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Changes in thermal quality of the environment along an elevational gradient affect investment in thermoregulation by Yarrow's spiny lizards

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body temperature; cost-benefit model; ectotherms; thermal quality; thermoregulation; *Sceloporus jarrovii*.

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Abstract

Body temperature affects physiological processes and, consequently, is assumed to have a large impact on fitness. Lizards need to thermoregulate behaviourally to maintain their body temperature within a range that maximizes performance, but there are costs associated with thermoregulation. The thermal quality of an environment directly affects the amount of time and energy that must be invested by an individual to maintain an optimal body temperature for performance; time and energy are major costs of thermoregulation. According to Huey and Slatkin's (Q. Rev. Biol. 1976, 363) cost–benefit model of thermoregulation, lizards should only thermoregulate when the benefits outweigh the costs. Thus, in habitats of poor thermal quality, lizards should invest less into thermoregulation. We tested the hypothesis that the thermal quality of an environment dictates investment in thermoregulation across an elevational gradient. Increases in elevation are accompanied by decreases in temperature and therefore thermal quality. We recorded body temperatures of Yarrow's spiny lizards (*Sceloporus jarrovii*) at ten talus slopes along an elevational gradient of over 1000 m. We found a significant positive relationship between elevation and effectiveness of thermoregulation, opposite to the prediction of the cost–benefit model of thermoregulation. This suggests that the disadvantages of thermoconformity may be greater than the costs of thermoregulating as habitats become more thermally challenging.

Introduction

Body temperature (T_b) has a significant impact on organismal performance (e.g. the ability to run, feed and interact socially; Huey & Stevenson, 1979) and consequently is assumed to have a large effect on fitness (Christian & Tracy, 1981; Huey & Kingsolver, 1989). The ability to maintain a T_b near the optimal body temperature (T_o) allows animals to achieve maximum performance (Angilletta, 2009). A T_b far from T_o has negative effects on proximate measures of fitness such as locomotion, food acquisition (Zhang & Ji, 2004) and predator avoidance (Huey & Kingsolver, 1989) as well as impacts on more ultimate measures of fitness such as reproductive output (Halliday *et al*., 2015). The reduction in performance associated with a T_b far from T_o is asymmetrical, being more precipitous at T_b above T_o than below T_o (Bulté & Blouin-Demers, 2006). Thus, individuals that can maintain their T_b near T_o maximize performance and, thus, it is assumed that individuals who regulate T_b close to T_o maximize fitness (Huey & Kingsolver, 1989; Zhang & Ji, 2004; Angilletta, 2009; Halliday *et al*., 2015).

The T_b of ectotherms is primarily determined by the temperature of the surrounding environment, which can vary markedly through space and time (Huey & Stevenson, 1979; Huey & Kingsolver, 1989; Angilletta *et al*., 2002). Despite this variation in operative environmental temperatures (T_e: the T_b a non-thermoregulating animal would experience), ectotherms are able to maintain T_b that is closer to T_o, and within a narrower range than T_e, through behaviour (Huey & Stevenson, 1979; Seebacher & Franklin, 2005). Shuttling between hot and cold microhabitats, controlling body posture and regulating activity times are common behavioural mechanisms used for temperature regulation by reptiles (Cowles & Bogert, 1944; Stevenson, Peterson & Tsuji, 1985; Adolph, 1990). Behavioural thermoregulation helps to buffer the thermal heterogeneity of the environment (Angilletta, 2009).

The extent to which reptiles regulate T_b varies across species and environments. Thermoregulatory strategies range from thermoconformity (Ruibal, 1961), where the organism does not thermoregulate and T_b matches T_e, to perfect thermoregulation where behaviour is used to adjust T_b within a very narrow range of temperatures (Adolph, 1990). The variation both within and between species in thermoregulatory strategies is assumed to be related to the associated costs and benefits of thermoregulation (Huey & Slatkin, 1976). The main benefit of thermoregulation is to increase organismal performance (Huey

& Slatkin, 1976). The main costs of thermoregulation are energy and time loss because energy and time spent thermoregulating or waiting for conditions that allow thermoregulation are unavailable for other important activities such as foraging and mating. Thermoregulation could also make lizards more susceptible to predation because it usually requires exposure (Huey, 1974). The cost–benefit model of thermoregulation (Huey & Slatkin, 1976) predicts that as the costs of thermoregulation increase, thermoregulatory effort should decrease. Interestingly, a recent mathematical formalization of Huey & Slatkin's (1976) conceptual and graphical model confirmed that its general predictions are upheld, but that perfect thermoregulation is never an optimal strategy and that under certain conditions thermoregulation may increase when costs increase (Alford & Lutterschmidt, 2018).

Different environments pose different challenges to a thermoregulating organism. The thermal quality (d_e) of an environment directly affects how much time and energy must be expended to maintain T_b within the preferred temperature range of a species (T_{set}). A habitat of low thermal quality is one where T_e is far from T_{set}, making it more difficult to maintain an optimal T_b (Hertz, Huey & Stevenson, 1993). Recent work has indicated that the cost of thermoregulation depends not only on how far, on average, T_e is from T_{set}, but also on the spatial arrangement of available T_e (Sears *et al*., 2019). For a given mean T_e, thermoregulation is more costly when thermal resources are clumped rather than dispersed (Sears & Angilletta, 2015; Sears *et al*., 2016). Under Huey & Slatkin's (1976) cost–benefit model of thermoregulation, thermoconformity is expected in habitats of low thermal quality where the costs of thermoregulation are high. It has also been argued that thermoconformity may be widespread in species that live in tropical areas (Ruibal, 1961; Shine & Lambeck, 1985; Shine & Madsen, 1996; Kapsalas *et al*., 2018). Tropical reptiles are exposed to environmental temperatures that are less variable daily and seasonally and almost always near their T_{set} so they can maintain an optimal T_b without incurring significant costs. Under these conditions, optimal body temperatures are still important, but regulating temperature requires so little effort that this regulation is unimportant (Shine & Madsen, 1996), and so, thermoconformity is the adopted strategy.

Most data on reptilian thermoregulation have been collected from temperate-zone lizards (Schall & Pianka, 1978; Blouin-Demers & Nadeau, 2005; Pianka *et al*., 2017; Ortega & Martín-Vallejo, 2019) that are small-bodied and experience wide daily and seasonal fluctuations in T_e. In this type of environment, a lizard must invest considerable time and effort into thermoregulation if it is to maintain a high and stable T_b (Cowles & Bogert, 1944). Support for the central prediction of Huey & Slatkin's (1976) cost–benefit model of thermoregulation has come from species that live in environments where maintaining T_b close to T_o is relatively inexpensive in terms of time and energy (Huey & Webster, 1976; Hertz & Huey, 1981; Hertz *et al*., 1993). Studies on temperate-zone reptiles, however, have contradicted this central prediction of the cost–benefit model of thermoregulation (Burns, 1970; Brown & Weatherhead, 2000; Blouin-Demers & Weatherhead, 2002; Row & Blouin-Demers, 2006; Edwards & Blouin-Demers, 2007; Aguado & Braña, 2014) and so have some experimental studies (Basson *et al*., 2016). In addition, an extension of Huey & Slatkin's (1976) cost–benefit model to include high-temperature environments concluded that lizards should increase thermoregulatory effort as thermal quality declines (Vickers *et al*., 2011). It may be that the physiological disadvantages of thermoconforming are very low in environments where T_e is close to T_{set} because even without thermoregulation T_b is close to T_o (Blouin-Demers & Nadeau, 2005). In environments where T_e is far from T_{set}, however, the cost of thermoconformity might be more important because it would result in T_b very far from T_o, yielding poor performance and may thus force species in more challenging habitats to thermoregulate more carefully despite the high costs (Blouin-Demers & Nadeau, 2005).

Evidently, cold environments are particularly challenging for reptiles because thermal constraints have direct effects on performance and activity (Lourdais *et al*., 2013; Bouazza *et al*., 2016; Ortega, Mencía & Pérez-Mellado, 2016). Correspondingly, at high latitudes and elevations, thermal constraints are highest (Addo-Bediako, Chown & Gaston, 2002) resulting in low thermal quality (Patterson, 2018). High elevations give rise to short reproductive seasons, frequent storms and extreme weather compared to lower elevations (Körner, 2007). There are fewer species adapted to live in thermally challenging environments (Blouin-Demers & Weatherhead, 2001; Herczeg, 2006; Besson & Cree, 2010; Lourdais *et al*., 2013; Bouazza *et al*., 2016; Ortega *et al*., 2016). Previous studies on lizard thermoregulation across elevational gradients have indicated that T_b decreases (Diaz de la Vega-Pérez *et al*., 2019; Gilbert & Miles, 2019; Senior *et al*., 2019) or remains unchanged (Burns, 1970; Zamora-Camacho, Reguera & Moreno-Rueda, 2016) with elevation despite the decrease in ambient temperature, but these studies were conducted on few populations or across narrow elevational gradients, thus limiting inferential power and representativity. Behavioural thermoregulation in harsh environments, although costly, may be required to buffer against the impact of temperature variation (Huey, Hertz & Sinervo, 2003; Basson *et al*., 2016) and extreme temperatures (Vickers *et al*., 2011; Woods, Dillon & Pincebourde, 2015) on performance, but to further our understanding of how investment in thermoregulation changes with thermal quality, we must look at several populations facing a gradient of thermal environments.

We studied ten populations of Yarrow's spiny lizards (*Sceloporus jarrovii*) on talus slopes across an elevational gradient of 1100 m in the Chiricahua Mountains of southeastern Arizona, USA (Fig. S1), to investigate the relationship between investment in thermoregulation and elevation. *S. jarrovii* is an ideal study species because it is abundant in rocky habitats and can be found along a wide elevational gradient of approximately 1500–2800 m (Ellis-Quinn & Simon, 1991). Talus slopes provide a structurally homogenous habitat for comparison across an elevational gradient (Fig. S2). In other habitats, vegetation changes with elevation, likely affecting the thermal quality and consequently the thermoregulatory opportunities (Lara-Reséndiz *et al*., 2014).

We tested the hypothesis that the thermal quality of an environment dictates investment in thermoregulation. Specifically,

we tested the central prediction of Huey & Slatkin's (1976) cost–benefit model of thermoregulation that lizards living in thermally superior habitats (at lower elevations in our study) should invest more in thermoregulation, keeping in mind that empirical data (e.g. Blouin-Demers & Nadeau, 2005) and recent extensions of the model (e.g. Vickers *et al*., 2011) contradict this central prediction.

Materials and methods

Study species and sites

The Yarrow's spiny lizard (*Sceloporus jarrovii*) is a moderate-sized (mean snout-vent length = 9.7 cm, Cox & John-Alder, 2007), heliothermic (gains heat from the sun) lizard that feeds on arthropods (Simon, 1975) and whose range spans from southeastern Arizona to northern Mexico (Ballinger, 1979). *S. jarrovii* is viviparous and breeds in fall, while birth occurs in spring and early summer. We collected data from ten populations living on talus slopes, ranging in elevation from 1634 m to 2700 m, within the Chiricahua Mountains of southeastern Arizona, USA (Figs. S1 and S2). From 2 May to 23 July 2017, a period encompassing the full range of temperature variation during the active season, we systematically alternated our visits between sites of high and low elevation to control for the seasonal changes in ambient temperature at different elevations across the study period. We visited sites for 3-day periods (referred to as a capture session) and then returned to the same site for a second capture session within 14–17 days. Four sites were visited for a third capture session to increase the sample sizes.

Field sampling

Each day, we caught lizards (510 individual lizards and a total of 1020 lizards captures, Table S1) by rod and lasso during their active period. The capture location of each lizard was marked with a hand-held GPS unit (accuracy ± 3 m), and individuals were released at their capture location the same day.

Lizards were uniquely marked with a felt tip marker on the head and stomach (Jones & Ferguson, 1980; Simon & Bissinger, 1983). The sex of each lizard (185 males and 325 females) was determined based on the presence (males) or absence (females) of enlarged post-anal scales, body size (Cox, 2006; Gilbert & Lattanzio, 2016) and colouration. Snout-vent length (SVL) was measured with digital calipers (±0.1 mm). Lizards were weighed with a digital scale (±0.01 g) to aid in determining reproductive status of females, as pregnant females of this species maintain a lower T_b in the field, presumably to speed embryo development (Beuchat & Ellner, 1987). In addition, we gently palpated the abdomen of females to determine whether or not they were pregnant.

Field active body temperature (T_b)

Immediately after a lizard was captured, we measured skin surface temperature (T_{sk}; n = 1020) 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 (Marler & Moore, 1991; Langkilde & Shine, 2006). Validation studies have indicated that T_{sk} gives an accurate estimate of cloacal temperature in small lizards (Herczeg, 2006; Hare, Whitworth & Cree, 2007; Besson & Cree, 2010; Carretero, 2012; Bouazza *et al*., 2016), including *S. jarrovii* (Beal, Lattanzio & Miles, 2014; Gilbert & Lattanzio, 2016). To measure T_{sk}, we used the procedure described in Andrews (2008) and 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. We used T_{sk} as a proxy for T_b.

Preferred body temperature range (T_{set})

T_{set} 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 (Huey, 1991; Hertz *et al*., 1993). T_{set} is assumed to include the optimal temperature for performance and is a highly conserved trait of a species (Angilletta & Werner, 1998). We used the T_{set} range for adult *S. jarrovii* (30.4–33.2 °C) from the same populations calculated by Patterson (2018) as the central 50% (25th–75th quartiles) of selected body temperatures in a laboratory thermal gradient. This T_{set} range is consistent with previous studies on *S. jarrovii* (Beal, Lattanzio & Miles, 2014; Gilbert & Lattanzio, 2016) and other species within the genus *Sceloporus* (Sartorius *et al*., 2002; Schuler, Sears & Angilletta, 2011; Lara-Reséndiz *et al*., 2014; Table S2).

Operative environmental temperature (T_e)

T_e represents the equilibrium temperature of an inanimate object (one lacking physiological or behavioural controls) with the same thermal characteristics as the study animals. The random distribution of T_e in a habitat describes the null distribution of T_b expected in non-thermoregulating animals (Bakken, 1992; Hertz *et al*., 1993). We used cylindrical copper models painted grey to approximate the reflectance of *S. jarrovii* (Shine & Kearney, 2001), and iButton (±0.5 °C) temperature data loggers (Thermochron iButton DIS1921G-F5) were placed inside to record T_e every minute. These models were validated by Patterson (2018), and the correlation between lizard and model temperatures was very high (R^2 = 0.98). Each sampling day at each site, three models were deployed; one in each of the three primary microhabitats available to *S. jarrovii* living on talus slopes: on a rock in the sun, under a rock and on a rock in the shade. The relatively simple structure of talus slopes, their consistency across elevations and the fine-grain of available microhabitats (Fig. S2) greatly reduce the issues associated with spatial heterogeneity of available thermal resources when assessing habitat thermal quality (Sears & Angilletta, 2015; Vickers & Schwarzkopf, 2016). Models were rearranged randomly each day within the microhabitats to ensure representativity of T_e. We averaged daily T_e from each copper model (3 per day) across 15-min intervals because lizards are mobile

and can readily move between microhabitats (Fig. S2). Consequently, the T_e they experience would likely converge on the mean T_e among the microhabitats rather than equilibrate to the T_e experienced within individual microhabitats (Bakken, 1992; Hertz *et al*., 1993; Seebacher & Shine, 2004).

Thermal quality (d_e)

We used the d_e index proposed by Hertz *et al*. (1993) to measure thermal quality at each site. For each T_e, we calculated a corresponding d_e value. d_e was calculated as the absolute deviation between T_e and the nearest limit of T_{set}. When T_e was above T_{set}, the deviation was measured from the upper bound of T_{set} and from the lower bound of T_{set} when T_e was below T_{set}. When T_e was within T_{set}, d_e was equal to zero.

Accuracy of body temperature (d_b)

We used the d_b index proposed by Hertz *et al*. (1993) to measure the accuracy of body temperature. For each T_b, we calculated a corresponding d_b value. d_b was calculated as the absolute deviation between T_b and the nearest limit of T_{set}. When T_b was above T_{set}, the deviation was measured from the upper bound of T_{set} and from the lower bound of T_{set} when T_b was below T_{set}. When T_b was within T_{set}, d_b was equal to zero.

Effectiveness of thermoregulation (d_e–d_b)

Because our T_e and T_b sampling were not continuous, we used T_e at the time a lizard was captured as a measure of the thermal environment available to the individual. We extracted the mean T_e and corresponding mean d_e for the 15-min time interval during which each individual was captured. Thus, for each of the 1020 T_b collected, there was an associated d_e value. Finally, the effectiveness of thermoregulation was calculated as d_e–d_b (Blouin-Demers & Weatherhead, 2001). In small ectotherms, like *S. jarrovii*, where the heating and cooling rates of the animals and of the physical models are similar, the comparison of d_b and d_e provides a reliable indicator of whether the animals are actively regulating their body temperatures towards T_{set} (Seebacher & Shine, 2004). This index measures the departure from thermoconformity (d_e–d_b = 0) and the investment into thermoregulation: how much closer is the T_b of the animal to T_{set} than is the randomly available T_e. Positive values indicate some degree of thermoregulation, while negative values represent avoidance of thermally favourable habitats.

Data analyses

All data were analysed using R version 3.4.1 (R Core Team, 2017). To determine how thermal quality varied with elevation, we constructed a linear mixed-effects model (LMM) (package: lme4, function: lmer; Bates *et al*., (2014)), including time of day and Julian date as continuous predictor variables and site as a random effect. To test the prediction that lizards living in thermally superior habitats (at low elevation in our study) thermoregulate more effectively, we constructed a LMM for d_e–d_b including elevation as a continuous predictor variable. 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 (male, pregnant female and non-pregnant female) to incorporate reproductive status and to control for sex and reproductive differences in T_b (Mathies & Andrews, 1997). SVL controls for the influence of size on T_b (Gilbert & Lattanzio, 2016). 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 possible site effects, other than elevation.

Results

General thermal ecology

Virtually all lizards (over 98%) were captured while on a rock in the sun. The distribution of T_b and T_e for the active season indicated that *S. jarrovii* tended to select habitats that allowed them to be warmer, on average, than the environment and to avoid extreme temperatures (Table S3). The mean T_b of *S. jarrovii* was higher than the mean T_e (27.8 ± 0.1°C vs. 25.9 ± 0.2°C; Fig. 1, Table S3). T_b was within 1°C of T_{set} for 31% of observations.

Thermal quality and elevation

Throughout the active season, T_e ranged from 1.8°C to 43.8°C (mean of 25.9 ± 5.9°C) and d_e ranged from 0°C to 28.6°C (mean of 5.3 ± 4.9°C) across all 10 study sites. Unsurprisingly, T_e increased with time of day at each site. Mean daily T_e for each hour showed much variation across elevations (Table S3). At low elevation, mean maximum T_e often exceeded T_{set} for ~3 h per day. Minimum daily T_e for each hour rarely reached the lower bound of T_{set} at any elevation. Mean daily T_e within T_{set} per hour decreased as elevation increased, with mean T_e never reaching T_{set} at the highest elevations, indicating the habitat available to lizards was more thermally challenging at high elevations (Fig. 2). Likewise, thermal quality decreased significantly (8°C per 1000 m) with elevation (conditional $R^2 = 0.61$, $F = 9.29$, d.f. = 1, 8, $P = 0.02$; Fig. 3).

Effectiveness of thermoregulation and elevation

Values of the d_e–d_b index ranged from −12.7 to 20.5°C (mean = 3.6 ± 0.1°C).

Males thermoregulated more effectively than females ($t = 2.42$, df = 615, $P = 0.02$); however, the difference was less than one degree (males: 4.0 ± 0.2°C, females: 3.4 ± 0.1°C). The mean d_e–d_b of pregnant females (4.4 ± 0.25°C) was significantly higher than that of non-pregnant females (2.8 ± 0.2°C; $t = 5.22$, df = 446, $P < 0.001$), indicating that

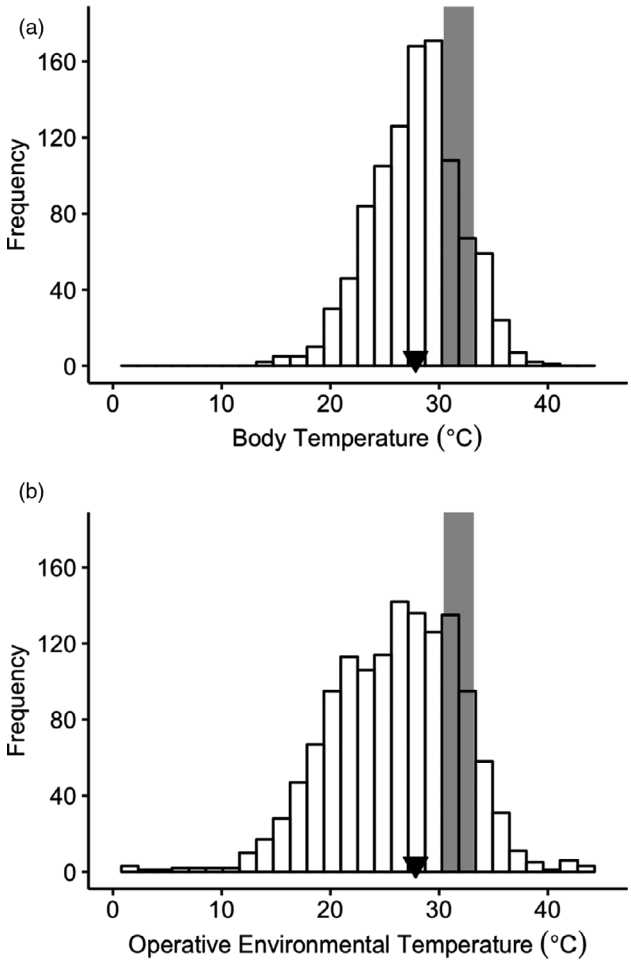

Figure 1 Frequency distributions of (a) the body temperature (T_b) of Yarrow's spiny lizards (*Sceloporus jarrovii*) and of (b) the operative environmental temperatures (T_e) during the daily active period at ten talus slopes from 2 May to 23 July 2017 in the Chiricahua Mountains, Arizona, USA. Shaded bars indicate the preferred temperature range (T_{set}) of the species. Triangles represent the means.

pregnant females thermoregulate more effectively than non-pregnant females. Interestingly, d_e–d_b increased significantly with elevation (conditional $R^2 = 0.38$, $F = 9.13$, d.f. = 1, 8, $P = 0.02$; Fig. 4, Table S4) which is opposite to the central prediction of Huey & Slatkin's (1976) cost–benefit model of thermoregulation.

Discussion

Cold climates are particularly challenging for ectothermic animals because the thermal environment constrains physiological performance and activity (Gvoždík, 2002; Lourdais *et al*., 2013). We demonstrated that the quality of the thermal environment affected investment in thermoregulation by *S. jarrovii*, although in the opposite direction than that predicted by Huey & Slatkin's (1976) cost–benefit model of thermoregulation. Although studies have made comparisons between populations at different latitudes (Ellner & Karasov, 1993; Andrews, 1998) and elevations (Bouazza *et al*., 2016; Trochet *et al*., 2018; Wu *et al*., 2018), the vast majority of studies make comparisons between only two or three populations (e.g. Burns, 1970; Ballinger, 1973; Grant & Dunham, 1990; Diaz, 1997; Olsson & Shine, 2002; Iraeta, Salvador & Díaz, 2013; Diaz de la Vega-Pérez *et al*., 2019; Gilbert & Miles, 2019; Senior *et al*., 2019), thus limiting inferential power and representativity. To the best of our knowledge, our study is the first where lizards were sampled at numerous sites evenly spaced along a wide altitudinal gradient.

At high elevations, d_e was higher, indicative of low thermal quality. Despite these differences in thermal quality, lizards maintained very similar T_b during activity across the elevational gradient, which is consistent with other studies of *Sceloporus* lizards across an elevational range of more than 2500 m (Burns, 1970; Andrews, 1998). During the day, lizards were more effective thermoregulators where thermal quality was lower (high elevation). These results are consistent with those of a global analysis of the effect of thermal quality on thermoregulation of lizards that indicated that poor thermal quality led to higher effectiveness of thermoregulation (Blouin-Demers & Nadeau, 2005), with a mathematical formalization of Huey & Slatkin's (1976) cost–benefit model that indicated that thermoregulatory effort is predicted to increase under certain conditions when thermal quality decreases (Alford & Lutterschmidt, 2018), with an extension of Huey & Slatkin's (1976) cost–benefit model to include high temperatures that also predicted that thermoregulatory effort should increase when thermal quality decreases (Vickers *et al*., 2011), and with experimental manipulations of thermal quality (Basson *et al*., 2016). The explanation Blouin-Demers & Nadeau (2005) proposed was that the physiological disadvantages of thermoconformity are small in thermally benign habitats (high thermal quality) because T_b is close to T_o even in the absence of thermoregulatory behaviour in such habitats. In thermally challenging habitats (low thermal quality), however, an animal that does not thermoregulate will experience T_b far from T_o and thus much reduced performance that may compromise survival. Thus, the high fitness costs associated with thermoconformity in poor thermal quality environments may select for careful thermoregulation in such habitats, contrary to the central prediction of Huey & Slatkin's (1976) cost–benefit model of thermoregulation. Studies of other reptiles at the northern edge of their distribution, where T_e rarely allows for T_o to be achieved, have also shown that reptiles invest more in thermoregulation in poorer thermal quality habitats (Blouin-Demers & Weatherhead, 2001; Row & Blouin-Demers, 2006; Edwards & Blouin-Demers, 2007; Picard, Carrière & Blouin-Demers, 2011; Aguado & Braña, 2014). In montane habitats, the environment is highly variable, and thus, the negative consequences of thermoconformity are high. For example, the mean T_e was 17°C at our highest elevation site, well below the preferred body temperature of *Sceloporus* lizards. If a lizard were to thermoconform to that temperature, performance would be poor and fitness would thus be compromised.

Physical properties of animals such as colouration and size influence thermoregulation and may differ across elevational

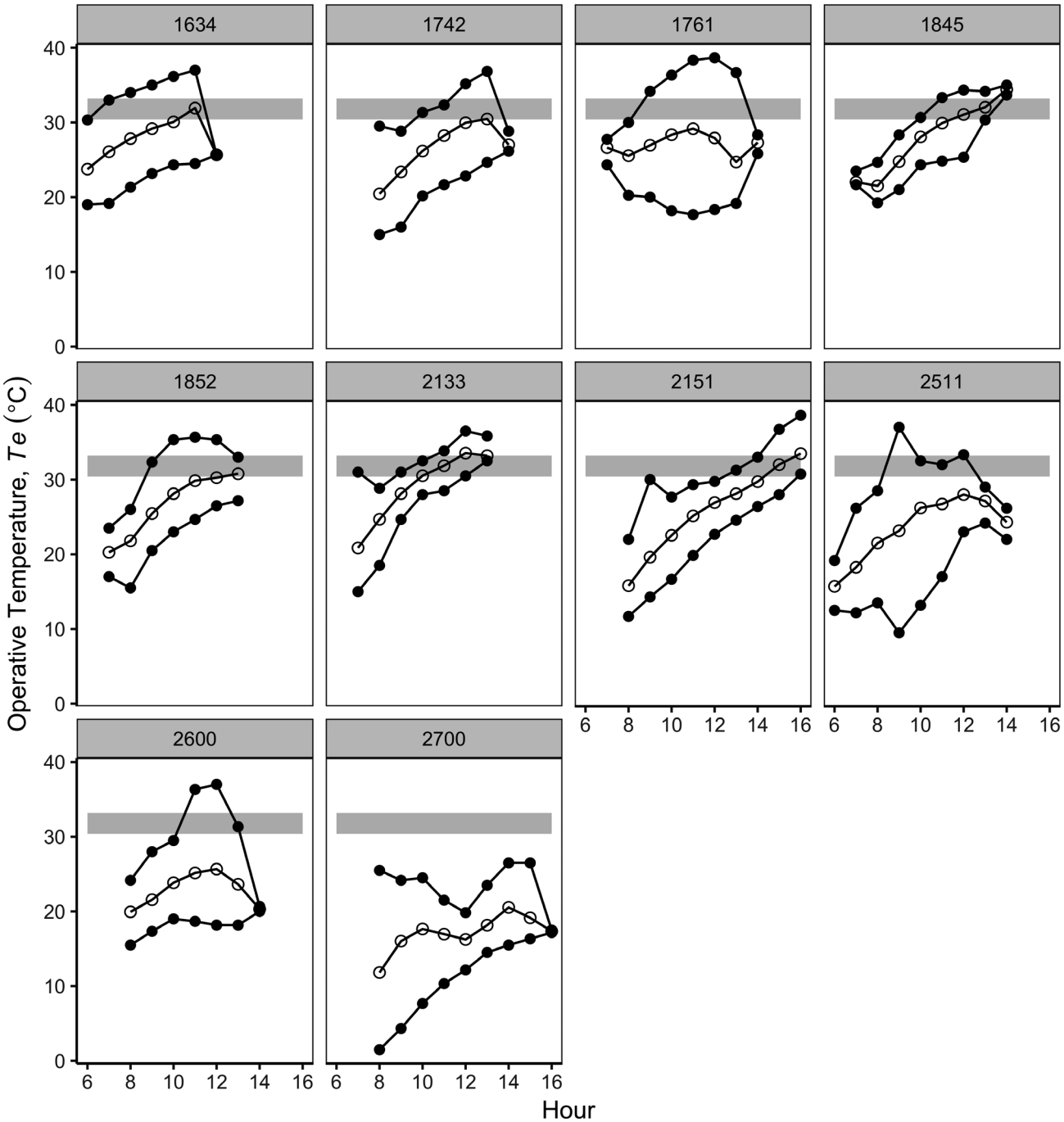

Figure 2 Mean hourly operative environmental temperatures (T_e) during the active season for ten talus slopes in relation to the preferred body temperature (T_{set}, shaded area) of Yarrow's spiny lizards (*Sceloporus jarrovii*) in the Chiricahua Mountains, Arizona, USA. Solid points indicate mean maximum and minimum T_e. Open points indicate the mean T_e. Elevation (in m) is indicated above each plot.

gradients. Some lizards modify their skin colour for heat absorption (Middendorf & Simon, 1988; Bouazza *et al*., 2016). For example, the high-elevation Atlas day gecko (*Quedenfeldtia trachyblepharus*) exhibits darker colouration when air temperatures are low (Bouazza *et al*., 2016). Likewise, the ability of *S. jarrovii* to dramatically change colour has been observed in the field (Middendorf & Simon, 1988; Sherbrooke *et al*., 1994). *S. jarrovii* darken to maximize heat gain until T_o has been achieved, after which they lighten. Body size also influences thermoregulation because larger individuals have higher

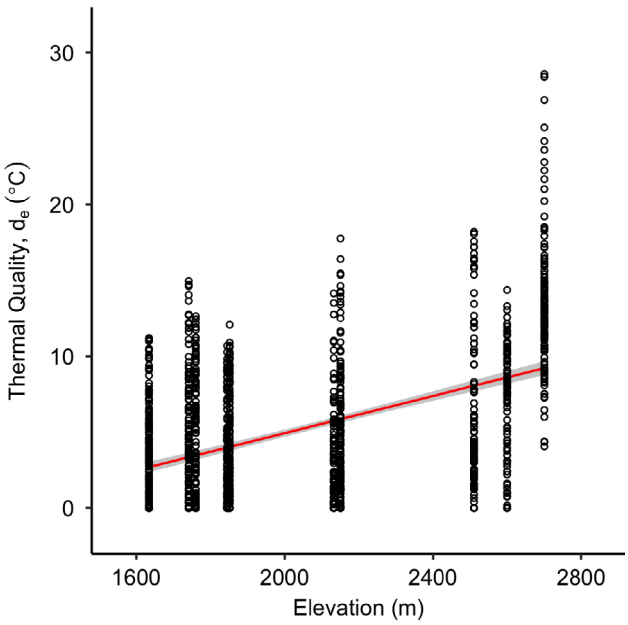

Figure 3 The relationship between thermal quality (d_e) and elevation at ten talus slopes occupied by Yarrow's spiny lizards (*Sceloporus jarrovii*) in the Chiricahua Mountains, Arizona, USA. Thermal quality decreases as elevation increases. Overlaid regression line in red and 95 % confidence interval in grey. [Colour figure can be viewed at wileyonlinelibrary.com]

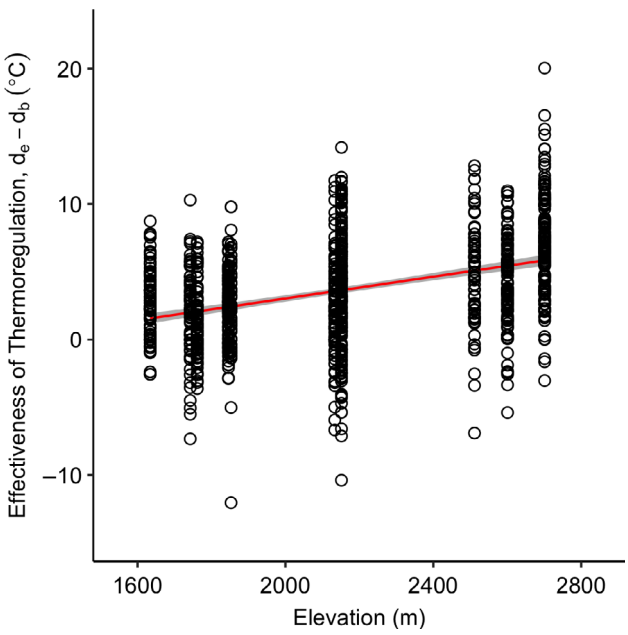

Figure 4 The relationship between the effectiveness of thermoregulation (d_e–d_b) and elevation at ten talus slopes occupied by Yarrow's spiny lizards (*Sceloporus jarrovii*) in the Chiricahua Mountains, Arizona, USA. Overlaid regression line in red and 95% confidence interval in grey. [Colour figure can be viewed at wileyonlinelibrary.com]

heat capacities and dissipate heat more slowly. Differences in body size of *Psammodromus algirus* at higher elevations result in a slower cooling rate (Zamora-Camacho *et al*., 2016). Body size of *S. jarrovii* increases with elevation (Ballinger, 1973; Patterson, 2018), probably because larger lizards have higher chances of surviving the colder winters of high elevations (Zani, 2008).

Although thermal quality is an important cost of thermoregulation and is one that varies considerably along an elevational gradient, we acknowledge that there may be other costs that affect thermoregulation in *S. jarrovii*. For instance, differences in predation risk affect thermoregulation; male common lizards (*Zootoca vivipara*) respond to predator scent simulated in the laboratory by decreasing their accuracy of thermoregulation (Herczeg *et al*., 2008) demonstrating that costs with immediate effects on fitness (i.e. survival or future reproduction) can override the benefits of optimized physiological performance accomplished by accurate thermoregulation (Herczeg, 2006; Herczeg *et al*., 2008). If predation risk is influencing lizard thermoregulation, the effect cannot be separated from the direct effect of thermal quality of the habitat, unless predation risk is quantified. At low elevations, there are more documented predators of *S. jarrovii* (Ballinger, 1973), and thus, spending time thermoregulating may have greater mortality costs than at higher elevations resulting in less investment in thermoregulation. In our study, the number of lizards with autotomized tails, a proxy for predation risk (Patterson, 2018), was not higher at low elevations. We note that autotomized tails only show the proportion of lizards that survived encounters with predators and is thus an imperfect proxy for predation risk. Lizards in highly productive environments may also have more time available for thermoregulation (Pianka & Pianka, 1970). However, Patterson (2018) did not detect a relationship between food availability for *S. jarrovii* and elevation over a three-year period in the same populations. In addition, for *S. jarrovii* it is unlikely that food availability affects thermoregulation because they are sit-and-wait predators (Simon, 1975), thus thermoregulation and foraging can probably be done simultaneously.

In lizards, the mechanism underlying variation in thermoregulatory behaviour has long been assumed to be phenotypic plasticity (Cowles & Bogert, 1944; Huey *et al*., 2003; Buckley *et al*., 2015). To maintain preferred body temperatures across a range of environmental conditions, lizard populations vary behaviours directly associated with thermoregulation such as microhabitat use, timing of activity and basking frequency (Huey & Webster, 1976; Huey *et al*., 2003). Using reciprocal transplant experiments, different behaviours associated with thermoregulation have been found to be phenotypically plastic such as perch height in *Sceloporus* lizards (Adolph, 1990) and light-use in short-horned lizards (*Phrynosoma herandesi*; Refsnider *et al*., 2018). This plasticity can help buffer a species from climate change in the short-term (Kearney *et al*., 2009; Huey *et al*., 2012), but confers a risk of extinction over the long-term. For example, avoiding exposed and sunny microhabitats during the hottest periods of the day may provide a buffer from the selective pressures imposed by these hotter microhabitats. Recent work has suggested that evolutionary adaption may promote

long-term persistence of lizards in altered thermal environments (Gilbert & Miles, 2019). Using reciprocal transplant experiments would help determine whether effectiveness of thermoregulation is a phenotypically plastic trait or one that has a genetic basis in *S. jarrovii*. This would also help shed light on the ability of this species to cope with decreased activity times imposed by climate warming.

In conclusion, we found that *S. jarrovii* thermoregulate more effectively in habitats of poorer thermal quality at high elevations, which is opposite to the central prediction of Huey & Slatkin's (1976) cost–benefit model of thermoregulation, but consistent with recent empirical data (e.g. Blouin-Demers & Nadeau, 2005) and theoretical advances (e.g. Vickers *et al*., 2011; Alford & Lutterschmidt, 2018). Across an elevational gradient where the costs of thermoregulation become higher with increasing elevation, it appears that the disadvantages associated with thermoconformity when thermal quality is low are more important in influencing investment into thermoregulation than the costs incurred for thermoregulation by *S. jarrovii*. Future studies should use telemetry or implanted data loggers to measure body temperatures continuously and explore in more detail daily and seasonal variation in thermoregulation across an elevational gradient both when lizards are active on the surface and inactive under rocks.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Number of individual Yarrow's spiny lizards (*Sceloporus jarrovii*) captured from ten talus slopes within the Chiricahua Mountains, Arizona, USA. Total number of captures in parentheses.

Table S2. Preferred body temperatures (T_{set}) selected in a laboratory thermal gradient by lizards from the genus *Sceloporus*. Any experimental conditions are noted.

Table S3. Mean (±1 SE), minimum, and maximum operative environmental temperatures (T_e, °C), mean and maximum thermal quality (d_e, °C), percentage of T_e within T_{set}, and mean, minimum, and maximum body temperatures (T_b, °C) recorded at ten talus slopes across an elevational gradient within the Chiricahua Mountains, Arizona, USA occupied by Yarrow's spiny lizards (*Sceloporus jarrovii*).

Table S4. Estimates and 95 % confidence intervals (CI) from the linear mixed-effects model of the index of effectiveness of thermoregulation (d_e–d_b) of Yarrow's spiny lizards (*Sceloporus jarrovii*) at ten talus slopes in the Chiricahua Mountains, Arizona, USA. The fixed effects include elevation, snout-vent length (SVL), sex, time of day, and Julian date. The random effects include lizard ID nested in site. Fixed effects with CI that do not include zero are bolded.

Figure S1. Location of study sites on talus slopes (n = 10) located within six canyons spanning an elevational gradient of 1700 to 2700 m in the Chiricahua Mountains, Arizona, USA.

Figure S2. Typical talus slope (n = 10) studied within six canyons spanning an elevational gradient of 1700 to 2700 m in the Chiricahua Mountains, Arizona, USA.