Differences in thermal quality affect investment in thermoregulation by lizards

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Abstract

Body temperature affects physiological processes and, consequently, has 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 is a major cost of thermoregulation because it directly affects the time and energy that must be invested by an individual to achieve and maintain an optimal body temperature for performance. According to the cost-benefit model of thermoregulation, lizards should only thermoregulate when the benefits outweigh the costs of doing so. Thus, in habitats of poor thermal quality, individuals should thermoregulate less. Using two systems, an elevational gradient and a pair of habitats that vary in the amount of solar radiation they receive, I tested the hypothesis that investment in thermoregulation by lizards is dictated by the associated costs of thermoregulating. Temperature, and thus thermal quality, decreases with elevation. I found a significant positive relationship between elevation and effectiveness of thermoregulation of Yarrow's spiny lizards (*Sceloporus jarrovii*). When comparing thermoregulation of ornate tree lizards (*Urosaurus ornatus*) living in the thermally superior open-canopy wash habitat or the closed-canopy upland habitat, I found that habitat type was a significant predictor of accuracy of body temperature. In the poorer quality habitat, lizards had smaller deviations of body temperature from their preferred temperature range. Overall, I conclude that the thermal quality of a lizards' environment impacts their thermoregulation in the opposite direction than predicted by the cost-benefit model of thermoregulation. This suggests that the disadvantages of thermoconformity may be greater than the costs thermoregulating as habitats become more thermally challenging.

Resumé

La température corporelle affecte les processus physiologiques et, donc, l'aptitude. Les lézards doivent ajuster leur comportement de thermorégulation pour maintenir une température corporelle qui maximise leur performance. Cependant, il y a des coûts associés à la thermorégulation. Ces coûts peuvent être influencés par la qualité thermique d'un environnement en affectant directement le temps et l'énergie qu'un individu doit investir pour obtenir et maintenir une température corporelle qui favorise la performance. Selon le modèle coût-bénéfice de la thermorégulation, les lézards devraient réguler leur température seulement lorsque les bénéfices surpassent les coûts associés. Ainsi, dans les habitats de faible qualité thermique, les individus devraient moins investir dans la thermorégulation. Dans deux systèmes, un gradient altitudinal et des paires d'habitats qui ne reçoivent pas la même radiation solaire, j'ai testé l'hypothèse que l'investissement en thermorégulation dépend des coûts associés à la thermorégulation. La température, et donc la qualité thermique, diminue avec l'altitude. J'ai identifié une relation positive significative entre l'altitude et l'efficacité de la thermorégulation chez le lézard épineux de Yarrow (*Sceloporus jarrovii*). En comparant la thermorégulation du lézard arboricole orné (*Urosaurus ornatus*) entre un habitat sans canopée de qualité thermique élevée et un habitat avec canopée fermée, j'ai observé que le type d'habitat était un prédicteur significatif de la température corporelle. Dans l'habitat de plus faible qualité, la température corporelle des lézards variait très peu de la gamme de températures préférées. Je conclus donc que l'effet de la qualité thermique de l'environnement sur le comportement de thermorégulation des lézards identifié dans cette étude est à l'opposé de la prédiction du modèle coût-bénéfice de la thermorégulation. Ceci suggère que les désavantages de la conformité thermique semblent être plus élevés que les coûts liés à la thermorégulation lorsque les habitats sont de faible qualité thermique.

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~Enjoy the journey~

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Tb	body temperature
To	optimal body temperature
Tset	preferred body temperature range
Te	operative environmental temperature
de	thermal quality measured as the absolute deviation between *Te* and *Tset*
db	accuracy of Tb measured as the absolute deviation between *Tb* and *Tset*
de-db	index of effectiveness of thermoregulation
Ex	thermal exploitation index
CT min	critical thermal minimum
CT max	critical thermal maximum
UID	unique lizard identification
SVL	snout-vent length
Tsk	skin surface temperature
IRT	infrared laser thermometer
LMM	linear mixed-effects model
CI	confidence interval

General Introduction

Body temperature (*Tb*; Table 1-1) has a significant impact on organismal performance (e.g. the ability to run, feed and interact socially; Huey and Stevenson 1979) and consequently has a large effect on fitness (Christian and Tracy 1981, Huey and Kingsolver 1989). The ability to maintain a *Tb* within an optimal (*To*; Table 1-1) and often narrow range allows animals to achieve maximum performance (Angilletta 2001). A *Tb* outside of the optimal range has negative effects on proximate measures of fitness such as locomotion, food acquisition (Zhang and Ji 2004) and predator avoidance (Huey and Kingsolver 1989) as well as impacts on more ultimate measures of fitness, such as reproductive output (Halliday et al. 2015b).

Endotherm and ectotherm are terms used to broadly categorize animals based on how they regulate *Tb*. Endotherms maintain a high and constant *Tb* through metabolic heat production (Seebacher and Franklin 2005). It requires a large amount of energy to regulate and maintain internal thermal conditions and processes over a wide range of environmental temperatures (Bennett and Ruben 1979). Endotherms generally maintain a higher *Tb* than their environments which allows them to be active under a broad range of conditions. In contrast, ectotherms have negligible metabolic heat generation (Huey and Kingsolver 1989). Because of this low metabolic rate, ectotherms have limited physiological control over their *Tb* and are thus dependent on other mechanisms of temperature regulation (Bennett 1980; Huey and Kingsolver 1989).

Thermoregulation is any active regulatory process (behavioural and or/physiological) that functions to maintain *Tb* as close as possible to a preferred temperature range (*Tset*; Table 1-1) which includes the optimal *Tb* for performance (Hertz et al. 1993). Although fluctuations in the thermal environment can alter an ectotherm's *Tb*, the potential impact of those fluctuations on performance can be buffered by behavioural thermoregulation that enables ectotherms to avoid extreme temperatures and to be active at *Tb* that enhances performance (Huey and Stevenson 1979, Huey 1982, Huey and Kingsolver 1989). Shuttling between shade and sun or hot and cold microhabitats (Cowles and Bogert 1944), changing posture to maximize surface-area-to-volume ratio for heat exchange (Huey 1974), and regulating activity times (Stevenson et al. 1985) are common behavioural adjustments made by reptiles to achieve *Tb* close to *Tset*. In addition, slight physiological responses, for instance regulation of peripheral blood flow, improve the efficiency of these behavioural mechanisms by modifying the rate at which *Tb* may change during a particular behavioural strategy (reviewed in Seebacher and Franklin 2005).

The extent of thermoregulation varies by species and environment. There is a continuum of thermoregulatory strategies that range from thermoconformity to perfect thermoregulation. An individual is considered a thermoconformer when its *Tb* matches the operative temperature (*Te*; Table 1-1) measured throughout the environment (Ruibal 1961). Perfect thermoregulation is achieved when an individual is able to maintain *Tb* within *Tset* across a range of *Te*. Huey and Slatkin (1976) developed the cost-benefit model of lizard thermoregulation to explain the differences in thermoregulatory strategies used both between and within species. The mathematical model assumes that the extent of thermoregulation is adjusted to maximize net energy gain. The model evaluates the optimal extent of thermoregulation as the benefits of thermoregulation subtracted from the costs of thermoregulation during some specified period of time (Huey and Slatkin 1976), Originally designed for lizards, this model has been applied to a wide variety of reptilian species (turtles: Edwards and Blouin-Demers 2007, Picard et al. 2011; snakes: Row and Blouin-Demers 2006, Blouin-Demers and Weatherhead 2001, Lourdais et al. 2013). This model recognizes that the maintenance of a particular *Tb* by a reptile generally involves both a benefit (e.g. increased performance) and a cost (in time, energy, or risk). Thus, precise thermoregulation should be demonstrated only when the benefits exceed the costs.

Thermoconformity should be the expected strategy in circumstances where thermoregulatory behaviour would impose such high costs to the organism that precise thermoregulation is not worthwhile (Huey and Slatkin 1976).

The costs and benefits of thermoregulation are complex and need not be mutually exclusive. The relationship between temperature and performance is described by a gradual increase in performance as *Tb* increases to *To* (Figure 1-1) followed by a rapid decline as *Tb* surpasses *To* (Huey and Kingsolver 1989). Performance peaks within a narrow range of temperatures, often close to the species preferred temperature range (*Tset*) (Hertz et al. 1993, Angilletta 2001). Temperatures below or above *To* result in decreased proximate (Angilletta 2001, Zhang and Ji 2004, Fernández and Ibargüengoytía 2012) and ultimate measures (Halliday et al. 2015a) of fitness. Consequently, the main benefit of thermoregulation is increased fitness via increased performance as it allows for the maintenance of *Tb* close to *Tset*. Intuitively, there are also costs of thermoregulating that are mainly associated with missed opportunities. The time and energy spent thermoregulating cannot be spent on other important activities such as foraging, territory defense, and subsequent mating (Huey 1974). Energetic costs of thermoregulating become prominent in heterogenous landscapes where the distance to travel between suitable microhabitats is great (Basson et al. 2016, Sears et al. 2016). In addition, thermoregulating may also increase conspicuousness to and encounter rate with predators (Huey 1982). Therefore, the trade-off between these costs and benefits of thermoregulation should dictate the extent to which an organism thermoregulates.

Even though reptiles use behavioural thermoregulation to compensate for unsuitable habitats, their success depends on the availability of suitable thermal microhabitats (Huey and Slatkin 1976, Sears et al. 2016). The thermal quality (*de*; Table 1-1) of a habitat determines how far *Te* is from the species *Tset* (Hertz et al. 1993). From a reptile's perspective a habitat of high thermal quality is one in which the reptile can easily maintain its *Tb* within its *Tset*. In habitats of low thermal quality more time and energy must be expended to attain a *Tb* close to *Tset*. Consequently, there is an energetic cost associated with living in habitats where *Te* is far from *Tset* (low thermal quality) as reptiles will need to devote more time and energy to maintaining *Tb* within *Tset*. Reptiles prefer habitats of higher thermal quality (Row and Blouin-Demers 2006, Picard et al. 2011, Halliday and Blouin-Demers 2016, Paterson and Blouin-Demers 2018) and there are fitness costs associated with low thermal quality habitats (locomotor performance: Blouin-Demers and Weatherhead 2008, growth rate: Besson and Cree 2010, Brewster et al. 2013, Patterson et al. 2017, reproductive success: Halliday and Blouin-Demers 2016). Therefore, according to the cost-benefit model of thermoregulation, a reptile should invest more in thermoregulation when the habitat thermal quality is high because the associated costs are lower than those in habitats of poor thermal quality.

Most data on reptilian thermoregulation are from studies of temperate-zone reptiles, especially small diurnal lizards living in areas such as deserts, where the range of environmental temperatures means that a lizard must allocate considerable time and effort to thermoregulation if it is to maintain a high and stable *Tb*. However, for the majority of reptile species, which are found in the tropics (see Schall and Pianka 1978), temperature regulation may be unimportant (Shine and Madsen 1996, Kapsalas et al. 2018). For water pythons (*Liasis fuscus*) living in tropical Australia, the thermal environment is so benign that the snakes do not need to expend much time or energy in modifying their *Tb* behaviourally. Water pythons were rarely observed overtly basking, they did not select microhabitats based on temperature, and their activity was maintained year-round (Shine and Madsen 1996). Therefore, if optimal *Tb*'s are always easily attainable, as in the case of water pythons in Australia, without incurring significant costs then thermoregulation may be virtually irrelevant to the day-to-day activities of a reptile.

Literature on the applicability of the cost-benefit model of thermoregulation both in the laboratory and in natural environments is equivocal. Some studies conducted in the laboratory (Withers and Campbell 1985, Herczeg 2006) and in thermally benign environments (Huey and Webster 1976, Hertz and Huey 1981, Hertz et al. 1993, Shine and Madsen 1996) support the predictions of the cost-benefit model. However, studies conducted in temperate environments have found the opposite pattern to the predictions of the model (Blouin-Demers and Weatherhead 2001a, 2002, Row and Blouin-Demers 2006, Edwards and Blouin-Demers 2007, Picard et al. 2011, Brewster et al. 2013). In thermally challenging environments, reptiles invest more in thermoregulation, despite the costs, likely because the disadvantages of thermoconformity are much higher when the thermal quality (*de*) is low than when it is high (Blouin-Demers and Weatherhead 2001a, Blouin-Demers and Nadeau 2005). A comparative study of lizard species at the global scale further support this idea (Blouin-Demers and Nadeau 2005). It indicated that there was either no relationship between *de* and thermoregulation or that there was more investment in thermoregulation in habitats of lower *de*. The cost-benefit model of thermoregulation was designed as a within species test, so the authors suggested that a more appropriate test of the model would be to quantify investment in thermoregulation of a given species when exposed to habitats of different thermal qualities.

Numerous indices that are used to measure the extent of thermoregulation have been developed and modified throughout the years. Originally, thermoregulation was extrapolated from frequency distributions of field active *Tb* and ambient temperature (Cowles and Bogert 1944). Heath (1964) presented evidence that any object, even a beer can, may appear to thermoregulate if thermal mass is not considered. Eventually, Hertz et al. (1993) accounted for thermal mass and included the notion that an organism has a thermal goal (set point range, *Tset*) and is not just trying to be different from the environment. Hertz et al. (1993) stressed the importance of three variables: set point range (*Tset*), field active body temperatures (*Tb*), and operative environmental temperature (*Te*). *Tset* is measured in a laboratory thermal gradient in the absence of any costs. Field active *Tb* is recorded with implanted loggers, cloacal probes, or infrared laser thermometers. *Te* is typically measured by physical models of the study animals and represent the temperature that a non-thermoregulating organism would experience within its environment. These variables are then used to compare the absolute deviations of body or environmental temperature from *Tset*.

The most commonly used measures of thermoregulation are the effectiveness of thermoregulation index (*de-db*; Table 1-1, Blouin-Demers and Weatherhead 2001) and the thermal exploitation index (*Ex*; Table 1-1, Christian and Weavers 1996). The accuracy of body temperature (*db*; Table 1-1, Hertz et al. 1993) is the extent to which *Tb* measured in the field matches *Tset*, regardless of whether the animal is actively thermoregulating. *db* is measured as the mean deviation of *Tb* from *Tset*. Thus, a high value of *db* indicates low accuracy of *Tb* because on average *Tb* is far from *Tset*. The thermal quality of the habitat (Hertz et al. 1993) is the extent to which *Te* matches *Tset*. *de* is measured as the absolute deviation between *Te* from *Tset*. A higher value of *de* is indicative of a habitat of lower thermal quality.

The effectiveness of thermoregulation is calculated as the difference between *de* and *db* (*de-db*). This is an open-ended index where thermoconformity has a value of zero, positive values represent thermoregulation, and negative values indicate avoidance of thermally favourable habitats. The magnitude of departure from zero represents the effectiveness of thermoregulation. How an animal exploits (*Ex*) its thermal environment is another index used to quantify thermoregulation (Christian et al. 1996). *Ex* is calculated as the percentage of time when *Tb* is within *Tset* when *Te* indicates that *Tb* within *Tset* can be achieved. The greater the *Ex* value the more the animal exploits the thermal environment when the environment is permissive.

Although these indices are widely used in studies of thermoregulation in various reptilian species, their limiting assumptions warrant further discussion. Typically, *Te* is measured by physical models placed throughout the environment (Hertz et al. 1993), but usually with no consideration of their temporal or spatial structure (Vickers and Schwarzkopf 2016a) despite their importance in thermoregulation (Sears et al. 2011, 2016, Basson et al. 2016, Vickers and Schwarzkopf 2016b). Through spatially explicit models (models that consider spatial distribution of resources), it has been demonstrated that when thermal resources are more dispersed through space, ectotherms thermoregulate more accurately (Sears and Angilletta 2015). In addition, using the absolute deviations (*Tb* from *Tset* and *Te* from *Tset*) assumes that overheating and overcooling are equally costly (Hertz 1993). This is not the case for real organisms (Vickers et al. 2011; Figure 1-1) because performance declines more precipitously above *To* than below. When calculating thermal quality (*de*), it is typically averaged across microhabitats. The major assumptions with this are that (1) organisms use each microhabitat equally, (2) there are no associated costs of travelling between microhabitats, and (3) an organism's *Tb* reaches equilibrium at each site they encounter (Seebacher and Shine 2004). Different models have been developed to accommodate these limitations (individual-based null model: Vickers and Schwarzkopf 2016, individual-based spatially explicit model: Sears et al. 2011, Basson et al. 2016, Sears et al. 2016) but these more complex models have been applied mostly to simulations and controlled laboratory settings.

It is argued that a successful theory of thermoregulation is one that considers the abundance and distribution of thermal resources in space (Angilletta 2009), but using these models in the field is challenging. Spatially explicit models account for the spatial heterogeneity and structure of a habitat which influences whether an organism can maintain *Tb* within *Tset* and the cost it incurs in doing so (Angilletta 2009, Sears and Angilletta 2015, Sears et al. 2016). Although these models may be ideal, the applicability of spatially explicit models to natural environments is limited. Making conclusions about whether a resource, for example, a particular microhabitat is used above, in proportion to, or below its availability is dependent on various components that the researcher deems as available to the animal (Johnson 1980). Secondly, for these spatially explicit models to be used in a real, complex, natural landscape one must be able to accurately sample every nuance of the environment and its relative availability from an organism's perspective. Many temperate-zone lizards spend most of the day under rocks or in other retreats (Huey 1982) and depending on the thermal properties of their retreat site they may experience very different *Te* from those associated with above ground activity (Christian et al. 1984, Peterson 1987). Sampling retreats, however, is difficult, especially for small-bodied ectotherms that can use equally as small retreats (e.g. under bark or leaf litter). Finally, spatial heterogeneity is more important to the thermoregulatory performance of larger organisms, because small animals, such as small lizards, can reach equilibrium with their environment rapidly (Bell 1980) and most movements result in thermal changes (Christian and Tracy 1981, Christian et al. 2006). Although spatially explicit approaches are great in theory and would more accurately represent the true costs of thermoregulation, there are major hurdles in applying them to field studies in complex habitats.

Objective

The goal of my thesis was to test the hypothesis that investment in thermoregulation by lizards is dictated by the associated costs. I tested this hypothesis with two study systems and used the predictions made from the cost-benefit model of lizard thermoregulation. For chapter one, I used ten populations of Yarrow's spiny lizards (*Sceloporus jarrovii*) occupying talus slopes along a wide elevational gradient. Consistent with the cost-benefit model of thermoregulation, I predicted that as elevation increases, and thermal quality decreases, lizards would invest less in thermoregulation. For chapter two, I used two habitat types, both occupied by the ornate tree lizard (*Urosaurus ornatus*), that were adjacent to one another yet they differed in the amount of solar radiation they receive and thus their thermal quality. I predicted that lizards would invest less in thermoregulation in the habitat with low thermal quality than in the habitat with higher thermal quality.

Significance

Unfortunately, rapid warming of environments has and will continue to have considerable impacts on biodiversity (Walther et al. 2002). To cope with this changing World, organisms have primarily used behavioural strategies to shift habitats over space and time (Bradshaw and Holzapfel 2006, Sinervo et al. 2010, Harley 2011). Although in a warming World organisms may be able to more readily reach body temperatures that promote physiological performance, excessive temperatures will constrain thermoregulation by limiting activity times. Sinervo et al. (2010) found that local extinction of lizards has already begun due to the impact of thermal constraints on activity time resulting in decreased foraging ability. They projected that by 2080 over 40 % of lizard species in Mexico will go extinct (Sinervo et al. 2010).

Thermal quality will change as environments continue to experience effects of anthropogenic warming. Understanding the impact thermal quality can have on thermoregulation is important in the light of climate change. Monitoring entire ecosystems is time consuming and costly (Shah et al. 2015); however, identifying habitats that can serve as models for climate change impacts at the broader scale can help illuminate global patterns. By studying latitudinal (Mcgraw et al. 2015) and elevational gradients (Bässler et al. 2010, Shah et al. 2015) it is possible to reconstruct the effect of changing climates. Studies across latitudinal gradients are challenging due to the associated costs of time and travel. Elevational gradients show similar habitat and temperature changes, but are more accessible and feasible to study. Climate change has been most rapid at high latitudes and elevations (Sinervo 2010, Shah et al. 2015). Thus, my elevational gradient study will help shed light onto the potential effects of climate change on thermoregulation and my habitat pair study will help shed light onto the ability of terrestrial ectotherms to respond to climate change via behavioural adaptation.

Note to readers:

Both chapters of this thesis have been prepared as manuscripts and content overlaps between them, specifically throughout the introduction and methods sections.

CHAPTER 1

Changes in thermal quality along an elevational gradient affect investment in thermoregulation by Yarrow’s spiny lizards (*Sceloporus jarrovii*)

Introduction

Physiological processes such as locomotor speed, prey capture and growth rate are strongly linked to temperature (Huey 1982, Huey and Kingsolver 1989, Seebacher and Franklin 2005) and are optimized within a narrow range of body temperatures (*Tb*; Table 1-1) (Huey 1982, Huey and Kingsolver 1989, Angilletta et al. 2002). Physiological performance generally increases slowly from the critical thermal minimum (*CT min*) to the optimum body temperature (*To*; Table 1-1) and then decreases rapidly as temperature approaches the critical maximum (*CT max*) (Huey and Stevenson 1979, Angilletta et al. 2002; Figure 1-1). Thus, individuals that can maintain their body temperature (*Tb*) within the optimal range maximize performance and have higher fitness (Huey and Kingsolver 1989, Zhang and Ji 2004, Angilletta 2009, Halliday et al. 2015).

Although maintaining *Tb* within an optimal range is essential for maximizing performance, the *Tb* of ectotherms is primarily determined by the heat obtained from the surrounding environments, which can vary readily through space and time (Huey and Stevenson 1979, Huey and Kingsolver 1989, Angilletta et al. 2002). Despite this variation in operative environmental temperatures (*Te*; Table 1-1), ectotherms are able to maintain *Tb* that is closer to *To* and within a narrower range than *Te*, through behaviour (Huey and Stevenson 1979, Seebacher and 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 and Bogert 1944, Huey 1982, Stevenson et al. 1985, Adolph 1990). Behavioural thermoregulation helps to buffer thermal heterogeneity of the environment (Angilletta 2009).

The extent to which reptiles regulate *Tb* varies across species and environments. Thermoregulatory strategies range from thermoconformity (Ruibal 1961), where the organism does not thermoregulate and *Tb* matches *Te*, to perfect thermoregulation where behaviour is used to adjust *Tb* within a narrow range (Adolph 1990). The variation seen both within and between species in their thermoregulatory strategies is assumed to be related to the associated costs and benefits of thermoregulation (Huey and Slatkin 1976). The main benefit of thermoregulation is physiological as most physiological processes are optimized within a narrow range of *Tb* (Huey and Slatkin 1976). The main costs of thermoregulation are energy and time loss because time and energy spent thermoregulating or waiting for conditions that allow thermoregulation is not available for other important activities such as foraging and mating (Huey 1974). The cost-benefit model of thermoregulation makes the fundamental prediction that as the costs of thermoregulation increase, thermoregulatory effort should decrease and individuals should thermoconform.

Different environments pose different types and degrees of challenge to a thermoregulating organism. The thermal quality (*de*; Table 1-1) of an environment directly affects how much time and energy must be expended to maintain *Tb* within the preferred temperature range of a species (*Tset*; Table 1-1). A habitat of low thermal quality is one where *Te* is far from *Tset*, making it more difficult to maintain an optimal *Tb* (Hertz et al. 1993). Under the cost-benefit model, thermoconformity is expected in habitats of low thermal quality where the costs of thermoregulation are high. However, it has been argued that thermoconformity may be widespread in species that live in tropical areas (Shine and Lambeck 1985, Shine and Madsen 1996, Kapsalas et al. 2018), which account for the majority of reptile species. Tropical reptiles are exposed to environmental temperatures that are almost always near their *Tset* and so they can maintain an optimal *Tb* 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 and Madsen 1996) and so thermoconformity is the adopted strategy.

Most data on reptilian thermoregulation have been collected from temperate-zone lizards (Shine and Madsen 1996) that are small-bodied and experience wide daily and seasonal fluctuations in *Te*. In this type of environment, a lizard must invest considerable time and effort into thermoregulation if it is to maintain a high and stable *Tb* (Cowles and Bogert 1944). Support for the predictions made by cost-benefit model of thermoregulation have been presented for species that experience relatively benign thermal environments (Huey and Webster 1976, Hertz and Huey 1981, Hertz et al. 1993). However, studies on temperature-zone reptiles have contradicted these predictions (Brown and Weatherhead 2000, Blouin-Demers and Weatherhead 2002, Row and Blouin-Demers 2006, Edwards and Blouin-Demers 2007). For example, both watersnakes (*Nerodia sipedon*; Brown and Weatherhead 2000) and black rat snakes (*Elaphe obsoleta*; Blouin-Demers and Weatherhead 2001a) at their northern limit in Canada are fairly precise thermoregulators despite their challenging thermal environment. Authors suggest that the physiological disadvantages of thermoconforming are very low in thermally benign environments because even without thermoregulation *Tb* is close to *To*. However, in thermally challenging environments, the cost of thermoconformity might be more important because it would result in *Tb* very far from *To* and may force species in more challenging habitats to thermoregulate more carefully.

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 et al. 2016). Correspondingly, at high latitudes and elevations, thermal constraints are highest (Addo-Bediako et al. 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 and Weatherhead 2001a, Herczeg 2006, Besson and Cree 2010, Lourdais et al. 2013, Bouazza et al. 2016, Ortega et al. 2016). Previous studies on lizard thermal ecology across elevational gradients have found that body temperatures at low and high elevations do not differ significantly, despite the decrease in ambient temperature (Burns 1970, Zamora-Camacho et al. 2016). Behavioural thermoregulation in harsh environments, although costly, may be required to buffer against the impact of temperature variations (Huey et al. 2003) and extreme temperatures (Woods et al. 2015) on performance, but to further our understanding of how investment in thermoregulation changes with thermal quality, we must look at populations facing a gradient of thermal environments.

For this study, I used ten populations of Yarrow's spiny lizards (*Sceloporus jarrovii,* Figure 1-2) on talus slopes across an elevational gradient of 1100 m in the Chiricahua Mountains of southeastern Arizona, USA to investigate whether investment in thermoregulation changes across an elevational gradient. *S. jarrovii* is an ideal study system because it is abundant in rocky habitats and can be found along a wide elevational gradient of approximately 1500–2800 m (Ellis-Quinn and Simon 1991), making it feasible to study the majority of the elevational distribution. Talus slopes are comprised of large rock outcroppings which limit vegetative growth and provide a homogenous habitat for comparison across an elevational gradient. In other habitat types, vegetation changes with elevation, likely affecting the thermal quality and consequently the thermoregulatory opportunities across elevational gradients due to habitat structure (Lara-Reséndiz et al. 2014).

I tested the hypothesis that the thermal quality of an environment dictates investment in thermoregulation by lizards. Specifically, I tested the prediction arising from the cost-benefit model of thermoregulation that lizards living at lower elevations, and thus thermally superior habitats, should invest more in thermoregulation.

Methods

Ethical note

This research was conducted with a State of Arizona Scientific Collection Permit (SP771492), permission from the U. S. Forest Service (Douglas Ruppel), and approved by the University of Ottawa Animal Care Committee (BL-2812).

Study species and sites

The Yarrow's spiny lizard (*Sceloporus jarrovii*) is a moderate-sized (average snout-vent length = 9.7 cm, Cox and John-Alder 2007) heliothermic (gains heat from the sun) lizard whose range spans from southeastern Arizona to northern Mexico (Ballinger 2013). *S. jarrovii* feed on a variety of arthropods (Simon 1975, Watters 2010). Their density is largely dependent on the amount of rock and number of rock crevices that serve as refuges from predators and unsuitable temperatures (Huey and Kingsolver 1989, Sabo 2003). *S. jarrovii* is regularly observed basking on rocks, close to rock crevices. Both sexes defend territories and maintain stable home ranges throughout the summer months (Ruby 1977). They are viviparous and females are able to store sperm over the winter and delay embryonic development until temperatures rise in the spring (Beuchat 1986), a supposed adaptation to occupying high elevation (Tinkle and Gibbons 1977).

I conducted this research from 2 May to 23 July 2017 at ten talus slopes (Figure 1-3) ranging in elevation from 1634 m to 2700 m (Table 1-2) within the Chiricahua Mountains of southeastern Arizona, USA (Figure 1-4). The vegetation surrounding the sites ranged from encinal vegetation (i.e. oaks, junipers) at low elevations to coniferous forest (i.e. Douglas fir, ponderosa pine) at high elevations (Bennett et al. 1996, Patterson 2018).

I systematically alternated my visits between sites of high and low elevation to help control for the seasonal changes in ambient temperature at different elevations across the study period (Table 1-3). I visited sites in 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. The maximum inter-capture session interval was 30 days.

Field data collection

Each day, I caught lizards by rod and noose (510 lizards caught 1020 times; Table 1-4) during their daily active period (from sunrise until it became too hot and they retreated under rocks). Individuals were caught between 1 (n = 257) and 8 times (n = 1) and excluding individuals only caught once, lizards were caught an average of approximately three times. There were daily fluctuations in the time and length of the active period due to the position of the slope relative to the rising sun, as well as daily variation in temperature and precipitation (earliest capture: 06:16 MST, latest capture: 16:02 MST, 92 % of captures before 12:00 MST). 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 on the same day.

I assigned each lizard a unique number for identification (UID) and marked this number on both their head and stomach using a felt tip marker to allow for repeated measures of individuals (Jones and Ferguson 1980, Simon and Bissinger 2011). This identification method is non-permanent and is shed off with the skin (non-continuously) approximately every 3–8 weeks (Todd 2005). For lizards that were shedding at the time of capture, I carefully removed the scales on the head and stomach region before marking it. UIDs were still visible after the maximum number of days between visits at a given site (Figure 1-5). In addition, I was able to use size, sex, and unique characteristics such as medical cauterized markings from Patterson (2018) and tail autonomy, to confirm my identification if there were any doubts. Because both males and females of *S. jarrovii* maintain stable territories (Ruby 1978), on occasion I was able to use GPS locations of repeat captures to confirm UIDs. Therefore, I assumed that I was able to identify re-caught lizards reliably and all statistical analyses treated lizards UIDs as independent.

I determined the sex of each lizard (185 males caught 338 times and 325 females caught 682 times; Table 1-4) based on the presence (males) or absence (females) of enlarged post-anal scales (Figure 1-6), size (males are bigger than females; Angilletta et al. 2004, Cox 2006, Gilbert and Lattanzio 2016), and colouration (blue on throat and flanks is more prominent in males). Snout-vent length (SVL) was measured using digital calipers (± 0.1 mm). SVL is the preferred metric for measuring size in lizards because body mass typically fluctuates with variation in stomach contents, fat storage, and reproductive status (Dunham 1978, Haenel and John-Alder 2002). In addition, body mass was measured using a digital scale (± 0.01 g) to aid in determining reproductive status of females, as gravid females of this species maintain a lower *Tb* in the field to increase embryo fitness (Beuchat and Ellner 1987).

Field active body temperature

I recorded the time (to the nearest minute) it took to capture each lizard because lengthy pursuits may influence body temperature (*Tb*) due to stress or prolonged exposure in the sun. Immediately after a lizard was captured by noose, skin surface temperature (*Tsk*) was measured (n = 1020) as an estimate of *Tb* using an infrared laser thermometer (IRT) pointed at the cloaca (see Supplementary material for laser calibration). *Tsk* is particularly suited for small-bodied lizards whose *Tb* are easily influenced by handling, both due to stress and heat transfer (Marler and Moore 1991, Langkilde and Shine 2006). Validation studies have indicated that *Tsk* gives an accurate estimate of cloacal temperature in small lizards (Herczeg 2006, Hare et al. 2007, Besson and Cree 2010, Carretero 2012, Bouazza et al. 2016), including *S. jarrovii* (Beal et al. 2014, Gilbert and Lattanzio 2016). To measure *Tsk* 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. In subsequent sections, *Tb* will indicate *Tsk*.

Preferred body temperature range

The preferred body temperature range or set-point range (*Tset*) of a species is determined by allowing individuals to select *Tb*'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). *Tset* is assumed to include the optimal temperature for performance and is a highly conserved trait of a species. For example, Angilletta and Werner (1998) found that *Tset* for the marbled gecko (*Christinus marmoratus*) differed by less than a degree for the same species recorded in 1994 and in 1966 (Light et al. 1966). For my research, I used the *Tset* range for adult *S. jarrovii* (30.4–33.2 °C) calculated by Patterson (2018) as the central 50 % (25th–75th quartiles) of selected body temperatures in a laboratory thermal gradient, which is consistent with previous studies on *S. jarrovii* and other species within the genus *Sceloporus* (Table 1-5).

Accuracy of body temperature

The difference between field active *Tb* and *Tset* (i.e. accuracy of body temperature, *db*) indicates how closely ectotherms achieve *Tb* within the preferred range for the species (Huey 1982). I measured *db* following Hertz et al. (1993) by calculating the deviation of *Tb* from *Tset* in absolute values. When *Tb* was over *Tset*, the difference between *Tb* and the upper bound of *Tset* was used to measure *db*. When *Tb* was below *Tset*, the difference between *Tb* and the lower bound of *Tset* was used to measure *db*. When *Tb* was within *Tset*, the *db* value calculated was zero. The magnitude of departure of *Tb* from the upper or lower bounds is a measure *db*. Note that deviations of equal magnitude above and below *Tset* are deemed of equal physiological importance (Hertz et al. 1993); however, we know that deviations above the upper bound of *Tset* are more problematic for organisms because the decline in performance is much sharper (see Figure 1-1).

Operative environmental temperature

To evaluate whether ectotherms are actively thermoregulating, information on the distribution of *Tb* that a non-thermoregulating animal would achieve is needed (Heath 1964, Huey et al. 1977). Operative environmental temperature (*Te*), the result of biophysical and morphological factors that influence an ectotherm's *Tb*, represents the equilibrium temperature of an inanimate object (one lacking physiological or behavioural controls) with the same thermal characteristics as the study animals. *Te* are traditionally measured with physical models, with similar characteristics as the animal (i.e. shape, size, colour), placed throughout the various microhabitats available (Bakken 1992). For small ectotherms, hollow metal (typically copper) or plastic models provide an accurate estimate of the *Tb* that a non-thermoregulating animal would achieve due to their limited capacity to control rates of heat exchange (Angilletta 2009). Bakken (1992) suggested that lizards of less than 0.03 kg, such as *S. jarrovii*, can be assumed to have zero heat capacity and so the *Te* values measured with physical models are an accurate representation of the *Tb* of non-thermoregulating lizard. The random distribution of *Te* in a habitat describes the "null" distribution of *Tb* expected in non-thermoregulating animals (Christian and Tracy 1985, Hertz et al. 1993).

I made *S. jarrovii* models from 6 cm by 2 cm copper tubes (Figure 1-7) which were painted grey to approximate the reflectance of *S. jarrovii* (Shine and Kearney 2001). iButton (± 0.5 °C) temperature data loggers (Thermochron iButton DIS1921G-F5, Dallas Semiconductor, Sunnyvale, California) were placed inside to record *Te* every minute. The ends of the model were sealed by rubber stoppers. These models were validated by Patterson (2018).

To record *Te*, I placed the models daily in 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 (normally near the base of the slope). Overall, 97.5 % of lizards were caught in one of these three microhabitats, so I assumed these microhabitats accurately represent the microhabitats used by *S. jarrovii* on talus slopes. Models were rearranged randomly each day of capture within the microhabitats to better capture the spatial heterogeneity of *Te*. I averaged daily *Te* from each copper model (3 per day) across 15-minute intervals because lizards are mobile and can readily move between microhabitats. Consequently, the *Te* they experience would likely converge on the average *Te* among the microhabitats rather than equilibrate to the *Te* experienced within individual microhabitats (Bakken 1992, Hertz et al. 1993, Seebacher and Shine 2004).

Thermal quality

Patterson (2018) found a strong positive correlation between elevation and thermal quality (*de*), indicating that *de* is poorer at high elevations and that elevation can be used as a proxy for *de*. To verify this pattern, I used the *de* index proposed by Hertz et al. (1993) to measure thermal quality at each site. For each *Te*, I calculated a corresponding *de* value. I calculated *de* as the absolute deviation between *Te* and the nearest limit of the *Tset*. When *Te* was above *Tset*, the deviation was measured from the upper bound of *Tset* and the lower bound of *Tset* when *Te* was below *Tset*. Thus, I calculated *de* every 15 minutes for each lizard capture session.

Effectiveness of thermoregulation

There are various indices of thermoregulation. Hertz et al. (1993) highlighted the importance of comparing the extent to which an animal maintains its *Tb* within *Tset* (accuracy of body temperature, *db*) to the degree to which the habitat allows *Tb* to be within *Tset* (thermal quality, *de*). In small ectotherms, like *S. jarrovii*, where the heating and cooling rates of the animal and physical models are similar, the comparison of *db* and *de* provides a reliable indicator of whether the animals are actively regulating their body temperatures towards *Tset* (Seebacher and Shine 2004).

I calculated the effectiveness of thermoregulation as the difference between *de* and *db* (Blouin-Demers and Weatherhead 2001a). This index measures the departure from thermoconformity (*de-db* = 0). It incorporates information on both the thermal quality of the habitat (*de*) and the body temperatures (*Tb*) achieved and determines a measure of the investment in thermoregulation by an animal. Positive values indicate some degree of thermoregulation while negative values represent avoidance of thermally favourable habitats. The magnitude of departure from zero (thermoconformity) is a measure of effectiveness of thermoregulation: how much closer is the *Tb* of the animal to *Tset* than is the randomly available *Te*.

Because my *Tb* sampling was sporadic, it was more appropriate to only use *Te* at the time the individual was captured as a measure of the thermal environment available to the individual. I extracted the mean *Te* and mean *de* for the 15-minute time interval during which each individual was captured. Thus, for each lizard capture (n = 1020) I had a *Tb* measurement and an associated *Te* and *de* value. When calculating the indices to examine differences in thermoregulation I assumed that all habitats were available to the lizards and I averaged *de* for all microhabitats. By determining if effectiveness of thermoregulation by *S. jarrovii* at different elevations varies, I established whether broad trends in thermal quality result in changes in investment in thermoregulation.

Statistical analyses

Main analyses

I first explored the potential relationships between my individual predictor and response variables using scatterplots. Linear mixed effects model (LMM) assumptions were examined using SjPlot (Ludecke 2015). I did not detect any violations of model assumptions including linearity, normality, homoscedasticity, independence of residuals, and normal distributions of the random effects. When I had multiple predictor variables in a model, variance inflation factors were all below 2, so multicollinearity was not an issue (O'Brien 2007). Full mixed-model conditional R^2 values were calculated using the r.squaredGLMM() function (MuMIn package, Barton 2018). Partial R^2 values were calculated using r2beta() function (r2glmm package, Jaeger 2017).

To determine how thermal quality varies with elevation, I used a linear mixed-effects model (LMM) (package: lme4, function: lmer; Bates et al. 2014). I included elevation, my variable of interest, as a continuous fixed effect. I also included time of day and Julian date as a continuous fixed effect. I included site as a random effect.

To determine how elevation affects lizard thermoregulation I constructed a separate LMM for *Tb* and *de-db.* I included elevation, my variable of interest, as a continuous fixed effect. Because the data were collected in the field, I included various biologically relevant control variables that affect body temperature of lizards. Sex was recorded as a three-factor variable to incorporate reproductive status (male, non-gravid female, and gravid female). It was included in the model as a fixed effect to control for sex and reproductive differences in *Tb* (Mathies and Andrews 1997). SVL was included as a fixed effect to control for the influence of size on *Tb* (Gilbert and Lattanzio 2016). I included Julian date of capture and time of day as continuous fixed effects to control for the increase in temperature over the season and during the day, respectively. The time it took to capture a lizard may influence *Tb* due to increased exposure to sun or stress, so I included this variable as a continuous fixed effect. Since I assigned each individual a UID unique to their site of capture, I incorporated lizard UID as a random effect to control for repeated captures. Likewise, I included site as a random effect to control for any possible site effects, other than elevation (e.g. position of slope).

Additional analyses

Length of the daily active period could not be measured directly as the last capture time was dependent on factors independent of the lizards (i.e. length of time required to process lizards already caught, etc.). Therefore, to approximate the start of the daily active period at each site, I calculated the fifth percentile of capture times for each day. The first capture of each day is too sensitive to outliers. To examine how the start of the daily activity period varied with elevation, I used LMM with fifth percentile of capture as the response variable; elevation as a continuous fixed effect; and month and site as random effects. I used month instead of Julian date of capture because there is only one response variable (fifth percentile of capture) for each day, therefore a random intercept cannot be calculated for each day; month does control for broad changes in activity throughout the active season. I also examined how lizard capture times varied with elevation using LMM with capture time as the dependent variable; elevation as a continuous fixed effect and Julian date of capture and site as random effects. Although I recognize that ambient temperature may affect these response variables, ambient temperature is highly correlated with elevation, so I did not include it in my models.

All data were analyzed using R Version 3.4.1 (R Core Team, 2017). Although I first analysed my dependent variables without control variables, all conclusions regarding the main effects of interest were based on models including controls. I evaluated significance of my fixed effects using Type III ANOVA (package: car, function: Anova). Degrees of freedom for F tests were generated using Kenward-Roger approximation (Bolker et al. 2009).

Results

Thermal quality and elevation

After condensing into 15-minute intervals, a total of 1359 *Te*'s were recorded and a corresponding *de* value was calculated. Throughout the active season, *Te* ranged from 1.8 °C to 43.8 °C (mean of 25.9 ± 5.9 °C) and *de* ranged from 0 °C to 28.6 °C (mean of 5.3 ± 4.9 °C) across all sites (Table 1-6). Throughout the active season, mean *Te* never reached the lower bounds of *Tset* at any elevation. Maximum *Te* values were higher than the upper bound of *Tset* at all elevations with the exception of the highest site. Minimum *Te* values were always below the lower bounds of *Te* at each site (Figure 1-8).

Te increased with time of day at each site. Mean daily *Te* for each hour showed much variation across elevations. At low elevation mean maximum *Te* often exceeded *Tset* for ~3 hours. Minimum daily *Te* for each hour rarely reached the lower bound of *Tset* at any elevation. Mean daily *Te* within *Tset* per hour decreased as elevation increased, with mean *Te* never reaching *Tset* at the highest elevation sites (Figure 1-9), indicating the habitat available to lizards was more thermally challenging at high elevations.

I used *de* for each time bin and percentage of time *de* was equal to 0 (*Te* within *Tset*) at each site as a measure of thermal quality. When exploring the raw effects of elevation on thermal quality, thermal quality decreased significantly (*de* more positive) with elevation ($R^2 = 0.21$, coefficient = 0.006, 95 % CI = 0.005–0.007, F = 357.7, df = 1, 1357, $p < 0.001$; Figure 1-10). Likewise, thermal quality decreased significantly (8 °C per 1000 m) with elevation when controlling for confounding variables ($R^2 = 0.61$, coefficient = 0.008, 95 % CI = 0.002–0.009, F = 9.29, df = 1, 8, $p = 0.016$; Figure 1-9). The percentage of time when de = 0 decreased significantly with elevation ($R^2 = 0.56$, coefficient = -0.020, 95 % CI = -0.027–-0.006, F = 9.88, df = 1, 67, $p = 0.008$; Figure 1-11). Therefore, I conclude that thermal quality decreases with elevation. These trends are consistent with Patterson (2018).

Body temperature and elevation

Across all elevations, *Tb* ranged from 14.4 °C to 39.9 °C (mean ± SE = 27.8 ± 0.1 °C) and males had significantly higher *Tb* than females (t = 1.93, df = 1018, p = 0.055); however, the difference was less than one degree which is within the accuracy of the IRT (males: 28.2 ± 0.2 °C, females: 27.7 ± 0.2 °C). As expected, the mean *Tb* of non-gravid females (28.0 ± 0.2 °C) was significantly higher than the mean *Tb* of gravid females (27.1 ± 0.3°C; t = 2.51, df = 680, $p = 0.010$) however, the difference was again less than one degree.

The distribution of *Tb* and *Te* 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. The mean *Tb* of lizards was higher than the mean *Te* (27.8 ± 0.1 °C vs. 25.9 ± 0.2 °C, respectively; Figure 1-12).

Tb decreased significantly with elevation in the absence of any control variables with an estimated slope of -0.0026 (95 % CI = -0.0033–0.0019, $R^2 = 0.05$, F = 56.09, df = 1, 1018, $p < 0.001$), however in the presence of control variables, the relationship between *Tb* and elevation was marginally non-significant with a similar estimated slope of -0.003 (95 % CI = -0.006–0.0002, $R^2 = 0.32$, F = 4.17, df = 1, 9, $p = 0.07$; Table 1-7, Figure 1-13).

Effectiveness of thermoregulation and elevation

Values of the *de-db* index ranged from -12.7 to 20.5 °C (mean (± SE) = 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: 4.04 ± 0.2 °C, females: 3.40 ± 0.1 °C). The mean *de-db* of gravid females (4.42 ± 0.25 °C) was significantly higher than the mean *de-db* of non-gravid females (2.84 ± 0.17 °C; t = 5.22, df = 446, $p < 0.001$), indicating that gravid females thermoregulate more effectively than non-gravid females, on average.

Effectiveness of thermoregulation (*de-db*) increased significantly with elevation in the absence of any control variables with an estimated slope of 0.004 (95 % CI = -0.0033–-0.0046, $R^2 = 0.14$, F = 161, df = 1, 1018, $p < 0.001$). In the presence of control variables, elevation was still a significant predictor of *de-db* with an estimated slope of 0.005 (95 % CI = 0.002–0.007, $R^2 = 0.38$, F = 9.13, df = 1, 8, $p = 0.02$, Table 1-8, Figure 1-14).

Daily activity period and elevation

Lizard activity began later in the day as elevation increased in the absence of any control variables ($R^2 = 0.09$, coefficient = 0.0009, 95 % CI = 0.0002–0.0016, F = 7.599, df = 1, 67, $p = 0.007$; Figure 1-15). Controlling for seasonal changes and site effects resulted in elevation not being a significant predictor of the start of daily activity ($R^2 = 0.47$, coefficient = 0.0007, 95 % CI = -0.0005–0.0018, F = 1.19, df = 1, 8, $p = 0.26$; Figure 1-15). When examining the raw effects between all capture times of lizards across elevations I found a significant positive linear relationship ($R^2 = 0.05$, coefficient = 0.0009, 95 % CI = 0.0007–0.0012, F = 52.95, df = 1, 1018, $p < 0.001$; Figure 1-16). However, when controlling for seasonal changes and site effects, the relationship was no longer significant ($R^2 = 0.31$, coefficient = 0.0065, 95 % CI = -0.0004–0.0017, F = 1.34, df = 1, 9, $p = 0.185$, Figure 1-16).

Discussion

In general, my data support the hypothesis that the thermal quality of an environment affects investment in thermoregulation by lizards, although in the opposite direction than predicted by the cost-benefit model of thermoregulation. Thermal quality, measured by *de*, decreased along the elevational gradient resulting in higher costs of thermoregulation as elevation increased. The effectiveness of thermoregulation by lizards, measured by *de-db*, also varied with elevation but instead of thermoregulation increasing in low-cost habitats (lower elevation), thermoregulation increased in high-cost, low thermal quality habitats (higher elevation), which is contrary to the predictions of the cost-benefit model of thermoregulation. This is the first study to my knowledge that tested the cost-benefit model of thermoregulation on multiple populations of the same species faced with different costs. Although studies have made comparisons between populations at different latitudes (Ellner and Karasov 1993, Andrews 1998) and elevations (Bouazza et al. 2016, Lu et al. 2018, Trochet et al. 2018), the majority make comparisons between only two and three populations (e.g. Burns 1970, Ballinger 1973, Grant and Dunham 1990, Diaz 1997, Olsson and Shine 2002, Iraeta et al. 2013) and studies quantifying thermoregulation using standard indices of thermoregulation such as thermal quality are scarce but are useful for testing the broad applicability of the cost benefit model of thermoregulation.

At high elevations, *de* was higher and lizard activity began later in the day indicative of low thermal quality. Despite these differences in thermal quality, lizards maintained very similar *Tb* 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 meta-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 and Nadeau 2005). The explanation these authors proposed was that the physiological disadvantages of thermoconformity are small in thermally benign habitats (high thermal quality) because *Tb* is close to *To* 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 *Tb* far from *To* 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 the cost-benefit model of thermoregulation.

The cost-benefit model of thermoregulation emphasizes that the cost of thermoregulating increases as the thermal quality of a habitat decreases but the disadvantage of thermoconformity may be more important than previously considered and may force species or individuals in more challenging habitats to thermoregulate more carefully than species or individuals in benign habitats. Studies of other reptilian species at the northern edge of their distribution in Canada, where *Te* rarely allows for *To* to be achieved, have also shown that reptiles invest more in thermoregulation in poorer thermal quality habitats (Blouin-Demers and Weatherhead 2001a, Row and Blouin-Demers 2006, Edwards and Blouin-Demers 2007, Picard et al. 2011, Aguado and Braña 2014). In mountain habitats, such as the Chiricahua Mountains of south eastern Arizona, the environment is highly variable and thus the consequences of thermoconformity are greater. For example, the mean *Te* was 17 °C at the highest elevation site in my study. If a lizard were to thermoconform to that temperature performance would be so poor that survival, and thus fitness would be compromised.

Although the cost-benefit model of thermoregulation has been seminal to research on thermoregulation, there are some short-comings that limit its broad applicability. The cost-benefit model was inspired by the thermoregulatory behaviour of *Anolis* lizards in the Caribbean (Huey and Slatkin 1976), a thermally benign environment. When assessing the costs and benefits of thermoregulation in this type of environment, there is little consequence to being a thermoconformer because *Tb* that allow for high performance are achieved without thermoregulation. However, the model fails to consider the scenario where the disadvantages of thermoconformity outweigh the costs of thermoregulation in habitats that are thermally-challenging. Another problem with the cost-benefit model of thermoregulation is that it assumes the costs and benefits of thermoregulation are independent of one another which is not realistic in nature. For example, the costs of thermoregulating in thermally-challenging habitats are high because a significant amount of time and energy is required to find thermoregulatory opportunities in addition to the opportunity cost of spending time in a microhabitat where activities other than basking cannot occur. Concurrently, the benefit of thermoregulating is also high because non-thermoregulating animals experience low *Tb* and poor performance. More laboratory experiments would help reveal the influence of costs and benefits, both separately and together, on thermoregulatory behaviour.

Physical properties of animals such as colouration and size influence thermoregulation and may differ across elevational gradients. Some lizards are known to modify their skin colour for heat absorption. (Clusella-Trullas et al. 2007, Bouazza et al. 2016, Middendorf and Simon 1988). 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 and Simon 1988, Sherbrooke et al. 1994). *S. jarrovii* will darken their colouration to maximize heat gain until *To* has been achieved, after which their skin lightens. Body size has also been linked to thermoregulation as individuals with larger body sizes have higher heat capacities and dissipate heat more slowly. Differences in body size of Algerian *Psammodromus algirus* at higher elevations results in a slower cooling rate (Zamora-Camacho et al. 2013). Body size of *S. jarrovii* increases with elevation (Ballinger 1973,1979, Patterson 2018), apparently because lizards with larger body sizes have higher chances of surviving the winter (Civantos et al. 1999, Zani 2008). I found that body size was a significant predictor of thermoregulation with larger individuals thermoregulating more effectively.

Although thermal quality is an important cost of thermoregulation, and is one that varies considerably along an elevational gradient, I acknowledge that there are likely other costs that may constrain *S. jarrovii* ability to thermoregulate across an elevational gradient. Differences in predation pressures affect thermoregulation. For example, male common lizards (*Zootoca vivipara*) respond to predator scent simulated in the laboratory by decreasing their accuracy of thermoregulation (*Tb* within *Tset*) (Herczeg et al. 2008), demonstrating that costs with immediate effects on fitness (i.e. predation or reproduction) can override the benefits of optimised physiological performance accomplished by accurate thermoregulation (Herczeg 2006, Herczeg et al. 2008). At low elevations, there are more documented predators of *S. jarrovii* (Ballinger 1979) and thus spending time thermoregulating may have greater mortality costs than at higher elevations resulting in less investment in thermoregulation. Although, in my study, the number of lizards with autotomized tails, a proxy for predation rates (Patterson 2018), was not higher at low elevations (there was no significant relationship with elevation). Also, lizards in high-productivity environments have more time available for thermoregulation (Pianka and Pianka 1970). However, Patterson (2018) did not detect a relationship between *S. jarrovii* food availability and elevation over a three-year period. In addition, for *S. jarrovii* it is unlikely that food availability affects thermoregulation because they are sit-and-wait predators (Simon 1975) and do not actively hunt their prey, thus thermoregulation and foraging are probably done simultaneously.

Using *de* as a measure of thermal quality is currently the most applicable index for natural studies, but this index does not consider the spatial arrangement of *Te* (Sears et al. 2016). Presumably organisms must move more when microhabitats with optimal temperatures become rare, thus the energetic cost of locating these rare microhabitats is greater. In a sandy arena, *S. jarrovii* thermoregulated more accurately with a dispersed distribution of shade and sun than with a clumped distribution of sun and shade, suggesting that the spatial arrangement of surface *Te* is important to thermal quality (Sears et al. 2016). When preferred microclimates are more dispersed throughout an area, the distances between them are smaller allowing individuals to thermoregulate more effectively while expending less energy (Sears et al. 2011). Although talus slopes are different sizes and shapes, shade surface temperatures are likely less important for thermoregulation because refuge sites are easily accessible at every point in the habitat underneath the loose rocks and are several degrees cooler than the surface (Patterson 2018). In a homogenous habitat like a talus slope, the spatial arrangement is of surface temperatures is less likely to influence the accuracy of thermoregulation.

Preferred body temperatures are strongly conserved within lizard species, even across diverse thermal environments (Bogert 1949, Angilletta Jr. et al. 2004, Buckley et al. 2015). I used the same *Tset* to make comparisons between populations along an elevational gradient. Although *Tset* is stable across environmental clines (Zamora-Camacho et al 2013, Diaz et al. 2006) it has been argued that plasticity in *Tset* has largely been ignored and may play an important role in how lizards cope with daily and seasonal changes in thermal conditions (Gvoždík 2012). *Tset* may stay stable across elevational gradients because ectotherms buffer selection pressure of thermal environment on *Tset* through behavioural thermoregulation (Bogert 1949, Stevenson 1985). Alternatively, ectotherms may select warmer (Conover and Schultz 1995) or colder (Levinton 1983) *Tset* across an elevational gradient to maximize performance in less favorable conditions. The wall lizard (*Podacris muralis*) and common lizard (*Zootoca vivipara*) from high elevation populations selected lower preferred temperatures in a laboratory gradient than lizards from low elevation populations (Trochet et al. 2018). The authors suggest that lizards from cold climates may be physiologically adapted to low temperature, with the ability to reach optimal functioning at lower temperatures than individuals from low elevation (Trochet et al. 2018).

In lizards, the mechanism underlying variation in thermoregulatory behaviour has long been assumed to be phenotypic plasticity (Cowles and 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 and 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 and Miles 2017). Using reciprocal transplant experiments would help determine whether *S. jarrovii* effectiveness of thermoregulation is a phenotypically plastic trait or one that has a genetic basis. This would also help shed light on this species ability to cope with decreased activity times imposed by climate warming.

In conclusion, I found that *S. jarrovii* thermoregulate more effectively in habitats of poorer thermal quality, which is opposite to the predictions of the cost-benefit model of thermoregulation. Across an elevational gradient where the costs of thermoregulating become greater 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*. To the best of my knowledge, this is the first study to conduct a more rigorous within-species test, using standard indices of thermoregulation, of the cost-benefit model of thermoregulation on multiple populations faced with varying costs. 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.

Tables and Figures

Table 1-1. Definitions of the symbols and indices used in the quantification of thermoregulation adapted from Hertz et al. (1993).

Symbol or index	Definition
Tb	Field active body temperature of study animal (measured with cloacal probes or infrared laser thermometers)
Tset	Preferred body temperature range (typically measured by central 50 % of the distribution of body temperatures in a laboratory thermal gradient)
Te	Operative environmental temperature: body temperatures that a non-thermoregulating animal would experience (typically measured with copper models placed randomly around the habitat)
db	Accuracy of body temperature (measured as mean of the deviations of field body temperatures from preferred body temperature range)
de	Thermal quality (measured as the mean deviations of the operative environmental temperatures from the preferred body temperature range)
de-db	Index of the effectiveness of thermoregulation (Blouin-Demers and Weatherhead 2001)
Ex	Thermal exploitation (measured as the time in which the body temperatures of animals are within the preferred body temperature range divided by the time available for animals to have their body temperatures within the preferred range, as indicated by the operative environmental temperatures, Christian and Weavers (1996))

Table 1-2. Coordinates (UTM, Zone 12R) of ten talus slopes and their corresponding elevation (m) in the Chiricahua Mountains, Arizona, USA where Yarrow's spiny lizards (*Sceloporus jarrovii*) were studied from 2 May to 23 July 2017. Note: Map of study sites in Figure 1-4.

Site	Elevation	E	N
Sulphur Canyon 4	1634	674776	3523405
South Fork 1	1742	671060	3525387
South Fork 3	1761	671484	3526096
Price Canyon 1	1845	664829	3515395
Price Canyon X	1852	664977	3515315
Rucker Canyon 2	2133	661683	3519503
Rucker Canyon 5	2151	663274	3519157
Saulsbury Trail 3	2511	660861	3527455
Rustler's Canyon F	2600	661850	3529510
Rustler's Canyon 1	2700	662040	3529401

Table 1-3. Date of capture sessions of Yarrow's spiny lizards (*Sceloporus jarrovii*) at ten sites within the Chiricahua Mountains, Arizona, USA. Number of capture sessions per site ranged from six to ten depending on sample size.

Date	Site	Elevation	Capture session
	Block 1 Sites		
02-May-17	Rucker Canyon 5	2151	1
03-May-17	Rucker Canyon 5	2151	2
04-May-17	Rucker Canyon 5	2151	3
05-May-17	South Fork 1	1742	1
07-May-17	South Fork 1	1742	2
08-May-17	South Fork 1	1742	3
11-May-17	Saulsbury Trail 3	2511	1
12-May-17	Price Canyon X	1852	1
13-May-17	Price Canyon X	1852	2
14-May-17	Price Canyon X	1852	3
17-May-17	Rustler's Canyon 1	2700	1
18-May-17	Rustler's Canyon 1	2700	2
19-May-17	Rucker Canyon 5	2151	4
20-May-17	Rucker Canyon 5	2151	5
21-May-17	Rucker Canyon 5	2151	6
23-May-17	South Fork 1	1742	4
24-May-17	South Fork 1	1742	5
25-May-17	South Fork 1	1742	6
26-May-17	Saulsbury Trail 3	2511	2
27-May-17	Saulsbury Trail 3	2511	3
28-May-17	Saulsbury Trail 3	2511	4
30-May-17	Price Canyon X	1852	4
31-May-17	Price Canyon X	1852	5
01-Jun-17	Price Canyon X	1852	6
02-Jun-17	Rustler's Canyon 1	2700	3
04-Jun-17	Price Canyon X	1852	7

05-Jun-17	Price Canyon X	1852	8
06-Jun-17	Price Canyon X	1852	9
07-Jun-17	Rustler’s Canyon 1	2700	4
08-Jun-17	Rustler’s Canyon 1	2700	5
09-Jun-17	Rustler’s Canyon 1	2700	6
10-Jun-17	Price Canyon X	1852	10
Block 2 Sites			
12-Jun-17	Sulphur Canyon 4	1634	1
13-Jun-17	Sulphur Canyon 4	1634	2
14-Jun-17	Sulphur Canyon 4	1634	3
15-Jun-17	Rucker Canyon 2	2133	1
16-Jun-17	Rucker Canyon 2	2133	2
17-Jun-17	Rucker Canyon 2	2133	3
18-Jun-17	Saulsbury Trail 3	2511	5
20-Jun-17	South Fork 3	1761	1
21-Jun-17	South Fork 3	1761	2
22-Jun-17	South Fork 3	1761	3
23-Jun-17	Rustler’s Canyon F	2600	1
24-Jun-17	Rustler’s Canyon F	2600	2
25-Jun-17	Rustler’s Canyon F	2600	3
27-Jun-17	Price Canyon 1	1845	1
28-Jun-17	Price Canyon 1	1845	2
29-Jun-17	Price Canyon 1	1845	3
30-Jun-17	Sulphur Canyon 4	1634	4
01-Jul-17	Sulphur Canyon 4	1634	5
02-Jul-17	Sulphur Canyon 4	1634	6
04-Jul-17	South Fork 3	1761	4
05-Jul-17	Rucker Canyon 2	2133	4
06-Jul-17	Rucker Canyon 2	2133	5
07-Jul-17	Rucker Canyon 2	2133	6
08-Jul-17	South Fork 3	1761	5
09-Jul-17	South Fork 3	1761	6
11-Jul-17	Rustler’s Canyon F	2600	4

12-Jul-17	Rustler’s Canyon F	2600	5
13-Jul-17	Rustler’s Canyon F	2600	6
14-Jul-17	Price Canyon 1	1845	4
15-Jul-17	Price Canyon 1	1845	5
16-Jul-17	Price Canyon 1	1845	6
18-Jul-17	Sulphur Canyon 4	1634	7
19-Jul-17	Sulphur Canyon 4	1634	8
20-Jul-17	Sulphur Canyon 4	1634	9
21-Jul-17	South Fork 3	1761	7
22-Jul-17	South Fork 3	1761	8
23-Jul-17	South Fork 3	1761	9

Table 1-4. Number of Yarrow's spiny lizards (*Sceloporus jarrovii*) captured from ten sites within the Chiricahua Mountains, Arizona, USA. Total number of captures in parentheses.

Site	Elevation	Adult Males	Adult Females	Juvenile Males	Juvenile Females	Total
Sulphur Canyon 4	1634	7 (13)	20 (52)	4 (6)	8 (9)	39 (80)
South Fork 1	1742	10 (22)	23 (51)	-	-	33 (73)
South Fork 3	1761	11 (20)	13 (43)	9 (11)	9 (9)	42 (83)
Price Canyon 1	1845	12 (22)	23 (64)	6 (6)	12 (15)	53 (107)
Price Canyon X	1852	8 (12)	17 (38)	-	-	25 (50)
Rucker Canyon 2	2133	15 (27)	24 (57)	9 (11)	9 (10)	57 (105)
Rucker Canyon 5	2151	42 (83)	73 (137)	-	-	115 (220)
Saulsbury Trail 3	2511	16 (25)	19 (37)	-	-	35 (62)
Rustler's Canyon F	2600	15 (40)	27 (71)	-	-	42 (111)
Rustler's Canyon 1	2700	21 (40)	48 (89)	-	-	69 (129)
Total		157 (304)	287 (639)	28(34)	38(43)	510 (1020)

Table 1-5. Preferred body temperatures (*Tset*) selected in a laboratory thermal gradient by lizards from the genus *Sceloporus*. Any experimental conditions are noted.

Reference	Species	Adult *Tset*	Juvenile *Tset*
Patterson et al. (2017)	*S. jarrovii*	-	Fed: 30.6–33.2 °C Fasted: 30.5–33.1 °C High food diet: 30.9–34.0 °C Low food diet: 30.9–33.5 °C
Gilbert and Lattanzio (2016)	*S. jarrovii*	-	Male: 33.0 °C Female: 32.8 °C
Sears et al. (2016)	*S. jarrovii*	32.7–34.9 °C	-
Beal et al. (2014)	*S. jarrovii*	Fasted Male: 33.1–34.9 °C Fasted Female: 32.4–34.5 °C Fed Male: 32.1-37.2 °C Fed Female: 24.1-36.5 °C	-
Schuler et al. (2011)	*S. jarrovii*	Fasted:31.2–34.7 °C Fed: 30.7–34.5 °C	-
Lara-Reséndiz et al. (2014)	*S. lineolateralis* *S. poinsettii*	28.8–31.7 °C 29.4–33.1 °C	-
Sartorius et al. (2002)	*S. arenicolus*	33.9–37.2 °C	-
Angilletta (2001)	*S. undulatus*	32.9 °C	-
Andrews et al. (1999)	*S. bicanthalis* *S. aeneus*	35.5 °C 34.9 °C	-
Mathies and Andrews (1995)	*S. scalaris*	35.6 °C	-

Table 1-6. Mean (± 1 SE), minimum, maximum operative environmental temperatures (*Te*, °C), mean (± 1 SE), maximum thermal quality (*de*, °C) and percentage of *Te* within *Tset* recorded at ten sites across an elevational gradient within the Chiricahua Mountains, Arizona, USA occupied by Yarrow's spiny lizards (*Sceloporus jarrovii*).

Elevation	*Te*			*de*		
	Mean	Minimum	Maximum	Mean	Maximum	% = 0
1634	27.82 ± 0.34	19.20	36.76	3.63 ± 0.24	11.20	18
1742	26.77 ± 0.43	15.43	26.48	4.35 ± 0.36	14.97	21
1761	27.67 ± 0.46	17.74	38.42	4.32 ± 0.33	12.66	22
1845	27.35 ± 0.37	19.72	34.98	3.43 ± 0.31	10.68	24
1852	28.50 ± 0.44	18.33	43.79	4.24 ± 0.27	12.07	15
2133	28.53 ± 0.39	16.24	36.29	2.67 ± 0.31	14.16	28
2151	26.33 ± 0.38	12.64	37.97	4.49 ± 0.34	17.76	16
2511	24.50 ± 0.53	12.20	33.10	6.02 ± 0.51	18.20	8
2600	23.66 ± 0.41	16.02	36.32	7.00 ± 0.37	14.38	6
2700	17.05 ± 0.38	1.81	26.32	13.35 ± 0.38	28.59	0

Table 1-7. Partial R^2, estimates and 95 % confidence intervals (CI) from the linear mixed-effects model of body temperatures (*Tb*) of Yarrow's spiny lizards (*Sceloporus jarrovii*) at ten sites in the Chiricahua Mountains, Arizona, USA. The fixed effects include elevation, snout-vent length (SVL), sex, time of day, Julian date and latency to capture. The random effects include lizard UID and site.

Fixed effects	Partial R^2	Estimate	2.5 %	97.5 %
Intercept	-	20.37	12.72	28.05
SVL	0.014	0.47	0.23	0.71
Male	0.002	0.47	-0.16	1.12
Non-gravid female	0.000	0.15	-0.53	0.84
Elevation	0.062	-0.003	-0.05	-0.0002
Julian date	0.009	0.02	-0.004	0.03
Time of day	0.080	0.82	0.65	0.99
Latency to capture	0.003	0.03	-0.001	0.06

Table 1-8. Partial R^2, estimates and 95 % confidence intervals (CI) from the linear mixed-effects model of effectiveness of thermoregulation index (*de-db*) of Yarrow's spiny lizards (*Sceloporus jarrovii*) at ten sites in the Chiricahua Mountains, Arizona, USA. The fixed effects include elevation, snout-vent length (SVL), sex, time of day, Julian date and latency to capture. The random effects include lizard UID and site.

Fixed effects	Partial R^2	Estimate	2.5 %	97.5 %
Intercept	-	-7.01	-13.87	0.04
SVL	0.003	0.19	-0.03	0.40
SexM	0.002	0.39	-0.19	0.97
SexNG-F	0.000	-0.07	-0.72	0.53
Elevation	0.125	0.004	0.002	0.007
Julian date	0.031	0.03	0.002	0.04
Time of day	0.024	-0.40	-0.56	-0.24
Latency to capture	0.009	-0.05	-0.08	-0.02

Table 1-9. Number of lizards captured and total number of field active body temperatures (*Tb*), in parentheses when given, from field studies on lizard thermal biology.

Reference	Species	Sample size
Kapsalas et al. (2018)	Ocellated skink (*Chalcides ocellatus*)	14
Sagonas et al. (2017)	Peloponnese wall lizard (*Podarcis peloponnesiacus*) Balkan wall lizard (*Podarcis tauricus*) Common wall lizard (*Podarcis muralis)*	85 89 57
Ortega et al. (2017)	Aurelio's rock lizard (*Iberolacerta aurelioi*)	37
Kapsalas et al. (2016)	Italian wall lizard (*Podarcis siculus*)	30
Bouazza et al. (2016)	Atlas day gecko (*Quedenfeldtia trachyblepharus)*	1338
Aguado and Braña (2014)	Cyren's rock lizard (*Iberolacerta cyreni*)	52
Maia-Carneiro et al. (2012)	Brazilian sand lizard (*Liolaemus lutzae*)	221
Güizado-Rodríguez et al. (2011)	Bunchgrass lizard (*Sceloporus palaciosi*)	52
Gadsden and Estrada-Rodriguez (2007)	Yarrow's spiny lizard (*Sceloporus jarrovii*)	149
Herczeg et al. (2004)	Common lizard (*Zootoca vivipara*)	73
Bauwens et al. (1999)	Girdled lizard (*Cordylus macropholis*)	105
Bauwens et al. (1996)	Iberian wall lizard (*Podarcis hispanica atrata*)	193
Adolph (1990)	Western fence lizard (*Sceloporus occidentalis*) Sagebrush lizard (*Sceloporus graciosus*)	529
Hertz and Huey (1981)	Largehead anole (*Anolis cybotes*)	278
Burns (1970)	Yarrow's spiny lizard (*Sceloporus jarrovii*)	208 (247)

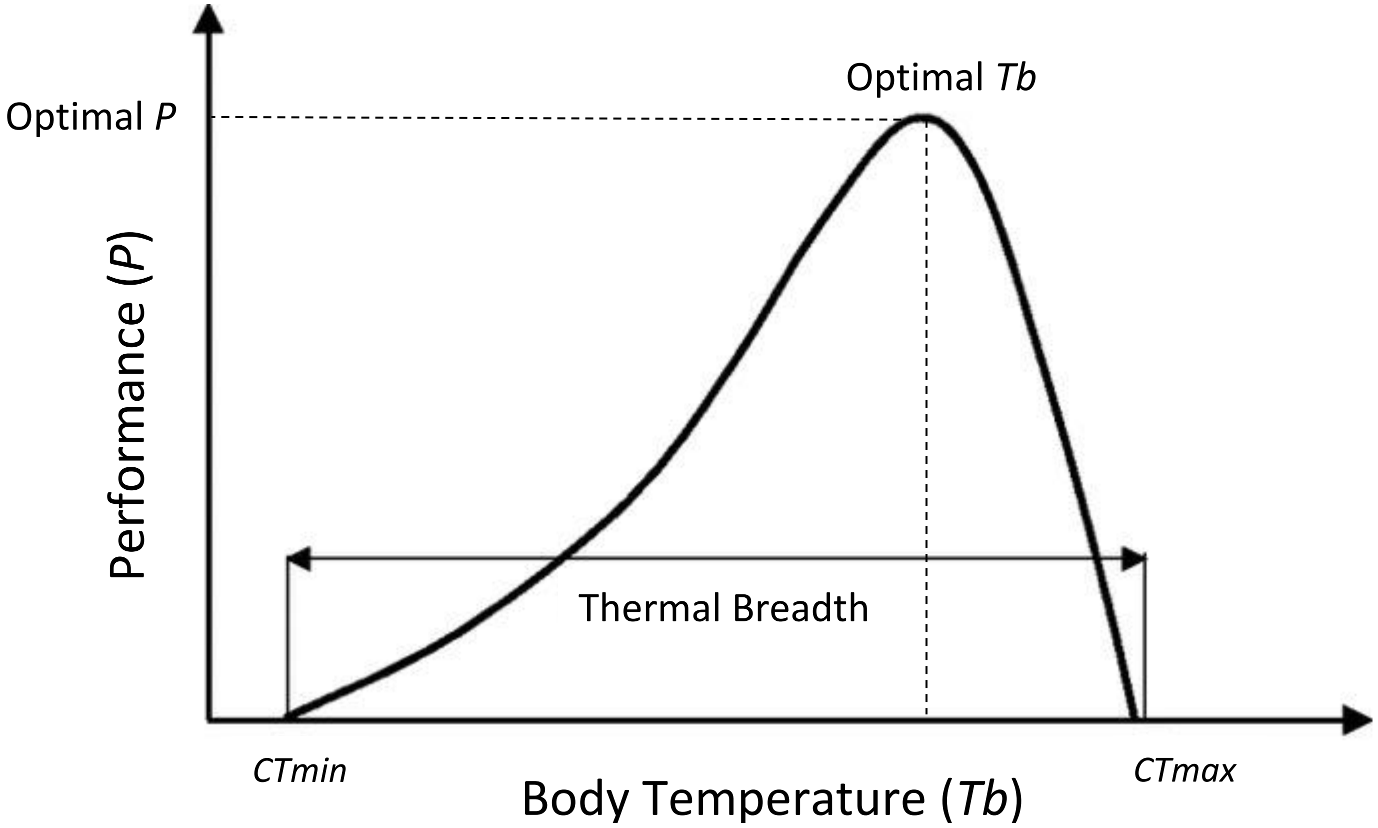

Figure 1-1. General thermal performance curve which relates some parameter representative of organismal performance (e.g. running speed, feeding rate, growth rate, reproductive output) to body temperature. The thermal breadth represents the range of tolerable temperatures and optimal temperature indicates the body temperature at which performance reaches its peak. Modified from Angilletta (2009).

Figure 1-2. An adult Yarrow's spiny lizard (*Sceloporus jarrovii*) basking on a rock at Rucker Canyon 5 talus slope. This species is distinguished by their black collar with white border. Photo taken by Nicolas Ouellette.

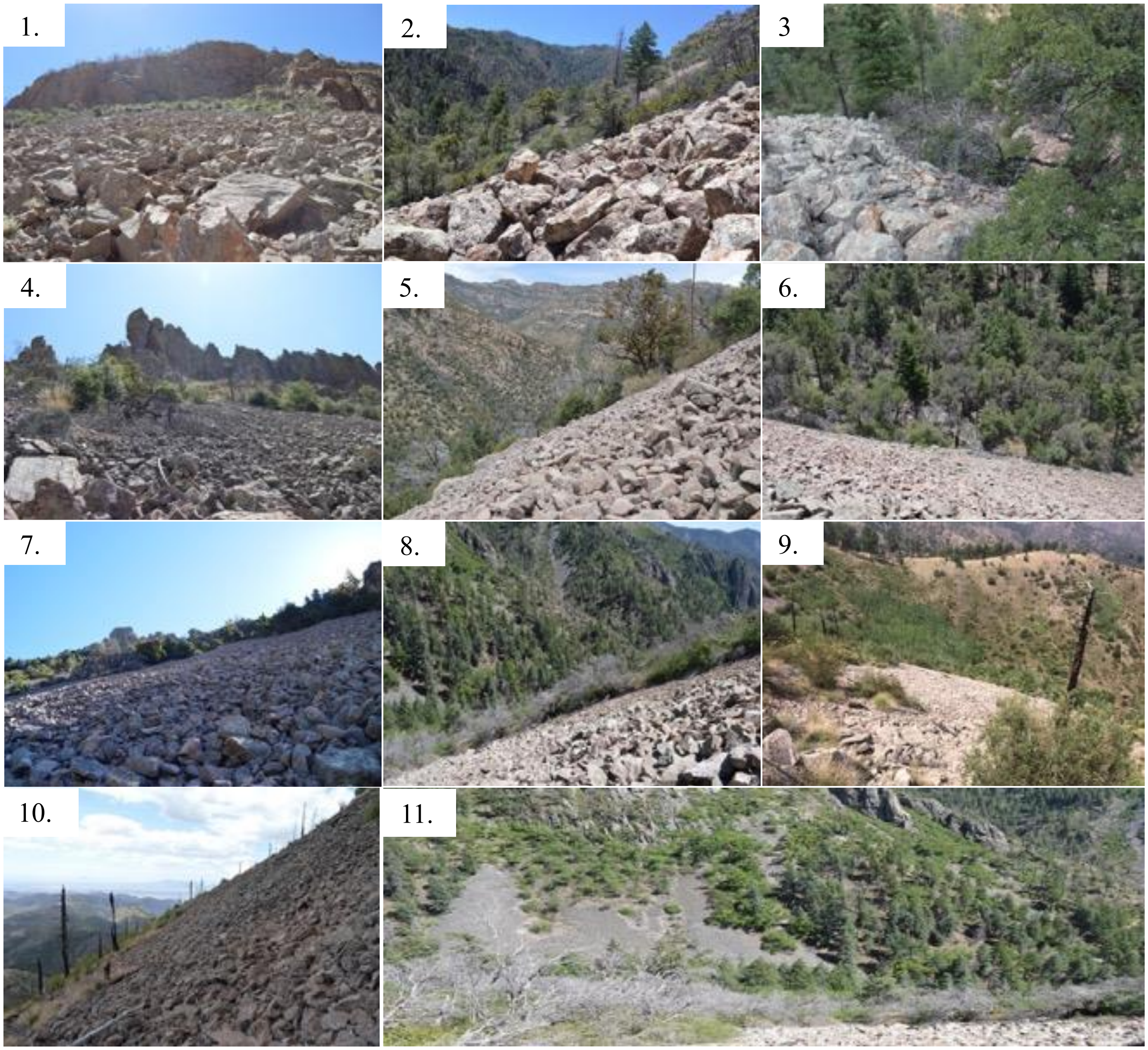

Figure 1-3. Talus slopes are comprised of large rocky outcroppings with limited vegetative growth on the slope, providing structurally homogenous habitats across an elevational gradient. Panel 1-10 are images taken from the lowest to highest elevation talus slope site in the Chiricahua Mountains, Arizona, USA. Panel 11 is an aerial image of a talus slope site.

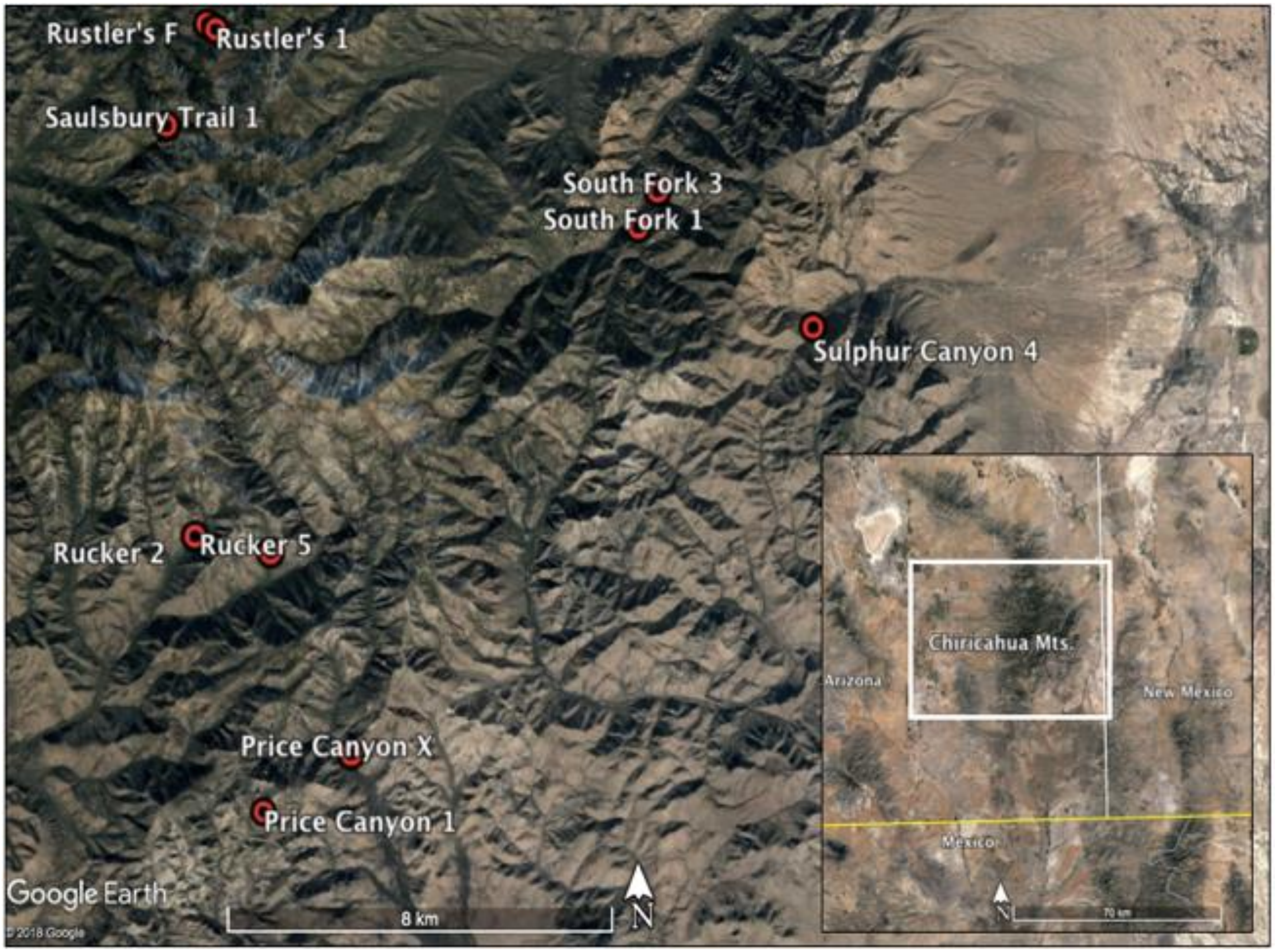

Figure 1-4. Location of talus slope study sites (n = 10) located within six canyons spanning an elevational gradient of ~1700-2700 m throughout the Chiricahua Mountains, Arizona, USA.

Figure 1-5. Photographs showing the degree of visibility of the UID assigned using felt tip marker to lizard #19 initially on June 25, 2017 (A) and 16 days later, July 11, 2017 (B).

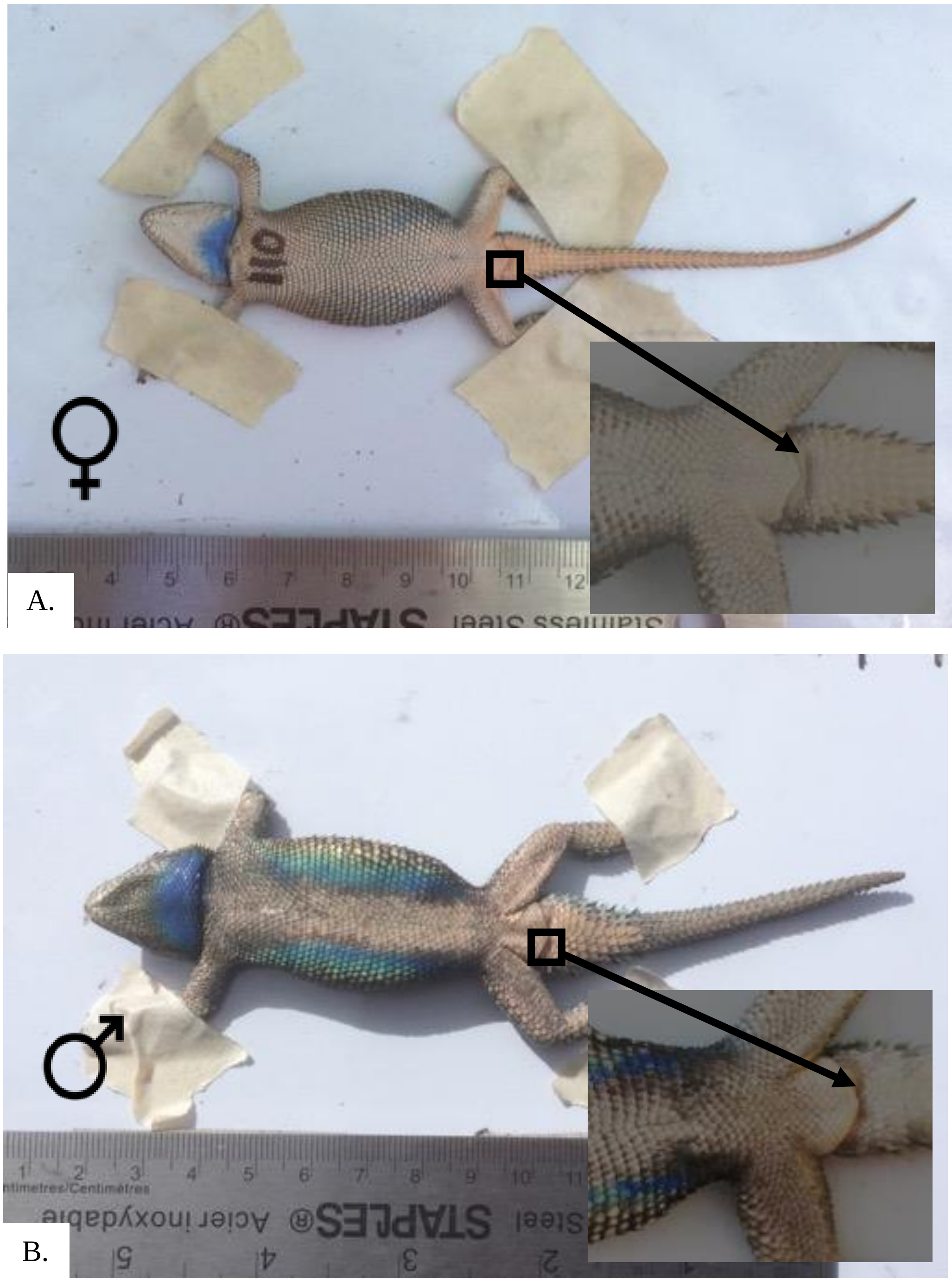

Figure 1-6. A visual comparison of the ventral side of adult female (A) and adult male (B) Yarrow's spiny lizards (*Sceloporus jarrovii*) from Chiricahua Mountains, Arizona, USA. Males are identified by their more dominant blue colouration and presence of enlarged post-anal scales.

Figure 1-7. Physical models of Yarrow's spiny lizards (*Sceloporus jarrovii*) made of hollow copper piping, painted grey to mirror the reflectance of these lizards. Ruler included for scale in centimetres.

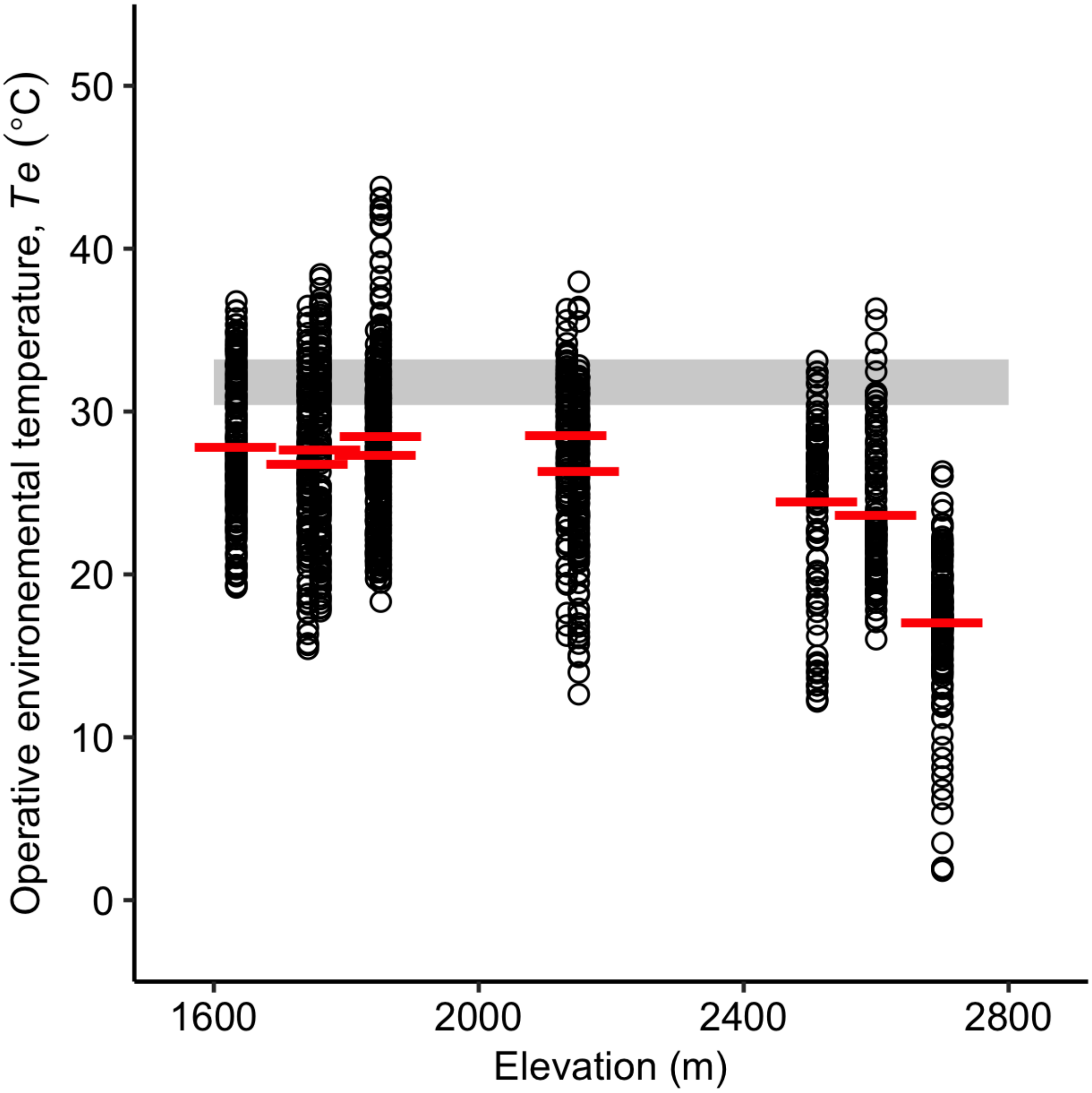

Figure 1-8. Operative environmental temperatures (*Te*, °C) as a function of elevation (m) in the Chiricahua Mountains, Arizona, USA. The grey shaded bar indicates the preferred body temperature (*Tset*) for Yarrow's spiny lizards (*Sceloporus jarrovii*). Red horizontal lines indicate mean *Te*.

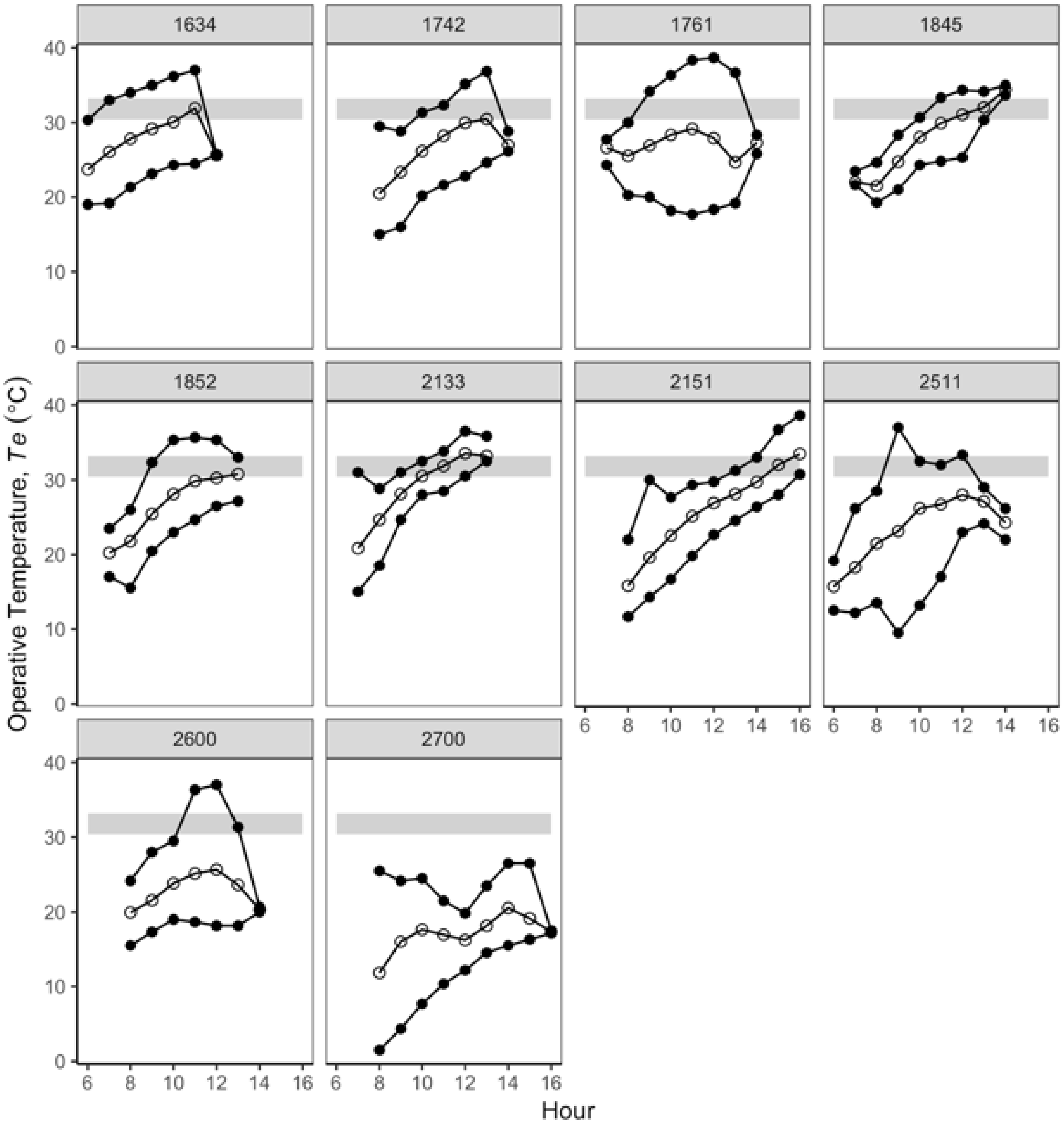

Figure 1-9. Mean hourly operative environmental temperatures (*Te*, °C) during the active season for each site (elevation in metres) in relation to the preferred body temperature (*Tset*, shaded area) of Yarrow's spiny lizards (*Sceloporus jarrovii*) in the Chiricahua Mountains, Arizona, USA. Solid points indicate mean maximum and minimum *Te*. Open points indicate the mean *Te*.

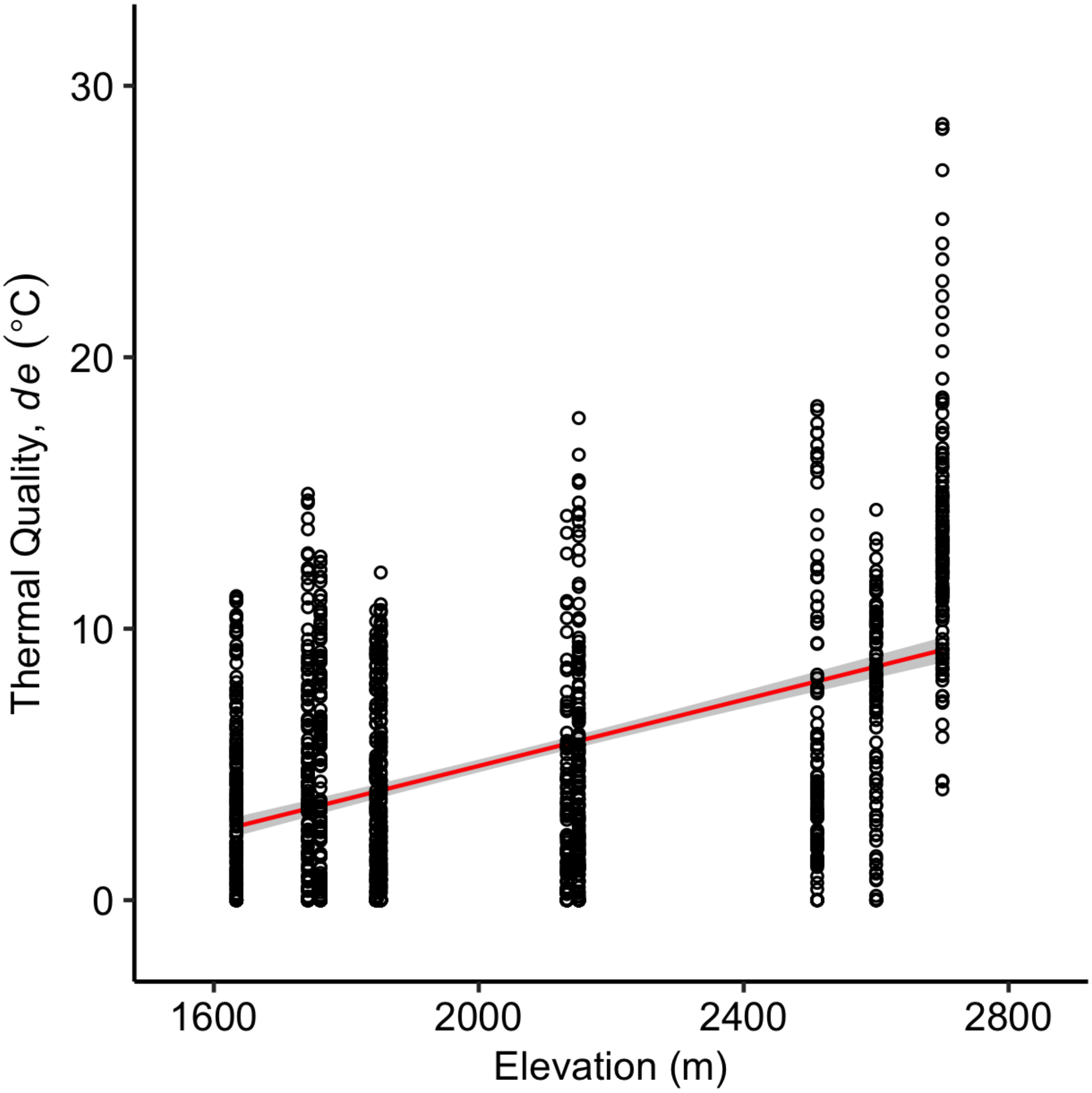

Figure 1-10. The relationship between thermal quality (*de*, °C) as a function of elevation (m) at ten talus slope sites occupied by Yarrow's spiny lizard (*Sceloporus jarrovii*) in the Chiricahua Mountains, Arizona, USA. Thermal quality decreases as elevation increases. Overlaid regression line in red and 95 % confidence interval in grey.

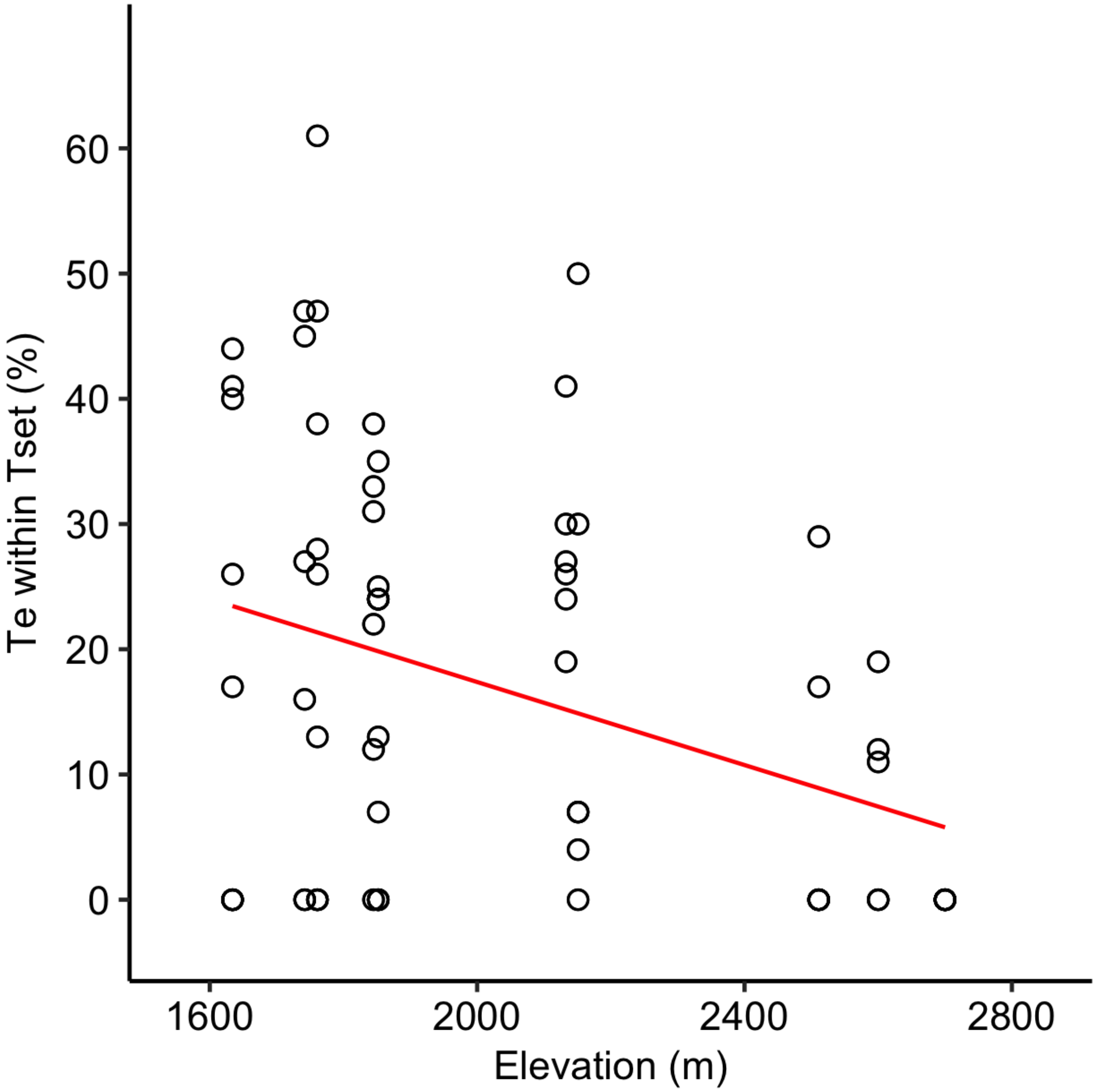

Figure 1-11. Percentage of operative environmental temperatures (*Te*, °C) within preferred temperature range (*Tset*) of Yarrow's spiny lizards (*Sceloporus jarrovii*). Overlaid regression line in red.

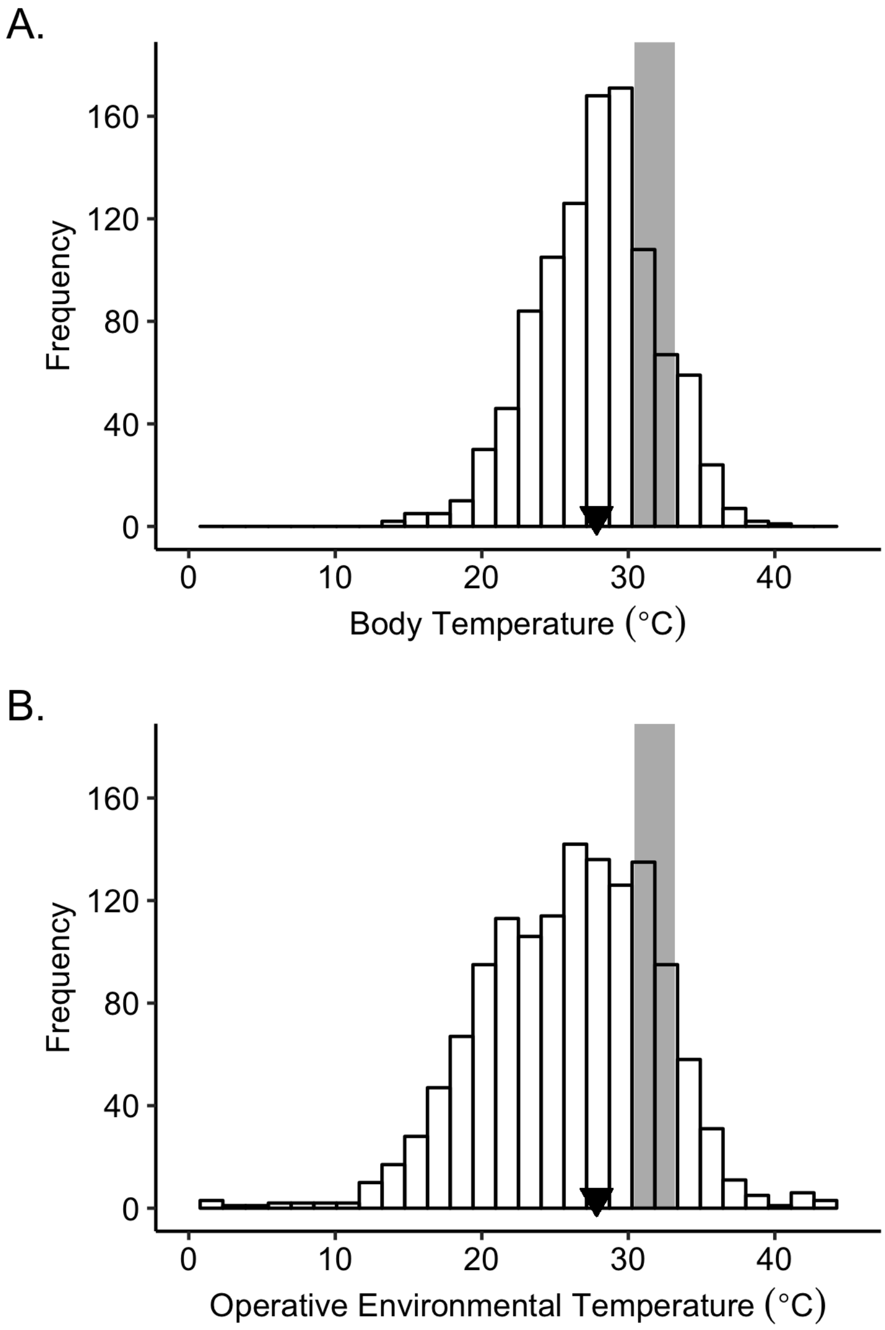

Figure 1-12. Frequency distributions of A) the body temperature (*Tb*, °C) of Yarrow's spiny lizard (*Sceloporus jarrovii*) B) the operative temperatures (*Te*, °C) during the daily active period at ten talus slope sites from 2 May to 23 July 2017 in the Chiricahua Mountains, Arizona, USA. Shaded bars indicate preferred temperature range (*Tset*) of the species. Triangles represent the mean.

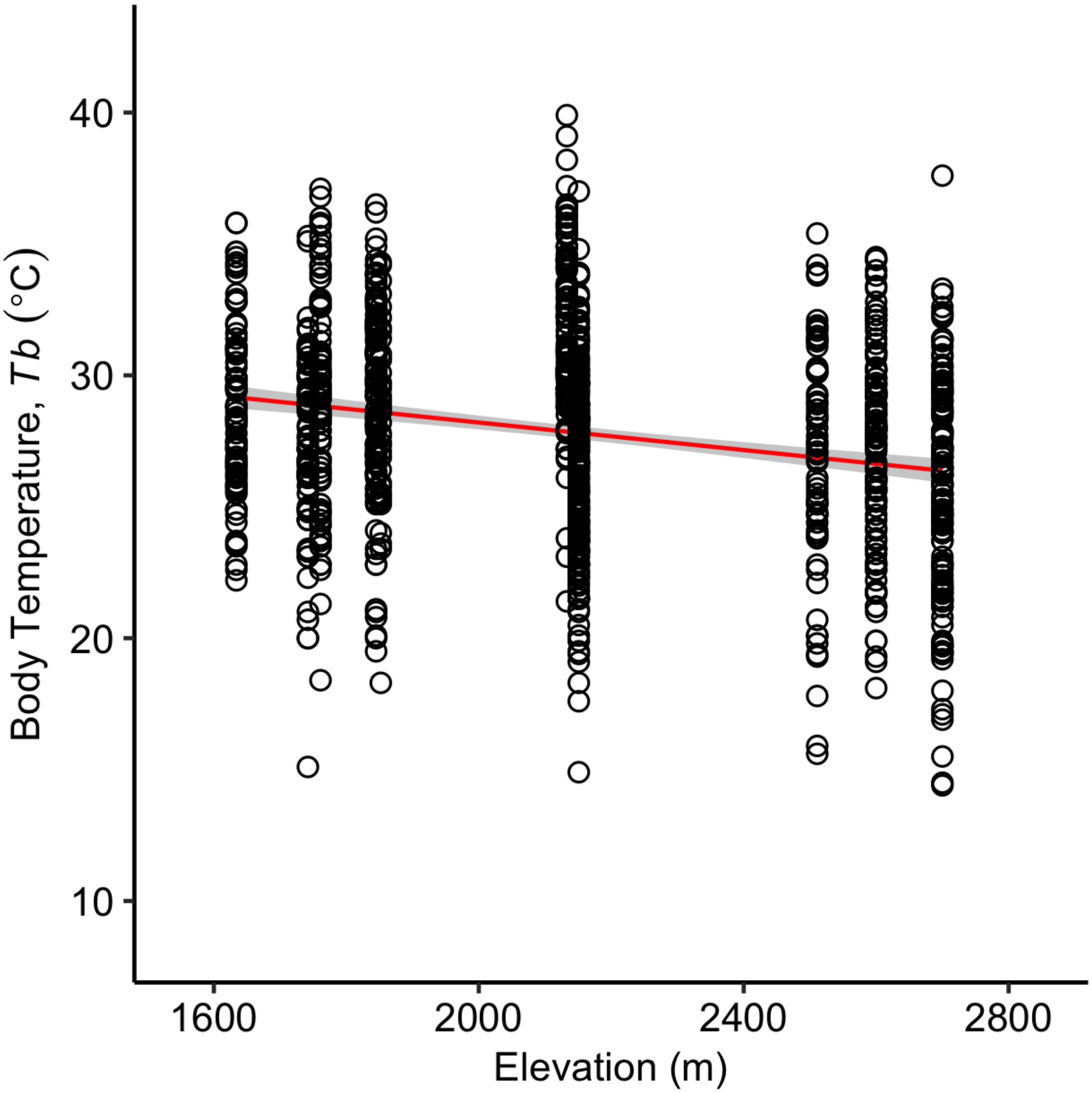

Figure 1-13. The relationship between Yarrow's spiny lizard (*Sceloporus jarrovii*) body temperature (*Tb*, °C) and elevation (m) in Chiricahua Mountains, Arizona, USA. Overlaid regression line in red and 95 % confidence interval in grey.

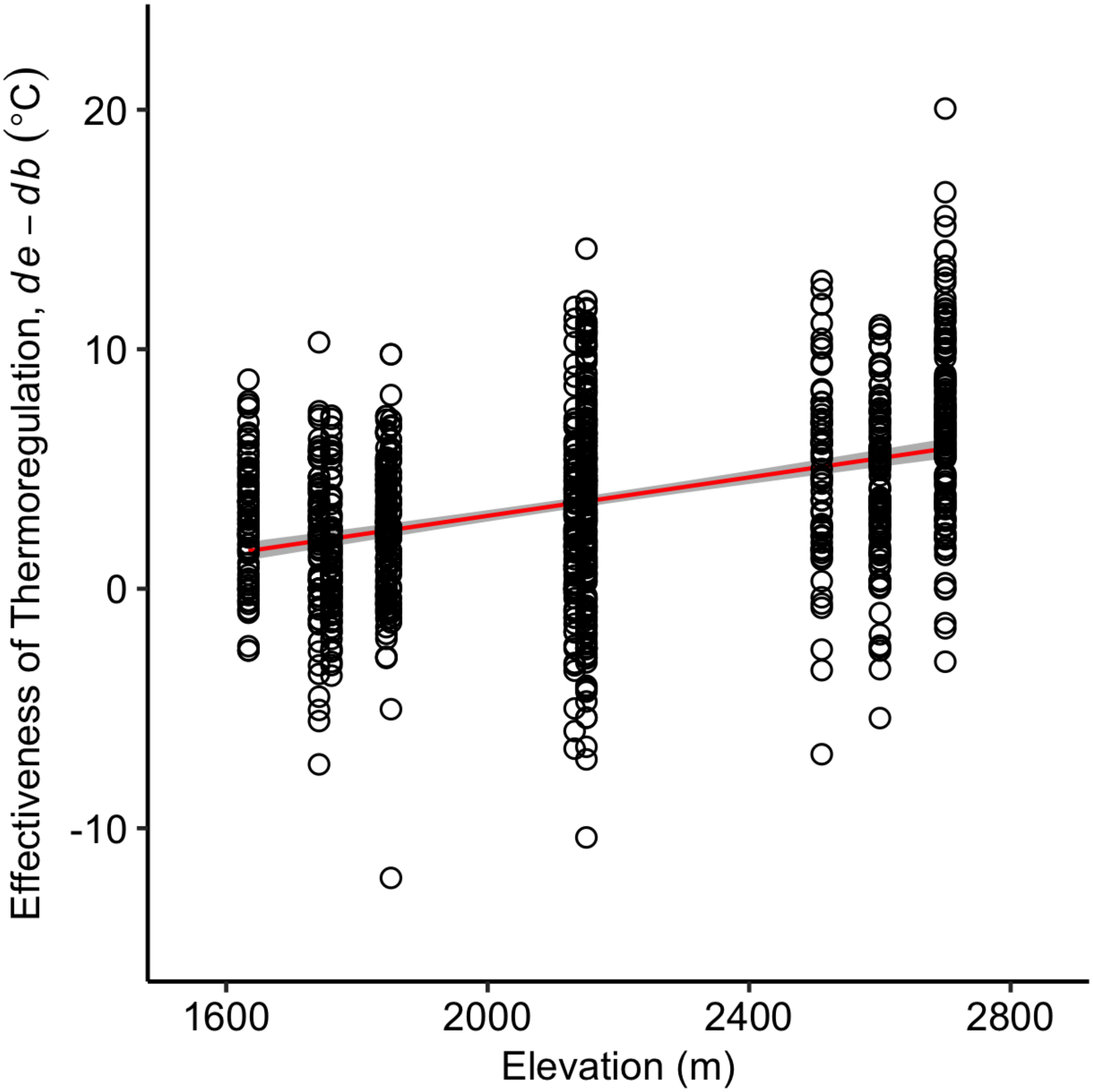

Figure 1-14. The relationship between *de-db* index of effectiveness of thermoregulation as a function of elevation (m) of Yarrow's spiny lizard (*Sceloporus jarrovii*) in the Chiricahua Mountains, Arizona, USA. Overlaid regression line in red and 95 % confidence interval in grey.

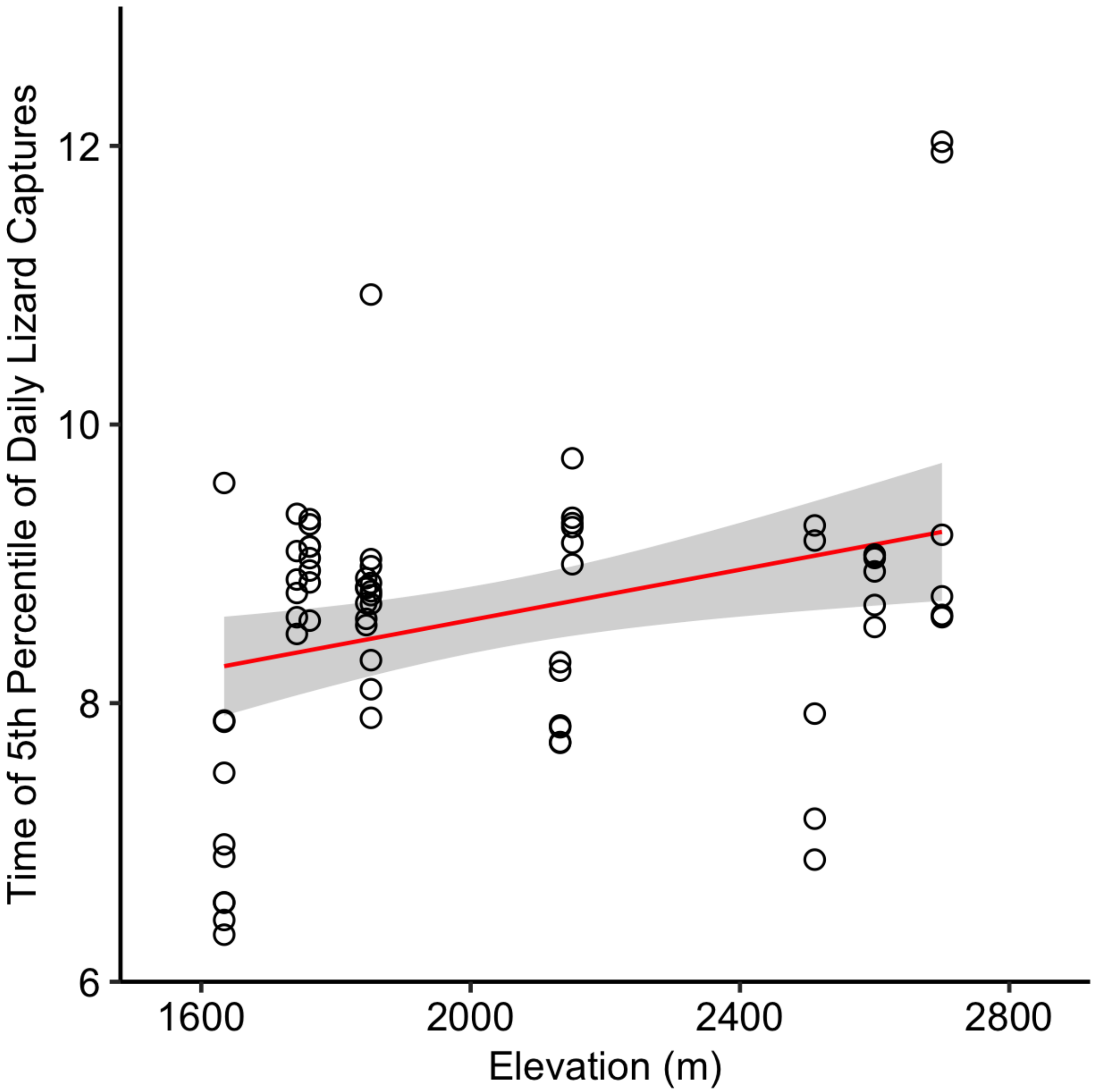

Figure 1-15. Fifth percentile of daily Yarrow's spiny lizard (*Sceloporus jarrovii)* captures as a function of elevation (m) in the Chiricahua Mountains, Arizona, USA. Overlaid regression line in red and 95 % confidence interval in grey.

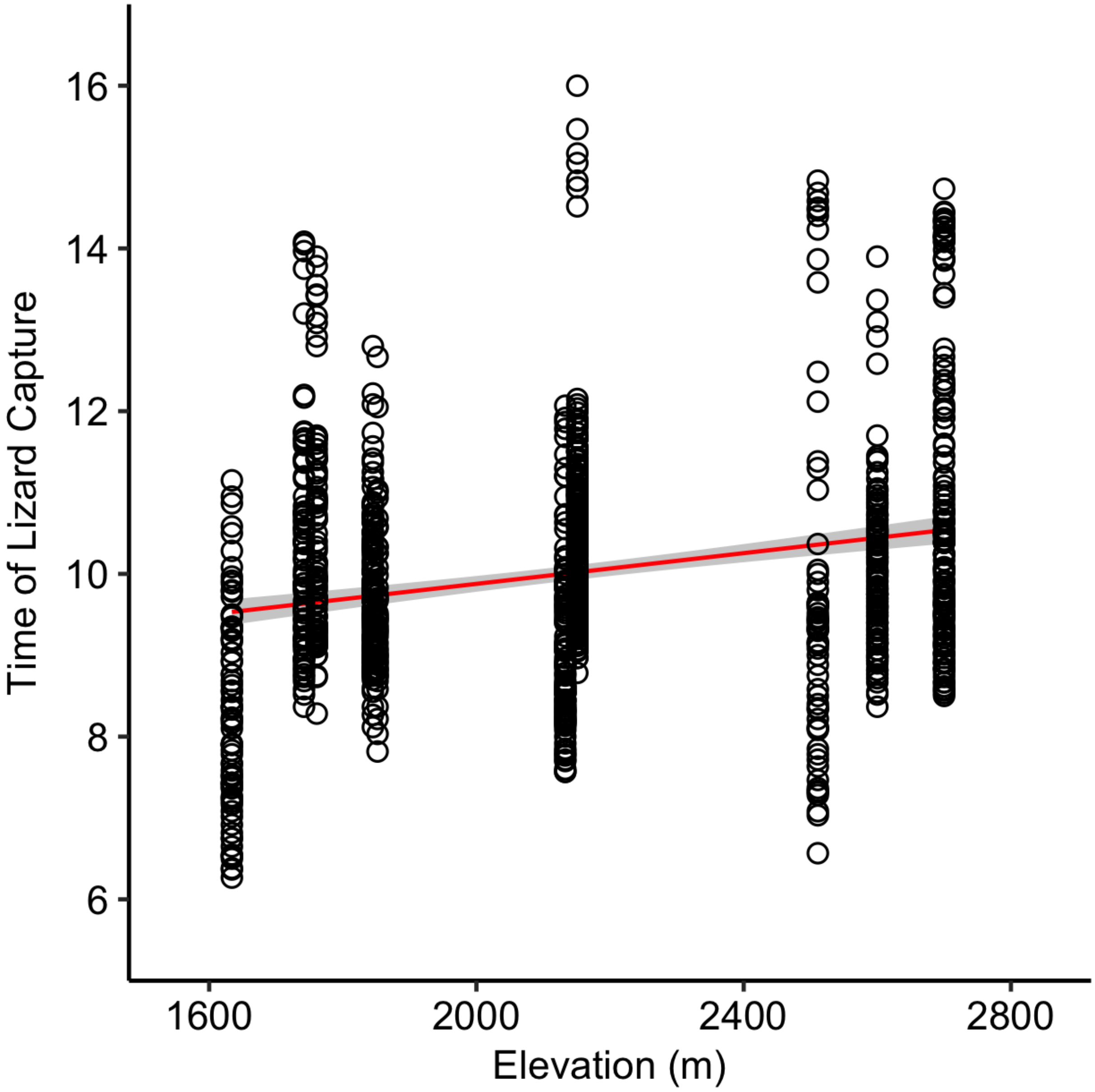

Figure 1-16. Time of Yarrow’s spiny lizard (*Sceloporus jarrovii*) captures as a function of elevation (m) in the Chiricahua Mountains, Arizona, USA. Overlaid regression line in red and 95 % confidence interval in grey.

Supplementary material for Chapter 1

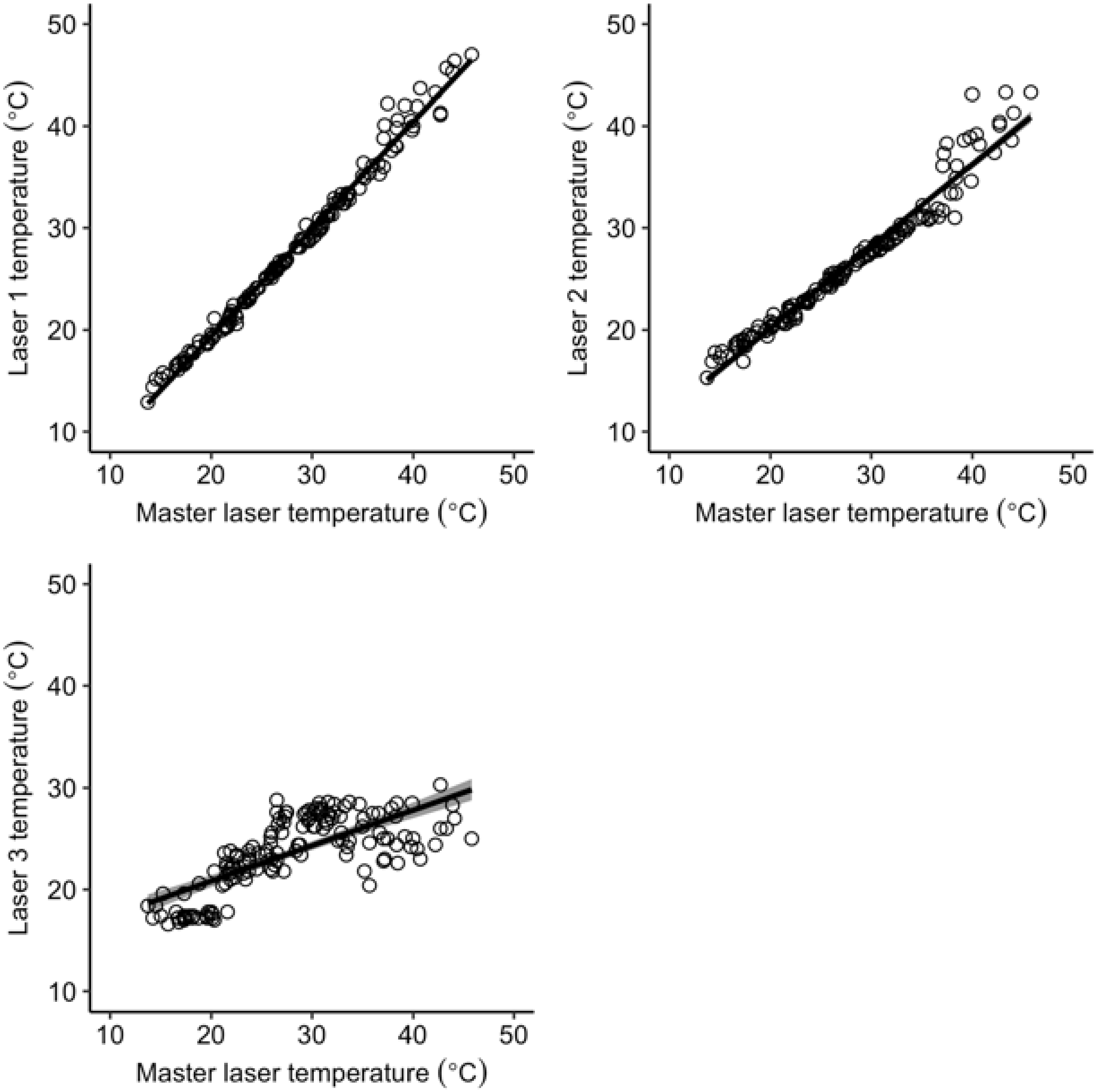

Figure 1-S1. The relationship between the temperature readings, made on rock heaters over three trials in the laboratory, of the "master" laser thermometer and the other laser thermometers used in the field. Overlaid regression line in black and 95 % confidence interval in grey.

Laser thermometer calibration

In September 2017, I performed a laser calibration in the lab in order to correct for the small variances in *Tb* readings of Yarrow's spiny lizards (*Sceloporus jarrovii*) between laser thermometers used in the field. Using reptile rock heaters (Zoo Med™ReptiCare©) and an external heat lamp I took temperature readings at the same time with each laser thermometer across the temperature gradient experienced by lizards in the field (~10 °C–40 °C). I repeated the measurements 3 times. I then used regressions to predict the temperature of each laser as a function of my "master" laser (Fluke 566 infrared thermometer, Fluke Corporation, Everett, Washington, USA).

There was a high correlation between master laser thermometer and the three other laser thermometers (laser 1: $R^2 = 0.99$, laser 2: $R^2 = 0.96$, laser 3: $R^2 = 0.54$ (Figure 1-S1). The mean difference between the three lasers from the master were 0.22 °C, 1.40 °C and 4.29 °C. These values are within or at least very close to the accuracy (± 1.1 °C) of the laser thermometer. Only 4 % of total lizard *Tb* readings in the field were taken with laser 3. Despite its poorer performance, I used the linear equation to compute corrected *Tb* readings that I then used for all subsequent analyses.

CHAPTER 2

Differences in thermoregulation by ornate tree lizards (*Urosaurus ornatus*) between two habitats that differ in thermal quality

Introduction

Although environmental temperatures vary tremendously through space and time, most organisms regulate their body temperature (*Tb*; Table 1-1) within a narrow range. The ability to respond to environmental thermal gradients and maintain a *Tb* within this narrow range, is beneficial for optimization of physiological processes (Huey and Bennett 1987). For instance, a *Tb* 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 *Tb* (Halliday et al. 2015b). Consequently, *Tb* has direct implications for fitness of animals.

Ectotherms are of particular interest when considering *Tb* and its effects on performance due to their limited ability to regulate *Tb* through metabolism (Huey and Kingsolver 1989). Because ectotherms have low metabolic rates, they have limited physiological control over their *Tb* and are dependent on other mechanisms of thermoregulation (Bennett 1980, Huey and Kingsolver 1989). As compared to endotherms, ectotherms use a much more energetically affordable strategy of temperature regulation through behaviour. By altering their behaviour, ectotherms are able 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 (Hertz and Huey 1981, Stevenson et al. 1985, Adolph 1990). Using behavioural thermoregulation, ectotherms are able to maintain an optimal body temperature (*To*; Table 1-1) and respond to environmental temperature changes (Huey and Stevenson 1979, Seebacher 2005, Glanville and Seebacher 2006).

Not all ectotherms thermoregulate to the same extent. Thermoregulatory strategies can range from thermoconformity, where the organism does not thermoregulate and *Tb* matches the environmental temperatures (Ruibal 1961), to active and nearly perfect thermoregulation, where behaviour is used to adjust *Tb* within a narrow range of *Tb* (Sartorius et al. 2002b). Differences in the costs and benefits of thermoregulation are assumed to account for this variation. The main benefit of thermoregulation is that it allows organisms to obtain a *Tb* that optimizes their fitness (Huey and Slatkin 1976). 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 (Pianka and Pianka 1970, Huey and Slatkin 1976). 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 *Tb* in heterogenous 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 *Tb* within its preferred body temperature range (*Tset*; Table 1-1) is a habitat of high thermal quality (Huey 1991, Hertz et al. 1993). 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 *Tb* close to *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 *To*.

Although there has been support for the predictions of the cost-benefit model of thermoregulation both in the field and in the laboratory (Huey 1974, Huey and Webster 1976, Withers and Campbell 1985, Hertz et al. 1993, Herczeg 2006), studies conducted in thermally-challenging climates have cast doubt on the general applicability of the model (Blouin-Demers and Weatherhead 2001, Blouin-Demers and Nadeau 2005, Row and Blouin-Demers 2006, Edwards and Blouin-Demers 2007, Picard et al. 2011, Aguado and Braña 2014, Bouazza et al. 2016). The most rigorous test of the cost-benefit model of thermoregulation to date used a global comparative approach of 22 lizard species and found that poor thermal quality lead 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 *Tb* that is far from *To* 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 *Tb*. Therefore, even without thermoregulation, an animal living in the tropics will attain a

Tb close to *Tset* with little or no effort. For water pythons living in the tropics of Australia, the 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 *Tb* 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 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. Here, I tested the hypothesis that thermal quality of a habitat dictates investment in thermoregulation by ornate tree lizards (*Urosaurus ornatus*; Figure 2-1). To test this hypothesis, I used two adjacent habitats that contrast in their thermal quality. Although tree lizards exploit a wide variety of habitat types throughout their broad North American distribution (Herrel et al. 2001), trees and boulders are their most commonly used microhabitats (Smith 1996, Herrel et al. 2001). I used ten study sites that each straddled the same two habitat types: 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 *Tset* (32.2–36.0°C) for a longer period in the day than the upland habitat. I 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.

Methods

Ethical note

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).

Study species and sites

The ornate tree lizard (*Urosaurus ornatus*) is a small diurnal heliothermic (gains heat from the sun) lizard. Both sexes defend territories and maintain small stable home ranges throughout the summer months (M'Closkey et al. 1987). The ornate tree lizard is oviparous and females may lay more than one clutch per year (Haenel 2011). Tree lizards are one of the most abundant lizard species in the USA (Tinkle and Dunham 1983); they occupy a variety of habitat types from desert flatlands with sparse vegetation to juniper-oak and pine-oak woodlands (Smith and Ballinger 1995). For this study, I 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 2018a). The wash is comprised of predominantly rocks and fallen logs and is largely devoid of vegetation, whereas the upland consists of pine-oak woodlands (Figure 2-2). 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 2018a).

I studied tree lizards at ten sites throughout Cave Creek Canyon in the Chiricahua Mountains of southeastern Arizona, USA from 1 May to 21 July 2018 (Table 2-1). Each site extended 300 m along the wash and extended 50 m into the adjacent upland (Figure 2-3). Sites were separated by at least 300 m which is further than tree lizard dispersal distance (Paterson

2018). Part way through the season, I extended the wash by between 100 m and 300 m to increase the sample size in the wash. Capture sessions were on approximately a 10-day cycle (Table 2-2), and each site was visited between seven and nine times. Site 3 was abandoned after the second capture session due to poor capture success.

Field data collection

Each day, I caught lizards by rod and noose (832 lizards captured 1251 times; Table 2-3) during their daily active period (earliest capture 06:34 MST, latest capture16:41 MST). Individuals were captured between 1 (n = 554) and 7 times (n = 1) and excluding individuals only captured once, lizards were captured an average of approximately 2.5 times. 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. There were daily fluctuations in the time and length of the active period due to the location of the site relative to the rising sun, as well as daily variation in temperature and precipitation. Overall, 99 % of captures were between 7:00 MST and 16:00 MST. 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, I assigned each lizard a unique number for identification (UID) and marked this number on both their head and stomach using a felt tip marker to allow for repeated measures of individuals. This marking technique has been used for reliable identification in other small lizard species (Jones and Ferguson 1980, Simon and Bissinger 2011). This identification method is non-permanent and is shed off with the skin (non-continuously) approximately every three to eight weeks (Todd 2005). For lizards that were shedding at the time of capture, I carefully removed the scales on the head and stomach region before marking. In addition, I was able to use size, sex, and unique characteristics such as medical cauterized markings from Paterson (2018), tail autonomy, and throat colouration to confirm my identification if there were any doubts. Because both male and female tree lizards maintain small and stable territories (M'Closkey et al. 1987, Thompson and Moore 1991) on occasion I was able to use GPS locations to confirm UIDs. However, due to the high tree lizard density at my sites there may still have been some unaccounted pseudoreplication, but because I used spot-sampling and *Tb* is so variable among individuals within a day, treating some *Tb* measurements as independent even if they may not have been should not unduly impact the biological significance of the effects obtained.

I determined the sex of each lizard 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 (Figure 2-4). Snout-vent length (SVL) was measured using digital calipers (± 0.1 mm). SVL is the preferred metric for measuring size in lizards because body mass typically fluctuates with variation in stomach contents, fat storage, and reproductive status (Dunham 1978, Haenel and John-Alder 2002). In addition, body mass was measured 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).

Field active body temperature

I recorded the time (to the nearest minute) it took to capture each lizard because lengthy pursuits may influence *Tb* due to stress or prolonged exposure in the sun. Immediately after a lizard was captured, skin surface temperature (*Tsk*) was measured as an estimate of *Tb* using an infrared laser thermometer (IRT) pointed at the cloaca. *Tsk* is particularly suited for small-bodied lizards whose *Tb* are easily influenced by handling, both due to stress and heat transfer (Marler and Moore 1991, Langkilde and Shine 2006). Validation studies have indicated that *Tsk* gives an accurate estimate of cloacal temperature (*Tb*) in small lizards (Herczeg 2006, Hare et al. 2007, Besson and Cree 2010, Carretero 2012, Bouazza et al. 2016). To measure *Tsk* 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. In subsequent sections, *Tb* will indicate *Tsk*.

Preferred body temperature range

The preferred body temperature range or set-point range (*Tset*) of a species is determined by allowing individuals to select *Tb*'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). *Tset* is assumed to include the optimal temperature for performance and is a highly conserved trait of a species (Light et al. 1966, Angilletta and Werner 1998). For my research, I used the *Tset* range for adult tree lizards (32.2–36.0 °C) calculated by Paterson and Blouin-Demers (2018a) 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 (Licht 1965, Gilbert and Miles 2016)

Accuracy of body temperature

The difference between field active *Tb* and *Tset* (Huey 1982) indicates how closely ectotherms achieve *Tb* within the preferred range for the species (i.e. accuracy of body temperature, *db*). I measured *db* following Hertz et al. (1993) by calculating the deviation of *Tb* from *Tset* in absolute values. When *Tb* was over *Tset*, the difference between *Tb* and the upper bound of *Tset* was used to measure *db*. When the *Tb* was below *Tset*, the difference between *Tb* and the lower bound of *Tset* was used to measure *db*. When *Tb* was within *Tset*, the *db* value calculated was zero. The magnitude of departure of *Tb* from the upper or lower bounds is a measure of *db*. Note that deviations of equal magnitude above and below *Tset* are deemed of equal physiological importance (Hertz et al. 1993); however, we know that deviations above the upper bound of *Tset* are more problematic for organisms because the decline in performance is much sharper (see Figure 1-1).

Operative environmental temperature

To evaluate whether ectotherms are actively thermoregulating, information on the distribution of *Tb* that a non-thermoregulating animal would achieve is needed (Heath 1964, Huey et al. 1977). Operative environmental temperature (*Te*), the result of biophysical and morphological factors that influence an ectotherm's *Tb*, represents the equilibrium temperature of an inanimate object (one lacking physiological or behavioural controls) with the same thermal characteristics as the study animals. *Te* is traditionally measured with physical models, with similar characteristics as the animal (i.e. shape, size, colour), placed throughout the various microhabitats available (Bakken 1992). For small ectotherms, hollow metal (typically copper) or plastic models provide an accurate estimate of the *Tb* that a non-thermoregulating animal would achieve due to their limited capacity to control rates of heat exchange (Angilletta 2009). 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 *Te* values measured with physical models are an accurate representation of the *Tb* of non-thermoregulating lizard. The random distribution of *Te* in a habitat describes the "null" distribution of *Te* expected in non-thermoregulating animals (Christian and Tracy 1985, Hertz et al. 1993).

Due to the small body size of tree lizards, I measured *Te* with temperature loggers (± 0.5ºC, Thermochron iButton DIS1921G-F5, Dallas Semiconductor, Sunnyvale, California) painted brown to reflect the thermal properties of tree lizards (Figure 2-5). These thermal models were validated by Paterson and Blouin-Demers (2018a). 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 of lizards in each habitat. I 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.) (Cowles and Bogert 1994, Christian et al. 1983). In my observations where perch location was noted (n = 1101), 98 % of lizards perched on trees, logs or rocks, so I assumed these microhabitats accurately represent the microhabitats used by tree lizards in the wash and upland habitats. I 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.

Thermal quality

Thermoregulatory performance of an organism depends on the frequency distribution of microhabitats in its environment (Tracy and Christian 1986). Typically, these distributions have been quantified by the index *de* (Hertz et al. 1993), which equals the absolute difference between an animals preferred temperature and the mean operative temperature of its environment. *de*, however, is a relatively simplistic descriptor of thermal quality that is suitable only for habitats that are structurally similar and provide homogenous thermoregulatory opportunities, such as the talus slopes of Chapter 1. For more structurally complex habitats, such as the upland in this study, averaging *Te* across space and time does not provide information about the relative availability or spatial structure of microhabitats of an environment. Specifically, in the upland habitat, it is difficult to adequately measure the range of refuge temperatures available to tree lizards due to the complex nature of the habitat. There are many structural components such as trees, logs, fallen bark, rocks, and leaf litter that could provide refuge for tree lizards and measuring each of their relative availabilities is a monumental challenge. For this reason, I chose to quantify thermal quality in the wash and upland habitat following Paterson and Blouin-Demers (2018a).

Thermal quality was measured in each habitat with temperature loggers whose readings were compared to the species' *Tset*. To quantify the thermal quality of each habitat, I calculated the proportion of the day that a lizard could achieve *Tset*. Instead of calculating an average *Te*, which assumes I was able to sample all microhabitats in proportion to their relative availability, which I do not believe is possible, for each minute the models were deployed, I calculated the maximum and minimum daily *Te* available to lizards in a habitat. I considered *Tset* achievable as long as the maximum temperature was above the lower bound of *Tset* and the minimum temperature was below the upper bound of *Tset* (Paterson and Blouin-Demers 2018a).

Statistical analyses

I first explored the potential relationships between my individual predictor and response variables using scatterplots. Linear mixed effects model (LMM) assumptions were examined using SjPlot (Ludecke 2015). I did not detect any violations of model assumptions including linearity, normality, homoscedasticity, independence of residuals, and normal distributions of the random effects. When I had multiple predictor variables in a model, variance inflation factors were all below 2, so multicollinearity was not an issue (O'Brien 2007). Mixed-model conditional R^2 values were calculated using the r.squaredGLMM() function (MuMIn package, Barton 2018). Partial R^2 values were calculated using r2beta() function (r2glmm package, Jaeger 2017).

To compare thermal quality between habitats, I used a LMM (package: lme4, function: lmer; Bates et al. 2014) to test whether the proportion of the day a lizard could achieve *Tset* was related to Julian date and habitat type. I included site as a random effect because I measured thermal quality multiple days per site.

To test whether habitat had an effect on *Tb* and *db* I constructed separate LMM. I included habitat, my variable of interest, as a fixed effect. Because the data were collected in the field, I included various biologically relevant control variables that affect body temperature of lizards. Sex was recorded as a three-factor variable to incorporate reproductive status (male, non-gravid female and gravid female). Sex was included in the model as a fixed effect to control for differences in *Tb* between sex and/or reproductive state. SVL was included as a fixed effect to control for the influence of size on *Tb*. I included Julian date of capture and time of day as continuous fixed effects to control for the increase in temperature over the season and during the day respectively. The time it took to capture a lizard may influence *Tb* due to increased exposure to sun or stress, so I included this variable as a continuous fixed effect. Since I assigned each individual a UID unique to their site of capture, I incorporated lizard UID as a random effect to control for repeated captures. Likewise, I included site as a random effect to control for any possible site effects. I also included thermometer ID to control for any differences in laser thermometers used by researchers catching and measuring body temperatures of lizards.

Results

Thermal quality of habitats

A total of 72 048 *Te*'s were recorded in both habitats over 71 field days. Throughout the active season, *Te* ranged from 9.5 ºC to 78 ºC (mean ± SE = 37.4 ± 0.05 ºC) in the wash and from 10 ºC to 66 ºC (mean ± SE = 30.5 ± 0.03 ºC) in the upland. In general, lizards could reach *Tset* earlier in the day in the wash habitat than in the upland habitat and could remain active at *Tset* later in the day in the wash habitat (Figure 2-6). The proportion of the day that *Tset* 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, $p < 0.001$; Figure 2-6). Therefore, the wash habitat had higher thermal quality than the upland habitat, consistent with Paterson and Blouin-Demers (2018a).

Body temperature

In total, I recorded 690 lizard *Tb* measurements in the upland and 561 in the wash (Table 2-3). Across both habitats, *Tb* ranged from 15.5 ºC–38.6 ºC (31.5 ± 0.1 ºC) throughout the active season. There was no significant difference between mean *Tb* of males (n = 632; 31.4 ± 0.2 °C) and females (n = 619; 31.5 ± 0.1 °C) (t = 0.72, df = 1249, 95 % CI = -0.253–0.546, $p = 0.472$). Likewise, there was no significant difference between the mean *Tb* of gravid females (n = 150; 31.9 ± 0.3 °C) and non-gravid females (n = 469; 31.5 ± 0.2 °C) (t = 1.27, df = 273, 95 % CI = -1.028–0.224, $p = 0.207$).

When examining differences in lizard *Tb* between habitat types, I found no significant difference (t = 1.61, df = 1176, 95 % CI = -0.072–0.735, $p = 0.107$) between the mean *Tb* of lizards caught in the upland (n = 690; 31.6 ± 0.1 °C) and the wash (n = 561; 31.3 ± 0.2 °C). There was a marginally non-significant effect of habitat type on *Tb* ($R^2 = 0.29$, F = 3.35, df = 1, 940, 95 % CI = -0.703–0.015, $p = 0.061$; Table 2-4, Figure 2-7) when controlling for confounding variables and the estimated difference between habitats was very small (0.3 °C).

Accuracy of body temperature

There was no significant difference between mean *db* of males (n = 632; 1.86 ± 0.1 °C) and females (n = 619; 1.78 ± 0.1 °C) (t = -0.51, df = 1248, 95 % CI = -0.369–0.217, $p = 0.614$; Figure 2-8). Likewise, there was no significant difference between the mean *db* of gravid females (n = 150; 1.59 ± 0.2 °C) and non-gravid females (n = 469; 1.84 ± 0.1 °C) (t = 1.19, df = 306, 95 % CI = -0.169–0.686, $p = 0.235$).

When examining differences in lizard *db* between habitat types, I found a significant difference (t = -2.11, df = 1187, 95 % CI = -0.614–-0.022, $p = 0.035$) between the mean *db* of lizards caught in the upland (n = 690; 1.68 ± 0.1 °C) and the wash (n = 561; 2.00 ± 0.1 °C). The deviations of lizard *Tb* from *Tset* (*db*) ranged from 0 to 16.7 °C (mean ± SE = 2.0 ± 0.1°C) in the wash and from 0 to 15.8 °C (mean ± SE = 1.7 ± 0.1 °C) in the upland. There was a significant effect of habitat type on *db* when controlling for confounding variables ($R^2 = 0.23$, F = 3.92, df = 1, 939, 95 % CI = 0.009–0.562, $p = 0.044$; Table 2-5, Figure 2-9) where lizards in caught in the upland have a slightly lower *db* (more accurate) than lizards caught in the wash. In addition, 45 % of the lizards captured in the upland had *Tb* within *Tset*, whereas the wash only had 39 % and lizards in the upland were closer to *Tset* when I caught them (80 % of *Tb* measurements were within 3 ºC of *Tset*).

Discussion

In Chapter 1, I demonstrated that thermal quality impacts the effectiveness of thermoregulation by Yarrow’s spiny lizards (*Sceloporus jarrovii*) in the opposite direction than predicted by the cost-benefit model of thermoregulation. Spiny lizards thermoregulated more effectively as elevation increased despite the corresponding increase in costs of thermoregulation that are associated with high elevations (poorer thermal quality). In this chapter, I showed that thermoregulation by ornate tree lizards (*Urosaurus ornatus*) is also affected by the thermal quality of the habitat in which they reside. Consistent with Paterson and Blouin-Demers (2018b), I 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 (*Te* within *Tset*) for a longer daily duration than the upland, indicative of higher thermal quality. Tree lizards caught in the lower thermal quality upland habitat more accurately (*db*) regulated their body temperatures (*Tb*) within their preferred temperature range (*Tset*). 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 *Te* in the wash = 37.4 ± 0.05 ºC and in the upland = 30.5 ± 0.03 ºC).

Because of the numerous microhabitats available in the upland and wash habitat, using standard indices such as *de* (Hertz et al. 1993) and *de-db* (Blouin-Demers and Weatherhead 2001a) 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 I sampled (on rocks, on logs, and on trees), I believe I was able to accurately sample the microhabitats used during activity. It seems reasonable to assume that lizards are always able to seek refuge from hot temperatures, as they do not die during the day when temperatures exceed their critical maximum body temperature. Therefore, what limits lizard activity should be the surface temperatures. In the wash, lizards were able to reach their preferred body temperature earlier in the day and maintain it for a longer duration than in the upland. As the environmental temperatures increased throughout the day, lizard *Tb* in both habitats increased; however, there was not a significant difference in *Tb* (0.3 °C) between lizards caught in the wash versus the upland, despite the difference in thermal quality. Surprisingly, upland lizards, maintained body temperatures closer to the optimal temperature (*db*, measured as the absolute deviation of *Tb* from *Tset*).

The thermal exploitation index (*Ex*) has been used in research on reptilian thermoregulation (Christian and Weavers 1996, Table 2-6). *Ex* can range from 0 % to 100 %, and is 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 animals' *Tb* is within *Tset* divided by the time available for them to achieve *Tb* within *Tset* as indicated by *Te*. The higher the *Ex* value, the more the animal exploits its thermal environment when that environment is permissive. Although *Ex* could not be calculated here due to measuring spot-samples of *Tb*, I can still use its logic. In the upland, lizards had smaller *db* values (mean 1.7 °C) than lizards caught in the wash (mean 2.0 °C) despite the fact that *Tset* is available for less time in the upland (lower thermal quality). If upland lizards are more accurately regulating their *Tb*, with less time to achieve *Tb* = *Tset*, 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 *Tb* within *Tset*; 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, my 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, Row and Blouin-Demers 2006, Edwards and Blouin-Demers 2007, Bouazza et al. 2016). In a comparative global analysis on 20 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 *Tb* is close to *Tset*. 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 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*) forgoes basking, decreasing its accuracy of body temperature, following a simulated risk of predation (Herczeg et al. 2008). Paterson and Blouin-Demers (2018a) 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 foraging. Thermoregulatory costs should be low in landscapes 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. This may have made thermoregulation more costly in the wash.

In conclusion, I found that tree lizards maintain *Tb* closer to *Tset* in the upland habitat despite the lower thermal quality, which is opposite to the predictions of the cost-benefit model of thermoregulation. Between habitats that differ in the amount of solar radiation they receive, it appears that the disadvantages of thermoconfomity 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 more evidence that even in less thermally challenging environments, small differences in thermal quality between habitats still impact lizard thermoregulation.

Tables and Figures

Table 2-1. Coordinates (UTM, Zone 12R) of ten study sites in the Chiricahua Mountains, Arizona, USA where ornate tree lizards (*Urosaurus ornatus*) were studied from 1 May to 21 July 2018. Note: Map of study sites in Figure 2-3.

Study Site	E	N
1	667700	3530564
2	667397	3533052
3	668088	3528306
4	668081	3533752
5	673919	3530657
6	669406	3529429
7	667943	3530998
8	666727	3532199
9	668271	3530541
10	667781	3533355

Table 2-2. Date of capture sessions of ornate tree lizards (*Urosaurus ornatus*) at ten sites within the Chiricahua Mountains, Arizona, USA. Number of capture sessions per site ranged from seven to nine depending on sample size.

Date	Capture Session	Site
01-May-18	1	1
12-May-18	2	1
23-May-18	3	1
03-June-18	4	1
14-June-18	5	1
25-June-18	6	1
05-July-18	7	1
14-July-18	8	1
24-May-18	1	2
25-May-18	2	2
05-June-18	3	2
15-June-18	4	2
26-June-18	5	2
01-July-18	6	2
11-July-18	7	2
02-May-18	1	3
11-May-18	2	3
24-May-18	3	3
03-May-18	1	4
13-May-18	2	4
27-May-18	3	4
07-June-18	4	4
17-June-18	5	4
27-June-18	6	4
07-July-18	7	4
04-May-18	1	5
15-May-18	2	5

26-May-18	3	5
06-June-18	4	5
18-June-18	5	5
28-June-18	6	5
06-July-18	7	5
18-July-18	8	5
05-May-18	1	6
17-May-18	2	6
29-May-18	3	6
08-June-18	4	6
19-June-18	5	6
29-June-18	6	6
08-July-18	7	6
15-July-19	8	6
02-July-18	9	6
06-May-18	1	7
18-May-18	2	7
30-May-18	3	7
09-June-18	4	7
20-June-18	5	7
30-June-18	6	7
10-July-18	7	7
19-July-18	8	7
08-May-18	1	8
19-May-18	2	8
31-May-18	3	8
10-June-18	4	8
21-June-18	5	8
09-May-18	1	9
20-May-18	2	9
01-June-18	3	9
12-June-18	4	9
23-June-18	5	9
03-July-18	6	9

12-July-18	7	9
17-July-18	8	9
21-July-18	9	9
10-May-18	1	10
22-May-18	2	10
02-June-18	3	10
13-June-18	4	10
22-June-18	5	10
04-July-18	6	10
13-July-18	7	10

Table 2-3. Number of adult ornate tree lizards (*Urosaurus ornatus*) captured, with total number of lizards captured in parentheses, in the Chiricahua Mountains, Arizona, USA.

	Upland			*Wash*		
Site	Female	Male	Total	Female	Male	Total
1	27(32)	18(21)	45(53)	12(19)	15(19)	27(38)
2	30(37)	29(43)	59(80)	28(39)	22(32)	50(71)
3	1(1)	3(3)	4(4)	1(1)	1(1)	2(2)
4	46(60)	44(64)	90(124)	47(61)	50(66)	97(127)
5	19(27)	16(28)	35(55)	25(33)	26(40)	51(73)
6	22(29)	34(59)	56(88)	20(39)	14(24)	34(63)
7	32(41)	23(37)	55(78)	27(35)	19(24)	46(59)
8	22(36)	18(28)	40(64)	1(1)	4(4)	5(5)
9	21(28)	31(37)	52(65)	16(22)	20(25)	36(47)
10	25(42)	30(37)	65(79)	25(36)	26(40)	51(76)
Total	255(333)	246(357)	501(690)	202(286)	197(275)	399(561)

Table 2-4. Partial R^2, estimates and 95 % confidence intervals (CI) from the linear mixed-effects model of ornate tree lizard (*Urosaurus ornatus*) body temperature (*Tb*) collected from ten sites in the Chiricahua Mountains, Arizona, USA. The fixed effects include habitat, snout-vent length (SVL), sex, time of day, Julian date and latency to capture. The random effects include lizard UID, site and thermometer ID.

Fixed effects	Partial R^2	Estimate	2.5 %	97.5 %
Intercept	-	17.62	14.595	20.678
SVL	0.030	1.72	1.22	2.22
Male	0.004	-0.73	-1.30	-0.15
Non-gravid female	0.003	-0.61	-1.21	0.01
Wash	0.002	-0.34	-0.70	0.01
Julian date	0.000	-0.0003	-0.009	0.009
Time of day	0.123	-0.57	0.50	0.66
Latency to capture	0.004	-0.04	-0.07	-0.01

Table 2-5. Partial R^2, estimates and 95 % confidence intervals (CI) from the linear mixed-effects model of accuracy of body temperature (*db*) of ornate tree lizards (*Urosaurus ornatus*) collected from ten sites in the Chiricahua Mountains, Arizona, USA. The fixed effects include habitat, snout-vent length (SVL), sex, time of day, Julian date and latency to capture. The random effects include lizard UID, site and thermometer ID.

Fixed effects	Partial R^2	Estimate	2.5 %	97.5 %
Intercept	-	10.39	8.09	12.64
SVL	0.024	-1.16	-1.54	-0.77
Male	0.003	0.45	0.01	0.90
Non-gravid female	0.002	0.39	-0.08	0.86
Wash	0.003	0.29	0.009	0.56
Julian date	0.000	0.001	-0.006	0.01
Time of day	0.080	-0.34	-0.40	-0.28
Latency to capture	0.003	0.03	0.002	0.05

Table 2-6. Summary of studies that have used the thermal exploitation index (*Ex*; Christian and Weavers 1996). This index is calculated as the time in which an animals' body temperature (*Tb*) is within the preferred temperature range (*Tset*) divided by the time available for the animal to have its *Tb* within *Tset*.

Reference	Taxon
Bauwens et al. (1996)	Lizard
Brown and Weatherhead (2000)	Snake
Blouin-Demers and Weatherhead (2001a)	Snake
Blouin-Demers and Weatherhead (2001b)	Snake
Blouin-Demers and Weatherhead (2002)	Snake
Sartorius et al. (2002)	Lizard
Fitzgerald et al. (2003)	Snake
Blouin-Demers and Nadeau (2005)	Lizard
Catenazzi et al. (2005)	Lizard
Christian et al. (2006)	Lizard
Edwards and Blouin-Demers (2007)	Turtle
Crane and Greene (2008)	Snake
Smith et al. (2008)	Lizard
Besson and Cree (2010)	Lizard
Picard et al. (2011)	Turtle
Millar et al. (2012)	Turtle
Rowe et al. (2014)	Turtle
Rowe et al. (2017)	Turtle

Figure 2-1. Photograph of an ornate tree lizard (*Urosaurus ornatus*) basking on a log. They are small-bodied, heliothermic lizards that are abundant in many habitats.

Figure 2-2. Photographs of the two habitats used to study investment in thermoregulation by ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains, Arizona, USA. (A) upland habitat (B) wash habitat.

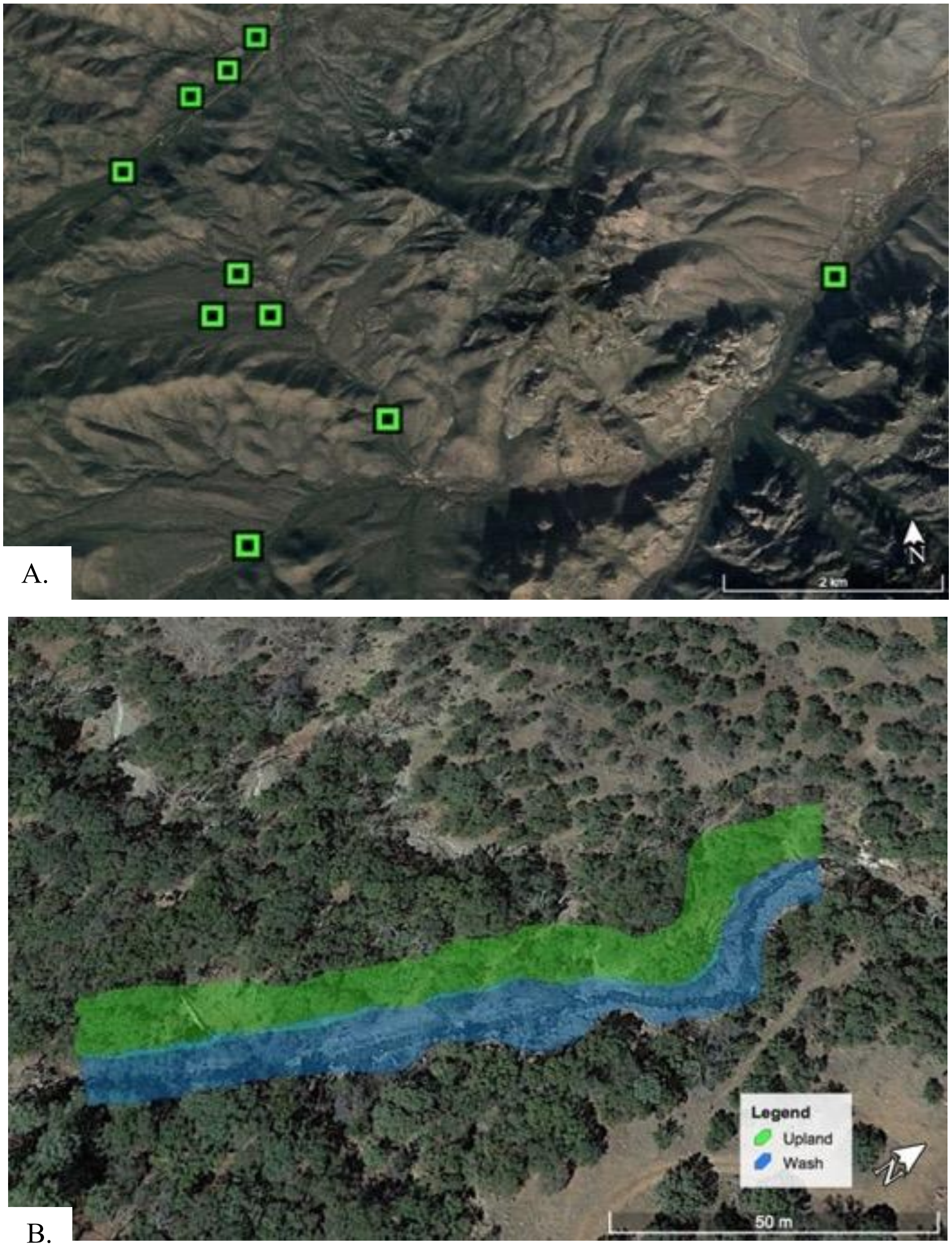

Figure 2-3. (A) Location of study sites of ornate tree lizards (*Urosaurus ornatus*) in the Chiricahua Mountains, Arizona, USA. (B) The two habitat types at one representative site (site 10) showing the upland (green) and wash (blue) habitat used by lizards.

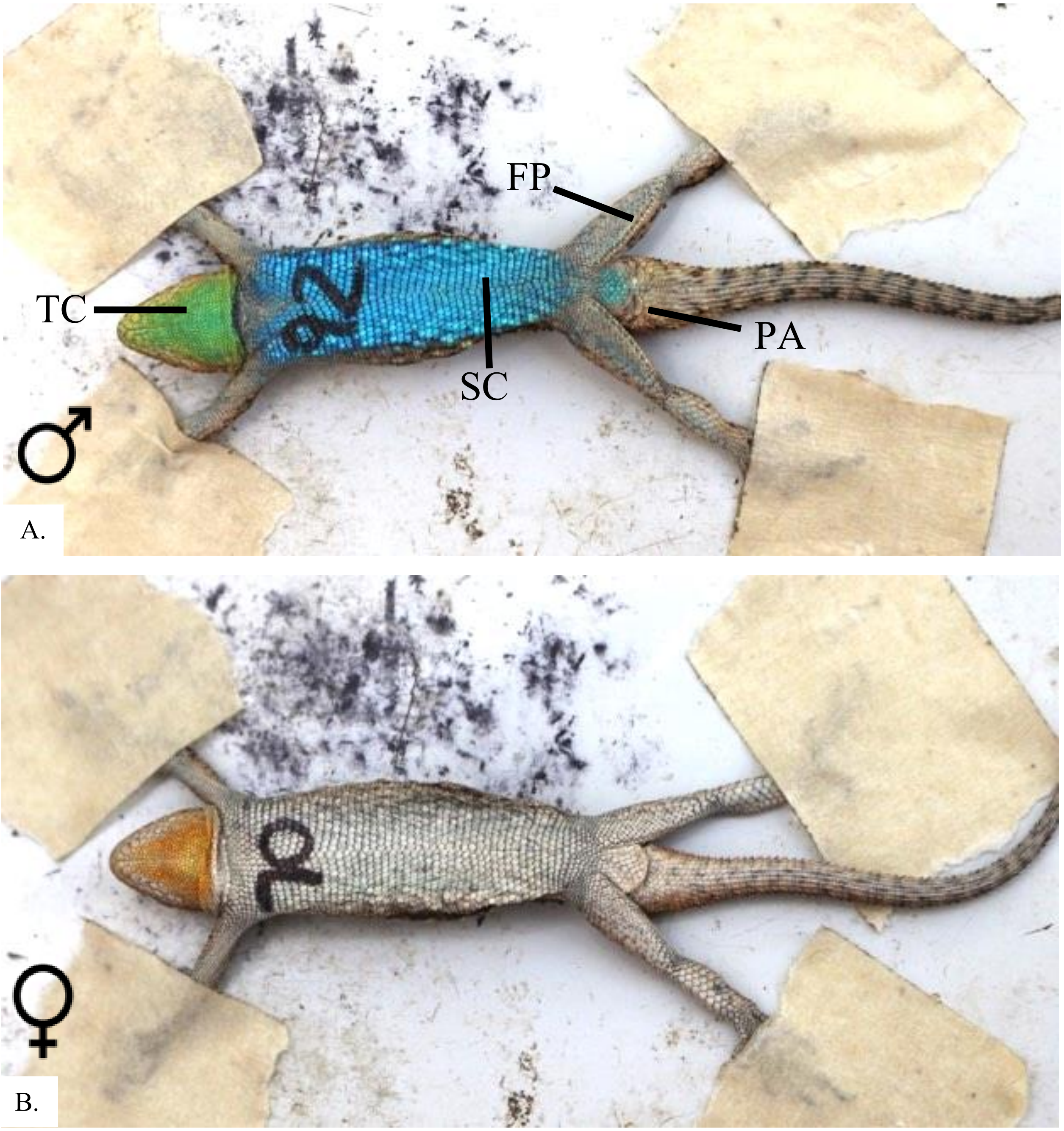

Figure 2-4. A visual comparison of the ventral side of an adult male (A) and adult female (B) ornate tree lizard (*Urosaurus ornatus*) from the Chiricahua Mountains, Arizona, USA. Males are identified by their enlarged post-anal scales (PA) and femoral pores (FP), as well as their stomach (SC) and throat (TC) colouration.

Figure 2-5. Physical models of ornate tree lizards (*Urosaurus ornatus*) made by painting a Thermochron iButton DIS1921G-F5 temperature logger brown to mirror the reflectance of these lizards. Models were placed throughout ten sites in the Chiricahua Mountains, Arizona, USA. Ruler included for scale in centimetres.

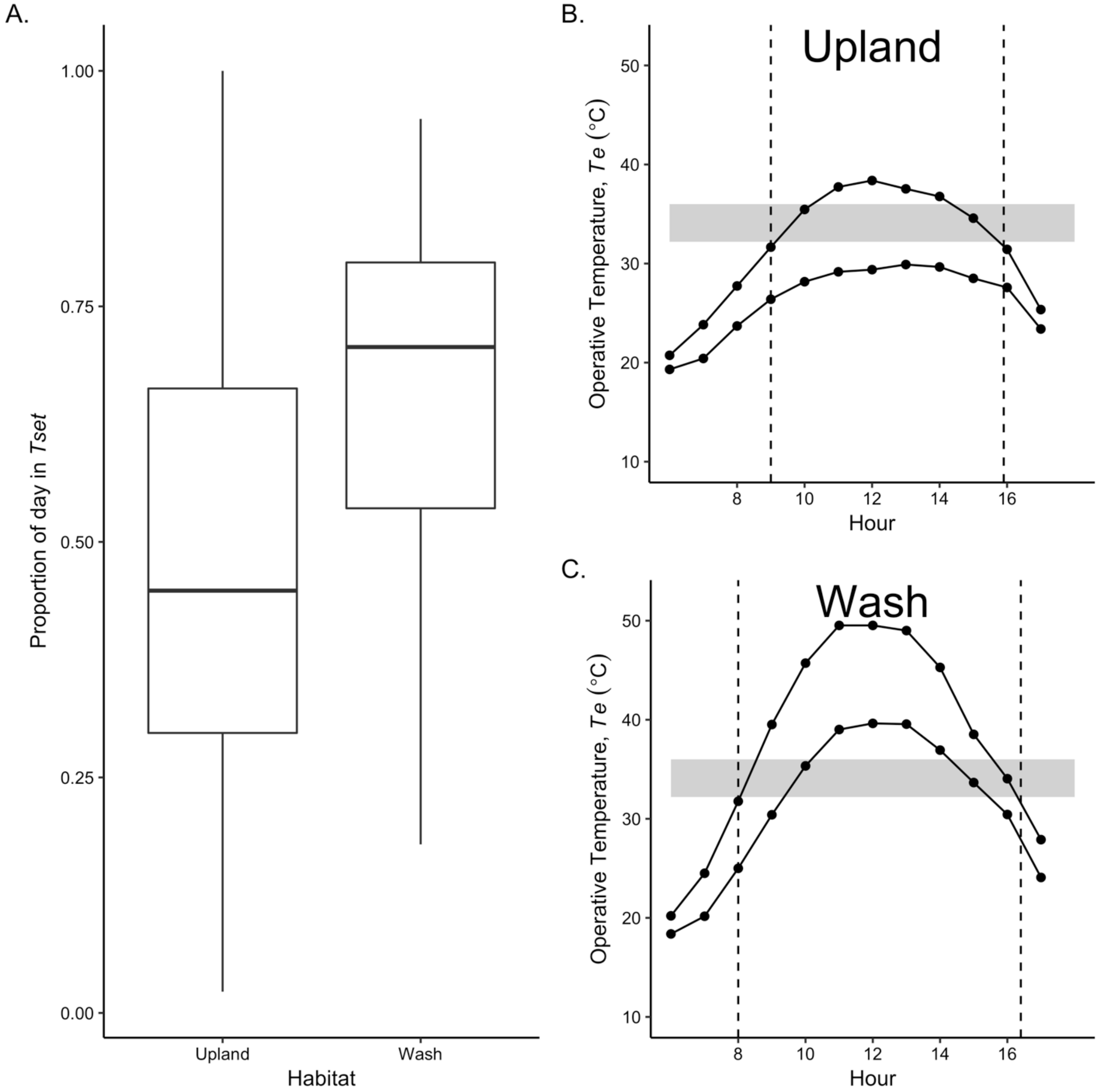

Figure 2-6. A) The proportion of daily operative temperatures (*Te*, °C) that are within the preferred range of body temperatures (*Tset*) of ornate tree lizards (*Urosaurus ornatus*) is higher in the wash than in the upland. Thermal quality of B) upland and C) wash habitats showing the mean daily maximum and minimum *Te* for each hour (solid lines) in relation to *Tset* (shaded area) of ornate tree lizards.

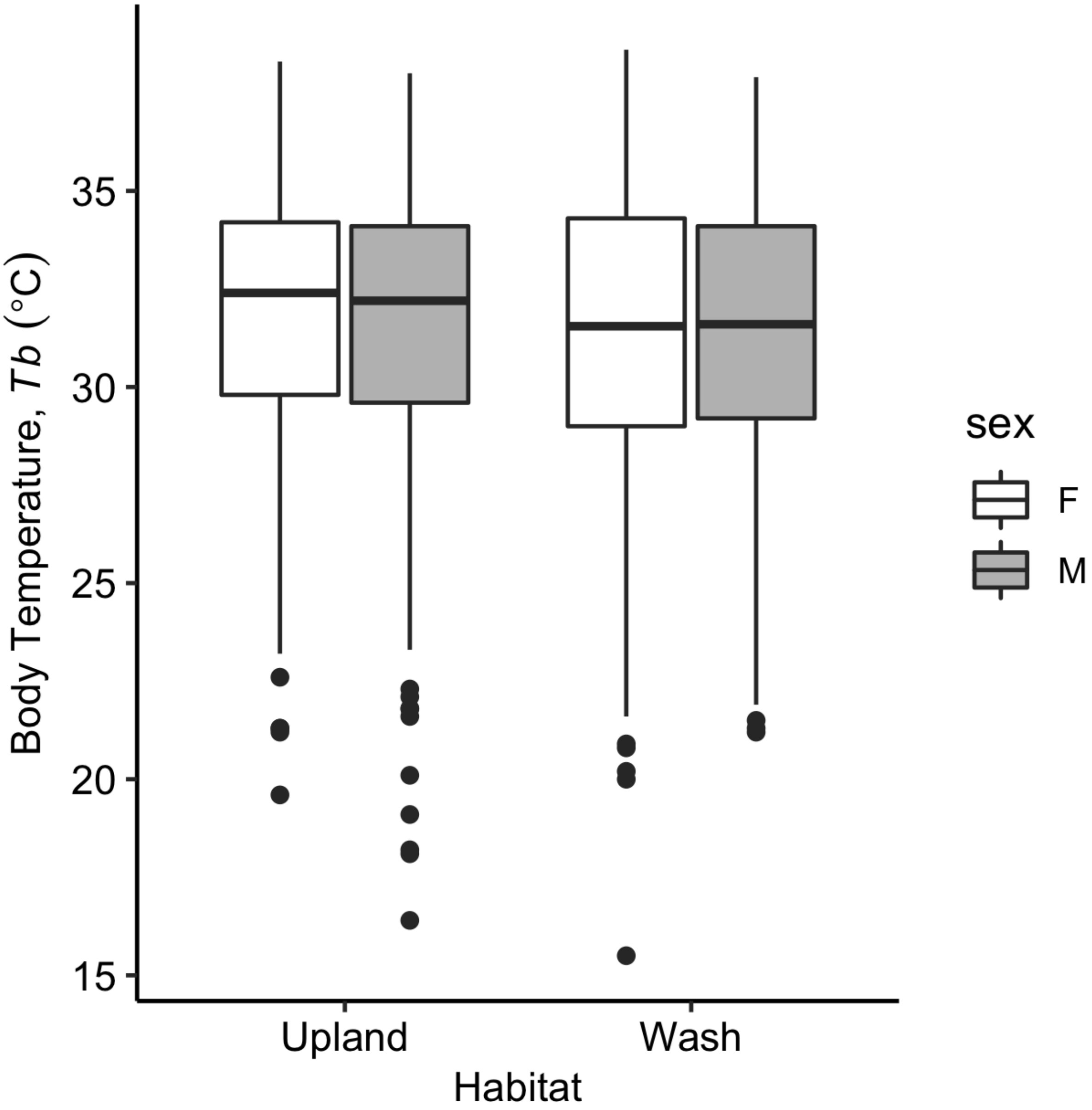

Figure 2-7. Boxplot of ornate tree lizard (*Urosaurus ornatus*) body temperatures (*Tb*, ℃) measured at ten sites in the Chiricahua Mountains, Arizona, USA from 1 May to 21 July, 2018.

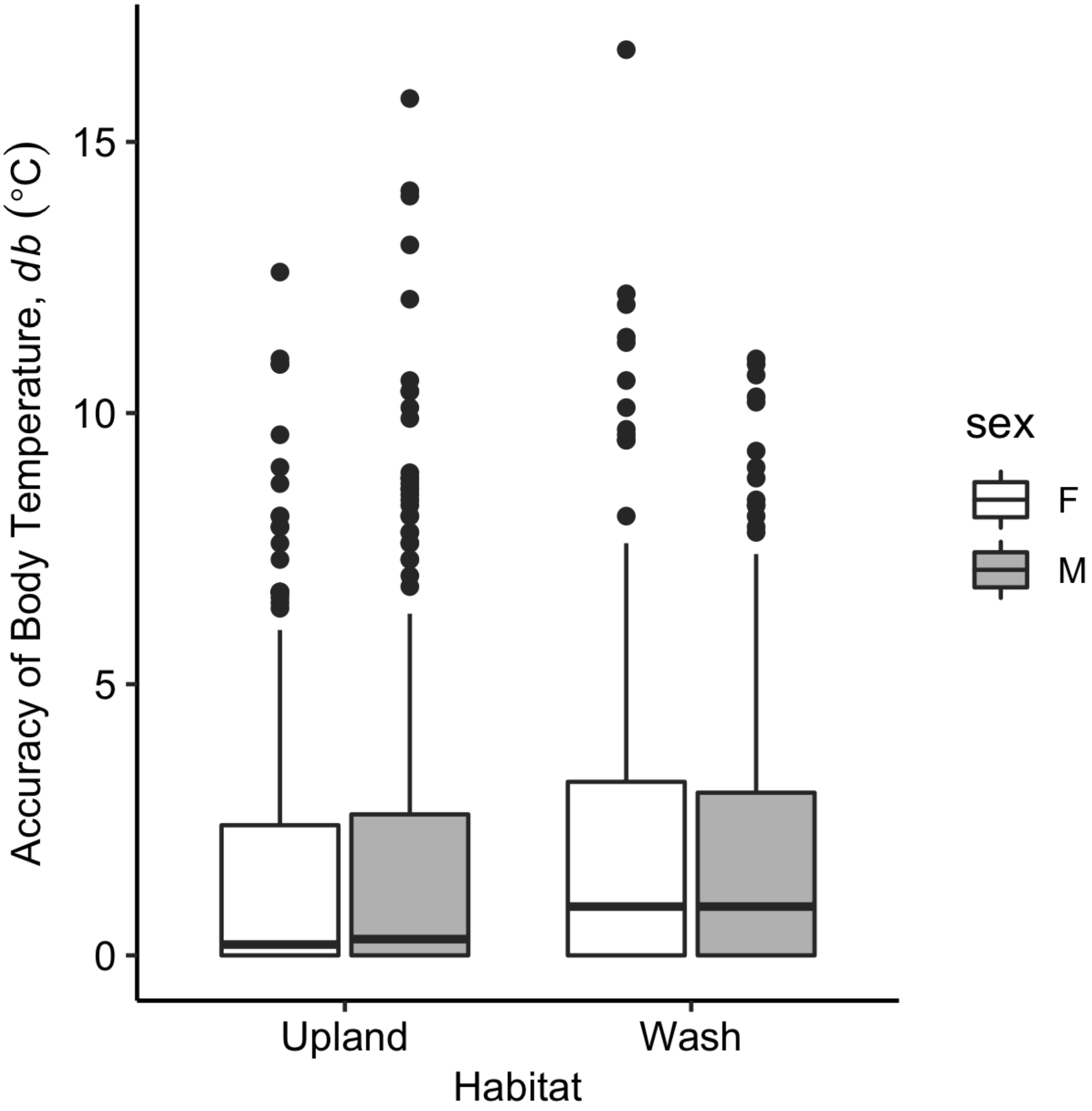

Figure 2-8. Boxplot of ornate tree lizard (*Urosaurus ornatus*) accuracy of body temperature index (*db*, °C) at ten sites in the Chiricahua Mountains, Arizona, USA from 1 May to 21 July, 2018. Lizards in the upland habitat have significantly smaller *db* values than the wash.

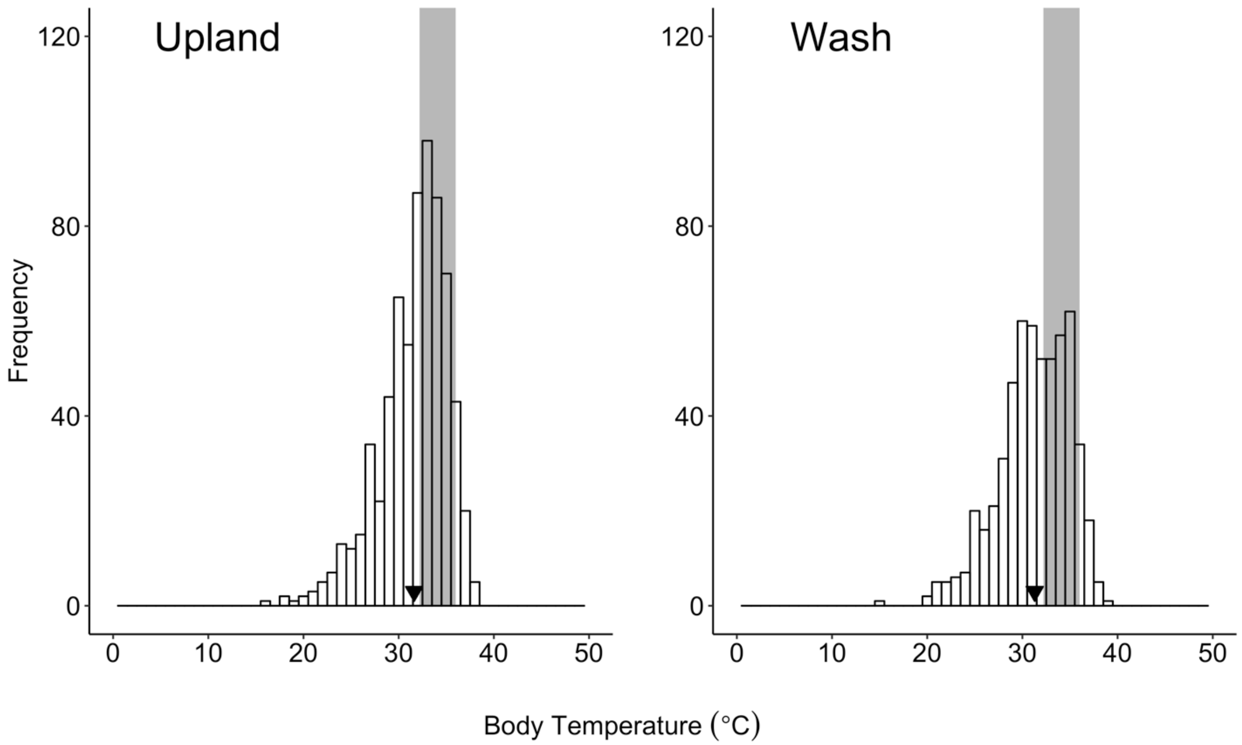

Figure 2-9. Frequency distributions of body temperatures (*Tb*, °C) of ornate tree lizards (*Urosaurus ornatus*) in upland (n = 690) and wash (n = 561) habitats at ten sites in the Chiricahua Mountains, Arizona, USA from 1 May to 21 July, 2018. Shaded bars indicate preferred temperature range (*Tset*) of the species. Triangles represent the mean.

General Conclusion

The general goal of my thesis was to test the hypothesis that thermal quality affects thermoregulation by lizards. According to the cost-benefit model of thermoregulation (Huey and Slatkin 1976), which has been central to studies on reptilian thermoregulation since it was proposed in the late 1970s, thermoregulation should depend on thermal quality. The main prediction of the model is that lizards should only thermoregulate when the benefits outweigh the costs of doing so (Huey and Slatkin 1976). Specifically, I attempted to determine whether lizards living in habitats of low thermal quality (high cost) invest less in thermoregulation. I used two systems to test this prediction: an elevational gradient and a pair of adjacent habitats that differ in the amount of solar radiation they receive.

Overall, I showed that lizards occupying low thermal quality environments invest more into thermoregulation than in high thermal quality environments. At high elevation, thermal constraints are high and, correspondingly, thermal quality is low. The Yarrow's spiny lizard (*Sceloporus jarrovii*) living on talus slopes along an elevational gradient thermoregulated more effectively as elevation increased (Chapter 1). In addition, the ornate tree lizard (*Urosaurus ornatus*) thermoregulated more accurately in a closed-canopy upland habitat (lower thermal quality) than in an open-canopy wash habitat (Chapter 2). Combined, I provide one of the most rigorous tests to date of the main prediction of the cost-benefit model of thermoregulation. I have shown that the disadvantages of thermoconforming may have been underestimated in low thermal quality environments.

Implications

Lizards cannot evolve rapidly enough to current climate change projections because of genetic limitations of thermal preference (Huey et al. 2003). Behavioural thermoregulation allows lizards to buffer environmental variation, which enables species to persist during climate change in the short term (Buckley et al. 2015), but can confer a risk of extinction over the long term. For ectotherms such as lizards, effective thermoregulation requires access to preferred microhabitats (Hertz et al. 1993). For a lizard that functions within a narrow range of body temperatures, climate severely restrict activity over space and time (Sinervo et al. 2010, Sears et al. 2011). Such constraints are manifested as decreased activity when environments become too hot or too cold. In some environments, warming could eliminate populations that are present today (Buckley et al. 2015, Sinervo et al. 2010). Even when environmental conditions permit thermoregulation, this behaviour requires time and energy that reduces time for other functions (Huey and Slatkin 1976, Angilletta 2009). If preferred microhabitats become less common or less accessible, the cost of thermoregulation may exceed the benefit (Huey and Slatkin 1976, Angilletta 2009).

As climates continue to warm, it will undoubtedly continue to affect lizard populations. Since 1975, 12% of local Mexican lizard populations have gone extinct and a projected 40 % will become extinct by 2080 (Sinervo et al. 2010). Although the effects of climate change on lizards is an important area of research, it is still not clear how exactly climate change will affect lizard populations. Some predict that range shifts will force certain populations (i.e. high elevation, forest habitat dwellers) to extinction (Huey et al. 2009, Sinervo et al. 2010). Whereas other studies suggest lizards will benefit from the predicted warming (Logan et al. 2013). In either case, my thesis helps illuminate the link between thermal quality and investment in thermoregulation and can be used to further study the potential outcomes of climate change.

Limitations of methodology

The evidence I found for thermal quality impacting lizard thermoregulation is strong, but there are several limitations that warrant some discussion. First, I used spot-sampling to measure lizard *Tb* and calculate indices such as *db* and *de-db*. Although I recognize that using high-resolution telemetry or implanted data loggers would have been better, it was not possible due to the small body size of both lizard species studied. Because I obtained large samples on both species, much larger than most studies that have used spot-sampling for studies on thermoregulation (see Table 1-9), I was still able to achieve high statistical power. However, I was only able to paint a picture of lizard thermoregulation during activity. Second, there are inherent challenges when conducting observational studies. One limitation is that I cannot control for other potential costs of thermoregulation, other than thermal quality, that may cause a similar response. Another difficulty faced by studies of thermoregulation in natural environments is accurately describing the thermal quality of the available habitats. For this reason, the way I measured thermal quality differed between Chapter 1 and 2. I chose to abandon the most commonly used index of thermal quality (*de*; Hertz et al. 1993) in Chapter 2 due to the structural complexity of the habitat types. Unlike the talus slopes, which are structurally homogenous, the habitats used in Chapter 2 are more complex and I felt that I could not accurately sample the various available microhabitats in proportion to their availability to obtain a representative mean *de*. Finally, I am limited to making inferences about lizard thermoregulation in the temperate regions. These patterns may not hold true in tropical environments where the issue is often not trying to gain heat, but instead seek refuge from extreme temperatures (Shine and Madsen 1996). In this case, regulation of *Tb* may be relatively unimportant.

Future directions

There are three fruitful avenues for future research that stem from my thesis. 1) The use of high-resolution telemetry or implanted data loggers to measure body temperatures continuously and to explore in more detail daily and seasonal variation in thermoregulation. 2) Common garden or reciprocal transplant experiments with lizards from high and low elevation or from wash and upland habitats would help illuminate whether effectiveness of thermoregulation is a phenotypically plastic trait or whether there is a genetic basis. 3) More laboratory experiments, such as Herczeg (2006) and (Sears et al. 2016), are warranted to tease apart the costs and benefits of thermoregulation and to assess their effect on thermoregulatory behaviour.

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