CONNECTING ENVIRONMENTAL AND MANAGEMENT FACTORS WITH NORTHERN BOBWHITE (COLINUS VIRGINIANUS) MOVEMENT AND HABITAT USE

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Abstract: Temperature is highly variable across space and time at multiple scales, shapes landscape pattern, and dictates ecological processes. Recently, gaining knowledge on the thermal ecology of vulnerable species has been a major focal point of ecological studies, and this focus has been heightened by predicted temperature increases associated with global climate change. For example, although ground nesting birds are susceptible to heat extremes across many reproductive stages (i.e., nesting, brood-rearing), the mechanistic drivers of site selection for these species are not well established, especially from a thermal perspective. We characterized the thermal landscape and assessed site selection of a small ground-dwelling bird species (northern bobwhite; *Colinus virginianus*, hereafter bobwhite) during two life stages. Specifically, we measured black bulb temperatures (T_{bb}) at random stratified points (n=312), bobwhite nest sites (n=87) and brood locations (n = 266) at the Packsaddle WMA in western Oklahoma, USA. We observed that the landscape was thermally heterogeneous and exhibited variation in T_{bb} up to 40˚C during peak diurnal heating, demonstrating a wide array of thermal choices available to nesting and brood-rearing bobwhites. The landscape also displayed a prevalence for thermal extremes (i.e., T_{bb} >50˚C), which were substantially moderated by tall woody cover. Accordingly, bobwhites selected nest and brood sites that substantially moderated T_{bb}. For example, nest sites moderated T_{bb} by more than 12˚C compared to random landscape sites, and successful nests remained on average 6˚C cooler than unsuccessful nests on days experiencing ambient temperatures ≥ 39˚C. At 15:00 h, broods selected thermal refuges that moderated T_{bb} on average 10.4˚C more than landscape sites and exhibited behavioral thermoregulation through reduced movement and by occupying more moderate microclimates in taller woody cover. Our modeled climate projections suggest that future thermal extremes will increase in intensity and extent across the landscape, as well as, at bobwhite nest and brood sites. These results highlight how landscapes can moderate thermal extremes and demonstrate how thermal complexity at organism-specific scales can dictate habitat selection. In the future, the management of thermal space for ground-nesting birds should focus on providing structural heterogeneity to promote thermal choices across life stages.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

LANDSCAPE PATTERN IS CRITICAL FOR THE MODERATION OF THERMAL EXTREMES

Abstract

Temperature is highly variable across space and time at multiple scales, shapes landscape pattern, and dictates ecological processes. While our knowledge of ecological phenomena is vast relative to many landscape metrics, thermal patterns which shape landscape mosaics are largely unknown. To address this disconnect, we investigated the thermal landscape across multiple temporal and spatial scales. Specifically, we assessed black bulb temperature (T_{bb}) at intervals as small as 15 min across 3 years and compared that to vegetation structure. We found that the thermal landscape was highly heterogeneous and displayed a prevalence for thermal extremes (i.e., T_{bb} >50˚C). During peak diurnal heating (14:00) tall woody cover moderated T_{bb} by 7˚C times X's more than bare ground, herbaceous or low woody cover. When ambient temperature (T_{air}) exceeded 40˚C, 98.4%, and 73.3% of T_{bb} measurements were ≥40˚C and ≥50˚C, respectively. Our findings demonstrate that local interactions between vegetation and temperature can create thermal patterns that shape dynamic landscape mosaics across space and time, and that very small portions of the landscape can be substantially buffered from thermal extremes. Landscape heterogeneity maximizes thermal complexity across landscapes providing greater potential thermal options for organisms. However, modeled climate projections suggest that far greater thermal extremes will be possible across increasingly larger swaths of the landscape in the future making such assessments increasingly critical.

Introduction

Abiotic and biotic components of landscape structure (e.g., vegetation and terrain features) shape landscape pattern, and in turn, drive ecological processes (Turner et al. 2001). For example, the juxtaposition of thermal patterns across space and time influence ecosystem function by dictating decomposition, nutrient cycling, evaporation, and heat flux (Hobbie et al. 1996, Rosenberg et al. 1983). Fine scale thermal and heat flux (Hobbie et al. 1996, Rosenberg et al. 1983). Fine scale thermal environments also regulate the life stages, daily activity, and thermoregulation of organisms (Sartorius et al. 2002, Angilletta 2009, Sears et al. 2011). Consequently, both regional distributions of plants and animals, as well as fine scale constraints on the movement and resource use of individual organisms are simultaneously dictated by thermal patterns (Peterman and Semlitsch 2013, Lawson et al. 2014). Despite influencing a variety of ecological phenomena, as well as being subject to scale dependency and high variability across space and time, temperature remains an understudied component of landscape pattern (Saunders et al. 1998, Faye et al. 2014).

The distribution of possible temperatures across landscapes are considerably broader than the thermal tolerances of most organisms (Gilchrist 1995). As a result, the spatial variation of microclimate (i.e., thermal heterogeneity) dictates how and when organisms utilize landscape patches based on their thermal preferences and limits (Campbell and Norman 1998, Angilletta 2009). Microclimate is formed by the collective effects of physical factors such as ambient temperature, solar radiation, and wind that determine the thermal conditions near ground level (Porter and Gates 1969, Rosenberg et al. 1983). Importantly, the survival of some individuals is often contingent upon the immediate accessibility of thermally-moderated microclimates (i.e., refuges) during extreme heat events (Suggitt et al. 2011). Further, species persistence requires regional landscape features that shelter populations from climatic extremes (i.e., refugia) (Ashcroft et al. 2010). Identifying both local thermal refuges and broad scale thermal refugia requires an understanding of the capacity of landscapes to buffer against thermal extremes, and accordingly has become a topic of significant importance recently in ecological studies (Keppel and Wardell-Johnson 2012, Moritz and Agudo 2013year, Hovick et al. 2014).

Ecosystem function and biological diversity are widely accepted as being affected by heterogeneity (Christensen 1997, Wiens 1997, Fuhlendorf et al. 2006). Patchiness of vegetation structure remains the most commonly investigated facet of heterogeneity, however, other fundamental aspects such as microclimate have received less attention (Limb et al. 2009). In addition to terrain features (i.e., slope and aspect) which influence thermal mosaics (Bennie et al. 2008), the spatio-temporal variation of microclimate across landscapes is strongly influenced by the interaction of temperature and vegetation structure and composition (Saunders et al. 1998, Jenerette et al. 2011, Shut et al. 2014). Consequently, the resulting configuration of thermal environments dictates the options available to organisms, especially during extreme temperatures (Guthery et al. 2005, Carroll et al. 2015). For example, discrete woody plants can substantially modulate fine scale thermal environments through blocking solar radiation (Vetaas et al. 1992) and provide critical thermal refuge for taxa, ranging from ectothermic reptiles (Attum and Eason 2006, Attum et al. 2013) to endothermic birds (Hiller and Guthery 2005, McKechnie et al. 2012, Carroll et al. 2015) and mammals (Chappell and Bartholomew

1981, van Beest et al. 2012). Although it is acknowledged that the interaction between vegetation and temperature is scale dependent (Saunders et al. 1998), the magnitude and spatio-temporal variation of thermal buffering resulting from this interaction is poorly understood. Much of this lack of understanding is a byproduct of past research which has typically focused on large scale climate variation across regions, with much less attention given to examining the relationship between vegetation and climate at local patch scales (Weiss et al. 2004). In fact, recognition of how landscape patterns vary at multiple scales is critical for investigating the complexities of ecological processes (Price et al. 2010, Price et al. 2013, Seabrook et al. 2014). Therefore, the common practice of examining thermal landscapes at ≥1 km scales can overlook fine scale variation in thermal patterns resulting from site-specific factors (Suggitt et al. 2011, Logan et al. 2013, Potter et al. 2013). Overcoming this discrepancy is especially important given that determining the scales at which organisms make selection choices is a key question in landscape ecology (Wiens 1989, Graf et al. 2005, Jackson and Fahrig 2012).

Understanding the thermal heterogeneity present across landscapes is critical now and will become more critical in the future due to climate change. Increases in both the frequency and intensity of extreme temperature events due to climate change (IPCC 2013) are predicted to alter the pattern juxtaposition of thermal environments across landscapes (Opdam and Wascher 2004). Already, temperature increases and thermal extremes have been implicated in the reduced fitness and survival of a wide range of species (Sinervo et al. 2010, du Plessis et al. 2012, Moses et. al 2012), and these negative impacts are predicted to worsen (Huey et al. 2010, Sinervo et al. 2010, du Plessis et al. 2012, Cunningham et al. 2013, Moses et. al 2012). For example, broad scale increases in thermal extremes have already been shown to translate to fine scales, causing cascading effects within lizard species whereby constraints on activity (e.g., growth, reproduction, feeding) have led to actual species extinctions (Sinervo et al. 2010). Nonetheless, information on how broad scale shifts in regional climates manifest at local scales is scarce (Parmesan 2006, Varner and Dearing 2014), but will be integral for assisting ecologists in disentangling the complex ways that these changes will occur (Helmuth et al. 2005, Angilletta 2009). Moreover, an understanding of the location and timing of climate change impacts on ecological communities remains largely unclear (Helmuth et al. 2005), especially regarding the role of landscapes as moderators of thermal extremes (Sears et al. 2011, Potter et al. 2013).

The purpose of this study was to investigate the relationship between local variation in thermal environments (abiotic) and vegetation structure (biotic), and the resulting landscape mosaics that they synergistically produce. To accomplish this, we assessed site-specific factors influencing spatial and temporal variability in landscape configuration (i.e., temperature and vegetation structure) under a range of thermal conditions, and up-scaled those measurements to elucidate landscape patterns (Liang and Schwartz 2009, Guillevic et al. 2012). Finally, we modeled how thermal patterns may be altered under future climate change projections in order to provide a linkage between complex thermal landscapes and anticipated changing environmental conditions.

Methods

Study Area

Our study site is located on the 7,956 ha Packsaddle Wildlife Management Area (WMA) managed by the Oklahoma Department of Wildlife Conservation in western Oklahoma. Precipitation ranges from 241.81 - 746.6 mm, with an average of 554.4 mm per year from 1994 – 2013 for this location (Arnett Oklahoma Mesonet Site; Oklahoma Mesonet 2013). Prone to high heat events, summer temperatures in the region can reach an average of 25 days per year > 37.8˚C (Arndt 2003).

The vegetation in this landscape consists of shrubs and mixed grasses and is dominated by sand shinnery oak (*Quercus havardii*). In addition to sand shinnery oak, other shrubs include sand sagebrush (*Artemisia filifolia*), sand plum (*Prunus angustifolia*) and aromatic sumac (*Rhus aromatica*) (DeMaso et al. 1997, Vermeire and Wester 2001). Herbaceous plants include little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), sideoats grama (*Bouteloua curtipendula*), blue grama (*Bouteloua gracilis*), western ragweed (*Ambrosia psilostachya*), Texas croton (*Croton texensis*) and prairie sunflower (*Helianthus petiolaris*) (DeMaso et al. 1997, Peterson and Boyd 1998). Tall woody cover primarily consists of sand shinnery oak mottes (≥ 2 m in height), but also hackberry (*Celtis occindentalis*), soap berry (*Sapindus drummondii*), black locust (*Robinia pseudoacacia*) and cottonwood (*Populus deltoides*). The terrain on the study area is generally flat to rolling.

Data Collection

Data were collected during summers of 2012-2014. To quantify patterns in thermal environments (i.e., thermal heterogeneity) and to assess the distribution of temperatures under thermal extremes, we measured black bulb temperature (T_{bb}). By combining ambient temperature, solar radiation, and wind effects into a single numeric index, T_{bb} provides a proxy for environmental conditions and can be used to evaluate variation in microclimates across the landscape (Porter and Gates 1969, Campbell and Norman 1998). It is closer to the thermal conditions that an organism experiences than ambient temperature (Helmuth et al. 2010). We used steel spheres painted flat black (hereafter, black bulbs) and placed them at ground level (101.6 mm-diameters; 20 gauge thickness) to measure T_{bb} (Guthery et al. 2005, Allred et al. 2013, Hovick et al. 2014). Each black bulb was fitted with a temperature probe suspended in the center and connected to a HOBO U12 data logger (Onset Corporation, Bourn, Massachusetts, USA) which recorded T_{bb}.

Because biophysical and ecological detail is reduced when studies rely solely on broad scale climate parameters to generalize fine scale thermal environments (Sears et al. 2011, Duarte et al. 2012), we quantified site-specific T_{bb} within diurnal periods. To assess spatial variation in thermal patterns across the landscape, we used a stratified random sampling approach to distribute sampling locations proportional to available vegetation cover classes and across the distribution of slope and aspect features within the study area as mapped using ArcGIS 10.3 (Environmental Systems Research Institute, Redlands, California, USA). Vegetation cover was assessed using an IKONOS multispectral image with 2 m spatial resolution collected during summer 2013.

Specifically, a supervised classification using 125 points with known vegetation cover was used to create and train a thematic layer of cover classes on the study area. The resulting map was further refined through ground-truthing at 215 points prior to and following map creation. Cover classes were categorized as bare ground, herbaceous, low woody and tall woody (≥2 m). To evenly distribute points across the available slope and aspect features on the study area, we calculated spatial topographic variables using ArcGIS 10.3 (ESRI, Redlands, California, USA). Specifically, we used a 1/3 arc second Nation Elevation Dataset (10 m resolution; https://gdg.sc.egov.usda.gov/) Digital Elevation Map (DEM) to calculate aspect (0-360˚) and slope (0-90˚). The range of terrain aspect at sampling points (0 - 337˚) was similar to that available on the landscape (0 - 358˚). Terrain slope at sampling points ranged from 0 – 23.30˚ and similarly 99.8% of this flat to rolling landscape had a slope of less than 24˚ (87% and 62% were less than 7˚ and 1.5˚, respectively). Therefore, sampling sites were adequately distributed across the landscape to capture variability in both vegetation and topographic features.

To account for structural heterogeneity and to assess fine scale thermal variation, we quantified thermal environments using sampling arrays consisting of 3 black bulbs connected to a single data logger. Arrays were arranged so that one black bulb was positioned at each random point and also at 2 m and 4 m from each random point in a randomly determined cardinal direction to assess fine scale variation in T_{bb}. We conducted sampling during June, July and August of each year of the study, and measured T_{bb} at 312 random points across 15 minute intervals for 24 hours. This sampling effort resulted in over 120,000 individual T_{bb} measurements. At 3 on-site meteorological stations situated 2 m above ground level, average hourly ambient temperature (T_{air}) and solar radiation (S_{rad}) were measured to compare broad environmental conditions with site-specific T_{bb}. T_{bb} was paired with T_{air} and S_{rad} measured from the nearest meteorological station for analysis. T_{bb} was sampled under a similar range of T_{air} at bare ground (19.48 – 40.50˚C), herbaceous (16.70 – 41.88˚C), low woody (19.66 – 41.88˚C) and tall woody (19.91 – 40.84˚C) cover types (Table 1).

To investigate biotic factors influencing site and scale specific thermal heterogeneity and buffering, we examined vegetation structure at each sampling location. Cover classes at each sampling point were classified as bare ground (i.e., no vegetation), herbaceous, low woody, and tall woody cover (< 2 m). Percent cover of litter, bare ground, grass, forb and woody cover was estimated within a 0.5 m^2 quadrat (modified from Daubenmire 1959) centered over each black bulb (Hovick et al. 2014). In 8 compass directions (cardinal and sub-cardinal), overhead vegetation obstruction was also measured by aiming a digital carpenter’s level affixed to a 2 m pole at the top of the nearest vegetation and recording the angle (Kopp et al. 1998).

Analyses

We used multiple regression using an AIC model selection framework to assess the influence of environmental variables (T_{air}, S_{rad} and their interaction), terrain features (i.e., slope, aspect and their interaction) and vegetation cover (i.e., bare ground, herbaceous, low woody and tall woody cover and their interaction with S_{rad}) on T_{bb} as the dependent variable. Aspect data was circular and thus was arcsine-transformed prior to analysis resulting in values represented as eastness and northness (Roberts 1986, Nadyeina et al. 2014). We also assessed the relative importance of each terrain and vegetation variable singularly in models that each contained T_{air}, and S_{rad} given that these variables are known to explain a large portion of the variation in T_{bb} (Hovick et al. 2014). Models were ranked by AIC value and models within ΔAIC = 2 were considered to have similar explanatory power (Burnham and Anderson 2010). Possible collinearity among variables was assessed with a Pearson's correlation test prior to analysis and correlation was less than 0.40 for all variables (range; -0.008 – 0.40) except for low woody and herbaceous cover (0.78). Therefore, herbaceous cover was not included as a variable in candidate models. Prior to analysis, T_{bb} measurements were averaged across each hourly period (Logan et al. 2013) to allow for comparisons with hourly averages of T_{air}. Models were ranked by AIC value and models within ΔAIC = 2 were considered to have similar explanatory power (Burnham and Anderson 2010). Additionally, because T_{bb} is assumed to be linear function of T_{air} (Gunderson and Leal 2012, Logan et al. 2013), we used simple linear models of T_{bb} as a function of T_{air} to descriptively depict the residuals in T_{bb} occurring among each cover type during comparatively warm periods, when $T_{air} \geq 25^{\circ}C$, which was the main focus of this study (Hovick et al. 2014).

To determine if rates of T_{bb} amplification varied among cover classes, we calculated the difference between T_{bb} measurements and the simultaneously recorded T_{air} value ($T_{bb} - T_{air}$) for each cover class. This standardized difference depicts to what degree cover specific T_{bb} is amplified for a given T_{air} experienced broadly on the study area. We also investigated the role of vegetation in modulating T_{bb} using one-way analyses of variance (ANOVA; Zar 1984) with T_{bb} measurements as a dependent variable and cover classes and vegetation parameters (i.e., angle of obstruction and percent cover [bare ground, litter, grass, forb, and woody]) as independent variables. Multiple comparisons were made using a Tukey multiple comparison test (Zar 1984) following significant ANOVA. Differences were deemed significant at the $p < 0.05$ level.

Mean (±SE) hourly T_{bb} recorded during 24 hour daily periods (00:00 – 23:00) within each cover class were calculated to examine temporal variability in T_{bb} among cover types and to assess thermal heterogeneity throughout diurnal periods. To assess spatial variation in T_{bb} among random point, 2 m, 4 m, and landscape sites, we calculated variances within each site category and compared T_{bb} measurements using Welch's t-tests for each site combination. Along with space and time, we also recorded T_{bb} across a wide range of T_{air} conditions and thus, were able to examine the distribution of T_{bb} in discrete categories as T_{air} increased. To assess shifts in T_{bb} concomitant to changes in T_{air}, we calculated proportions of T_{bb} at intervals of <20˚C, 20 to <25˚C, 25 to <30˚C, 30 to <35˚C, 35 to <40˚C, 40˚C - <45˚C, 45˚C - <50˚C and ≥50˚C across T_{air} intervals of 20 to <25˚C, 25 to <30˚C, 30 to <35˚C, 35 to <40˚C and ≥40˚C. We used categories spaced at 5˚C intervals given that T_{bb} varies across ranges of T_{air} and for ease of interpretation. Alterations in thermal space across the landscape were further examined by calculating proportions of T_{bb} observed across T_{air} ranges for each vegetation cover type.

Finally, we predicted what T_{bb} will occur across the landscape given future climate projections. To account for possible non-uniform rates of increase in T_{bb} among cover classes, we used the resulting linear equations and slope coefficients from the simple linear models to model projections of T_{bb}. Specifically, we calculated the T_{air} that was experienced at 14:00 (i.e., the hottest period of the day) using the mean T_{bb} recorded and the specific linear equation for each cover type. We then added the projected ambient temperature increase to the resulting T_{air} value and solved for the new projected

T_{bb} under end of century low (2.7˚C increase in T_{air}) and high emission (4.6˚C increase in T_{air}) climate change scenarios (www.climatewizard.org, Girvetz et al. 2009). For our projections of future T_{bb}, we averaged available climate scenarios for the study area as predicted by both climate change scenarios. Discrete values of current and future T_{bb} modeled for low and high emission climate scenarios were assigned to pixel values in ArcGIS 10.3 for each cover type in order to display potential changes in the thermal landscape. T_{bb} was mapped based on natural breaking points in observed T_{bb} values (< 42˚C, ≥ 42˚C to <50˚C, and ≥ 50˚C) and because these intervals also hold biological relevance given that temperatures >50˚C can denature proteins and prohibit biotic processes needed for life (Calder and King 1974, Larcher 1991).

Results

We found that this shrub-dominated landscape was composed of a mosaic of thermally heterogeneous T_{bb} that ranged from 27 to 79˚C (Figure 1). When T_{air} exceeded 39˚C, we observed that T_{bb} was capable of exceeding 70˚C, with a large portion of the landscape reaching > 50˚C (Figure 1). Of the suite of multiple regression candidate models, the global model received the greatest support based on AIC ranking (Table 1). All other candidate models had ΔAIC > 2 indicating a lack of relative support. Among models that included T_{air}, S_{rad} and their interaction along with 1 single terrain (slope or aspect) or vegetation variable (cover class), the model containing tall woody covered received substantially greater support than models for any other variable (Table 2). Nevertheless, this model had very low relative support among the full suite of candidate models.

Although we observed that many factors (i.e., abiotic and biotic) in combination drive T_{bb}, specific patch characteristic (e.g., cover class) were associated with substantial differences in observed T_{bb} across the landscape. Linear models demonstrate that T_{bb} among tall woody cover remained cooler than in other cover types (Figure 2). For example, T_{bb} among cover classes were significantly different ($F_{3, 21864} = 57.0$, $p < 0.0001$) and tall woody cover provided mean T_{bb} that was more than 4˚C cooler than low woody, bare ground, and herbaceous cover for all measurements (Table 3) and more than 10˚C cooler during peak diurnal heating (14:00 hr). Interestingly, mean T_{bb} for bare ground was similar to herbaceous cover and low woody ($p > 0.05$), but the T_{bb} for herbaceous cover differed from low woody cover ($p <0.05$) (Table 3). For example, we observed maximum $T_{bb} > 70$˚C in low woody and bare ground cover types and T_{bb} approaching nearly 80˚C in herbaceous cover types, but in woody cover types, T_{bb} peaked at only 63˚C (Table 3).

We observed both spatial and temporal variation in T_{bb} observations. Temporally, T_{bb} did not appear to differ between cover classes from 20:00 – 06:00, but exhibited considerable disparity throughout the rest of the day (07:00 – 19:00) (Figure 3). We observed substantial heterogeneity during mid-day and afternoon periods (12:00 – 14:00) (Figure 3) and tall woody cover exhibited the most moderated thermal environments across the full range of temporal variability. Spatially, we found that variances were similar among all spatial scales that we assessed (range; 137.8 - 140.8), especially at the finest point scale (137.8) and broadest landscape scale (139.5). Additionally, we found that local scale T_{bb} did not differ between point and 4 m sites ($t= -0.147$, $df=11612.3$, p=0.88), point and 2 m sites (t= -0.165, df=11638.7, p=0.87), and 2 m and 4 m sites (t= -0.312, df=11630.4, p= 0.76).

Specifically, diurnal distributions of T_{bb} demonstrated that during mid-day, tall woody cover provided microsites that were on average 10.22˚C, 10.74˚C, and 12.7˚C less than low woody, bare and herbaceous cover types, respectively. Standardized differences ($T_{bb} – T_{air}$) in the magnitude of thermal environments at tall woody cover types were 0.81˚C compared to 5.71˚C at low woody, 6.77˚C at bare, and 6.95˚C at herbaceous cover types ($F_{3, 17433} =$ 149.4, $p < 0.0001$) (Figure 4). Therefore, tall woody cover moderated T_{bb} relative to T_{air} by 7.05, 8.35, and 8.59 times more than low woody, bare and herbaceous cover types, respectively (Figure 4). The greater thermal buffering capacity (i.e., reduced T_{bb}) observed at tall woody cover types corresponded to greater angle of obstruction with tall woody cover than other vegetation cover types. Angle of obstruction at tall woody cover was 5, 3, and 0.3 X's greater than at bare ground, herbaceous or low woody cover types, respectively ($F_{3, 919} =$ 394.1, $p < 0.0001$) (Figure 5).

Pronounced thermal heterogeneity was evident across a wide range of T_{air} conditions ranging from 20 - > 40˚C, and comparatively moderated thermal environments became increasingly scarce as T_{air} increased (Table 4). For example, 86.8% and 98.4% of T_{bb} measurements exceeded 40˚C at T_{air} ranging from 35 to < 40˚C and ≥ 40˚C, respectively (Table 4). Furthermore, the prevalence of thermal extremes was demonstrated by our finding that 49% and 73.3% of T_{bb} measurements exceeded 50˚C at T_{air} ranging from 35 to < 40˚C and ≥ 40˚C, respectively (Table 4). Interestingly, distributions of T_{bb} measurements in tall woody cover also exhibited different distributional patterns than the other 3 cover types at T_{air} >35˚C (Figure 6). Specifically, 52.2% of T_{bb} values in tall woody cover remained below 40˚C, compared to 6.5% for bare ground, 7.9% for herbaceous and 13.8% for low woody categories.

We found that during peak heating (14:00), mean T_{bb} averaged within bare ground, herbaceous and low woody cover (93% of the total landscape) exceeded 50˚C while T_{bb} in tall woody cover (7% of the total landscape) was 41.5˚C, substantially buffering against conditions prevalent on the surrounding landscape (Figure 7). When modeling future conditions under the low emission scenario, tall woody cover shifted to 45.8˚C, while the remainder of the landscape remained >50˚C, reaching up to 57.5˚C for low woody, 58.5˚C for bare ground, and 60.8˚C for herbaceous cover types. Under the modeled high emission scenario, the entire landscape exceeded 50˚C, with T_{bb} for tall woody, low woody, bare ground and herbaceous cover types being 55.0˚C, 61.2˚C, 62.9˚C and 65.5 ˚C, respectively (Figure 7).

Discussion

Our results demonstrate that thermal landscapes should be viewed as scale dependent mosaics that exhibit variability across space and time resulting from the synergistic relationship of both abiotic and biotic factors. We found that T_{bb} across the landscape was driven by many environmental, terrain, and vegetation factors in concert. Accordingly, we observed a high degree of thermal heterogeneity, which resulted in a diversity of potential thermal choices for organisms. The thermal landscape was prone to extreme T_{bb} during bouts of high ambient temperature and solar radiation, creating a scarcity of thermally-moderated microsites. Compared to other cover classes, tall woody cover substantially buffered extreme temperatures further supporting the hypothesis that landscapes can serve as moderators of thermal extremes (Suggitt et al. 2011, Hovick et al. 2014). These findings also substantiate the premise that the interaction of vegetation and temperature can be informative for making assessments of fine scale thermal environments (Saunders et al. 1998).

Interestingly, our observation that the thermal landscape exhibited the potential for experiencing T_{bb} exceeding 70˚C was similar to observations from studies in other regions, including the tallgrass prairie in Oklahoma where T_{bb} exceeded 70˚C and Mescalero sand dunes in New Mexico where T_{bb} exceeded 65˚C (Hovick et al. 2014, Sears et al 2011; Fig. 4). Moreover, during extreme heat (i.e., $T_{air} \geq 40$˚C), 98.4% and 73.3% of T_{bb} measurements exceeded 40˚C and 50˚C, respectively. Given that temperatures >50˚C can result in protein denaturation and the inhibition of biotic processes (Calder and King 1974, Larcher 1991), thermally buffered sites serve a critical landscape function, especially for species that require regular use of thermal refuges (Lagarde et al. 2012, Shi et al. 2014). In the face of thermal extremes during peak diurnal heating (14:00), tall woody cover moderated T_{bb} by more than 10˚C compared to other vegetation classes (e.g., bare ground, herbaceous and low woody), demonstrating that a comparatively small segment (7%) of the landscape substantially buffered microclimate. In addition, tall woody cover buffered T_{bb} 7 times more than bare ground, herbaceous and low woody cover at T_{air} >25˚C, demonstrating the degree to which vegetation components can dictate thermal environments. These findings have major ecological implications given that in order for organisms to obtain suitable microclimates, such microclimates must be available and accessible within the range of conditions occurring on the landscape (Faye et al. 2014). If thermally-moderated sites are juxtaposed so that they are distant from one another, the potential for ecological traps could be high for species seeking thermal refuge during the heat of the day or during extreme heat events.

For example, due to their limited mobility, Moorish tortoises (*Testudo graeca*) in Morocco require thermal refuges within 0.5 km of their diurnal position during hot summer conditions to avoid heat stress (Moulherat et al. 2014). Characterizations of thermal landscapes such as those in this study combined with behavioral and physiological data could serve to answer questions about how environmental conditions may induce ecological traps for species now and in the future (Van De Pol et al. 2010).

Although tall woody cover that had dense canopies (i.e., high angle of obstructions) was a significant moderator of site-specific microclimate, it only composed a small proportion of the total landscape (7%). Hence, any practice that reduces or prevents tall woody cover in regions where it is comparatively scarce would likely act to increasingly homogenize the thermal landscape towards more extreme conditions during high heat. However, landscape components that moderate thermal extremes may not always align with the other habitat needs of specific species. This disconnect can occur locally due to predation risks or foraging tradeoffs that could potentially override thermal considerations (Amo et al. 2004, Levy et al. 2012, Cunningham et al. 2015) or broadly given that structural features on the landscape that moderate extremes may not coincide with the habitat suitability thresholds for sustaining populations. Despite providing thermal buffering and promoting thermal heterogeneity, increases in woody plant abundance poses a major threat to many grassland bird species by altering the structure and composition of critical habitat space (Coppedge et al. 2004, Grant et al. 2004). As a result, woody plant encroachment in the Great Plains of the United States has led to substantial declines in species diversity and composition for grassland and shrub land birds (Engle et al. 2008), potentially creating a management conundrum that presents conservationist with a difficult challenge. Therefore, although characterizing thermal landscapes is critical for understanding the environments that organisms inhabit now and in the future, it will also be necessary that efforts to maximize the availability of thermally buffered sites consider the physiological tolerances of imperiled species and incur a minimal amount of degradation to overall habitat quality.

Along with exhibiting spatial variability, as indicated by the similarity of variances among each scale measured (i.e., point, 2 m, 4 m, and landscape), our results also agreed with previous studies that found that temperature is also subject to high temporal variability (Kustas et al. 2000, Raney et al. 2014). We observed that thermal conditions were spatially homogenous from 20:00 – 06:00 h indicating that organisms would face similar thermal conditions regardless of their position or patch selection on the landscape. However, thermal heterogeneity increasingly diverged among vegetation cover types throughout the day, peaking at 14:00 h providing further evidence that thermal landscapes, and the occurrence of thermal extremes, are temporally dynamic. Our findings of thermal variability at different times of the day were not unexpected, however, the differences (up to >10˚C) that we observed between tall woody cover and all other cover types were stark. During this period, organisms likely face a habitat selection conundrum because although the variability among potential thermal choices increases, available thermal environments become increasingly extreme. Therefore, these results also show the significance of acknowledging temporal variation in thermal patterns in assessments of ecological communities, especially given that short bouts (i.e., hours) of extreme heat may be more impactful or detrimental to species than increases in seasonal or yearly averages (Gilbert et al. 2004, Faye et al. 2014, Rezende et al. 2014).

The influence of climate change on biota remains uncertain yet holds a high potential for shifting the distributions of species and resulting in other "ecological surprises" (Williams and Jackson 2007). Therefore, it is critical that we better understand how climate change will alter potential risks to thermal exposure within ecological communities (Parmesan 2006). Our models of T_{bb} indicate that microclimates will continue to vary as ambient temperature (T_{air}) increases due to climate change, but will all be subject to far greater extremes. Under low emission climate scenarios, tall woody cover remained the only cover type with T_{bb} <50˚C (45.8˚C), while under high emission scenarios, the entire landscape experienced T_{bb} >50˚C representing highly extreme conditions from a biological standpoint (Calder and King 1974, Larcher 1991). Even though organisms may actually experience more moderate thermal conditions than those indicated by black bulb temperatures, such scenarios would also likely reduce the capacity of the landscape to provide refuge or refugia for species that are sensitive to thermal extremes. For example, in the absence of tall woody structure, northern bobwhites (*Colinus virginianus)* on the subtropical and semiarid periphery of their North American distribution would likely not persist during hot summer conditions due to excessive heat and solar radiation exposure (Guthery 2000). However, if increases in environmental heat loads reach a point where they overwhelm the ability of microsites to moderate T_{bb} within thermally tolerable limits for organisms, then the presence of previously viable thermal refuge may be rendered ineffective.

A key goal of landscape ecology is to investigate the structural features and patch configurations that ultimately create mosaic patterns (Wiens and Milne 1989). This assessment of current and future thermal environments provides a step towards understanding the role of abiotic factors as drivers of ecological complexity and increases our understanding of thermal landscapes now and in the future. Our findings reinforce that thermal landscapes should be viewed as dynamic systems that are subject to diverse spatio-temporal variation (Saunders et al. 1998) and are largely a by-product of the interaction between temperature and vegetation structure. Furthermore, these results underscore the important ecological relevance of landscape structure as agents for modulating thermal extremes. To provide thermal heterogeneity and thermal buffering, conservation practices should focus on preserving both vertical and horizontal vegetation structural heterogeneity to create complex thermal landscapes. This will maximize the capacity of landscapes to support a diversity of species and their wide-ranging thermal tolerances. In this study, tall woody cover was the primary component for the maximization of thermal buffering across the landscape, and without them, thermal patterns would shift towards increasingly greater and more homogenized extremes. However, our models of the changes in microclimatic conditions associated with future climate change suggest that landscapes will be subject to far greater thermal extremes across increasingly larger swaths of the landscape, subsequently increasing the need to understand the drivers of thermal patterns multiple scales.

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Table 1. Results of multiple regression models of black-bulb temperature (T_{bb}) modeled as a function of ambient temperature (T_{air}) and solar radiation (S_{rad}), slope, eastness aspect (East), northness aspect (North), as well as bare, low woody and tall woody cover and interactions. Models included T_{bb} measured during diurnal periods (11:00 – 15:00) at the Packsaddle WMA, Oklahoma, USA, 2012 – 2014 (n = 12,031). Models were ranked by AIC value.

Candidate Model	**AIC**	**ΔAIC**
T_{air}+ S_{rad}+ T_{air}*S_{rad} + Slope + East + North + Slope*North + Slope*East + Bare + Low Woody +Tall Woody + S_{rad}*Tall Woody + S_{rad}*Bare + S_{rad}*Low Woody	74138.2	0.0
T_{air}+ S_{rad}+ T_{air}*S_{rad} + Slope + East + North + Slope*North + Slope*East + Bare + Low Woody +Tall Woody + S_{rad}*Tall Woody + Srad*Tall Woody	74159.2	21.0
T_{air}+ S_{rad} + T_{air}*S_{rad} + Slope + East + North + Slope*North + Slope*East + Low Woody +Tall Woody +S_{rad}*Tall Woody + S_{rad}*Low Woody	74159.6	21.4
T_{air}+ S_{rad} + T_{air}*S_{rad} + Slope + East + Slope*North + Bare + Low Woody + Tall Woody + S_{rad}*Tall Woody + S_{rad}*Bare + S_{rad}*Low Woody	74210.5	72.3
T_{air}+ S_{rad} + T_{air}*S_{rad} + Slope + East+ North + Bare + Low Woody + Tall Woody + S_{rad}*Tall Woody + S_{rad}*Bare + S_{rad}*Low Woody	74227.8	89.6

Table 2. Models including environmental drivers of T_{bb} (T_{air}, S_{rad}, and their interaction) and single terrain and vegetation variables to assess their relative importance as predictors of T_{bb} during diurnal periods (11:00 – 15:00) at the Packsaddle WMA, Oklahoma, USA, 2012 – 2014 (n = 12,031). Models were ranked by AIC value.

Candidate Model	**AIC**	**ΔAIC**
$T_{air} + S_{rad} + T_{air}*S_{rad}$ + Tall Woody	74880.9	0.00
$T_{air} + S_{rad} + T_{air}*S_{rad}$ + Low Woody	75828.4	947.5
$T_{air} + S_{rad} + T_{air}*S_{rad}$ + Bare	75947.8	1066.9
$T_{air} + S_{rad} + T_{air}*S_{rad}$ + Slope	75995.2	1114.3
$T_{air} + S_{rad} + T_{air}*S_{rad}$ + North	75999.4	1118.5
$T_{air} + S_{rad} + T_{air}*S_{rad}$ + East	76002.7	1121.8
$T_{air} + S_{rad} + T_{air}*S_{rad}$	76002.4	1121.5

Table 3. Range of ambient temperature (T_{air}) and black-bulb temperature (T_{bb}) sampled in bare ground, herbaceous, low woody and tall woody cover types at the Packsaddle WMA, Oklahoma, USA, 2012-2014 (n = 22,190).

Vegetation Type	**T_{air} Range (˚C)**	**T_{bb} Range (˚C)**	**T_{bb} Mean (±SE)** [a]
Bare	19.48 – 40.50	18.28 – 72.55	37.98 (±0.32) AB
Herbaceous	16.70 – 41.88	17.83 – 79.56	38.57 (±0.13) A
Low Woody	19.66 – 41.88	17.89 – 75.81	37.48 (±0.15) B
Tall Woody	19.91 – 40.84	20.35 – 63.36	32.60 (±0.28) C

[a] All means with same letter were not significant different (P > 0.05) (Tukey's multiple comparisons).

Table 4. Proportion of black-bulb temperature (T_{bb}) experienced on the landscape across the ranges of ambient temperature (T_{air}) measurements sampled during 2012 - 2014 at the Packsaddle WMA, Oklahoma, USA, 2012-2014 (n = 4,576).

T_{air}	**20 - <25**	**25 - <30**	**30 - <35**	**35 - <40**	**≥40**
T_{bb}					
<20	14.00	0.69	0.00	0.00	0.00
20 - <25	77.60	33.02	0.48	0.00	0.00
25 - <30	7.61	46.80	11.28	0.17	0.00
30 - <35	0.67	9.11	21.05	2.60	0.00
35 - <40	0.150	5.87	16.09	10.61	1.60
40 - <45	0.060	3.02	17.07	16.71	8.82
45 - <50	0.000	1.13	16.97	20.91	16.31
≥50	0.000	0.31	17.06	49.00	73.26

Figure Legend

Figure 1.1 Distribution of black bulb temperatures (T_{bb}) observed at ambient temperature $T_{air} \geq 25^{\circ}C$ (i.e., warmer focal periods) at the Packsaddle WMA, Oklahoma, USA, 2012-2014 (n = 17,491).

Figure 1.2 Relationship of black bulb temperature (T_{bb}) as a function of ambient temperature (T_{air}) $\geq 25^{\circ}C$ (i.e., warmer focal periods) measured at bare ground, herbaceous, low woody, and tall woody cover types at the Packsaddle WMA, Oklahoma, USA, 2012-2014 (n = 17,491).

Figure 1.3. Daily variation (i.e., 24 hour period) in black bulb temperature (T_{bb}) distribution experienced at bare ground, herbaceous, low woody and tall woody cover types at the Packsaddle WMA, Oklahoma, USA, 2012-2014 (n = 22,189).

Figure 1.4. Standardized differences between black bulb temperature (T_{bb}) and ambient temperature (T_{air}) ($T_{bb} – T_{air}$) depicting the magnitude of relative thermal buffering at bare ground, herbaceous, low woody and tall woody cover types (n = 17,491) at $T_{air} \geq 25^{\circ}C$ (i.e., warmer focal periods) at the Packsaddle WMA, Oklahoma, USA, 2012-2014. Different letters denote statistical significance ($p < 0.05$).

Figure 1.5. Angle of obstruction (gray bars) and corresponding mean black bulb temperatures (T_{bb}) (black line) measured at bare ground, herbaceous, low woody and tall woody cover types at the Packsaddle WMA, Oklahoma, USA, 2012-2014.

Figure 1.6. Proportion of black-bulb temperature (T_{bb}) measured at bare ground (A), herbaceous (B), low woody (C) and tall woody (D) cover types measured at $T_{air} > 35^{\circ}C$

(i.e., comparatively extreme conditions) at the Packsaddle WMA, Oklahoma, USA, 2012-2014.

Figure 1.7. Thermal characterization of current (A), and future thermal conditions under low (B) and high (C) emission scenarios by 2080 at 14:00 hr at the Packsaddle WMA, Oklahoma, USA, 2012-2014. Mean T_{bb} <42˚C (blue), ≥42 - <50˚C (yellow) and ≥50˚C (red) shown.

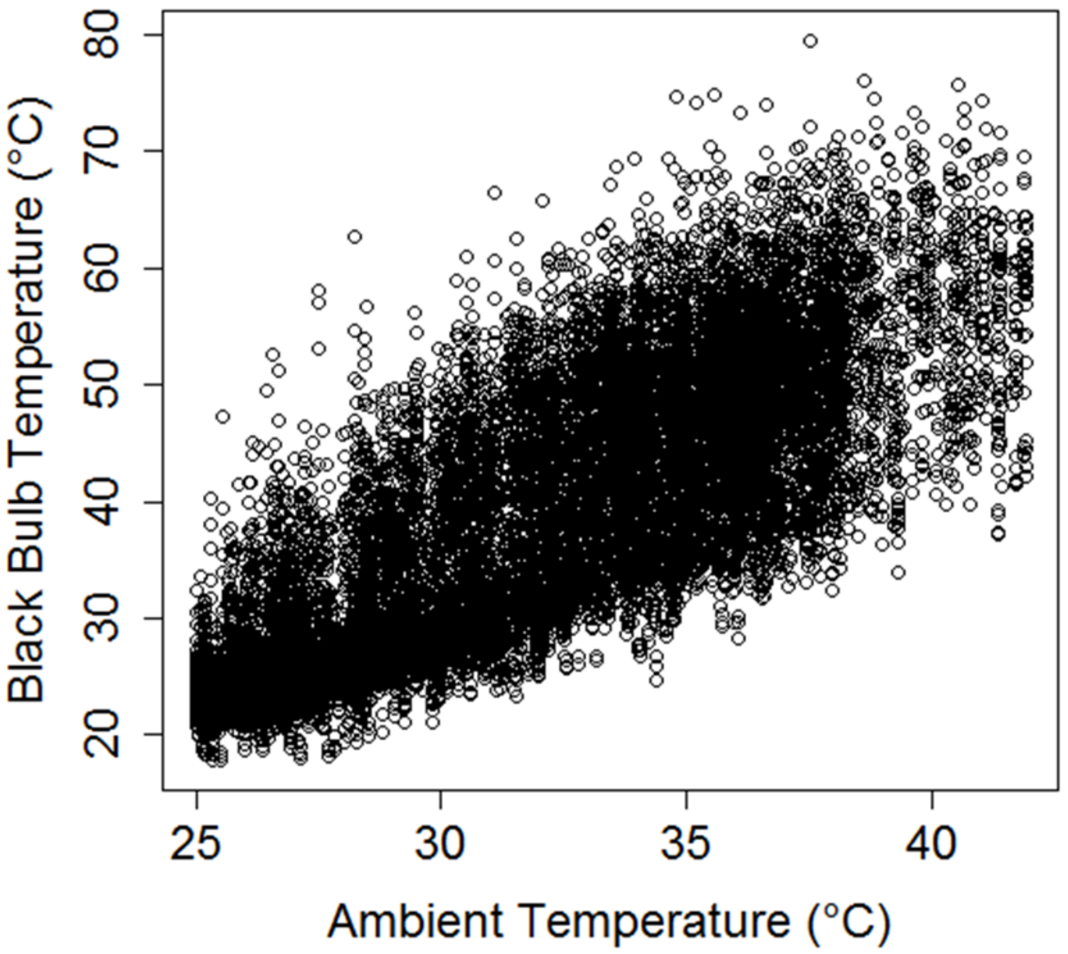

Black Bulb Temperature (°C)
20
30
40
50
60
70
80
25
30
35
40
Ambient Temperature (°C)

Figure 1.1.

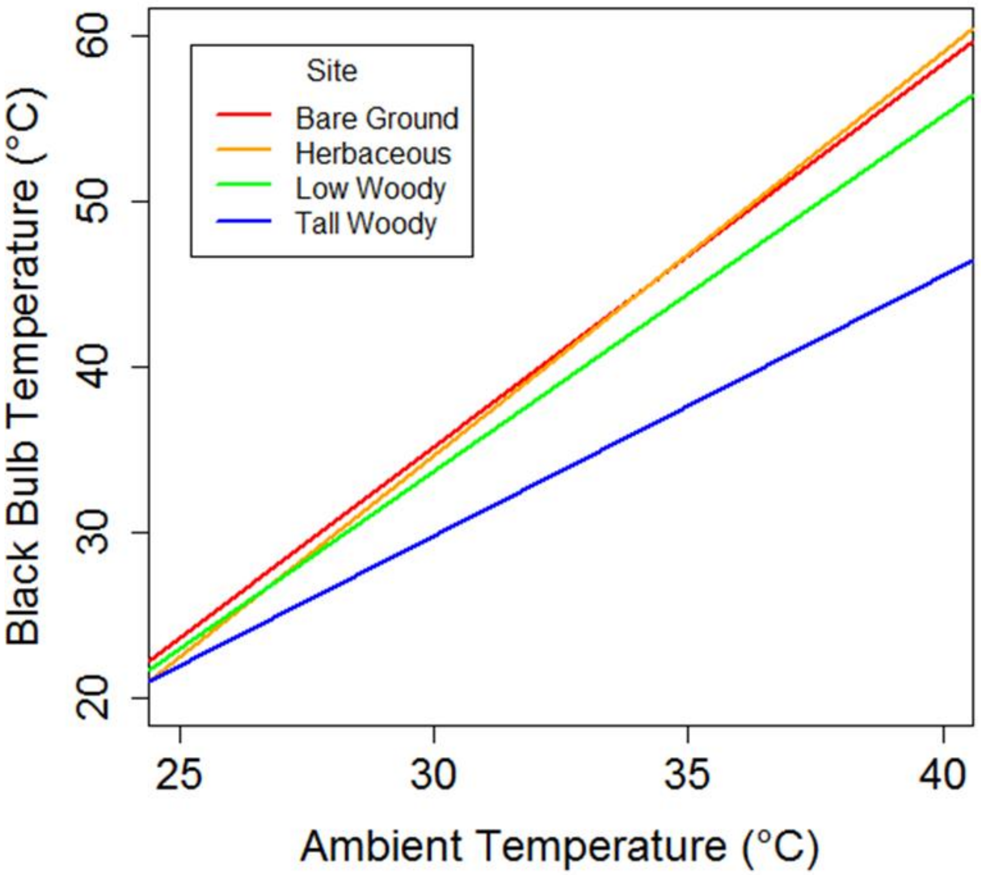

Site
Bare Ground
Herbaceous
Low Woody
Tall Woody
Black Bulb Temperature (°C)
20
30
40
50
60
25
30
35
40
Ambient Temperature (°C)

Figure 1.2.

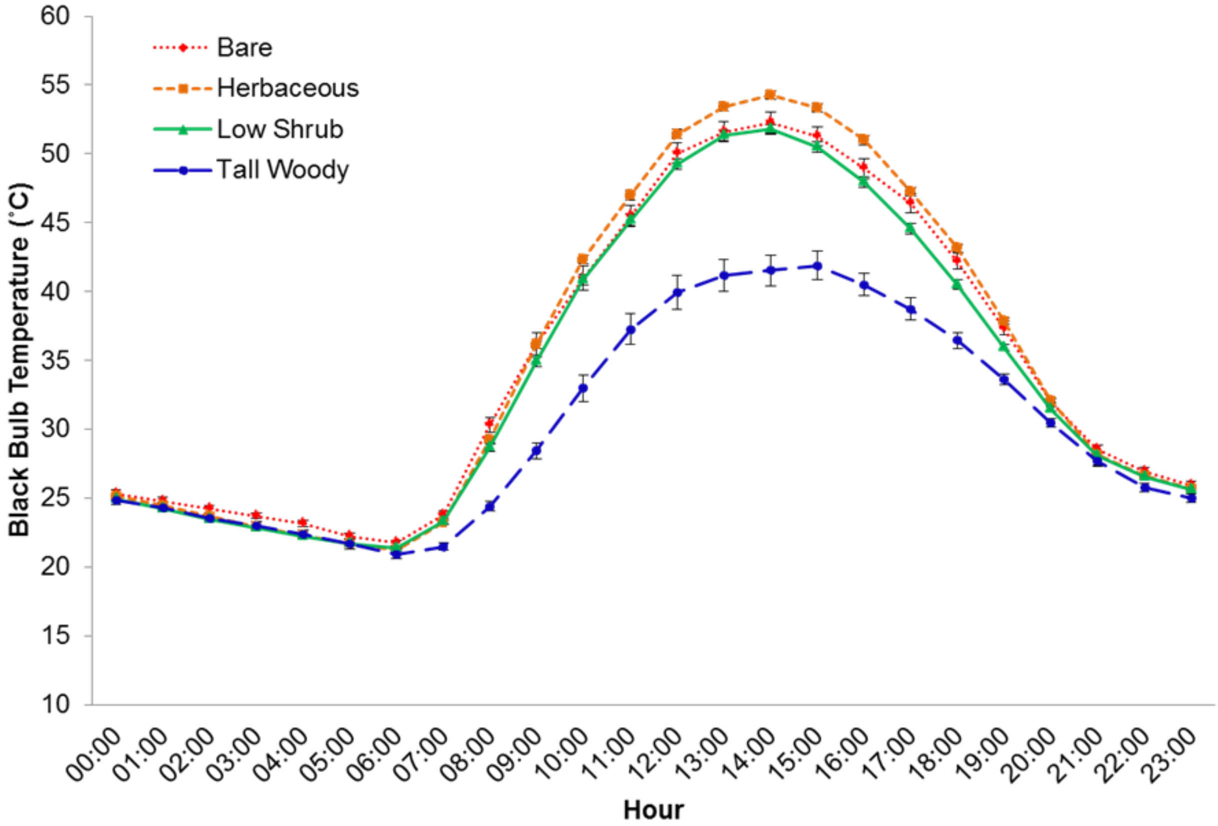
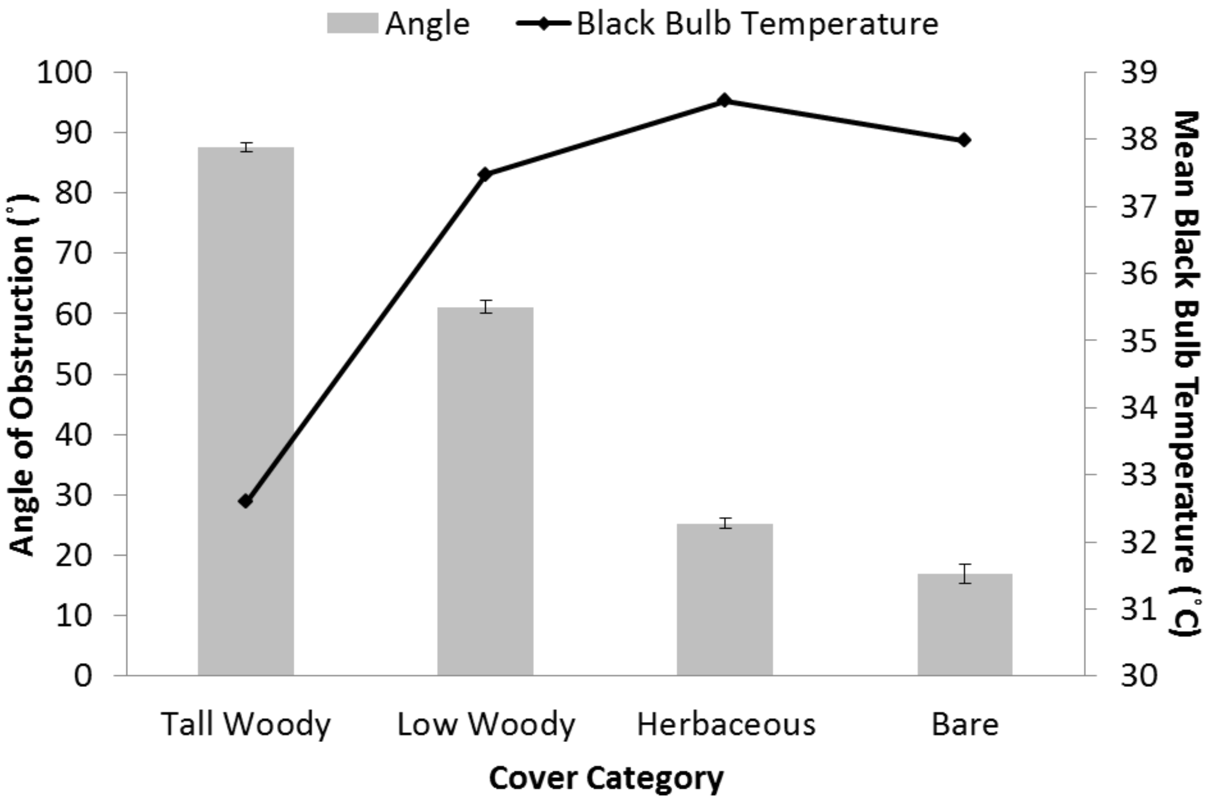

60
55
50
45
40
35
30
25
20
15
10
Black Bulb Temperature (˚C)
Bare
Herbaceous
Low Shrub
Tall Woody
00:00
01:00
02:00
03:00
04:00
05:00
06:00
07:00
08:00
09:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
20:00
21:00
22:00
23:00
Hour

Figure 1.3.


8
7
6
5
4
3
2
1
0
a
a
b
c
T_{bb} - T_{air} (˚C)
Bare
Herbaceous
Low Woody
Tall Woody
Vegetation Type

Figure 1.4.



Angle
Black Bulb Temperature
Angle of Obstruction (˚)
Mean Black Bulb Temperature (˚C)
100
90
80
70
60
50
40
30
20
10
0
39
38
37
36
35
34
33
32
31
30
Tall Woody
Low Woody
Herbaceous
Bare
Cover Category

Figure 1.5.

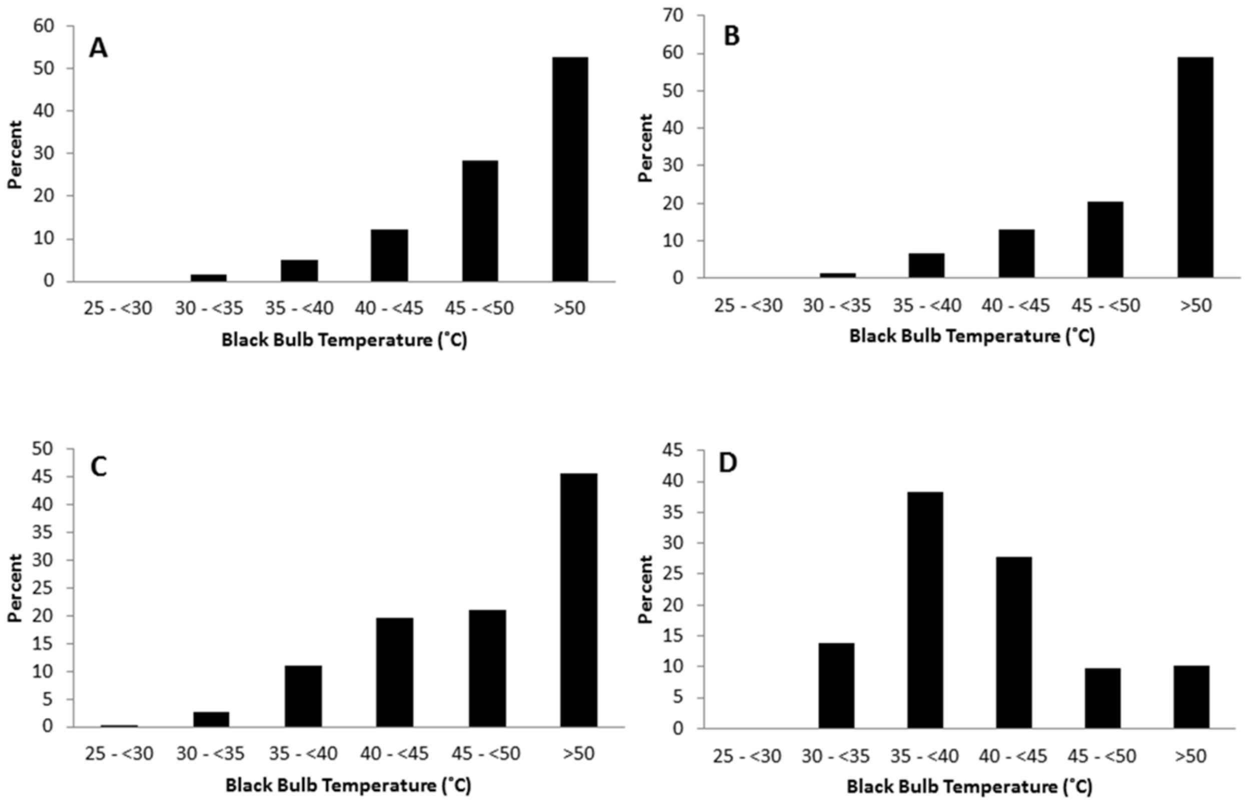

A
B
C
D
Percent
Black Bulb Temperature (˚C)
25 - <30
30 - <35
35 - <40
40 - <45
45 - <50
>50
0
10
20
30
40
50
60
70
5
15
25
35
45

Figure 1.6.

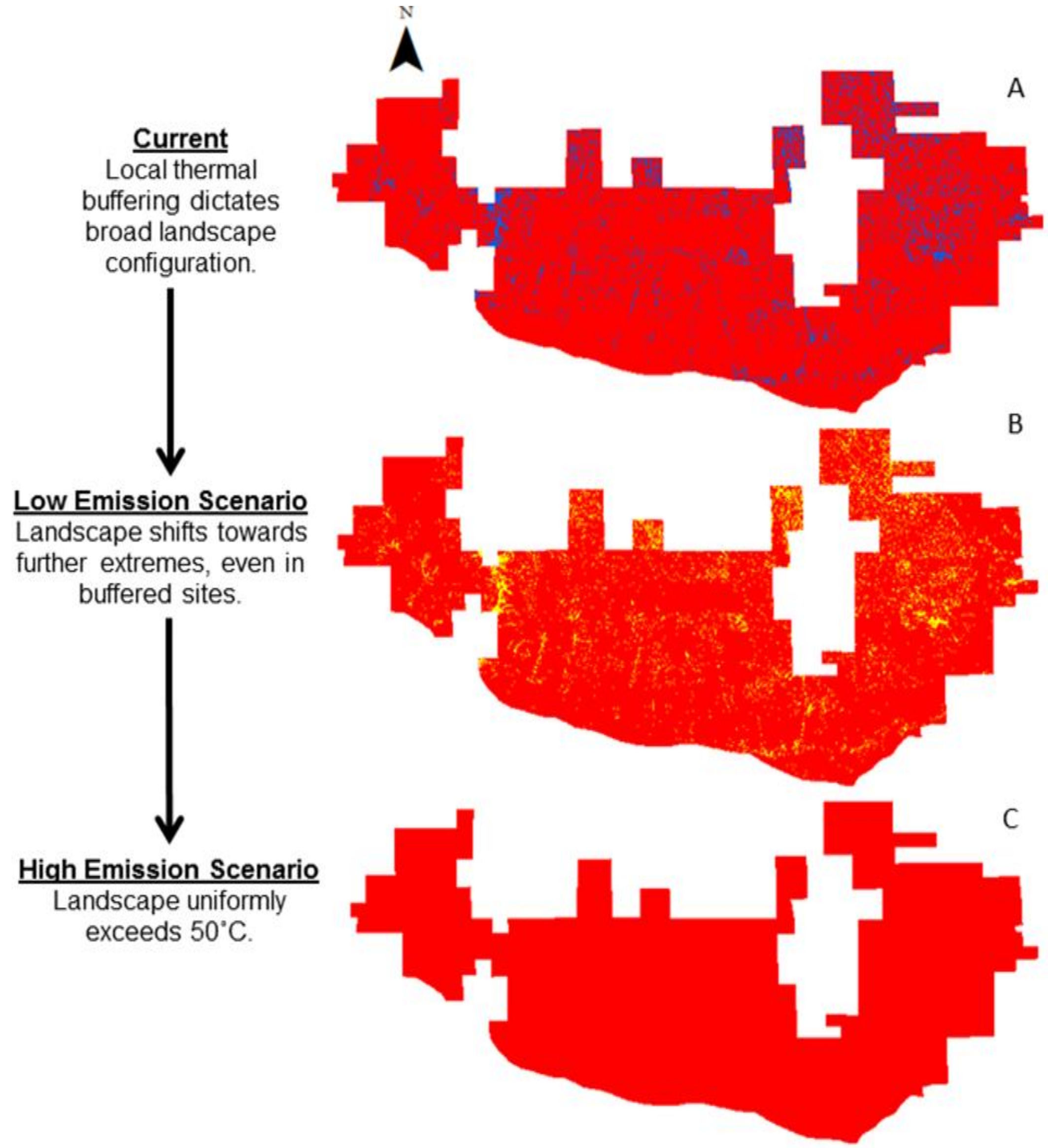

N
A
B
C
Current
Local thermal buffering dictates broad landscape configuration.
Low Emission Scenario
Landscape shifts towards further extremes, even in buffered sites.
High Emission Scenario
Landscape uniformly exceeds 50˚C.

Figure 1.7.

CHAPTER II

A GROUND-NESTING GALLIFORM'S RESPONSE TO THERMAL HETEROGENEITY: IMPLICATIONS FOR GROUND-DWELLING BIRDS

Abstract

The habitat selection choices that individuals make in response to thermal environments influence both survival and reproduction. Importantly, the way that organisms behaviorally respond to thermal environments depends on the availability and juxtaposition of sites affording tolerable or preferred microclimates. Although, ground nesting birds are especially susceptible to heat extremes across many reproductive stages (i.e., breeding, nesting, brood rearing), the mechanistic drivers of nest site selection for these species are not well established from a thermal perspective. Our goal was to assess nest site selection relative to the configuration of the thermal landscape by quantifying thermal environments available to a ground-nesting bird species inhabiting a climatically stressful environment. Using northern bobwhite (*Colinus virginianus*) as a model species, we measured black bulb temperature (T_{bb}) and vegetation parameters at 87 nests, 87 paired sites and 205 random landscape sites in Western Oklahoma during spring and summer 2013 and 2014. We found that thermal space within the study area exhibited differences in T_{bb} of up to 40˚C during peak diurnal heating, resulting in a diverse thermal landscape available to ground-nesting birds. Within this thermally heterogeneous landscape, nest sites moderated T_{bb} by more than 12˚C compared to random landscape sites. Furthermore, successful nests remained on average 6˚C cooler than unsuccessful nests on days experiencing ambient temperatures $\geq$ 39˚C. Models of future T_{bb} associated with 2080 climate change projections indicate that nesting bobwhites will face substantially greater T_{bb} throughout the landscape for longer durations, placing an even greater importance on thermal choices for nest sites in the future. These results highlight the capacity of landscape features to act as moderators of thermal extremes and demonstrate how thermal complexity at organism-specific scales can dictate habitat selection.

Introduction

Thermal environments place unavoidable behavioral and physiological constraints on all living organisms (Smith and Smith 2000, Angilletta 2009) and determine the outcome of critical life history periods (Dawson et al. 2005, Weber et al. 2011). Consequently, fine scale thermal limitations on reproductive stages can have significant population implications (Peterman and Semlitsch 2013, Lawson et al. 2014, Zhao et al. 2014). For example, extreme heat has been shown to cause adult, embryo, and chick mortality in endothermic birds (Kendeigh 1969, Salzman 1982, Webb 1987), as well as reduced hatching success and alterations of sex determination in ectothermic reptiles and amphibians (Duarte et al. 2012, Pike 2014). While it is widely acknowledged that ecological processes are scale dependent (Kotliar and Wiens 1990, McGill 2010), organisms have been shown to exploit the environment at numerous scales depending on their size, movement capabilities and life stage (van Beest et al. 2012, Peterman and Semlitsch 2013, Lawson et al. 2014). However, daily and hourly thermal decisions are made at comparatively finer scales which can be critical for reproductive success, fitness and survival (Dubois et al. 2009, Schofield et al. 2009, Cunningham et al. 2013). Additionally, studies that include temperature as predictors of biotic responses often focus on scales that are much coarser than the scale at which organisms exploit their environment (Austin and Van Niel 2011, Potter et al. 2013, Hannah et al. 2014). These discrepancies can create obstacles for understanding an organism's sensitivity to fine scale variation in thermal patterns, ultimately hindering assessments of species responses to future climate change (Logan et al. 2013, Varner and Dearing 2014). Heterogeneity is recognized as a primary mechanistic driver of broad scale ecosystem function and biological diversity, as well as fine scale patch use by organisms (Christensen 1997, Wiens 1997). Studies addressing the ecological effects of heterogeneity have typically focused on spatial and temporal variation in vegetation structure, leaving other basic components of heterogeneity, such as microclimate, understudied (Limb et al. 2009). Importantly, the spatial variation of microclimate (i.e., near ground climate) creates patterns of thermal heterogeneity across landscapes that directly impact behavior, thermoregulation, and overall fitness of organisms (Rosenberg et al. 1983, Angilletta 2009, Sears et al. 2011), as well as community assemblages (Perfecto and Vandermeer 2012, Patten et al. 2012). Within these thermally heterogeneous landscapes, specific microhabitats can also buffer against thermal extremes (e.g., ambient temperature and solar radiation) thereby augmenting the completion of reproductive stages such as nesting and incubation in birds (Walsberg 1981, Hovick et al. 2014, Hovick et al. 2015) and reptiles (Cowles and Bogert 1944, Shine 2005). However, the way that patterns of thermal environments influence the decisions made by individuals remains a question of high ecological importance Potter et al. 2013). This lack of understanding can hinder conservation efforts required for identifying and managing thermal space critical to species persistence (Ford et. al. 2013), but can be overcome by assessing both spatial and temporal aspects of site selection from a thermal perspective (Van beest et. al 2012).

Nest site selection is a behavioral activity that dictates the thermal environments that embryos are exposed to and ultimately convey early and critical influences on neonate fitness (Tieleman et al. 2008, Angilletta et al. 2009, Huang and Pike 2011, Durant et al. 2013). Although factors such as nest structure and incubation activity by adults are critical for successful incubation (Hansell and Deeming 2002, Mainwaring et al. 2014), landscape components can also be integral for providing a template of physical environments that can promote or constrain reproductive stages (Angilletta et al. 2009, Hovick et al. 2014) Because nest sites chosen by oviparous organisms are often fixed across space and time for the duration of the incubation period they remain stationary under fluctuating environmental conditions (Ricklefs and Hainsworth 1968, Huey 1991). Unlike reptile species that often locate nests in subterranean microhabitats that moderate temperatures (Cowles and Bogert 1944, Telemeco et al. 2009), most bird species select above ground nest sites, which further increases their potential exposure to thermal extremes and limit their choices for thermally moderated sites (Bennett et al. 1981). Additionally, nest site selection is tightly linked to predator avoidance, and tradeoffs between predation risk and thermal environments are complex and often confounded (Gloutney and Clark 1997, Wiebe and Martin 1998, Martin 2001). As a result, studies that assess both abiotic and biotic factors as selective pressures will provide a better understanding of the mechanistic basis for nest site selection and may also elucidate how these tradeoffs may be altered due to shifts in thermal space associated with future climate change (Martin 2001).

Ground-nesting bird species have been shown to be especially sensitive to high heat events at both individual and population levels (Goldstein 1984, Guthery et al. 2001, Patten et al. 2005, Albright et al. 2010). For example, levels of solar radiation have been shown to be the greatest predictor of greater prairie chicken (*Tympanuchus cupido*) nest success in the tall grass prairie of Oklahoma (Hovick et al. 2005). Additionally, northern bobwhite (*Colinus virginianus*; hereafter bobwhite*)* have been shown to be vulnerable to high temperatures throughout several reproductive periods (i.e., breeding, nesting, and brood rearing) (Guthery et al. 2001, Johnson and Guthery 1988, Guthery et al. 1988). For example, bobwhites in the Texas Panhandle of the United States commonly experienced hyperthermic conditions (≥39˚C) (Guthery et al. 2005) which are known to stimulate behavioral heat removal mechanisms such as refuge seeking and gular flutter (i.e., panting) (Guthery 2000). Moreover, when exposed to temperatures of 46˚C for a minimum of 1 hour bobwhite eggs experience 50% mortality (Reyna and Burggren 2012). As a ground-nesting species facing a widespread population decline (Sauer et al. 2011), bobwhites also experience reduced production and undergo population declines following high heat events in the western portion of their continental distribution (Guthery 2000). Because of this, bobwhites are an ideal species for assessing the impact of local thermal environments on fine scale site selection. Furthermore, individual bobwhites commonly exist on the edge of their thermal tolerance during summer heat extremes (Guthery et al. 2005, Guthery 2000) and therefore, are likely to be an excellent model species for assessing future climate change impacts on ground-dwelling birds.

A key component to understanding temperature constrained biotic processes involves quantifying thermal landscapes to better understand site selection decisions by organisms at multiple scales (Woods et al. 2014). Moreover, improving conservation efforts for thermally-sensitive species will require assessments of how both abiotic and biotic factors impact ecological processes (Limb et al. 2009); especially at a scale that reflects behavioral responses to diurnal thermal stress. For example, gaining a better understanding on how site selection choices are promoted or constrained by thermal heterogeneity will aid in disentangling the tradeoffs between microclimate and predation risk in dictating site selection (Hovick et al. 2014). Additionally, identifying the spatiotemporal positioning of thermally buffered sites at species-specific scales will also help focus conservation efforts on maintaining landscape components that modulate thermal conditions. In this study, our primary objective was to characterize thermal heterogeneity at scales relevant to ground-nesting birds. We hypothesized that in an environment prone to high heat, birds would select nests sites with structural characteristics that would confer thermal advantages by moderating temperature extremes. Therefore, we quantified thermal properties and vegetation characteristics at bobwhite nest sites, paired microsites, and random sites in order to assess the influence of proximate thermal environments on nest site selection and to determine the magnitude of potential differences in heat loads. We also assessed how the thermal conditions of nesting may be altered due to increased heat extremes as predicted by future climate change scenarios.

Materials and Methods

Study area

We studied the thermal ecology of nesting bobwhites at the Packsaddle Wildlife Management Area (WMA) in western Oklahoma, USA, which is near the western periphery of the North American bobwhite distribution. Packsaddle WMA is a 7,956 ha area owned and managed by the Oklahoma Department of Wildlife Conservation. The study area is dominated by sand shinnery oak (*Quercus havardii*), but other shrub species such as sand sagebrush (*Artemisia filifolia*), aromatic sumac (*Rhus aromatica*), and sand plum (*Prunus angustifolia*) are locally common (DeMaso et al. 1997, Peterson and Boyd 1998, Vermeire and Wester 2001). Common and co-dominant herbaceous species include little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), sideoats grama (*Boutelou curtipendula*), blue grama (*Boutelou gracilis*), western ragweed (*Ambrosia psilostachya*), Texas croton (*Croton texensis*) and prairie sunflower (*Helianthus petiolaris*). The study area occurs primarily on sandy Brownfield and Nobscott soil types (Wiedeman and Penfound 1960), and the terrain is mainly flat with 99.8% of the landscape < 24˚ and 62.1% of the landscape < 4.5˚ in slope. From 1994 – 2014, the region received yearly precipitation totals that averaged approximately 554.4 mm (range; 250 mm -750 mm) (Oklahoma Mesonet). Intense heat events are common during summer with mean temperatures exceeding 37.8˚C on average for 25 days per year (Arndt 2003). Mean maximum summer temperatures exceeding the point at which heat intake can surpass heat removal in bobwhites (39˚C) have also been documented (Oklahoma Mesonet).

Data collection

We captured bobwhites using funnel traps during winter and spring 2013 and 2014 and fitted each bobwhite with a 6 gram necklace VHF radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). Radio-marked bobwhites were monitored using radio-telemetry to locate nest sites and monitor nesting status. Following nest confirmation, nests were monitored daily (i.e., 6-7 days per week) during the 23 day incubation period (Guthery 2000) until fate (i.e., successful or unsuccessful) was determined. Nests were considered successful if at least one egg hatched (n = 54) and all other nests were considered unsuccessful regardless of the cause of failure and were assigned into a category of depredated (n = 29) or abandoned (n = 4). Based on the first and last dates that nests were located, nesting season duration lasted from 8-May to 26-September in 2013 and from 28-May to 12-August in 2014.

We measured black bulb temperature (T_{bb}) to investigate the thermal environments available to nesting bobwhites across the landscape relative to those at sites selected for nesting. T_{bb} provides an approximation of thermal environments that are experienced by an organism because it simultaneously incorporates ambient temperature, solar radiation, and wind effects into one interpretable metric (Campbell and Norman 1998). T_{bb} was measured using steel spheres (101.6 mm-diameter; 20 gauge thickness) painted flat black (hereafter, black bulbs), equipped with an ambient temperature (T_{air}) sensor suspended in the center, and situated at ground level (Guthery et al. 2005, Allred et al. 2013). Each black bulb was connected to a HOBO U12 data logger (Onset Corporation, Bourn, Massachusetts, USA) which recorded T_{bb} at 15 minute intervals for 24 hour periods at each thermal sampling site. The use of steel spheres as black bulbs has been a common approach for investigating the thermal aspects of site selection by gallinaceous birds, such as bobwhites, (Hiller and Guthery 2005, Guthery et al. 2005) as well as nest site selection by lesser prairie chickens *(Tympanuchus cupido)* (Hovick et al. 2014). Because black bulbs do not mimic the feather arrangement or coloration of our study species, our T_{bb} observations do not fully reflect the actual operative temperature or body temperature of bobwhites (Dzialowski 2005). We expect that steel sphere black bulbs are subject to greater thermal heat loads than bobwhites under the same environmental conditions given that we assumed that black bulbs had greater short wave absorptivity (~1) compared to that of bobwhites (0.78) (Calder and King 1974, Guthery et al. 2005). Therefore, our objective was not to directly replicate the temperatures experienced by bobwhites or their eggs, but rather, was to assess nest site selection in the context of thermal landscape heterogeneity. Thus, our use of T_{bb} measurements as a standardized proxy of the environment enabled us to examine nest selection relative to the thermal patterns of the surrounding landscape, as well as to calculate the magnitude of those differences.

We measured thermal environments at 87 nests by placing a black bulb inside each nest bowl to investigate site specific T_{bb} exposure. To avoid potential systematic bias associated with sampling successful nests later in the nesting cycle than unsuccessful nests, we standardized T_{bb} measurements for nest sites by recording T_{bb} immediately following hatching for successful nests and at the projected hatch date for unsuccessful nests (With and Webb 1993, Hovick et al. 2014). To determine whether bobwhites selected nest sites that were cooler than those predominantly available within this heterogeneous landscape, we measured T_{bb} at 205 landscape points distributed proportional to available vegetation types using a stratified random sampling approach in ArcGIS 10.3 (Environmental Systems Research Institute, Redlands, California, USA). Sampling of T_{bb} at landscape points was distributed regularly throughout nesting season. To control for variation in T_{bb} measured at nest sites, we simultaneously measured T_{bb} at paired sites located ≤ 2 meters from each nest. At these paired sites, black bulbs were placed at a location void of overhead cover and therefore provided a fine scale environmental control relative to nest microclimates (Johnson and Guthery 1988, Robertson 2009). While we expected that paired sites would experience higher T_{bb} than nests because of the lack of solar radiation blockage, they provided a way to obtain a relative measure of the magnitude of differences in thermal heat loads inside the nest compared to the environment outside the nest. Therefore, while comparisons between landscape points and nests provided an assessment of scale specific nest selection from a thermal perspective, paired control sites allowed us to examine potential heat loads that were possible within close proximity to nests.

To compare site specific T_{bb} measurements with simultaneously occurring macroclimate variables, we recorded ambient temperature (T_{air}) and solar radiation (S_{rad}) hourly at 3 onsite meteorological stations positioned 2 meters above ground level. Weather stations were distributed in an east-west orientation to match the boundaries of the study and were spaced < 7 km apart. Measurements of T_{air} and S_{rad} recorded from the meteorological station in closest proximity to each nest, paired microsite, or landscape point were used for analysis of site-specific T_{bb}. Means of hourly T_{bb} across each thermal sampling array were averaged for comparisons with hourly T_{air} measurement prior to analysis. Of the 252 days of nest monitoring in 2013 and 2014, only 30 (12%) days experienced $T_{air} \geq 39$˚C which has been identified as the point at which the heat accrual exceeds heat removal in bobwhites (i.e., hyperthermic threshold) (Guthery 2000). Accordingly, fewer nests were sampled on days with $T_{air} \geq 39$˚C (n=12) than on days with $T_{air} < 39$˚C (n=75) due the timing of extreme heat events, nest termination and sampling logistics. Nest and landscape T_{bb} were sampled under a similar range of T_{air} especially during periods of comparatively high temperatures which was a goal of our study (nest range: 7.31 – 43.30˚C; landscape range: 19.27 – 43.30˚C).

Vegetation structure is a primary driver associated with avian nest site selection and is a proxy for both protection from predation and thermal stress (Martin 1998). Therefore, we collected vegetation data at bobwhite nest sites and random landscape sites to examine site specific factors that could influence both thermal environments and predation exposure. Vegetation height and estimated percent cover of grass, forb, woody, litter, and bare ground cover were measured at each sampling point within a 0.5^2 meter quadrat (modified from Daubenmire) (Daubenmire 1959) centered over each black bulb (Hovick et al. 2014). To assess visual obstruction from terrestrial predators we used a Nudds board separated into 12 decimeter intervals (Nudds 1977) recorded at a distance of 7 meters from the nest site or landscape point (Guthery et al. 1981). We also measured the angle of obstruction directly above each sampling site (i.e., nest or landscape) given that vegetation can influence microclimate (i.e., blockage of solar radiation) and potential detection by predators (Hiller and Guthery 2005). Overhead angle of obstruction was quantified by aiming a digital carpenter's level affixed on a 2 meter pole at the top of the nearest vegetation in each of the 8 cardinal and sub-cardinal directions and recording the angle reading at each sampling point (Kopp et al. 1998). Vegetation sampling was conducted following nest termination to reduce disturbing nesting bobwhites and to standardize the timing of measurements across all nest sites (Saalfield et al. 2012).

Data Analyses

To depict thermal environments available to bobwhites during the nesting season, we modeled T_{bb} as a function of T_{air}, S_{rad}, and their interactions using regression analysis. Thus we accounted for T_{bb} being measured on different days. For all sites, T_{bb} was averaged by hour within diurnal periods (9:00 – 19:00) for each black bulb. We assessed the magnitude of differences in T_{bb} among nest sites and landscape sites by comparing standardized relative differences between T_{bb} and simultaneously recorded T_{air} (i.e., $T_{bb} - T_{air}$) experienced during the sampling period.

To evaluate the effects of *a priori* abiotic and biotic parameters on bobwhite nesting, we developed predictive models with nest fate (i.e., successful or unsuccessful) as a dependent variable based on T_{bb}, visual obstruction, angle of obstruction and vegetation height as dependent variables using logistic regression and AIC model selection. Nest fates were classified as "0" for successful nests (≥1 egg hatched) and "1" for unsuccessful nests (0 eggs hatched). We assessed possible collinearity among covariates with a Pearson's correlation test prior to analysis (range; -0.17 – 0.31), and each were subsequently included in candidate models. Candidate models were ranked using AIC model selection and top models with $\Delta AIC \leq 2$ were considered to have similar explanatory power (Burnham and Anderson 2002). We also converted model-averaged coefficients to odds ratios and 95% confidence intervals to indicate relative importance of variables and to provide an assessment of effect size. Thermal variation between successful and unsuccessful nests was analyzed using analysis of variance (ANOVA) (Zar 1984) to compare T_{bb} experienced on days with maximum $T_{air} < 39^\circ C$ (i.e., less extreme) and $T_{air} \geq 39^\circ C$ (i.e., more extreme), respectively. We used 39˚C as a threshold because it is the temperature at which heat loss is outpaced by heat accrual in bobwhites, resulting in the avoidance of thermal space exceeding 39˚C (Guthery 2000, Forester 1998), and therefore confers biological relevance for the species in this study. This threshold has also been used in studies on the thermal ecology of other gallinaceous species such as greater prairie chickens *Tympanuchus cupido* (Hovick et al. 2015).

We examined variation in vegetation parameters among nest sites and landscape points using ANOVA (Zar 1984). Visual obstruction, angle of obstruction, vegetation height, and percent cover of bare ground, litter, grass, forb, and woody plants were included as site specific variables that potentially influence nest selection through moderating thermal conditions, predation avoidance, or both. Differences between groups were considered significant at the $p < 0.05$ level for all analyses.

We used simple linear regression of T_{air} and T_{bb} measurements from this study to project T_{bb} under future climate scenarios in order to examine potential alterations in thermal space relevant to ground nesting birds. We used these simple linear model outputs rather than merely adding predicted T_{air} increases onto observed T_{bb} in order to better characterize potential changes in site-specific nest and landscape microclimates associated with future climate change. Therefore, we used models that were based on the distribution of T_{bb} observed in this study to elevate the accuracy and real-world applicability of our predictions. Projected T_{air} used to model future T_{bb} were obtained by averaging climate models for both high and low end of century (2080) carbon dioxide emission scenarios for western Oklahoma (www.climatewizard.org) (Girvetz et al. 2009). According to these average ambient temperature increases, T_{air} at the study area will increase by 2.7˚C and 4.6˚C for low and high emission scenarios, respectively. We compared our models of future T_{bb} at nests and landscape points to investigate whether thermal conditions differed across the same ranges of T_{bb} experienced, thus providing unbiased assessment of relative thermal conditions between groups.

Results

We found that the landscape exhibited substantial thermal heterogeneity with differences in T_{bb} ranging by up to 40˚C when $T_{air} > 35˚C$ (Fig 1A). Within this thermally heterogeneous landscape, nest sites moderated T_{bb} substantially more than locations on the surrounding landscape which exhibited the potential to reach $T_{bb} > 70˚C$ (Fig 1A-1B). Models of nest and landscape site T_{bb} showed that T_{air} and S_{rad} recorded at meteorological stations and their interaction were effective at explaining the variation in fine scale T_{bb} measurements (86%) (Table 1); however, site specific differences in microclimates were likely driven by fine scale vegetation cover.

Nest sites acted as buffers against thermal conditions occurring on the surrounding landscape by remaining warmer at $T_{air} < 28˚C$; yet cooler than landscape sites at $T_{air} > 28˚C$ (Fig 1B). Furthermore, we observed that the thermal buffering provided by nest sites substantially decoupled nests from surrounding conditions by reducing the amplification of T_{bb} relative to that of landscape (Fig 2). Specifically, standardized mean differences (±SE) between T_{bb} and T_{air} (i.e., T_{bb} - T_{air}) were more than twice as much at landscape sites (5.4˚C greater) during diurnal periods (09:00 -19:00) (Fig 2). Under the assumption that nest and landscape T_{bb} remained relatively consistent within 15 minute sampling periods, this difference of 5.4˚C would result in an additional 1,620 degree-minutes of additional heat loads during the hottest parts of the day (11:00 – 16:00 h) (i.e., 5.4˚C x 5 h x 60 min/h) (Johnson and Guthery 1988). Although nest sites moderated microclimates more than the surrounding landscape, we also observed the potential for extreme T_{bb} at sites selected for nesting. As expected, we observed temporal differences between nest T_{bb} and paired control site T_{bb} throughout the day, however, differences were substantial (Fig 3). Specifically, discrepancies in T_{bb} increased incrementally and peaked during the afternoon concomitant to daily T_{air} and S_{rad} maximums. Not only was average nest T_{bb} cooler than at paired sites or landscape sites, maximum T_{bb} recorded at nests was more than 10˚C less (61.9˚C) than at microsites (72.1˚C) or landscape points (72.1˚C).

Logistic regression models identified T_{bb} as the primary single variable predicting nest success ($p < 0.05$) and the odds of nests being unsuccessful increased with increases in T_{bb} (i.e., hotter nest sites). Specifically, the candidate model containing nest as a lone variable produced an AIC ranking that was substantially better (ΔAIC $\geq$16) than any other models containing single vegetation variables (i.e., visual obstruction, angle of obstruction or vegetation height) (Table 2). T_{bb} was included in each of the top 8 candidate models and had the strongest effect on nest survival (Table 2) demonstrating that it was a more important variable than the vegetation structure variables that we examined as proxies for potential predation risk. However, significant improvements in AIC rankings were achieved when T_{bb} and vegetation variables were included together in candidate models (Table 2). Specifically, the top 2 candidate models received similar statistical support (ΔAIC <2) and included T_{bb} and angle of obstruction as well as T_{bb}, angle of obstruction and vegetation height, respectively (Table 2). The four top candidate models accounted for 98% of the Akaike weight (w_i) (Table 2) and were used to identify model-averaged coefficients used to solve for odds ratios and 95% confidence intervals. Odds ratios were 1.025 (95% CI, 1.00-1.04), 1.01 (95% CI, 1.00-1.02), 0.86 (95% CI, 0.54-1.38) and 1.0 (95% CI, 0.92-1.09) for T_{bb}, angle of obstruction, visual obstruction and vegetation height, respectively. Additionally, differences in T_{bb} between nest fates were temporally explicit with the most pronounced variability occurring during mid-day and afternoon periods on extreme heat days ($T_{air} \geq 39$˚C) (Fig 4A). Interestingly, mean T_{bb} between the 48 successful and 27 unsuccessful nests on days with maximum $T_{air} < 39$ ˚C ($F_{1, 805} = 0.034$, $p = 0.85$) (n=75) (Fig 4B) were similar. However, mean T_{bb} at the 6 successful nests were on average 6 C˚C cooler than at the 6 unsuccessful nests sampled on days experiencing maximum $T_{air} \geq 39$˚C ($F_{1,130} = 6.56$, $p < 0.05$) (n=12) (Fig. 4A).

The moderated microclimates selected by bobwhites as nest sites also afforded different vegetation structure than those at landscape sites. For example, angle of obstruction (71.61˚ ± 2.4) was significantly greater at nest sites than at landscape sites (41.45˚ ± 1.9) ($F_{1, 290} = 80.94$, $p < 0.0001$). Similarly, lateral visual obstruction (6.81dm ± 0.20) at nest sites was also significantly greater than at landscape sites (5.96 dm ± 0.22) ($F_{1, 290} = 5.23$, $p < 0.05$). Moreover, greater percent grass and woody cover and less bare ground cover occurred at nest sites compared to landscape sites (Fig 5), however no differences were found between litter or forb cover. Mean vegetation height (±SE) was similar between successful (0.74 meters ± 0.03) and unsuccessful nests (0.73 meters ± 0.06) and each offered similar lateral visual concealment ($F_{1, 85} = 1.72$, $p = 0.19$) and overhead obstruction ($F_{1,85} = 0.69$, $p = 0.41$). When examining other fine scale vegetation parameters among successful and unsuccessful nests, we found no differences ($p > 0.10$) in any of the vegetation cover variables that were measured.

The study area consists of 50% herbaceous cover and 37% in low shrub cover (unpublished data) and of the 87 nests, 49.4% and 50.6% of the 87 nests were located in grass and shrub cover, respectively. Nest success was 58% in nests positioned in grass and 66% in nests positioned in shrubs. Nests located in shrub and grass cover provided similar T_{bb} on days with maximum $T_{air} < 39^{\circ}C$ ($F_{1, 805} = 0.13$, $p = 0.72$) ($n = 75$), however, shrub cover provided substantially cooler thermal conditions than grass cover on days when maximum $T_{air} \geq 39^{\circ}C$ ($F_{1, 130} = 9.26$, $p < 0.005$) ($n = 12$).

Simple linear models of T_{bb} as a function of T_{air} explained, 77% and 73% of the variation in site-specific T_{bb} measured at nest and landscape sites, respectively. Our models of T_{bb} associated with future climate change indicate that nesting bobwhites will face substantially greater T_{bb} for longer durations (Fig 6). Specifically, we found that future thermal conditions on the landscape could potentially exceed T_{bb} of 50˚C from 12:00 – 16:00 for low emission scenarios and from 11:00 – 17:00 for high emission scenarios (Fig 6). However, while nest sites generally offered much less severe environments than those occurring on the landscape, nests sites will also potentially experience a substantial increase in exposure to thermal extremes for longer durations in the future. For example, under present conditions, mean T_{bb} at nest sites remained less than 39˚C for the entire day but will exceed 39˚C for at least 4 hours of the day under low emission scenarios and at least 6 hours of the day under high emission scenarios (Fig 6).

Discussion

These results provide a linkage between thermal moderation as a component of landscape function and the biologically meaningful response of a ground-nesting bird species. We found that the thermal landscape was highly heterogeneous and provided an extensive variety of microclimates available to ground-nesting birds. Specifically, we observed that T_{bb} differences ranged up to 40˚C among microhabitats across the landscape when $T_{air} > 35^{\circ}C$, demonstrating that certain portions of the landscape moderate thermal environments considerably more than others. Our findings also revealed the potential for high thermal extremes (> 70˚C) occurring on the landscape, further substantiating the importance of thermal choices for ground-dwelling birds to obtain suitable microhabitats for nesting. Moreover, a reduction in thermal heterogeneity or loss of thermally-buffered microhabitats would likely have negative impacts on ground-nesting bird species once a threshold of intolerable thermal space was reached. Therefore, management practices that maintain the heterogeneity of vegetation and thermal environments inherent in shrub landscapes will likely benefit nesting bobwhites by promoting thermally complex matrices of shrubs and grasses, some of which serve as locations for nest sites. Importantly, our models show that reductions of thermally suitable space and greater heat extremes will increasingly confront nesting bobwhites as a result of climate change, suggesting that the impacts of thermal environments on critical reproductive stages is a notable concern for future conservation of species constrained to near ground climates.

The landscape sampled in this study was prone to extreme T_{bb} that regularly exceeded 50˚C during several hours of the day. These findings have major biological implications given that the lethal body temperature for most birds, including bobwhites is 47˚C (Kendeigh 1969, Guthery 2000) and that the lethal egg temperature for bobwhites (50% mortality) has been reported for eggs exposed to 46˚C for as little as 1 hour (Reyna and Burggren 2012). In response to these thermal extremes, bobwhite nest sites offered cooler and less variable thermal conditions than those on the surrounding landscape. Furthermore, ground level T_{bb} at paired control sites was subject to substantial temporal variation and displayed the potential for extremes; however, proximate extremes were greatly mitigated at nest sites. Differences between nest and landscape site T_{bb} were especially greatest on the hottest days (by on average more than 6˚C), demonstrating that thermally-buffered sites likely aided in reducing thermal stress during the reproductive cycle. Using a similar approach, a recent study in the tall grass prairie of Oklahoma observed that greater prairie-chickens (*Tympanuchus cupido*) exhibited similar responses to thermal environments as bobwhites in this study did; specifically, sites selected for nests substantially moderated landscape thermal conditions and successful nests exhibited cooler T_{bb} than unsuccessful nests (Hovick et al. 2014). These similarities demonstrate that nest site selection by ground-nesting birds in two different vegetation communities has an explicit thermal context and reinforces the importance of fine scale thermal heterogeneity for the future persistence of these species.

Habitat selection has been shown to result from the synergistic effects environmental patterns as well as vegetation structure which confer impacts on animals that are scale dependent 9Avgar et al. 2013, Van Moorter et al. 2013, Seabrook et al. 2014). Although these factors can often be confounded (Hiller and Guthery 2005), examining microclimatic conditions at selected locations and the surrounding landscape is a step towards understanding the spatio-temporal trade-offs associated with habitat selection (Hovick et al. 2014). Nest sites in our study were less exposed overhead, provided significantly greater grass and woody cover than those predominately available on the landscape, and were correlated with moderated microclimates. Our finding that T_{bb} was the better single predictor of nest fate suggests that nest success during extreme heat may have been a result of moderated microclimate rather than protection from nest predators. However, top models included both $T_{bb,}$ angle of obstruction and vegetation height, demonstrating the complexity of the microclimate-predation risk tradeoffs involved in nesting.

Long term temperature averages can be informative for broadly assessing bird population responses to climate (La Sorte and Jetz 2010), however, the regularity and intensity of thermal extremes occurring at hourly or diurnal scales are also critical (McKechnie et al. 2012), yet less studied. Interestingly, we found that nest site T_{bb} was similar between successful and unsuccessful nests on less extreme days (<39˚C), however, successful nests moderated T_{bb} by more than 6˚C compared to unsuccessful nests on days of extreme heat (≥ 39˚C). Although our methodology precluded us from gaining a direct linkage between nest fate and T_{bb} at the time of nest failures, the contrast of the pattern that we observed based on relative T_{bb} differences was stark and suggests that further research is needed. The potential importance of this pattern is further elevated given that the range of thermal conditions ensuring successful incubation is narrow and short bouts of extreme high temperatures can be lethal to embryos (Guthery 2000, Reyna and Burggren 2012). In addition, differences in site-specific microclimate conditions among successful and unsuccessful nests during extreme heat may be highly impactful they are likely missed by studies assessing environmental conditions at coarser scales.

A key component to understanding the ecological impacts of future climate change will require knowledge on how critical life history periods may be influenced by proximate thermal environments (Potter et al. 2013, Cavallo et al. 2015). Broad scale climate change will likely shift the juxtaposition of fine scale thermal regimes relevant to organisms (Angilletta 2009, Davies et al. 2006), yet the magnitude and spatial distribution of these shifts are poorly understood (Sears et al. 2011). We found that although broad scale climate greatly influences microclimates, biologically relevant thermal buffering decoupled nest sites from regional conditions (i.e., meteorological station data) as well as microclimates on the surrounding landscape. However, under current conditions nests showed the potential for reaching extremely high mean T_{bb} on occasion and our models indicate that thermal extremes will become increasingly exacerbated with the higher projected temperatures. For example, we found that under high emission scenarios mean T_{bb} experienced at nest sites may reach 44˚C at nest sites and 60˚C at landscape sites. Given that bobwhites have been shown to avoid thermal space ≥ 39˚C, nest sites will commonly experience suboptimal T_{bb}. Therefore, incubating bobwhites and their embryos will be exposed to substantially more extreme T_{bb} for longer durations despite the relative thermal buffering provided by nest sites. Furthermore, given that temperatures ≥ 50˚C exceed both the lethal body temperature for birds (Kendeigh 1969) and the temperature threshold that precludes most biotic life (Calder and King 1974, Larcher 1991), our models suggest that few microhabitats across the landscape will be available to ground nesting avifauna during summer.

Answering ecological questions has historically been hindered by examinations of broad scale patterns that lack local scale relevance (Forman and Godron 1986, Kotliar and Wiens 1990). Moreover, the common practice of assessing scales larger than those experienced by study organisms can inhibit our knowledge about how individuals exploit thermal landscapes, especially in the face of climate change (Varner and Dearing 2014). We provide evidence that heterogeneous landscapes provide microhabitats that moderate thermal extremes and were consequently selected as nest sites by bobwhites. By incorporating detailed assessments of thermal environments as a part of the experimental design, future studies would be better suited to bridge the gap between broad scale climate patterns and the microclimates that organisms experience. For example, thermally induced ecological traps could reduce populations through the inhibition of required for reproductive success (Wong and Candolin 2015), especially in cases where preferred microclimates become fewer and farther between. Therefore, identifying whether animals will respond to increased future thermal stresses by dispersing to tolerable environments, adapting to thermally-stressful conditions (Moritz and Agudo 2013), or perishing will be critical to guide conservation efforts. Our findings show that diurnal and hourly thermal constraints and heat load exposure on ground-nesting birds will likely be exacerbated due to increased high heat associated with climate change. As a result, the need for an increased conservation focus on the mitigation of thermal extremes is likely urgent. Furthermore, these findings demonstrate that the management of thermal space for ground-nesting birds should focus on providing structural complexity that allows species to make hierarchical nest selection decisions at both landscape and fine scales.

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Tables

Table 1. Model outputs for black bulb temperature (T_{bb}) as a function of ambient temperature (T_{air}) and solar radiation (S_{rad}) at northern bobwhite nest sites and landscape sites at the Packsaddle WMA, Oklahoma, USA (2013 – 2014) (n = 7,008).

		Slope Parameter			Fit
Site Modeled	Intercept	T_{air}	S_{rad}	T_{air} X S_{rad}	R^2
Nest*	2.39	0.90	0.00097	0.00030	0.86
	(±0.43)	(±0.018)	(±0.0012)	(±0.000044)	
Random*	-1.96	1.03	0.0091	0.00025	0.86
	(±0.57)	(±0.021)	(±0.0017)	(±0.000052)	

*Denotes significance at the level of $p < 0.001$.

Table 2. Logistic regression candidate model rankings for variables affecting northern bobwhite nest success at the Packsaddle WMA, Oklahoma, USA (2013-2014). Black bulb temperature (i.e., T_{bb}), angle of obstruction, visual obstruction, and vegetation height (i.e., height) were variables included in candidate models

Candidate Model	**K[a]**	**AIC**	**ΔAIC**	**w_i[b]**
T_{bb} + Angle	3	1241.7	0.0	0.38
T_{bb} + Angle Obstruction + Height	4	1241.9	0.2	0.34
T_{bb} + Visual Obstruction + Angle	4	1243.7	2.2	0.13
Global	5	1243.7	2.2	0.13
T_{bb} + Visual Obstruction + Height	4	1249.4	7.5	< 0.01
T_{bb} + Visual Obstruction	3	1251.0	9.1	< 0.01
T_{bb}	2	1251.6	9.7	< 0.01
T_{bb} + Height	3	1252.3	10.4	< 0.01
Angle Obstruction	2	1267.6	25.7	< 0.01
Angle Obstruction + Height	3	1268.8	27.1	< 0.01
Angle Obstruction + Visual Obstruction	3	1269.3	27.6	< 0.01
Visual Obstruction + Height	3	1271.4	29.7	< 0.01
Visual Obstruction	2	1271.4	29.7	< 0.01
Null	1	1272.4	30.7	<0.01
Height	2	1273.7	31.8	< 0.01

[a] Number of parameters

[b] Akaike weight

Figure Legend

Figure 2.1. (A) Distribution of diurnal black bulb temperature (T_{bb}) observed from 09:00 – 19:00 h (n = 3,212) and (B) linear models of T_{bb} as a function of ambient temperature (T_{air}) recorded during the full sampling period (00:00 – 24:00 h) (B) at northern bobwhite nest and landscape sites at the Packsaddle WMA, Oklahoma, USA (2013 -2014) (n = 7,008).

Figure 2.2 Differences (T_{bb} – T_{air}) between diurnal black bulb temperature (T_{bb}) and ambient temperature (T_{air}) (±SE) measured from 09:00 – 19:00 h at northern bobwhite nest (n = 87) and landscape sites (n = 205) at the Packsaddle WMA, Oklahoma, USA (2013 - 2014).

Figure 2.3. Mean black bulb temperature (T_{bb}) (±SE) measured from 09:00 – 19:00 h at northern bobwhite nests (light gray) (n = 87) and paired control sites (dark gray) (n = 87) at the Packsaddle WMA, Oklahoma, USA (2013 -2014).

Figure 2.4. (A) Mean black bulb temperature (T_{bb}) (±SE) measured from 09:00 – 19:00 at successful (n=54) (dashed line) and unsuccessful (n=33) northern bobwhite nests (solid line) on days when maximum ambient temperature (T_{air}) was ≥ 39˚C (n=12) and (B) < 39˚C (n=75) at the Packsaddle WMA, Oklahoma, USA (2013 -2014).

Figure 2.5. Percent vegetation cover measured at northern bobwhite nest (n = 87) and landscape sites (n = 205) at the Packsaddle WMA, Oklahoma, USA (2013 – 2014). Asterisks denote significant differences at the $p < 0.05$ level within cover categories.

Figure 2.6. Black bulb temperature (T_{bb}) (±SE) measured at northern bobwhite nest sites (green) and random landscape sites (red). Marker shape denotes observed conditions (square) and those associated with projected increases in T_{air} as predicted by the low (circle) and high (triangle) emission end of century scenario ensemble averages at the Packsaddle WMA, Oklahoma, USA, 2013 - 2014 (n=7,008).

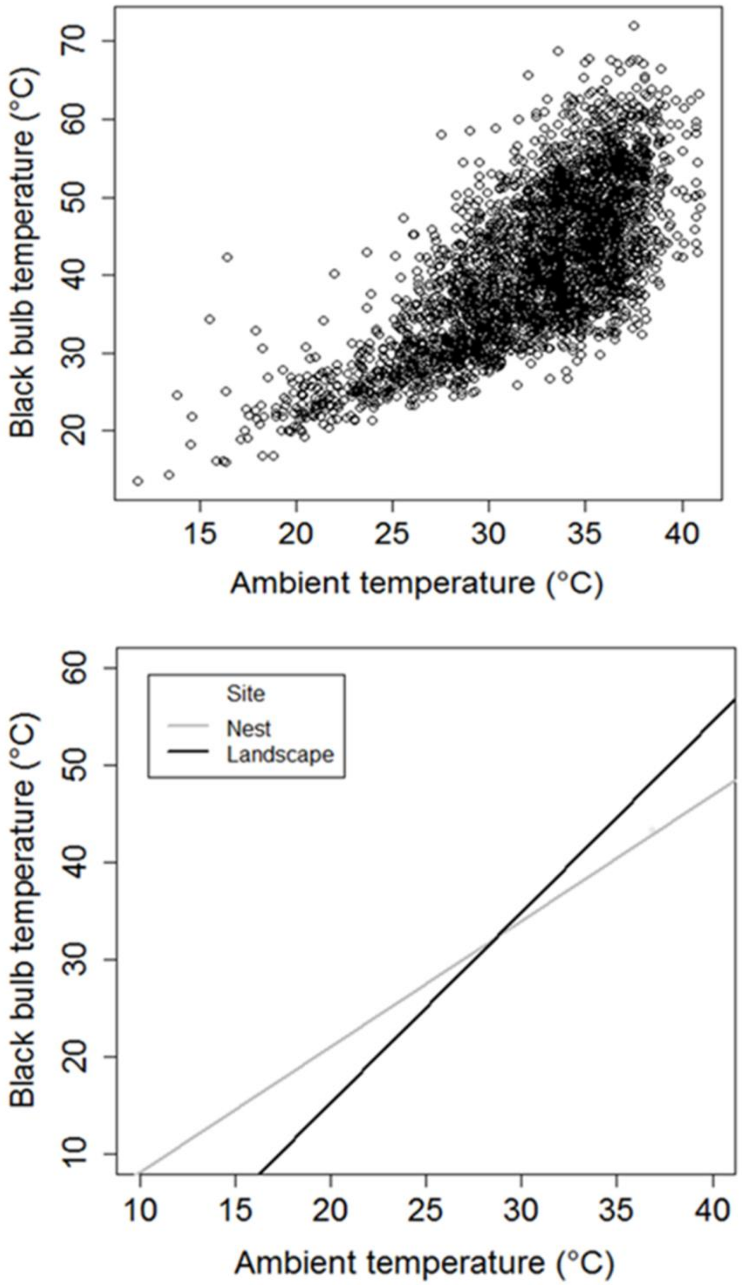
Black bulb temperature (°C)
70
60
50
40
30
20
15
20
25
30
35
40
Ambient temperature (°C)
Black bulb temperature (°C)
60
50
40
30
20
10
Site
Nest
Landscape
10
15
20
25
30
35
40
Ambient temperature (°C)

Figure 2.1.

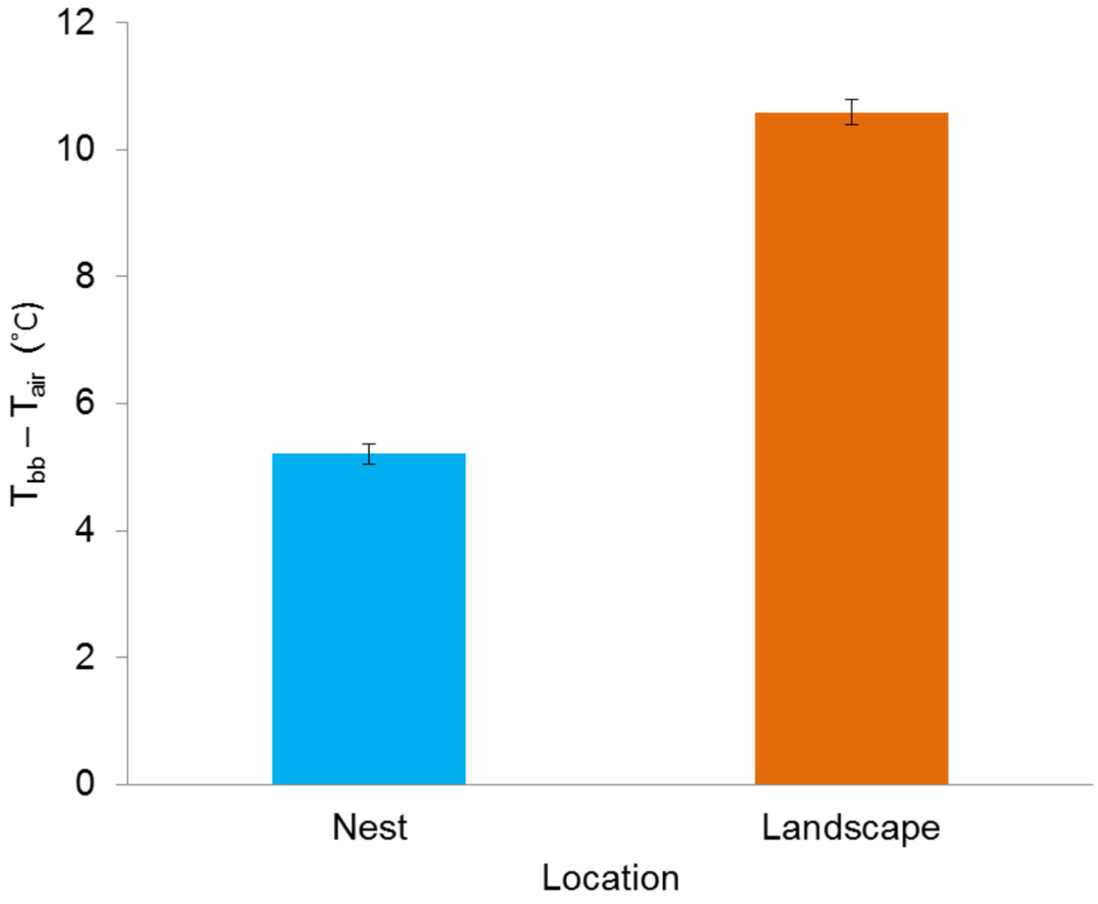

Figure 2.2.

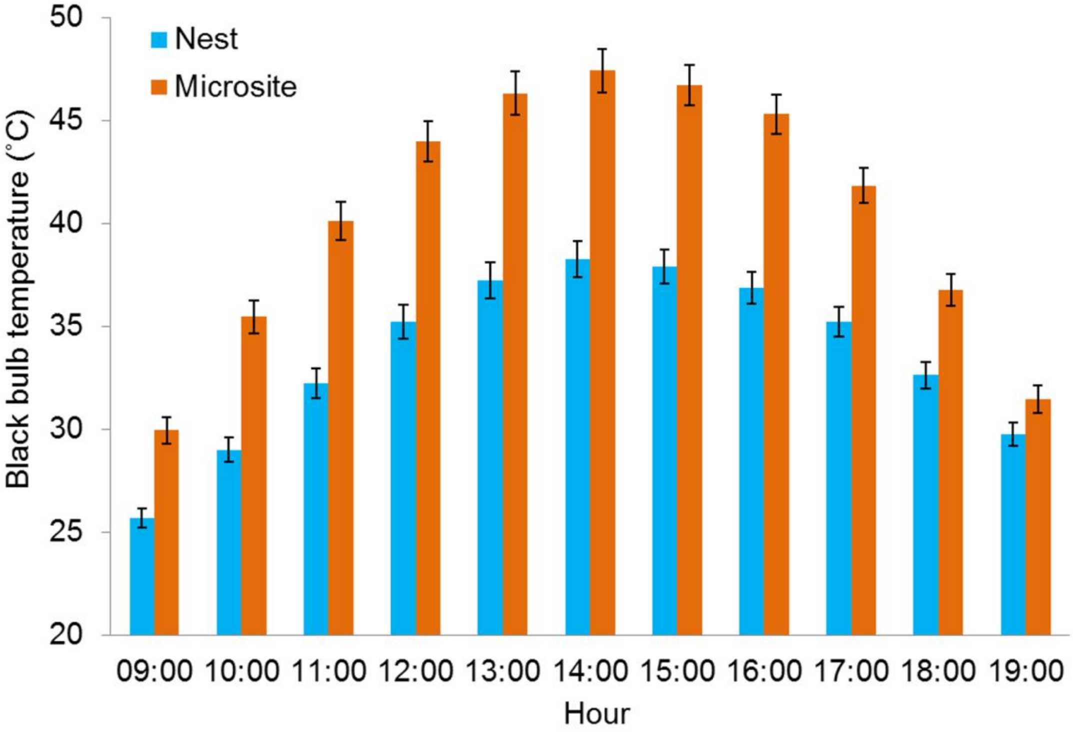
50
45
40
35
30
25
20
Black bulb temperature (˚C)
Nest
Microsite
09:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
Hour

Figure 2.3.

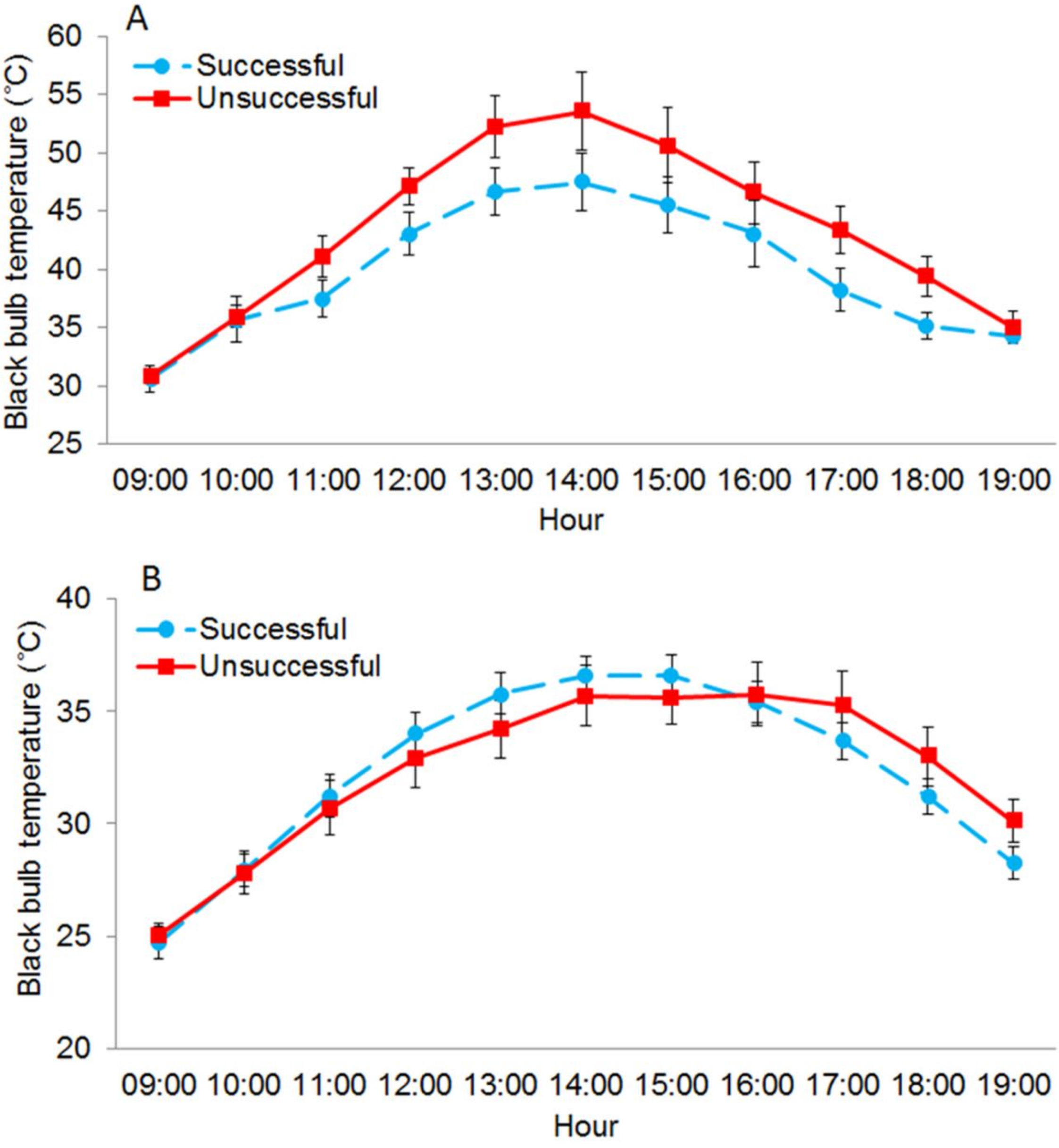
A
Successful
Unsuccessful
Black bulb temperature (°C)
60
55
50
45
40
35
30
25
09:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
Hour
B
Successful
Unsuccessful
Black bulb temperature (°C)
40
35
30
25
20
09:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
Hour

Figure 2.4.

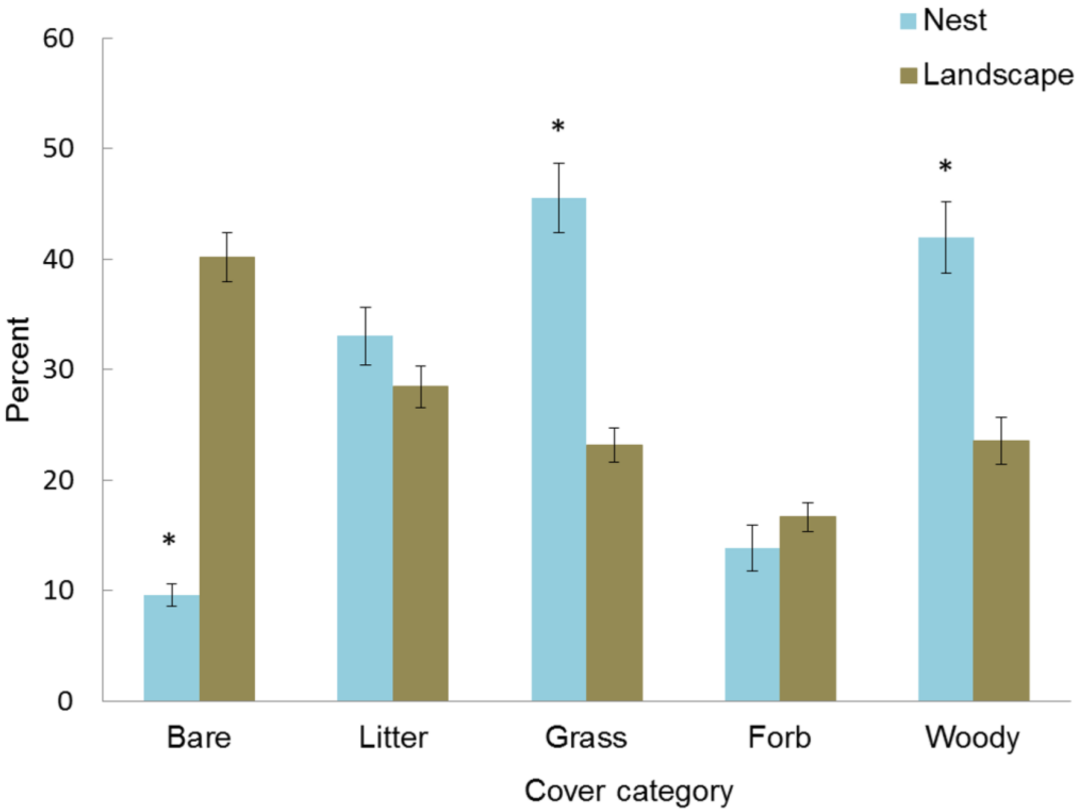
Nest
Landscape
60
50
40
30
20
10
0
Percent
*
*
*
Bare
Litter
Grass
Forb
Woody
Cover category

Figure 2.5.

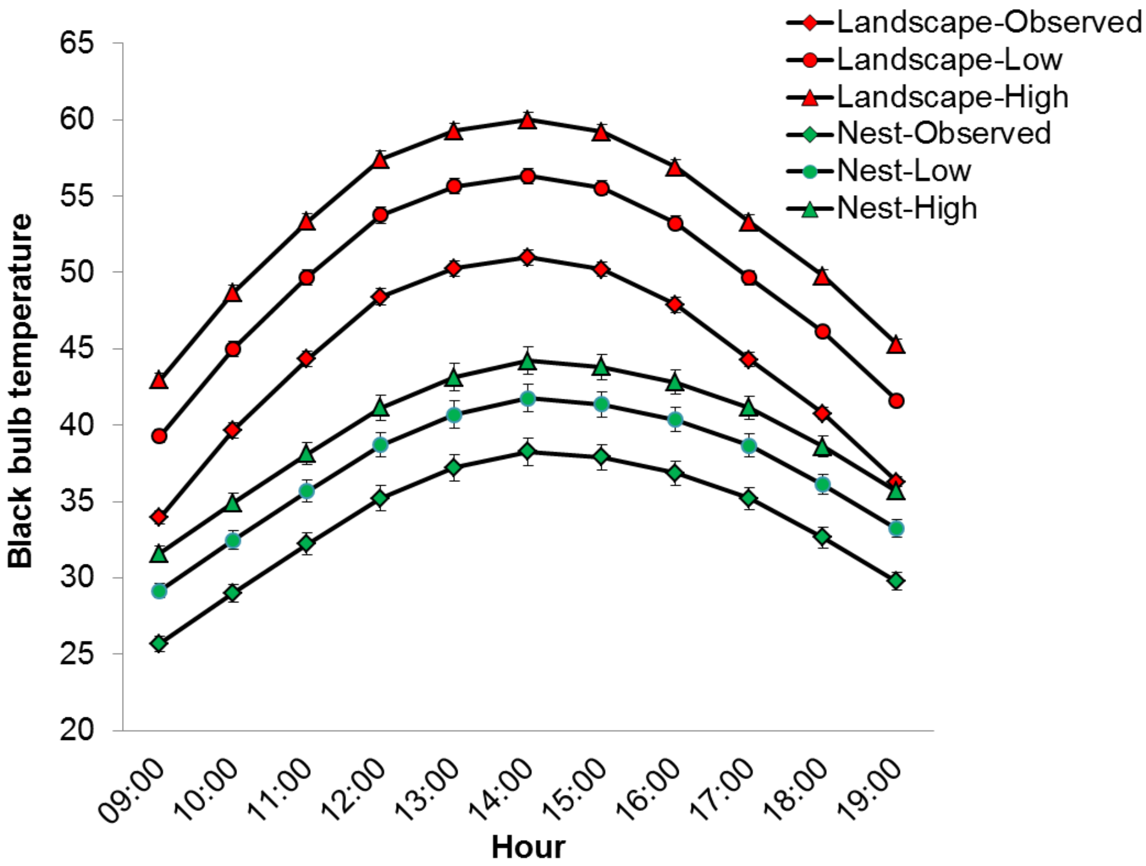
Landscape-Observed
Landscape-Low
Landscape-High
Nest-Observed
Nest-Low
Nest-High
Black bulb temperature
65
60
55
50
45
40
35
30
25
20
09:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
Hour

Figure 2.6.

CHAPTER III

THERMAL PATTERNS CONSTRAIN DIURNAL BEHAVIOR OF A GROUND-DWELLING BIRD

Abstract

Recently, gaining knowledge about thermal refuges for vulnerable species has been a major focal point of ecological studies, and this focus has been heightened by predicted temperature increases associated with global climate change. To better understand how organisms respond to thermal landscapes and extremes, we investigated the thermal ecology of a gallinaceous bird species (northern bobwhite; *Colinus virginianus,* hereafter bobwhite) during a key life history period. Specifically, our study focused on the brood-rearing period of precocial bobwhite chicks associated with brood-attending adults. We measured site-specific black bulb temperatures (T_{bb}) and vegetation characteristics across 38 brood tracking days and 68 random landscape sites to assess thermal patterns at scales relevant to broods. We observed that the landscape was thermally heterogeneous, exhibiting variation in T_{bb} up to 40˚C during peak diurnal heating demonstrating a wide array of thermal choices available to broods. At 15:00 h, broods selected thermal refuges that moderated T_{bb} on average up to 10.4˚C more than landscape sites. Moreover, broods exhibited behavioral thermoregulation through reduced movement and by occupying more moderate microclimates that afforded taller vegetation structure during high heat. Modeled climate projections suggest that future T_{bb} in thermal refuges will approach those currently avoided on the landscape, emphasizing the need for future conservation plans that acknowledge fine scale thermal space in climate change scenarios. These findings underline that studying both abiotic and biotic factors at scales relevant to organisms can increase our understanding of how thermally heterogeneous landscapes provide thermal choices under extreme conditions.

Introduction

Thermal environments impact all organisms on Earth (Brock 1967, Angilletta 2009), and are a primary component of a population's fundamental niche (Hutchinson 1957, Magnuson et al. 1979, Kearney and Porter 2004). Although temperature (e.g., operative temperature and ambient temperature) has been widely accepted as a driver of ecological processes (Smith and Smith 2000, Begon et al. 2006), detailed information on how fine scale variation in thermal patterns influence individuals remains unclear, especially during thermal extremes (Suggitt et al. 2011, Potter et al. 2013). An organism's fitness and survival are contingent upon its physiological and behavioral response to proximate thermal variation and subsequently, its ability to control body temperature (Hafez 1964, Huey 1991, Smit et al. 2013). However, if thermally buffered microsites cannot be obtained, extreme heat exposure can cause body temperature to reach lethal limits if heat load surpasses the animals thermoregulatory capacity for heat dissipation (Cowles and Bogert 1944, Porter and Gates 1969, Cunningham et al. 2013a). For example, large scale heat related die offs have been documented for birds in Australia (Finlayson 1932, Towie 2009) and in the deserts of the southwestern United States of America (Miller 1963). Moreover, air temperatures of large portions of landscapes in both semi-arid and subtropical regions can exceed lethal thermal thresholds for birds during hot conditions (Goldstein 1984, Guthery et al. 2001). Therefore, a better understanding of how landscapes moderate thermal environments, as well as how organisms exploit thermally buffered sites (i.e., refuge), will be a critical component of species conservation especially in light of future climate change (Hovick et al. 2014).

The fitness of mobile organisms is dictated by their ability to use spatio-temporal variation of resources and environmental conditions between patches resulting in beneficial, neutral, or detrimental impacts (Brown and Orians 1970, Wiens 1976). Accordingly, organisms position themselves in specific microclimates across the landscape to buffer themselves from excessive heat loads (Huey 1991). Microclimate is defined as near ground climate (Rosenberg et al. 1983), and spatio-temporal variation in microclimate shapes thermal heterogeneity across the landscape (Angilletta 2009, Suggitt et al. 2014). Although the juxtaposition of microclimates are key in determining the habitat use and physiological responses of organisms, ecological research often overlooks how landscapes moderate thermal extremes and drive biotic patterns (Chen et al. 1999). Moreover, macro-scales (> 1 km^2) are commonly used as proxies of organism responses to thermal environments, however, microclimates at scales relevant to those experienced by study species are rarely assessed, leading to misunderstandings about how organisms utilize microclimates within thermal landscapes (Helmuth et al. 2010, Sears et al. 2011, Gunderson and Leal 2012). Additionally, because certain portions of the landscape moderate extreme temperatures more than others, thermal heterogeneity can determine the availability of thermal choices obtainable to organisms at both broad and fine scales (Limb et al. 2009, Hovick et al. 2014, Goller et al. 2014).

Northern bobwhite (*Colinus virginianus*) (hereafter, bobwhite) is an r-selected gallinaceous bird species (Guthery and Brennan 2007) that is heavily constrained by high temperatures on the southern and western edges of its distribution (Hiller and Guthery 2005, Guthery et al. 2001). Being a species of conservation concern that is undergoing a widespread decline (Brennan 1991, Sauer et al. 2011), bobwhites are also a fitting model species for assessing refuge use and behavioral responses to thermal heterogeneity for two primary reasons. First, adult bobwhites inhabiting the western portion of their distribution likely already exist on the edge of their physiological thermal limits during hot conditions (Forrester et al. 1998, Guthery et al. 2001). Thus, bobwhites are potentially a representative species for assessing organism responses to thermal extremes. Second, unlike many small mammal or reptile species that utilize subterranean retreats to mitigate extreme heat (Huey et al. 1989, Sharpe and Van Horn 1999), ground birds are constrained to above ground thermal environments which increases their potential exposure to thermal extremes (Dawson 1982, Wolf et al. 1996).

Recently, ecological studies have stressed the importance of gaining knowledge about the conservation of species that are vulnerable to high temperatures by studying how microsites mitigate thermal conditions relevant to impending climate change (Potter et al. 2013, Scheffers et al. 2014, Hannah et al. 2014). However, sensitivity to climatic variation is not static across life history periods of species, and therefore, vulnerability can be higher during some periods than others (Moritz and Agudo 2013). For example, exposure to high temperatures or solar radiation can impact young birds through direct lethal effects (Salzman 1982) or sub-lethal effects such as reduced growth or survival due to decreased foraging time (Goldstein 1984, Cunningham 2013a). In our study, we hypothesized that groups of precocial bobwhite chicks (hereafter, broods) would respond behaviorally to proximate thermal variation across the landscape within diurnal cycles, and that these responses would be most pronounced on the hottest days. Our main objective was to investigate how landscapes moderate thermal extremes and to examine the behavioral adjustments (i.e., movement and patch use) of broods in response to variations in thermal patterns, especially during thermally stressful periods (i.e., actual exposure). Furthermore, we sought to quantify the relative thermal benefits associated with those behavioral adjustments; specifically, the thermal conditions that broods would be exposed to had they not occupied thermal refuge (i.e., potential exposure). Finally, we modeled the potential diurnal thermal conditions that broods may be exposed to as a result of future climate change in order to better understand how temperature increases will impact the availability of thermal space.

Methods

Study area

We studied bobwhite thermal ecology in a shrub-dominated landscape located on the western periphery of the continental bobwhite distribution. The study site encompasses 7,956 ha and is located on the Packsaddle Wildlife Management Area (WMA) in western Oklahoma, which is owned and managed by the Oklahoma Department of Wildlife Conservation. The vegetation at Packsaddle WMA is dominated by sand shinnery oak (*Quercus havardii*), yet herbaceous plants and other shrubs are also common (Vermeire and Wester 2001). A detailed description of the vegetation community on the study area is provided by DeMaso et al. (1997). Locally (< 30 km from the study site), average annual precipitation from 1994 – 2013 ranged from 241.81 - 746.6 mm with an average of 554.4 mm per year (Arnett Oklahoma Mesonet Site; Oklahoma Mesonet 2013). Furthermore, this region can be subject to frequent and intense heat during summer, experiencing an average of 25 days annually at temperatures in excess of 37.8˚C (Arndt 2003). Mean high summer temperatures exceeding 39˚C are also possible (Arnett Oklahoma Mesonet Site; Oklahoma Mesonet 2013).

Data collection

We captured adult bobwhites from February – April 2013 and 2014 and fitted them with a 6 gram necklace radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). Via radio telemetry, we monitored 92 nests located by tracking 220 adult bobwhites during the 2013 and 2014 breeding season to determine nest fate (i.e., successful or unsuccessful). Successful hatching (i.e., ≥ 1 egg hatched) occurred at 51 nests. Bobwhite broods were randomly selected from the pool of available marked broods for diurnal telemetry monitoring resulting in 19 different broods tracked across 38 days during the study. Because of logistical constraints such as the periodic loss of broods to predation, some broods were tracked on more than one sampling day. On each brood sampling day, a single brood was monitored via radio-telemetry on the brood-attending adult, and locations were recorded at 07:00, 09:00, 11:00, 13:00, 15:00, 17:00, and 19:00 h. Broods were located at each time period and were not radio-tracked continuously between locations. We located broods using the homing technique (White and Garrott 1990) at a distance of approximately 15-20 meters which has been shown to be appropriate for locating quail with minimal disturbance (Goldstein 1984, Goldstein and Nagy 1985). This general technique has been a standard radio-telemetry approach for locating gallinaceous bird broods, including bobwhites (Taylor and Guthery 1994, Martin et al. 2009). During tracking, we observed no noticeable response of broods to the presence of observers, and no brood-attending adults or chicks were flushed during radio-tracking events. Due to vegetation structure and the cryptic behavior of broods, visual observations on adults or chicks were rare. However, to improve the accuracy of our radio-locations, we attempted to confirm each brood location by searching for chick feces, tracks, feathers, or evidence of dusting (Johnson and Guthery 1988). In addition, we confirmed that broods were associated with the radio-marked adult by checking roost sites for the presence of chick feces, by flushing broods, or by observing brood-tending displays by the adult within two days of each brood-tracking event (Taylor and Guthery 1994).

We measured black bulb temperature (T_{bb}) to assess patterns in thermal conditions (i.e., thermal heterogeneity) and to acquire an index of thermal conditions at brood locations and at random points on the landscape. T_{bb} consolidates ambient temperature, solar radiation, and wind effects into a single value to approximate the conditions that an organism is experiencing (Campbell and Norman 1998) and provides a means to assess microclimate conditions (Porter and Gates 1969). To obtain a proxy of environmental temperature, we measured T_{bb} using steel spheres (101.6 mm-diameter; 20 gauge thickness) painted flat black (hereafter, black bulbs), positioned at ground level (Guthery et al. 2005, Allred et al. 2013, Hovick et al. 2014). We elected to use steel spheres because they have been used in previous studies on the thermal ecology of galliforms including bobwhites and were specifically used to link thermal environments to bird behavior and site selection (Hiller and Guthery 2005, Guthery et al. 2005, Hovick et al. 2014). However, T_{bb} measurements do not replicate the color and feather composition of real birds and thus, do not provide a direct linkage between the thermal environment and operative temperature or body temperature (Dzialowski 2005). Therefore, given our assumption that the short wave absorptivity of radiation on our black bulbs is 1 compared to 0.78 for bobwhites (Calder and King 1974, Guthery et al. 2005), we expect that steel spheres experience higher thermal heat loads than bobwhites. Despite these limitations, quantifying T_{bb} provided an ecologically relevant means to obtain a proxy of the environmental temperature that broods were exposed to throughout the day. Moreover, assessing T_{bb} allowed for a comprehensive depiction of thermal environments at brood locations relative to those in their surroundings at fine spatial and temporal scales.

A temperature probe was suspended in the center of each black bulb and T_{bb} was recorded with four channel HOBO data loggers (U12-008, Onset Corporation, Bourn, Massachusetts, USA). To thoroughly characterize the thermal environment at brood locations, T_{bb} at patches used by broods were measured using thermal arrays consisting of four black bulbs connected to a single data logger. Because each data logger was equipped with four data ports, thermal arrays were arranged so that one black bulb was placed at the estimated brood location point, and three black bulbs were placed in three randomly determined cardinal directions at a distance of 4 m from the estimated brood point. To avoid unnecessarily disturbing broods, we deployed thermal sampling arrays prior to 07:00 h on the day following a brood-tracking event, under similar weather conditions. Thus, each thermal-sampling array began recording T_{bb} at the same time of day and recorded T_{bb} for equivalent durations within days.

We recorded T_{bb} at brood use sites on 38 tracking days at one minute intervals for 24 hours to characterize relative site specific T_{bb} exposure at fine temporal scales. To sample T_{bb} available across the landscape, a stratified random sampling approach was used to distribute random points proportional to available vegetation types within the study area using ArcGIS 10.3 (Environmental Systems Research Institute, Redlands, California, USA). Landscape T_{bb} was measured at 68 of these randomly selected sites, and these sites were sampled across 15 minute intervals for 24 hours on days that brood locations were sampled. This sampling effort allowed us to obtain over 1,500,000 individual T_{bb} measurements at brood and landscape sites. To provide a broad scale environmental context to site-specific T_{bb}, we measured average hourly ambient temperature (T_{air}) and solar radiation (S_{rad}) (W/m^2) at three onsite meteorological stations positioned 2 m above ground level. Data from the nearest meteorological station to each brood location or random landscape site were used for analysis of environmental variables. Brood and landscape T_{bb} were sampled under a similar range of T_{air} (brood range: 11.09 – 40.83˚C; landscape range: 19.85 – 40.92˚C). Thus, brood sites experienced similar T_{air} as landscape sites, especially during warmer focal periods.

This study focused on investigating thermal conditions, which provide one dimension of habitat use across time and space (Huey 1991). To further examine the mechanisms of thermal moderation from the perspective of a ground-dwelling bird inhabiting a shrub community, we also assessed vegetative structure at brood sites and random landscape sites. Specifically, we estimated percent cover of litter, bare ground, grass, forb and woody cover within a 0.5^2 m quadrat (modified from Daubenmire; Daubenmire 1959) centered over each black bulb (Hovick et al. 2014). Because the study site is primarily composed of low shrub, herbaceous vegetation, and bare ground, vegetation height at brood locations was categorized as < 1 m, 1-2 m, or ≥ 2 m. At each sampling point, we quantified overhead vegetation obstruction (i.e., overhead canopy cover) by aiming a digital carpenter’s level attached to a 2 m pole at the top of nearest vegetation in 8 compass directions (cardinal and sub-cardinal) and recorded the angle (Kopp et al. 1998).

Data Analyses

To characterize thermal conditions relevant to broods, we modeled site specific T_{bb} for brood locations and random landscape sites relative to T_{air} and S_{rad} recorded at onsite weather stations using regression analysis. T_{bb} was averaged by hour (07:00 – 19:00 h) across each thermal sampling array and the resulting values were averaged for comparisons with hourly averages of T_{air} included in models. To enhance ecological relevance, site-specific T_{bb} from brood locations were classified as active (07:00, 09:00, and 19:00 h locations), transition (11:00 and 17:00 h locations), and refuge periods (13:00 and 15:00 h locations). These categories were based on previous literature indicating that adult bobwhites curtail movement during the heat of the day (Hiller and Guthery 2005). We used a repeated-measures ANOVA to compare site-specific T_{bb} during peak diurnal heating (11:00 -17:00) with site-specific hourly temperatures as repeated measures recorded across active, transition, and refuge sites.

To examine movement patterns and distance traveled throughout diurnal periods, we calculated the Euclidean distance and standard errors between brood locations for each daily sampling period using ArcGIS 10.3 (Environmental Systems Research Institute, Redlands, California, USA) (Beasely and Rhodes 2010, Lohr et al. 2011). We used $T_{bb} \geq 39^{\circ}C$ outlined by Forrester et al. (1998) as the temperature at which heat gain outpaces heat loss in bobwhites as a threshold to examine possible changes in movement on days with maximum T_{air} of $< 39^{\circ}C$ and $\geq 39^{\circ}C$.

Because vegetation characteristics can substantially decouple microclimates from macroclimates (Varner and Dearing 2014), we tested for differences between vegetation parameters among brood locations and landscape sites to assess the ability of site specific vegetation to moderate T_{bb}. Accordingly, vegetation height categories among activity periods were analyzed using a Pearson's Chi-squared test. Differences in vegetation parameters (e.g., bare ground cover, litter cover, grass cover, forb cover, woody cover, and angle of obstruction) among activity periods were analyzed using ANOVA. When ANOVA reported significant differences, multiple comparisons were made using a Tukey multiple comparison test (Zar 1984). Differences were deemed significant at the $p < 0.05$ level.

To investigate potential changes in the diurnal distributions of T_{bb} accessible to broods in the future, we used simple models of site specific T_{bb} as a function of T_{air} to project changes in T_{bb} linked with global climate change predictions. The resulting models enabled us to represent potential future thermal characteristics of brood habitat at fine temporal scales (i.e., every two hours) during diurnal periods. We followed the assumption that T_{bb} is a linear function of T_{air} (Gunderson and Leal 2012, Logan et al. 2013) however, to provide greater ecological detail to our models, we used model outputs as the basis for our projections of brood and landscape T_{bb}. Because the impacts of climate change on organisms will be expressed at fine temporal scales (Angilletta 2009), we used site specific models of T_{bb} as the basis for our future projections to allow us to account for non-uniform changes in T_{bb} throughout diurnal cycles relevant to broods. Thus, resulting linear equations and coefficient estimates from model outputs were used to project T_{bb} from projected T_{air} increases for the region containing the study area based on ensemble averages for both end of century high (4.6˚C increase in T_{air}) and low (2.7˚C increase in T_{air}) emission scenarios (www.climatewizard.org, Girvetz et al. 2009).

Results

Landscape T_{bb} variability

The distribution of diurnal T_{bb} measurements ranged from 12.95 – 73.17˚C across sampling locations throughout the study. Moreover, we observed that differences in T_{bb} available to broods of up 40˚C were possible when T_{air} exceeded 39˚C (Fig. 1), demonstrating that the variability in thermal conditions was greatest at high T_{air}.

Diurnal T_{bb} exposure

Our sampling effort resulted in 38 diurnal brood tracking days and 68 random landscape sites. Brood locations were consistently and often substantially cooler than landscape sites during diurnal periods (Fig. 2). Moreover, mean T_{bb} differences between landscape sites and brood locations were most pronounced during peak daily heating periods (Fig. 2). For example, mean T_{bb} at 15:00 h for landscape sites exceeded T_{bb} at brood locations by 10.4˚C (Fig. 2). We found that diurnal T_{bb} exposure at brood locations was lowest during morning and evening periods and increased throughout the day, peaking during mid-day and afternoon periods (Fig. 2). However, while brood locations were substantially buffered against more extreme thermal conditions available in the surrounding landscape, in some cases by more than 10˚C, mean T_{bb} at brood locations still reached considerably high levels (Fig. 2). For example, we observed mean T_{bb} of 44.70˚C and 42.78˚C for 13:00 and 15:00 h locations, respectively (Fig. 2).

Potential diurnal T_{bb} exposure and thermal benefits of refuge sites

In addition to mitigating thermal extremes on the landscape, refuges selected by broods provided conditions that buffered them from climate extremes occurring in the surrounding area, and relative to locations occupied during other periods of the day (Fig. 2 and Fig. 3). For instance, T_{bb} was comparatively homogenous at 07:00 and 19:00 h (i.e., active sites), however, the remaining periods of the day experienced distinct thermal heterogeneity among brood locations (Fig. 3). Moreover, the greatest thermal heterogeneity occurred during the hottest periods of the day (Fig. 1, Fig. 3). Models of site –specific T_{bb} that included T_{air}, S_{rad} (i.e., solar radiation) and their interaction as variables had sufficient explanatory power accounting for 74 - 86% of the variation measured at active, transition, refuge, and landscape sites (Table 1), and confirm the importance of T_{air} and S_{rad} in assessments of site-specific T_{bb}.

Behavior and role of habitat selection

During periods of peak heating (11:00 – 17:00 h), when thermal decisions are likely most critical, mean T_{bb} differed among active, transition, and refuge sites (ANOVA: $F_{2, 1838} = 15.32$, $p < 0.001$). Moreover, had broods remained at the active sites that they occupied during morning or evening periods rather than seeking refuge sites, T_{bb} exposure would have been up to 5˚C greater (Fig. 3). Correspondingly, distances moved were greatest during morning and evening periods (active period) when T_{bb} was lowest, and were least during midday and afternoon periods (refuge periods) when T_{bb} was greatest. Broods observed in our study had mean (±SE) minimum daily movement of 392.3 ±34 m, with 69%, 25% and 6% of distances moved occurring during active, transition, and refuge periods, respectively. Specifically, mean brood movement pooled across broods was greatest from 17:00 - 19:00 h (101.29 ± 9.84 m) and 07:00 - 09:00 h (84.32 ± 10.15 m) and was least from 13:00 - 15:00 h (24.59 ± 4.32 m) ($n=38$ tracking days). As hypothesized, mean differences in movement across tracking intervals throughout the day were greatest on days when maximum T_{air} was $\geq 39^\circ$C and was reduced to 9.48 (± 4.0) m from 13:00 – 15:00 h (Fig. 4). In addition, mean brood movement was approximately 11.5-fold greater from 07:00 – 09:00 h than from 13:00 – 15:00 h on days when maximum T_{air} were $\geq 39\ ^\circ$C. On comparatively milder days ($T_{air} < 39^\circ$C), mean brood movement was two-fold greater from 07:00 – 09:00 h than from 13:00 – 15:00 h. Therefore, we found that broods maximized movement during the coolest periods of the day, especially on the hottest days.

As a general pattern, we observed that broods utilized microsites affording different vegetation structure throughout diurnal periods, with the most pronounced differences observed at refuge sites (Fig. 5 and Fig. 6). We found significant differences in vegetation height categories among active, transition, refuge, and landscape sites ($X^2 = 85.01$, $p < 0\ .001$, $df = 4$), and broods generally selected taller shrub cover during hotter times of the day (Fig. 6A). Specifically, 92% of active site locations were in patches with < 1 m tall shrubs, compared to 31% in refuge sites (Fig. 6A). Angle of obstruction (i.e., overhead cover) differed significantly among all activity periods ($F_{2,\ 261} = 54.47$, $p < 0.001$) and was greatest at refuge sites (i.e., coolest sites) and least at active sites (Fig. 6B). Significant differences for percent bare ground, litter, grass, and woody cover parameters were found among activity periods, however, we found no differences in percent forb cover among activity periods (Table 2). Percent woody cover was greatest at refuge sites and least at active sites (Table 2), however, landscape sites afforded lower percent woody cover than all brood sites (Table 2). Additionally, litter cover was greater at refuge sites than at active or landscape sites. Conversely, bare ground was greater at active and landscape sites than at refuge sites (Table 2), suggesting that at fine scales the presence of bare ground was associated with higher T_{bb}.

Susceptibility to climate change

Simple linear models including T_{air} had adequate explanatory power in predicting T_{bb} (62 – 69%) (Table A1) and provided a straightforward way to describe non-uniform site specific changes in T_{bb} across diurnal periods resulting from climate change. As expected, our models indicate that brood rearing cover will become substantially hotter for greater portions of the day by 2080 (Fig. 7). However, we observed that brood locations will potentially reach mean T_{bb} of up to 48.5˚C and 51.1˚C, even in sites selected for thermal refuge (13:00 h), and simultaneous mean landscape T_{bb} will reach up to 58.9˚C and 62.4˚C at low and high emission scenarios, respectively (Fig. 7). In both climate change scenarios, T_{bb} at brood locations will exceed 39˚C, the point at which heat intake outpaces heat loss in bobwhites (Forrester et al. 1998), earlier in the day and for longer durations (Fig. 7). Models show that even for low emission scenarios, T_{bb} on the landscape will exceed 39˚C by 09:00 h and will remain above 39˚C through 19:00 h (Fig. 7). Therefore, these estimates demonstrate that bobwhites will be exposed to suboptimal thermal conditions that they currently avoid. Moreover, T_{bb} exceeding 47˚C on the landscape may occur from 11:00 – 17:00 h for both low and high emission scenarios.

Discussion

We found highly heterogeneous thermal environments with variations in T_{bb} by up to 40˚C, indicating a wide array of thermal choices available to organisms within diurnal periods. T_{air} and S_{rad} were drivers of site-specific microclimate at scales relevant to broods, and taller vegetation with greater overhead cover was associated with moderated T_{bb}. In addition, our findings suggest that thermal heterogeneity and thermal extremes influenced diurnal brood behavior as demonstrated by the rapid adjustments that broods made in their response to changing thermal conditions, which were especially apparent on the hottest days. These results further emphasize the importance of including both biotic and abiotic factors in investigations on ecological phenomena (Limb et al. 2009).

To prevent or mitigate thermal stress, individuals confronted with extreme heat must seek out thermally-buffered microsites that serve as thermal refuges (Scheffers et al. 2014). We observed that broods in this study exhibited the ability to behaviorally modify their exposure to thermal extremes by moving to, and occupying, refuge sites that moderated T_{bb} by an average of up to 10˚C compared to the surrounding landscape. Importantly, refuge sites also acted as buffers against prevalent thermal extremes on the landscape. However, although refuge sites substantially moderated thermal extremes, they provided thermal conditions that are likely sub-optimal ($T_{bb} \geq 39$˚C). While vegetation and the cryptic behavior of bobwhites precluded observing behavioral responses to heat stress, our findings indicate that bobwhites may require panting or gular fluttering to mitigate heat accrual on a potentially daily basis. Furthermore, our models indicate that broods will be exposed to substantially greater and more extreme T_{bb} at all times of the day and for longer durations according to future climate scenarios. Specifically, although refuge sites significantly moderated T_{bb} relative to the landscape, future mean T_{bb} of over 50˚C and 60˚C will be possible in sites selected for thermal refuge as well as throughout the landscape, respectively. These findings demonstrate a thermal conundrum which has broad implications for species responses to climate change; specifically, refuge sites will likely become more critical yet also simultaneously hotter (i.e., less suitable), making extreme thermal space increasingly unavoidable.

Compared to sites used at other periods of the day or on the landscape, refuge sites consisted of taller woody structure, denser overhead canopies, and corresponded to the coolest thermal environments. This suggests that tall, dense woody cover decoupled refuge sites from the prevailing environmental conditions occurring on the landscape, especially thermal extremes. These physiognomic features are consistent with heat mitigating conservation recommendations for birds inhabiting arid regions (McKechnie et al. 2012). However, protection from both predators and detrimental thermal space can often be confounding factors for influencing habitat use, primarily because the avoidance of both risks often requires similar structural vegetation characteristics (Hiller and Guthery 2005). Nevertheless, while major thermal-predation avoidance tradeoffs may be necessary at moderate T_{air}, the risks of thermal stress or hyperthermia during extreme heat are virtually equivocal to those associated with predators as both are linked with potential death (Forrester et al. 1998). Moreover, similar to predation avoidance, thermal extremes can limit time spent engaged in foraging activities that are critical for growth and development of young birds (Goldstein 1984). For example, lower body mass and delayed fledging dates have been associated with exposure to thermal extremes in altricial common fiscal (*Lanius collaris*) chicks in South Africa (Cunningham et al. 2013b). Additionally, bobwhites chicks are precocial and rely on foraging for arthropods to meet their daily nutritional requirements for growth and development (Guthery 2000, Moorman et al. 2013), primarily during morning and evening. Therefore, increased thermal extremes could potentially restrict time available for foraging and could contribute to further population declines. Importantly, our findings suggest that the activity of broods was highly constrained during peak heating, warranting more research on the energetic costs of refuge use, especially as it pertains to ground dwelling birds regularly exposed to high heat.

While these findings suggest that site specific vegetation should be considered as a key component in assessments of thermal exposure on organisms to thermal extremes, fine scale observations on organism-environment relationships have also been shown to have major implications for broad-scale spatial patterns and processes (Angilletta et al. 2009). In our study, thermal refuges consisting of tall woody cover provided critical thermal cover yet makes up a small portion of the landscape on our study area (~7%; unpublished data). This certainly indicates possible conservation concerns because limited accessibility to refuges could potentially create ecological traps inhibiting the completion of critical life history periods. The importance of this topic is increasingly elevated considering that thermal extremes resulting in individual mortality and species extinctions are predicted to increase in regularity due to climate change (McKechnie and Wolf 2010, Sinervo et al. 2010).

Identifying critical microsites that buffer thermal extremes will be an important component of future conservation, especially for climatically-vulnerable species confronted by increased heat events associated with global climate change (Seabrook et al. 2014). However, scales relevant to organisms are often overlooked in studies that examine organism responses to thermal landscapes or potential increases in future thermal extremes (Sears et al. 2011). Unfortunately, this presents researchers and conservationists with information disconnects regarding organisms and their environment (Flint and Flint 2012, Potter et al. 2013). Helping to bridge this gap, the fine scale spatio-temporal variation of thermal conditions enumerated in this study provides a basis to examine organism responses to dynamic thermal landscapes at relevant site-specific scales. Furthermore, these findings underscore the importance of quantifying thermal environments that would otherwise be missed by less temporally rigorous sampling approaches. For example, we found that on the hottest days bobwhites maximized movement during the 07:00 h active period when the thermal landscape between sites were comparatively homogenous. This behavioral response suggests that broods may have been preemptively preparing for upcoming diurnal heat extremes by maximizing movement and feeding bouts when the thermal landscape was uniformly moderate. Future research examining the importance of these behavioral adjustments will be needed to better understand possible energetic costs and constraints on fitness associated with increased heat extremes. In addition, we show that thermal refuges may only be exploited at very specific times that are often during periods that are critical for survival. Thus, our findings emphasize that thermally heterogeneous landscapes can provide organisms with an array of thermal choices and that identifying refuge sites that moderate thermal extremes will assist in guiding future species conservation efforts.

A key goal of thermal ecology is to determine how thermal heterogeneity influences an organism's perception of its surroundings (Angilletta 2009, Tonolla et al. 2010). Importantly, thermal heterogeneity can allow organisms to make decisions for selection of the most opportune thermal conditions relative to those accessible (Goller et al. 2014). We found that a structurally and thermally heterogeneous landscape allowed broods to behaviorally alter the thermal conditions that they were exposed to by occupying sites that moderated thermal extremes. However, given that increases in intensity, frequency, and extent of extreme heat are predicted to occur as a result of climate change (IPCC 2013), many species will likely face greater thermal stresses that will negatively impact fitness and survival (Sinervo et al. 2010, du Plessis et al. 2012). This study provides a snapshot of the diurnal thermal extremes that confront a small ground-dwelling bird, and its behavioral adjustments to those extremes, during a life history period that is critical to its growth and development. We suggest that if ground-dwelling birds are to persist in thermally harsh regions, microsites that provide thermal refuge will be critical; however, individuals and populations will likely need to endure more extreme and more persistent diurnal heat exposure even in sites selected as thermal refuge.

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Tables

Table 1. Results of regression models of diurnal T_{bb} modeled as a function of T_{air}, S_{rad} and their interaction at active (07:00, 09:00, and 19:00 h), transition (11:00 and 17:00 h), and refuge (13:00 and 15:00 h) northern bobwhite brood and landscape sites, at the Packsaddle WMA, Oklahoma, USA, 2013 – 2014 (n = 4,355 hourly means). Interaction terms of T_{air} and S_{rad} were not significant for active and transition sites and thus were not included as parameters.

		Slope Parameter			Fit
Site Modeled	Intercept	T_{air}	S_{rad}	T_{air} X S_{rad}	R^2
Active*	-3.06	1.06	0.02		0.86
	(±0.63)	(±0.02)	(±0.0004)		
Transition*	-0.60	0.97	0.017		0.83
	(±0.76)	(±0.03)	(±0.0005)		
Refuge*	-2.75	1.05	0.025	0.00031	0.83
	(±1.22)	(±0.04)	(±0.0023)	(±0.000076)	
Landscape*	-7.36	1.25	0.027	-0.00027	0.74
	(±2.34)	(±0.76)	(±0.0055)	(±0.00016)	

*$P < 0.001$

Table 2. Vegetation cover (%) measured at active (07:00, 09:00, and 19:00 h), transition (11:00 and 17:00 h), and refuge (13:00 and 15:00 h) northern bobwhite brood and landscape sites, at the Packsaddle WMA, Oklahoma, USA, 2013 – 2014 (n = 335). Means with different letters are significantly different (Tukey's HSD, $p < 0\ .05$) among activity periods.

	Activity Period, Means (±SE)			
Cover	Active	Transition	Refuge	Landscape
Bare^{**}	36.3^{A}	$29.4^{A,B}$	23.30^{B}	$39.6^{A,C}$
	(±2.3)	(±2.7)	(±2.7)	(±3.0)
Litter^{**}	30.8^{A}	$37.0^{A,B}$	44.5^{B}	$29.1^{A,C}$
	(±1.8)	(±2.6)	(±2.8)	(±2.8)
Grass^{*}	$19.8^{A,B}$	$17.4^{A,B}$	14.2^{A}	24.2^{B}
	(±1.6)	(±2.0)	(±1.5)	(±2.3)
Forb	14.7^{A}	10.3^{A}	9.4^{A}	14.25^{A}
	(±1.5)	(±2.0)	(±1.6)	(±1.4)

Woody**	33.1^{A} (±2.3)	50.2^{B} (±3.5)	63.8^{C} (±3.0)	22.1^{D} (±2.8)

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*$P < 0.01$

**$P < 0.001$

Figure Legends

Figure 3.1. Distribution of T_{bb} observed at $T_{air} \geq 20^\circ C$ (i.e., warmer focal periods) at the Packsaddle WMA, Oklahoma, USA, 2013 - 2014 (n = 4,120 mean hourly T_{bb} measurements). The solid line represents a 1:1 ratio.

Figure 3.2. Mean T_{bb} (±SE) measured at active (07:00, 09:00, and 19:00 h), transition (11:00 and 17:00 h) and refuge (13:00 and 15:00 h) northern bobwhite brood and landscape sites during diurnal periods (07:00 – 19:00 h) at the Packsaddle WMA, Oklahoma, USA, 2013 - 2014 (n = 2,345 hourly means).

Figure 3.3. Diurnal variation (07:00 – 19:00 h) in mean T_{bb} distribution by minute at active (07:00, 09:00, and 19:00 h), transition (11:00, and 17:00 h), and refuge (13:00 and 15:00 h) northern bobwhite brood sites at the Packsaddle WMA, Oklahoma, USA, 2013 - 2014 (n = 5,460 mean T_{bb} measurements by minute). Lines indicate the potential diurnal heat loads experienced at brood sites.

Figure 3.4. Diurnal variation (07:00 – 19:00 h) in mean northern bobwhite brood movement (±SE) on days experiencing maximum $T_{air} < 39^\circ C$ (n = 27) (blue) and on days experiencing maximum $T_{air} \geq 39^\circ C$ (n = 11) (red), at the Packsaddle WMA, Oklahoma, USA, 2013 - 2014.

Figure 3.5. Example of northern bobwhite brood locations observed on a summer day at the Packsaddle WMA, Oklahoma, USA. (A-C) Brood locations at 07:00, 09:00, and 11:00 h time periods, respectively. (D) Brood location at 13:00 and 15:00 time periods.

Figure 3.6. (A) Vegetation height categories at active, transition, and refuge northern bobwhite brood sites (n = 266). (B) Angle of obstruction (±SE) measured at active, transition and refuge sites (n = 266) at the Packsaddle WMA, Oklahoma, USA, 2013 - 2014. Means with different letters are significantly different (Tukey's HSD, $p < 0.05$).

Figure 3.7. T_{bb} measured at northern bobwhite brood sites (green) and random landscape sites (red). Marker shape denotes observed conditions (square) and those associated with projected increases in T_{air} as predicted by the low (circle) and high (triangle) emission end of century scenario ensemble averages at the Packsaddle WMA, Oklahoma, USA, 2013 - 2014 (n = 2,345 hourly means).

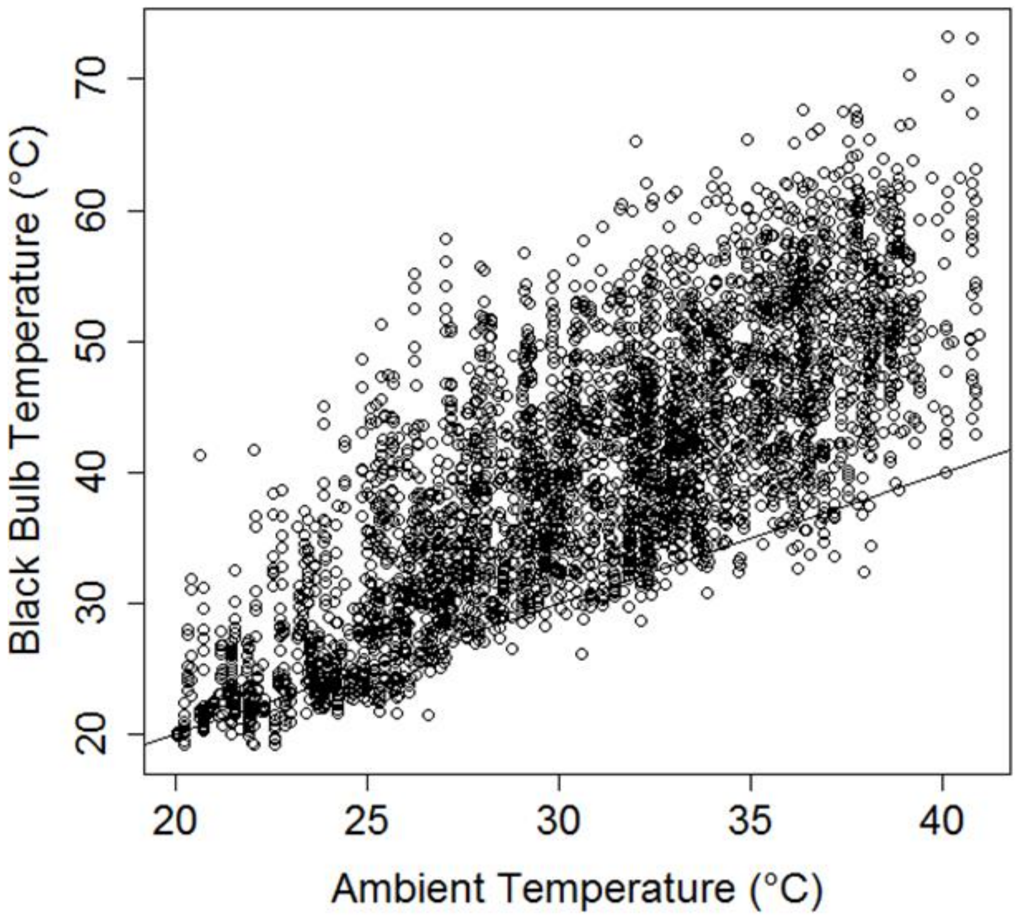

Black Bulb Temperature (°C)
20
30
40
50
60
70
20
25
30
35
40
Ambient Temperature (°C)

Figure 3.1.

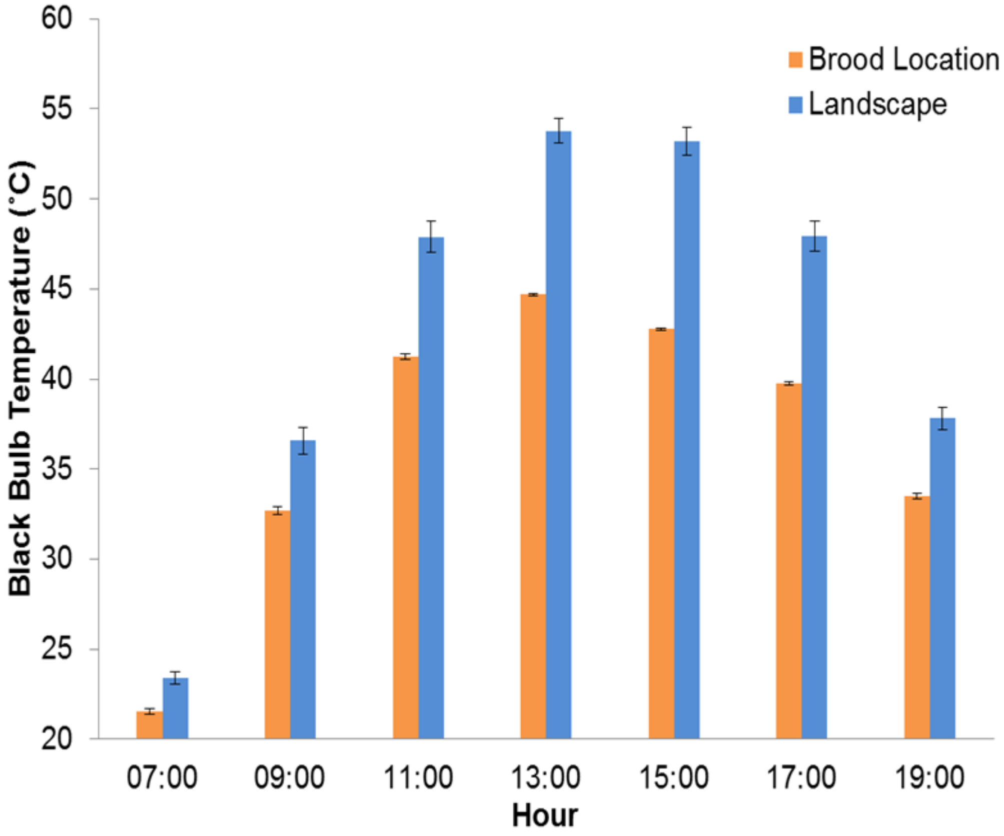
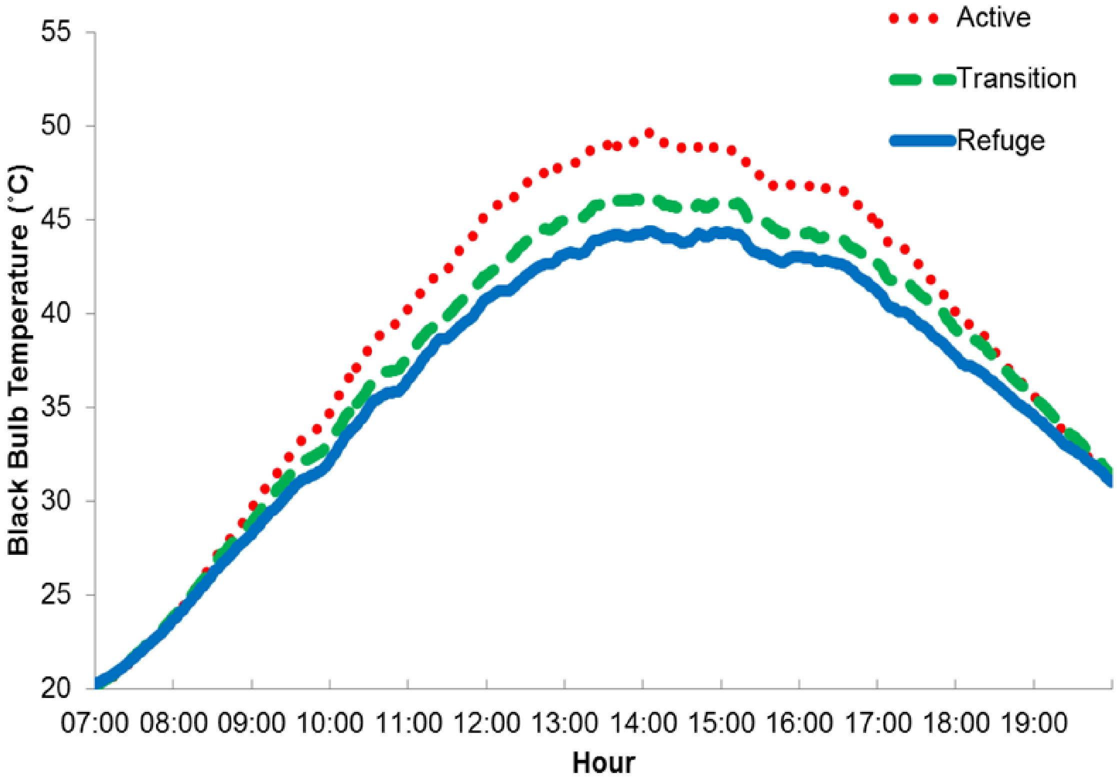

60
55
50
45
40
35
30
25
20
Black Bulb Temperature (˚C)
Brood Location
Landscape
07:00
09:00
11:00
13:00
15:00
17:00
19:00
Hour

Figure 3.2.



Active
Transition
Refuge
Black Bulb Temperature (˚C)
55
50
45
40
35
30
25
20
07:00
08:00
09:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
Hour

Figure 3.3.

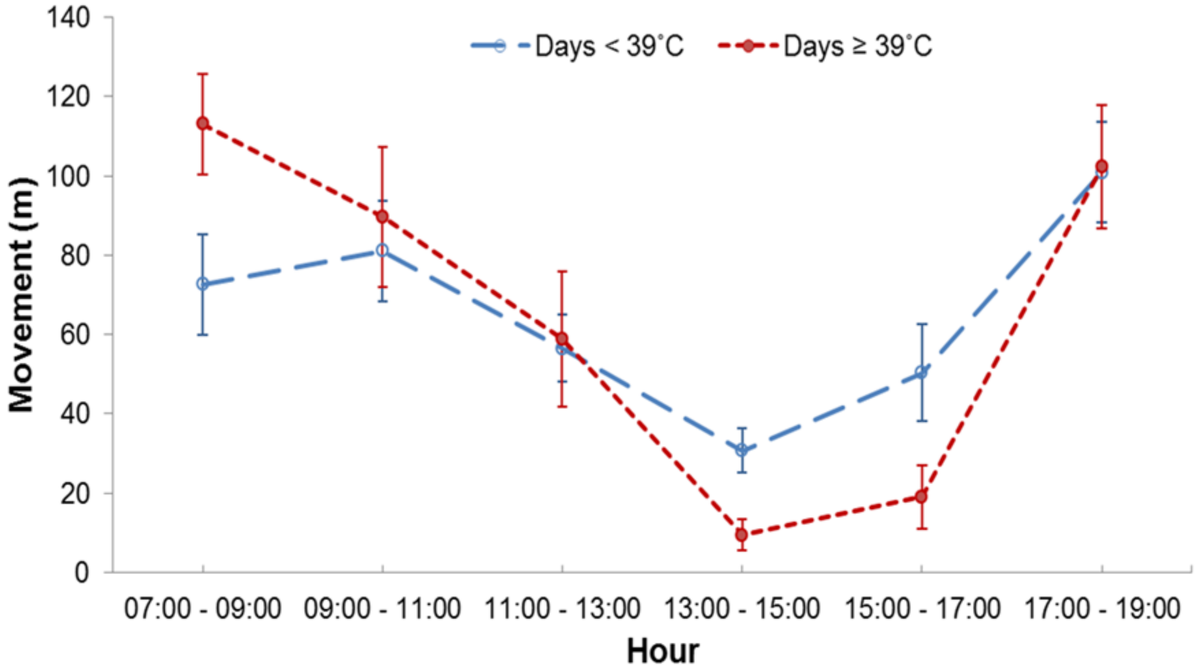

140
120
100
80
60
40
20
0
Movement (m)
Days < 39˚C
Days ≥ 39˚C
07:00 - 09:00
09:00 - 11:00
11:00 - 13:00
13:00 - 15:00
15:00 - 17:00
17:00 - 19:00
Hour

Figure 3.4.

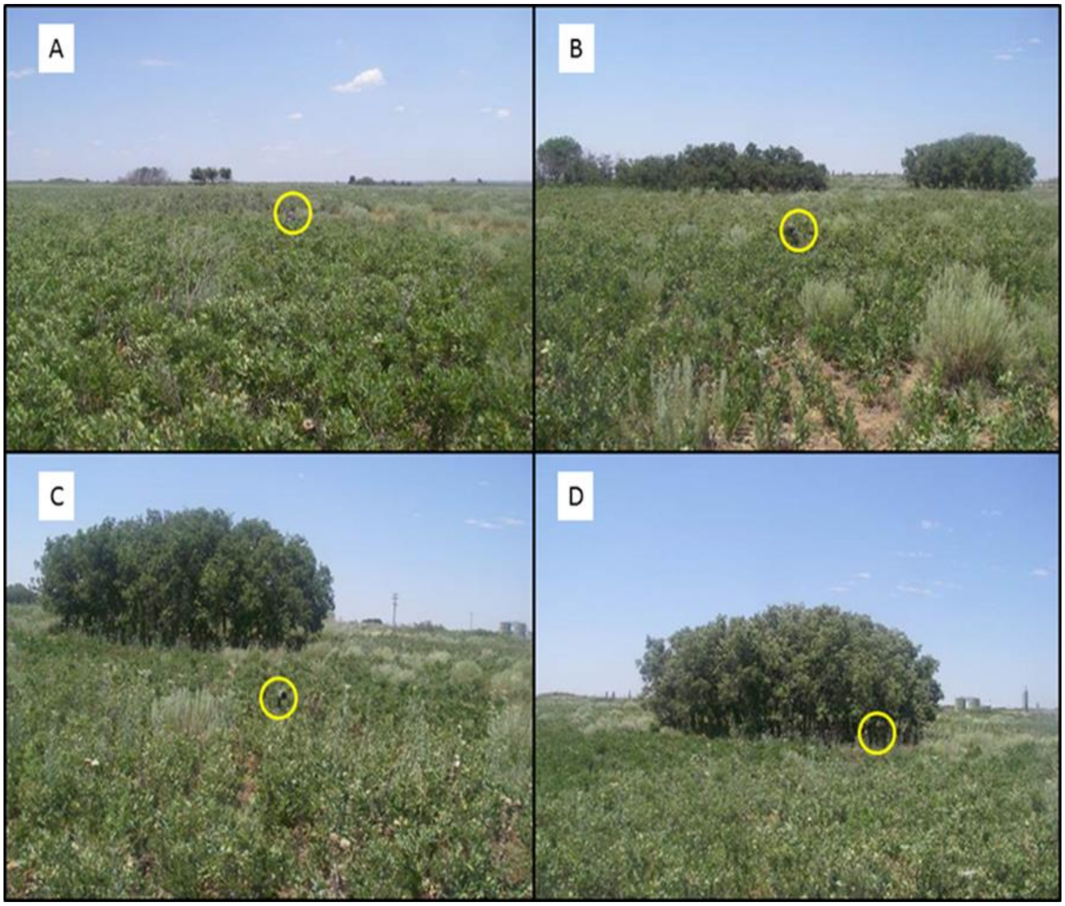


Figure 3.5.

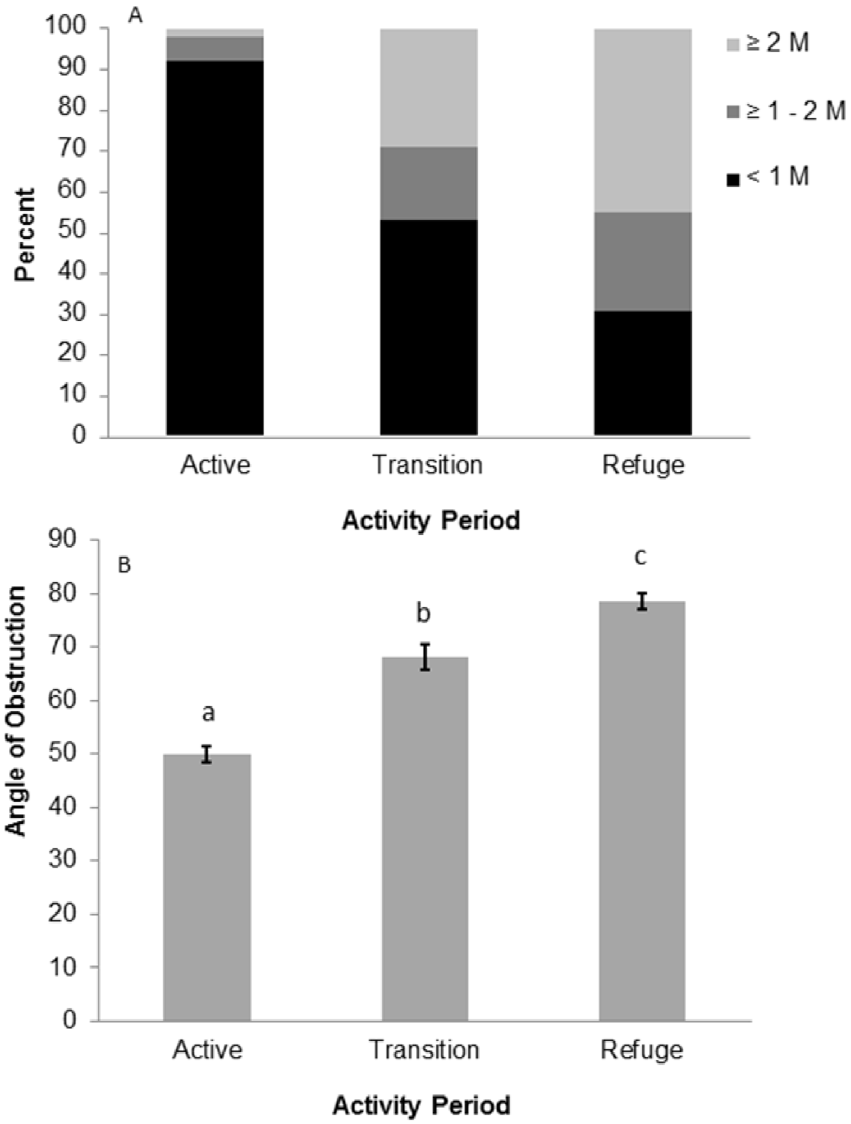
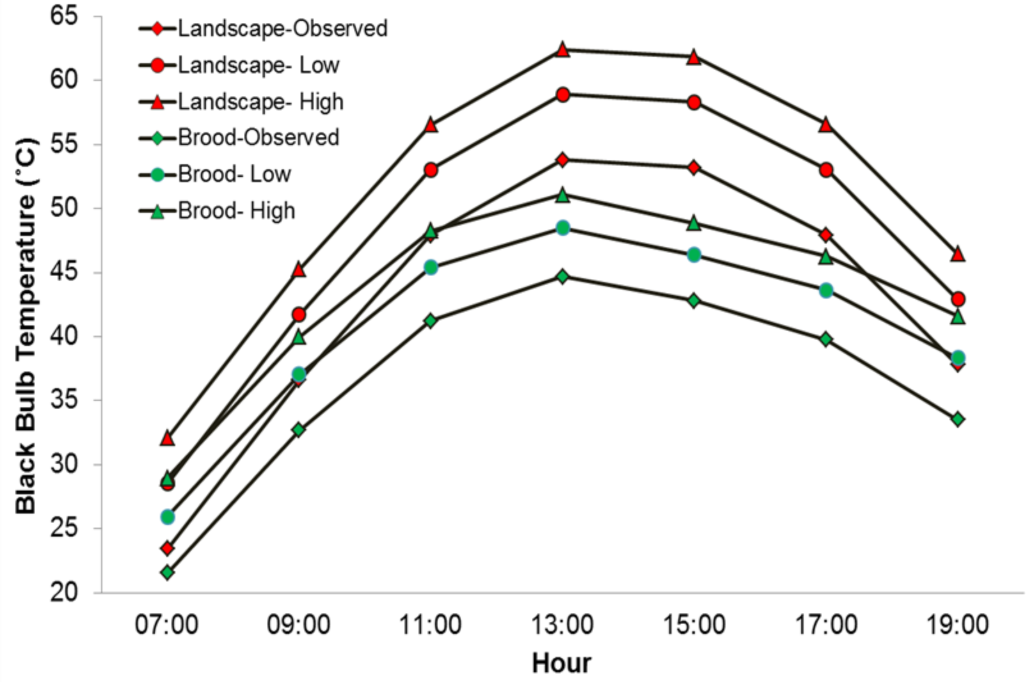

A
100
90
80
70
60
50
40
30
20
10
0
Percent
Active
Transition
Refuge
Activity Period
≥ 2 M
≥ 1 - 2 M
< 1 M
B
90
80
70
60
50
40
30
20
10
0
Angle of Obstruction
a
b
c
Active
Transition
Refuge
Activity Period

Figure 3.6.



65
60
55
50
45
40
35
30
25
20
Black Bulb Temperature (˚C)
Landscape-Observed
Landscape- Low
Landscape- High
Brood-Observed
Brood- Low
Brood- High
07:00
09:00
11:00
13:00
15:00
17:00
19:00
Hour

Figure 3.7.

CHAPTER IV

RESPONSE OF NORTHERN BOBWHITE MOVEMENTS AND HABITAT USE TO MANAGEMENT-DRIVEN DISTURBANCE

Abstract

Similar to many North American grassland and shrubland bird species, northern bobwhite (*Colinus virginianus*) populations have undergone a widespread decline throughout a large portion of their historical distribution more than 50 years. Surprisingly, although few species have received as much research or management attention as northern bobwhites, and despite inhabiting fire-adapted grassland and shrublands across much of their continental distribution, bobwhite behavior relative to disturbance (e.g., fire and grazing) are poorly understood. To assess bobwhite behavioral responses following dormant season burning (Jan-Mar; 2012-2014), we monitored radio-marked northern bobwhites across time since fire treatments (0-12, ≥12-24, ≥24-36, ≥36 months post fire) at the Packsaddle Wildlife Management Area in Western Oklahoma. We found that covey home range (76.9 ha ±5.9 [SE]) was substantially larger in extent than those reported in previous studies but was also highly variable (range; 12 - 270 ha). Mean covey home ranges were greater in the 0-12 months post fire patches (93.4 ±13.8) than in ≥ 24-36 months post fire patches (43.9 ±7.1) ($F_{3, 53} = 3.22$, $p < 0.05$). Spring dispersal movements were highly variable (range; 227.8 to 7,070.8 m) and differed among years. Time since fire, age of individuals, or sex of individuals were not correlated with differences in dispersal movements. Calculations of Ivlev's Electivity Index indicated that bobwhites avoided sand sagebrush during the covey and dispersal periods in both years. Also, during dispersal, bobwhites avoided herbaceous cover and exhibited preference for sand plum during both years. Our findings suggest a mostly neutral effect of prescribed fire on bobwhite spring dispersal movements, but time since fire likely influences bobwhite covey home range size. In addition, these results also provide further evidence that bobwhites can occupy a diverse variety of vegetation configurations (Guthery 1999, Guthery 2000) across patchy landscapes subjected to large scale disturbance.

Introduction

Northern bobwhite (*Colinus virginianus;* hereafter bobwhite) populations have undergone a widespread decline throughout a large portion of their historical range for more than 50 years (Stoddard 1931, Brennan 1991, Sauer et al. 2011). In the Southern Great Plains, the decline has been less extensive than in the southeastern United States (Rollins 2002, Sauer et al. 2011), but nevertheless, these populations have also declined (Peterson 2001, Sauer et al. 2011). Habitat loss and fragmentation due to conversion, anthropogenic development, and large scale fire suppression are considered major contributors to bobwhite population declines (Brennan 1991, Fies et al. 2002, Peterson et al. 2001, Brennan and Kuvlesky 2005). As a result, the preservation and management of remaining habitat is becoming an increasingly critical component of bobwhite conservation. Bridging the gap between management practices and future conservation goals will require understanding how bobwhites respond to habitat alterations at scales that are similar to the scale of management applied on the landscape (Fies et al. 2002, Wellendorf and Palmer 2009, Cook et al. 2009). More than 35 years have passed since Renwald et al. (1978) pointed out the lack of knowledge regarding bobwhite responses to prescribed fire in the western portion of its distribution; yet, data regarding the impacts of prescribed fire on bobwhite ecology remain somewhat ambiguous (Carter et al. 2002, Wilson and Crawford 1979, Ransom and Schulz 2007).

Ecosystems in the Great Plains of the United States were historically shaped by the synergistic disturbance effects of fire and grazing by herbivores (i.e., pyric herbivory) (Fulhendorf et al. 2009), resulting in mosaic patterns of vegetation which create critical habitat for a diverse assemblage of avian species (Fuhlendorf et al. 2006, Hovick et al.

2014, Hovick et al. 2015). Accordingly, restoring pyric herbivory has been recommended for the conservation of native grassland and shrubland avifauna populations (Fuhlendorf et al. 2006, 2009; Hovick et al. 2014, 2015) which have experienced substantial and widespread declines across North America (Herkert 1995, Peterjohn and Sauer 1999, Brennan and Kuvlesky 2005). Surprisingly, although few species have received as much research or management attention as bobwhites (Hernandez and Guthery 2012), and despite inhabiting fire-adapted shrublands across much of their distribution, topics related to bobwhite ecology and disturbance (e.g., fire and grazing) are poorly understood (Maas et al. 2003). For example, research results addressing bobwhite responses to prescribed fire are mixed and contradictory in the western portion of the bobwhite distribution, specifically Oklahoma and Texas (Baumgartner 1946, Wilson and Crawford 1979, Carter et al. 2002), which promotes further confusion regarding the identification of management goals. As a result, the use of fire as a management practice in the more arid western distribution for bobwhites has been cautiously applied, and discretion has often been recommended (Carter et al. 2002, Wilson and Crawford 1979, Ransom and Schulz 2007). Ultimately, identifying the influence of disturbance on bobwhite ecology and maximizing conservation efforts will require more information on how bobwhites behaviorally respond to heterogeneous landscapes (Cook et al. 2009), especially following disturbances such as prescribed fire.

Many aspects of the distribution, dynamics, and genetic composition of populations are dictated by dispersal (Greenwood 1980, Jamieson and Zwickel 1983), yet, the population and management implications of dispersal movements are poorly understood for many species (Forero et al. 1999, MacDonald and Johnson 2001, Trakhtenbrot et al. 2005), including birds (Walters et al. 2000). Moreover, dispersal is a scale-dependent process that determines the spatial distribution of individuals and populations across space and time (Brown and Orians 1970). However, dispersal rates can vary due to demographic factors (i.e., age and sex of individuals, population size) (Newton and Marquiss 1982), as well as habitat quality or landscape configuration (Opdam 1991, Pulliam and Danielson 1991, Lin and Batzli 2001). For example, changes to structural features on the landscape resulting from management actions could potentially impact the way that animals perceive or experience their surroundings, and ultimately could affect habitat quality for a given species. Therefore, assessing animal movement patterns, such as dispersal, can increase our understanding of how individuals and populations utilize landscapes, and also provide an informative way to evaluate the impact and effectiveness of management actions (Cook et al. 2009). For bobwhites, dispersal reaches its highest annual frequency during spring following covey break-up (Townsend et al. 2003, Fies et al. 2002, Cook et al. 2009) and ultimately influences the spatial distribution of breeding bobwhites across the landscape (Errington 1933, Lehmann 1946). Although dispersal has been suggested as a potentially critical process helping to sustain bobwhite populations in the western portion of their distribution, little is known about actual dispersal dynamics in this region (Townsend et al. 2003), especially following landscape level disturbances (e.g., prescribed fire).

Our objective in this study was to assess how disturbance on the landscape, specifically prescribed fire, applied at the pasture level, influences bobwhite space use and movement. We measured bobwhite covey home ranges (i.e., second order selection; Johnson 1980) to assess spatial responses to time since fire at a scale similar to the scale of management on the study area (i.e., macro-habitat level). We also calculated spring dispersal movements in order to explore how landscape level habitat manipulation impacts bobwhite behavior during the breeding season. Finally, we examined how bobwhites utilized vegetation patches (i.e., third order selection; Johnson 1980) during both covey and spring dispersal periods to better understand bobwhite habitat use at local scales.

Methods

Study Area

We investigated bobwhite movement and habitat use across a shrub and mixed grass landscape at the Packsaddle Wildlife Management Area (WMA) in western Oklahoma, USA, during winter and spring 2013–2014. Packsaddle WMA (7,956 ha) is owned and managed by the Oklahoma Department of Wildlife Conservation. The vegetation at the study area mostly consists of shrubs and grasses and is dominated by sand shinnery oak (*Quercus havardii*). In addition to sand shinnery oak, other shrubs include sand sagebrush (*Artemisia filifolia*), sand plum (*Prunus angustifolia*) and aromatic sumac (*Rhus aromatica*) (DeMaso et al. 1997, Vermeire and Wester 2001). Herbaceous species such as little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), sideoats grama (*Bouteloua curtipendula*), blue grama (*Bouteloua gracilis*), western ragweed (*Ambrosia psilostachya*), Texas croton (*Croton texensis*) and prairie sunflower (*Helianthus petiolaris*) are common (DeMaso et al. 1997, Peterson and Boyd 1998). Regionally, mean annual precipitation ranges from 241.8 - 746.6 mm, averaging 554.4 mm per year from 1994 – 2013 (Arnett Oklahoma Mesonet Site; Oklahoma Mesonet 2013).

Prescribed fire and grazing are the two primary habitat management practices on the study area with wildlife conservation and management as the primary goal. Prescribed fires are mostly conducted during the dormant season and approximately 1,372 ha and 1,821 ha of the study area were burned by ODWC personnel from late January to late March 2013 and 2014, respectively. Stocking rate of livestock 1.6 per/AUM and grazing was distributed across 11 individual pastures totaling 4,983 ha from April 1 – August 15 during each year of the study.

Capture and Radio-monitoring

During fall and winter 2013 and 2014, we trapped bobwhites using baited Stoddard style funnel traps (Stoddard 1931). Traps were distributed across the study area in order to maximize the potential to capture bobwhites, but also to obtain adequate coverage of the study area. Traps were checked twice a day in the morning and evening. We weighed each captured bobwhite and determined sex and age using sexually dimorphic plumage identifiers and age specific characteristics of wing features (Leopold 1939, Leopold 1945, Rosene 1969). Each captured bobwhite weighing > 130 g (n = 350) was fitted with a 6 g radio-transmitter equipped with an 8 hr mortality sensor (Advanced Telemetry Systems, Isanti, Minnesota, USA) and banded with a uniquely numbered aluminum leg band (size 7; National Band and Tag, Newport, Kentucky, USA).

We monitored bobwhites via radio-telemetry using the homing technique (White and Garrott 1990) to determine covey locations during winter and individual bird locations during spring. At each bird location, we circled radio-marked individuals at a distance of 15-20 m and recorded an estimated distance and bearing from the observer to the covey (i.e., winter) or individual (i.e., spring) as well as the dominant vegetation type at the location. We obtained 2-3 locations per week for coveys during the covey period and 4-7 locations per week for individuals during the spring dispersal. We used movement data to determine covey break-up dates and considered covey break-up to have occurred when one or more individuals of a covey were no longer affiliated with their respective covey (Liberati and Gates et al. 2012). The period following covey break-up and prior to nest initiation was designated as the spring dispersal period. We located nests by searching the locations of both males and females when radio-telemetry indicated that they were in the same location for two consecutive days. Clutch size was recorded at each nest site, and we estimated nest initiation dates by back-dating nest sites confirmed through radio-telemetry using the assumption that 1 egg was laid per day (Rosene 1969, Lehmann 1984). We censored birds that were captured after the earliest observed covey break-up (17-March-2013 and 21-March-2014, respectively) because it is possible that dispersal movements had already occurred, as well as those that died during the dispersal period and thus did not have equal time to undergo breeding season movement (Liberati and Gates 2012). The spring dispersal period was defined as the period between covey break-up and nest initiation for nesting birds or median nest initiation date for birds that were not observed nesting (22-May-2013, and 25-May-2014, respectively). We searched for missing birds using a combination of techniques including intensively searching a 3 km circle surrounding the most recent bird location, checking for signals from high terrain points on the study area, as well as driving surrounding public roads with a truck mounted dipole omni-directional antenna (Advance Telemetry Systems, Isanti, Minnesota).

Covey Home Range

To determine covey home range (i.e., second order selection) we used the Geospatial Modeling Environment to calculate fixed kernel density estimates (Worton 1987, Worton 1989) for coveys with at least ≥ 20 locations (Taylor et al. 1999, Singh et al. 2010, Peters et al. 2015). For coveys used in home range analysis, radio-locations per covey ranged from 20-75 locations and averaged 42.2 locations during the covey period, totaling 942 and 1,634 independent radio-locations in 2013 and 2014, respectively. We used maximum likelihood cross-validation to estimate smoothing parameters given that it is considered an appropriate estimation method when sample sizes are relatively low (Horne and Garton 2006) and calculated 95% isopleths (ha) for each covey. Euclidean distance was measured from the location immediately following covey break-up through nest initiation to assess spring dispersal movements using ArcGIS 10.3 (ESRI, Redlands, California, USA). We compared covey home ranges and dispersal distances of bobwhites across time since fire by designating a covey or individual into an *a priori* category if >50% of radio-locations fell within a treatment interval (<12 months, ≥12 – 24 months, ≥24 – 36, and ≥36 months post fire). One covey was removed from time since fire comparisons because proportions of locations were each less than 50% of the total locations and were distributed across 3 different time since intervals (i.e., 0-12, >12-24 and >36 months post fire).

We examined variation in covey home range sizes among years, time since fire intervals and their interactions using a two-way anova ANOVA (Zar 1984). Because home range estimate distributions were right-skewed, we applied a $\log_n$ transformation prior to analysis (Singh et al. 2010). When significant differences were reported by ANOVA results, we tested for differences among year and time since fire category combinations using a Tukey's test. We deemed differences significant at the $p < 0.05$ alpha level.

Spring Dispersal

Maximum dispersal distances were calculated by measuring the Euclidean distance between individual bird locations at the last measured location prior to the onset of covey break-up to the farthest location observed during the dispersal period prior to nest initiation using ArcGIS 10.3 (ESRI, Redlands, California, USA). Dispersal distance distributions were non-normal and thus, were $\log_n$ transformed prior to analysis (Liberati and Gates 2012). To assess the extent of the study area that was traversed by dispersing bobwhites, we estimated the minimum area covered by bobwhites during the dispersal period by calculating fixed kernel density estimates (Worton 1987, Worton 1989) using the Geospatial Modeling Environment. Variables potentially influencing bobwhite dispersal area traversed were assessed using generalized linear mixed models. Models were fit using the "lme" package in program R and parameters were estimated using restricted maximum likelihood estimation (Zuur et al. 2009, R Development Core Team 2012). Models included covey id as a random effect and year, age, sex, and time since fire (with two-way interactions) as *a priori* explanatory variables that we considered as factors that may influence bobwhite dispersal (i.e., response variable). Therefore, models included both demographic and management-related parameters to better understand bobwhite dispersal across a landscape managed with fire and grazing practices at a broad scale. Candidate models consisted of single and covariate combinations and relative model plausibility was assessed using Akaike Information Criterion (AIC) (Akaike 1973, Burnham and Anderson 2002).

Habitat Use

To investigate bobwhite habitat use at the patch level (i.e., third order selection) during both the covey and dispersal period, we calculated the proportion of locations in each of the 4 most common vegetation cover types (herbaceous, sand shinnery, sand sage brush, and sand plum) on the study area. Other cover types on the landscape such as roads, water, and closed canopy forests were not analyzed as these cover types are not typically considered as being suitable habitat for bobwhites. We delineated available vegetation cover on the study area using a 2 m spatial resolution multispectral IKONOS satellite image collected during summer 2013. We conducted a supervised classification using 125 points at locations with known vegetation cover in ArcGIS 10.3 (ESRI, Redlands, California, USA). We then created and trained a thematic layer of cover types for the extent of study area, which was refined with an additional 215 ground truth points to aid in map creation. Habitat use data recorded at radio-locations obtained during the covey and dispersal periods were used to calculate the proportion of locations observed in each vegetation type, and the mapped vegetation layer was used to calculate proportions of available vegetation types. To determine bobwhite selection among vegetation patches, we used Ivlev's electivity index (E_i) : $E_i = (o_i - a_i)/(o_i+a_i)$, where o_i equals the proportion utilized by individual i and a_i equals proportion available for any given habitat characteristics (e.g. vegetation type) (Ivlev 1961, Jacobs 1974). For analysis, the values of ai were constrained to the study area. Outputs range from -1 (avoidance) to +1 (preference) with 0 indicating a neutral response equivalent to availability (Manly et al. 2002). We calculated indices for each radio-marked bobwhite during dispersal and covey periods by year and derived mean indices and standard errors for each vegetation type.

Results

Covey Home Range

We estimated covey home ranges for 22 and 39 coveys in 2013 and 2014, respectively. Observed covey home ranges were highly variable during both years (2013: 31 - 270 ha; 2014: 12 – 160 ha) and the mean across years (76.9 ha ±5.9 [SE]) was substantially larger in extent than reported in previous studies (Table 1). Additionally, we found that covey home ranges were larger in 2013 (100.54 ha ±11.83 [SE]) than in 2014 (63.62 ha ±5.32 [SE]) ($F_{1, 53}$= 5.06, $p < 0.05$), and also varied among time since fire ($F_{3, 53}$ = 3.22, $p < 0.05$). Specifically, covey home ranges were smaller in ≥24 - <36 months post fire patches than in <12 month post fire treatments ($p < 0.05$; Tukey's test) (Figure 1). We found no statistically significant differences in covey home range sizes among other time since fire categories and the interaction between time since fire and year was not significant ($F_{2, 53}$ = 1.65, $p = 0.20$).

Spring Dispersal

We analyzed spring dispersal movements for 98 individuals represented by 37 individual coveys. Timing of covey break-up ranged from 25 March to 26 April in 2013 and 17 March to 25 April in 2014. During the dispersal periods, movement data were censored for birds that were captured after covey break-up (n=74 individuals), died prior to or during the dispersal period (n=162 individuals), were lost for >3 consecutive days during the dispersal period (n = 12 individuals), or were lost permanently (n = 4 individuals). Because some birds were lost during the dispersal periods, our movement rates are likely an underestimation of bobwhite spring dispersal (Cook et al. 2009). Median nest initiation date was 22May in 2013 and 25May in 2014. Observed spring dispersal distances were highly variable among individual bobwhites during both years of the study, with distances ranging from 227.6 to 7,070.8 m (Table 2; Figure 2), however, 96.5% of observed dispersal movements were <5,000 m and 51.8% were <1,000 m (Figure 3).

Generalized linear mixed models with covey id analyzed as a random effect demonstrated that neither demographic (i.e., age and sex) or time since fire parameters had model support for explaining variation in bobwhite dispersal distances (Table 3). Juveniles of both sexes exhibited greater variation in the distributional spread of dispersal movements than observed for adults, these differences were not significant (Figure 2). The most plausible candidate model included year as a single explanatory variable, which had a ΔAIC > 2 than that of any other candidate models indicating statistical support for the effect of year on bobwhite dispersal (Burnham and Anderson 2002) (Table 3). Furthermore, the regression coefficient for year included as a variable in the top model was significant ($p = 0.01$). No other candidate models including age, sex, time since fire or their interactions exhibited regression coefficients that were significantly correlated with maximum dispersal distances (Table 3).

Similar to our findings for dispersal distances, the minimum area traversed by bobwhites during dispersal was also highly variable among individuals and ranged from 24-741 ha and 13-1,463 ha in 2013 and 2014, respectively, but were greater on average in 2013 (208.7 ha) than in 2014 (147.1 ha) (Figure 4). Using generalized linear mixed models we found that the most plausible candidate model included year as a single covariate (AIC = 275.0) which was the only variable correlated with area covered during dispersal ($p = 0.002$) for any candidate models (Table 3). The candidate model that included year and time since fire ($\Delta AIC < 2$) also had equivalent support relative to the suite of analyzed models (Table 3). AIC rankings for all other candidate models were >2, indicating low relative model support (Burnham and Anderson 2002) (Table 3).

Habitat Use

For all vegetation types, we found that Ivlev's electivity index for both positive (preference) and negative (avoidance) were all within 0.6 of neutral selection (Manly et al. 2002) indicating that neither selection nor avoidance of vegetation patches was particularly strong. However, we observed the consistent pattern that bobwhites avoided sand sagebrush during the covey and dispersal periods in both years (Figure 5). During the covey period, preference for sand shinnery oak was weak in 2013, but was avoided in 2014, while other woody cover (e.g., fragrant sumac, hackberry) was avoided during both years (Figure 5). In the dispersal period, bobwhites avoided herbaceous cover and exhibited preference for sand plum during both 2013 and 2014 (Figure 5). Use of shinnery oak in the dispersal period was similar to that observed during the covey period; specifically, shinnery oak was preferred in 2013 but avoided in 2014 (Figure 5).

Discussion

Although previous studies have provided important information on the diversity, productivity and survival of bird species relative to efforts aimed at restoring natural disturbance regimes (e.g., fire and grazing interactions) (Coppedge et al. 2008; Hovick et al. 2011, 2012, 2015), more information on the behavioral responses (e.g., dispersal, space use) of birds to management actions are needed to better inform future conservation practices (Sutherland et al. 2000). For example, uncertainty exists over the efficacy of prescribed fire for bobwhite habitat management (Renwald et al. 1978), especially on sites where large portions of the landscapes are burned. Our findings suggest a mostly neutral effect of prescribed fire on bobwhite spring dispersal movements, but do suggest that time since fire influences bobwhite covey home range. In addition, these results also provide further evidence that bobwhites can occupy a diverse variety of vegetation configurations (Guthery 1999, Guthery 2000) across patchy landscapes subjected to large scale disturbance. We also demonstrate that connecting behavioral ecology (e.g., movement and habitat use) with the scale of habitat management can help to elucidate behavioral responses associated with management prescriptions.

In the past, fire has been suggested as being detrimental to bobwhites, specifically, by causing coveys to disperse from recently burned areas (Baumgartner 1946). However, we did not observe mass dispersal of birds from the current year burns (0 - <12 months post fire), but we did find that mean bobwhite covey home range was substantially larger in the 0 - <12 and ≥ 36 months post fire treatments (93.4 ha and 80.5 ha, respectively) than in ≥24 – 36 months post fire treatments (43.9 ha). The occupation of smaller home ranges is typically considered to be advantageous largely because the energetic costs associated with movement as well as the risk of encountering predators can increase with home range size (Powell 2000, Yoder et al. 2004, Whitaker et al. 2007). Moreover, larger home range size has often been attributed to limited forage availability and poor habitat quality for numerous species (Zabel et al. 1995, Pasinelli 2000, Moorcroft et al. 2006, Whitaker et al. 2007), including bobwhites (Singh et al. 2010). Therefore, bobwhites in more recent burns (e.g., 0 - <12 months post fire) may have been required to traverse greater distances to obtain suitable cover, resulting in the greatest mean covey home ranges observed. Conversely, ≥24 – 36 months post fire treatments afforded the smallest observed home ranges which may have provided comparatively optimal tradeoffs between forage availability and protection from predators thereby reducing the need for coveys to move across the landscape. Interestingly, ≥24 – 36 time since fire treatments also align the time period shown to result in the rapid recovery (i.e., within 3 years) of sand shinnery oak to pre-fire structure and composition following fire (Harrell et al.2001).

We found that bobwhites in our study had mean covey home ranges (76.9 ha) that were considerably larger in extent than those reported in studies conducted in other regions (Table 2), and are more similar to other sympatric Great Plains galliforms such as scaled quail (*Callipepla squamata*) (range: 70.8 – 239.6 ha; Wallmo 1956). Additionally, the home range sizes that we observed far exceeded those typically attributed to excellent (<5 ha) and good (<40 ha) bobwhite habitat (Wiseman and Lewsi 1981, Dixon et al. 1996, Guthery et al. 2004, Singh et al. 2010). Poorer resource availability associated with lower productivity in more arid regions such as western Oklahoma could be a possible explanation for the substantial differences in covey home range sizes observed in this study compared to those reported from other more mesic regions. A second possibility is that the openness of the landscape in our study area caused bobwhites to perceive their surroundings at broader scales than those inhabiting other more densely vegetated regions (Powell 2000) of their surroundings. Hunting pressure has also been suggested as a cause of increases in home range size for ruffed grouse (*Bonasa umbellus*) (Whitaker et al. 2007) and greater movement in bobwhites (Stoddard 1931, Williams et al. 2000). Therefore, hunting pressure on the study area may have disturbed bobwhite coveys causing them to utilize larger portions of the landscape during the winter.

We found that bobwhites preferred specific vegetation types during both the covey and dispersal period. Specifically, bobwhites preferred sand plum demonstrating the importance of this shrub species for bobwhites across a substantial portion of the year. The greater overall selection exhibited for sand plum than any other vegetation patch among years and periods (i.e., dispersal and covey) has important management implications given that sand plum makes up a comparatively small portion of the landscape. Conversely, our findings agree with previous studies demonstrating that bobwhites avoid sand sagebrush during winter (i.e., covey period) in the western portion of their distribution (Guthery et al. 2005, Hiller et al. 2007). Although, sand sagebrush and herbaceous cover were each avoided in the dispersal period during both years, managers should consider that both have been found to provide important nesting habitat for bobwhites (Townsend et al. 2001, Hiller et al. 2007, unpublished data). The lack of strong selection or avoidance (>0.6) for any vegetation type agrees with previous studies that have demonstrated that many species of gallinaceous birds require a diverse array of configurations afforded by the juxtaposition of varying vegetation structure and composition across the landscape.(Guthery 1999, Guthery 2000, Fuhlendorf and Engle 2001).

Variation in movement and space use of animals can be influenced by many factors including resource availability, environmental conditions, density dependent factors relating to fluctuations in population size, as well as general population dynamics (e.g., age and sex ratios) (Crimmins et al. 2015). Therefore, causes of the significant effect of year on bobwhite dispersal distance and minimum area covered during dispersal that we observed are likely complex and driven by a wide range of factors. Although greater dispersal by juveniles is a common characteristic of avian populations (Howard 1960), and has been documented for bobwhites (Fies et al. 2002, Smith et al. 1982), we found no difference in maximum observed dispersal movements between sex or age classes (Table 1). These findings demonstrate that dispersal movements were not contingent upon demographic parameters measured in our study. However, other factors such as population density and resource availability have been identified as drivers of dispersal movements in a wide range of taxa (Greenwood 1980, Herzig 1995), including birds (Greenwood 1980, Matthysen 2005), and may have contributed to our observations.

Interestingly, the broad scale application of fire and grazing across the study area did not appear to negatively impact short term space use or movement by bobwhites; specifically, individuals were not attracted to or repelled by varying time since fires occurring on the landscape. Unlike in the eastern United States, fire has been met with more scrutiny than in drier regions (Kuvlesky et al. 2007), primarily because lower annual rainfall and productivity may shift the habitat needs of bobwhites to later seral stages than those required in more mesic eastern regions (Rollins 2002, Spears et al. 1993). However, we found that bobwhites did not exhibit substantial differences in dispersal movements in response to differing seral stages occurring within time since fire treatments (e.g., 0-12 months vs. > 36 months' time since fire), despite that each year of the study experienced below average annual precipitation compared to the annual mean for 1994-2014 (Arnett Oklahoma Mesonet Site; Oklahoma Mesonet 2013).

In the future, improving our understanding of how species perceive, traverse and utilize structurally heterogeneous landscapes will help to maximize conservation benefits for diverse groups of biota. Importantly, disturbance associated with fire and grazing is both a short term driver of structural heterogeneity and bird diversity (Fuhlendorf et al. 2006, Hovick et al. 2014, Hovick et al. 2015) as well as a necessity for maintaining rangeland ecosystems in the long term (Fuhlendorf et al. 2006, Engle et al. 2008). Based on our findings, prescribed fire applied across large portions of the landscape appeared to have a mostly neutral effect on bobwhite dispersal movements and align with the knowledge that the species evolved in disturbance prone grasslands and shrublands (Knick et al. 2005, Fuhlendorf and Engle 2004, Fuhlendorf et al. 2009). However, space use was influenced by time since fire during the covey period and how these differences convey ecological costs and benefits to bobwhites. Regardless, we suggest that although maintaining fine scale habitat features are a critical component for maintaining bobwhite populations (Brennan 1991), addressing the ongoing bobwhite decline will also require more information on the impacts of landscape level habitat use (Taylor et al.1999).

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Tables

Table 1. Summary of home range estimates observed in previous studies on northern bobwhite conducted in the United States.

Study	**Study Site**	**Mean Home Range (ha)**
Dixon et al. 1996	S.E. SC	11.1
Singh et al. 2010	S. FL	69.3
Liu et al. 2002	E. TX	10.1
Wiseman and Lewis 1981	N.E. OK	4.6
Hiller et al. 2007	TX Panhandle	27.1
Madison et al. 2000	KS	42.7
This Study	W. OK	76.9

Table 2. Mean dispersal movements (±SE) and ranges of radio-marked northern bobwhites at the Packsaddle Wildlife Management Area in western Oklahoma, USA, 2013 – 2014 .

Year	**Sex**	**N**	**Dispersal Distance (m)**	**Dispersal Range (m)**
2013	Male	22	1,636.0 (±242.2)	483.6 – 4,420.5
	Female	27	1,863.1 (±295)	425.3 – 6,421.4
2014	Male	32	1,273.6 (±206.2)	350.8 – 4,705.3
	Female	32	1,694.7 (±320.4)	227.83 – 7,070.8
Pooled	Male	54	1,421.3 (±157.5)	350.8 – 4,705.3
	Female	59	1,771.8 (±218.5)	227.83 – 7,070.8

Table 3. Generalized linear model rankings of spring dispersal distance movements and minimum area traversed during dispersal by radio-marked northern bobwhites at the Packsaddle Wildlife Management Area in western Oklahoma, USA, 2013 – 2014. Candidate models with ΔAIC ≤5 shown (n=98).

Dispersal Category	**Model**	**AIC**	**ΔAIC**	**w_i**
Distance	Year	243.49	0.00	0.68
	Year + Age	246.42	2.93	0.16
	Year + Sex	247.09	3.6	0.11
	Age	248.50	5.0	0.05
Minimum Area Traversed	Year	275.0	0.00	0.56
	Year + TSF	276.90	1.90	0.22
	Year +Sex	278.06	3.10	0.12
	Year +Age	278.24	3.24	0.11

Figure Legend

Figure 4.1. Mean covey home ranges (±SE) of northern bobwhites within different time since fire (TSF) categories at the Packsaddle Wildlife Management Area in western Oklahoma, USA, 2013 – 2014 (n = 60). Different letters denote statistical significance among categories ($p < 0.05$)

Figure 4.2. Distribution of dispersal movements of radio-marked adult female (AF), adult male (AM), juvenile female (JF) and juvenile male (JM) northern bobwhites at the Packsaddle Wildlife Management Area in western Oklahoma, USA, 2013 – 2014. Box plots represent 25th and 75th percentile boundaries, inside lines indicate the median, whiskers show the 10th and 90th percentiles, and open circles display outliers (n = 112).

Figure 4.3. Frequency distribution of distance traveled by radio-marked northern bobwhites from covey break-up through nest initiation during the spring dispersal period at the Packsaddle Wildlife Management Area in western Oklahoma, USA 2013 – 2014 (n = 114).

Figure 4.4. Mean minimum area traversed (±SE) by dispersing radio-marked northern bobwhites from covey break-up through nest initiation at the Packsaddle Wildlife Management in western Oklahoma, USA, 2013 - 2014 (n = 114).

Figure 4.5. Habitat selection by northern bobwhites during the covey (A) and dispersal (B) periods at the Packsaddle Wildlife Management Area, USA (2013 - 2014). Preference was assessed with Ivlev's electivity index (±SE) (n = 3,499 locations).

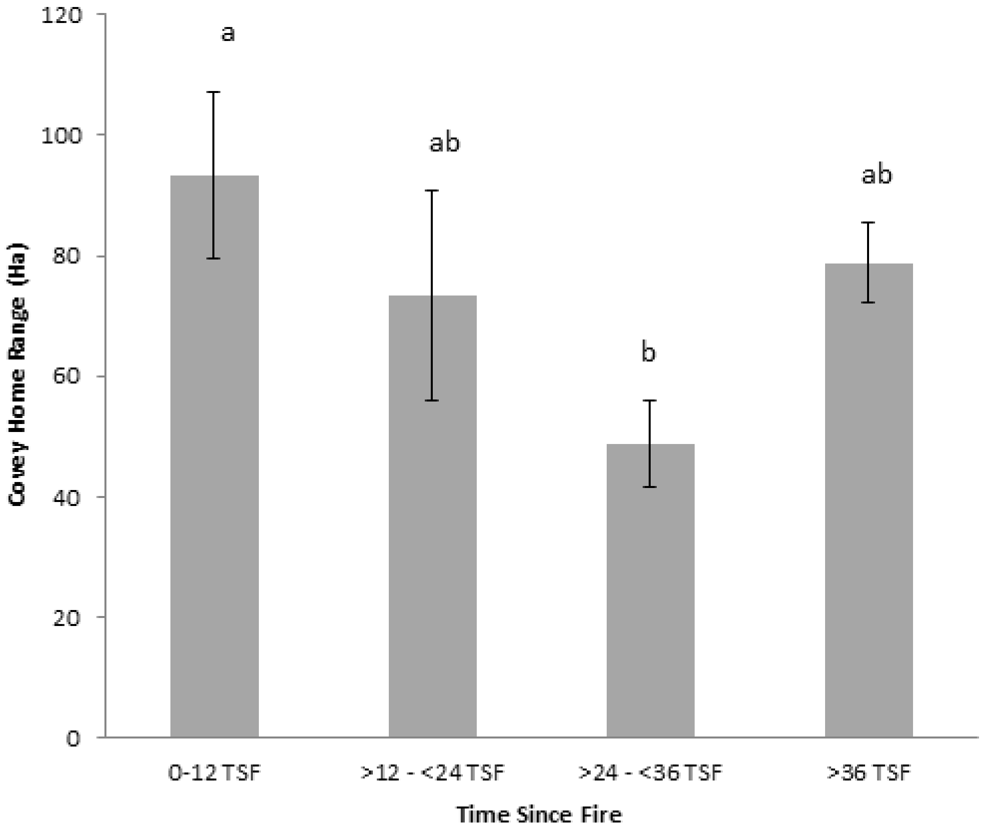

120
100
80
60
40
20
0
Covey Home Range (Ha)
a
ab
b
ab
0-12 TSF
>12 - <24 TSF
>24 - <36 TSF
>36 TSF
Time Since Fire

Figure 4.1.

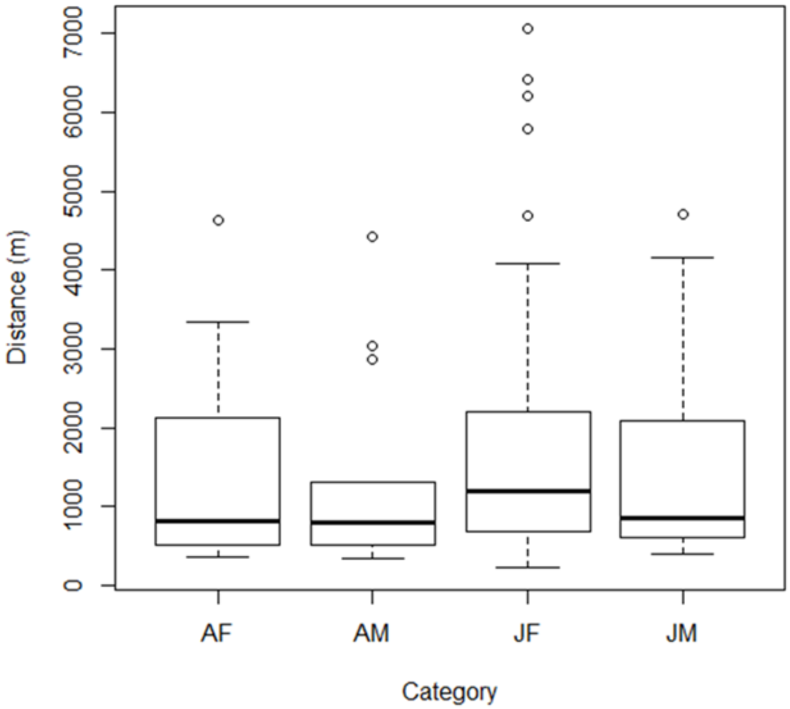
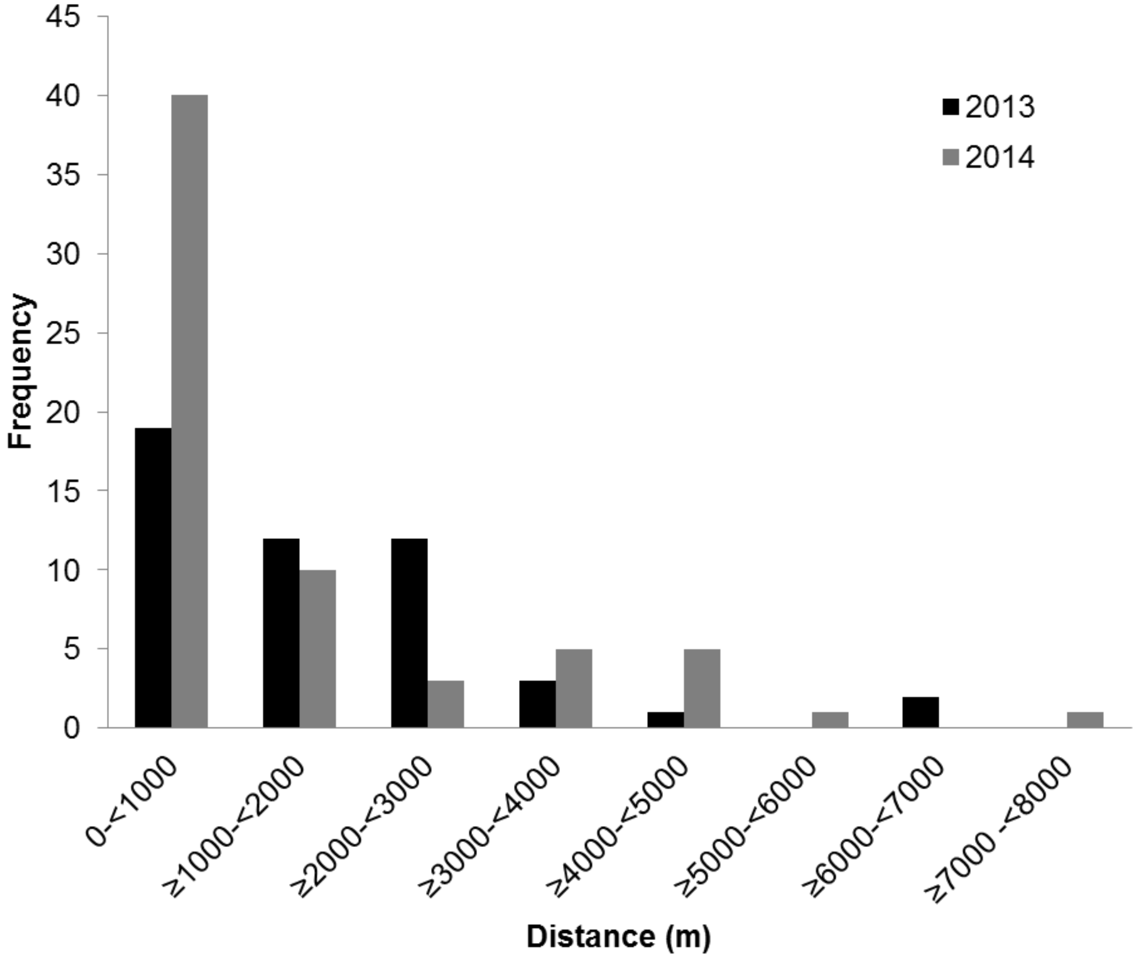

Distance (m)
0
1000
2000
3000
4000
5000
6000
7000
AF
AM
JF
JM
Category

Figure 4.2.



45
40
35
30
25
20
15
10
5
0
Frequency
■ 2013
■ 2014
0-<1000
≥1000-<2000
≥2000-<3000
≥3000-<4000
≥4000-<5000
≥5000-<6000
≥6000-<7000
≥7000 -<8000
Distance (m)

Figure 4.3.

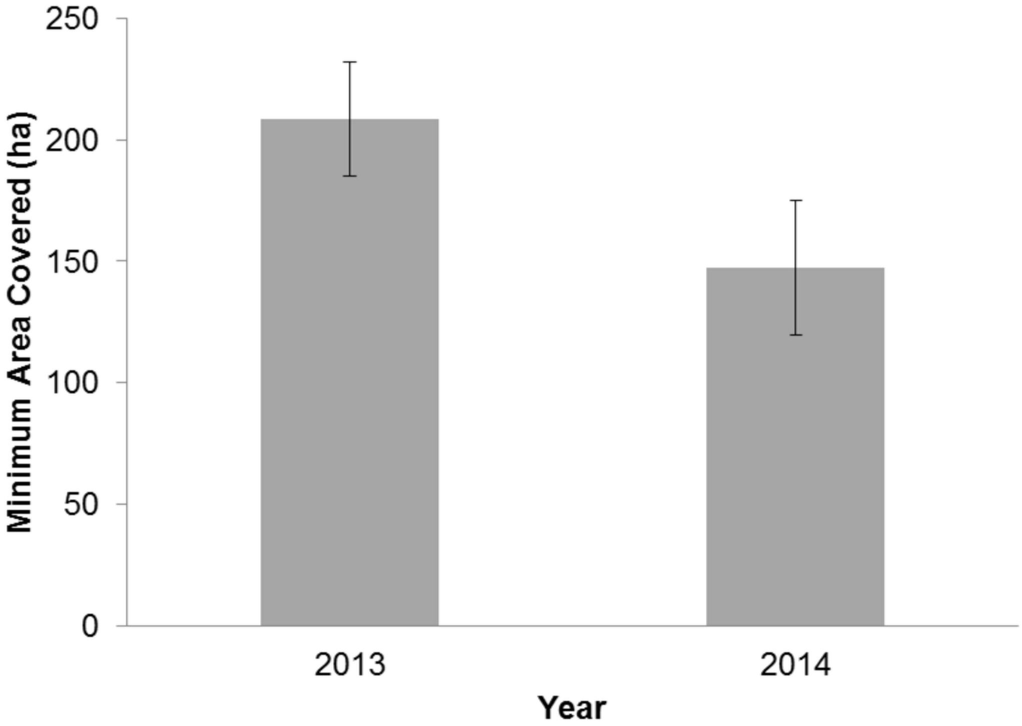


Figure 4.4.

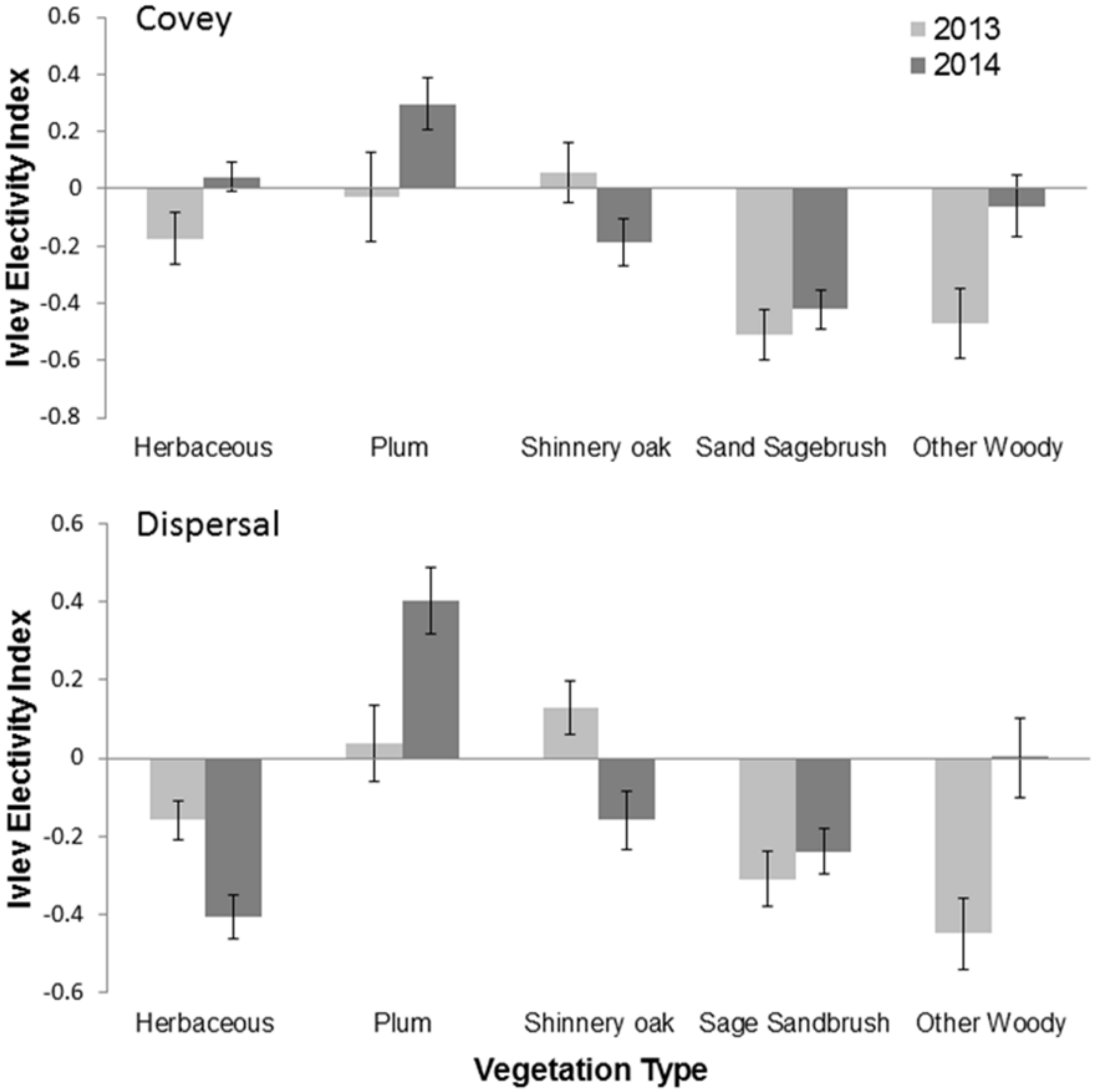

Covey
2013
2014
Ivlev Electivity Index
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
Herbaceous
Plum
Shinnery oak
Sand Sagebrush
Other Woody
Dispersal
Ivlev Electivity Index
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
Herbaceous
Plum
Shinnery oak
Sage Sandbrush
Other Woody
Vegetation Type

Figure 4.5.

VITA

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