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The effect of body posture on available habitat and activity-time in a lizard: Implications for thermal ecology studies

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ABSTRACT

Ectothermic animals contend with variable environmental temperature through behavioral thermoregulation, including selection of activity-times and microhabitat spaces with suitable operative temperatures. Thus, an important component to understanding the influence of temperature on animals is through the assessment of thermal constraints on time and space usage. Thermal ecologists have recognized that postural adjustments are an important part of behavioral thermoregulation. However, the impact of postural adjustments on available space and time has received little attention. We hypothesized that postural adjustments would significantly affect the thermal availability of space and time for surface activity. To test our hypothesis, we used data collected over a four-year study of the thermal ecology of Eastern Collared Lizards (*Crotaphytus collaris*) in Arkansas. We used a novel approach to model three distinct postures used by *C. collaris*, and to assess the impact of posture on available space and time. For our study species and habitat, posture had a significant impact on several indices of available space and time including: a) a 13% increase in length of the reproductive activity season, b) a 35% increase in the frequency distribution of habitat within active body temperature range and c) a 42% increase in average thermal quality index. We conclude that posture can significantly impact space and time available for surface activity in species that employ it for thermoregulation. Thus, a clearer understanding of the thermal constraints on time-space usage in ectotherms requires consideration of the impact of posture on the spatiotemporal distribution of thermally suitable microhabitats.

1. Introduction

Temperature affects organisms on multiple scales, from molecular to whole-animal processes (Hochachka and Somero, 1973; Huey, 1982), and from species distributions to ecosystem interactions (Porter and Gates, 1969; Gilman et al., 2010). Understanding how rising air temperatures will influence organisms is critical to predicting ecological impacts of climate change. The ability of many animals to adjust behaviorally to changing environmental temperatures is often underappreciated in climate change studies (Huey and Tewksbury, 2009). Recent work suggests that behavioral thermoregulation will play a key role in buffering the negative impacts of climate warming on ectotherms (Kearney et al., 2009; Huey et al., 2012). For many animals, behavioral thermoregulation includes selection of activity-times and microhabitat spaces with suitable environmental temperatures (Porter and Tracy, 1983). Thus, an important approach for predicting the impact of changing environmental temperatures on animals is through estimation of available time and space for activity (Sinervo et al., 2010; Sears et al., 2011) . However, one important component of behavioral thermoregulation, adjustment of body posture, has received little attention in terms of its impact on estimation of available space and time.

The effect of posture on the biophysical properties of animals is well known (DeWitt, 1971; Muth, 1977a; Stevenson, 1985). Postural adjustments can influence several biophysical properties such as radiative, conductive, convective and evaporative heat flux rates (Porter and Gates, 1969; Bakken and Gates, 1975). Thus, posture can play an important role in determining T_b (body temperature; see Box 1 for a glossary of thermal-biology terms) and heating/cooling rates that animals experience in a given micro-environment. For example, Porter et al. (1994) showed that adjustments in posture can influence the metabolic rate of birds and mammals as a result of variation in heat transfer properties. One of the earliest observations of the potential importance of posture in the thermal biology of animals was by Cowles and Bogert (1944), in their discussion of “thermal control through behavior” in desert lizards. Since 1944, posture has been shown to influence the thermal ecology of several ectotherms including: grasshoppers (Chappell, 1983), dragonflies (Anderson et al., 1979), snakes (Dmi'el and Borut, 1972; Ayers and Shine, 1997), marine iguanas

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Box 1

A glossary of thermal-biology terms

d_e – habitat thermal quality; absolute difference between T_{SET} and T_e

***electroformed* OTMs** – hollow copper OTM replicas of the target species.

h_r – hours of restriction: the time where temperatures are predicted to be too hot or cold for surface activity.

MIN_{ACT} – minimum activity threshold; average percentage of OTMs within T_{ACT} when *C. collaris* initiated, or ceased surface-activity.

OTM – operative temperature model; physical model that estimates the operative temperature (T_e) of the study organism.

OTM_{IDEAL} – modeling method that uses one of three OTM types (compressed, unmodified or stilted) based on the mean T_e of the habitat at that time (parameterized from observations on *C. collaris* use of posture with respect to mean T_e; Fig. 3a) to estimate T_e distribution.

$OTM_{UNMODIFIED}$ – modeling method that uses a single OTM type (unmodified OTM) to estimate T_e distribution.

restrictive T_b – T_bs too hot or cold for voluntary surface activity.

T_{ACT} – voluntary surface-active T_b range.

T_b – body temperature.

T_e – operative environmental temperature; a single temperature index of the equilibrium temperature of an object with zero heat capacity and the same thermodynamic properties as the study organism in the same microclimate.

thermal time constant – time for the temperature of an object to change by ~ 63% of the differential between the initial temperature and the ambient temperature.

T_{SET} – the range of T_bs selected by the study species in a laboratory setting.

(Bartholomew, 1966; White, 1973), crocodiles (Seebacher, 1999), turtles (Grayson and Dorcas, 2004) and several surface-active lizard species (i.e. Heatwole, 1970; Pearson, 1954; Losos, 1985; Martin et al., 1995; McConnachie et al., 2009).

In terrestrial ectotherms, postural adjustments impact two physical characteristics that influence heat flux rates. First, posture influences the animal's shape, and in turn, surface-area to volume ratios (Porter and Tracy, 1983), the amount of surface-area in contact with the substrate and the amount of surface-area exposed to the sun/wind/radiating substrate. Second, posture can impact position and orientation, which influences the distance of the animal from the substrate and the orientation to the sun/wind/radiating substrate (Stevenson, 1985; DeWitt, 1971). In turn, variation in these two physical characteristics influences heat flux rates including: conduction (i.e. amount of heat flux to the body surface through the substrate), convection (i.e. fluid dynamics and amount of surface within the wind profile), radiation (i.e. surface area exposed to long and short-wave radiation) and evaporation (i.e. amount of surface exposed to the air) rates (Porter and Gates, 1969).

Several studies have provided evidence that ectotherms use posture as a means to behaviorally thermoregulate (i.e. White, 1973; Tracy et al., 1979; Waldschmidt and Tracy, 1983; Stanton-Jones et al., 2018). For example, *Callisaurus dracanoides* uses an elevated posture when T_b is high, a prostrate posture when T_b is low, and a tail-down posture when T_b is intermediate (Muth, 1977b). Adopting the prostrate posture when air temperatures are colder than substrate temperatures increases the rate of heat gained through conduction, relative to the tail-down or elevated postures (DeWitt, 1971; Muth, 1977a). Alternatively, adopting the elevated posture reduces the rate of heat gained through conduction while increasing heat loss to the air (convection) compared to the tail-down posture (DeWitt, 1971). Therefore, adjusting posture based on the current heat load can allow an ectotherm to behaviorally thermoregulate in a single microhabitat. However, standard procedures for investigating the thermal ecology of ectotherms involve modeling T_e (Box 1; Bakken, 1976) of target species using a single posture. Therefore, studies of thermal ecology typically lack information on postural adjustments in the study species.

We postulated that if posture is an important component of thermal ecology then it should impact estimates of the available space and time for surface activity. For example, posture could allow an ectotherm to extend surface activity for a longer period (e.g. by adopting the prostrate posture at sunset when environmental heat loads are low) before it experiences *restrictive* T_bs (Box 1), thus increasing available activity-time. Similarly, if posture allows an organism the opportunity to occupy a greater proportion of the habitat at a given time (e.g. by adopting an elevated posture in microhabitats with high heat loads), then this would be an example where posture increases the available activity-space for that organism.

The goal of this study was to investigate the impact of posture on the estimated available space and time for surface activity in a diurnal lizard; the Eastern Collared Lizard (*Crotaphytus collaris*). We evaluated the impact of posture using data collected during a four-year thermal ecology study on a *C. collaris* population in Northern Arkansas. First, we tested for an association between *C. collaris* posture and T_b or environmental heat load. Next, we characterized the impact of postural adjustments on steady state T_b of *C. collaris*. Lastly, we addressed the influence of posture on available space and time by asking: 1) does postural adjustment allow *C. collaris* the opportunity to occupy a greater proportion of habitat during typical activity times, and 2) does postural adjustment provide *C. collaris* the opportunity to extend their estimated daily surface activity time?

2. Methods

2.1. Study system and C. collaris posture

Our study was conducted on a single *C. collaris* population in Northern Arkansas at a site along the White River in the Ozark National Forest. The habitat at this site consists of xeric-limestone prairie, with large expanses of exposed bedrock within a savannah-woodland matrix. We made weekly visits from late April through late August from 2013 to 2016. Posture used by *C. collaris* are similar to those reported by Muth (1977b) and DeWitt (1971) of other surface-active lizards (Fig. 1a–c). Postures can be categorized based on several characteristics including: body shape, area of contact with the substrate, distance of body from substrate, head and tail position, and geometry of the body plane to the substrate (DeWitt, 1971; McConnachie et al., 2009). However, we chose to classify postures into three categories similar to that reported by Muth (1977b): 1) Elevated; forelimbs and hind-limbs extended and the body completely off of the substrate (Figs. 1a), 2) Intermediate; forelimbs extended (or partially so) and posterior of ventral surface in contact with substrate (Figs. 1b), and 3) Prostrate; all of ventral surface in contact with substrate (Fig. 1c). Frequently, lizards adopted postures not included in these three categories for short periods of time (i.e. during courtship displays, mating, patrolling territories and while pursuing prey items). However, in instances where posture could not be immediately categorized for an individual, the observer could typically wait 3–5min and the lizard would adjust into one of the three

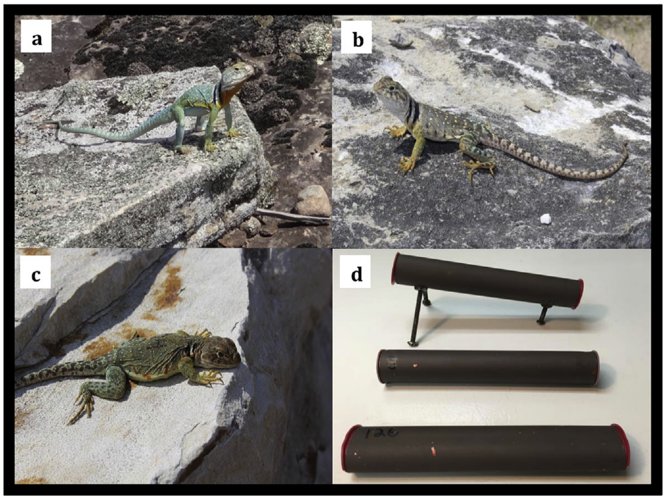

Fig. 1. a–d: Images of *C. collaris* postures: **a**) elevated, **b**) intermediate, and **c**) prostrate**. d)** Image of the three OTM types used in study. Stilted OTM (top OTM; corresponding to an elevated lizard, Fig. 1a), unmodified OTM (middle OTM; corresponding to a lizard in intermediated posture, Fig. 1b) and compressed OTM (bottom OTM; corresponding to prostrate lizard, Fig. 1c.).

categories. In the majority of observations, lizard posture could be confidently placed into one of the three categories immediately.

2.2. OTM construction

We used three types of operative temperature models (OTM; Box 1; Bakken et al., 1985) for this study, all of which consisted of a 12 cm length of copper pipe (~2.0 cm outside diameter). We used a preserved *C. collaris* specimen (9.8 cm SVL; University of Arkansas zoological collection) to estimate surface area variables of a mean adult sized lizard in the study population (~9.6 cm SVL; Brewster et al., 2018) to compare to OTMs. The pipe dimensions were chosen as a compromise between the mean adult SVL of *C. collaris* in the population and a cylinder with a similar surface area (~100 cm^2) as an adult *C. collaris* (~105 cm^2). Models were painted using spray paint (Valspar™, Labrador Brown, #85046) with a similar mean percent reflectance value (11.7%) as reported for *C. collaris* (10.6% Porter, 1967). We inserted a single iButton™ temperature data logger (Maxim Integrated Products) wrapped with a piece of aluminum screening material (to keep the iButton suspended in the center of the OTM) inside each OTM, and used a plastic plug (Mocap™, T-series tapered plug) to cover the ends of the pipe. We used an unmodified OTM (painted copper pipe, described above) to mimic the biophysical properties of *C. collaris* in the intermediate posture (unmodified OTM; Fig. 1d). The unmodified OTM had approximately 3 cm^2 of ventral surface in contact with substrate (on a flat surface), compared to approximately 4 cm^2 of an actual lizard in the intermediate posture. To mimic the biophysical properties of a lizard in the elevated posture (stilted OTM; Fig. 1d), we modified OTMs to match the mean distance above the surface of an elevated adult *C. collaris* (~3.5 cm at the coronal and radial center of the body). We fastened two 4.5 cm bolts (2.5 mm diameter, drilled and fastened using appropriate size nuts) at one end of the OTM, and a single 2.5 cm bolt at the opposite end of the OTM. To mimic the biophysical properties of a lizard in the prostrate posture (compressed OTM), we dorsoventrally compressed the copper pipe of an OTM (using a bench vise) to an approximately 1.0 cm dorsoventral height and an approximately 2.5 cm lateral width (Fig. 1d). The compressed OTM had approximately 18 cm^2 of ventral surface in contact with the substrate (on a flat surface), compared to approximately 20 cm^2 of an actual adult lizard in the prostrate posture.

2.3. OTM validation

To test for a linear relationship between *C. collaris* T_b and the T_e estimate of the three OTM types used, we made comparisons of animals in a given posture to the T_e of an OTM with a corresponding posture. We captured one-year-old and above *C. collaris* opportunistically, and only on days with low cloud and wind conditions. Upon observing a stationary lizard, we approached the animal to within 5 m and waited a minimum of 15min before attempting to capture the lizard by noose. The minimum time before capture was chosen to allow at least two thermal time-constants (Box 1; ~6.5min for the mean *C. collaris* body size in our population; based on the regression from Grigg et al., 1979) to elapse, thus insuring the animal was at or near steady state T_b. If at any point the animal's posture changed categories, or if it moved from the microhabitat location, the time to attempt capture was reinitiated. Immediately after capturing an individual, its cloacal T_b was recorded using a quick read digital thermometer, and the appropriate OTM type (corresponding with posture adopted by the lizard) was placed in its exact location. Once the OTM had reached equilibrium (OTM time constant ~3.5min), we recorded T_e using a quick read digital thermometer. If weather conditions changed (cloud cover or wind), the procedure was started over or excluded. This model validation procedure is similar to that reported by Grant and Dunham (1988) and allowed us to compare the steady state T_b of lizards in each of the three posture categories, to that of the corresponding OTM type. We used major-axis regression to assess the linear relationship between T_e and T_b.

2.4. T_e sampling

We used a total of one hundred OTMs, placed at fifty microsites across the habitat. We arranged OTMs along five 10 m transects and designated transects randomly (randomizing the distance and direction of each transect from the center of the site) across the habitat. Models were placed 1 m apart, along each transect. At each microsite, we randomly assigned orientation of OTMs (East–West or North–South). We programmed iButtons™ to record T_e estimates every 20 min, for ten-day time blocks, at two-time periods (May and late June to early July). We removed days with heavy cloud cover or rain from our dataset, leaving us with seven days early and seven days late season for comparisons. Microsites at the study site included exposed bedrock, loose sand/gravel or sparsely covered native grass substrates with intermittently distributed sandstone boulders and boulder piles. The study site has a relatively low tree density, so the majority of microsites were in full sun throughout the day.

2.5. *Crotaphytus collaris* use of posture

We used two different methods to quantify *C. collaris* use of posture with respect to heat loads experienced by surface active individuals. First, we recorded postures adopted by *C. collaris* simultaneously while recording the mean T_e of the habitat (using the unmodified OTMs only). Here, we used mean T_e as an index of the average environmental heat load impingent on surface active animals. We then compared the frequency of animals in a given posture to the range of mean T_es. Second, we opportunistically captured surface-active *C. collaris* (from 2013 to 16), and recorded T_bs and the posture adopted by those animals. We then compared the frequency of animals in a given posture to T_b. For both frequency of posture comparisons, residuals fit normality assumptions and we used ANOVA for statistical comparisons.

2.6. Posture and steady state T_b

We evaluate the impact of posture on *C. collaris* steady state T_b if they were to remain in the intermediate posture instead of adopting the prostrate posture when heat loads were low or the elevated posture when heat loads were high. We compared T_bs of individuals to an unmodified OTM opportunistically and using similar capture procedures as discussed above (see *2.3 OTM validation*). Comparisons were made between a validated unmodified OTM and the T_b of individuals in either the prostrate or elevated postures. We made comparisons at times when air temperatures (measured with a quick read thermometer, in the shade at 1 m above the surface) were near the observed threshold of restricting surface activity in our population and all remaining individuals on the surface were in the prostrate (air temperatures below 27 °C) or elevated (air temperatures above 37 °C) postures. Thus, by using the unmodified OTMs validated to *C. collaris* in the intermediate posture (see *2.3 OTM validation*), we were able to predict the T_b of a lizard if it were to adopt the intermediate posture instead of the elevated or prostrate posture, near the air temperature thresholds for surface activity. Data on the predicted difference in T_b among postures fit normality assumptions and were analyzed using ANOVA.

2.7. Modeling T_e

Our objective was to model T_e under two scenarios: 1) assuming *C. collaris* postural adjustments have no impact on available space and time estimation, and all microsites can be modeled with a single (intermediate) posture ($\text{OTM}_{\text{UNMODIFIED}}$; Box 1), and 2) assuming *C. collaris* adjusts posture to one of the three categories (prostrate, intermediate and elevated) based on mean T_e at that time ($\text{OTM}_{\text{IDEAL}}$; Box 1). To model $\text{OTM}_{\text{UNMODIFIED}}$, we placed an unmodified OTM at every-other microsite (25 microsites). To model $\text{OTM}_{\text{IDEAL}}$, we placed three OTMs (one of each type placed side-by-side oriented in the same direction) at the remaining microsites (25 microsites). In all replicates (time points), we used data on only one of the three OTM types to estimate T_e for $\text{OTM}_{\text{IDEAL}}$. To determine which OTM type to use at each time point, we used the mean T_e thresholds where *C. collaris* adjusted from the intermediate to prostate posture, and the intermediate to elevated posture. To estimate these T_e thresholds, we recorded the mean T_e when the frequency of postures used by *C. collaris* intersected between postures (prostrate-intermediate posture = 33.5 °C; intermediate-elevated posture = 39.5 °C; Fig. 2a). Thus, to model T_e based on $\text{OTM}_{\text{IDEAL}}$ we used the compressed OTMs when mean T_e was below 33.5 °C, and the stilted OTMs when mean T_e was above 39.5 °C. When mean T_e was within 33.5–39.5 °C, we used the unmodified OTMs. Therefore, our comparisons were between twenty-five microsites modeled solely with unmodified OTMs ($\text{OTM}_{\text{UNMODIFIED}}$), and twenty-five microsites modeled by one of three OTM types (compressed, unmodified and stilted), based on mean T_e at that time point ($\text{OTM}_{\text{IDEAL}}$).

We used T_b data collected over the four-year study to estimate the range of T_bs for voluntary surface activity (T_{ACT}; Box 1). We used the central 99% of all T_bs recorded from surface active lizards (31.2–42.6 °C) as our metric of T_{ACT} (Grant and Dunham, 1990). We used the percent of OTMs within T_{ACT} to quantify the spatiotemporal frequency distribution of available T_e (Grant, 1990). A second metric for quantifying the availability of suitable T_e is the estimate of the "thermal quality" of habitat (Hertz et al., 1993). Thermal quality (d_e; Box 1) is estimated by calculating the absolute difference between T_{SET} (Box 1) and T_e. Although the concept of T_{SET} has been criticized in the literature (Currin and Alexander, 1999; and references therein), its use in thermal ecology studies is still common. Thus, to make our estimates comparable to other thermal ecology studies that are based on T_{SET}, we utilized the d_e estimation. We used the central 60% of all T_bs selected by *C. collaris* in a laboratory gradient (34.8–38.1 °C; Firth et al., 1989) as our metric for $\text{T}_{\text{SET.}}$ We note that d_e does not directly estimate available time or space (instead, it measures absolute differences between T_e and T_{SET}) for surface activity. However, it can be used as a metric to compare thermal quality of habitats (Diaz, 1997; Blouin-Demers and Weatherhead, 2001; Bakken and Angilletta, 2014), and thus represents an additional method to test the impact of posture on available habitat for surface activity.

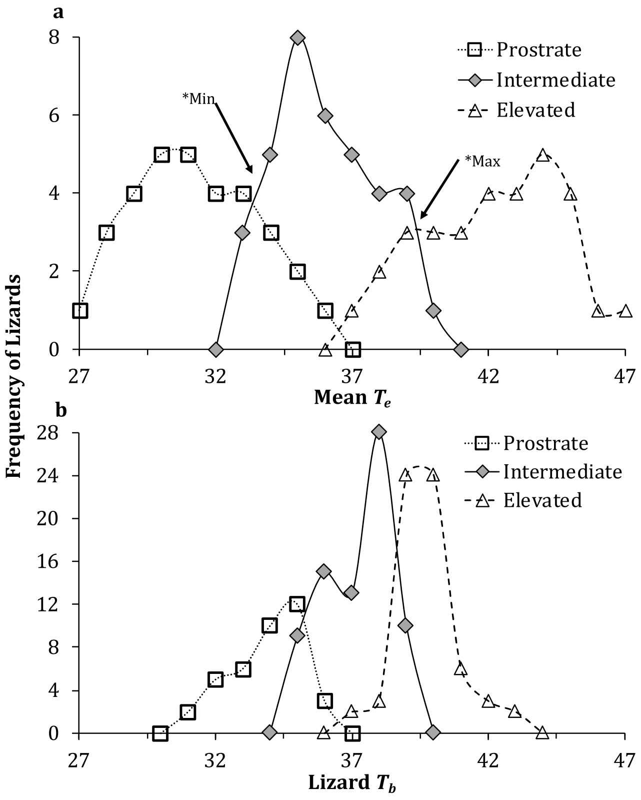

Fig. 2. a–b: Frequency of *C. collaris* in prostrate, intermediate and elevated postures as a function of: **a)** mean T_e of the habitat and **b)** individual lizard T_b. * = intersection points between intermediate-prostrate postures (Min = 33.5 °C); and intermediate-elevated postures (Max = 39.5 °C). Intersection points used to parametrize minimum and maximum mean T_e thresholds for $\text{OTM}_{\text{IDEAL}}$.

2.8. Hypothesis testing

2.8.1. Hypothesis #1: Available habitat

We tested the null hypothesis that posture does not increase the proportion of available habitat that is in the thermally suitable range for *C. collaris* surface activity. To test this hypothesis, we compared the percentage of suitable habitat (% OTMs within T_{ACT}) over a range of typical days and conditions throughout the activity season. We compared twenty-five microsites with unmodified OTMs only ($\text{OTM}_{\text{UNMODIFIED}}$), to twenty-five microsites with OTMs in the ideal posture at that time ($\text{OTM}_{\text{IDEAL}}$). Daily comparisons were made from 7:00am to 9:00pm, at 20min intervals, on four separate days (sunny day in May, June and July, and a cloudy day in June). We chose these four days (out of the 14 total days we had data for) to represent relatively typical daily climatic conditions across the *C. collaris* reproductive season in Arkansas (mid-April to mid-July; Brewster et al., 2018). The frequency distribution of T_e data did not fit normality assumptions. Thus, we used Wilcoxon signed rank test to assess differences in available habitat between $\text{OTM}_{\text{UNMODIFIED}}$ and $\text{OTM}_{\text{IDEAL}}$. If posture does not increase the space available for *C. collaris* surface-activity, then we did not expect a statistically significant increase in the proportion of thermally suitable habitat modeled with $\text{OTM}_{\text{IDEAL}}$ compared to $\text{OTM}_{\text{UNMODIFIED}}$.

2.8.2. Hypothesis#2: Available activity-time

Here we tested the null hypothesis that posture does not increase the time available that is in the thermally suitable range for surface activity in *C. collaris*. To test this hypothesis, we compared the number of hours where the proportion of T_e within T_{ACT} is at or above the minimum threshold for surface activity (MIN_{ACT}; Box 1). To determine the $\mathrm{MIN}_{\mathrm{ACT}}$, we conducted a pilot study using thirty unmodified OTMs, and estimated the average percentage of OTMs within $\mathrm{T}_{\mathrm{ACT}}$ when lizards initiated or ceased surface-activity. We recorded eleven observations of $\mathrm{MIN}_{\mathrm{ACT}}$ in 2014 on the study population, with a mean of 10.3% (SE ± 1.95) of OTMs within $\mathrm{T}_{\mathrm{ACT}}$. Thus, we used 10% as our $\mathrm{MIN}_{\mathrm{ACT}}$ threshold to compare available time within $\mathrm{T}_{\mathrm{ACT}}$ between microsites modeled with $\mathrm{OTM}_{\mathrm{UNMODIFIED}}$ to microsites modeled with $\mathrm{OTM}_{\mathrm{IDEAL}}$ (see *2.7 Modeling T_e*). Comparisons were made by summing the total hours per day (from 7:00am to 9:00pm, at 20min intervals) where the habitat was greater than $\mathrm{MIN}_{\mathrm{ACT}}$ (10%). Daily time estimates were made across seven days in mid-May (early reproductive season) and seven days in late June (late reproductive season). Available activity-time data fit normality assumptions and were analyzed using ANOVA with model-type and day as a fixed effect. If posture does not increase the available time for surface-activity of *C. collaris*, then we did not expect a statistically significant increase in the available time for surface activity for habitat modeled with $\mathrm{OTM}_{\mathrm{IDEAL}}$, compared to $\mathrm{OTM}_{\mathrm{UNMODIFIED}}$.

2.8.3. Hypothesis #3: Thermal quality (d_e)

We tested the null hypothesis that posture does not improve the thermal quality index (d_e) of available habitat for *C. collaris*. Using the same model parameters as our previous two hypotheses (modeling 25 microsites with $\mathrm{OTM}_{\mathrm{IDEAL}}$ and 25 microsites with $\mathrm{OTM}_{\mathrm{UNMODIFIED}}$) we estimated d_e over seven days early and seven days late season (from 7:00am to 9:00pm). Daily mean d_es fit normality assumptions and were analyzed using ANOVA with model-type and day as a fixed effect. If posture does not improve the thermal suitability of habitat for *C. collaris*, then we should find no statistically significant decrease in mean d_e of habitat modeled with $\mathrm{OTM}_{\mathrm{IDEAL}}$ compared to $\mathrm{OTM}_{\mathrm{UNMODIFIED}}$.

3. Results

3.1. OTM validation

In all three OTM to lizard T_b comparisons, relationships were isometric with slopes indistinguishable from 1.0 and intercepts indistinguishable from 0.0 (Fig. 3). For the compressed OTM to lizards in the prostrate posture, the intercept was 0.485 (95% CI from -4.890 to 5.082) and slope was 1.019 (95% CI from 0.875 to 1.189). For the unmodified OTM to lizards in the intermediate posture, the intercept was -1.847 (95% CI from -7.755 to 3.27) and the slope was 1.009 (95% CI from 0.875 to 1.165). For the stilted OTM to lizards in the elevated posture, the intercept was -1.589 (95% CI from -11.31 to 6.322) and the slope was 0.989 (95% CI from 0.802 to 1.218; Fig. 3).

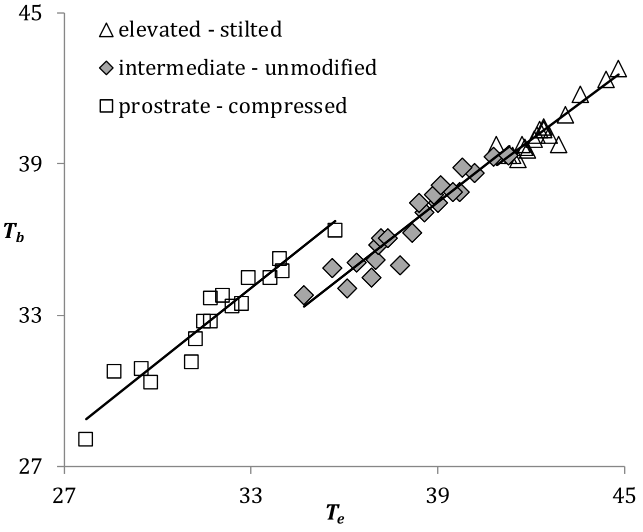

Fig. 3. Linear relationships between T_e and T_b of *C. collaris* in three postures. Stilted OTM to lizards in an elevated posture ($r^2 = 0.87$), unmodified OTM to lizards in an intermediate posture ($r^2 = 0.91$) and compressed OTM to lizards in a prostrate posture ($r^2 = 0.93$).

3.2. *Crotaphytus collaris* use of posture

Body temperature (T_b) of *C. collaris* was significantly different among the three postures (mean prostrate = 33.8 °C, mean intermediate = 37.2 °C, mean elevated = 39.7 °C; $F_{1,182} = 566.8$, $P < 0.001$; Fig. 2b). Similarly, mean T_e was significantly different among the three postures adopted by lizards (grand means for prostrate = 31.6 °C, intermediate = 36.3 °C and elevated = 43.2 °C; $F_{1,101} = 238.6$, $P < 0.001$; Fig. 2a). We used the mean T_e where the frequency of prostrate and intermediate postures intersected (33.5 °C); and the frequency of intermediate and elevated postures intersected (39.5 °C) to parameterize $\mathrm{OTM}_{\mathrm{IDEAL}}$ across time-points (Fig. 2a; see Methods, *2.7 Modeling T_e*).

3.3. Posture and steady state T_b

We made a total of 10 OTM to T_b comparisons when air temperatures were near the threshold for surface activity. When air temperatures were near the minimum for surface-activity, lizard T_bs would have been an estimated 2.4 °C colder (range of 2.3–2.8 °C) if they were to adopt the intermediate posture instead of the prostrate posture ($F_{1,8} = 12.3$, $P = 0.008$). When air temperatures were near the maximum for surface-activity, lizard T_bs would have been an estimated 3.8 °C hotter (range of 3.3–4.4 °C) if they were to adopt the intermediate posture instead of the elevated posture ($F_{1,8} = 29.5$, $P = 0.0006$).

3.4. Hypothesis testing

3.4.1. Hypothesis #1: Available habitat

Null: Posture does not increase the proportion of available habitat that is in the thermally suitable range for *C. collaris* surface activity. On all four days, the proportion of suitable habitat was statistically greater for $\mathrm{OTM}_{\mathrm{IDEAL}}$ compared to $\mathrm{OTM}_{\mathrm{UNMODIFIED}}$ (Wilcoxon signed rank, $P < 0.001$ all four days; Fig. 4a–d). Differences in the mean proportion of OTMs within $\mathrm{T}_{\mathrm{ACT}}$ were greatest on the warmest days (Sunny day July, $\mathrm{OTM}_{\mathrm{IDEAL}}$ = 54.7% vs. $\mathrm{OTM}_{\mathrm{UNMODIFIED}}$ = 31.2%; Sunny day June, $\mathrm{OTM}_{\mathrm{IDEAL}}$ = 49.5% vs. $\mathrm{OTM}_{\mathrm{UNMODIFIED}}$ = 28.5%), compared to cooler days (Cloudy day June, $\mathrm{OTM}_{\mathrm{IDEAL}}$ = 60.5% vs. $\mathrm{OTM}_{\mathrm{UNMODIFIED}}$ 42.8%; Sunny day May, $\mathrm{OTM}_{\mathrm{IDEAL}}$ = 60.2% vs. $\mathrm{OTM}_{\mathrm{UNMODIFIED}}$ 45.5%; Fig. 4a–d).

3.4.2. Hypothesis#2- Available activity-time

Null: Posture does not increase the time available that is in the thermally suitable range for surface activity in *C. collaris*. In both early and late season, $\mathrm{OTM}_{\mathrm{IDEAL}}$ had statistically greater daily hours for activity (hr/day where T_e was within $\mathrm{T}_{\mathrm{ACT}}$) than $\mathrm{OTM}_{\mathrm{UNMODIFIED}}$ (early season: $F_{1,6} = 8.7$, $P = 0.026$; late season; $F_{1,6} = 17.98$, $P = 0.005$; Fig. 5). The mean hours available for activity were greater for both $\mathrm{OTM}_{\mathrm{UNMODIFIED}}$ and $\mathrm{OTM}_{\mathrm{IDEAL}}$ in the late season compared to early season (Fig. 5).

3.4.3. Hypothesis #3: Thermal quality (d_e)

Null: Posture does not improve the thermal quality index (d_e) of available habitat for *C. collaris*. The mean daily d_e of available habitat across the activity season was significantly lower for $\mathrm{OTM}_{\mathrm{IDEAL}}$ (early season, 5.7 °C, SE = 0.55; late season, 3.6 °C, SE = 0.62) than for $\mathrm{OTM}_{\mathrm{UNMODIFIED}}$ (early season, 7.9 °C, SE = 0.39, $F_{1,11} = 11.1$, $P < 0.01$; late season, 8.1 °C, SE = 4.3, $F_{1,11} = 48.5$, $P < 0.001$).

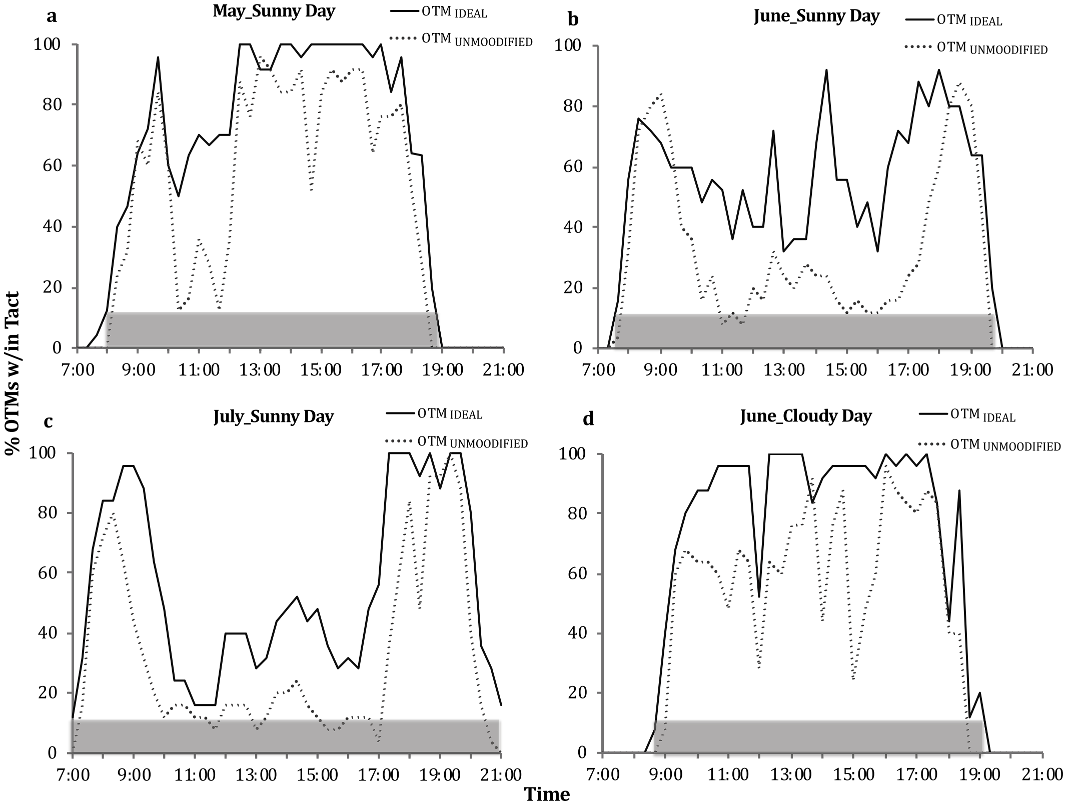

Fig. 4. a–d: Comparison of T_e (% of OTMs within T_{ACT}) modeled with $OTM_{UNMODIFIED}$ vs OTM_{IDEAL} over a typical sunny day in **a)** May, **b)** June and **c)** July; and **d)** a typical cloudy day in June. Shaded area represents the average minimum threshold for surface activity (MIN_{ACT} = 10%) observed by lizards in the study population.

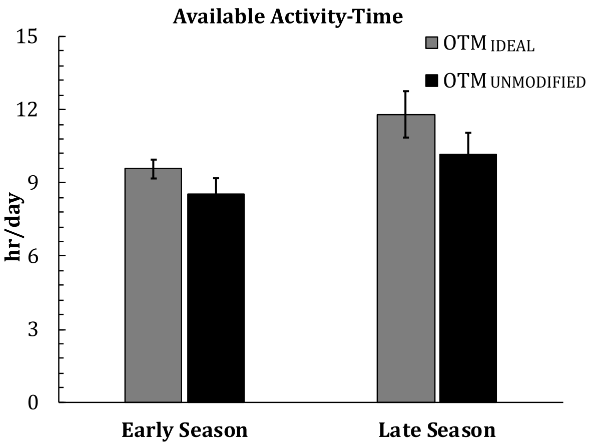

Fig. 5. Mean hr/day and SE of early (n = 7d) and late (n = 7d) seasons for habitat modeled: 1) exclusively by OTMs in the intermediate posture ($OTM_{UNMODIFIED}$) and, 2) by OTMs in the optimal posture at that time (prostrate, intermediate or elevated; OTM_{IDEAL}). hr/day measured as number of hours where a minimum of 10% of OTM's are within voluntary active T_b (T_{ACT} = 32.1–42.6 °C).

4. Discussion

The goal of this study was to assess the influence of posture on the available time and space for surface activity in *C. collaris*. We found an association between *C. collaris* posture and both T_b and mean T_e (Fig. 3a and b). We recognize that *C. collaris* do not adjust posture as a function of mean T_e per se, but rather by the T_e they (individually) experience in the microhabitat they occupy. However, our data suggest that mean T_e provides a reasonable proxy for the heat load that most lizards experience at a given time (at least at this study site), as indicated by the timing of postures adopted by *C. collaris*. Our data also suggested that posture can have a marked effect on the heat flux rates experienced by *C. collaris*, depending on the environmental heat load at that time. Taken together, these two results (*C. collaris* use of posture and the impact of posture on steady state T_b) implicate posture as an important means of behavioral thermoregulation in *C. collaris*.

Our data also suggest that altering posture affords *C. collaris* increased available space and time for surface activity. By adjusting posture favorably with environmental heat loads (mean T_e) throughout the day, *C. collaris* is able to occupy a greater spatial portion of the habitat during normal activity times without experiencing restrictive T_bs (Fig. 4a–d). The difference in the proportion of available habitat within T_{ACT} for *C. collaris* that remain in the intermediate posture ($OTM_{UNMODIFIED}$) compared to animals that adjust posture (OTM_{IDEAL}) was greatest on the days with higher heat loads (sunny June and July days; Fig. 4b and c). The difference in magnitude of useable habitat among days is partially explained by the greater buffering effect that the elevated posture provides *C. collaris* when heat loads are high, compared to the effect of prostrate posture when heat loads are low (see Results; *3.3 Posture and steady state* T_b). Nonetheless, our data suggest that even on colder days, *C. collaris* can greatly improve the useable proportion of habitat by adjusting posture (Fig. 4a, d).

Second, our results suggest that posture can significantly increase the activity-time available for *C. collaris* before experiencing restrictive T_bs. If *C. collaris* used only the intermediate posture ($OTM_{UNMODIFIED}$), they would have an average of 11–14% fewer hours per day (early or late season, respectively) for surface activity, compared to lizards that adjust posture (OTM_{IDEAL}: Fig. 5). Our results also indicate that by adjusting posture, *C. collaris* experience an approximately 42% improvement in thermal quality of the habitat (d_e) than if they ignored posture. The improvement in thermal quality implies *C. collaris* would have an easier time maintaining T_b within T_{SET}, potentially facilitating optimal physiological performances (e.g. digestion and sprint speed), by adjusting posture.

4.1. OTMs used in this study

The benefits of using electroformed OTMs (Box 1; Bakken and Gates, 1975) over cylinder shaped OTMs have been discussed in the literature (Bakken and Angilletta, 2014). In short, electroformed OTMs are designed to mimic the surface area and shape of the actual organism (Walsberg and Wolf, 1996), thus improving the odds that they will match the biophysical properties of the study animal. Nonetheless, several studies have successfully approximated T_e of the target organism using cylinder shaped models (i.e. Peterson et al., 1993; Diaz, 1997; Wills and Beaupre, 2000; Row and Blouin-Demers, 2006; Stanton-Jones et al., 2018). In the present study, we also found cylinder OTMs to provide a good approximation of the study organisms, indicated by our validation data (Fig. 3). We note that modeling T_e in a species that uses three postures requires three times the number of OTMs to reach the same sample size. With the significant costs associated with electroformed OTMs (time and money; Bakken, 1992; Watson and Francis, 2015), we believe our methodology provides an accurate and cost-effective approach to modeling T_e of ectotherms that use multiple postures.

4.2. The importance of posture in *C. collaris*

Our data show the importance of space and time characterization to understanding ecological patterns in the study population. For example, T_e estimates based on $\text{OTM}_{\text{UNMODIFIED}}$ suggest that *C. collaris* surface activity should be bimodal and cease at mid-day (Fig. 4c). Yet even on days hotter than the "typical" sunny July day modeled here, *C. collaris* at this site remained surface active through the entire day by adopting elevated postures and restricting most of their activity to elevated (i.e. on top of a large rock) or shaded microhabitats. Alternatively, estimates based on $\text{OTM}_{\text{IDEAL}}$ correctly predicted that lizards should have the opportunity to remain surface active through the hottest part of the day by adopting the elevated posture and restricting activity to microhabitats with the lowest heat loads (i.e. large rocks and shaded microhabitats).

Similarly, our predictions about total number of hours available for surface activity across the reproductive season were also impacted by posture. Our results suggested fewer hours available for daily activity (1.0–1.6hr; early and late season, respectively) for $\text{OTM}_{\text{UNMODIFIED}}$ compared to $\text{OTM}_{\text{IDEAL.}}$ With an approximately 90-day reproductive season length (Brewster et al., 2018), this would be an estimated 112 fewer hr (~13% shorter reproductive season) for surface activity for $\text{OTM}_{\text{UNMODIFIED}}$, compared to $\text{OTM}_{\text{IDEAL}}$. Thus, our study suggests posture has important implications for *C. collaris* space and time availability that may have implications for the species ecology and life history as well.

4.3. Is *C. collaris* the exception or the rule?

The target species in this study is a surface-active, diurnal lizard. The estimated difference in steady state T_b among postures in this study (up to ~4.3 °C), is consistent with estimates in another surface-active lizard (*Callisaurus dracanoides,* ~6 °C, Bakken, 1989; ~4 °C, Muth, 1977b). Indeed, the magnitude of variation in T_b associated with posture will vary among species, depending on factors such as body size, morphology and the range of climatic conditions that occur for that species (Stevenson, 1985; Muth, 1977a). Thus, it is difficult to know what impact posture has on time and space utilization in other species. We suspect that for some terrestrial ectotherms, posture may be a minor or even negligible influence on their thermal ecology. For example, posture will likely be of minor importance for nocturnal species or species that spend all of their time in full shade (e.g. in full canopy, or leaf litter). However, with the breadth of taxa reported in the literature that use posture for thermoregulatory purposes, we suspect that *C. collaris* may represent more of the "rule" than the "exception" in sun-basking, terrestrial ectotherms.

4.4. Implications for studies of thermal ecology

Current methods for modeling T_e (Bakken and Gates, 1975; Hertz et al., 1993; Bakken and Angilletta, 2014) typically lack information on postural adjustments. Our results suggest that in species that can and do use posture to buffer restrictive T_bs, omitting this information could lead to underestimation of available space and time for activity. The potential impact of errors in T_e estimations on inferences about thermal ecology have been addressed in the literature. Bakken and Angilletta (2014) showed that habitat modeled with a ± 2 °C systematic error would result in large effects on thermal indices (i.e. d_e, thermoregulatory effectiveness, and available surface activity-time), ranging from 8 to 32%. In our study, the difference in T_b*s* among postures (up to 4.3 °C) exceeds the ± 2 °C modeled by Bakken and Angilletta (2014). Similarly, variation in estimates of available time and d_e modeled with $\text{OTM}_{\text{UNMODIFIED}}$ versus $\text{OTM}_{\text{IDEAL}}$ mirrored (13% difference in activity-time) or exceeded (42% difference in d_e) those reported by Bakken and Angilletta (2014).

A relatively recent practice in thermal ecology studies is to model extinction risk of lizards to climate change by estimating hours of restriction (h_r; Box 1; Sinervo et al., 2010; Lara-Reséndiz et al., 2015). The h_r methodology assumes that when climate change causes activity-time to reach some minimum threshold for a particular species, that species will go extinct. Since ectotherms must balance competing functions of time and mass-energy budgets, all while contending with the available thermal environment (Dunham et al., 1989), the h_r methodology is based on a critical component of ectotherm life histories: activity-time budgets (Adolph and Porter, 1993). However, current studies using the h_r methodology do not incorporate the potential variance in available activity-time associated with posture. Our findings suggest that in studies that make inferences based on the interaction between temperature and the availability of space and time, an assessment of the target species use of posture is warranted.

5. Conclusions

Our study presents a novel approach to investigating and quantifying the influence of postural adjustments on the thermal ecology of a terrestrial ectotherm. Our data show the importance of postural adjustments to the available space and time for *C. collaris*. Based on the frequency of ectotherm species in the literature that use posture as a means of behavioral thermoregulation, we conclude that posture can play a significant role in the available space and time for surface activity in species that use this behavior. A key component to predicting the biological impacts of climate change includes understanding the effects of rising air temperatures on the space and time budgets of ectotherms. Thus, our findings imply that posture can be an important component to accurately predict the impacts of changing temperatures on ectotherms that use it for behavioral thermoregulation. We urge investigators to consider the potential effects of posture in their target species, and when appropriate, account for variation in this behavior when making inferences associated with space and time utilization.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2019.03.006.

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