

## Landscapes as a moderator of thermal extremes: a case study from an imperiled grouse

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**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.

**Key words:** climate change; fire; grazing; operative temperature; pyric herbivory; tallgrass prairie; *Tympanuchus cupido*.

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### 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 Clark 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 Clark 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 (Gabrielsen et al. 1991, Swain 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 m<sup>2</sup> quadrat centered over black spheres both at the nest bowl and the surrounding micro-sites. Additionally, we mea-

sured 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., 12:00–04:00 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 (°C) and solar radiation (watts/m<sup>2</sup>) 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 environ-

ments 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 ~3°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 ~5°C cooler at peak daytime temperatures than micro-sites (Fig.

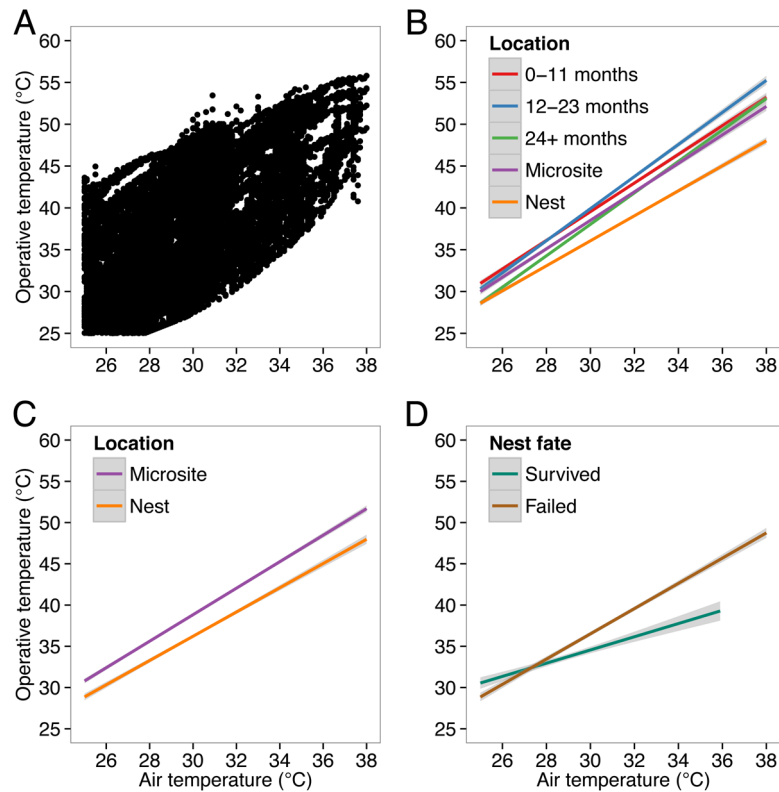


Fig. 1. (A) Modeled data showing range of operative temperatures that result when air temperatures are  $\geq 25^{\circ}\text{C}$  in tallgrass prairie managed with interacting fire and grazing. (B) Linear models of landscape patches from time since focal disturbance (i.e., fire and grazing), micro-site, and nest operative temperatures using modeled data. (C) Differences between nests and micro-sites within two meters of the nest bowl. Nests were nearly  $4^{\circ}\text{C}$  cooler at  $36^{\circ}\text{C}$  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  $6^{\circ}\text{C}$  cooler at  $36^{\circ}\text{C}$  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.

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). Parameter abbreviations:  $T_{\text{air}}$  = air temperature;  $S_{\text{rad}}$  = solar radiation.

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

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 3–6°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°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

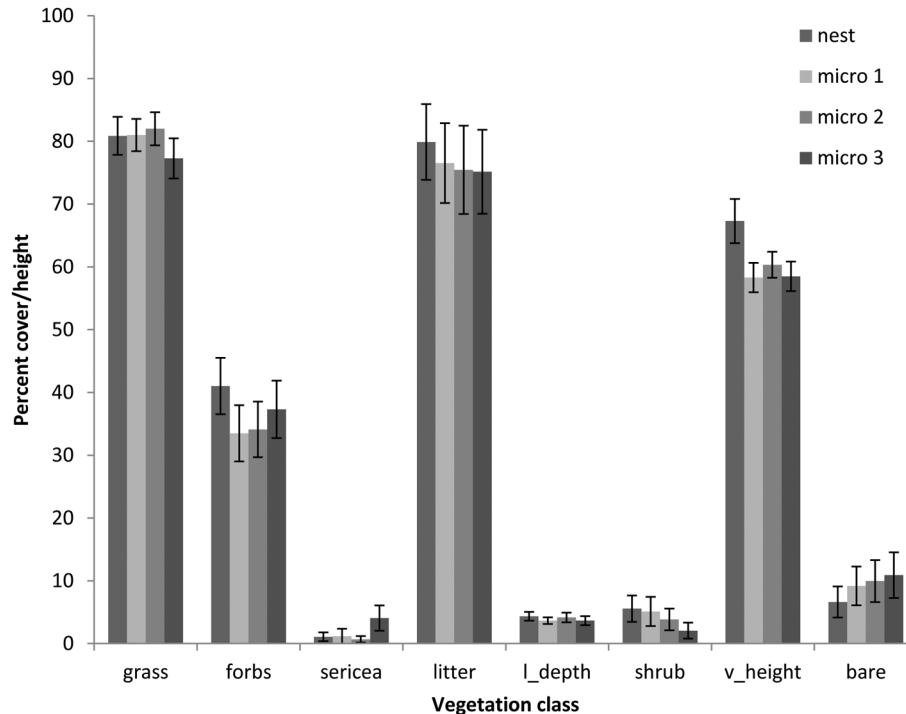


Fig. 2. Vegetation characteristics ( $\pm$ SE) measured at nest sites and micro-sites at the Tallgrass Prairie Preserve, Oklahoma, USA (2011–2012).

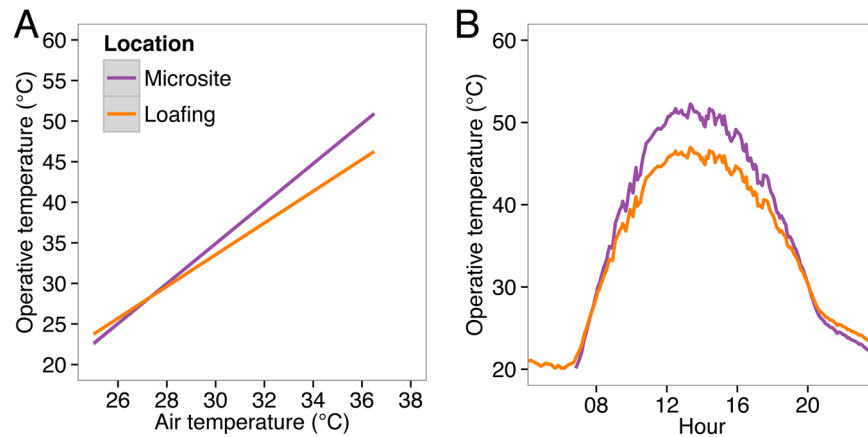


Fig. 3. (A) Linear model of operative temperature as a function of air temperature at mid-July loafing sites and surrounding micro-sites of Greater Prairie-chickens. (B) Average hourly operative temperature at loafing sites and the surrounding micro-sites during mid-July at the Tallgrass Prairie Preserve,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

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

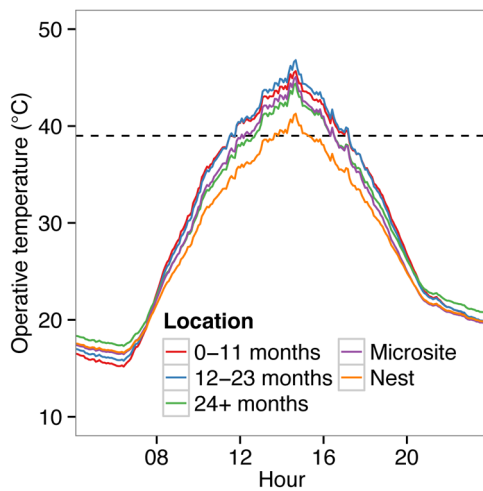


Fig. 4. Average hourly daytime operative temperature for the landscape (separated as patches resulting from time since focal disturbance), micro-sites, and nests at the Tallgrass Prairie Preserve, Oklahoma, USA (2011–2012). The dotted line represents a hyperthermic threshold (39°C) at which prairie grouse potentially become hyperthermic (i.e., physically incapable of dissipating heat) and must seek a cooler environment.

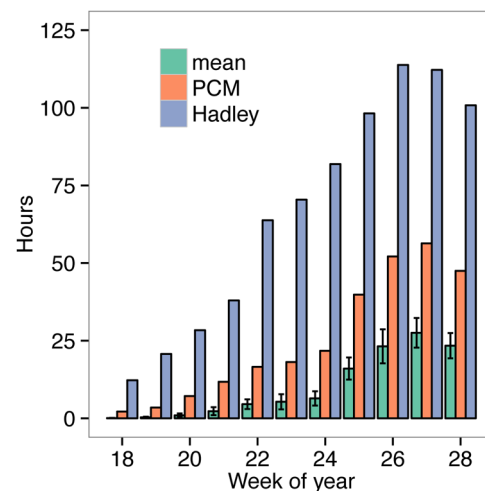


Fig. 5. Thermal stress on incubating females measured as the number of hours/week that exceeds 31°C air temperature. Bars represent the long term mean temperatures from 1 May–15 July for 1994–2012 ( $\pm$ SE), and the projected stress on hens as determined by the high emissions end-of-century scenarios 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).



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 (Holecheck 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 and Wardell-Johnson 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°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 (Larson 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  $p > 0.05$ ) 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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