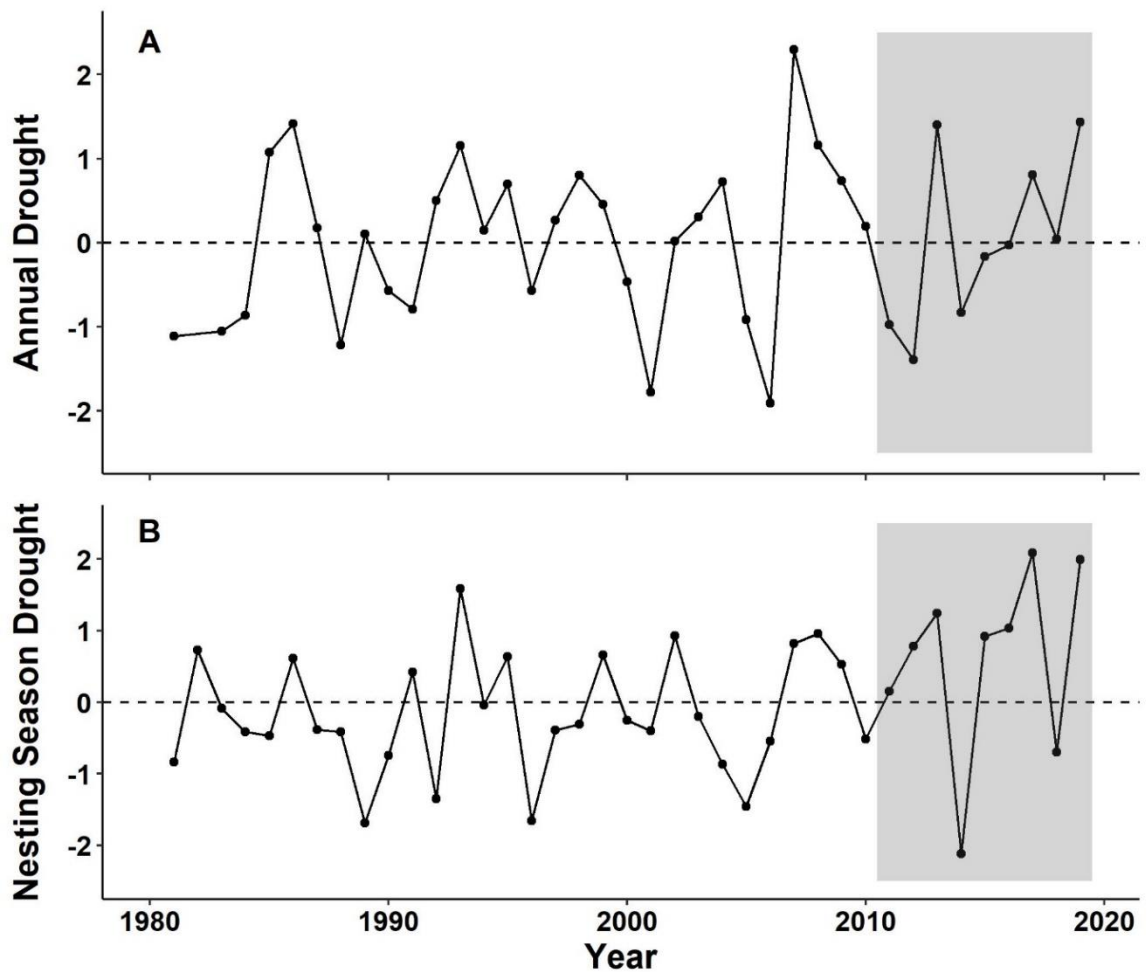
APPENDIX C

Figure C1. Total A) number of invertebrates and B) biomass of invertebrate captured in each size class by sweep-net samples conducted at prairie-chicken active and refuge locations and random landscape locations in patches that are 0-12, 13-24, and > 24 months post fire in Osage County, Oklahoma, USA in 2018 and 2019. Invertebrate sizes were measured in millimeters and biomass was measured in grams.



APPENDIX D

Figure D1. Drought conditions for the A) entire year (January to December) and B) the greater prairie-chicken nesting season (April to June) from 1981 to 2019 in Osage County, Oklahoma. The grey box indicates the period for which Greater Prairie-Chicken nesting activity was monitored. Drought conditions were calculated using SPEI indices where positive values indicate wet periods and negative values indicate dry periods.



APPENDIX E

Table E1. AIC_c values for intermediate modeling stages comparing models describing the effects of time trends, characteristics of the nest and hen, drought, and daily weather variables on daily nest success for Greater Prairie-Chicken nests monitored in Osage County, Oklahoma between 2011 and 2019. Model development followed a multi-step process where we developed a base model from the nest age, time of season and hen nest characteristics variables, then assessed the importance of weather variables relative to this base model. For each step in the model building process we only considered modes that resulted in a > 2 AIC_c improvement over the best model from the previous step as being supported.

Model	<i>k</i>	AIC _c	ΔAIC _c	<i>w</i>	Deviance
<i>Step 1: Base Model Development</i>					
<i>Nest Hen Characteristics</i>					
Age + Time + Hen Age	5	898.8	0	0.4	890.8
Age + Time + Transmitter Type	5	900.1	1.35	0.2	892.1
Age + Time	4	900.4	1.7	0.17	894.4
Age + Time + Clutch Size		902.10	1.98	0.10	894.08
Age + Time + Nest Attempt		902.18	2.06	0.09	894.17
Age + Time + Time Since Fire		902.27	2.15	0.09	894.26
<i>Step 2: Drought Variable Selection</i>					
<i>Drought Conditions</i>					
Age + Time + Nesting Season Drought	6	892.94	0.00	0.92	884.93
Age + Time	5	900.44	7.50	0.02	894.43
Age + Time + Preceding Summer Drought	6	900.57	7.63	0.02	892.56
Age + Time + Year-long Drought	6	901.58	8.64	0.01	893.57
Age + Time + Six-month Drought	6	901.98	9.04	0.01	893.97
Age + Time + Early Spring Drought	6	902.08	9.14	0.01	894.07
<i>Step 3: Daily Weather Variables</i>					
<i>Precipitation</i>					
Age + Time + Nesting Season Drought + Extreme Rainfall	7	885.99	0.00	0.44	873.96
Age + Time + Nesting Season Drought * Extreme Rainfall	8	887.35	1.36	0.22	877.33
Age + Time + Nesting Season Drought + Daily Rainfall	7	888.17	2.18	0.15	878.15
Age + Time + Nesting Season Drought * Daily Rainfall	8	889.17	3.18	0.09	877.14
Age + Time + Nesting Season Drought	6	892.94	6.95	0.01	884.93

Table E1. Continued

Daily Temperature

Age + Time + Nesting Season Drought * Maximum Temperature	8	888.78	0.00	0.40	876.75
Age + Time + Nesting Season Drought * Average Temperature	8	889.48	0.70	0.28	877.45
Age + Time + Nesting Season Drought * Minimum Temperature	8	892.18	3.40	0.07	880.15
Age + Time + Nesting Season Drought	6	892.94	4.16	0.05	884.93
Age + Time + Nesting Season Drought + Average Temperature	7	894.06	5.29	0.03	884.05
Age + Time + Nesting Season Drought + Maximum Temperature	7	894.24	5.46	0.03	884.22
Age + Time + Nesting Season Drought + Minimum Temperature	7	894.71	5.93	0.02	884.69

Table E2. AICc values for intermediate modeling stages comparing models describing the effects of characteristics of the nest and hen, drought, and weather during the two months prior to nesting on nest incubation start date for Greater Prairie-Chicken nests monitored in Osage County, Oklahoma between 2011 and 2019. For each variable set, only the model that resulted in a > 2 AICc change in model fit over the best model from the previous step were considered supported. k indicates the number of parameters, w indicates the model weight within a variable set, and LL is the $-\log(\text{likelihood})$.

Model	k	AICc	Δ AICc	w	LL
<i>Step 1: Nest Hen Characteristics</i>					
Nest Attempt	3	1185.58	0	0.99	-589.71
Clutch Size	3	1194.87	9.29	0.01	-594.35
Time Since Fire	3	1277.91	92.33	0	-635.87
Intercept Only	2	1308.79	123.21	0	-652.36
Hen Age	3	1309.27	123.69	0	-651.56
<i>Step 2: Drought Conditions</i>					
Nest Attempt + Year Long Drought	4	1159.54	0	0.99	-575.64
Nest Attempt + Early Spring Drought	4	1169.48	9.94	0.01	-580.61
Nest Attempt + Preceding Summer Drought	4	1171.22	11.69	0	-581.48
Nest Attempt + Six-Month Drought	4	1173.59	14.06	0	-582.66
Nest Attempt	3	1185.58	26.04	0	-589.71
Nest Attempt + Preceding Winter Drought	4	1187.19	27.65	0	-589.46
<i>Step 3: Early Spring Conditions</i>					
Nest Attempt + Year Long Drought + Average Daily Mean Temperature	5	1154.31	0	0.26	-571.96
Nest Attempt + Year Long Drought + Average Daily Maximum Temperature	5	1154.72	0.41	0.21	-572.16
Nest Attempt + Year Long Drought + Average Daily Minimum Temperature	5	1155.55	1.24	0.14	-572.57
Nest Attempt + Year Long Drought * Average Daily Temperature	6	1156.33	2.02	0.09	-571.88
Nest Attempt + Year Long Drought * Average Daily Maximum Temperature	6	1156.79	2.48	0.07	-572.11
Nest Attempt + Year Long Drought * Average Daily Minimum Temperature	6	1157.49	3.18	0.05	-572.46
Nest Attempt + Year Long Drought	4	1159.54	5.23	0.02	-575.64
Nest Attempt + Year Long Drought + Total Precipitation	5	1160.56	6.25	0.01	-575.08
Nest Attempt + Year Long Drought * Total Precipitation	6	1162.38	8.07	0	-574.91

Table E3. AICc values for intermediate modeling stages comparing models describing the effects of characteristics of the nest and hen, drought, and weather during the two months prior to nesting on nest incubation start date for Greater Prairie-Chicken nests monitored in Osage County, Oklahoma between 2011 and 2019. For each variable set, only the model that resulted in a > 2 AICc change in model fit over the best model from the previous step were considered supported. k indicates the number of parameters, w indicates the model weight within a variable set, and LL is the $-\log(\text{likelihood})$.

Model	k	AICc	Δ AICc	w	LL
<i>Step 1: Nest Hen Characteristics</i>					
Nest Attempt	3	618.06	0	0.99	-305.95
Incubation Start Date	3	597.35	10.53	0.01	-295.59
Time Since Fire	3	611.92	25.1	0	-302.88
Intercept Only	2	630.15	43.33	0	-313.03
Hen Age	3	632.12	45.3	0	-312.97
<i>Step 2: Drought Conditions</i>					
Nest Attempt + Year Long Drought	4	611.57	0	0.42	-301.15
Nest Attempt + Six-month Drought	4	611.01	0.44	0.34	-301.37
Nest Attempt + Early Spring Drought	4	611.96	1.39	0.21	-301.85
Nest Attempt + Preceding Winter Drought	4	617.53	6.95	0.01	-304.63
Nest Attempt + Preceding Summer Drought	4	618.06	7.48	0.01	-304.89
Nest Attempt	3	618.06	7.49	0.01	-305.95
<i>Step 3: Early Spring Conditions (final model set)</i>					
Nest Attempt + Year Long Drought + Mean Daily Maximum Temperature	5	605.59	0	0.25	-297.6
Nest Attempt + Year Long Drought + Mean Daily Average Temperature	5	606.81	1.22	0.14	-298.2
Nest Attempt + Six-month Drought * Mean Daily Maximum Temperature	6	607.11	1.52	0.12	-297.27
Nest Attempt + Six-month Drought + Mean Daily Maximum Temperature	5	607.56	1.97	0.09	-298.58
Nest Attempt + Year Long Drought * Mean Daily Maximum Temperature	6	607.73	2.13	0.09	-297.58
Nest Attempt + Year Long Drought + Mean Daily Average Temperature	6	608.63	3.03	0.06	-298.03
Nest Attempt + Year Long Drought + Mean Daily Minimum Temperature	5	608.76	3.16	0.05	-299.18
Nest Attempt + Six-month Drought + Mean Daily Average Temperature	5	609.03	3.44	0.05	-299.31
Nest Attempt + Six-month Drought * Mean Daily Average Temperature	6	609.94	4.34	0.03	-298.69
Nest Attempt + Year Long Drought + Mean Daily Minimum Temperature	6	610.08	4.48	0.03	-298.75
Nest Attempt + Year Long Drought	4	610.57	4.98	0.02	-301.15
Nest Attempt + Year Long Drought + Total Rainfall Accumulation	5	610.79	5.19	0.02	-300.19
Nest Attempt + Six-month Drought	4	611.01	5.42	0.02	-301.37
Nest Attempt + Six-month Drought + Mean Daily Minimum Temperature	5	611.42	5.83	0.01	-300.51
Nest Attempt + Six-month Drought * Total Rainfall Accumulation	6	611.85	6.25	0.01	-299.64
Nest Attempt + Six-month Drought + Total Rainfall Accumulation	5	612.84	7.25	0.01	-301.22
Nest Attempt + Six-month Drought + Mean Daily Minimum Temperature	6	613.07	7.47	0.01	-300.25
Nest Attempt + Six-month Drought + Total Rainfall Accumulation	6	615	9.4	0	-301.21

VITA

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Doctor of Philosophy

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Londe D.W., R.D. Elmore, C.A Davis, S.D. Fuhlendorf, B. Luttbeg, T. Hovick, and J. Rutledge. 2020. Weather influences multiple reproductive components of Greater Prairie-Chickens. *Journal of Wildlife Management*.

Londe D.W., R.D. Elmore, C.A Davis, S.D. Fuhlendorf, B. Luttbeg, T. Hovick and J. Rutledge. *In review*. Fine-scale habitat selection moderates trade-offs between food availability and temperature in a ground-dwelling grouse. *Behavioral Ecology*.