

Thermal patterns constrain diurnal behavior of a ground-dwelling bird

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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.

Key words: climate change; *Colinus virginianus*; conservation; landscape; microclimate; northern bobwhite; operative temperature; thermal heterogeneity; thermal refuge.

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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 tem-

perature) 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 km²) 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 (Helmut 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, Goller et al. 2014, Hovick 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 (Guthery et al. 2001, Hiller and Guthery 2005). 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, Hannah et al. 2014, Scheffers 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 et al. 2013a). In our study, we hypothesized that groups of precocial bobwhite chicks (hereafter, broods) would respond behaviorally to proxi-

mate 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 to 2013 ranged from 241.81 to 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 to April 2013 and 2014 and fitted them with a 6 g 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 m 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., ther-

mal 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 (Guthery et al. 2005, Hiller and Guthery 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 h 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 m² 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).

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; Beasley and Rhodes 2010, Lohr et al. 2011). We used $T_{bb} \geq 39^\circ\text{C}$ 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 $<39^\circ\text{C}$ and $\geq 39^\circ\text{C}$.

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° to 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

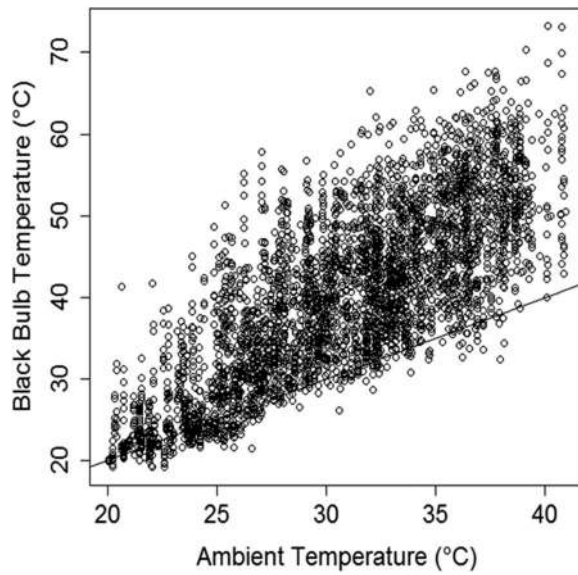


Fig. 1. Distribution of T_{bb} observed at $T_{air} \geq 20^{\circ}\text{C}$ (i.e., warmer focal periods) at the Packsaddle WMA, Oklahoma, USA, 2013–2014 ($n = 4,120$ mean hourly T_{bb} measurements). The solid line represents a 1:1 ratio.

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 (Figs. 2 and 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 (Figs. 1 and 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 (\pm 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 to 19:00 h (101.29 ± 9.84 m) and 07:00 to 09:00 h (84.32 ± 10.15 m) and was least from 13:00 to 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 $\geq 39^{\circ}\text{C}$ and was reduced to $9.48 (\pm 4.0)$ m from 13:00 to 15:00 h (Fig. 4). In addition, mean brood

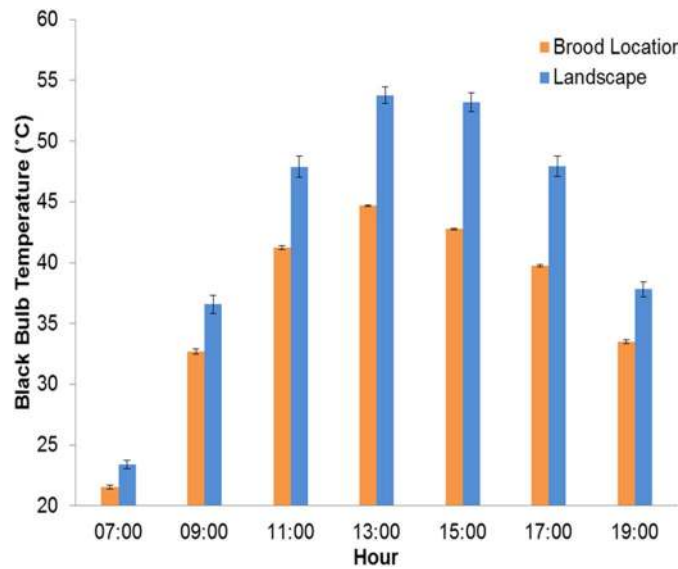


Fig. 2. Mean T_{bb} (\pm SE) measured at active (07:00, 09:00, and 19:00 h), transition (11:00 and 17:00 h) and refuge (13:00 and 15:00 h) northern bobwhite brood and landscape sites during diurnal periods (07:00–19:00 h) at the Packsaddle WMA, Oklahoma, USA, 2013–2014 ($n = 2,345$ hourly means).

movement was approximately 11.5-fold greater from 07:00 to 09:00 h than from 13:00 to 15:00 h on days when maximum T_{air} were $\geq 39^{\circ}\text{C}$. On comparatively milder days ($T_{air} < 39^{\circ}\text{C}$), mean

brood movement was two-fold greater from 07:00 to 09:00 h than from 13:00 to 15:00 h. Therefore, we found that broods maximized movement during the coolest periods of the

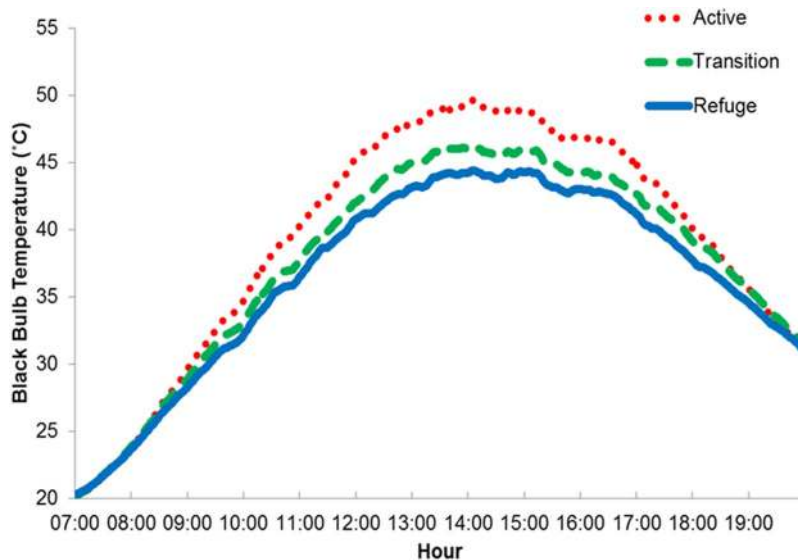


Fig. 3. Diurnal variation (07:00–19:00 h) in mean T_{bb} distribution by minute at active (07:00, 09:00, and 19:00 h), transition (11:00, and 17:00 h), and refuge (13:00 and 15:00 h) northern bobwhite brood sites at the Packsaddle WMA, Oklahoma, USA, 2013–2014 ($n = 5,460$ mean T_{bb} measurements by minute). Lines indicate the potential diurnal heat loads experienced at brood sites.

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.

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

* $P < 0.001$.

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 (Figs. 5 and 6). We found significant differences in vegetation height categories among active, transition, refuge, and landscape sites ($\chi^2 = 85.01$, $p < 0.001$, $df = 4$), 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–

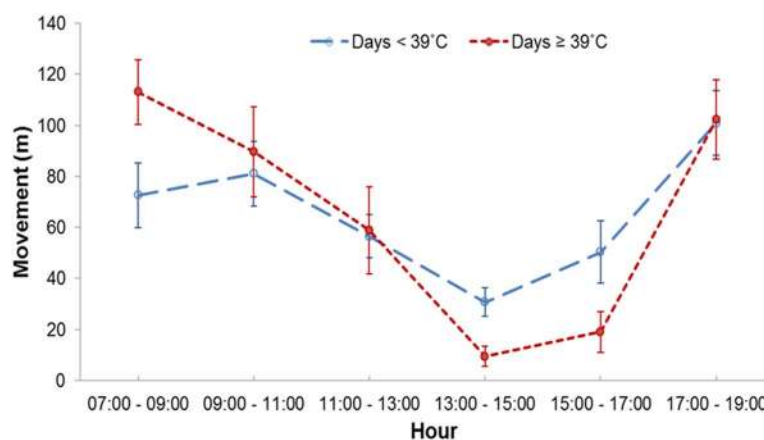


Fig. 4. Diurnal variation (07:00–19:00 h) in mean northern bobwhite brood movement (\pm SE) on days experiencing maximum $T_{air} < 39^\circ\text{C}$ ($n = 27$) (blue) and on days experiencing maximum $T_{air} \geq 39^\circ\text{C}$ ($n = 11$) (red), at the Packsaddle WMA, Oklahoma, USA, 2013–2014.

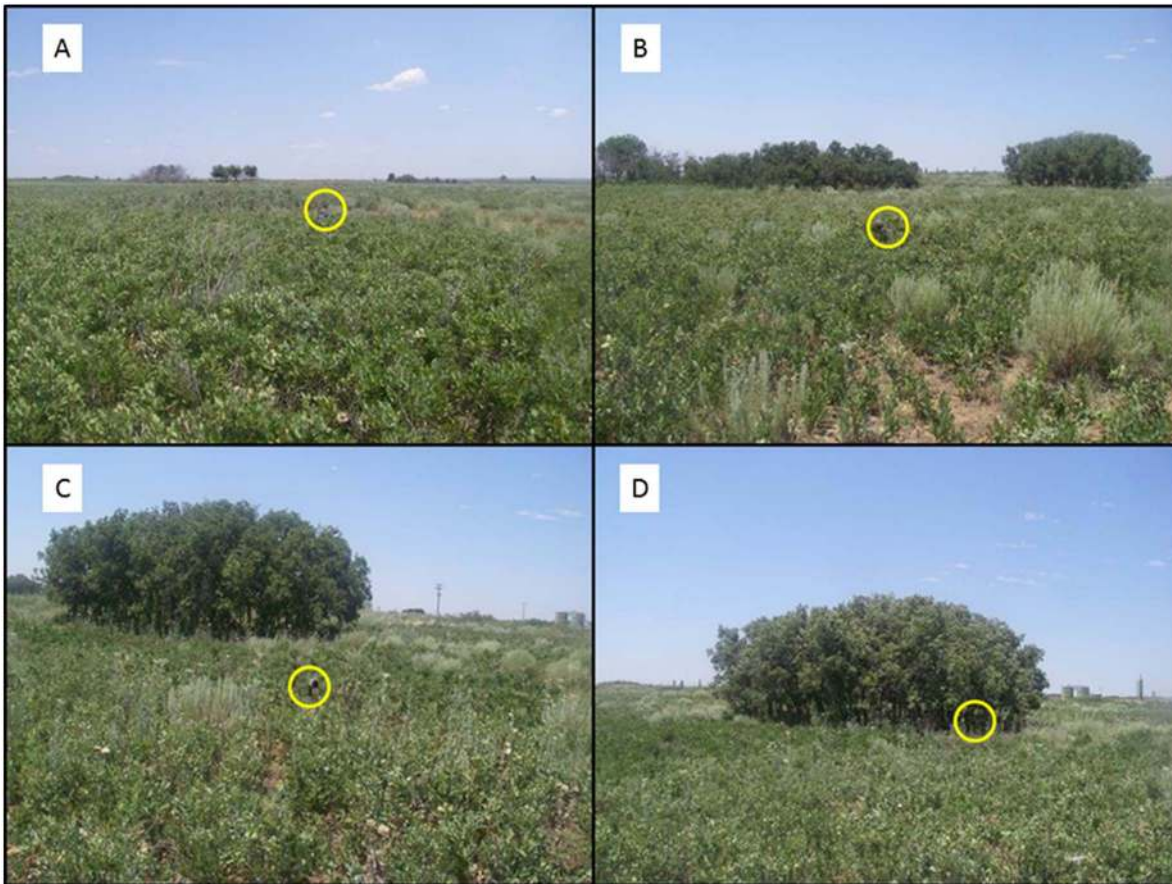


Fig. 5. Example of northern bobwhite brood locations observed on a summer day at the Packsaddle WMA, Oklahoma, USA. (A–C) Brood locations at 07:00, 09:00, and 11:00 h time periods, respectively. (D) Brood location at 13:00 and 15:00 time periods.

69%; Appendix: 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 to 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

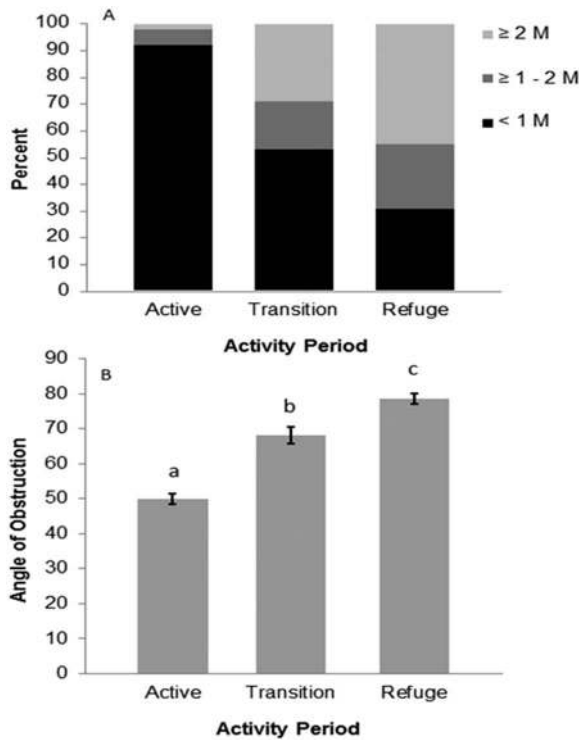


Fig. 6. (A) Vegetation height categories at active, transition, and refuge northern bobwhite brood sites ($n = 266$). (B) Angle of obstruction (\pm SE) measured at active, transition and refuge sites ($n = 266$) at the Packsaddle WMA, Oklahoma, USA, 2013–2014. Means with different letters are significantly different (Tukey’s HSD, $p < 0.05$).

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 ($T_{bb} \geq 39^\circ\text{C}$). 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

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 (mean with SE in parentheses; $n = 335$). Means with different letters are significantly different (Tukey’s HSD, $P < 0.05$) among activity periods.

Cover	Activity period			
	Active	Transition	Refuge	Landscape
Bare**	36.3 ^A (± 2.3)	29.4 ^{A,B} (± 2.7)	23.30 ^B (± 2.7)	39.6 ^{A,C} (± 3.0)
Litter**	30.8 ^A (± 1.8)	37.0 ^{A,B} (± 2.6)	44.5 ^B (± 2.8)	29.1 ^{A,C} (± 2.8)
Grass*	19.8 ^{A,B} (± 1.6)	17.4 ^{A,B} (± 2.0)	14.2 ^A (± 1.5)	24.2 ^B (± 2.3)
Forb	14.7 ^A (± 1.5)	10.3 ^A (± 2.0)	9.4 ^A (± 1.6)	14.25 ^A (± 1.4)
Woody**	33.1 ^A (± 2.3)	50.2 ^A (± 3.5)	63.8 ^C (± 3.0)	22.1 ^D (± 2.8)

* $P < 0.01$.

** $P < 0.001$.

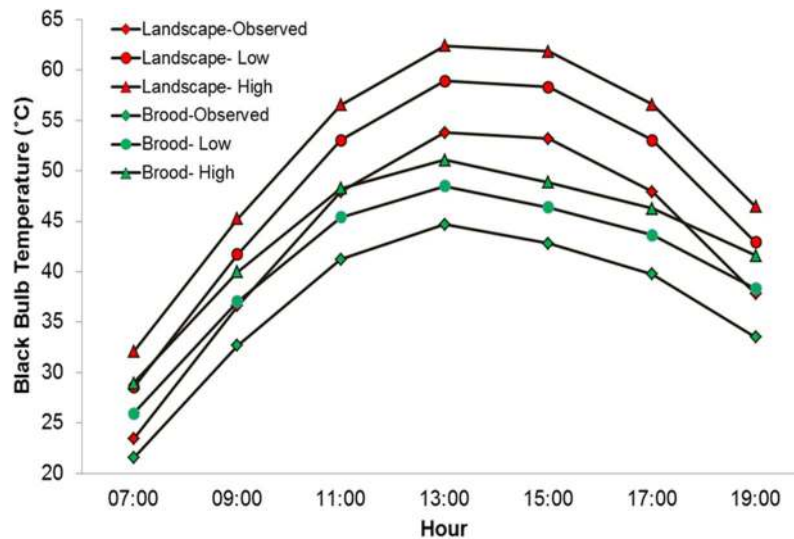


Fig. 7. T_{bb} measured at northern bobwhite brood sites (green) and random landscape sites (red). Marker shape denotes observed conditions (square) and those associated with projected increases in T_{air} as predicted by the low (circle) and high (triangle) emission end of century scenario ensemble averages at the Packsaddle WMA, Oklahoma, USA, 2013–2014 ($n = 2,345$ hourly means).

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 (McKeechnie 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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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

The Appendix is available online: <http://dx.doi.org/10.1890/ES15-00163.1.sm>