



# Thermal refuge affects space use and movement of a large-bodied galliform

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## ABSTRACT

Temperature affects every organism on Earth and has been argued to be one of the most critical factors influencing organisms' ecology and evolution. Most organisms are susceptible to landscape temperature ranges that exceed their thermal tolerance. As a result, the distribution of landscape features that mitigate thermal extremes can affect movement and space use of organisms. Using Rio Grande wild turkey (*Meleagris gallopavo intermedia*) as a model species, we measured black bulb temperature throughout the diurnal period and identified vegetation characteristics at wild turkey locations and random landscape locations. We observed that the thermal landscape was highly heterogeneous with temperature varying up to 52 °C at a given ambient temperature. Vegetation type strongly influenced temperature across space during daily peak heating, with taller vegetation types (woody vegetation > 2 m) having mean temperatures up to 8.95 °C cooler than the remainder of the landscape. However, these cooler vegetation types were uncommon, only accounting for 8.2% of the landscape. Despite the rarity of tall woody cover, wild turkey showed strong selection for this vegetation type particularly during peak daily heating with 74.9% of locations within 18 m of tree cover. Not only did wild turkey alter space use across time relative to temperature variation, but they also altered movement. We found that on the hottest days ( $\geq 35$  °C), wild turkeys decreased movement by three fold during peak heating, while movement on cooler days ( $< 30$  °C) was uniform. Collectively, our data provide evidence that space use and movement for large avian species can be influenced by the thermal environment, and that the thermal environment is an important component of habitat for a species.

## 1. Introduction

Temperature affects every organism on Earth and has been argued to be one of the most critical factors influencing organisms' ecology and evolution (Brock, 1967). Specifically, temperature influences animal physiology, distribution, home range, reproduction, and survival. Organisms experience and respond to their thermal environment on a scale comparable to their size and mobility (Heath, 1965; Chelazzi and Calzolari, 1986). Temperature is accepted to be a driver of ecological processes (Smith and Smith, 2000; Begon et al., 2006) and so understanding how temperature variation across landscapes affects space-use and patterns of movement will help better explain what constitutes habitat for a species.

Most organisms are susceptible to landscape temperature ranges that exceed their thermal tolerance (Gilchrist, 1995; Williams and Tieleman, 2005). Understanding the thermal tolerance of a species and how the thermal environment may constrain habitat selection is rarely

considered in habitat selection studies (Tuff et al., 2016). Endotherms can make physiological adjustments for greater heat dissipation (Calder, 1974; Williams and Tieleman, 2005) as well as behavioral modifications such as reducing activity or seeking shade in tall woody vegetation (Wolf, 2000). As a result, the distribution of landscape features that mitigate thermal extremes affect an organism's daily movement and space use (Ageillette, 2009; Melin et al., 2013). Survival may even hinge on the availability of these thermally buffered landscape features, especially during extreme heat events where usable space on the landscape may drastically change or decrease (Suggitt et al., 2011; Tanner et al., 2016; Elmore et al., 2017). In particular, the microclimate, which includes physical factors such as ambient temperature, solar radiation, wind, and humidity directly around an organism, is critical for survival and space use (Porter and Gates, 1969). Identifying a species range in thermal tolerance and the features that provide thermal refuge is critical for conservation and management (Guthery, 1997). Equally as important as the spatial distribution of thermal refuge

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is understanding when these thermal refuges are available as they may shift across time. For example, an organism's space use on the landscape may be constrained during extreme climactic events compared to more moderate temperatures. Extreme cold and hot periods both constrain the timing of availability and amount of usable space on the landscape. However, the amount and location of usable space available during hot and cold periods differs, indicating that different vegetation types and structures are needed to buffer against these extreme temperature events (Tanner et al., 2016). Previous literature has often focused on measures of central tendency to determine thermal constraints on organisms (Dunbar et al., 2009). However, averaging organisms' usable space on an annual or seasonal scale does not appropriately identify thermal refuge available on the landscape that may be necessary for survival during variable and perhaps discrete environmental conditions (Tanner et al., 2016). Identifying the discrete temporal and spatial environmental conditions that constrain organisms' habitat selection can increase our ability to manage species.

Heterogeneity is widely recognized as a driver of biodiversity and ecosystem function (Christensen, 1997; Wiens, 1997). It has primarily been associated with spatial and temporal variation of vegetation structure and composition, though other facets of landscape heterogeneity such as microclimate are essential yet understudied (Limb et al., 2009). The spatial and temporal variation of microclimate, created by heterogeneity of vegetation, can generate variable locations that differ dramatically spatially across landscapes providing organisms with thermal heterogeneity (Hovick et al., 2014; Carroll et al., 2016). This variation provides microclimates that both far exceed ambient temperatures and those that buffer against extreme ambient temperatures. For example, tall woody vegetation provides shade and has been demonstrated to provide 10–12 °C cooler locations than open herbaceous vegetation because herbaceous vegetation is often subjected to high levels of solar radiation (Carroll et al., 2016). The interactions between vegetation composition/structure and temperature strongly influence the characteristics of microsites (Saunders et al., 1998; Schut et al., 2014; Tuff et al., 2016) and in turn, dictate which locations are usable to organisms during bouts of temperature extremes (Guthery, 2000; Melin et al., 2013; Carroll et al., 2015b, 2016). Tall woody vegetation has been shown to provide critical thermal refuge for both ectotherms (Burrow et al., 2001; Attum et al., 2013) and endotherms (McKechnie et al., 2012; Melin et al., 2013; Carroll et al., 2015a, 2015b). Understanding thermal characteristics of different vegetation types and the scale that individuals make behavioral adjustments and movement decisions based on temperature is essential for conservation and management decisions (Wiens, 1989; Porter et al., 2002; Jackson and Fahrig, 2012; Tuff et al., 2016).

Increases in annual global temperature, as well as an increase in the frequency and intensity of extreme temperature events (IPCC, 2013), are predicted to alter thermal patterns across landscapes (Opdam and Wascher, 2004). Landscapes that already experience high heat and aridity are predicted to experience the greatest increases (Meehl and Tebaldi, 2004). Temperature increases and thermal extremes have been implicated in local extinctions (Sinervo et al., 2010), mass mortality events (Welbergen et al., 2008; Towie, 2009; McKechnie et al., 2012), reductions in long-term survival (Moses et al., 2012), and constraints on activity (Gundersen and Leal, 2016). While all organisms are influenced by their thermal environment (Brock, 1967; Angilletta, 2009), most avian species are particularly vulnerable to elevated temperatures because they are predominately active and above ground during the day (Wolf et al., 1996; McKechnie and Wolf, 2010).

The Rio Grande wild turkey (*Meleagris gallopavo intermedia*) is a large generalist gallinaceous species (Rioux et al., 2009) that can tolerate a wide range of vegetation types. Previous studies focused on small and medium-sized galliforms have found strong patterns of space use selection influenced by thermal heterogeneity for both nesting (Carroll et al., 2018; Grisham et al., 2016; Hovick et al., 2014; Larsson et al., 2013; Raynor et al., 2018) brooding (Bell et al., 2010; Carroll

et al., 2015a; Guthery, 2000), and adult locations (Guthery, 2000; Tanner et al., 2016). Space use and movement of wild turkey is known to be influenced by tree cover (Phillips et al., 2011; Collier et al., 2017). Wild turkey require trees for roosting at night which at least partially explains selection for woody cover during periods of the day. However, the mechanism for diurnal selection has not been thoroughly explored and is likely related to the thermal environment. How strongly thermal variation affects the space use of a large galliform such as wild turkey is unknown.

Rio Grande wild turkey (hereafter, wild turkey) is native to Texas, Oklahoma, and Kansas in the Southern Great Plains of the United States where summer ambient temperatures often exceed 35 °C (Arndt, 2003) and tall woody vegetation can be sparse. Wild turkey has been known to temporally select varying vegetation types throughout the day including herbaceous and riparian areas (Collier et al., 2017). These varying vegetation types likely have highly variable thermal conditions, but this has not been quantified spatially or temporally for this species. Further, temperature variation at fine temporal scales and how it affects habitat selection is almost completely unexplored for any avian species. Because wild turkey are birds that are active during the day, they are likely susceptible to high ambient temperatures and levels of solar radiation. These characteristics and the discrete nature of potential thermal refuge make wild turkey an ideal species to investigate the influence of the thermal environment on movement and space use especially during periods of high heat. Our objectives were to 1) describe the thermal heterogeneity of a landscape and examine how wild turkey use the landscape to moderate periods of peak heating and 2) to characterize the microclimates wild turkey use during peak heating. Therefore, we quantified both thermal and vegetation characteristics at wild turkey diurnal locations and random landscape points to identify how spatial variation in vegetation and temporal variation can influence animal behavior.

## 2. Methods

### 2.1. Study site

We studied the thermal ecology of wild turkey in western Oklahoma on Packsaddle Wildlife Management Area (WMA). The Oklahoma Department of Wildlife Conservation (ODWC) owns and manages the 7956 ha property. The study site is predominately composed of mixed-grass prairie and sand shinnery oak (*Quercus havardii*). Other shrubs include sand sagebrush (*Artemisia filifolia*), sand plum (*Prunus angustifolia*) and aromatic sumac (*Rhus aromatica*) (DeMaso et al., 1997). Common 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 predominately consists of hybrid sand shinnery/post oak mottes (*Quercus havardii* × *Quercus stellata*) but also contains cottonwood (*Populus deltoides*), black locust (*Robinia pseudoacacia*), hackberry (*Celtis occidentalis*), and soap berry (*Sapindus drummondii*). Hybrid shinnery oak are small trees that grow in groups or "mottes". These trees can grow 6 or more meters tall and are found amid the low-growing shinnery oak (Peterson and Boyd, 1998).

From 1994–2017, the region received an average precipitation of 571.25 mm per year (Arnett Oklahoma Mesonet Site; Oklahoma Mesonet, 1994–2016). Summer temperatures in the area can reach 37.8 °C on average for 15 or more days per year (Arndt, 2003). The area includes sandy Nobscot, Nobscot-Brownfield, and Pratt-Tivoli soils (DeMaso et al., 1997), has rolling hills and contains partially wooded draws. Management practices used on Packsaddle WMA consist mainly of prescribed fire and grazing. Prescribed fire has been used as a consistent management technique since 2004 with most burns conducted during the dormant season. The study site is grazed uniformly at a

stocking rate of 1 steer per 7.3 ha from April 1 to August 15 of each year.

## 2.2. Data collection

We captured wild turkeys in the spring of 2016 and 2017 using modified walk-in funnel traps (Davis, 1994). We fitted female wild turkeys with solar powered 70 g backpack-style GPS transmitters that have  $\pm 18$  m error (Microwave Telemetry, Inc., Columbia, MD). Transmitters generally recorded 7 locations during the day (8:00, 10:00, 12:00, 14:00, 16:00, 18:00, and 20:00 h) from 15 March to 15 September during each year.

To investigate the thermal environment across the landscape and assess potential thermal selection of wild turkey during the periods of potentially high thermal stress, we measured black bulb temperature during June–August of each year. Black bulbs are steel spheres (101.6 mm-diameters; 20 gauge thickness) painted flat black that contain a temperature probe suspended in the center of each sphere and connected to a HOBO U12 data logger (Onset Corporation, Bourn, Massachusetts, USA). Black bulb temperatures provide closer estimates of thermal conditions an organism is experiencing than does ambient temperature because they provide a proxy for operative temperature (Campbell and Norman, 1998; Guthery et al., 2005). Operative temperature incorporates ambient temperature, solar radiation, and wind convection into a single metric (Dzialowski, 2005). We attached three total spheres to each data logger, one at the center point (turkey location or random landscape location), and the other two distributed 6 m away in a random cardinal direction to form a thermal sampling array to characterize the thermal conditions at a given point. As the thermal environment can vary tremendously at very small spatial scales (Hovick et al., 2014), we used three spheres at each point to better capture the small-scale variation at that point while also accounting for telemetry error. To measure the black bulb temperature of wild turkey locations, we deployed thermal sampling arrays on the day following telemetry download (typically within three days of data acquisition) only if similar temperature and solar radiation conditions were forecast. In this way, we were not assessing the precise thermal environment the wild turkey experienced, but modeling an index of thermal conditions at turkey and random locations across space and time to evaluate thermal variation, drivers of thermal variation, and thermal selection by wild turkeys. Each day, a random wild turkey was chosen, with the constraint that we did not sample an individual more than once per week. We placed thermal arrays at all seven daytime GPS locations for each selected wild turkey. All arrays were placed at the respective telemetry locations before 08:00 and data were recorded every 15 min from 08:00–20:00 h. In this way, we were able to collect temperature data during the entire diurnal period of GPS telemetry (8:00–20:00 h).

To capture thermal variation of the landscape, we selected the four most common vegetation types on the study site [herbaceous, shinnery oak, hybrid shinnery oak, and tree cover (tall woody vegetation > 2 m excluding hybrid shinnery oak)]. We then used a combination of data collected during the study and points used from a previous study conducted on Packsaddle WMA. We used or collected thermal data on each vegetation type by randomly choosing 30 points per vegetation type (2012–2017) resulting in 120 vegetation points. Vegetation was delineated using Maximum Likelihood Supervised Classification method from 2-meter resolution satellite imagery. A total of 319 known vegetation polygons were used to train and create a map of vegetation types on the study area. Our four vegetation types accounted for 90.09% (50.97%, 30.40%, 6.43%, and 2.29% for herbaceous, shinnery oak, hybrid shinnery oak, and tree cover, respectively) of the total vegetation coverage on the landscape. We measured black bulb temperature at random landscape locations with the same black bulb array design as the wild turkey locations. At each random location, we deployed a data logger and three thermal spheres to take black bulb temperature every 15 min from 07:30–20:30 h. To compare site-specific black bulb

temperature measurements to ambient temperatures, we recorded ambient temperature every hour at an onsite meteorological station. Because the meteorological station recorded averaged hourly temperatures, we averaged the black bulb temperatures that were recorded every 15 min by hour as well so that we could compare ambient and black bulb temperatures on the same temporal scale. Hour 20 was omitted from the analysis since we only collected data until 20:30 h, leaving only two 15 min intervals to be averaged instead of four. We used ANOVA and multiple pairwise-comparisons to determine differences in temperature between vegetation types.

To determine the frequency wild turkeys use vegetation types over the course of the day, we overlaid wild turkey GPS locations with our vegetation map and extracted vegetation values for each point. We used Ivlev's electivity index to determine selection or avoidance of vegetation types by wild turkey (Ivlev, 1961; Jacobs, 1974). A value of +1 indicates complete selection for a vegetation type, while a value of -1 indicates complete avoidance. Each GPS point taken at hour 20 was omitted from this analysis because of its proximity to when wild turkey use the roost, and we did not want to overestimate the frequency of tree cover use because of roosting behavior.

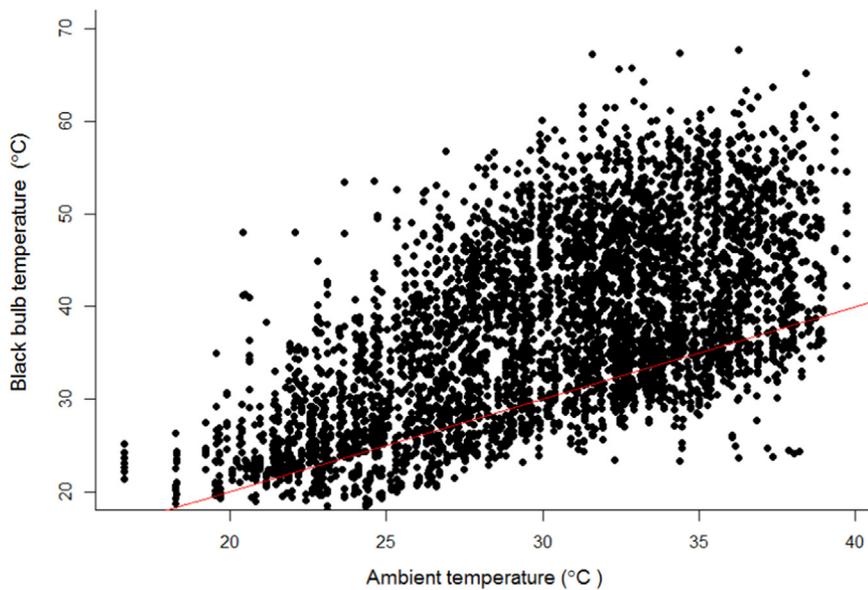
To examine daily movement patterns of wild turkey, we calculated the distance moved between two consecutive GPS locations (spanning two hours) for all wild turkey telemetry locations. If a transmitter was unable to record a GPS point, we discarded that 2-h period. During May through August, we had a successful fix frequency of about 98%. We then averaged the movement data into three categories, days that experienced maximum air temperatures  $\geq 35^\circ\text{C}$ ,  $< 35^\circ\text{C}$  and days  $< 30^\circ\text{C}$  to evaluate the effect of temperature on wild turkey movement across the 2-h time periods. Previous laboratory research suggests that wild turkey show signs of heat stress through panting, dropping wings, and extending neck and snood (fleshy protuberance above the beak) at ambient temperatures above  $35^\circ\text{C}$  (Buchholz, 1996). Therefore, we used this threshold to investigate possible differences in mean daily movement between days that experienced maximum air temperatures  $< 30^\circ\text{C}$ ,  $< 35^\circ\text{C}$  and  $\geq 35^\circ\text{C}$ . We used an ANOVA and multiple pairwise comparisons to determine differences in movements over the three categories of days.

## 3. Results

We found that the landscape had high thermal variability with differences in black bulb temperature ranging up to  $52^\circ\text{C}$  when ambient temperatures are  $> 30^\circ\text{C}$  (Fig. 1). We observed black bulb temperatures that were up to  $13.9^\circ\text{C}$  cooler than ambient temperatures as well as black bulb temperatures that exceeded  $70^\circ\text{C}$  (Fig. 1).

Variable vegetation types provided different ranges of black bulb temperature throughout the day with considerable disparity occurring during the midday when ambient temperatures and solar radiation levels are highest (Fig. 2). Tree cover and hybrid shinnery oak vegetation types (the taller vegetation types) provided the most moderated temperatures throughout the day especially during peak heating (Fig. 2). Tree cover was the coolest of all vegetation types with black bulb temperatures averaging  $3.65^\circ\text{C}$ ,  $8.17^\circ\text{C}$ , and  $8.95^\circ\text{C}$  cooler than hybrid shinnery oak, shinnery oak and herbaceous vegetation types, respectively, during the heat of the day (Table 1).

Our study site was primarily herbaceous (52.94%) and shinnery oak (28.79%) vegetation types (Fig. 3). Only 8.22% of the landscape was composed of taller vegetation types (1.99% tree cover and 6.23% hybrid shinnery oak). We found that wild turkey strongly selected for tree cover (Fig. 4). Depending on the time of day, wild turkey selected for this vegetation type six to eleven times more than what was available on the landscape (Fig. 3). While this selection is apparent during all times of the day, it was especially strong during hours of peak heating. Hybrid shinnery oak was also selected more than expected by random chance during peak heating, but this selection was much less than selection for tree cover (Fig. 4). We found that shinnery oak was used



**Fig. 1.** Relationship between black bulb temperature and ambient temperature recorded from 08:00–19:00 h at Packsaddle Wildlife Management Area, Oklahoma, USA during June–August (2016–2017). The red line represents a 1:1 linear relationship. Data points below this line are areas of thermal refuge at a given ambient temperature ( $n = 14,764$ ). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

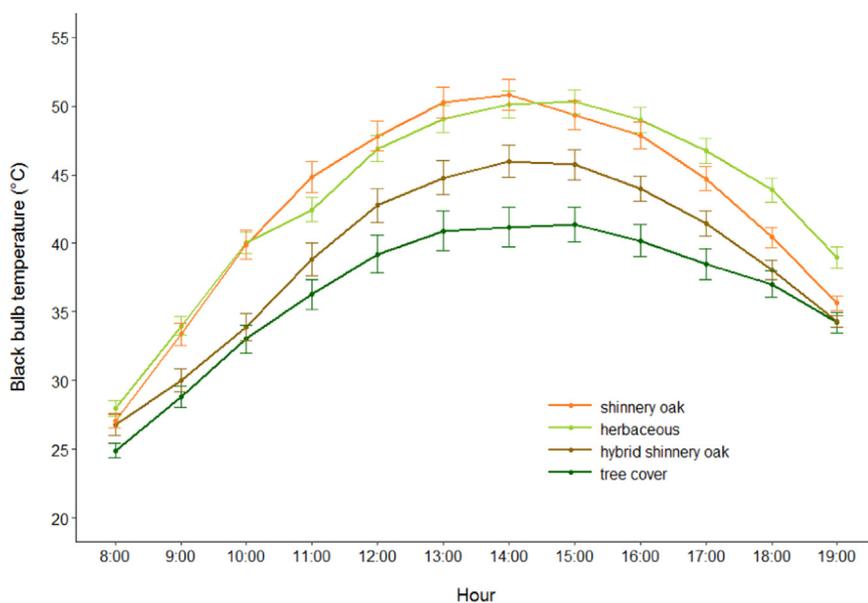
approximately in proportion to availability and wild turkey tended to avoid herbaceous vegetation and developed land at all times of the day (Fig. 4).

We further found that wild turkey altered their movement patterns over the course of the day on hotter days, but no difference in movement was detected during peak heating on cooler days. Specifically, on days  $< 30\text{ }^{\circ}\text{C}$ , wild turkey movement did not differ between consecutive locations excluding the period just prior to roosting where turkey move greater distances to find suitable roosting trees (Fig. 5). However, on days that included temperatures  $< 35\text{ }^{\circ}\text{C}$ , wild turkey altered their movement patterns during midday when ambient temperatures and solar radiation levels were the highest. During these days, wild turkey moved most in the early and late hours of the day and decreased their mean movement by 117 m during peak heating (Fig. 5). On days experiencing maximum temperatures  $\geq 35\text{ }^{\circ}\text{C}$ , wild turkey altered their movement patterns further during peak heating. Specifically, wild turkey mean movement was  $234.16\text{ m} \pm 6.69$  during 8:00–10:00 h and declined more than threefold to  $74.34\text{ m} \pm 3.31$  during midday (12:00–14:00 h). After peak heating, average movement again increased. The difference in mean movement between days  $< 30\text{ }^{\circ}\text{C}$  and

days  $\geq 35\text{ }^{\circ}\text{C}$  during peak heating was 126.83 m (Fig. 5).

#### 4. Discussion

We found that the thermal landscape was highly heterogeneous with temperature varying up to  $52\text{ }^{\circ}\text{C}$  at a given ambient temperature. Vegetation type strongly influenced temperature across space during daily peak heating, with taller vegetation types having mean temperatures up to  $8.95\text{ }^{\circ}\text{C}$  cooler than the remainder of the landscape. However, these cooler vegetation types were uncommon, only accounting for 8.2% of the landscape. Despite the rarity of tall woody cover, wild turkey showed strong selection for this vegetation type, particularly during peak daily heating. Not only did wild turkey alter space use across time relative to temperature variation, but they also altered movement. We found that on the hottest days ( $\geq 35\text{ }^{\circ}\text{C}$ ), wild turkeys decreased movement by three fold during peak heating, while movement on cooler days ( $< 30\text{ }^{\circ}\text{C}$ ) was uniform. Our data provide evidence that the thermal environment can influence space use and movement for large avian species, and that the thermal environment is an important component of habitat for a species.



**Fig. 2.** Variation in average back bulb temperatures ( $\pm$  SE) recorded in herbaceous, shinnery oak, hybrid shinnery oak, and tree cover at different times of the day (8:00–19:00 h) at Packsaddle Wildlife Management Area, Oklahoma, USA during June–August (2012–2017). Both hybrid shinnery oak and tree cover were significantly cooler than shinnery oak and herbaceous vegetation during peak mid-day heating. Tree cover was significantly cooler than hybrid shinnery oak during peak mid-day heating ( $n = 2598$ ).

**Table 1**

Range of ambient temperature  $T_{\text{air}}$  and black bulb temperature  $T_{\text{bb}}$  sampled from peak heating (12:00–16:00 h) in herbaceous, shinnery, hybrid shinnery, and tree cover at the Packsaddle Wildlife Management Area, Oklahoma, USA during June–August (2012–2017).

Vegetation type	$T_{\text{air}}$ range (°C)	$T_{\text{air}}$ mean (°C)	$T_{\text{bb}}$ range (°C)	$T_{\text{bb}}$ mean ( $\pm$ SE)
Herbaceous	25.85–39.36	34.31 $\pm$ (0.15)	25.58–64.10	49.08 ( $\pm$ 0.44) <sup>a</sup>
Shinnery	25.85–41.01	34.27 $\pm$ (0.19)	22.35–67.29	48.30 ( $\pm$ 0.52) <sup>a</sup>
Hybrid shinnery	26.51–41.87	35.56 $\pm$ (0.20)	27.48–72.43	43.78 ( $\pm$ 0.59) <sup>b</sup>
Tree cover	26.51–38.51	34.51 $\pm$ (0.16)	25.68–64.50	40.13 ( $\pm$ 0.51) <sup>c</sup>

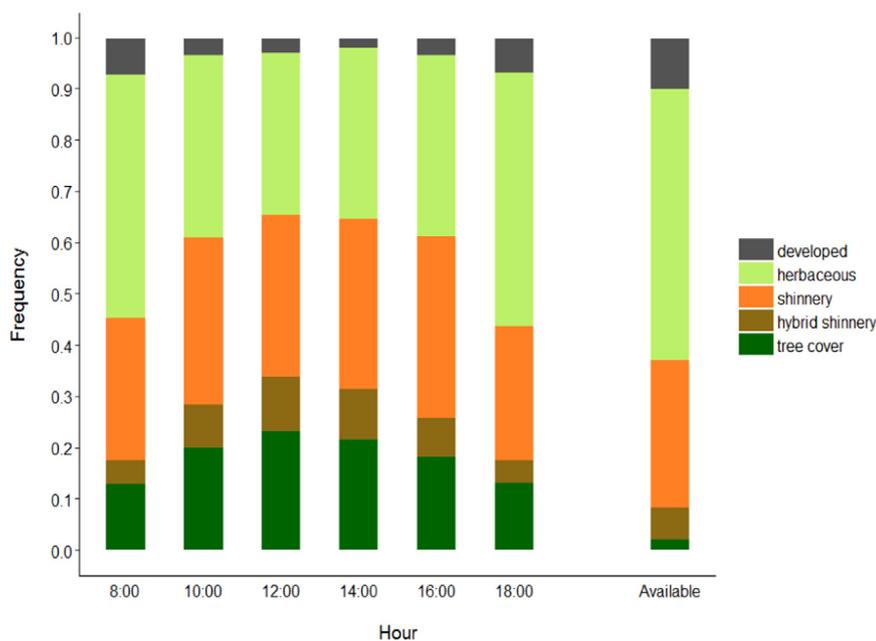
Notes: Different superscript letters denote significant differences (Tukey's multiple comparisons,  $p < 0.05$ ). Ambient temperature corresponds to days vegetation type was taken ( $n = 1029$ ).

Heterogeneity in vegetation across the landscape provides a wide array of thermal options. When ambient temperatures and levels of solar radiation are high, organisms can mitigate the stress of thermal extremes by moving to or occupying cooler microclimates that may be influenced by vegetation types (e.g., tall vegetation that offers shade). The distribution of these thermal refuges across the landscape may dictate the amount of usable space available to organisms, which suggests that available habitat is variable depending on temperature and other environmental conditions (Tanner et al., 2016). During periods of high heat, the amount of usable space may be substantially reduced by the distribution of thermal refuges accessible to organisms (Tanner et al., 2016), due to vegetation structure and composition. Different vegetation types and structures provide varying temperatures to organisms, meaning high heat events may make some vegetation types too hot to inhabit as they exceed the organism's thermal tolerance (Tuff et al., 2016). However, if the landscape provides heterogeneity in vegetation, organisms may be provided with sufficient locations that thermally buffer high temperatures (Fig. 6). In some cases, the persistence of both endotherm (Guthery, 2000) and ectotherm (Lagarde et al., 2012; Attum et al., 2013) populations may be contingent upon the presence of thermal refuge during these high temperatures.

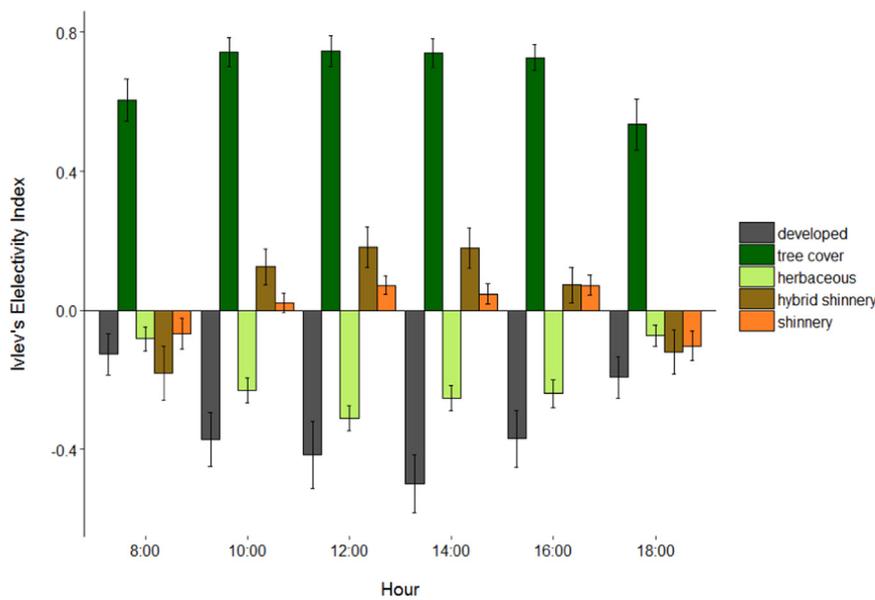
In our study, thermal refuge made up a small portion of the landscape which likely constrained the total usable space for some organisms during times of thermal extremes. Wild turkey responded to this spatially discrete thermal refuge by selecting for it and a reduction of movement as a function of daily temperature variation. However, other factors besides temperature obviously affect habitat selection. Specifically, we found that while wild turkey strongly selected for tree cover that had a mean temperature of  $40.13\text{ }^{\circ}\text{C} \pm 0.51$ , selection for

hybrid shinnery oak, which was nearly as cool as tree cover ( $43.78\text{ }^{\circ}\text{C} \pm 0.59$ ), was less selected for. The difference in selection was likely due to a combination of thermal and vegetation structure differences. Hybrid shinnery tends to have a denser understory structure compared to tree cover. Wild turkey rely on sight to avoid potential predators and prefer loafing in open understory (Baker, 1978 and Baker et al., 1980) which may help explain their stronger selection for tree cover. This illustrates the multifaceted and hierarchical decision-making within habitat selection. Individuals make habitat selection decisions based on many different factors in their environment (food, water, predators, temperature, etc.) and prioritize those that are more important at any given point in time and space. Thermal variation is but one aspect of habitat selection, but it does happen to be one that is often overlooked in most habitat selection studies. This is relevant to wild turkey habitat selection, which has been previously well studied. While wild turkey are known to require tree cover for roosting, no previous studies have documented that thermal variation largely explains habitat selection during diurnal periods and that trees (at least some trees) provide thermal refuge. Having this mechanistic understanding of habitat selection can allow managers to better determine the appropriate spatial arrangement of woody cover, which are clearly not only used for roosting cover by this species. This is but one example of how understanding the mechanism of habitat selection can completely change the application.

Studying long-term temperature averages and climate over a landscape can be informative for broad-scale questions relevant to animal distributions, population fluctuations, and species persistence (Dunbar et al., 2009). However, small-scale changes in temperature over the course of the day influences animal behavior and movement. Further,



**Fig. 3.** Frequency of wild turkey telemetry locations within each vegetation type at different times of the day (8:00–18:00) at Packsaddle Wildlife Management Area, Oklahoma, USA (2016–2017). The frequency each vegetation type was available across the landscape is represented in the right-most bar. Wild turkey selected for tree cover greater than expected at random and this selection was greatest during mid-day hours ( $n = 12,623$ ).

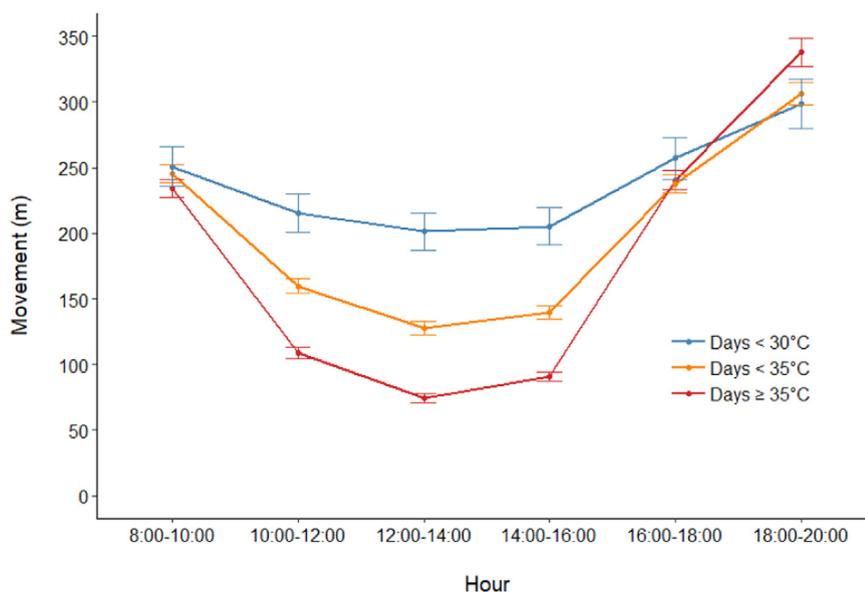


**Fig. 4.** Ivlev's electivity index indicating wild turkey vegetation selection (positive values) or avoidance (negative values) for different times of the day (8:00–18:00) at Packsaddle Wildlife Management Area, Oklahoma USA (2016–2017). Bars represent means (n = 32; wild turkey), error bars are standard errors. Wild turkey selected for tree cover at all times of the day and avoided herbaceous vegetation and developed land, especially during peak heating.

the availability of thermal refuges to organisms in times of thermal stress can have profound effects on habitat selection and in some cases even discrete stochastic weather events can affect animal survival (Tanner et al., 2016). Previous studies suggest that different species of reptiles (Sears et al., 2011; Attum et al., 2013), birds (Carroll et al., 2015a, 2015b), and mammals (Melin et al., 2013), select for thermal buffering when temperatures begin to exceed their thermal tolerances. Our study also indicated that wild turkey similarly make space use decisions based on discrete vegetation types that are cooler than the majority of the landscape. Wild turkey selected for taller vegetation types during periods of extreme heat. These vegetation types provided thermal buffering against extreme ambient temperatures throughout the day. In addition to changes in behavior, a reduction in activity or movement is a common strategy for organisms to moderate heat loads (Wolf, 2000). We found wild turkey did indeed reduce movement during peak heating especially during high temperatures. On the hottest days ( $\geq 35^\circ\text{C}$ ), wild turkeys decrease movement by three fold during peak heating, while on cooler days ( $< 30^\circ\text{C}$ ) movement was consistent throughout the day until movement to roost trees at sunset. This suggests that wild turkey alter movement patterns based on temperature

and not just time of day. The variation in movement over hours of the day and between days indicates that temporal variation in temperature affects space use at multiple scales (Tanner et al., 2016).

Additionally, organisms have been shown to mitigate thermal extremes during critical life stages. Exposure to high temperatures and solar radiation can affect the selection of nesting locations and nest success (Hovick et al., 2014, 2018). Several different species of grouse have been demonstrated to choose cooler nesting locations than what is available in the surrounding landscape (Hovick et al., 2014; Raynor et al., 2018) and select more or less exposed sites based on the ambient temperature (Larsson et al., 2013). During early stages of development, exposure to heat may directly cause chick mortality (Salzman, 1982), or decrease foraging time leading to reduced growth or survival (Goldstein, 1984; Cunningham et al., 2013). Extreme temperatures also change brood behavior and movement. For example, northern bobwhite (*Colinus virginianus*) were found to move their broods to tall vegetation that provides thermal cover and decrease movement to reduce the amount of energy expended (Carroll et al., 2015b). Our study provides evidence that organisms can mitigate thermal extremes on a daily basis when choosing loafing locations and not just during critical



**Fig. 5.** Variation in mean wild turkey movement ( $\pm$  SE) at different times of the day (8:00–20:00 h) on days experiencing maximum air temperature  $< 30^\circ\text{C}$  (blue) (n = 21) on days where maximum temperatures were  $< 35^\circ\text{C}$  (orange) (n = 84) and days experiencing maximum air temperatures  $\geq 35^\circ\text{C}$  (red) (n = 66) at Packsaddle Wildlife Management Area, Oklahoma, USA, 2016–2017 (Multiple pairwise comparisons,  $p < 0.05$ , significance corresponds to non-overlapping error bars). Wild turkey minimized their movements as mid-day temperatures increased (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

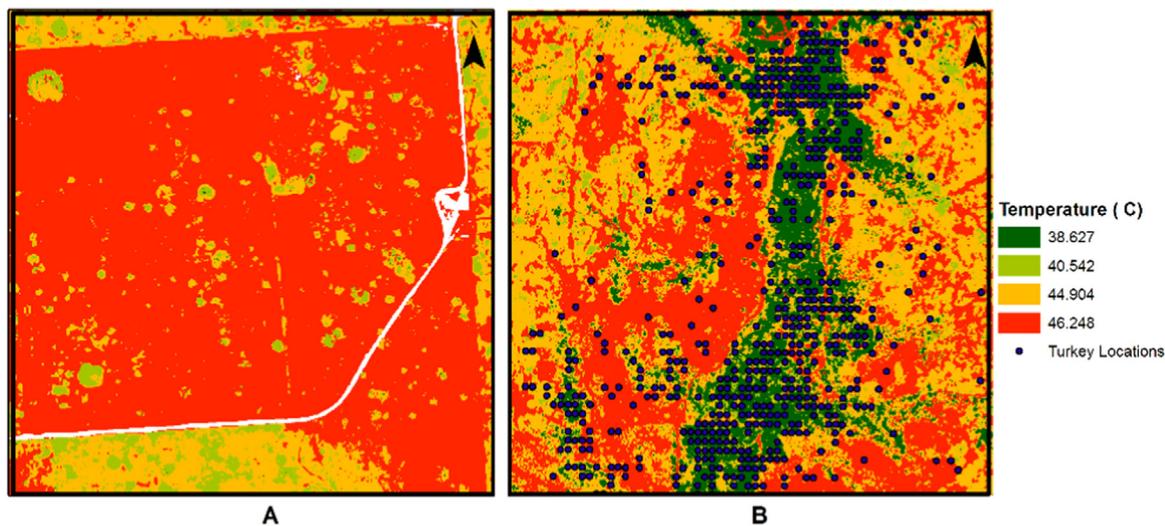


Fig. 6. Spatial variation of available mean black bulb temperatures across a homogenous landscape (A) and a relatively heterogeneous landscape (B) during midday peak heating on Packsaddle Wildlife Management Area, Oklahoma, USA (2016–2017). Each panel is one square kilometer of the study site. The more homogenous landscape (A) offers fewer thermally buffered choices to wild turkey as seen by the large areas of red. This portion of the study site is characterized by mainly herbaceous vegetation. The relatively heterogeneous portion of the landscape (B) provides a wide array of thermal options due to patches of trees (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

life stages such as nesting and brood rearing. Further, our data suggest that organisms can actively choose to buffer against extreme temperatures by selecting cooler locations and reducing movement in discrete time intervals (< 2 h). While this finding is intuitive given the limited previous findings, little empirical data exist documenting fine scale intra-daily behavior modifications relative to landscape thermal variation. Though active heat dissipation through adjustments in behavior, movement, and physiology is beneficial to organisms, it may incur costs such as increased demand for energy, reduced foraging efficiency, reduced rate of water intake, and constrain metabolic functions such as growth and reproduction (Sinervo et al., 2010; du Plessis et al., 2012; Smit et al., 2016). The increase in wild turkey movement that we documented from 18:00–20:00 h on days  $\geq 35^\circ\text{C}$  (Fig. 5) may be a compensating mechanism to increase foraging opportunities that were restricted during midday due to extreme temperatures. Prioritizing foraging and cover selection decisions along with altering movement patterns could be increasingly important with future predictions of increased temperatures and extreme thermal events (IPCC, 2013).

Thermal landscapes are dynamic systems that vary spatially and temporally (Saunders et al., 1998). Our study suggests that the structural heterogeneity (spatial) of a landscape provides a broad range of thermal options for organisms, especially during periods of high heat (temporal). The interaction of temperature and vegetation is a primary driver in the variation of microenvironments that allows organisms to alter the thermal conditions they experience by modifying behavior and space use. We found that discrete vegetation patches (tall woody vegetation) offer optimal thermal refuge during midday and on days with relatively high temperatures. These isolated vegetation patches that provide protection from solar radiation and extreme heat are important because temperature moderation may play a foundational role in organisms' selection of habitat. A reduction in thermal refuge would likely be detrimental to species that often experience landscape temperatures that exceed their thermal limits by offering fewer sites to moderate extreme temperature. Specifically for the Rio Grande wild turkey, discrete patches of taller woody cover appear to be important components of habitat during high temperature periods. While other subspecies of wild turkey are also known to select for woody cover for roosting, this woody cover may not be as limiting on the landscape. Collectively, our data provide evidence that organism space use and movement can be influenced by the thermal environment. Studying thermal characteristics of landscapes allows us to better understand

how and why these thermal factors affect space use and when they may be most critical. By including temperature, we get a more informed picture of when and why individuals select certain vegetation types and landscape features. This additional data helps to make more informed management decisions. Based on our findings, conservation practices should be directed towards maintaining vegetation and structural heterogeneity to ensure a wide range of thermal choices are available across landscapes to support organisms and their thermal tolerances.

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