



Ornate tree lizards (*Urosaurus ornatus*) thermoregulate less accurately in habitats of high thermal quality

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ABSTRACT

Temperature plays a critical role for ectotherm performance and thus for fitness. Ectotherms, since unable to regulate their body temperature internally, use behavioural thermoregulation to maintain their body temperature within a range that maximizes performance. According to the cost-benefit model of thermoregulation, investment into thermoregulation is dictated by the trade-off between the costs and benefits of thermoregulating. The thermal quality of the environment is a major cost of thermoregulation because it directly affects the amount of time and energy that must be invested by an individual to achieve and maintain an optimal body temperature. Thus, in habitats of poor thermal quality, lizards should thermoregulate less. Using *Urosaurus ornatus* living at 10 sites each straddling two adjacent habitats (wash and upland), we tested the hypothesis that investment in thermoregulation is dependent on the thermal quality of the habitat. We found that the wash habitat had higher thermal quality indicated by a longer duration when optimal body temperatures could be reached. Lizards had more accurate body temperatures in the upland despite its poorer thermal quality. These results suggest that discrepancies in thermal quality between adjacent habitats affect investment in thermoregulation by lizards, but in a direction opposite to the main prediction of the cost-benefit model of thermoregulation.

1. Introduction

Although environmental temperatures vary tremendously through space and time, most organisms regulate their body temperature within a narrow range. The ability to respond to environmental thermal gradients and maintain a T_b within this narrow range is beneficial for the optimization of physiological processes (Huey and Bennett, 1987). For instance, a T_b outside of this optimal range can have negative effects on locomotor performance, food acquisition (Zhang and Ji, 2004), and predator avoidance (Huey and Kingsolver, 1989). More ultimate measures of fitness, such as reproductive output, are also linked to T_b (Halliday et al., 2015). Consequently, T_b has direct implications for the fitness of animals.

Ectotherms are of particular interest when considering T_b and its effects on performance due to their limited ability to regulate T_b through metabolism (Huey and Kingsolver, 1989). Because ectotherms have low metabolic rates, they have limited physiological control over their T_b and are dependent on other mechanisms of thermoregulation

(Bennett, 1980; Huey and Kingsolver, 1989). As compared to endotherms, ectotherms use a more energetically affordable strategy of temperature regulation through behaviour. By altering their behaviour, ectotherms are able to control heat gain or loss through conduction, convection, evaporation, and radiation (Angilletta, 2009). Common behavioural strategies include basking, changing body posture (Huey, 1974), selecting particular microhabitats and activity periods (Adolph, 1990; Hertz and Huey, 1981; Stevenson et al., 1985). Using behavioural thermoregulation, ectotherms are able to maintain a T_o and respond to environmental temperature changes (Glanville and Seebacher, 2006; Huey and Stevenson, 1979; Seebacher, 2005).

Not all ectotherms thermoregulate to the same extent. Thermoregulatory strategies can range from thermoconformity, where the organism does not thermoregulate and T_b matches the environmental temperatures (Ruibal, 1961), to active and nearly perfect thermoregulation, where behaviour is used to adjust T_b within a narrow range (Sartorius et al., 2002). Differences in the costs and benefits of thermoregulation are assumed to account for this variation (Huey and

Abbreviations: T_b , body temperature; T_o , optimal body temperature; T_{set} , preferred body temperature; T_{sk} , skin temperature; d_b , accuracy of body temperature; T_e , operative environmental temperature; d_e , thermal quality; SVL, snout-vent length; LMM, linear mixed model; d_e-d_b , effectiveness of thermoregulation; E_x , thermal exploitation index

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Slatkin, 1976). The main benefit of thermoregulation is that it allows organisms to obtain a T_b that optimizes their fitness. The main costs associated with thermoregulation are related to the energy and time invested in seeking thermoregulatory opportunities. Also, for lizards in particular, many thermoregulatory behaviours involve movements that would increase conspicuousness to and the rate of encounter with predators (Huey and Slatkin, 1976; Pianka and Pianka, 1970). The cost-benefit model of thermoregulation developed by Huey and Slatkin (1976) is used to predict how much an individual should invest in thermoregulation considering these energetic costs and benefits. Intuitively, the model predicts that organisms should thermoregulate precisely when the associated costs of thermoregulation are low.

Despite the ability of many ectotherms to maintain appropriate T_b in heterogeneous thermal environments, even a careful thermoregulator is limited by available temperatures (Angilletta, 2009). Exposure to extreme temperatures, whether high or low, even for a short duration, may result in highly reduced performance (Gilchrist, 1995) or death. The cost-benefit model of thermoregulation postulates that characteristics of the physical environment are the primary factors to be considered when determining how much energy should be invested in thermoregulation (Huey and Slatkin, 1976). From an ectotherm's perspective, a habitat in which it can easily maintain its T_b within its T_{set} is a habitat of high thermal quality (Hertz et al., 1993; Huey, 1991). As environmental temperatures deviate from the optimal range for performance, the thermal quality of the habitat decreases and individuals must devote more time and energy into thermoregulation to achieve T_b close to (Huey and Slatkin, 1976). Consequently, there are more missed opportunities in low thermal quality habitats and, as a result, costs increase. Therefore, when all else is equal, an organism is expected to invest more in thermoregulation in a habitat of high thermal quality than in a habitat of low thermal quality because the costs of thermoregulation are lower in a habitat of high thermal quality where the environmental temperatures are closer to.

Although there has been support for the predictions of the cost-benefit model of thermoregulation both in the field and in the laboratory (Herczeg, 2006; Hertz et al., 1993; Huey, 1974; Huey and Webster, 1976; Withers and Campbell, 1985), studies conducted in thermally-challenging climates have cast doubt on the general applicability of the model (Aguado and Braña, 2014; Blouin-Demers and Nadeau, 2005; Blouin-Demers and Weatherhead, 2001a; Bouazza et al., 2016; Edwards and Blouin-Demers, 2007; Picard et al., 2011; Row and Blouin-Demers, 2006). The most rigorous test of the cost-benefit model of thermoregulation to date was a global comparative approach of 20 lizard species that indicated that poor thermal quality leads to higher effectiveness of thermoregulation, contrary to the central prediction of the cost-benefit model of thermoregulation. The authors suggested that in thermally-challenging habitats the disadvantages of thermoconformity may be greater than the costs of thermoregulation. An animal that does not thermoregulate in an environment that is thermally-challenging will experience a T_b that is far from T_o resulting in reduced performance. Consequently, thermoregulation takes place despite the high cost (Blouin-Demers and Nadeau, 2005).

It has also been argued that, for most reptiles, thermoregulation may be unimportant (Shine and Madsen, 1996). The majority of reptiles occur in the tropics, in thermally-benign habitats, where thermoconformity has little consequence because environmental temperatures are close to optimal T_b . Therefore, even without thermoregulation, an animal living in the tropics will attain a T_b close to T_{set} with little or no effort. For water pythons living in the tropics of Australia, the thermal environment allows the snakes to select from a wide range of microhabitats with little or no cost and so regulating temperature requires little effort and has been considered unimportant (Shine and Madsen, 1996). In addition, the cost-benefit model of thermoregulation assumes that the primary aim of thermoregulatory behaviour for an animal is to attain a T_b that is higher than those experienced in the absence of thermoregulatory behaviour (Hertz et al., 1993). In tropical

environments, this is probably not the case and the main challenge is to cool down, not to heat up (Shine and Madsen, 1996).

The extent of thermoregulation required by an individual or species is highly dependent on the environment in which it resides and investigating thermoregulation in populations faced with different thermal challenges is warranted to understand the impact of thermal quality of an environment on thermoregulation. We tested the hypothesis that thermal quality of an environment dictates investment in thermoregulation. To test this hypothesis, we used two adjacent habitats that are occupied by tree lizards and contrast in their thermal quality. We used ten study sites each straddling the two habitats: an open-canopy, dry, rocky stream bed habitat (wash) and a closed-canopy, treed habitat (upland). Paterson and Blouin-Demers (2018) found that the wash habitat has higher thermal quality, allowing lizards to achieve their T_{set} for a longer period in the day than the upland habitat. We predicted that, if the cost-benefit model of thermoregulation is correct, tree lizards should invest less in thermoregulation in the upland habitat where the thermal quality is lower.

2. Materials and methods

2.1. Study sites and species

The ornate tree lizard (*Urosaurus ornatus*) is a small lizard that is abundant across the southwestern USA and northern Mexico (Tinkle and Dunham, 1983) and that occupies a variety of habitats (Smith and Ballinger, 1995). For this study, we used adjacent treed (upland) and open-canopy creek bed (wash) habitats in canyon bottoms because these habitats provide an obvious difference in structure that impacts thermoregulatory opportunities (Paterson and Blouin-Demers, 2018). The wash is comprised predominantly of rocks and fallen logs and is largely devoid of vegetation, whereas the upland consists of pine-oak woodlands. The difference in habitat structure affords the wash more solar radiation at ground level than the closed-canopy upland resulting in differing thermal quality for lizards (Paterson and Blouin-Demers, 2018). From 1 May to 21 July 2018, we collected data at ten sites throughout Cave Creek Canyon within the Chiricahua Mountains of southeastern Arizona, USA. Each site extended 300 m along the wash and extended 50 m into the adjacent upland. Sites were separated by at least 300 m which is further than tree lizard dispersal distance (Paterson and Blouin-Demers, 2018). Capture sessions were approximately on a 10-day cycle, and each site was visited between seven and nine times.

This research was conducted with a State of Arizona Scientific Collection Permit (SP622205), permission from the U. S. Forest Service (Douglas Ruppel), and approved by the University of Ottawa Animal Care Committee (BL-2812-R1).

2.2. Field data collection

Each day, we caught lizards by rod and noose (832 lizards captured 1251 times) during their daily active period. The habitat type, wash or upland, was recorded upon initial sighting. Overall, 21% of recaptured individuals (61/278) switched between wash and upland habitats on at least one occasion. The capture location of each lizard was marked with a hand-held GPS unit (accuracy ± 3 m) and lizards were placed individually into uniquely numbered cloth bags until processing, after which individuals were released at their capture location on the same day.

During processing, lizards were uniquely marked with a felt tip marker on the head and stomach (Jones and Ferguson, 1980; Simon and Bissinger, 2011). The sex of each lizard (399 males and 433 females) was determined based on the presence (males) or absence (females) of enlarged post-anal scales and femoral pores, body size (males are bigger than females), and colouration. Snout-vent length (SVL) was measured using digital calipers (± 0.1 mm). Lizards were weighed using a digital

scale (± 0.01 g) to aid in determining reproductive status of females because reproduction has been shown to alter the body temperature of lizards (Beuchat, 1986; Braña, 1993; Smith and Ballinger, 1994).

2.3. Field active body temperature (T_b)

Immediately after a lizard was captured, T_{sk} was measured as an estimate of T_b using an infrared laser thermometer pointed at the cloaca. T_{sk} is particularly suited for small-bodied lizards whose T_b are easily influenced by handling, both due to stress and heat transfer (Langkilde and Shine, 2006; Marler and Moore, 1991). Validation studies have indicated that T_{sk} gives an accurate estimate of cloacal temperature in small lizards (Besson and Cree, 2010; Bouazza et al., 2016; Carretero, 2012; Hare et al., 2007; Herczeg, 2006). To measure T_{sk} we followed the guidelines outlined by Hare et al. (2007): emissivity set at 0.95 and the thermometer was oriented in-line with the body axis. In subsequent sections T_b indicates T_{sk} .

2.4. Preferred body temperature range (T_{set})

T_{set} of a species is normally determined by allowing individuals to select T_b 's within a laboratory thermal gradient that lacks any ecological costs that may influence temperature regulation in the field (Hertz et al., 1993; Huey, 1991). T_{set} is assumed to include the optimal temperature for performance and is a highly conserved trait of a species (Angilletta and Werner, 1998; Light et al., 1966). We used the T_{set} range for adult tree lizards ($32.2\text{--}36.0^\circ\text{C}$) at the same study sites calculated by Paterson and Blouin-Demers (2018) as the central 50% (25th–75th quartiles) of selected body temperatures, which is consistent with the preferred body temperatures of tree lizards measured by other researchers (Gilbert and Miles, 2016; Licht, 1965).

2.5. Accuracy of body temperature (d_b)

The difference between field active T_b and T_{set} (Huey, 1982) indicates how closely ectotherms achieve T_b within the preferred body temperature range for the species (i.e. accuracy of body temperature, d_b). We measured d_b following Hertz et al. (1993) by calculating the deviation of T_b from T_{set} in absolute value.

2.6. Operative environmental temperature (T_e)

To evaluate whether ectotherms are actively thermoregulating, information on the distribution of T_b that a non-thermoregulating animal would achieve is needed (Heath, 1964; Huey and Pianka, 1977). Bakken (1992) suggested that lizards of less than 0.03 kg, such as tree lizards, can be assumed to have zero heat capacity and so the T_e values measured with physical models are an accurate representation of the T_b of non-thermoregulating lizard. We determined T_e every minute from iButton ($\pm 0.5^\circ\text{C}$) temperature loggers (Thermochron DIS1921G-F5) painted brown to reflect the thermal properties of tree lizards. These thermal models were validated for use with tree lizards by Paterson and Blouin-Demers (2018).

Because lizard activity such as foraging, guarding territories, and mating is limited by environmental temperatures at the surface (not inside refuges), models were randomly placed on rocks, logs, and tree trunks (at 1.5 m height) to represent common perching areas ($n = 1101$, 98% of lizard observations) of lizards in each habitat. We assumed that lizards were always able to seek refuge from hot surface temperatures in the numerous hiding locations available (under bark, under leaf litter, under rocks, under logs, etc.) (Christian et al., 1983; Cowles and Bogert, 1944). Models were rearranged randomly each day within the microhabitats to better capture the spatial heterogeneity of T_e ; however, we did not attempt to capture every nuance of microhabitat variability with this method, but rather aimed to establish general thermal properties of active surface temperatures available to

tree lizards in each habitat type.

2.7. Thermal quality

Thermal quality was measured in each habitat with temperature loggers whose readings were compared to the species' T_{set} . To quantify the thermal quality of each habitat, we calculated the proportion of the day that a lizard could achieve T_{set} . Instead of calculating a mean T_e , which assumes we were able to sample all microhabitats in proportion to their relative availability, for each minute the models were deployed, we calculated the minimum and maximum T_e available to lizards in a habitat. T_{set} was considered achievable as long as the maximum temperature was above the lower bound of T_{set} and the minimum temperature was below the upper bound of T_{set} (Paterson and Blouin-Demers, 2018).

2.8. Statistical analyses

All data were analyzed using R Version 3.4.1 (R Core Team, 2017). To compare thermal quality between habitats, we used a LMM (package: lme4, function: lmer; Bates et al., 2014) to test whether the proportion of the day a lizard could achieve T_{set} was related to Julian date and habitat type using site as a random effect. To test the prediction that lizards living in poor quality habitats thermoregulate less accurately, we constructed a LMM for d_b including habitat as a fixed effect. Because the data were collected in the field, we included in the model biologically relevant control variables that affect T_b of lizards. Sex was recorded as a three-factor variable to incorporate reproductive status (male, non-gravid female, and gravid female) to control for sex and reproductive differences in T_b . SVL controls for the influence of size on T_b . Julian date and time of day controlled for increases in temperature over the season and during the day, respectively. We incorporated random effects with lizard ID nested in site to control for repeated captures and site effects. Finally, we also included thermometer ID to control for any potential differences in laser thermometers used by researchers catching and measuring body temperatures of lizards.

3. Results

3.1. Thermal quality of habitats

A total of 72 048 T_e 's were recorded in both habitats over 71 field days. Throughout the active season, T_e ranged from 9.5°C to 78°C (mean $\pm$ SE = $37.4 \pm 0.05^\circ\text{C}$) in the wash and from 10°C to 66°C (mean $\pm$ SE = $30.5 \pm 0.03^\circ\text{C}$) in the upland. In general, lizards could reach T_{set} earlier in the day in the wash habitat than in the upland habitat and could remain active at T_{set} later in the day in the wash habitat. The proportion of the day during which T_{set} could be achieved was almost 20% higher in the wash than in the upland ($R^2 = 0.13$, coefficient = 0.17, 95% CI = 0.10–0.25, $F = 19.9$, $DF = 1,129$, $P < 0.001$, Fig. 1). Therefore, the wash habitat had higher thermal quality than the upland habitat, consistent with Paterson and Blouin-Demers (2018).

3.2. Accuracy of body temperature

In total, we recorded 690 lizard T_b in the upland and 561 in the wash. Across both habitats, T_b ranged from 15.5°C to 38.6°C ($31.5 \pm 0.1^\circ\text{C}$) throughout the active season (Fig. 2). There was no significant difference between mean d_b of males ($n = 632$; $1.86 \pm 0.1^\circ\text{C}$) and females ($n = 619$; $1.78 \pm 0.1^\circ\text{C}$) ($t = -0.51$, $DF = 1248$, 95% CI = $-0.369\text{--}0.217$, $P = 0.614$). Likewise, there was no significant difference between the mean d_b of gravid females ($n = 150$; $1.59 \pm 0.2^\circ\text{C}$) and non-gravid females ($n = 469$; $1.84 \pm 0.1^\circ\text{C}$) ($t = 1.19$, $DF = 306$, 95% CI = $-0.169\text{--}0.686$,

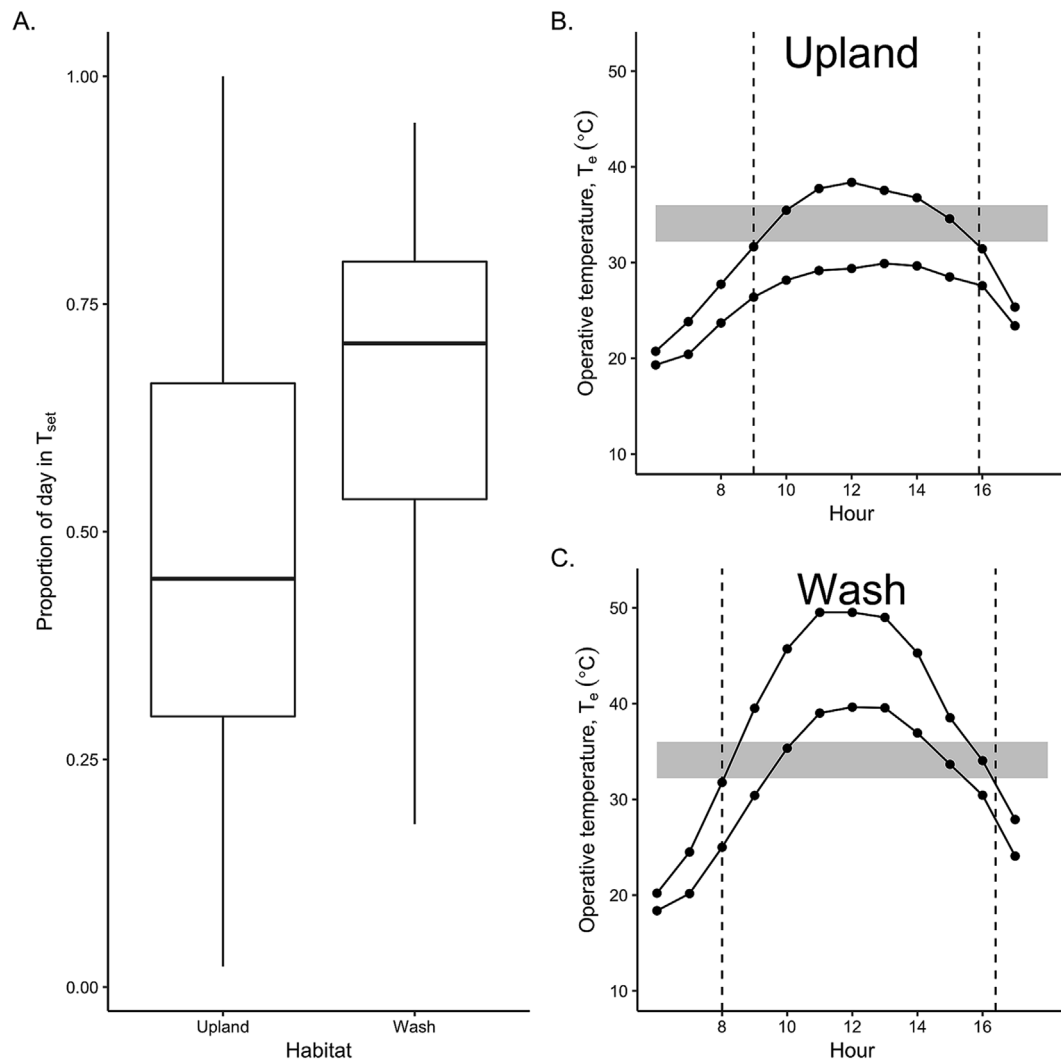


Fig. 1. A) The proportion of operative temperatures (T_e) that are within the preferred range of body temperatures (T_{set}) of ornate tree lizards (*Urosaurus ornatus*) is higher in the wash than in the upland. Thermal quality of B) upland and C) wash habitats showing the mean daily maximum and minimum T_e for each hour (solid lines) in relation to T_{set} (shaded area) of ornate tree lizards.

$P = 0.235$).

When examining differences in lizard d_b between habitat types, we found a significant difference ($t = -2.11$, $DF = 1187$, 95% $CI = -0.614$ – 0.022 , $P = 0.035$) between the mean d_b of lizards caught in the upland ($n = 690$; 1.68 ± 0.1 $^{\circ}\text{C}$) and the wash ($n = 561$; 2.00 ± 0.1 $^{\circ}\text{C}$) (Fig. 3). The deviations of lizard T_b from T_{set} (d_b) ranged from 0 to 16.7 $^{\circ}\text{C}$ (mean $\pm$ SE = 2.0 ± 0.1 $^{\circ}\text{C}$) in the wash and from 0 to 15.8 $^{\circ}\text{C}$ (mean $\pm$ SE = 1.7 ± 0.1 $^{\circ}\text{C}$) in the upland. There was a significant effect of habitat type on d_b ($R^2 = 0.23$, $F = 3.92$, $DF = 1$, 939, 95% $CI = 0.009$ – 0.562 , $P = 0.044$) where lizards caught in the upland had a lower d_b (more accurate) than lizards caught in the wash. In addition, 45% of the lizards captured in the upland had T_b within T_{set} , whereas 39% of the lizards captured in the wash had T_b within T_{set} . Also, lizards in the upland were closer to T_{set} when we caught them (80% of T_b measurements were within 3 $^{\circ}\text{C}$ of T_{set}) (Fig. 4).

4. Discussion

We showed that thermoregulation by tree lizards is affected by the thermal quality of the habitat in which they reside. Consistent with Paterson and Blouin-Demers (2018), we found a difference in the thermal quality of two structurally different, but adjacent habitat types: an open-canopy dry, rocky streambed habitat (wash) and a closed-

canopy treed habitat (upland). The wash allowed tree lizards to achieve their preferred body temperature (T_e within T_{set}) for a longer duration each day than the upland, indicative of higher thermal quality. Tree lizards caught in the lower thermal quality upland habitat more accurately regulated their T_b within T_{set} . This study provides strong evidence that there is an important link between habitat thermal quality and investment in thermoregulation by tree lizards, even in adjacent habitat types where temperatures regularly reach their preferred temperature range, but due to differences in structure, still differ in thermal quality (mean T_e in the wash = 37.4 ± 0.05 $^{\circ}\text{C}$ and in the upland = 30.5 ± 0.03 $^{\circ}\text{C}$).

Because of the numerous microhabitats available in the upland and wash habitat, using standard thermoregulation indices such as d_e (Hertz et al., 1993) and d_e - d_b (Blouin-Demers and Weatherhead, 2001b) to compare the thermal quality of these habitats posed major challenges. Due to the complexity of both the wash and upland habitats (e.g. trees, rocks, logs, leaf litter etc.) it was not possible to accurately sample tree lizards' microhabitats in proportion to their relative availability, and this was especially problematic for refuge microhabitats. Because 98% of the lizards captured were perched on the surface microhabitats sampled (on rocks, on logs, and on trees), we believe we were able to accurately sample the microhabitats used during activity. It seems reasonable to assume that lizards are always able to seek refuge from

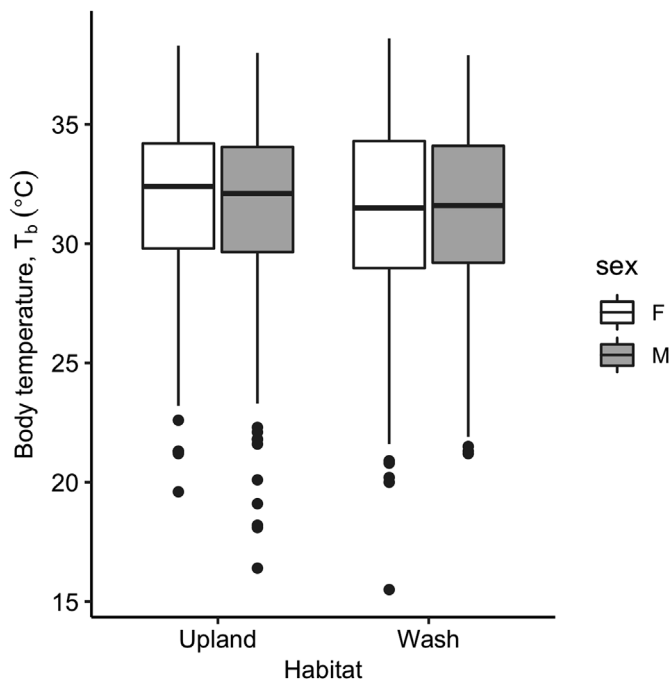


Fig. 2. Boxplot of ornate tree lizard (*Urosaurus ornatus*) body temperatures (T_b) measured at ten sites in the Chiricahua Mountains, Arizona, USA from 1 May to 21 July 2018.

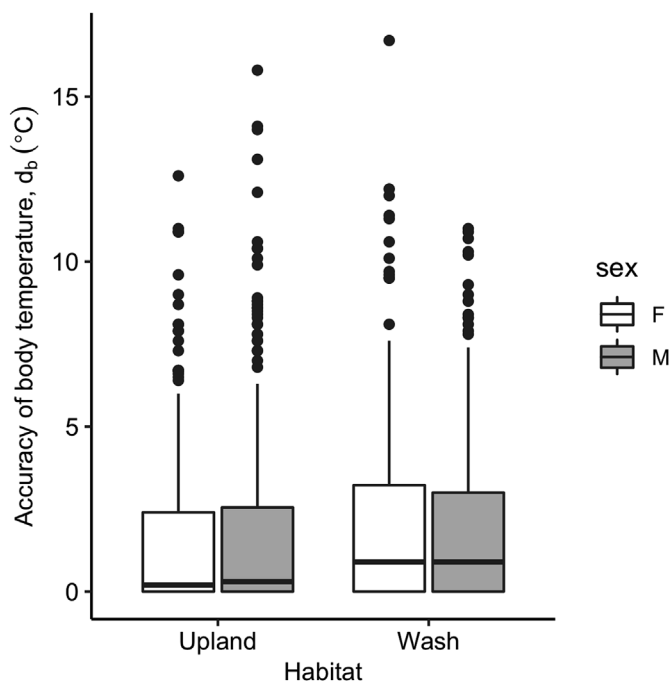


Fig. 3. Boxplot of ornate tree lizard (*Urosaurus ornatus*) accuracy of body temperature index (d_b) at ten sites in the Chiricahua Mountains, Arizona, USA from 1 May to 21 July 2018. Lizards in the upland habitat have significantly smaller d_b values than the wash.

hot temperatures, as they do not die during the day when temperatures exceed their critical maximum T_b . Therefore, what limits lizard activity should be the surface temperatures. In the wash, lizards were able to reach T_{set} earlier in the day and maintain it for a longer duration than in the upland. As the environmental temperatures increased throughout the day, lizard T_b in both habitats increased; however, there was no significant difference in T_b (0.3°C) between lizards caught in the wash

versus the upland, despite the difference in thermal quality. Surprisingly, upland lizards maintained T_b closer to T_{set} (d_b).

E_x has been used to index reptilian thermoregulation (Bauwens et al., 1996; Blouin-Demers and Weatherhead, 2001a; Catenazzi et al., 2005; Christian and Weavers, 1996; Rowe et al., 2017; Sartorius et al., 2002) as a measure of the extent to which an individual (or species) exploits the available thermal environment. It is calculated as the amount of time an animal's T_b is within T_{set} divided by the time available for them to achieve T_b within T_{set} as indicated by T_e (E_x can range from 0% to 100%). The higher the E_x value, the more the animal exploits its thermal environment when that environment is permissive. Although E_x could not be calculated in this study due to measuring T_b intermittently, we can still apply its logic. In the upland, lizards had smaller d_b values (mean = 1.7°C) than lizards caught in the wash (mean = 2.0°C) despite the fact that T_{set} is available for less time in the upland (lower thermal quality). If upland lizards are more accurately regulating their T_b , with less time to achieve $T_b = T_{set}$, then the upland lizards must be investing more into thermoregulation.

Contrary to the central prediction of the cost-benefit model of thermoregulation (Huey and Slatkin, 1976), instead of tree lizard thermoregulation increasing in the low-cost, high thermal quality habitat (wash), tree lizard thermoregulation was lower in the wash. When thermal quality is low, there are high costs for lizards to maintain T_b within T_{set} , such as energy and time loss, as well as an increased risk of predation (Huey, 1974; Huey and Slatkin, 1976). Although it seems reasonable to assume that the optimal amount of thermoregulation for an ectotherm is determined by some trade-off between costs and benefits, these results suggest that the main cost of thermoregulation identified in the original cost-benefit model of thermoregulation, thermal quality, is insufficient to explain investment into thermoregulation by tree lizards.

The disadvantages of thermoconformity may explain why the cost-benefit model of thermoregulation has not been supported, at least in temperate zone reptiles that experience highly variable diurnal temperatures (e.g. Blouin-Demers and Weatherhead, 2002; Bouazza et al., 2016; Edwards and Blouin-Demers, 2007; Row and Blouin-Demers, 2006). In a comparative global analysis on 20 diurnal lizard species, Blouin-Demers and Nadeau (2005) found that lizards invested more in thermoregulation in low thermal quality environments and offered the explanation that the physiological disadvantages of thermoconformity are very low when the thermal environment is benign because even without thermoregulation T_b is close to T_{set} . The cost-benefit model of thermoregulation puts more emphasis on the idea that the cost of thermoregulation increases as the thermal quality of the habitat decreases. However, in thermally-challenging climates (i.e. temperate forests, hot deserts), the disadvantages of thermoconformity may be more important and may force individuals to thermoregulate more carefully than in thermally benign habitats. In a low thermal quality environment, a lizard that does not thermoregulate carefully will perform so poorly that it may not survive, and so lizards must thermoregulate more carefully in low thermal quality habitat despite the high costs.

Thermal quality is not the only cost faced by thermoregulating tree lizards. Due to their small body size, predation risk is likely another important cost. In the open-canopy wash habitat, basking lizards are clearly more visible to aerial predators. Lizards can shift their investment into thermoregulation in response to costs with possible immediate negative fitness effects, such as predation. For example, in an experimental study where the thermal environment was held constant, the common lizard (*Zootoca vivipara*) forwent basking, decreasing its accuracy of body temperature, following a simulated risk of predation (Herczeg et al., 2008). Paterson and Blouin-Demers (2018) measured natural food availability in the wash and upland and found that the wash had significantly more food than the upland, so it is unlikely that wash lizards thermoregulated less accurately due to increased time spent foraging. Thermoregulatory costs should be low in landscapes

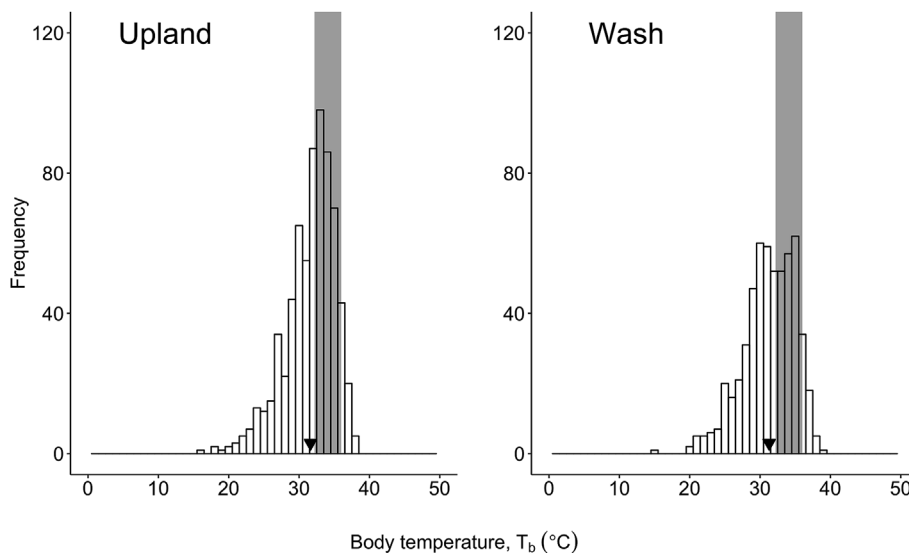


Fig. 4. Frequency distributions of body temperatures (T_b) of ornate tree lizards (*Urosaurus ornatus*) in upland ($n = 690$) and wash ($n = 561$) habitats at ten sites in the Chiricahua Mountains, Arizona, USA from 1 May to 21 July 2018. Shaded bars indicate the preferred temperature range (T_{set}) of the species. Triangles indicate the mean.

where an abundance of optimal microhabitats reduces the distance that animals need to travel between shade and sun (Sears et al., 2016). An animal that moves a greater distance or basks more often could not only attract the attention of a predator, but also expends more time and energy locating suitable microhabitats. In a semi-natural arena, Sears et al. (2016) demonstrated that Yarrow's spiny lizards thermoregulate more accurately in habitats where the preferred microhabitats were dispersed instead of clumped. The upland habitat is more spatially complex than the wash and provides more dispersed microhabitats than the more homogenous wash. The fine-scale spatial arrangements of thermally suitable microhabitats may have made thermoregulation more costly in the wash.

4.1. Conclusions

In summary, we found that tree lizards maintain T_b closer to T_{set} in the upland habitat despite the lower thermal quality, which is opposite to the central prediction of the cost-benefit model of thermoregulation. It appears that the disadvantages of thermoconformity when the thermal quality is low may be more important in influencing investment into thermoregulation by tree lizards than the costs incurred for thermoregulation. This study provides evidence that even small differences in thermal quality between habitats still impact lizard thermoregulation. To determine whether this pattern holds true outside of the activity period of lizards, future studies should use high-resolution telemetry or implanted data loggers to measure T_b continuously and to explore in more detail the daily and seasonal variation in thermoregulation. A more complete understanding of the interactions between environmental temperatures and T_b may provide insights into the potential impacts of climate change on habitat selection and fitness of ectotherms (e.g. Buckley et al., 2015).

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Appendix A. Supplementary data

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