

RESTORED HETEROGENEITY AS A
CONSERVATION STRATEGY FOR GRASSLAND
BIRDS

By

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CONSERVATION STRATEGY FOR GRASSLAND
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Abstract: Grasslands are inherently dynamic in space and time evolving with frequent disturbance from fire and herbivores. Throughout much of the world, grasslands have been converted and fragmented and many remaining grasslands have become homogenous as a consequence of human actions. As a result, ecosystem function has declined and biodiversity loss has led to decreased ecological services. Of particular concern are highly imperiled grassland birds which have experienced greater population declines than any other habitat associated guild of birds in North America. Conservation efforts that restore heterogeneity to grasslands through the re-coupling of fire and grazing may be an effective strategy for stabilizing or increasing grassland bird populations. We examined Greater Prairie-Chicken (*Tympanuchus cupido*) ecology, breeding bird community diversity and stability, and non-breeding bird community diversity and patch occupancy in tallgrass prairie with restored structural and compositional heterogeneity. We found that Greater Prairie-Chickens selected for patches with greater time since fire and grazing and that taller vegetation increased nest survival. Additionally, nests that survived were in cooler environments and prairie-chickens displayed fine scale thermal habitat selection as nest sites were nearly 4°C cooler than micro-sites within 2 meters of nests. We found that heterogeneity increased breeding bird community diversity and that increased heterogeneity resulted in greater community stability over time. Finally, non-breeding bird community diversity increased as a result of structural heterogeneity and occupancy modeling revealed that certain species selected for varying patches along a disturbance gradient (i.e, recently disturbed to relatively undisturbed) that resulted from fire and grazing dependent heterogeneity. Our findings add to a growing body of literature supporting the use of fire and grazing to create a shifting grassland mosaic that increases vegetation structural and compositional heterogeneity and maximizes native biodiversity within rangeland ecosystems through the conservation of natural patterns and processes. Additionally, these data provide evidence that variation in grassland structure resulting from the fire-grazing interaction may be important in moderating thermal environments and highlights the complex and interactive effects of restored ecological processes on ecosystems. We recommend future management efforts in rangelands focus on restored disturbance process to increase heterogeneity and improve grassland bird conservation.

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CHAPTER I

Landscapes as a Moderator of Thermal Extremes: A Case Study from an Imperiled Grouse

Abstract

The impacts of climate driven change on ecosystem processes and biodiversity are pervasive and still not fully understood. Biodiversity loss, range shifts, and phenological mismatches are all issues associated with a changing climate that are having significant impacts on individuals and ecosystems alike. Investigating and identifying effective management strategies that can conserve vulnerable species should be the focus of current and future climate change research. We investigated thermal properties of habitat for an imperiled grouse (Greater Prairie-chicken; *Tympanuchus cupido*) in tallgrass prairie characterized by heterogeneous fire and grazing (the fire-grazing interaction). We examined operative temperature at varying scales relevant to grouse and used historic and forecasted climate data to estimate thermal stress during nesting activities. We found that heterogeneous grasslands have high thermal variability with operative temperature ranging as much as 23°C across the landscape. Grouse exhibited strong selection for cooler thermal environments as nest sites were as much as 8°C cooler than the surrounding landscape, and fine-scale differences in thermal environments were nearly 4°C cooler than sites within 2 m of nests. Additionally, forecasted climate scenarios indicate grouse will experience 2-4 times the number of hours above thermal stress thresholds, emphasizing the need for informed conservation management. Overall, these data provide evidence that variation in grassland structure resulting from the fire-grazing interaction may be important in moderating thermal environments and highlights the complex and interactive effects of restored ecological processes on ecosystems.

Introduction

The impacts of climate driven change on ecosystems are widespread and pervasive (Parmesan and Yohe 2003). Changes in the environment have increased biodiversity loss, impacted range shifts, and created phenological mismatches (Thomas and Lennon 1999, Both and Visser 2005, Dawson et al. 2011). Of these, biodiversity loss is the least reversible form of global change, and has been observed recently in numerous taxonomic groups (Novacek and Cleland 2001, Dawson et al. 2011). In addition, extinction risks are predicted to rise through the next century in response to global climate change (Maclean and Wilson 2011). Understanding how species and populations respond to these changes is a problem for ecologists worldwide, and identifying and evaluating effective management strategies that can conserve vulnerable species should be a central tenant of global change research.

The importance of high temperature extremes in influencing species distribution and fitness has long been appreciated (Begon et al. 2006). Therefore, temperature regulation or amelioration of thermal extremes can be an important landscape function (Matala et al. 2013). Despite this, thermal ecology has received much less research focus than other facets of wildlife ecology. Limited evidence suggests that avian nest-site preferences are influenced by microclimatic conditions (Gloutney and Clarke 1997), and that nest temperature can have impacts on energy and water budgets of both avian parents and young (Dawson et al. 2005). Furthermore, research on Northern Bobwhites (*Colinus virginianus*) suggests that thermal stress can have suppressive effects on reproduction through shortened laying seasons and nest abandonment (Guthery et al. 2005). In fact, it has been hypothesized that a large portion of the annual variation in reproduction of gallinaceous birds is associated with annual variation in heat loads in the near-ground environment (Guthery et al. 2005). If thermal extremes increase as a result of climate change as most models predict, it is

likely that many species will confront a trade-off between predation threat and thermal stress (Gloutney and Clarke 1997).

In addition to the effects of climate change, grassland species have faced numerous threats to conservation and biodiversity, primarily resulting from row crop agriculture and livestock production (Hoekstra et al. 2005). The tallgrass prairies of North America are no exception and are frequently labeled as endangered and a high conservation priority (Samson and Knopf 1996). These ecosystems are characterized by two major disturbances, fire and grazing, which drive and shape ecosystem structure and function (Collins and Wallace 1990, Anderson 2006). Many of the wild fauna within tallgrass prairies require landscapes with varied vertical structure and resources for food availability, predator avoidance, and thermoregulation, all of which will be affected by fire and grazing animals. Judging by the precipitous decline of many grassland birds, management throughout much of the remaining tallgrass prairie ecosystem has not adequately met these requirements (Robbins et al. 2002, Sauer et al. 2012). A contributing factor to this decline is likely the over-active disturbance regime that is used throughout much of the remaining tallgrass prairie in the central United States, which creates a homogeneous landscape void of patches with dense vegetation (Robbins et al. 2002). Not only does a lack of dense vegetation leave many grassland birds susceptible to predation (Robbins et al. 2002, Winter et al. 2005, Martin 2007), it reduces their benefits from wind protection, nocturnal radiative heat loss, and diurnal heat gain (Walsberg 1981).

Increased exposure resulting from reduced vertical vegetation structure can increase operative temperatures experienced by an organism (Guthery et al. 2005). Operative temperature incorporates energy flow between an animal and the environment and is primarily dependent upon radiation, air temperature, wind, and humidity (Dzialowski 2005). Collectively, these environmental variables determine the actual thermal environment experienced by an animal and influences their

body temperature, loss of moisture, and metabolic rate. From an organism's perspective it is important to recognize the difference between air temperature and operative temperature as air temperature alone may be misleading. For example, maintenance of metabolism accounts for 40-60% of daily energy expenditure in many avian species (Walsberg 1983) and thermal regimes of an animal's microhabitat potentially can have a strong influence on energetic costs (Swain 1991, Gabrielson et al. 1991, Martin 2001). Operative temperatures have become the standard tool for integrating environmental variables in an attempt to describe and understand the interaction between animals and their micro-environment and have been used for a wide variety of animal species (Hertz et al. 1994, Beaver et al. 1996, Forrester et al 1998, Fortin et al. 2000, O'Connor 2000).

Ecological processes that impact vegetation structure and composition are likely to affect microclimates for organisms inhabiting these systems (Matala et al. 2013). A conservation species of concern in the central United States that is potentially impacted by alterations in thermal regimes is the Greater Prairie-Chicken (*Tympanuchus cupido*; hereafter prairie-chicken). Prairie-chickens are an iconic tallgrass prairie species that have been referred to as indicator and umbrella species for this system, but they have undergone precipitous population declines over recent decades (Robbins et al. 2002, Pruett et al. 2009, McNew et al. 2012). The historic loss of tallgrass prairie for conversion to agriculture has undoubtedly contributed to declines (Johnsgard 1983), but more recently, a change in rangeland management resulting in landscape homogenization is blamed for their demise (Robbins et al. 2002). Annual biomass removal can result in decreased nest survival (McNew et al. 2012), but the synergistic effects of microclimate and predation are hard to separate and the role of microclimates has been explored very little. Improving our understanding of these potential trade-offs by properly quantifying thermal environments will improve future conservation efforts.

The shifting grassland mosaic that results from the interactive effects of fire and grazing across space and time creates a highly heterogeneous landscape that has potential to improve conservation of grassland organisms by minimizing effort to seek thermal refugia as climates continue to warm and become more extreme. Currently, most research and management focus on the main effects of fire and grazing independently, which decouples the inherent interactive effects of these disturbances. We believe assessing grasslands that are managed with interacting fire and grazing, similar to what tallgrass prairie developed under, will provide the best opportunity to understand thermal habitat selection and is critical for assessing habitat use in a way that will inform conservation of grasslands globally. Moreover, the prairie-chicken represents an ideal case study for examining thermal habitat use because of its conservation status, potential role as an indicator species, and evolutionary lineage from cold adapted ancestors thereby leaving it sensitive to rising global temperatures and thermal extremes (Johnsgard 1983, Pruett et al. 2009, PIF 2012). We hypothesized that prairie-chickens would seek habitats that lessened thermal stress during nesting and mid-day loafing relative to what was available in the surrounding landscape. Specifically, we investigated thermal environments at nest sites, loafing sites, and micro-sites relative to the broader landscape. This was done across a range of available vegetation patches that result from the spatio-temporal variation of the fire-grazing interaction. Additionally, we compared nest fates in relation to thermal environments, determined current thermal stress on breeding prairie-chickens, and projected future thermal stress on prairie-chickens using forecasted climate change scenarios.

Methods

Study area

We examined prairie-chicken habitat use at The Nature Conservancy's Tallgrass Prairie Preserve, located in northeast Oklahoma, USA. The preserve is a 16,000 ha area managed for biodiversity, and is located at southern most extent of the tallgrass prairie ecoregion and prairie-chickens range in North America. The plant community is primarily tallgrass prairie and dominant grasses include *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Panicum virgatum* L., and *Sorghastrum nutans* (L.) Nash (Allred et al. 2013). An on-site weather station records air temperature, solar radiation, and other weather parameters every five minutes (Brock et al. 1995).

The Tallgrass Prairie Preserve is managed in a way that restores the fire-grazing interaction, resulting in grassland structural heterogeneity (Hamilton 2007; Fuhlendorf et al. 2009). The structural heterogeneity becomes present through a series of positive and negative feedbacks as animals are allowed to select from areas that are recently burned and those that have greater time post fire (Archibald et al. 2005, Fuhlendorf et al. 2009, Allred et al. 2011). Nearly one-third of the preserve is burned on an annual basis and nearly 80% of fires are done in the dormant season with approximately 20% conducted during the growing season. The preserve has bison and cattle and both species are managed in a similar fashion with only perimeter fences present and animals are free to move within their respective units. Bison and cattle units are stocked with similar, moderate stocking rates (bison: 2.1 AUM/ha; cattle: 2.4 AUM/ha). Vegetation structure and composition at the preserve are driven by the interacting effects of fire and grazing and the corresponding out-of-phase succession from these disturbances (Fuhlendorf et al. 2006; Allred et al. 2011). For more detailed information on the management at the Tallgrass Prairie Preserve refer to Hamilton (2007).

Data Collection

We measured operative temperature to quantify the thermal environment of grouse and the tallgrass prairie landscape. To quantify thermal environments at the landscape scale, we recorded operative temperature by measuring air temperature inside the center of a black steel sphere (15 cm diameter) placed at ground level (Guthery et al. 2005, Allred et al. 2013). Sampling periods were weeklong and conducted twice during the breeding season (i.e., early May and mid-July) in 2011 and 2012. To capture spatial variation, we used three 50 m transects that varied in landscape features (e.g., time since fire, topography). Within each transect, two by two meter plots were established at 0, 25, and 50 m; operative temperature was recorded at every corner of each plot resulting in 12 sampling points per transect. Transects were moved daily during each sampling period to capture spatial variation and improve thermal landscape characterization (Allred et al. 2013).

We measured operative temperature at each nest site on the forecasted hatch date (i.e., known start of incubation plus 25 days) by placing one black sphere in the nest bowl and three spheres at random locations in the immediate area (<2 m) around the nest bowl. Operative temperature was recorded every five minutes for a 24 hour period at all 32 nests that were found and monitored during the course of this study. We used the forecasted hatch date to standardize deployment times and to prevent biasing samples by consistently measuring failed nests earlier than successful nests. We also recorded vegetation parameters such as grass, forb, bare ground, and litter coverage in a 0.5 m² quadrat centered over black spheres both at the nest bowl and the surrounding micro-sites. Additionally, we measured vegetation height and litter depth at each black sphere and took a measure of biomass structure at each nest using a Nudd's profile board (Nudds 1977, Guthery et al. 1981).

We collected thermal and vegetation data at prairie-chicken loafing sites during peak mid-day July temperatures in 2011 and 2012. We define loafing sites as areas occupied during the mid-day (i.e., 12-4 pm) by male or female prairie-chickens that were no longer nesting or with broods. We intentionally flushed birds from loafing sites and placed one black sphere in the location that was previously occupied by the bird (identified by depressed vegetation and/or feces). We also placed three spheres in the surrounding vegetation at a distance of 2 m in random directions as described for nest sampling. Black spheres were deployed for 24 hours and collected temperature data every five minutes. Vegetation measurements followed the same protocol described for nest sites.

Data analysis

We modeled operative temperature at prairie-chicken locations and across the landscape based on the interactive effects of air temperature and solar radiation. Both air temperature ($^{\circ}\text{C}$) and solar radiation (watts/m^2) were recorded every five minutes at an onsite Oklahoma Mesonet station (Brock et al. 1995). We limited our model to temperatures above 25°C to only examine thermal environments at warmer temperatures. Because operative temperatures were not all recorded on the same dates, we used the developed models to predict operative temperatures at prairie-chicken locations and across the landscape on the days that operative temperatures were measured at prairie-chicken nests and loafing sites. This modeled data was used when comparing operative temperatures and trends between prairie-chicken locations and across the landscape.

We used previously published thresholds to interpret and determine thermal stress experienced by prairie-chickens throughout the breeding season. To our knowledge this method has not been tested previously on prairie-chickens or any other grouse species, therefore we considered

thermal thresholds developed for Northern Bobwhites (Guthery et al. 2005). Research suggests that Northern Bobwhites begin to show signs of heat stress through gular fluttering near 31°C air temperature and that at an operative temperature of 39°C Northern Bobwhite become hyperthermic (i.e., individuals become physically incapable of heat dissipation; Guthery et al. 2005). We recognize that this does not represent the precise threshold at which prairie-chickens experience heat stress, but we feel it is a conservative number given the morphological and physiological differences between Northern Bobwhites and prairie-chickens and it represents the most rigorous examination of thermal stress on a Galliformes. Additionally, Northern Bobwhites and prairie-chickens overlap in most areas where prairie-chicken populations persist indicating that they do have exposure to similar abiotic factors and likely have some niche overlap. However, Northern Bobwhites have a more expansive range especially in southern regions of the United States, which is likely a result of their tolerance for warmer environments thereby emphasizing our point that the thresholds used herein are likely conservative and represent a best case scenario. Therefore, to qualitatively interpret thermal stress we modeled daily average operative temperature and compared hyperthermic (39°C operative temperature) levels across all sites. To get a more quantitative assessment of thermal stress we calculated the long term average (i.e., 1994-2012) air temperature during the breeding season (1 May-15 July) and summed the total hours per week that exceeded 31°C air temperature. We then used the increase in temperature predicted by the Hadley and the PCM high emissions scenario for the end of the century (i.e., 2080) to examine future thermal stress on breeding prairie-chickens. We chose the Hadley and the PCM models because they represent more liberal and conservative warming scenarios, respectively (<http://www.climatewizard.org> accessed 15 July, 2013).

Results

We found that heterogeneous grasslands have high thermal variability with operative temperature ranging as much as 23°C across the landscape when air temperatures are > 30°C (Fig. 1A), creating the opportunity for grouse and other organisms to seek thermal environments that maximize their chance for survival. As expected, operative temperatures in all environments increased linearly with air temperature, but the rate of increase varied among patches, micro-sites, and nests (Fig. 1B).

Modeled operative temperatures were cooler at nest sites than any other locations measured across the landscape (Fig. 1B), and all of our thermal models adequately explained the variation in operative temperature (Table 1). Moreover, modeled nest site environments were 4° C cooler than micro-sites within 2 m of the nest when air temperatures reached 38° C (Fig. 1C), and operative temperatures at nest sites had a narrower range and lower mean than micro-sites (Table 2). This difference between micro-sites and nests at such fine scales shows the high thermal variability within tallgrass prairie and implies that prairie-chickens are able to select for cooler, more moderate environments. Additionally, measurements of vegetation at nest sites and the micro-sites were similar for all parameters with the exception of vegetation height, which was significantly taller at nests than micro-sites ($F_{1,126} = 4.53, p < 0.05$) and suggests that shading could be driving operative temperatures at nest sites (Fig. 2). Furthermore, thermal environments were cooler at successful nests than failed nests (Fig. 1D), with successful nests being up to 6° C cooler at higher air temperatures. However, there were no statistical differences in vegetation height ($F_{1,29} = 0.84, p = 0.37$) or any of the other vegetation parameters measured at nests with different fates, possibly indicating that thermal environments at nests are influencing survival and not predator avoidance through nest concealment. Successful nests also had a more moderate rate of operative

temperature increase with air temperature (i.e., flatter slope) when compared to unsuccessful nests (Fig. 1D).

Examination of loafing data also revealed fine-scale selection for thermal environments with prairie-chicken mid-day loafing sites recorded at $\sim 3^{\circ}\text{C}$ cooler than the surrounding micro-sites when air temperatures reached 35°C (Fig. 3A). Furthermore, maximum operative temperature recorded at loafing sites reached 65.8°C while the mean maximum operative temperature at micro-sites was 72.44°C , and average hourly operative temperature at loafing sites was $\sim 5^{\circ}\text{C}$ cooler at peak daytime temperatures than micro-sites (Fig. 3B). Also, similar to vegetation parameters at nest sites, vegetation height was significantly taller at prairie-chicken loafing sites when compared to micro-sites within 2 m while all other vegetation parameters were similar ($F_{1,142} = 5.03$, $p < 0.05$).

Average hourly operative temperatures at nest sites were much cooler than other environments across the landscape (Fig. 4). In fact, during peak daytime heat nests have an operative temperature $3\text{--}6^{\circ}\text{C}$ cooler than the surrounding environment, and perhaps more importantly, nests only exceed an assumed hyperthermic threshold (i.e., 39°C operative temperature) for < 1 hour while other environments exceeded this threshold for > 4 hours (Fig. 4).

Modeling of long term, on-site temperature data (1994-2012) showed that during the warmest week of the breeding season prairie-chickens experience ~ 27 hours of temperatures exceeding 31°C . The addition of projected temperature increases using the PCM and Hadley high emissions scenarios for the end of the century suggested that prairie-chickens will experience 54 and 113 hours at temperatures $> 31^{\circ}\text{C}$, respectively (Fig. 5). If projected climate change scenarios are correct, prairie-chickens in the southern Great Plains will experience a 2-4 fold increase in the amount of thermal stress during peak summer temperatures than they have experienced over the last two decades.

Discussion

It has long been recognized that temperature plays a central role in ecology (Begon et al. 2006), yet research in this arena is lacking relative to other aspects of ecology. These results elevate our understanding of the importance of heterogeneity of thermal environments across multiple scales and demonstrate the importance of understanding habitat heterogeneity from a thermal perspective in the face of climate change. Moreover, they expose the thermal variability of tallgrass prairie with restored ecological processes, show that reproduction of imperiled grouse are correlated with thermal properties, and illustrate the complexity of thermal environments in plant communities that are often viewed as structurally simplistic (i.e., grasslands). Our findings may have profound implications when considered in the context of projected temperature increases resulting from climate change and the widespread management paradigm that focuses on uniform, moderate disturbance rather than a shifting mosaic comprised of patches with highly variable amounts of disturbance (Holocheck et al. 2004, Fuhlendorf et al. 2012). Furthermore, our findings indicate that thermal variation can occur at fine scales, but that thermal variation at multiple scales is maximized by varying focal disturbance across broad scales (Fig. 1A).

Maintaining structural variation for thermal refugia is going to be one of the most necessary landscape functions if native fauna are going to persist, and thermal refugia is only enabled by high local heterogeneity of the microclimate which allows the decoupling of local from regional environments (Dobrowski 2011, Keppell et al. 2012). A comparison of long term climatic data and projected temperatures showed a 2-4 fold increase in the number of hours exceeding suggested thermal stress levels (i.e., 31°C) during the hottest week of the breeding season (Fig. 5). This supports the claim that the importance of microclimate refugia will increase with climate change

(Suggitt et al. 2011), and emphasizes our need to understand thermal environments to improve conservation efforts. Maximizing sites for thermal refuge during extreme heat events will be necessary if grouse populations in southern regions of the United States are going to persist in light of climate projections.

This study demonstrates that habitat selection can be viewed through the lens of thermal environments and that landscapes function to moderate temperature regimes. As we hypothesized, prairie-chickens constructed nests in cooler environments relative to the surrounding landscape. It has been reported that egg temperatures $> 38^{\circ}\text{C}$ may kill embryos if exposed for prolonged periods and that the eggs of most species can withstand exposure up to 41°C for short intervals (Webb 1987). Therefore, at some level it is necessary for prairie-chickens to select nesting areas that minimize thermal loads if eggs are to maintain viability, and it appears that they are capable of doing this at fine spatial scales (i.e., within 2 m; Fig. 1C). Moreover, we found significantly taller vegetation around nest sites and nests that survived were in cooler environments than nests that failed to survive likely because amelioration of adverse environmental conditions on eggs, young, and incubating adults can greatly improve nesting success (Webb and King 1983, Walsberg 1985). Research from the southwestern United States found that ground nesting species declined by 12% following late summer heat waves and that ground-nesting species were more sensitive to thermal extremes than other avifauna (Albright et al. 2010). It has been hypothesized that increased temperatures result in higher predation rates because of increased activity in nest predators such as snakes (Morrison and Bolger 2002), or prolonged thermal stress may force incubating females to leave the nest site more frequently thereby increasing the opportunity for predators to detect nest locations.

Mid-day loafing sites of prairie-chickens were cooler than random sites within 2 m of prairie-chicken locations, and vegetation at prairie-chicken locations was taller than areas nearby. Northern Bobwhite showed similar hyperthermic avoidance behavior when selecting mid-day coverts in Texas by using areas of greater vegetation growth (Guthery et al. 2005), and Lesser Prairie Chickens (*Tympanuchus pallidicinctus*) in Oklahoma and New Mexico selected areas that were more exposed during cool seasons and less exposed during warm seasons, presumably to thermoregulate through more or less exposure to solar radiation (Larsson et al. 2013). Separating thermal habitat selection from predator avoidance behavior is highly confounded and complicated as it appears that areas of greater biomass are used for both (Guthery et al. 2005), but it is not unlikely that predator avoidance and hyperthermic avoidance behavior are acting in synergy and that management practices focused on biomass retention would benefit populations by improving conditions for both. Limited evidence from this study suggests that survival at nest sites was not driven by differences in vegetation parameters (i.e., all p-values > 0.05) between successful and unsuccessful nests, but there were significantly different thermal environments at nests that survived compared to those that did not, possibly indicating that thermal environments are impacting survival and not concealment from predators per se (Fig. 1D).

Our findings emphasize two main points. First, they stress the importance of managing for heterogeneous landscapes that create a broad range of thermal environments because the implications for ecological consequences of global climate change (Martin 2001). Increasing the range of available thermal environments allows organisms to select for areas that improve thermal regulation and afford energy for other metabolic processes (Gabrielson et al. 1991). By improving our understanding of how disturbances impact thermal environments we can improve conservation efforts. Second, our research emphasizes the need for more investigation of thermal environments, particularly the effects of focal disturbances that directly impact above ground biomass in

rangelands. A major focus of past research has operated under the assumption that biomass manipulations largely influence fauna as a result of predator avoidance (Guthery et al. 2005), and while this issue is largely confounded with thermal environments, we believe future research should emphasize the thermal aspect of ecology to determine the cues that fauna use in selection and how and when predator avoidance and thermal refugia act alone or in synergy to influence survival. Despite broadly recognizing the role of temperature (Begon et al. 2006), few studies actually investigate the role of temperature in determining habitat use or the dynamic interplay of thermal environments and natural disturbances. If we hope to conserve biodiversity as global changes become more extreme, it is necessary to take a proactive approach that maximizes species' opportunities for survival by recognizing a major role of landscapes is to function as a moderator of thermal extremes and it appears this is maximized by restoring ecological processes that create focal disturbance across broad scales.

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Table 1. Model fit, parameter estimates, and confidence intervals (parenthetically) describing thermal environments at nest sites, micro-sites (2 m), and landscape patches resulting from focal disturbance at the Tallgrass Prairie Preserve, Oklahoma, USA (2011-2012).

Location modeled	Parameters				Fit
	Intercept	T_{air}	S_{rad}	$T_{\text{air}} \times S_{\text{rad}}$	r^2
nest*	-2.90	1.01	0.01	0.00002	
	(-5.16, -0.63)	(0.92, 1.09)	(0.011, 0.018)	(-0.00010, 0.00014)	0.80
micro-site*	-3.30	1.02	0.02	0.00010	
	(-4.93, -1.66)	(0.96, 1.07)	(0.014, 0.019)	(0.000015, 0.00019)	0.79
landscape 0-11*	-12.69	1.44	0.04	-0.00078	
	(-13.53, -11.84)	(1.40, 1.46)	(0.039, 0.042)	(-0.00083, -0.00073)	0.89
landscape 12-23*	-9.17	1.29	0.03	-0.00023	
	(-10.13, -8.20)	(1.25, 1.32)	(0.024, 0.028)	(-0.00029, -0.00017)	0.87
landscape >24*	-3.62	1.08	0.01	0.00019	
	(-4.62, -2.60)	(1.04, 1.11)	(0.009, 0.013)	(0.00012, 0.00024)	0.85

* Indicates significance at a level of $p < 0.01$.

Table 2. Operative temperature recorded at Greater Prairie-chicken (*Tympanuchus cupido*) nest sites and micro-sites (2 m) at the Tallgrass Prairie Preserve, Oklahoma, USA from May-July in 2011 and 2012.

Location	mean (°C)	SE	range (°C)
micro 1	27.62	0.12	5.40 - 64.24
micro 2	28.17	0.12	6.62 - 65.79
micro 3	27.50	0.12	7.03 - 59.22
nest	26.64	0.10	7.03 - 57.24

Figure Legends

Figure 1. A) Modeled data showing range of operative temperatures that result when air temperatures are $\geq 25^{\circ}\text{C}$ in tallgrass prairie managed with interacting fire and grazing. B) Linear models of landscape patches resulting from time since focal disturbance (i.e., fire and grazing), micro-site, and nest operative temperatures using modeled data. C) Differences between nests and micro-sites within two meters of the nest bowl. Nests were nearly 4°C cooler at 36°C than the surrounding micro-sites. D) Linear models of successful and failed prairie-chicken nests at the Tallgrass Prairie Preserve, Oklahoma, USA (2011-2012). Successful nests experienced operative temperatures that were 6°C cooler at 36°C and had more moderate operative temperatures (i.e., flatter slope) than failed nests. Apparent survival trends were reported to show general relationships and because all nests were found at the onset of incubation by tracking marked individuals. Gray areas surrounding modeled lines represent 95% confidence intervals.

Figure 2. Vegetation characteristics (\pm SE) measured at nest sites and micro-sites at the Tallgrass Prairie Preserve, Oklahoma, USA (2011-2012).

Figure 3. A) Linear model of operative temperature as a function of air temperature at mid-July loafing sites and surrounding micro-sites of Greater Prairie-chickens. B) Average hourly operative temperature at loafing sites and the surrounding micro-sites during mid-July at the Tallgrass Prairie Preserve, Oklahoma, USA (2011-2012). Gray areas surrounding modeled lines represent 95% confidence intervals.

Figure 4. Average hourly daytime operative temperature for the landscape (separated as patches resulting from time since focal disturbance), micro-sites, and nests at the Tallgrass Prairie Preserve,

Oklahoma, USA (2011-2012). The dotted line represents a hyperthermic threshold (39°C) at which prairie grouse potentially become hyperthermic (i.e., physically incapable of dissipating heat) and must seek a cooler environment.

Figure 5. Thermal stress on incubating females measured as the number of hours/week that exceeds 31°C air temperature. Bars represent the long term mean temperatures from 1 May-15 July for 1994-2012 (\pm SE), and the projected stress on hens as determined by the high emissions end-of-century scenarios for the Hadley and PCM climate projection models. We used 31°C because it represents the best published estimate at which gallinaceous birds are reported to exhibit thermal stress (i.e., gular fluttering).

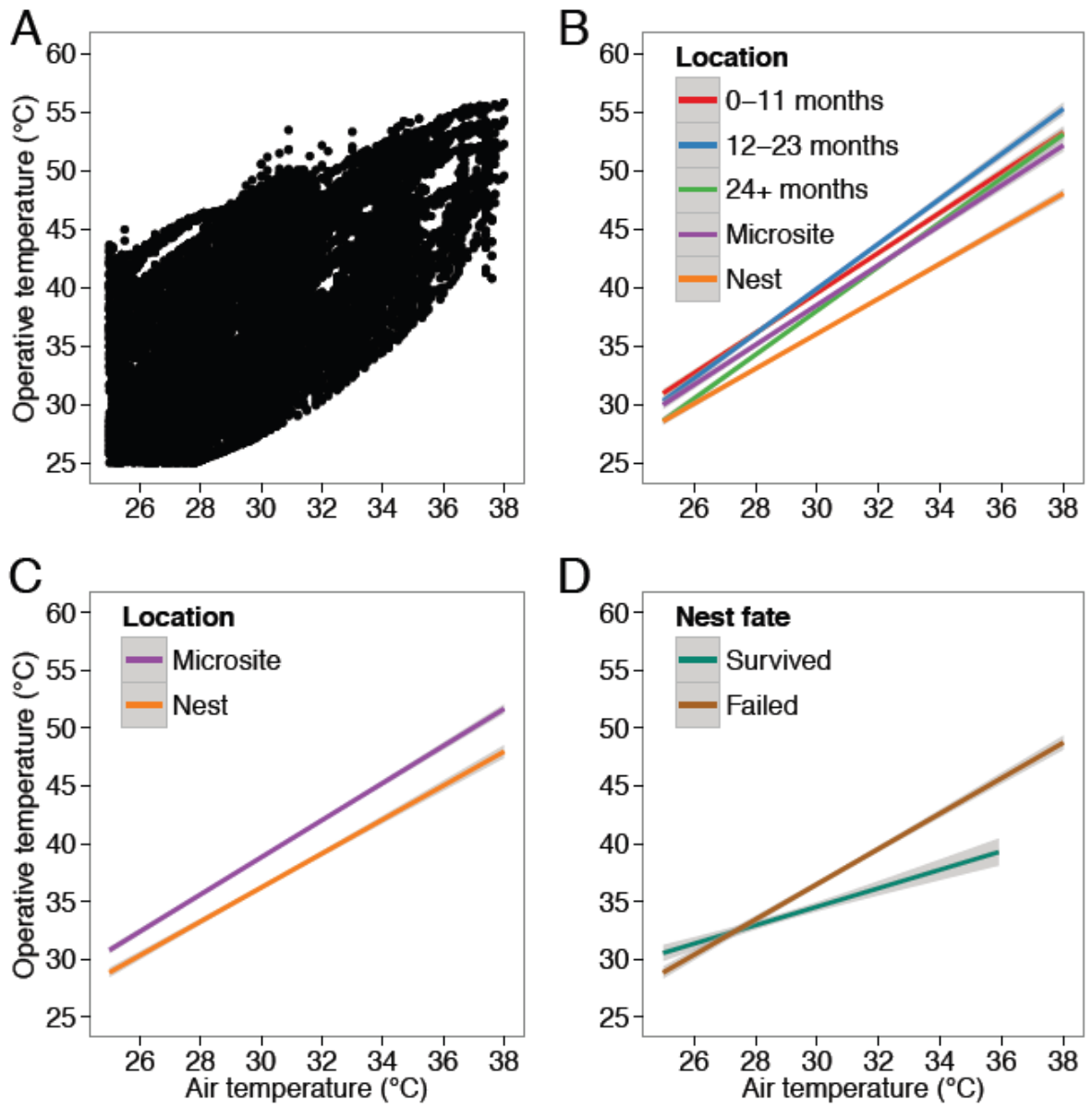


Figure 1.1.

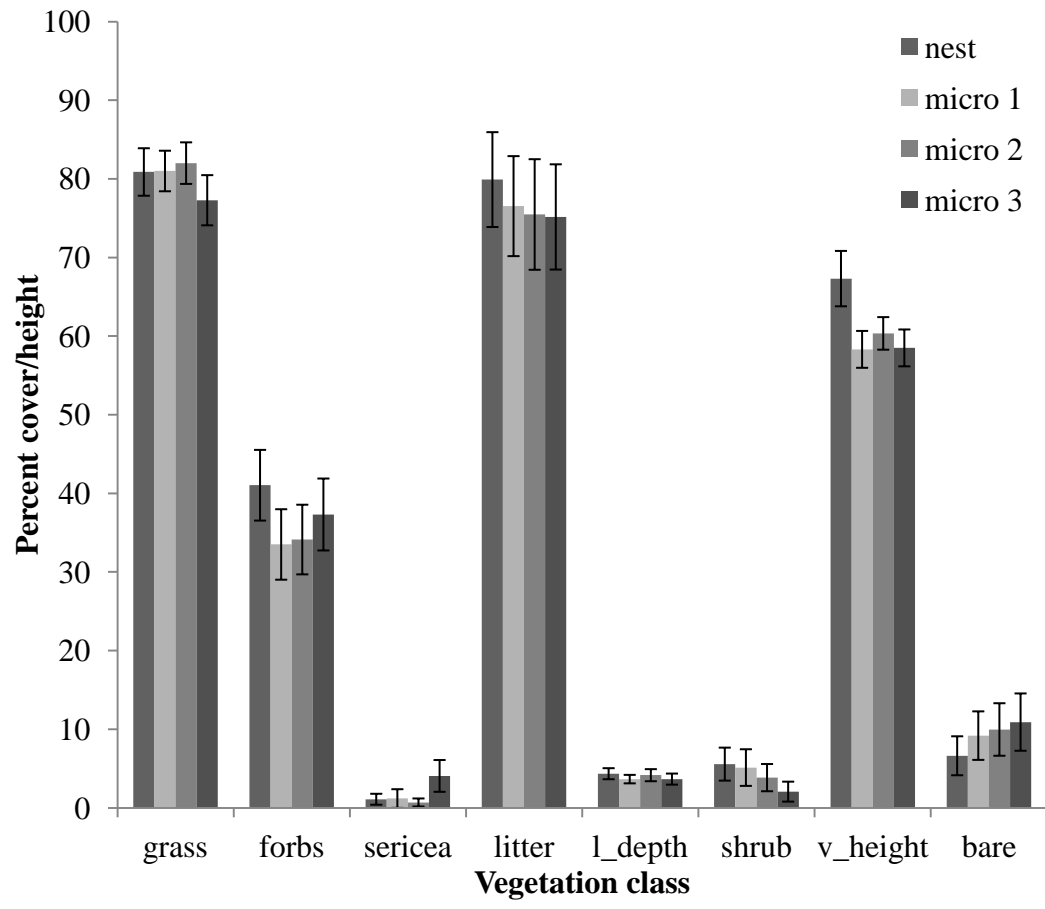


Figure 1.2.

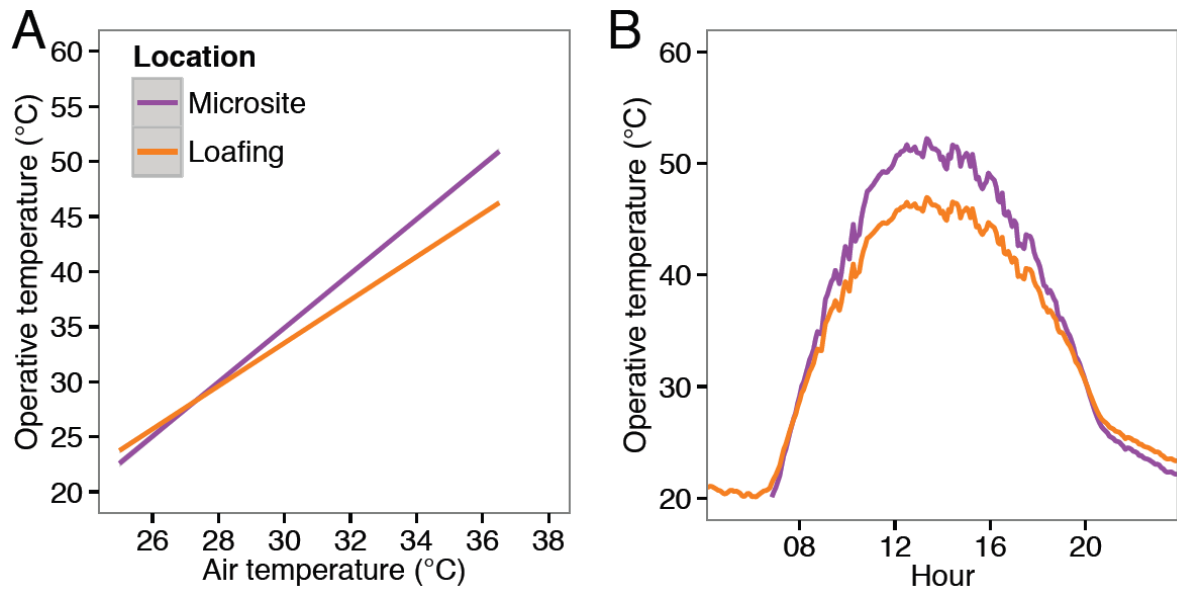


Figure 1.3.

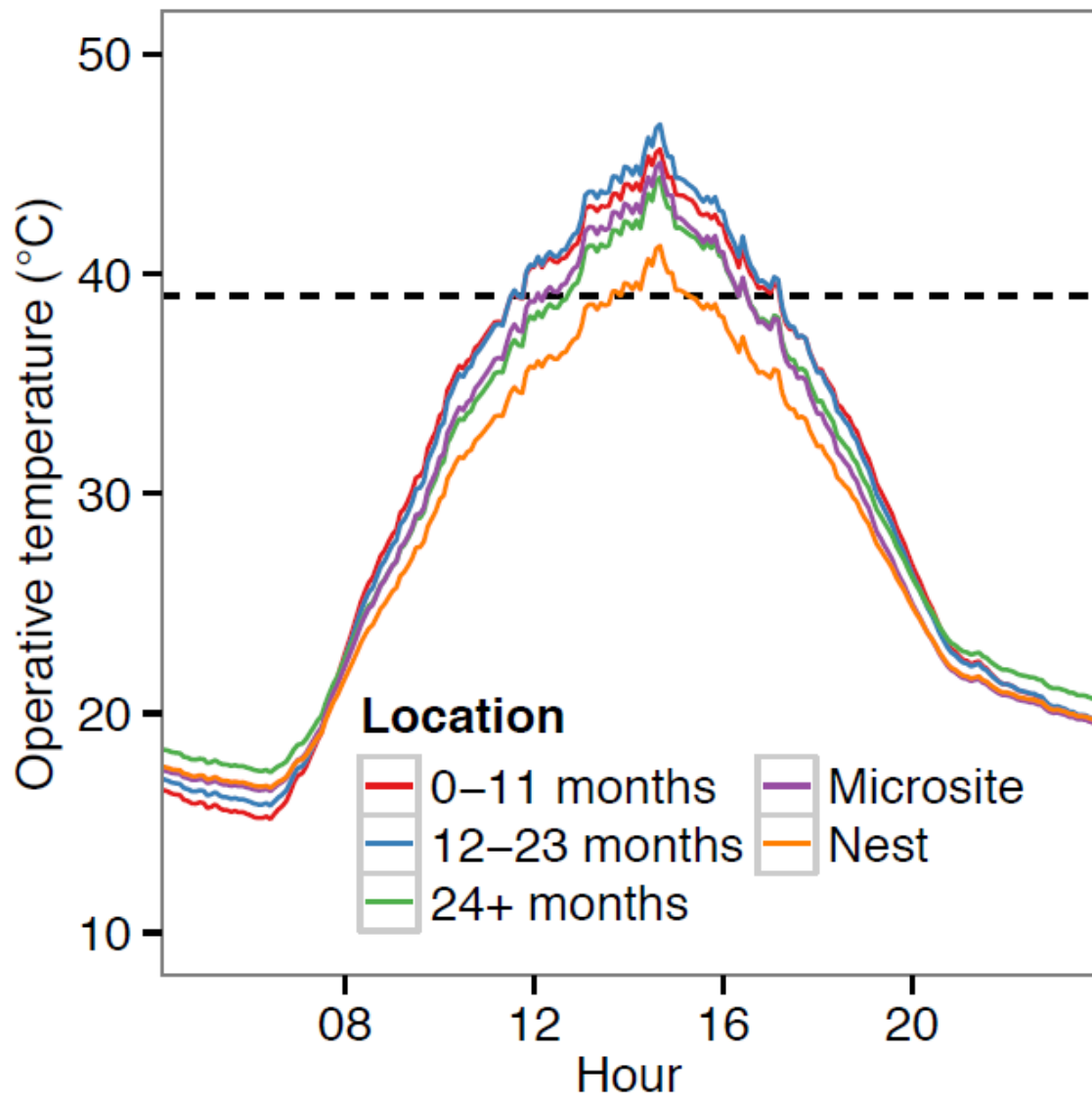


Figure 1.4.

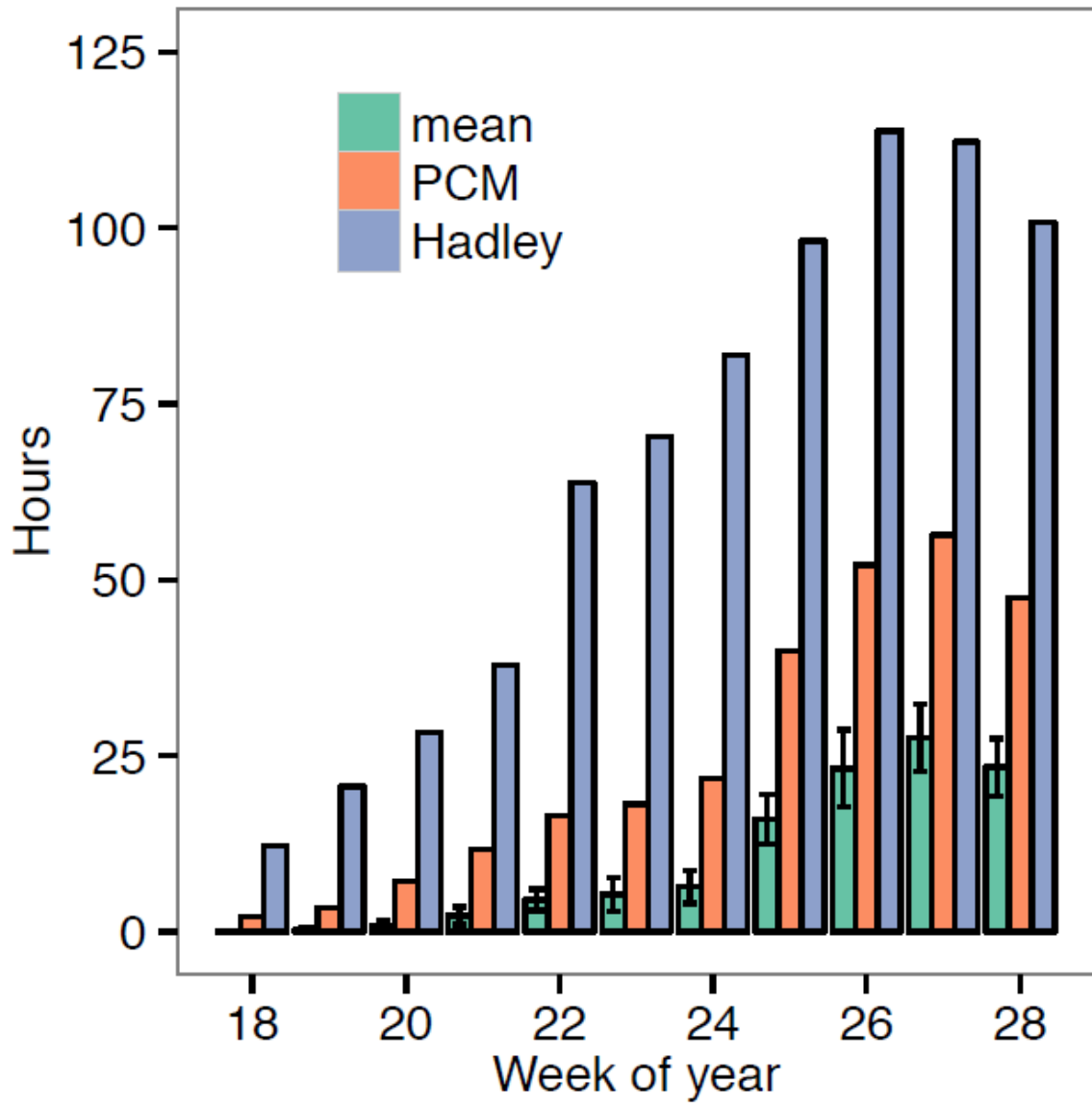


Figure 1.5.

CHAPTER II

Structural Heterogeneity Increases Diversity of Non-breeding Grassland Birds

Abstract

Grassland birds have experienced greater population declines than any other guild of birds in North America, and yet we know little about habitat use and the effects of management during their non-breeding period on wintering grounds. The paucity of information on wintering grassland birds limits our ability to develop effective conservation strategies. We investigated habitat use by the winter bird community in grasslands with restored heterogeneity resulting from the interactive effects of fire and grazing. We used 500 m line transects distributed across patches (i.e., <13, 13-24, and >24 months post disturbance) resulting from spring burning with growing season grazing (April-Sept) and quantified avian relative abundance, community structure, and probability of patch occupancy while accounting for imperfect detection. Grassland structure that resulted from the fire-grazing interaction created heterogeneity among patches that influenced avian habitat use during winter. Generalist birds such as the Savannah Sparrow (*Passerculus sandwichensis*) and meadowlarks (*Sturnella* spp.) were relatively common in all patch types while more specialized species such as the Smith's Longspur (*Calcarius pictus*) and Le Conte's Sparrow (*Ammodramus leconteii*) reached greatest abundance and probability of occupancy in the patches with the least and greatest time post disturbance, respectively. This research provides novel information on the response of wintering birds to restored ecological processes in grasslands and can improve efforts to create effective conservation strategies. Our findings add to a growing body of literature supporting the use of fire and grazing to create a shifting grassland mosaic that increases vegetation structural and compositional heterogeneity and maximizes native biodiversity within rangeland ecosystems through the conservation of natural patterns and processes.

Introduction

Grassland bird declines are a major conservation concern of the 21st century (Brennan and Kuvlesky 2005). Since the inception of the North American breeding bird survey, no other habitat-associated group of birds has undergone such drastic population declines (Sauer et al. 2012). While the historic loss of grasslands is undoubtedly a leading cause for grassland bird declines (Samson and Knopf 1996), it is likely that the cumulative effects of afforestation, mismanagement and intensification of production on rangelands, and increased fragmentation have acted in synergy to drive populations to their current low levels (Herkert 1994, Vickery et al. 1999, Brennan and Kuvlesky 2005). The impacts of these factors have typically been investigated using breeding birds, and data on non-breeding bird communities is generally lacking despite multiple claims that this is the period limiting avian populations (Wiens and Dyer 1975, Rappole and McDonald 1994, Peterjohn 2003). Grassland degradation in the southern United States may limit suitable wintering sites for many temperate grassland birds (Hunter 1990, Lymn and Temple 1991). The lack of data examining habitat use and survival of grassland birds during the non-breeding season limits our ability to apply effective conservation management (Herkert et al. 1996).

We must improve our knowledge of avian responses to management throughout the year to maximize conservation efforts for grassland birds. Grasslands are disturbance-dependent habitats that evolved with fire and grazing, which explains the affinity for certain grassland birds to inhabit specific patches that result from interacting fire and grazing disturbances (Knopf 1994, Hoekstra et al. 2005). Grasslands with fire and grazing still occurring in tandem typically apply these processes uniformly across the landscape, which results in homogenous vegetation structure and reduces grassland diversity (Robbins et al. 2002, Reinking

2005). This approach has been termed “management toward the middle” and reflects the intermediate disturbance model that has shaped rangeland management, but has failed to recognize the diverse needs of grassland organisms and the historically diverse structure of grasslands posited to have occurred pre-European settlement (Fuhlendorf and Engle 2001, Powell 2006, Fuhlendorf et al. 2012). Management aimed at uniform disturbance limits the amount of undisturbed patches across the landscape necessary for certain species life history traits and fulfills the habitat requirements of a limited suite of generalized bird species (Reinking 2005, Fuhlendorf et al. 2006, Powell 2008). The separation of the fire-grazing interaction can simplify rangeland communities and limit ecosystem structure and function (Fuhlendorf and Engle 2001, Hoekstra et al. 2005). While there is evidence that burning and grazing can act independently to influence grassland plant communities this typically does not result in structural heterogeneity that drives diversity in grassland bird communities (Valone and Kelt 1999, Davis 2004, Coppedge et al. 2008). Diverse communities of species require habitat heterogeneity that includes intensively disturbed habitats (i.e., bare ground and relatively short-statured vegetation) and habitats with minimal disturbance dispersed as a shifting mosaic across a complex landscape (Knopf 1994, Fuhlendorf et al. 2006, Fuhlendorf et al. 2009). Furthermore, the response of wildlife to disturbance processes, particularly birds, can vary greatly based on the duration and seasonal timing of disturbances (Brawn et al. 2001, Gregory et al. 2010).

Pyric herbivory, the ecological process through which fire drives grazing and grazing determines the probability of future fires, has been an effective strategy for improving habitat for breeding grassland birds (Fuhlendorf et al. 2006, Churchwell et al. 2008, Fuhlendorf et al. 2012, Hovick et al. 2012). Grasslands are inherently heterogeneous systems that vary functionally and structurally across multiple scales (Wiens 1997, Fuhlendorf and Smeins 1999). When fire and grazers are allowed to interact spatially and temporally across the landscape, it

results in a shifting mosaic that influences population dynamics and movement patterns of breeding native birds (Brawn et al. 2001, Fuhlendorf et al. 2006). Furthermore, heterogeneous grasslands create habitat that can support a more diverse bird community (Fuhlendorf et al. 2006), and have been shown to improve reproduction for grassland nesting birds (Churchwell et al. 2008, Hovick et al. 2012). Restoring heterogeneity to grasslands could improve over-wintering conditions for non-breeding birds by providing structural variation resulting from interacting fire and grazing disturbances that suits habitat needs of specialized species, thereby increasing avian diversity across the landscape.

Most grassland birds in North America are migratory, spending one-half or more of their annual cycle in migration or wintering areas (Herkert et al. 1996). Although the complexity of avian life cycles complicates conservation and management efforts, the extent and duration of seasonal movements by grassland birds emphasizes the need for information in areas other than the breeding grounds (Igl and Ballard 1999). Monitoring avian communities during winter is challenging. Inclement weather makes conducting surveys impractical, birds almost never vocalize during the non-breeding season, and flushing birds are hard to identify (Fletcher et al. 2000). These challenges are, in part, why non-breeding communities of grassland birds have received less research attention than breeding bird communities.

The limited number of studies that have examined winter bird communities typically report habitat use in the absence of disturbance, or they examine the affects of fire and grazing independently (Igl and Ballard 1999, Gordon 2000, Baldwin et al. 2007). Both of these scenarios are not commonly practiced in working grassland landscapes which makes application to conservation difficult. To effectively evaluate non-breeding bird communities in a way that maximizes the potential effect on management of grassland ecosystems, research should focus

on bird use of grasslands managed with fire and grazing. Therefore, we investigated non-breeding grassland bird habitat use in a landscape that is managed with interacting fire and grazing processes. Prescribed fires for this study took place in during the dormant season in early spring (i.e., March) and grazing took place throughout the growing season (April- Sept). We hypothesized that the interaction of fire and grazing would result in structural heterogeneity and the resulting differences in patch structure and composition would influence winter grassland bird abundance and patch occupancy. This work provides empirical support for managing grasslands to improve efforts for bird species of conservation concern during the non-breeding season and increases our general understanding of avian habitat associations during winter.

Methods

Study area

Our study was conducted at The Nature Conservancy's Tallgrass Prairie Preserve (hereafter, the preserve) in north eastern Oklahoma, USA from 2011-2013. This area comprises the southern extent of the Flint Hills region of the Great Plains and is part of the largest remaining tallgrass prairie in North America. The preserve is a 16,000 ha area dominated by a tallgrass prairie plant community. Dominant grasses include *Andropogon gerardii* Vitman, *Schizachyrium scoparium* Nash, *Panicum virgatum* L., and *Sorghastrum nutans* (L.) Nash. Dominant forbs at the preserve include ironweeds (*Veronia* spp.), milkweeds (*Asclepias* spp.), and ashy sunflower (*Helianthus mollis*). The climate of the preserve is temperate with hot summers and cool winters. During the course of this study (2011-2013) average high temperatures for January and February were 9.8°C and 10.2°C, respectively, while average low temperatures were -4.8°C and -3.0°C,

respectively. Precipitation totals for each calendar year prior to sampling were 93.6, 80.1, and 85.8 cm for 2010, 2011, and 2012, respectively. Snowfall occurred on three different occasions during the sampling period, but never persisted for >3 days. As a consequence, we avoided sampling during periods of snow cover.

The preserve is managed to restore the fire-grazing interaction, resulting in grassland structural heterogeneity (Hamilton 2007, Fuhlendorf et al. 2009). The structural heterogeneity becomes present as animals are allowed to select from areas that are recently burned and those that have greater time post fire (Archibald et al. 2005, Allred et al. 2011). Cattle management at the preserve is done across multiple pastures ranging from (430-980 ha), and are stocked at moderate rates (cattle: 2.4 animal unit months^{-ha}) using stocker steers that graze throughout the growing season (April-Sept), and all prescribed fires were conducted during spring (i.e., March-April) for this study.

Data Collection

We used permanent, 500 m line-transects to survey grassland birds during January and February from 2011-2013. Transects were distributed across three patches in each of four pastures with two transects in each patch (n = 24). Therefore, we examined three different patch types (0-12, 13-24, >24) resulting from time since fire and grazing and each patch-type was replicated four times (pastures). Patches were large with an average size of 119 ha and ranging from 61 – 227 ha. Transects were randomly placed within patches using ArcGIS 10.0 (ESRI 2011) but constrained so that transects were >150 m apart and >100 m from patch edges to ensure independence between sites and prevent any double counting. Sampling was conducted during daylight hours by one observer on days with winds less than 20 km/h and no precipitation (lg

and Ballard 1999). Surveys were conducted four times in 2011 and 2013 and three times in 2012. Birds can be surveyed throughout the day during the non-breeding season because daily activities do not peak as they do during the breeding season (i.e., dawn chorus; Fletcher et al. 2000). Each individual or group was identified to species by distinctive flight patterns, call notes, or coloration (Butler et al. 2009). When groups of individuals were encountered, we recorded them as a single detection and recorded the total number of individuals within the group. Additionally, we recorded environmental data at the start of each transect and for each survey day that could affect detection probabilities (wind, cloud cover, temperature, date, and time of day).

We collected vegetation data along each transect at the end of the sampling period. We measured vegetation in three plots situated at the start, middle, and end of transects to characterize the vegetation characteristics of each transect. Each plot was centered on the transect and had 0.5 m² quadrats distributed every 2.5 m for 10 m in each cardinal direction (n = 17). Within each quadrat we measured grass, forb, shrub, bare ground, and litter cover. Additionally, we measured litter depth and vegetation height within each quadrat and took a reading of vertical vegetation structure for the plot using a Nudd's board modified for grassland environments (Nudds 1977, Guthery 1981).

Data Analysis

We calculated relative abundances for the eight most frequently detected species. To do so, we divided the total number of detections for each species by the number of transects surveyed in each patch during each year of the study. This method standardized effort across years and allowed for simple patch-type comparisons across and among all species. We used this method

rather than estimating densities using program Distance because we frequently surveyed transects that had no detections and preliminary analysis indicated that several of the gregarious or large species had detection probabilities that did not decrease as distance from the observer increased (Buckland et al. 2001).

We used non-metric multi-dimensional scaling (NMDS) to assess similarity in bird species composition across habitat patches resulting from the fire-grazing interaction. Specifically, we used relative abundances and the “metaMDS” and “envfit” functions in the vegan package of program R to project a two dimensional summary of avian community habitat use (Oksanen et al. 2010). We chose to use the Bray-Curtis distance metric in NMDS because it is sensitive to differences in the most abundant species and less sensitive to infrequently encountered species (Pillsbury et al. 2011), which works well for the winter bird community because some species are detected very frequently while others are not. NMDS is iterative procedure that maximizes the rank-order correlation between Euclidean distance in ordination space and the values in the dissimilarity matrix. Therefore, axes are arbitrary and do not convey any real meaning. To interpret NMDS graphics one must know that species with shorter inner-point distances are more similar (i.e., similar patch use) than those with greater inner-point distances. Goodness-of-fit is measured through stress in NMDS, which is inversely proportional to the rank order of Euclidean distance correlations. We set our analysis at a level of two dimensions and assessed the stress values to make sure our selection of the number of dimensions adequately described these data.

We used an occupancy model framework in program MARK to evaluate site occupancy and detection probabilities for a subset of species of grassland birds during winter (White and Burnham 1999, MacKenzie et al. 2002). MARK uses a likelihood-based method for estimating

site occupancy rates when detection probabilities are < 1 and allows for the incorporation of covariates that can influence occupancy and detection rates. We only incorporated species that are considered grassland obligates (per Vickery et al. 1999) and for which we had >25 detections. Models assume there are no false detections and that sites are independent of one another, which we ensured through proper spacing of transects and combining detections for transects within the same patch (MacKenzie et al. 2002).

To assess occupancy dynamics, we created encounter histories for all surveys conducted from 2011-2013 indicating a 1 if the species was detected in a particular patch (i.e., time since fire) or a 0 for non-detections. Because detection is important in determining unbiased estimates of site occupancy, our first modeling procedure was to determine which covariates most influenced detection for each focal species. We examined the effects of temperature, wind, cloud cover, and annual variation on detection. After determining the best detection model, we then assessed the influence of time since fire and grazing on occupancy by entering user-specified covariates in the MARK design matrix. Because our primary objective was to examine bird habitat use in patches that result from the spatio-temporal interactions of fire and grazing, the only a priori covariate we examined was time since fire. We used this approach because time post fire and grazing affects plant community structure and composition (Fuhlendorf and Engle 2004, Winter et al. 2012), which is an important predictor of grassland bird site occupancy especially in large, intact grassland landscapes (Davis 2004, Fuhlendorf et al. 2006, Coppedge et al. 2008). Models were ranked using Akaike's information criterion adjusted for small sample sizes (AIC_c) and we followed the general information theoretic approach for assessing model fit (Burnham and Anderson 2002).

Results

We found that the interaction of fire and grazing resulted in a shifting mosaic of grassland patches as areas with greater time since fire and grazing supported taller, denser vegetation with greater litter cover, litter depth, and less bare ground cover than recently burned and grazed areas. In contrast, recently burned and grazed patches had high amounts of bare ground with relatively minimal litter cover and short vegetation structure (Fig. 1).

We detected 14 bird species across 144 km of transects and detection rates were low with an average of 2.4 detections km⁻¹. Recently burned and grazed patches had the fewest overall detections but the same species richness as patches 13-24 months since fire and grazing; patches with >24 months since fire and grazing had the most detections and the greatest avian richness. There were seven species that were detected in all three patches, one species detected in two patches, and six species that were only detected in one patch type. Many of these species are gregarious and detections averaged > 1 individual; group size averages were 1.07 (±0.03) for meadowlark spp. (*Sturnella* spp.), 1.05 (±0.02) for Savannah Sparrow (*Passerculus sandwichensis*), 3.40 (±1.01) for American Tree Sparrow (*Spizella arborea*), and 4.72 (±1.10) for Smith's Longspur (*Calcarius pictus*). All other species were only detected as single individuals.

Relative abundance data showed that Northern Harrier (*Circus cyaneus*), meadowlark spp., Savannah Sparrow, and American Tree Sparrow used a range of vegetation patches resulting from time since fire and grazing. In contrast, Smith's Longspur and Le Conte's Sparrow (*Ammodramus leconteii*), exhibited trends in habitat use with abundance maximized in the most recently disturbed and the most undisturbed patches, respectively (Fig. 2).

The NMDS ordination produced a good fit in two dimensions (stress = 0.01; Kruskal 1964) and accounted for 70% of the variance in the grassland bird abundance data. The ordination showed that bird community composition differed among the vegetation patches resulting from time since fire and grazing and patterns observed in relative abundance data were generally supported. Most strikingly, Le Conte's Sparrow, Smith's Longspur, and Sprague's Pipit (*Anthus spragueii*) utilized specific, opposite patch types. Le Conte's Sparrow was found in patches >24 months since fire and grazing while Smith's Longspur and Sprague's Pipit were in the most recently burned and grazed patches (Fig. 3). However, there was partial overlap in bird communities across patches as seen by clustering of individual species and the overlap of patch-hulls.

Patch occupancy for the four most abundant grassland birds complemented observed relative abundance data and community results, and indicated that some species are generalists whereas other species are specialists, selecting for specific patches that result from time since fire and grazing (Fig. 4). Savannah Sparrows trended towards occupying the most recently burned and grazed patches but this effect was not significant ($\beta = -0.56$, CI: -3.15, 2.03), reflecting the generality of habitat selection for that species. Similarly, disturbance did not have a significant effect on meadowlark patch occupancy ($\beta = 0.38$, CI: -0.86, 1.62). Smith's Longspur had a higher probability of occurrence in recently burned and grazed patches ($\beta = -0.81$, CI: -1.86, 0.23), whereas, Le Conte's sparrows had the highest probability of occupancy in patches with the greatest time since fire and grazing ($\beta = 18.6$, CI: 18.2, 19.1). All species had high detection rates and models for detection for two species were improved by inclusion of temporal or weather parameters (Table 1).

Discussion

Coupling fire and grazing to allow grazers to select among burned and unburned areas of the landscape has significant implications for breeding grassland birds (Fuhlendorf et al. 2006, Powell 2006, Coppedge et al. 2008, With et al. 2008). Our results now demonstrate the effects of restored fire and grazing processes on a winter bird community. Grazing animals preferentially select the most recently burned areas which increase the amount of bare ground and reduce standing biomass, while areas that have gone unburned accumulate litter and standing biomass over time (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006). The resulting structural heterogeneity provides greater suitability of habitat structure and increases the diversity of winter birds that can occur across the landscape (Fig. 5). Our work has important conservation implications as many have speculated that North American grassland bird populations are limited by habitat during the non-breeding season (Brooks and Temple 1990, Basili 1997), yet until now there was little empirical support for this. Our results support the hypothesis that the interaction of fire and grazing would result in structural heterogeneity of vegetation and the resulting differences in patch structure and composition would influence winter grassland bird abundances. Our findings uphold management recommendations that a mosaic of patchy disturbance across the landscape would provide suitable winter habitat for a wide range of bird species (Gabrey et al. 1999, Baldwin et al. 2007). Additionally, our conclusions are substantiated by recent work examining winter bird use in tallgrass prairie managed with interacting fire and grazing that found plant structure (i.e., height) mostly determined patch use (Monroe and O'Connell 2014).

Much of the previous work investigating winter bird community responses to disturbance have viewed fire and grazing as separate disturbances (Gabrey et al. 1999, Gordon 2000, Baldwin et al. 2007, Baldwin et al. 2010), or have examined the bird community in grasslands that are grazed in the absence of fire (Grzybowski 1982). Our study indicates that the spatial and temporal patterns of grazing and fire in combination may be important to conservation of non-breeding birds. While we did not explore the impacts of fire alone or grazing along, our results indicate that the structure that results from interacting fire and grazing is beneficial to broad suite of winter birds (Fuhlendorf and Engle 2004, Fuhlendorf et al. 2009). As a consequence of the grassland shifting mosaic that occurred in the presence of the fire-grazing interaction, areas most recently disturbed had the least amount of litter and vertical structure and created habitat for two bird species of conservation concern, Sprague's Pipit and Smith's Longspur. Both of these species have high continental concern rankings by Partners in Flight (PIF). Sprague's Pipit was encountered very infrequently during this study, but is a watchlist species and this information could help improve future management efforts (PIF 2012). Smith's Longspurs were relatively abundant and had the highest probability of patch occupancy in recently disturbed patches.

We observed that patches with the greatest time since fire and grazing had the tallest, densest vegetation with the most litter accumulation, and the greatest avian richness of all patches examined. Additionally, relatively undisturbed patches had the highest probability of occupancy by Le Conte's Sparrows, which occurred almost exclusively in areas of >24 months since fire and grazing. Our findings illustrate how the interaction of fire and grazing influence birds differently than either disturbance in isolation as previous research reported Le Conte's Sparrows reaching their greatest abundance in areas burned within the previous two years (Baldwin et al. 2007). Thus, decoupling these interacting disturbances under which grasslands

birds evolved with, can lead to recommendations which may deviate from historic conditions. Our work elucidates the complexity of grassland bird response to disturbance and illustrates that research outcomes can vary dependent on the timing, duration, and type of disturbance being examined. In particular, Le Conte's Sparrow winter ecology is poorly studied, and our results can be used to improve conservation efforts for this species by increasing grassland patches that have gone undisturbed for multiple years.

Patch selection by non-breeding birds likely reflects a combination of physiological constraints on their behavior and survival strategies (Pulliam and Enders 1971, Pulliam and Mills 1977). For example, Le Conte's Sparrows similar to most *Ammodramus*, are generally poor flyers that rely more heavily on cryptic behavior and running to try and avoid predators. As a result, they commonly have small and well-defined home ranges in winter (Baldwin et al. 2010). Additionally, it is possible that this solitary species seeks dense and tall vegetation structure for thermal protection from exposure to windy conditions common in the southern Great Plains during winter. Conversely, more gregarious species such as the Smith's Longspur and American Tree Sparrow reached highest abundances in recently burned and grazed patches. These species likely select patches that are recently disturbed with small amounts of litter and short vertical structure to enable easier access to food resources. They are able to select for open foraging patches as a result of reduced predation risk that occurs as a result of flocking behavior (Grzybowski 1983). Other commonly encountered species during this study showed a range of patch use and probably use some combination of access to resources, thermal needs, and predator avoidance to select patches.

Many of the species that we examined appear to use similar habitat structure during the non-breeding and the breeding seasons. For example, meadowlark species that we recorded

during winter exhibited very generalist behavior, similar to their patch use during the breeding season (Fuhlendorf et al. 2006, Pillsbury et al. 2011). Additionally, Le Conte's Sparrows were most abundant in undisturbed patches similar to the vegetation they are most abundant in during the breeding season (Igl and Johnson 1999), and Savannah Sparrows were widespread across all patch types reflecting their generalist approach to nesting habitat (Bollinger 1995). There may be exceptions to these trends (Igl and Ballard 1999, Baldwin et al. 2010), but based on our data when a range of habitat structure is available, many species seem to have an affinity for the same type of structure during breeding and non-breeding seasons. If this conclusion is true for a broad suite of species, simply knowing the over-wintering range for species of conservation concern would allow conservation efforts to focus on the proper structure type. Nonetheless, managing for a mosaic of structure would offer the greatest diversity of habitat types and would likely suit the requirements of the most species, similar to the results we report.

Our findings concur with breeding bird research from other rangeland systems that indicated bird community composition is dependent on variable patterns of fire and grazing (Knopf 1994, Skowno and Bond 2003, Krook et al. 2007, Reinkensmeyer et al. 2007, Gregory et al. 2010). This makes intuitive sense when you consider the historical disturbance regime of grasslands and the affinity of grassland breeding birds to select areas with specific, varying levels of biomass (Knopf 1994). Breeding bird abundance and diversity was increased in grasslands that mimicked historical disturbance regimes compared to management that promoted uniform vegetation structure across the landscape (Fuhlendorf et al. 2006, Coppedge et al. 2008). The consistent response of grassland birds during breeding and non-breeding seasons is a strong indication of the potential conservation value in managing for a structural mosaic. Moving forward, we argue that because of the long evolutionary history of fire and grazing in grassland

ecosystems, conservation research should focus on the interaction of fire and grazing and the resulting shifting mosaic in the landscape (Fuhlendorf et al. 2006, Fuhlendorf et al. 2012).

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Table 1. The best models examining weather and temporal effects on detection probabilities for the four most commonly encountered grassland bird species at the Tallgrass Prairie Preserve, Oklahoma, USA (2011-2013). In the table, p indicates the detection probability; LCI and UCI indicate the lower confidence interval and upper confidence interval, respectively.

Species	Model	p	LCI	UCI
Le Conte's Sparrow	constant	0.28	0.18	0.40
meadowlark spp.	constant	0.52	0.40	0.63
Savannah Sparrow	year	0.63 - 0.96	0.44	0.99
Smith's Longspur	cloud cover	0.90	0.61	0.98

Figure Legend

Figure 1. Observed vegetation characteristics in the non-growing season in patches that range in time since fire and grazing at the Tallgrass Prairie Preserve, Oklahoma, USA (2011-2013).

Figure 2. Relative abundances (detections per patch \pm SE) of the six most commonly encountered bird species in patches that range in time since fire and grazing at Tallgrass Prairie Preserve, Oklahoma, USA (2011-2013).

Figure 3. Non-metric multidimensional scaling plot for all bird species with >5 detections at the Tallgrass Prairie Preserve, Oklahoma, USA (2011-2013). The hulls around the perimeter of each patch are based on the site scores for each of the three patch types and species are projected based on species score. Species projected near each other indicate similar habitat use. Four letter codes represent the following species: NOHA = Northern Harrier, GRPC = Greater Prairie-Chicken, SPPI = Sprague's Pipit, ATSP = American Tree Sparrow, SAVS = Savannah Sparrow, LESP = Le Conte's Sparrow, SMLO = Smith's Longspur, and MESP = meadowlark species.

Figure 4. Occupancy probabilities for the most abundant grassland bird species in patches that range in time since fire and grazing at the Tallgrass Prairie Preserve, Oklahoma, USA (2011-2012). Four letter codes represent the following species: SAVS = Savannah Sparrow, LESP = Le Conte's Sparrow, SMLO = Smith's Longspur, and MESP = meadowlark species.

Figure 5. Characterization of the response of bird species during the non-growing season to interacting fire and grazing at the Tallgrass Prairie Preserve, Oklahoma, USA (2011-2013). Art work courtesy of Gary Kerby adapted from Fuhlendorf et al. (2009). Lines for each species are based on observed patch use.

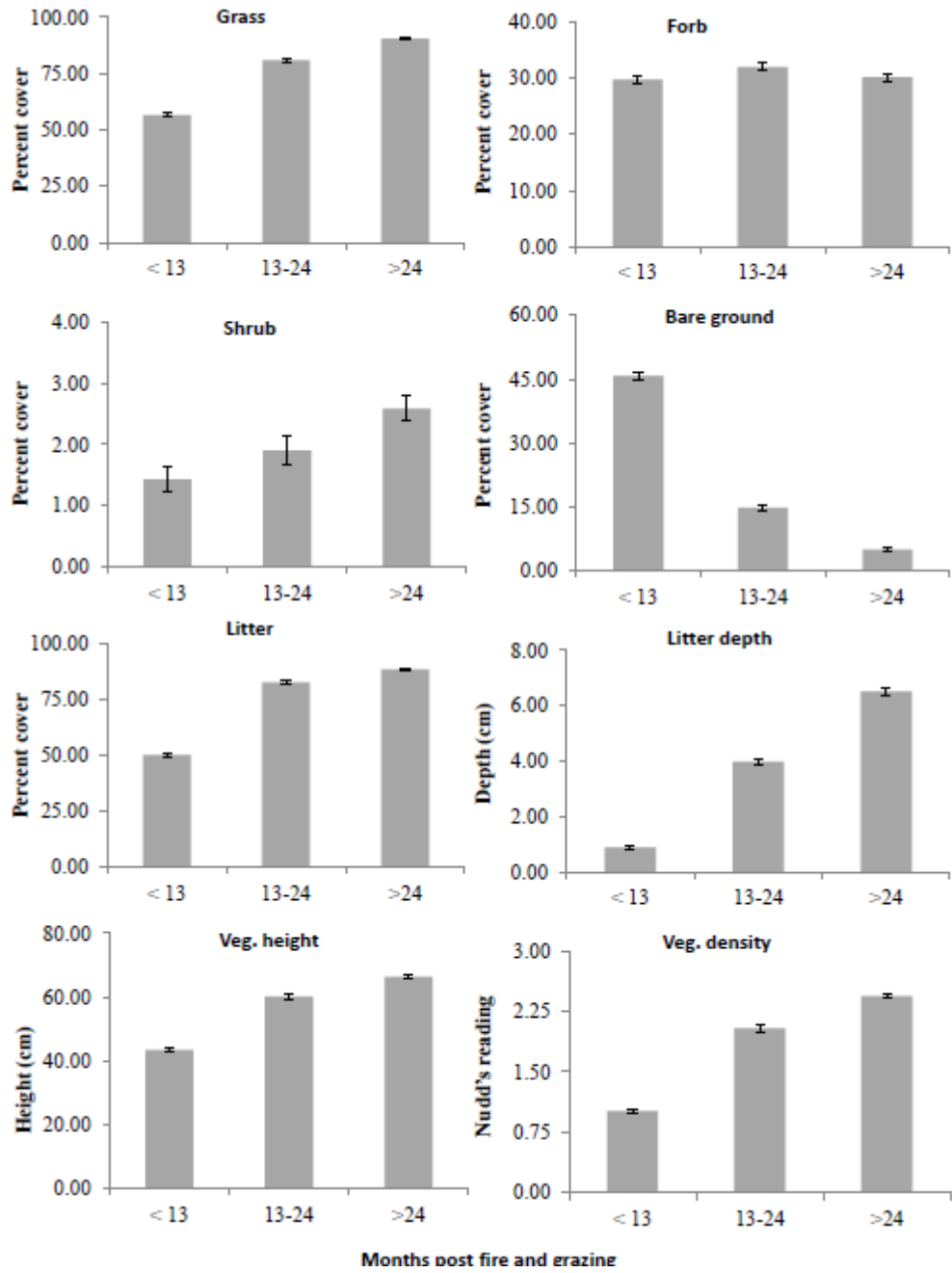


Figure 2.1.

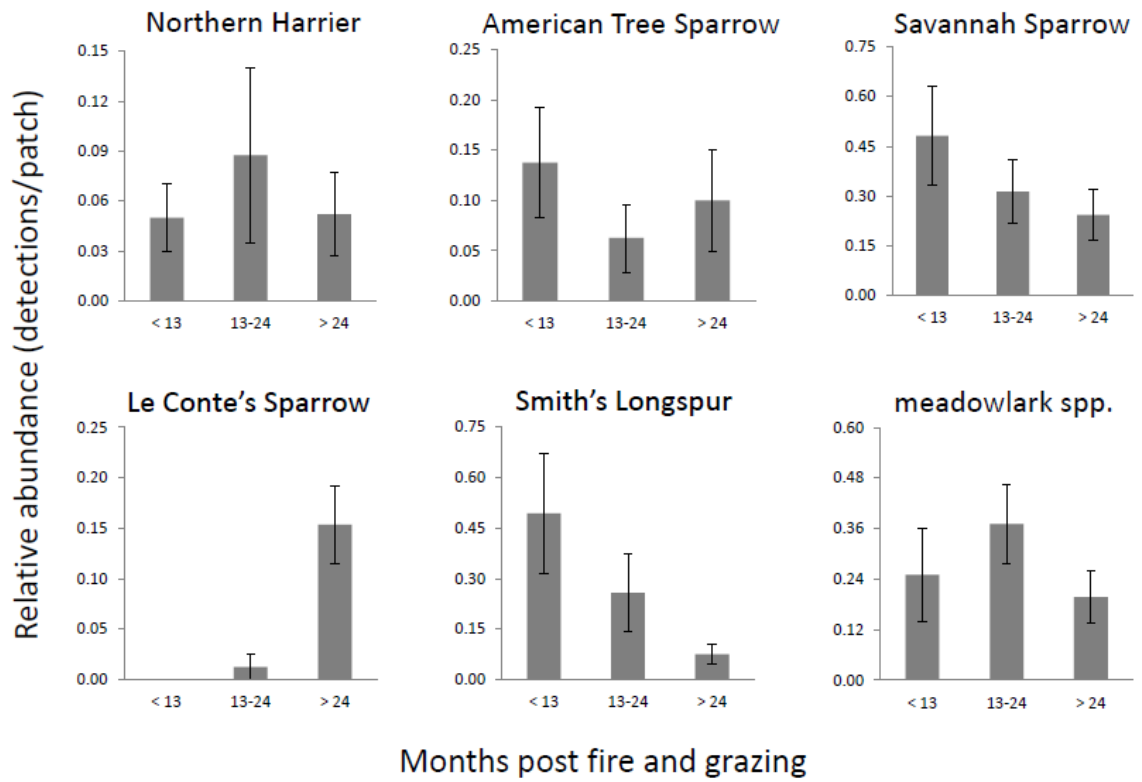


Figure 2.2.

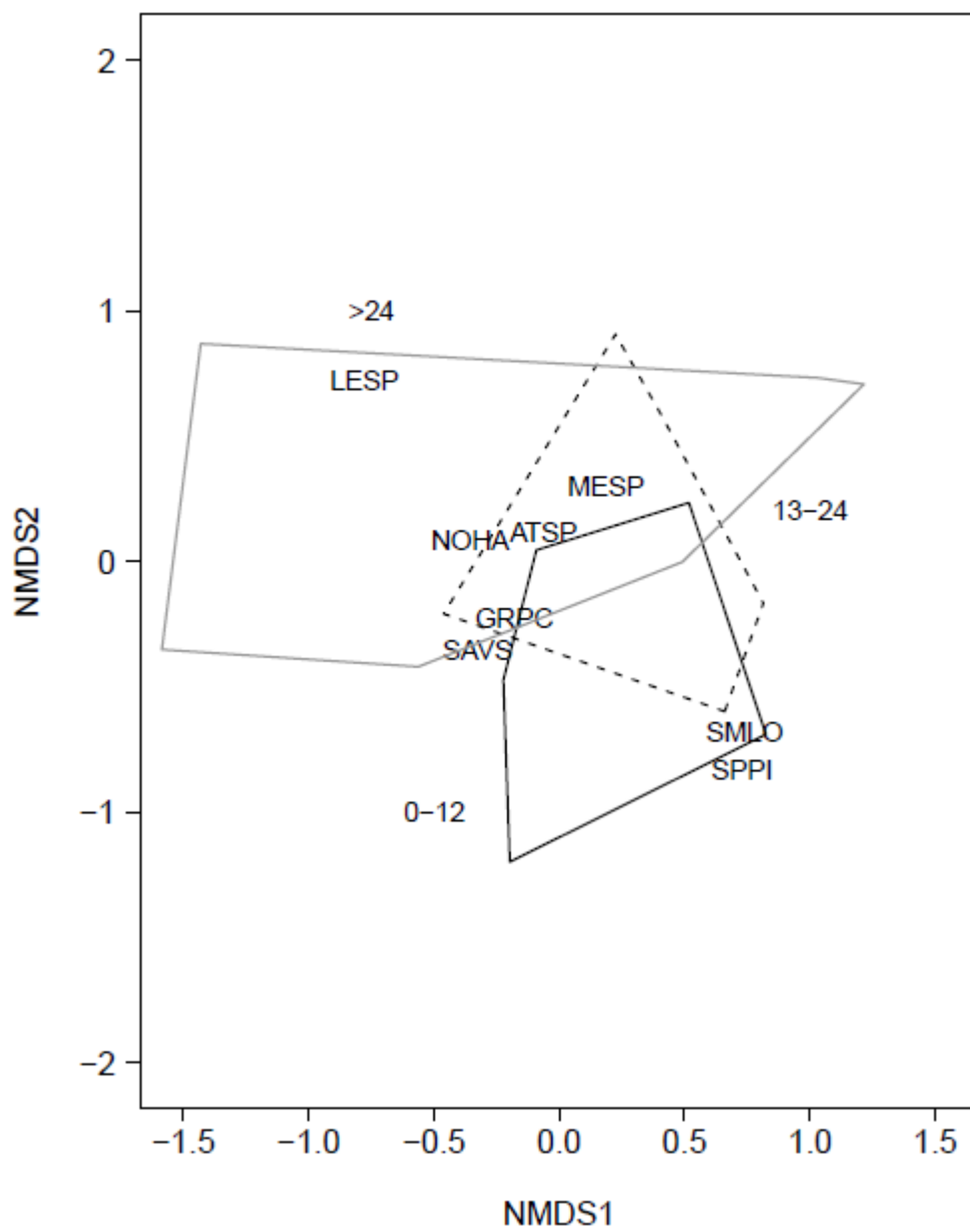


Figure 2.3.

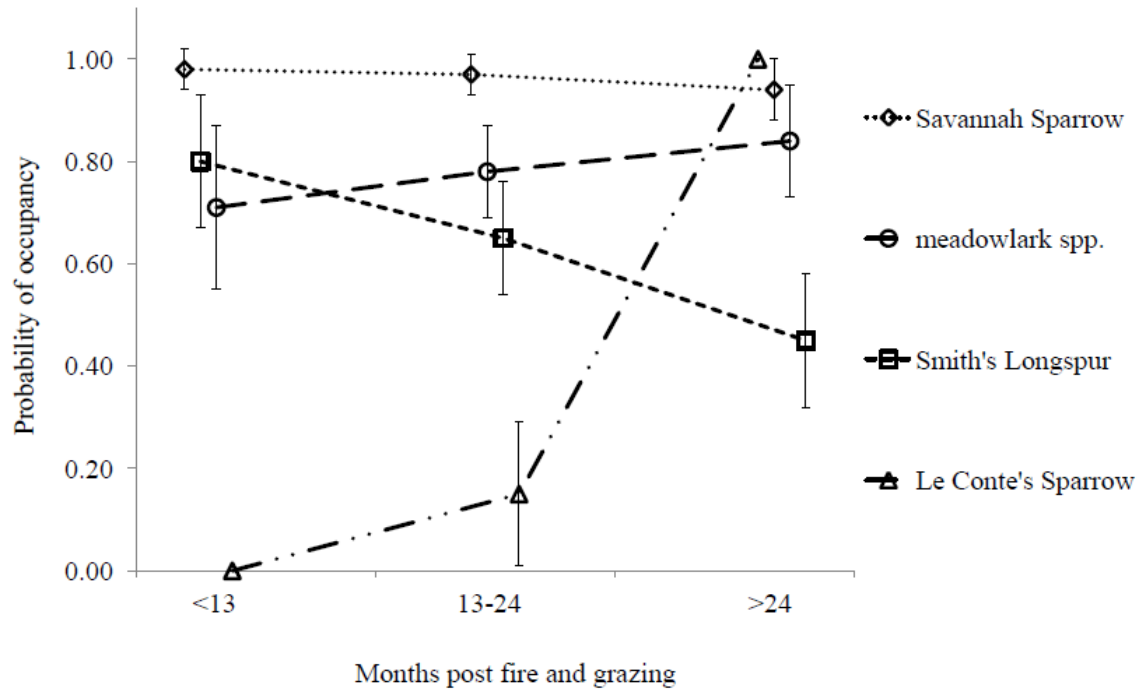


Figure 2.4.

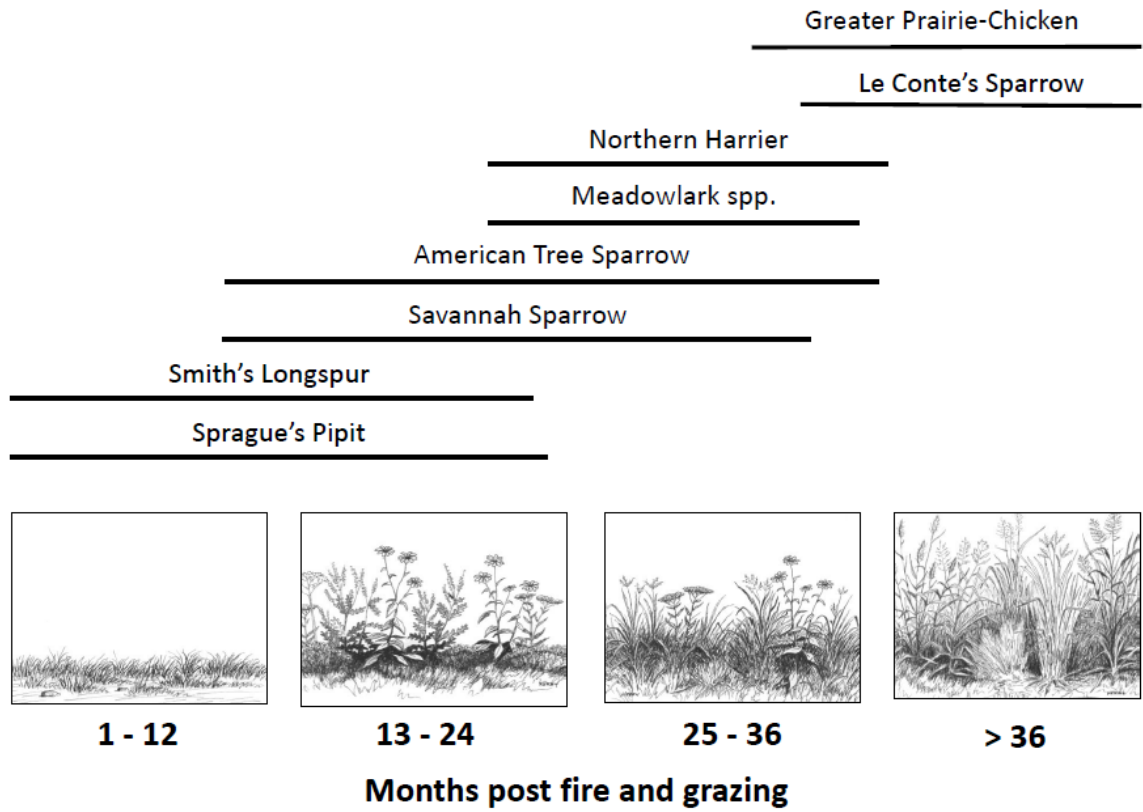


Figure 2.5.

CHAPTER III

Climate variability, Fire, and Oil in Grasslands: What drives Nest Site Selection and Survival of Greater Prairie-Chickens?

Abstract

Grasslands are highly imperiled as a result of widespread conversion for agricultural purposes and fragmentation and alteration from multiple human actions. Remaining grasslands are susceptible to mismanagement, energy extraction, and highly variable weather associated with global climate change which makes understanding the response of imperiled grassland species to these challenges important for informed conservation. We assessed Greater Prairie-Chicken (*Tympanuchus cupido*) survival and nest site selection in tallgrass prairie characterized by interacting fire and grazing disturbance and anthropogenic structures associated with oil extraction during three years of highly variable weather. We found that Greater Prairie-Chicken survival was negatively affected by solar radiation and there was a trend for decreased survival as the breeding season progressed. Focal disturbance was not found to impact survival directly, but vegetation height which is greatly influenced by fire and grazing processes had a positive effect on nest survival. Greater Prairie-Chickens chose nesting locations that maximized the amount of time post fire while minimizing the amount of tree cover and distance to lek sites. Future conservation efforts for Greater Prairie-Chickens needs to focus on variable disturbance regimes that create areas of residual biomass to increase vegetation height and potentially reduce the affects of solar radiation while decreasing woody vegetation encroachment into grasslands. Maintaining suitable nesting sites should maximize the potential for high reproduction in years when local weather variables are favorable.

Introduction

Grasslands are one of the most imperiled ecosystems in the world (Hoekstra et al. 2005). Loss of grassland environments have been widespread and as global changes accelerate, the threats to remaining grasslands are increasing. In North America, < 1% of tallgrass prairie remains and an estimated 80% of all grasslands have been converted for agricultural use (Samson and Knopf 1996; Noss et al. 1995). As a consequence, grassland organisms are highly threatened. Grassland birds specifically have experienced major population declines over the last half century (Vickery et al. 1999; Sauer et al. 2012). Additionally, changes in climate and an increase in energy infrastructure are new challenges that threaten conservation of remaining grassland landscapes. To improve future grassland conservation we must understand the relative impacts of management, anthropogenic structures, and local weather variables on grassland organisms.

Grasslands are disturbance prone ecosystems that depend on grazing and burning processes to drive and shape ecosystem structure and function (Collins and Wallace 1990; Anderson 2006). Traditionally, the application of burning and grazing in rangelands has been under a utilitarian paradigm and goals have been production-based, which has resulted in homogenous systems that are largely void of the heterogeneity that is inherent to rangelands (Holocheck et al. 2004; Anderson 2006). While these practices have been successful at reducing the effects of extreme grazing, they have limited heterogeneity and biodiversity (Fuhlendorf et al. 2012). More recently, however, the focus of conservation in rangelands has begun a paradigm shift that promotes the conservation of pattern and process through the restoration of natural disturbances (Fuhlendorf et al. 2009; Fuhlendorf et al. 2012). Because heterogeneity is the root of diversity, the use of fire driven grazing or pyric herbivory, can increase the breadth of niches available in rangeland environments thereby favoring diversity in grasslands and potentially improving long term stability in these systems (Otsfeld et al. 1997; Wiens

1997; Fuhlendorf et al. 2006). Recent studies in the Great Plains have consistently called for management that promotes patchy disturbance for conservation (Patten et al. 2007; With et al. 2008; Augustine and Sandercock 2011; McNew et al. 2012). Unfortunately, as the support for a shift in grassland conservation is occurring, new challenges are emerging as energy extraction in rangelands is increasing and global climate change is creating more extreme weather patterns (Lyon et al. 2003; Holloran et al. 2005; Obermeyer et al. 2011; IPCC 2013).

Energy extraction processes and the associated infrastructure can negatively affect native rangelands and imperiled grassland species (Kociolek et al. 2011; Obermeyer et al. 2011; Douglas et al. 2012). Many previously unfragmented natural landscapes are being developed to meet the demands of a growing human population (Lior 2008). In addition to the direct mortality threats posed by new energy infrastructure (Kunz et al. 2007; Wolfe et al. 2007; Kociolek et al. 2011), the avoidance or displacement associated with construction of structures in rangeland environments can be much greater than direct habitat loss resulting from development (Zeiler and Grünshauchner-Berger 2009; Pearce-Higgins 2012; Winder et al. 2014). Indirect loss of habitat can effectively limit the amount of usable space thereby reducing carrying capacities, or displacement can force individuals into novel environments and increase mortality risk (Dzialak et al. 2010; Holloran et al. 2010; Stoen et al. 2010). Finally, the increased direct and perceived fragmentation to grasslands that results from anthropogenic structures may exacerbate future challenges associated with greater climate variability by reducing species abilities to shift to suitable habitats in cooler environments (Pruett et al. 2009; Lawler et al. 2013).

Climate driven changes have increased biodiversity loss and understanding how species respond to a warming and more variable climate is a central challenge facing ecologists (Dawson et al. 2011). Climate changes are now occurring at unprecedented rates (IPCC 2013), which rises concerns for species extinctions in organisms that are unable to adjust (Veneir 1999). Moreover, changes are not uniform in

space or time and patterns can be complex as a result of interplay between region-specific and species-specific factors that are affected by local management (Tingley et al. 2013). Greater investigation of species responses to current weather conditions can aid in more accurate predictions of species' responses to future climate change and potentially inform conservation efforts allowing organisms to persist.

Increasing climate variability, management that promotes homogeneity and the construction of new energy structures in previously unfragmented rangelands are all challenges facing the imperiled Greater Prairie-Chicken (*Tympanuchus cupido*; hereafter "prairie-chicken"). Prairie-chickens have been referred to as an indicator and umbrella species of the tallgrass prairie ecosystem (Poiani et al. 2001; Pruett et al. 2009), but their long term persistence is questionable as they have experienced one of the greatest distribution contractions and population declines of any grassland species resulting in a vulnerable status by the International Union for Conservation (Schroeder and Robb 1993; Robbins et al. 2002; Birdlife International 2012). Remaining prairie-chicken populations are threatened by changes associated with rangeland practices, energy development, and a changing climate because of their complex life history traits and need for large, open landscapes (Johnsgard 2002; PIF 2012). Yet, the impacts of these potential threats have gone mostly unexamined. Previous research has proposed that rangeland practices that promote heterogeneity should be implemented, but few have examined prairie-chicken survival or habitat use in a landscape with interacting fire and grazing (Patten et al. 2007; McNew et al. 2012). Furthermore, until recently no research had investigated the impacts of energy development on prairie-chickens (McNew et al. 2012; Winder et al. 2013; Winder et al. 2014), and studies examining the impacts of oil and gas infrastructure are still lacking. Moreover, the direct influence of weather on prairie-chicken survival is largely unknown.

We examined Greater Prairie-Chicken nest survival and nest site selection in tallgrass prairie characterized by interacting fire and grazing disturbance and anthropogenic structures associated with oil extraction during three years of highly variable weather. This work took place on The Nature Conservancy's Tallgrass Prairie Preserve which is managed in a way that allows fire and grazing to interact by burning approximately one-third of the preserve each year and allowing large herbivores to select from burned and unburned portions of the landscape (Hamilton 2007). In addition, the preserve has undergone a resurgence of oil exploration in recent years which afforded us the unique opportunity to examine prairie-chicken nest survival and nest site selection in relation to management, energy infrastructure, and a gradient of weather extremes that occurred over the last three years (2011-2013) (Table 1). Our specific objectives were to: 1) test the influence of management (i.e., fire and grazing), energy infrastructure, and weather variables on nest survival of prairie-chickens, and 2) examine the relative role of management, energy infrastructure, and lek sites on nest site selection by prairie chickens.

METHODS

Study area

We examined prairie-chicken nest survival and selection across approximately 30,000 ha of tallgrass prairie managed with fire and grazing in Osage County, Oklahoma. This area lies at the southern end of the Flint Hills region and represents a portion of the largest remaining tallgrass prairie in the world (With et al. 2008). The plant community is primarily tallgrass prairie and dominant grasses include *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Panicum virgatum* L., and *Sorghastrum nutans* (L.) Nash. The climate is temperate with hot summers and cold winters with average temperatures (1971-2000) for May, June, and July of 26.7, 30.5, and 33.8°C and temperatures average 9.4, 7.9, and

11.7°C for December, January, and February, respectively. Average annual precipitation from 1971-2000 is 117.1 cm.

Data Collection

We trapped prairie-chickens using walk-in funnel traps during the springs of 2011-2013 (Schroeder and Braun 1991). Trapping started in mid-March and concluded in early May. We focused on leks with the most displaying males, but attempted to trap all leks with ≥ 5 males. We monitored traps each morning one hour prior to sunrise until lekking activity ceased or until we were forced to flush birds in order to retrieve trapped individuals.

We attached necklace-style radio transmitters to adult prairie-chickens at the time of capture. We used series A4100 transmitters weighing approximately 16 g (~1.5 % of the bird's body weight) and having an expected life span of 900 days (Advanced Telemetry Systems, Isanti, MN). We fitted females with transmitters at the time of capture and released them immediately after attachment. Females were then monitored every one to three days with daily checks after localizing in an area. We flushed females intentionally after they localized in the same area for three consecutive days to observe nest contents and record exact nest locations using a handheld GPS unit (Pitmen et al. 2006). Additionally, we marked nests by placing a large rock 5 and 10 m south of nest sites. To minimize disturbance after finding nests, females were monitored every 2 days at distances >100 m by triangulation of the radio signal. Once we determined that the female was no longer tending the nest, we revisited the nest site to determine nest fate. A nest was classified as successful if ≥ 1 egg hatched.

We measured vegetation at nest sites using a 0.5 m² quadrat centered over the nest location (Daubenmire 1959). Canopy cover was estimated for the following plant functional groups: grass-like,

forb, *Sericea lespedeza*, litter, bare ground, and shrub. We measured vegetation height and litter depth in each quadrat in standardized locations. Additionally, we visually estimated vegetation density using a Nudd's board adapted for grassland/shrubland use (Nudds 1977, Guthery 1981).

Weather variables were collected on-site at an Oklahoma Mesonet station (Brock et al. 1995). The weather station collects a variety of weather variables every 5 minutes, 365 days of the year. For the purposes of this study, we included variables that have been shown to affect nest survival in grouse or that we hypothesized may influence the ability of a predator to locate nests (Grisham et al. 2013, Hovick et al. 2014). The variables of interest included; maximum daily temperature, minimum daily temperature, daily precipitation total, average daily relative humidity, average daily barometric pressure, and average daily solar radiation.

Finally, we used ArcGIS 10.0 (ESRI 2011) and current satellite imagery to measure the distances to and densities of anthropogenic structures such as roads, oil and gas wells, and power poles. We hand digitized images to mark known well locations and used local expertise and ground-truthing to identify recently constructed infrastructure that was not on current imagery. Additionally, power poles were recorded with a Trimble© handheld GPS unit by hand as most power pole construction occurred recently and was not present on imagery.

Data Analysis

Nest survival

We used program MARK to model the relationship between prairie-chicken nest survival and management, anthropogenic structures, and local weather variables (White and Burnham 1999; Dinsmore et al. 2002). Program MARK uses a maximum-likelihood estimator and the use of a logit

function to derive daily survival probabilities. Additionally, MARK allows for the inclusion of covariates and comparison of *a priori* candidate models on the basis of Akaike's information criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002).

Our first step was to create four model groups based on temporal trends, management, anthropogenic structures, and weather variables. We then used Pearson's correlation to assess multicollinearity among variables within each group, retaining one variable from any highly correlated variable pairs ($r > 0.6$). We were left with five management, three anthropogenic, and four weather variables (Table 2). We then ran single-variable models in all four groups and ranked them based on their relative importance (AIC weight [w_i]) and in comparison to a null model. Single-variable models from each group that had greater relative importance than the null model and were within two AIC_c units of the best model for their respective model set were considered strongly supported and used to produce a "best" model set. To gauge the relative importance of each variable in the best model set, we ran all single, two-way, and three-way combinations of models using the strongly supported variables (Loss and Blair 2011). This method created the opportunity for each variable to be included in the same number of models within the best model set and allowed us to rank the relative importance of each variable on prairie-chicken survival. We calculated model-averaged parameter weights for each variable that was strongly supported by summing AIC weights (w_i) in the best model set and then dividing by the total number of models that each variable occurred in (Burnham and Anderson 2002). This allowed us to determine which parameters were most informative despite multiple competitive models ($\Delta AIC_c \leq 2$) (Arnold 2010).

Nest site selection

We used resource selection functions to determine nest site selection of prairie-chickens. Resource selection functions (RSF) are defined as any function that is proportional to the probability of use by an organism (Manly et al. 1993). The RSF method is highly applicable to natural resource management and can be a powerful tool when linked to a geographical information system (Boyce et al. 2002). We employed a binomial generalized linear model for our use versus availability sampling design where we assigned three random (available) points to each nest site point (use) (Allred et al. 2011). We randomly distributed three points within a 2 km radius buffer surrounding each nest site because our preliminary data showed that bird movement averaged approximately 1.5 km from leks to nest sites. Therefore, a 2 km buffer represented a realistic “available” area for nest site selection in this population. Additionally, we placed a 2 km buffer around each of the random locations to summarize available habitat to nesting prairie-chickens and used the information gathered within the random buffers and nest site buffers to populate the binomial generalized linear model. Similar to nest survival models, we examined management and anthropogenic structure parameters that have been identified as potential influences for nest selection in prairie-chickens or other gallinaceous birds (Hagen et al. 2004; Aldridge et al. 2007; McNew et al. 2012). We did not use weather parameters for this model because they are unlikely to influence site-selection at the scale of weather data available. Additionally, we used remote sensing to identify random locations and as such we do not report fine-scale vegetation parameters but instead used months post fire-grazing which impacts many of the fine-scale vegetation parameters in a predictable way (Fuhlendorf and Engle 2004; Allred et al. 2011; McGranahan et al. 2012). Additionally, we used Pearson’s correlation to assess multi-collinearity among variables within each group, retaining one variable from any highly correlated variable pairs ($r > 0.6$). This eliminated the inclusion of two anthropogenic variables as road densities were highly correlated with well densities so we removed road density variable, and well densities were highly correlated with distances to wells so we removed

distance to wells variable. We created one model set for nest site selection by comparing univariate models of all parameters of interest to a null, a global, and an additive model using variables from univariate models that had greater importance weights than the null model. All models were evaluated using Akaike's Information Criteria for small samples (AIC_c) and model weights (AIC weight [w_i]) (Burnham and Anderson 2002).

RESULTS

We attached transmitters to 40 female prairie-chickens and found a total of 47 nests (36 first attempts, 11 re-nests) from 2011-2013. The constant daily survival rate (DSR) for all nests and years combined was 0.9525 and when exponentiated over the 25-day incubation period, indicated that prairie-chickens in this population have ~30 % chance of a nest surviving until hatch. Using mean covariate estimates from our best program MARK survival model we found that prairie-chickens had ~34% chance of a nest surviving the 25-day incubation period, but survival estimates ranged from 9-92% depending on covariate values.

We used 12 covariates to examine the effects of management, anthropogenic structures, and local weather on the survival of 47 prairie-chicken nests with known fates. We found that local weather variables had the greatest impact on prairie-chicken survival while distance to and density of energy infrastructure had relatively little impact on estimated nest survival rates (Table 3). Survival of prairie-chicken nests was most influenced by solar radiation (parameter importance weight = 0.23), vegetation height (parameter importance weight = 0.13), and a linear temporal trend for decreased survival as the nesting season progressed (parameter importance weight = 0.11) (Table 3). Solar radiation was the most influential parameter with survival rates declining as solar radiation increased ($\beta = -0.13$ on a logit scale, $SE = 0.06$, $CI = -0.24$ to -0.02) (Fig. 1A). The linear survival trend showed a decrease in survival

throughout the breeding season ($\beta = -0.22$, $SE = 0.12$, $CI = -0.45$ to 0.007 ; Fig 1B) and greater vegetation height positively influence nest survival ($\beta = 0.02$, $SE = 0.01$, $CI = -0.005$ to 0.036 ; Fig 1C).

We used 48 nest site locations to determine the relative influence of management, anthropogenic structures, and lek locations on nest site selection for prairie-chickens. We found the amount of time recovery post fire, tree cover, and distance from lek sites were the most influential parameters in determining nesting locations. Additionally, oil and gas infrastructure in this landscape had relatively little impact on prairie-chicken nest placement (Table 4). Months post fire had the greatest impact of all parameters examined on prairie-chicken nest placement with birds seeking areas that maximized the amount of time elapsed since an area had previously burned, and prairie-chickens selected for nesting locations with minimal tree cover and areas that minimized distances from leks (Table 5).

DISCUSSION

Our results demonstrate the importance of local weather variables on prairie-chicken nest survival and are consistent with an emerging body of evidence emphasizing the importance of thermal environments and local weather parameters on gallinaceous bird habitat use and survival (Guthery et al. 2005; Grisham et al. 2013; Larson et al. 2013; Hovick et al. 2014). We found that increased solar radiation during the breeding season decreased the probability of nest survival. Solar radiation likely impacted nest survival through increased operative temperatures (Hovick et al. 2014)—an incorporation of energy flow between an animal and its environment that depends upon solar radiation, air temperature, wind, and humidity (Dzialowski 2005)—which can increase stress on incubating females and potentially kill embryos if nests are exposed for prolonged periods of time (Webb 1987). Solar radiation may have had greater impacts during the course of our study than during average weather years as both maximum

temperature and solar radiation reached levels outside the range recorded at the onsite weather station over the last two decades (Table 1). However, weather experienced during the course of this study may become more frequent as climate change predictions for the southern Great Plains are forecasting more extreme weather events with an increase in overall temperature (IPCC 2013). Conservation efforts that vary focal disturbance across broad scales can maximize thermal refugia and potentially limit the heat stress experienced by nesting Greater Prairie Chickens (Hovick et al. 2014).

Nest site selection was most influenced by variation in disturbance regimes, landscape patterning of vegetation communities, and proximity to known lek sites. These results highlight the importance of suitable conservation practices to manage landscapes for prairie-chickens and promote a discussion of how the proper utilization of scale in management can have the greatest impact on prairie-chicken populations. When managing for species with large home ranges that require relatively large and intact landscapes, conservation can be challenging and needs to be done at the appropriate scale (Noss et al. 1996). As such, we created a simple conceptual figure to elucidate the differences and challenges in attempting to manage for a species at fine scales without consideration of the status and condition of habitat at the broadest scale (e.g., watershed, region) (Fig. 2A). We illustrate that conservation efforts at fine-scales have high potential to influence prairie-chicken populations when landscapes are primarily contiguous grasslands (i.e., Flint Hills), which is supported by recent research from the Flint Hills suggesting conservation that alters disturbance regimes to affect nest site conditions can be highly effective (McNew et al. 2012; McNew et al. 2013). In contrast, conservation efforts at fine-scales in landscapes with high amounts of fragmentation are unlikely to improve the outlook for long term population persistence and efforts would be better spent focusing on a reduction of fragmentation at broad-scales (i.e., tree removal, prevention of new anthropogenic structures) (Fig. 2B).

We found little influence of anthropogenic structures on prairie-chicken nest survival or nest site selection, a similar finding to that reported for Lesser Prairie-Chicken nest survival (*Tympanuchus pallidicinctus*; Pitman et al. 2005), but contrasts the overall trends associated with grouse and energy infrastructure (Lyon et al. 2003; Walker et al. 2007; Harju et al. 2010; Hagen et al. 2011; Winder et al. 2014). There are several factors that likely influenced our results. First, our research area is dominated by a contiguous grassland landscape making the relative importance of grassland management and local weather parameters of greater importance than in more fragmented landscapes (Fig. 2). Second, use of home ranges throughout the year or long-term lek data may be more adequate measures of the influence of structures on grouse habitat use and behavior because nesting hens may use cues at scales that do not reflect behavior throughout the rest of the year (Walker et al. 2007; Harju et al. 2010; Hagen et al. 2011; Winder et al. 2014). Third, much of the energy infrastructure in this region has been on the landscape for >50 years and it is likely that new infrastructure and old infrastructure have different effects on prairie-chickens and parsing out the age of structures in future analysis may be more informative. Finally, most grouse species exhibit high site fidelity which may confound any perceived avoidance of structures in breeding areas (e.g., leks), but structures may affect the long term persistence by exhibiting a lag affect through an eventual decline as later generations begin to avoid previously used sites (Walker et al. 2007).

Our estimated nest survival rates were low relative to previously reported rates for prairie-chickens. Constant nest survival estimates were 29.6% for a 25-day exposure period, but survival estimates using the best MARK model ranged from 9-92% indicating nest survival can reach high levels under the right conditions. For comparison, if we extrapolate our daily survival estimate across a 35-day exposure period similar to previous research done in the Flint Hills (Augustine and Sandercock 2011; McNew et al. 2012), this population would only have a 18.2% chance of a nest surviving until hatch using the constant survival model, which despite being low, is still slightly higher than the rates recently

reported in the Flint Hills (2 – 16%, McNew et al. 2012). Additionally, nest survival was much lower during our study than the 50 % threshold recommended to maintain stable populations (Westemeier 1979), and was more similar to the range of rates (i.e., 31 – 39 %) that have been reported for isolated populations of prairie-chickens in Missouri (McKee et al. 1998; Ryan et al. 1998). Low nest survival in this population appears to be closely linked with weather parameters and may be a potential consequence of this being the southernmost extant population of (Greater) prairie-chickens, making them especially susceptible to warming trends, extreme heat events, and other factors that commonly confront populations on a species' range boundary (Sexton et al. 2009).

In conclusion, our results suggest that prairie-chickens will benefit from conservation practices that result in greater residual biomass as nest survival increased with greater vegetation height and birds preferentially selected nest sites with relatively greater amount of time since fire and grazing. Moreover, nest sites were selected in areas that minimized tree cover so spatially and temporally varying disturbance regimes that prevent woody encroachment while maintaining portions of the landscape that have gone unburned in multiple years may be the most beneficial. Our findings support previous recommendations for conservation efforts in the Flint Hills region of the Great Plains that suggested patchy grazing and fire disturbances to improve conditions for declining prairie-chicken populations (Pattern et al. 2007; Augustine and Sandercock 2011; McNew et al. 2012).

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Table 1. Local weather variables from the Tallgrass Prairie Preserve, OK, measured at a standardized Oklahoma Mesonet weather station. Local weather is summarized to contrast weather patterns from the fifteen years prior to the study with the extreme weather events that occurred during the three year study. Maximum temperature (°C) is the average maximum temperature for each day of the month, rainfall (cm) is the sum of all rainfall events in the month, solar radiation (Watts/m²) is the overall average of the averaged daily solar radiation recorded for every day of the month, and > 32 represents the number of days in the month where temperatures exceeded 32°C. The range of variable within each month is given parenthetically below the average value.

Month	15 years previous (1996-2010)				3 years of study (2011-2013)			
	Max temp.	Rainfall	Solar radiation	> 32	Max temp.	Rainfall	Solar radiation	> 32
April	30.44 (28-34)	3.87 (1.26-6.85)	18.97 (17.45-20.99)	0.43 (0-5)	32.60 (32-34)	6.46 (3.57-10.08)	18.53 (16.34-19.70)	0.33 (0-1)
May	31.67 (29-35)	4.55 (1.04-6.70)	21.60 (17.44-24.1)	0.93 (0-7)	32.78 (32-34)	5.07 (2.71-9.53)	21.17 (18.41-24.90)	1.33 (1-2)
June	33.57	6.14	23.57	4.86	36.48	2.95	25.92	13.33

	(32-37)	(0.94-12.76)	(20.19-25.54)	(0-15)	(36-38)	(2.89-2.99)	(25.75-26.22)	(8-21)
July	36.87	3.51	24.31	17.36	40.74	4.00	25.03	24.67
	(34-41)	(0.54-6.93)	(22.2-26.92)	(8-26)	(37-43)	(0.42-8.89)	(23.6-25.74)	(12-31)
August	38.26	3.16	21.67	18.79	41.29	3.75	21.38	20.00
	(34-42)	(0.01-9.46)	(18.64-24.4)	(7-28)	(36-44)	(3.40-4.14)	(20.95-21.76)	(13-25)
September	35.16	2.81	17.86	7.07	38.71	1.84	18.51	10.00
	(31-43)	(0.52-7.93)	(15.12-20.16)	(0-16)	(36-41)	(1.22-2.95)	(17.67-19.24)	(6-13)
October	31.31	3.73	13.17	0.79	30.37	2.85	14.19	0.00
	(27-36)	(0.94-8.27)	(10.15-15.71)	(0-3)	(30-31)	(0.65-4.72)	(13.03-15.98)	0

Table 2. Summary statistics for non-correlated variables used to examine nest survival of Greater Prairie-Chickens at the Tallgrass Prairie Preserve, OK, USA, 2011-2013.

Parameter/classification	Mean (SE)	Range	Definition
<i>Anthropogenic</i>			
distance to road	228.85 (29.00)	2.48 - 925.67	Distance from a nest to all road types (no paved roads in study area)
well density	12.24 (1.25)	0.00 - 27.07	Wells per square kilometer measured in 2 kilometer radius of the nest
distance to power-pole	1178 (89.72)	107.71 - 2602.67	Distance from a nest to the nearest power-pole
<i>Management</i>			
months post fire	21.19 (1.80)	2.00 - 46.00	Months elapsed since the last fire at the nest site
forb	41.85 (3.67)	3.00 - 86.00	Forb canopy cover in a 0.5 m ² quadrat placed over the nest bowl
litter	80.60 (4.40)	3.00 - 98.00	Litter cover in a 0.5 m ² quadrat placed over the nest bowl
litter depth	4.49 (0.54)	0.00 – 14.00	Litter depth in a 0.5 m ² quadrat placed over the nest bowl

vegetation height	65.49 (2.66)	26.00 - 119.00	Tallest piece of vegetation in a 0.5 m ² quadrat placed over the nest bowl
vegetation density	3.79 (0.13)	1.75 - 5.90	Cumulative score of Nudd's board reading taken at nest site
<i>Weather</i>			
maximum temperature	83.70 (1.45)	44.00 - 101.00	Daily maximum temperature recorded on site
relative humidity	71.88 (1.92)	43.00 - 98.00	Average daily relative humidity recorded on site
precipitation	0.14 (0.07)	0.00 - 4.32	Daily precipitation total recorded on site
solar radiation	23.73 (0.96)	3.45 - 30.67	Daily maximum solar radiation measured in watts/ m ² on site

Table 3. Models explaining the effects of temporal, anthropogenic, management, and local weather variables on Greater Prairie-Chicken nest survival at the Tallgrass Prairie Preserve, OK, USA, 2011-2013.

MODEL	ΔAIC_c^a	k^b	w^c	deviance
<i>Temporal models</i>				
linear trend	0.00	2	0.52	214.96
null	1.71	1	0.22	218.68
quadratic trend	1.72	3	0.22	214.66
year effects	5.09	3	0.04	218.03
<i>Anthropogenic models</i>				
null	0.00	1	0.36	218.68
distance to power-pole	0.38	2	0.30	217.05
distance to road	1.35	2	0.19	218.02
well density	1.74	2	0.15	218.41
<i>Management models</i>				
vegetation height	0.00	2	0.25	216.19

null	0.48	1	0.19	218.68
months post fire	0.69	2	0.18	216.87
litter depth	1.23	2	0.13	217.42
vegetation density	1.87	2	0.10	218.06
forb	2.29	2	0.08	218.48
litter	2.38	2	0.07	218.57

Weather models

solar radiation	0.00	2	0.71	210.73
maximum temperature	2.62	2	0.19	213.35
precipitation	5.44	2	0.05	216.17
null	5.94	1	0.04	218.68
relative humidity	7.91	2	0.01	218.63

Best models

solar radiation + veg. height ^d	0.00	3	0.29	208.50
solar radiation	0.21	2	0.26	210.73

solar radiation + linear trend	0.76	3	0.20	209.26
global	1.00	4	0.17	207.48
linear trend	4.44	2	0.03	214.96
linear trend + veg. height	4.61	3	0.03	213.11
veg. height	5.67	2	0.02	216.19
null	6.15	1	0.01	218.68

^a Akaike's Information Criterion adjusted for small sample sizes. Numbers are based on differences from the best model within each model set.

^b Number of parameters in each model.

^c Model weight.

^d AIC_c for best model = 214.54.

Table 4. Resource selection models investigating the influence of management, anthropogenic structures, and lek sites on Greater Prairie-Chickens nest site selection at the Tallgrass Prairie Preserve, OK, USA, 2011-2013.

Model	ΔAIC_c^a	k^b	w^c	deviance
fire + distance to lek + trees ^d	0.00	4	0.860	193.73
global	4.70	7	0.080	192.07
fire	5.60	2	0.050	203.45
trees	12.70	2	0.001	210.62
distance to lek	14.80	2	<0.001	212.70
null	16.00	1	<0.001	215.94
distance to road	16.20	2	<0.001	214.10
well density	17.80	2	<0.001	215.68
distance to power-pole	18.00	2	<0.001	215.92
anthropogenic	20.20	4	<0.001	213.89

^a Akaike's Information Criterion adjusted for small sample sizes. Numbers are based on differences from the best overall model.

^b Number of parameters in each model.

^c Model weight.

^d AIC_c for best model = 201.73.

Table 5. Parameter estimates for the best model describing factors that influence Greater Prairie-Chicken nest site selection at the Tallgrass Prairie Preserve, Oklahoma, USA, 2011-2013. All parameters were standardized prior to modeling so beta values indicate the relative importance on nest site selection.

Parameter	β	SE	LCI	UCI
Months post fire	0.64	0.18	0.30	1.00
Tree cover	-0.57	0.32	-1.34	-0.05
Distance to lek	-0.40	0.20	-0.81	-0.02

FIGURE LEGEND

Figure 1. Logistic regression curve showing daily survival probability for nesting Greater Prairie-Chickens as a function of A) solar radiation B) linear temporal trend and C) vegetation height at the Tallgrass Prairie Preserve, OK, USA from 2011-2013. Solar radiation and vegetation height values are based on range experienced during the course of the study. Day one of the nesting season corresponds to April 28th.

Figure 2. Conceptual model of two theoretical 10,000 ha landscapes to illuminate the differences in the relative importance of management at different scales as our nest site selection and survival results support the idea of filters acting to hierarchically influence site selection for prairie chickens. The focus of management in landscapes similar to much of the Flint Hills represented by panel A would likely benefit from management actions at finer scales because fewer filters exist to prevent prairie-chicken selection at the broadest scales (i.e., level I.), thereby leaving more land area that would be of suitable nesting cover for prairie-chickens if managed at the proper scale (i.e., altered burning regime, reduced herbicide, or reduced stocking rates). In contrast, management in landscapes similar to the Great Plains (B) would benefit from a focus on landscape scale habitat suitability with little focus on microhabitat (i.e., nesting conditions). As shown by the land area estimates and graphics, increased efforts at level III in landscape B has a maximum potential to restore 140 ha of nesting cover, whereas management at level III in landscape A has the potential to increase suitable nesting cover by 3,860 ha.

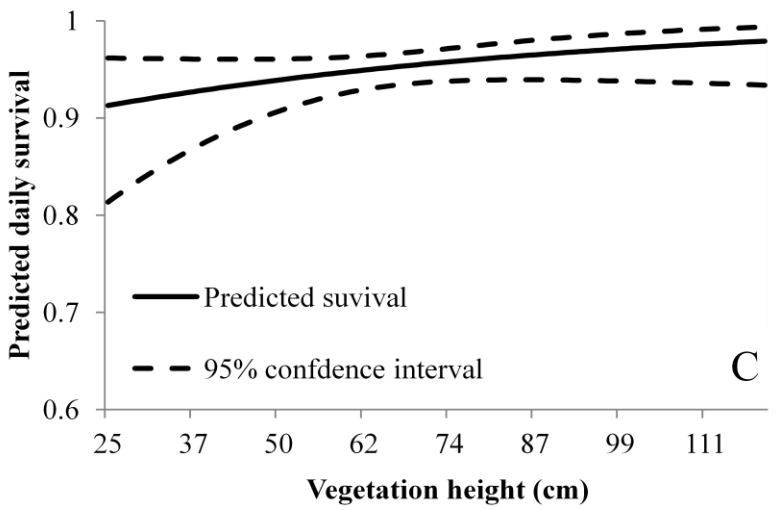
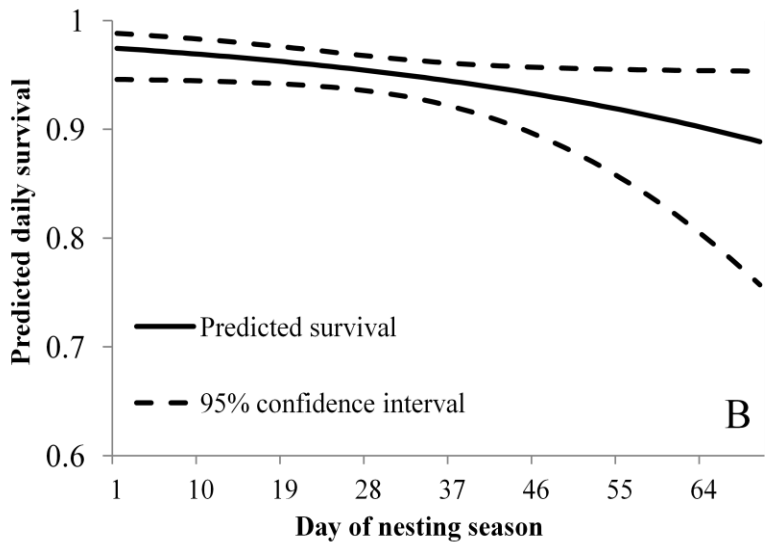
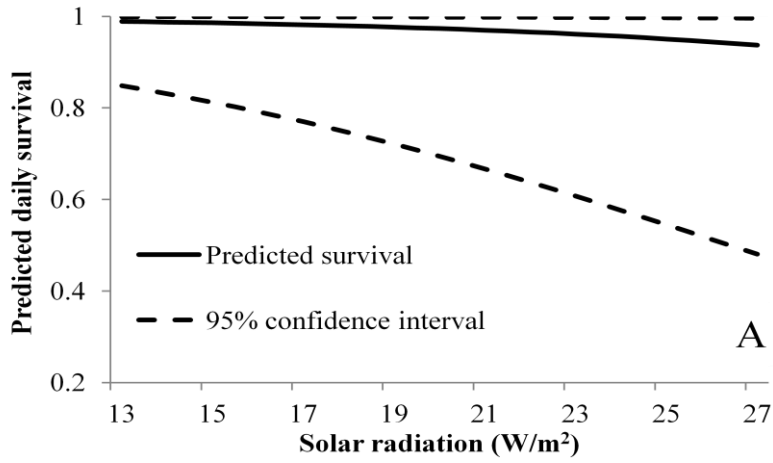


Figure 3.1.

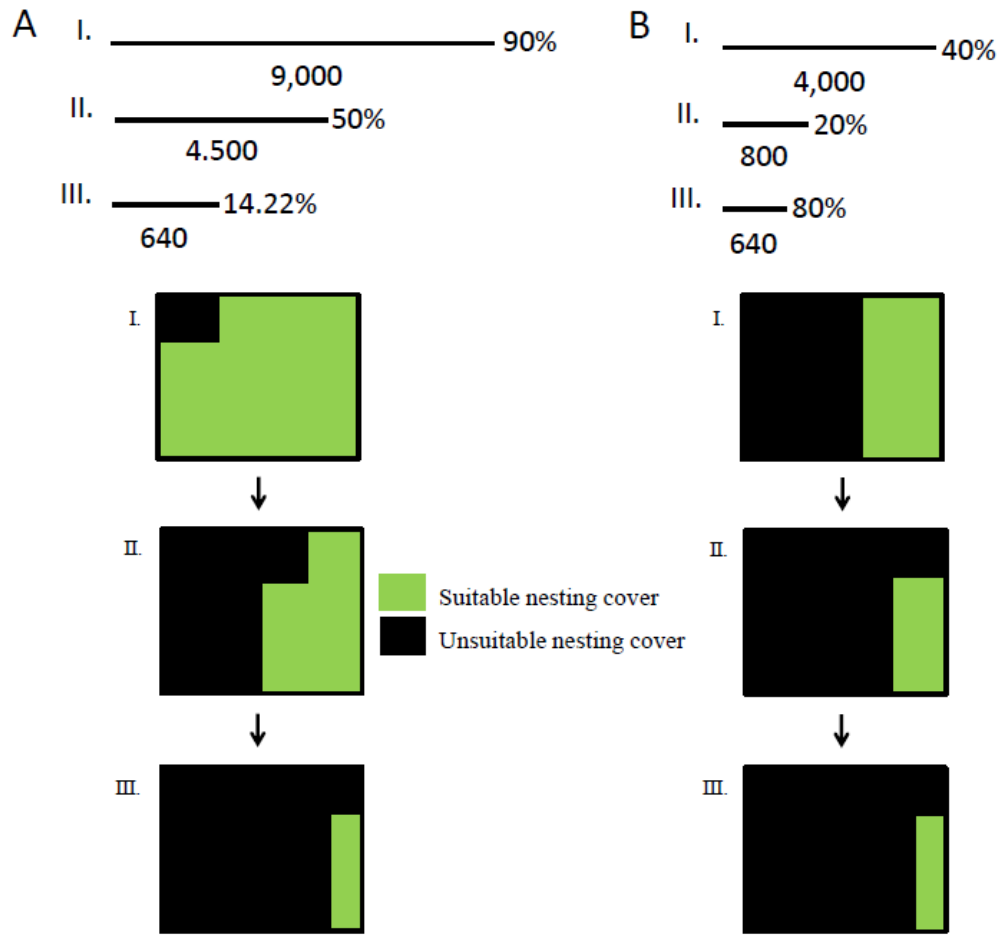


Figure 3.2.

CHAPTER IV

Spatial Heterogeneity Increases Diversity and Stability in Grassland Bird Communities

Abstract

Grasslands are inherently dynamic in space and time evolving with frequent disturbance from fire and herbivores. As a consequence of human actions, many remaining grasslands have become homogenous which has led to reduced ecosystem function, biodiversity loss, and decreased ecological services. Previous research has shown that restoring inherent heterogeneity to grasslands can increase avian diversity, but the amount of heterogeneity (i.e., number of patches or fire return interval) and the impact on avian community stability have yet to be investigated. We used a sophisticated experimental design to examine avian response to interacting fire and grazing across multiple experimental landscapes that represented a gradient of fire and grazing dependent heterogeneity. We used seven landscapes (480-900 ha) with varying levels of patchiness ranging from annually burned (one single patch) with spring only fires to a four year fire-return-interval with spring and summer fires (eight patches). This design created a range of heterogeneity as a result of pyric herbivory, an ecological process in which fire and grazing are allowed to interact in space and time. We found that greater heterogeneity across experimental landscapes resulted in increased avian diversity and stability over time. Turnover in the bird community, quantified as the sum of the range of detrended correspondence analysis axis scores, was nearly four times greater in the most homogenous pasture when compared to the most heterogeneous pasture. Heterogeneity driven by the fire-grazing interaction increased variation in the bird community within experimental landscapes and was dependent upon the number of patches. Species responses were consistently positively associated with increased heterogeneity at the pasture scale and within patch responses were most often related to litter cover, accumulation, and vegetation height. Overall, we found that increased fire and grazing dependent heterogeneity can result in high variability in the bird community at finer scales within patches but increased diversity and stability at broad landscape scales. We recommend future management efforts in rangelands focus on restored disturbance processes to increase heterogeneity and improve grassland bird conservation.

Introduction

The promotion of uniform and moderate grazing across rangelands has become a central paradigm for grassland management and while it has undoubtedly limited severe grazing on rangelands, it has greatly diminished the natural complexity of this biome (Fuhlendorf and Engle 2001). This simplification, or homogenization, of rangeland landscapes has resulted in a decline of ecosystem structure and function, ecosystem services, and overall biodiversity (Anderson 2006; Derner et al. 2009; Fuhlendorf et al. 2009). Recognition of the state of rangelands and an understanding of the importance of ecosystem complexity and heterogeneity has presented a challenge to ecologists and managers alike because it suggests the need for an alternative paradigm for ecosystem management (Fuhlendorf et al. 2012). Recent work suggests that because heterogeneity is the root of diversity (Otsfeld et al. 1997; Wiens 1997), a model for managing rangelands should promote the restoration of variability that is inherent to this system (Fuhlendorf et al. 2012). Heterogeneity in this context is derived from variability in vegetation structure, composition, density, and biomass which are highly dependent on fire and grazing processes and the interaction of these processes (Fuhlendorf and Engle 2001; Fuhlendorf and Engle 2004; Allred et al. 2011; McGranahan et al. 2012).

Historically, fire and grazing were key forces in the origin and maintenance of grass-dominated systems and their frequency, intensity, and effects have been variable in time and space at multiple scales (Steinauer and Collins 1996, Hoekstra et al. 2005). Recently, a model for managing rangelands that restores the interactive effects of fire and grazing through fire driven grazing, or pyric herbivory (Fuhlendorf et al. 2009), has shown that heterogeneity does in fact result in greater biodiversity when compared with models that promote homogeneity (Fuhlendorf et al. 2006). Pyric herbivory is an ecological process that results in a shifting grassland mosaic and heterogeneity at broad scales as

herbivores and fire interact through a series of positive and negative feedbacks (Fuhlendorf et al. 2009; McGranahan et al. 2012; Augustine and Derner 2013).

Few studies have addressed the direct influence of spatial heterogeneity on community temporal variability or how disturbance history alters the spatial scale of community stability over time (Wu and Loucks 1995; Foster et al. 2003). However, it is well supported that biological diversity contributes to ecosystem stability (Tilman 1996; Tartowski et al. 1997; Jiang and Pu 2009; Downing et al. 2014), and that biodiversity is a driver of many ecological processes and not simply a product of them (Naeem 2002). In most cases, however, the effects of diversity on stability have been investigated at lower trophic levels or highly controlled experiments and few studies have examined the effects of restored grassland heterogeneity on the stability of upper trophic levels such as the native bird community. In this circumstance, we define stability as a reduction in the temporal variability of an attribute within an ecosystem (Downing et al. 2014). Specifically, we will focus on population attributes associated with diversity of the grassland bird community (i.e., the temporal variability in species abundance and diversity).

There needs to be a better understanding of how the timing and scale of restored natural disturbance processes influence diversity and stability (Christensen 1997, Wiens 1997). It has been shown that high habitat heterogeneity can promote temporal stability through several mechanisms including stabilization of resources and increased refugia from minor disturbance or predation (Brown 2007), but this is likely depends on scale. Despite many conservation and restoration programs focused on generating and maintaining heterogeneity to promote biodiversity and system stability (Palmer et al. 1997; Benton et al. 2003; Carey 2003), there is limited empirical evidence supporting the impacts of restored heterogeneity at broad scales relevant to management or on terrestrial fauna. The implications of such research would be applicable to ecological theory and management practices simultaneously

(Micheli et al. 1999). Furthermore, a better understanding of the impacts of restored heterogeneity on community stability will improve conservation efforts because variation in community processes can decrease reliability of ecosystem processes (Naeem and Li 1997), reduce ecosystem services (Cardinale et al. 2012), and increase extinction risk (Pimm et al. 1995).

To improve our understanding of the impacts of restored heterogeneity on avian diversity, stability, and individual species abundances we investigated avian response to a gradient of fire and grazing dependent heterogeneity that resulted from pyric herbivory. We used a sophisticated experimental design across seven experimental landscapes that varied from annually burned (i.e., one patch) to a four year fire-return-interval with spring and late summer prescribed fires (i.e., eight patches). We hypothesized that greater landscape level heterogeneity would increase avian diversity and result in greater community stability over time, and that individual species abundances would vary greatly across the gradient of heterogeneity as a result of specific life history traits.

Methods

Study area

Our study took place on The Nature Conservancy's Tallgrass Prairie Preserve (TGPP) in northeast Oklahoma, USA from 2011-2013. This area comprises the southern extent of the Flint Hills region of the Great Plains and is part of the largest remaining tallgrass prairie in North America. The TGPP is a 16,000 ha area dominated by tallgrass prairie plant community. Dominant grasses include *Andropogon gerardii* Vitman, *Schizachyrium scoparium* Nash, *Panicum virgatum* L., and *Sorghastrum nutans* (L.) Nash. Dominant forbs at the preserve include ironweed (*Veronia spp.*), milkweed (*Asclepias spp.*), and ashy sunflower (*Helianthus mollis*). The climate is temperate with, with hot summers (average high of 31.4°C

for June 2011-2013) and cold winters (average low of -4.81°C for January 2011-2013). Precipitation during the growing season (Apr-Oct) was 478 mm, 624 mm, and 875 mm for 2011, 2012, and 2013, respectively.

Experimental design

Our sophisticated experimental design consisted of seven large-scale experimental landscapes within the TGPP to examine the affect of fire and grazing dependent heterogeneity on avian diversity, stability, and individual species abundances. Experimental landscapes varied in size from 430-980 ha (= 627 ha) and ranged from one patch (i.e., the entire experimental landscape) to eight patches (Fig. 1). Experimental landscapes had no interior fences and were enclosed by a single exterior fence for organizational purposes. The attraction and preference of grazing animals to recently burned areas creates structural heterogeneity and results in areas of low vegetation structure that are recently burned and grazed to areas of tall vegetation and dense litter that are unburned and ungrazed (Allred et al. 2011; McGranahan et al. 2012). Therefore, we created spatial heterogeneity within seven experimental landscapes by manipulating the number and relative size of burn patches. As patch number increases and the relative size of a patch decreases, grazing animals will concentrate more heavily on such a patch, increasing the level of heterogeneity within an experimental landscape (Allred et al., 2011). Each experimental landscape was assigned a fire return interval (i.e., 1,2,3, or 4) and a season of fire (i.e., spring only or spring and summer). Experimental landscapes with one to four patches were burned in the spring (March to April), while landscapes with four to eight patches were burned in the spring and summer (July to August). Application of fires began in 2008 and continued through 2013 and only one patch was burned per experimental landscape, season, and year. All experimental landscapes were in similar condition, with similar potential productivity.

Data collection

We used line-transect surveys to record the grassland bird community. Line transects are preferred to point counts in open habitats due to higher sampling efficiency and cryptic species are more likely to be observed (Buckland et al. 2001). We randomly placed 12, 200 m long transects in each of the 7 experimental landscapes (i.e., 84 transects total) because we were primarily interested in landscape level (to correspond to the heterogeneity gradient) responses to heterogeneity and therefore wanted equal sampling effort across experimental landscapes. Transects were placed greater than 100 m from experimental landscape borders and greater than 200 m from other transects. We conducted surveys from sunrise until 10:30 (CST), when grassland birds are most active (Ralph et al. 1993), and on days with no precipitation and wind speeds less than 15 km^{-hr}. On each transect, observers recorded every bird seen and heard within 50 m of the line. We limited observation to 50 m to maximize detectability and decrease potential observer error when identifying cryptic grassland species at long distances (Pillsbury et al. 2011). Additionally, observers recorded the species, sex, and perpendicular distance from the line for each encounter. We conducted surveys four times annually (~ every 10 days) from May 15 through July 10.

We measured plant community characteristics once each breeding season in mid June to correspond with avian surveys. We recorded vegetation at the mid-point of each transect and placed a 0.5 m² quadrat on the transect and sampled every 2.5 m in each cardinal direction for a distance of 10 m ($n = 17$ total quadrats/plot). We estimated canopy cover for the following plant functional groups: grass-like, forb, litter, bare ground, and shrub. Additionally, we measured vegetation height and litter depth in each quadrat and standardized these measurements by measuring the tallest live vegetation within each quadrat and measuring litter depth in the northwest corner of each quadrat. Finally, we measured

vegetation density using a Nudd's board adapted for grassland/shrubland use by observing the percentage of obstruction on a Nudd's profile board from a distance of 7.5 m away and an observer height of 1 m above ground level (Nudds 1977, Guthery 1981). We recorded vegetation densities in each cardinal direction at every plot.

Data analysis

We assessed grassland bird community diversity as a result of fire and grazing dependent heterogeneity at several levels. First, we focused on species diversity by calculating the Shannon Diversity index (H) at the experimental landscape level (Pillsbury et al. 2011). This diversity measure simultaneously takes into account the number of bird species present in an experimental landscape and the relative abundances of individual bird species. We overcame a potential drawback of diversity indices associated with obscured species identities by restricting our analysis to five grassland breeding birds that made up the majority of our detections. To explicitly examine the influence of heterogeneity on diversity, we ran a general linear model with the number of patches within an experimental landscape as our dependent variable and calculated diversity scores as our response variable. This approach allowed for an intuitive representation of the general effect of fire and grazing dependent heterogeneity on community level diversity.

To examine bird community composition responses and stability over time we subjected grassland bird abundance data for each experimental landscape to indirect gradient analysis using detrended correspondence analysis (DCA). DCA has been used to summarize general similarities and differences among grassland bird communities and can elucidate compositional dynamics over time (Collins 2000, Fuhlendorf et al. 2006). All analyses were conducted in Canoco 5.0 using default settings for DCA unconstrained ordination (Biometris and Šmilauer 2012). After conducting DCA we then used

loading scores for site samples (i.e., each experimental landscape and year combination) to project differences in avian community turnover over time. Differences in community composition are measured by standard deviation units, and therefore, experimental landscapes with a greater range of axis scores have the most turnover or change in the bird community, while those experimental landscapes with a smaller range in axis scores represent the most stable bird communities over time. In addition to projecting site scores to show relationships of dissimilarity in ordination space, we used the summed range of axis scores for each experimental landscape as a response variable in a general linear model to show the relationship between bird community stability and fire and grazing dependent heterogeneity.

We executed a separate DCA analysis to investigate finer scale patterns of community composition within patches. For this analysis, we performed an indirect gradient analysis using DCA on transect level bird abundances. We then used the individual DCA axis 1 site scores to calculate an average of all transects (i.e., 12 per experimental landscape) within an experimental landscape for each year of the study. Next, we calculated a standard deviation for the average site scores within each year. Then, we took an average of the standard deviation for each experimental landscape over the three years of the study and calculated a standard error of the averaged standard deviation. Finally, we used a general linear model to quantify the effect of fire and grazing dependent heterogeneity (i.e., the number of patches/experimental landscape) on transect level variation in the bird community (measured as average standard deviation across the three years of the study). Increased standard deviation in this analysis would indicate greater variability in the avian community at the transect scale over time, a result that you would expect at a fine scales within heterogeneous environments.

We addressed individual species responses to a fire and grazing dependent heterogeneity and using distance estimates from line-transect surveys and program Distance 6.0 (Thomas et al. 2010) to

calculate species-specific detection probabilities and densities. We then used density estimates to create general linear models for each of the five most abundant obligate breeding grassland bird species (sensu Vickery et al. 1999). We ran two linear models for each of the five species to assess the influence of the number of patches (i.e., level of heterogeneity) and the effect of fire return interval on individual species abundances. We realize that fire return interval and the number of patches are highly correlated (i.e., greater fire return intervals in this study will increase the number of patches), but to make our results most applicable to future conservation, separate analysis on the number of patches (heterogeneity) and fire return interval makes our results more interpretable.

Finally, we used transect level vegetation data to examine the influence of fine-scale, vegetation structure and composition that result from disturbance processes on individual species abundances. To do this, we used univariate general linear models that could explain relationships between individual species abundances and vegetation parameters that were measured at breeding bird transects. We used transect level vegetation parameters and species abundances because using landscape level means would average away the variation in patch level differences that are likely responsible for species selection of specific patch types that result from variable timing of fire and grazing processes. We ran a series of eight models for all five species of interest. After calculating Pearson correlation coefficients for vegetation components and removing those with values >0.60 , we only present the outcomes of models for the five uncorrelated vegetation parameters.

Results

We detected 5,534 individuals of 35 different bird species. Of the species detected, 12 were obligate grassland breeding birds, 10 were facultative grassland breeding birds, and 13 were shrubland, forest, or wetland associated species. However, the grassland bird community was dominated by five species that

made-up nearly 94% of all detections. The most frequently encountered species were Dickcissel (*Spiza americana*), Grasshopper Sparrow (*Ammodramus savannarum*), Eastern Meadowlark (*Sturnella Magna*), Henslow's Sparrow (*Ammodramus henslowii*), and Upland Sandpiper (*Bartramia longicauda*). No other species accounted for $\geq 1\%$ of the total detections. Therefore, all of our analyses focused on the five most abundant grassland breeding birds which have the greatest potential of being affected by varying levels of fire and grazing dependent heterogeneity.

Analysis of our seven experimental landscapes demonstrated that the grassland bird community is strongly dependent on the number of patches in the landscape and increased heterogeneity resulted in greater species abundances for nearly all species that we examined. Additionally, grassland heterogeneity, quantified as the variation in vegetation components, generally increased at the landscape scale with an increase in the number of patches within experimental landscapes (Fig. 2). As a result, we found a significant, positive linear relationship between landscape level spatial heterogeneity (patches) and grassland bird community diversity (Fig. 3).

Our examination of the bird community using DCA explained $>87\%$ of the variation in the grassland breeding bird community at the landscape level (Fig. 4A). Moreover, modeling of site scores from DCA showed there was a strongly significant, negative relationship between grassland bird community turnover and the number of patches in an experimental landscape (Fig. 4B), indicating increased heterogeneity at landscape scales resulted in more stable bird communities over time. In fact, the most homogenous experimental landscape experienced nearly four times greater turnover in the grassland bird community than the most heterogeneous experimental landscape across the three years of the study.

We found that greater heterogeneity resulted in increased variability over time within patches in our experimental landscapes (Fig. 5). In other words, experimental landscapes with the greatest

number of patches had transects with greater variation in the bird community over time. Transects in the experimental landscapes with the greatest number of patches averaged 0.48 standard deviation units across the three years ($SE \pm 0.10$) while the transects in the experimental landscapes with the fewest patches only averaged 0.15 standard deviation units ($SE \pm 0.01$). This result is reflected in the variation of vegetation parameters at a landscape level—experimental landscapes with few patches have little variability (i.e., range in SD) in vegetation parameters, while experimental landscapes with many patches have the most variable vegetation as a result of out-of-sequence successional recovery (Fig. 2).

The strength of individual species responses to heterogeneity varied, but four of the five focal species showed statistically significant or near significant increases in abundance as a result of increased heterogeneity at broad, landscape level scales (Fig. 6). Dickcissels, a generalist species and the most frequently detected bird in this study, were the only breeding bird examined that did not show a significant response to fire return interval or the number of patches in an experimental landscape. Three of five species examined had significant positive relationship with an increasing number of patches (i.e., heterogeneity) and variation in Henslow's Sparrow abundance was best explained by fire return interval (Fig. 6).

Within patches we found that litter cover, litter depth, and vegetation height were significant in explaining breeding bird abundances for most species (Table 1). Dickcissel, Henslow's Sparrow, and Eastern Meadowlark all showed positive relationships with litter depth or litter cover within patches while Grasshopper Sparrow abundance decreased with increasing litter depth, and Upland Sandpiper abundance was most explained by a negative association with vegetation height (Table 1).

Discussion

Grassland bird diversity was strongly correlated with increased heterogeneity and nearly all species reached maximum abundances in the most heterogeneous experimental landscapes. Many studies have reported a positive relationship between diversity and community stability (Tilman 1996; Brown 2003; Ives and Carpenter 2007; Jiang and Pu 2009; Downing et al. 2014), but few have examined how management actions relate to stability at upper trophic levels or across large landscapes. Our results give new evidence supporting the role of heterogeneity in the conservation of biodiversity and community stability in rangeland systems and substantiate the claims that spatial and temporal heterogeneity and complexity are critical elements in ecosystem function (Christensen 1997). This study used a sophisticated experimental design to overcome the traditional focus on binary statistics associated with heterogeneous versus homogenous conceptualizations, and it addressed the call for greater attention to complex landscape mosaics that examine how organisms respond to a gradient of patchiness (Wiens 1997). Furthermore, our results provide direct application to management as a result of our landscape scale real-world experimental design and stress the importance of variable disturbance patterns to improve conservation of breeding grassland birds.

We found that fire and grazing dependent heterogeneity increased variability in vegetation cover and structure at landscape scales. Differential timing of disturbance across the landscape creates a corresponding out-of-phase succession in vegetation within patches which in turn is responsible for greater heterogeneity at broad spatial scales and increased temporal heterogeneity at fine spatial scales (Fuhlendorf et al. 2006; Derner et al. 2009). This spatial heterogeneity of vegetation structure provides greater breadth of suitable niches for grassland bird species and increases the variety of grassland bird communities that can occur across the landscape (Fuhlendorf et al. 2006, Gregory et al. 2010, Little et al. 2012). Additionally, maximizing niche breadth can buffer against environmental shocks or threats

associated with predation and resource shortages (Brown 2003; Ives and Carpenter 2007). As a result, we found that experimental landscapes with greater heterogeneity had less turnover (measured as by variation in DCA axes 1 and 2) while those with more homogeneous structure experienced greater community turnover. This finding supports previous recommendations to increase the diversity of management practices used in the Great Plains to overcome the current state of homogeneity and improve grassland bird conservation (Rahmig et al. 2009).

Increased temporal stability in the avian community with increased landscape level heterogeneity may be explained through multiple mechanisms including increased resources and refugia and could be the result of a phenomenon commonly referred to as the portfolio effect—as the community diversifies, constancy increases over time (Doak et al. 1998; Tilman et al. 1998). Analogous to advice given by a financial consultant, the portfolio effect refers to increasing diversity so that the aggregate value (i.e., diversity, biomass, etc) will be less variable through time. In this case, patch diversity at broad scales created suitable environments that elevated species richness in the most heterogeneous experimental landscapes thereby creating a temporally stable avian community because of the complimentary or independent dynamics among species that perform similar ecosystem functions (Schindler et al. 2010).

Because heterogeneity is largely associated with spatial and temporal variability it is highly scale dependent and should be evaluated across several scales (Fuhlendorf and Smiens 1999). To address this, we examined community dynamics at the transect scale in addition to landscape scales. We found a strong positive association with transect level variation in species abundance and the number of patches in an experimental landscape. In other words, at fine scales heterogeneity increased temporal variability in the grassland bird community, but at broad spatial scales heterogeneity resulted in greater temporal stability. This fine-scale variation over time occurs as some specialized species select areas of low stature

grazing lawns in recently burned patches (i.e., Upland Sandpiper) while other species primarily select tall, mature unburned patches that occur through time as patches succeed post disturbance (i.e., Henslow's Sparrow). As a result, within patch diversity is high over time but low within a patch in a given breeding season. This temporal heterogeneity within patches demonstrates the dependence of grassland birds on disturbance and illustrates the variation in species composition as succession takes place over time.

Within patch selection was best explained by fine scale habitat associations at the transect scale which illustrated that litter cover, litter depth, and vegetation height were the most influential parameters affecting individual species abundances. Grassland birds select nesting habitats with very specific characteristics which suggests they evolved in grassland environments with highly variable disturbance regimes that created structurally diverse habitats (Cody 1985; Knopf 1996). Despite the specific affinities of each species for certain vegetation structure, no species reached maximum abundances in an experimental landscape with limited heterogeneity. This suggests that patches within the most heterogeneous experimental landscape create optimal nesting conditions, or that species may inherently select for more diverse landscapes because they can provide stabilization of resources and increased refugia from potential environmental stressors (Brown 2007).

Maintaining and restoring spatio-temporally variable disturbances that produce heterogeneity in herbaceous systems has increased diversity in multiple taxa (Fuhlendorf et al. 2006; Engle et al. 2008; Fuhlendorf et al. 2010), and has frequently been suggested as the best method to promote the conservation of grassland bird communities (Askins 2000, Walk and Warner 2000). This study now provides an approach that allows conservationists and land managers to understand how specific disturbance regimes can maximize individual species abundances, and perhaps more importantly, this research illustrates the significance of heterogeneity at broad scales to optimize avian diversity and

stability. Furthermore, our results on add to the growing body of work supporting the role of diversity in community stability and ecosystem function (Brown 2003; Loreau et al. 2003; Isbell et al. 2009; Downing et al. 2014).

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Table 1. Results of univariate regression showing the influence of vegetation components on grassland bird abundance within patches in experimental landscapes managed with pyric herbivory at the Tallgrass Prairie Preserve, Oklahoma, USA from 2011-2013. Univariate results indicate that most species are significantly impacted by litter accumulation and vegetation height—two components that are greatly influenced by fire and grazing processes within patches and moderated across experimental landscapes with multiple patches.

Vegetation component	Dickcissel		Grasshopper Sparrow		Eastern Meadowlark		Henslow's Sparrow		Upland Sandpiper	
	Estimate	r^2	Estimate	r^2	Estimate	r^2	Estimate	r^2	Estimate	r^2
Grass cover	0.05	0.02	-0.001	< 0.001	0.02	0.02*	0.06	0.14*	-0.008	0.02*
Forb cover	0.10	0.08*	-0.003	< 0.001	-0.001	< 0.001	-0.02	0.02*	-0.003	0.005
Litter cover	0.05	0.08*	< 0.001	< 0.001	0.02	0.06*	0.04	0.30*	-0.005	0.05*
Litter depth	0.49	0.06*	-0.18	0.04*	0.02	< 0.001	0.51	0.40*	-0.05	0.04*
Veg. height	0.23	0.27*	-0.02	0.009	0.02	0.02*	0.08	0.22*	-0.02	0.13*

* Denotes significance at p-value ≤ 0.05 .

Figure Legend

Figure 1. Experimental design at The Nature Conservancy's Tallgrass Prairie Preserve used to examine the influence of a gradient of fire and grazing heterogeneity on the grassland breeding bird community. Each box represents an exterior fence of an experimental landscape and below it we have included the number of patches within each landscape and the fire-return-interval (parenthetically). Dashed lines are hypothetical patch divisions created by discrete fire and focal grazing; no experimental landscape had interior fencing.

Figure 2. Landscape level vegetation heterogeneity shown as standard deviation of vegetation components measured along each breeding bird transect in experimental landscapes ranging from one to eight patches at the Tallgrass Prairie Preserve, OK, USA. Fire return interval for each experimental landscape given parenthetically.

Figure 3. Grassland bird community diversity represented as Shannon's Diversity Index in response to fire and grazing dependent heterogeneity across seven experimental landscapes at the Tallgrass Prairie Preserve, OK, USA.

*Denotes experimental landscape with two year fire return interval and spring and summer seasons of fire.

Figure 4. A) Bi-plot of detrended correspondence analysis showing axis 1 and axis 2 loadings of site scores representing bird community dissimilarity across a gradient of fire and grazing dependent heterogeneity at the Tallgrass Prairie Preserve, OK, USA. Polygons were formed by connecting the site scores for each experimental landscape for all three years of the study. Numbers in the center of polygons represent the number of patches resulting from pyric herbivory.

† Experimental landscape with four year fire return interval and spring only fire.

‡ Experimental landscape with two year fire return interval and spring and summer fires.

B) Sum of the range of detrended correspondence analysis axis 1 and axis 2 site scores as a function of fire and grazing dependent heterogeneity. A strong, negative relationship between the sum of axes scores and heterogeneity signifies less turnover in the avian community at landscape scales when more heterogeneity is present.

Figure 5. The standard deviation of detrended correspondence analysis axis 1 scores from within patch analysis showing grassland bird community variation as a function of the number of patches in seven experimental landscapes at the Tallgrass Prairie Preserve, OK, USA. Variation within patches increased with increasing heterogeneity and began to level-off in experimental landscapes with the greatest number of patches. Error bars are standard error.

Figure 6. The response of individual species to fire return intervals and the number of patches within an experimental landscape at the Tallgrass Prairie Preserve, OK, USA.

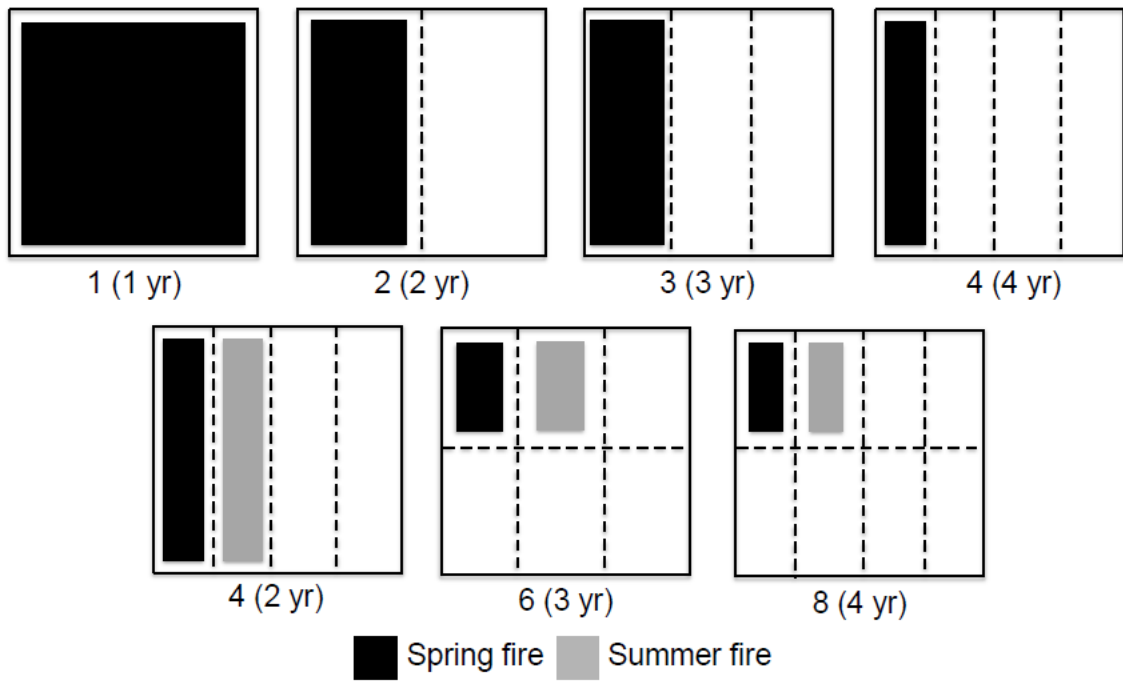


Figure 4.1.

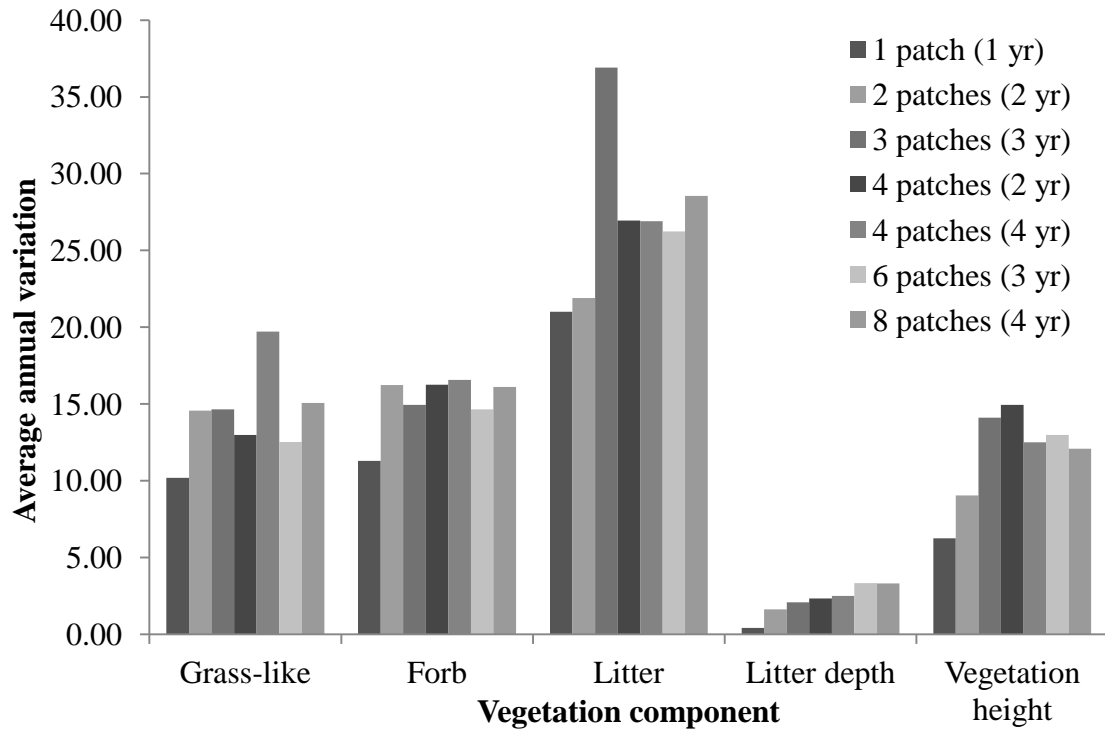


Figure 4.2.

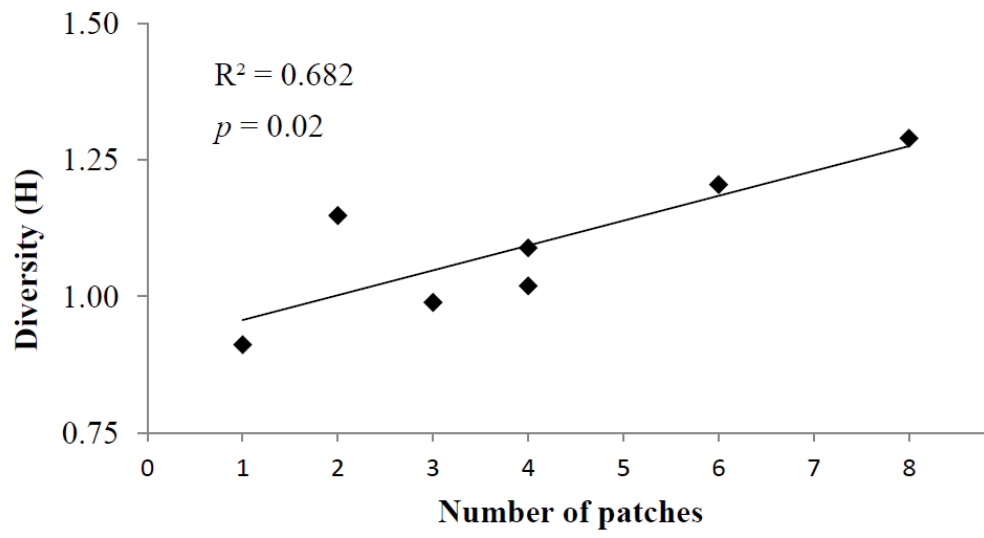


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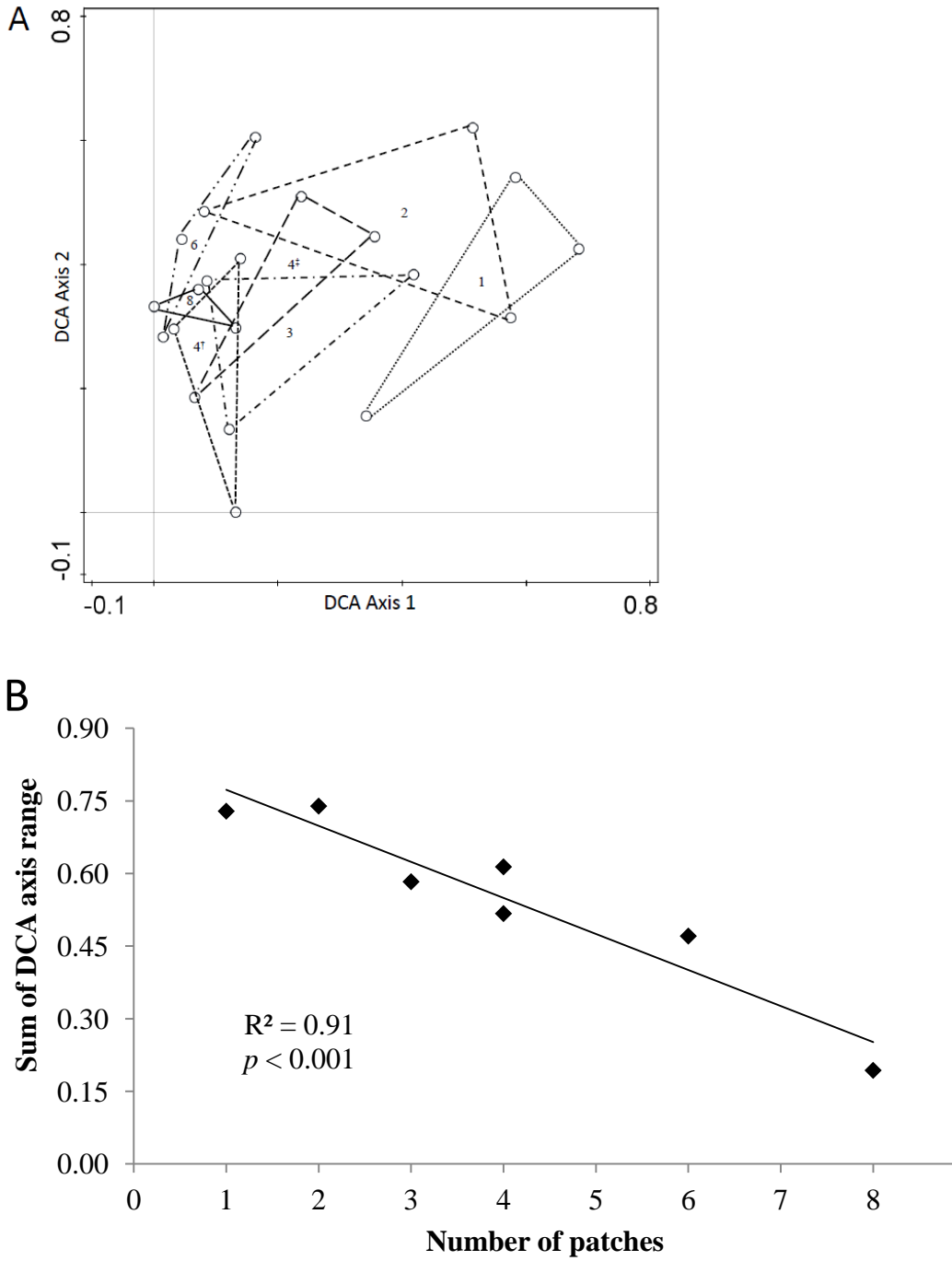


Figure 4.4.

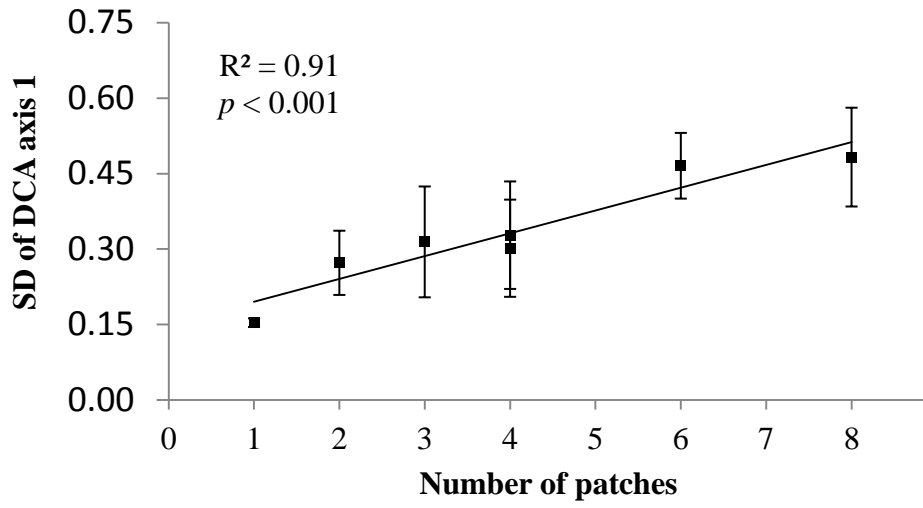


Figure 4.5.

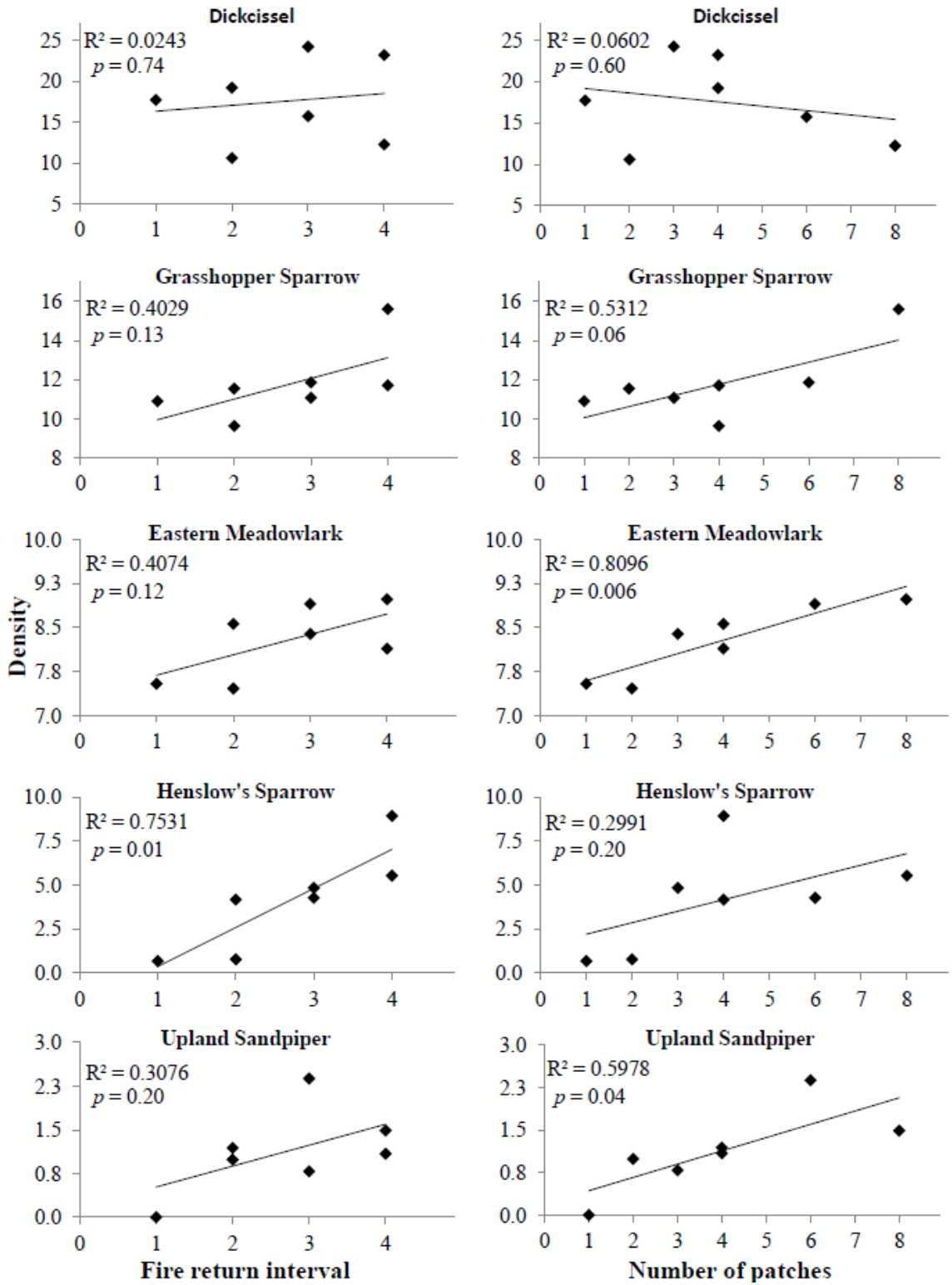


Figure 4.6.

VITA

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