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THERMOREGULATION IN TROPICAL LIZARDS.

PhD Thesis by Mathew Vickers.

Witty quotes:

“The [*lizard*] prefers comfort to pleasure, convenience to liberty, and a pleasant temperature to the deathly … consuming fire [*sic*].” Herman Hesse

“I wanted to call it: The Ins and Outs of cloacal thermometry” M Vickers, 2014

“The Harvard Law states: Under controlled conditions of light, temperature, humidity, and nutrition, the organism will do as it damn well pleases” Larry Wall, Author, creator, Perl language.

“An instant-read thermometer is your best bet for making sure that meat and fish are cooked to the proper temperature” Bobby Flay, Chef

1 Statement on the contribution of Others

Nature of Assistance	Contribution	Names, Titles, affiliations
Intellectual	Proposal writing	Prof Lin Schwarzkopf School of Marine and Tropical Biology James Cook University, Townsville Prof Ross Alford School of Marine and Tropical Biology James Cook University, Townsville
	Data analysis	Prof Lin Schwarzkopf Prof Ross Alford
	Editorial assistance	Prof Lin Schwarzkopf Prof Ross Alford Dr Ian Watson CSIRO Ecosystem Services
	Co Authors	Prof Lin Schwarzkopf Prof Ross Alford Dr Ben Phillips Department of Zoology University of Melbourne
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	Stipend	Australian Government Australian Research Council
Data collection	Field support	Justin Perry, Eric Vanderduys, Alex Kutt, Genevieve Perkins, Anders Zimny, Dr Carryn Manicom

Copyright statement

Ethics Statement

This research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council (NHMRC) Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th Edition, 2004 and the Qld Animal Care and Protection Act, 2001. The proposed research study received animal ethics approval from the JCU Animal Ethics Committee Approval Number #A1964 and A1527. Research was conducted under QPWS permit WISP12323413.

CoAuthorship

I have co-authors, Lin Schwarzkopf, Ross Alford, Carryn Manicom, and Ben Phillips. In all papers, I was the primary agent of the research, concept, original idea, data collection, analysis, and writing. Other people have helped in any aspects of these, in my data analysis, Ross Alford assisted me, in clarification and refinement of concepts, I was assisted by Lin Schwarzkopf and Ben Phillips.

Table of contents

Overview

Detail

Acknowledgements

From my perspective this thesis has been a long time in the making, and the making took more people than listed as Author: the workload for a thesis is too large for one person to shoulder, or at least for me to shoulder, and I suppose part of the PhD training is to be able to enlist, encourage, coerce, demand and blackmail people into assuming responsibility for some of that load. The first recruit was Professor Lin Schwarzkopf, who needed some amount of convincing to accept an unfunded project and an easily distracted and slow-paced, recalcitrant student, who regardless of every lesson and example still can't manage to get things organized in time. Lin has supported me in my endeavours since 2004, and I thank her for the opportunity to be part of her research group, where I learned so much. In particular Lin has helped me to articulate my ideas and communicate them in an effective manner, to describe convoluted concepts clearly and concisely. I imagine it was something like untangling the most heinous handful of headphone cord. On a middle-row airplane seat with burly people on each side. With a seat back tray laden with wine and soup in front of you. Flying through turbulence. While wearing an eye mask and juggling. Lin, I owe you a lot for this thesis, and I hope you got something out of it too. I'm writing these acknowledgements before I've finished, but if this gets printed, I can say at least: I finished it (and if it doesn't make it, no one will be any the wiser). It's not quite on time, but hopefully up to standard. Along the hall, and next in line is Professor Ross Alford, who has helped with many aspects of the thesis. In particular, Ross helped me to see further into my data and analysis, and to clarify and formalize my arguments.

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you’re own thesis. I am still not sure how you get so much shit done. I’ll wrap this up soon with a thank you to my parents and family. And lastly, to Theresa: thank you

List of Figures

333

Abstract

Thermoregulation is critically important for ectotherms, and there is a large body of literature on the topic. Much of the theory predicting aspects of behavioural thermoregulation stems from lizard biology, and there have been numerous developments in theoretical understanding over the past 30 years. Naturally, as the data increases, and more systems are understood, some of the basic theories and methods underpinning the study of any subject must be updated. New techniques in data collection and modeling improve predictive capacity and confidence in predictions, and can be used to further the understanding of behavioural thermoregulation.

As with many organismal processes, the execution of behavioural thermoregulation relies on balancing the costs and benefits, as described in the classic cost benefit model for behavioural thermoregulation written by Huey & Slatkin (1976). Costs of behavioural thermoregulation include the energetic cost of moving to locations at appropriate temperatures, but also more difficult-to-quantify costs, such as home range maintenance (assuming, for example that 'good' home ranges have many good temperatures), and interruption to foraging or mating time while thermoregulating. The benefit derived from body temperature control occurs because processes such as locomotion, digestion, and cognition are dependent on body temperature, which means, ultimately, that fitness is thermally dependent. The relationship between fitness and temperature is described by the thermal performance curve, which is a

characteristic asymmetrical inverted U shape, with the peak of the fitness hump (thermal optimum) nearer to the hot end than the cold. This asymmetry means overheating is more costly than overcooling and, I present a new cost-benefit model for behavioural thermoregulation that includes this asymmetry, considers the cost of failing to thermoregulate, and describes these costs and benefits in terms of fitness, rather than energetic cost alone. The key predictions of the model were that a) organisms should invest more (not less, as the previous model predicted) effort in thermoregulation as environmental temperature deviates from the thermal optimum; and b) to offset the increased cost of failing to thermoregulate at high temperatures, organisms will thermoregulate more effectively when it is hot than when it is cold (the previous model did not consider the case in which the environment is too hot). Both predictions of my new model were supported by data from three sympatric rainbow (*Carlia* spp.) skinks in tropical Australia, and by existing literature that did not support the predictions of the previous null model.

Quantifying the costs and benefits of thermoregulation relies on comparison of an organism’s body temperature with a null model, or model of a non-thermoregulator. Hertz, Huey & Stevenson (1993) formalized the first null model for behavioural thermoregulation, in which they standardized terminology: body temperature was defined as the temperature of a real organism; operative temperature was defined as the temperature of the null model (or non-thermoregulator). Here, I discuss the limitations of their null model, and propose a new null model that aims to overcome these limits. Originally, operative temperature was determined by placing static models randomly around in the environment, and creating indices describing the available environmental temperatures relative to the preferred body temperature of the modeled species. These indices were calculated using mean absolute differences between the temperature achieved by the physical null model and the organism's preferred body temperature, which was measured in a thermal gradient. Mean absolute differences do not correctly model the influence of the asymmetrical shape of the thermal performance curve, and its fitness consequences. Also, using overall mean temperatures obtained from static physical models assumes there is no spatial or temporal structure to environmental temperatures, and that the organism will reach thermal equilibrium at each site it attends.

Foraging strategies of organisms range from ambush to searching, which has broad implications for the level of activity, i.e., the tendency and frequency of movement, of individuals. Rather than static models, I created a computer model that used random walks through a detailed, spatio-temporally realistic thermal landscape to sample environmental temperature. To account for different foraging modes, walk rate can be tailored to match the organism of interest. Rather than using physical models of the organism to collect operative temperature, I used a differential equation to estimate operative temperature from the environmental temperatures that were measured using data loggers placed around the environment (iButtons™). Operative temperature was calculated as function (validated against real lizards) of environmental temperature, recent operative temperature, and the rate of temperature change. Using my model, operative temperature (i.e., the 'body' temperature of the non-thermoregulating computer model) can be calculated as often as desired, and I calculated it every second. Operative temperature and lizard body temperature were converted to a new metric, which I called Thermal Benefit, by transforming operative temperature using the thermal performance curve. Due to its relation to the thermal performance curve, thermal benefit incorporates the asymmetrical effects of being too hot versus too cold. The thermal benefit I calculated for the null model was a temporally integrated estimate of habitat thermal quality, and could be used to determine the difficulty of behavioural thermoregulation, in the sense that if null model thermal benefit was low, it is difficult for a behavioural thermoregulator to achieve preferred body temperature, and *vice versa*. If the assumptions of the null model are upheld, comparing the estimate of habitat quality obtained from a model with the thermal benefit obtained by real lizards indicates the real benefit gained by thermoregulation. I found that the thermal benefit gained by thermoregulation increased towards the middle of the day, as thermal quality decreased due to high environmental temperatures, suggesting that active lizards worked harder to maintain their preferred temperatures as the temperature of the environment increased over the day.

My random walk null model can be used to describe habitat in detail, and test specific hypotheses in thermal ecology. Global temperatures are apparently increasing, but the likely future changes in cloud cover are less clear. The increase in temperature is predicted to reduce the amount of potential daily activity time for ectotherms, which will impact their fitness, and may cause populations to decline in abundance. Cloud cover, on the other hand, influences lizard activity rates by changing the amount of solar radiation reaching the ground, and therefore, local temperatures, sometimes reducing available activity time by decreasing temperature. I used my null model to quantify the implications, in terms of thermal quality of the habitat, of cloudy versus sunny days in contemporary conditions, using 3 years of temperatures of lizard environments, in both winter and summer. The descriptions of habitat quality provided by the model were also calculated for a scenario with 3 °C of climate warming. The climate-warming scenario was also run with scenarios including a 30% increase, and a 30% decrease, in number of cloudy days per year. Overall, winter days had higher summed total thermal benefit scores than summer days and, in both seasons, cloudy days had higher total thermal benefit scores than sunny days. Thermal quality in summer decreased when I included climate warming, but in winter thermal quality increased enough to offset summer's decrease over the entire year: i.e., total annual thermal quality of the habitat was better when there was climate warming. Increasing cloud cover linearly increased thermal benefit in summer, because it buffered lethally hot conditions somewhat, although never enough to balance the negative effects on thermal benefit caused by increased environmental temperatures. If summer is a critical period in terms of activity, the effect of high temperatures may cause problems. This example demonstrates variability in the effect of changing temperature interacting with other environmental factors, such as cloud cover.

Studies predict that tropical ectotherms are at particular risk from climate change. Tropical species tend to be thermal specialists, and live in environments near, or even above, their thermal optimum. In the tropics, increasing temperatures should cause fitness to decrease, because environmental

temperatures often exceed thermal optima and maxima of most species. Using concepts generated while defining cost benefit model for thermoregulation and the new null model, I argue that, as thermal specialists, tropical ectotherms tend to be highly precise thermoregulators, and are particularly adept at thermoregulating in high temperature environments. I suggest that these traits could provide the behavioural buffer required to filter the negative effects of increased temperature, altering our expectations of the effect of climate change.

The uncertainty of some aspects of future climate, together with the unknown extent of buffering due to behavioural thermoregulation means that predictions of gloom or success for ectotherms are premature.

Chapter 1 Introduction

Ectotherms necessarily rely on their environment to increase and decrease their body temperatures. Global temperatures are increasing (Stocker *et al.* 2013), and increasingly, there is a focus on the future of ectothermic organisms and concern that warmer temperatures will adversely affect them. Many organisms, ectotherms in particular, thermoregulate behaviourally to control their body temperature, filtering out the worst of the habitat temperatures, and selecting the most appropriate, to optimize their body temperature. Much of the seminal work that informs our understanding of ectotherm thermoregulation is based on lizards (Cowles & Bogert 1944). Lizards are sensitive to their thermal environment (Bennett 1980; Grant & Dunham 1988; Autumn *et al.* 1999), abundant, and lend themselves to experimentation as they are large enough to accurately measure and estimate changes in body temperature, but small enough that changes can occur fast.

Ectotherm fitness is strongly tied to body temperature via the thermal performance curve (Figure 3-1). The total range over which an organism can survive is bounded by a critical thermal minimum and maximum, and performance and fitness are maximised somewhere between these limits, at the thermal optimum. Thermal performance curves and sensitivities are unique to each species (Deutsch *et al.* 2008), and within species, can be unique to each individual (Careau *et al.* 2008, 2014). The thermal performance curve, in its idealized form, is a summary of all of the physiological and physical processes that an organism must perform, and each process may have slightly different critical limits or optimum temperatures. Over evolutionary time, these processes tend to converge such that performance metrics (e.g. running speed) can be reliable proxies for a generalised relative fitness curve (Angilletta *et al.* 2002).

Despite variability in each trait's thermal dependence, the general form of the thermal performance curve has a typical shape (Huey & Kingsolver 1989). Reaction rate increases with increasing temperature from zero at the critical thermal minimum to one, and then decreases more sharply to zero at the critical thermal maximum (Figure 3-1). The curve is typically asymmetrical, in that the optimum is always closer to the maximum than the minimum, and this property underlies the theory that increasing global temperatures are a threat to ectotherms (Tewksbury, Huey & Deutsch 2008; Huey, Losos & Moritz 2010; Sinervo *et al.* 2010; but see Clusella-Trullas & Chown 2011). If an ectotherm currently lives at or near its thermal optimum, increased environmental temperatures will cause a fitness decrement if the organism does not change physiologically or behaviourally. Not responding to increasing environmental temperature will cause more of a decrement than would the same decrease in environmental temperature (Figure 2-1, Chapter 2, Vickers, Manicom & Schwarzkopf 2011). Temperature can act directly on fitness, or can be indirect; for example, increased temperatures can curtail activity time, which decreases an organism's capacity to acquire resources (Adolph & Porter 1993), and under climate change this is one mechanism predicted to cause species declines and extinctions (Sinervo *et al.* 2010; Huey *et al.* 2012; Kearney *et al.* 2013). Most organisms can thermoregulate in some way, but can have associated costs including the loss of water through evaporative cooling or respiration, altering body posture to increase or decrease exposure to ambient temperature, opening and closing opercula, or selecting suitable settlement habitat that is close to the thermal optimum. The goal of thermoregulation is, firstly, to keep organisms alive by maintaining body temperature within thermal limits, and secondly, to maximise fitness by maintaining body temperature near the thermal optimum (Martin & Huey 2008).

The primary mode of body temperature control in lizards is behavioural thermoregulation (Brattstrom 1965). A lizard can make use of warm and cool sites in space (Christian & Weavers 1996) and time (Grant & Dunham 1988), but more subtle variations also affect body temperature. Lizards can behaviourally thermoregulate by varying duration of exposure to incident radiation and the angle of exposure (the sun) or presenting surfaces to convective currents or conductive substrates (Bakken & Angilletta 2013). Interestingly, this is not constrained to lizards or even ectotherms: endotherms also engage in behavioural thermoregulation in offloading heat, or huddling, etc. (Adair & Adams 1983). Ideally, behavioural thermoregulation is beneficial because it maximises fitness by increasing the efficiency of processes such as digestion, or performance such as locomotion, or awareness, for improved prey capture or predator avoidance (Martin & Huey 2008). Of course, behavioural thermoregulation is not without associated costs. The costs can be difficult to measure, but include the energetic costs of movement to find appropriate locations and temperatures, being exposed to predators and competitors when thermoregulating, or when searching for a place at the correct temperature, and also rather indirect costs, such as missing opportunities for foraging, mating and other activities when thermoregulating (Huey 1974; Downes & Shine 1998; Hare *et al.* 2007). The first attempt to quantify the relative effects of costs and benefits on the probability of thermoregulatory behaviour was the cost-benefit model for thermoregulation (Huey & Slatkin 1976). This model posited that thermoregulatory effort should decrease as energetic costs associated with thermoregulation increase. This model was broadly supported, especially in habitats that were mild, but not dangerous (Herczeg *et al.* 2006, 2008), though some empirical results were not consistent with its predictions (Blouin-Demers & Nadeau 2005). The Huey and Slatkin (1976) model was developed for habitats where environmental temperatures are always below the critical thermal maximum of an organism; however, as the thermal environment becomes warmer, and therefore more dangerous, the cost of experiencing inappropriate temperatures becomes unacceptably high, because mortality may occur (Grant & Dunham 1988). Many reptiles live in hot, or at least seasonally hot, environments, and the cost-benefit model of Huey and Slatkin (1976) does not apply to them (Chapter 2, Vickers *et al.* 2011). In the second chapter of my thesis, I re-examined this model, and proposed a new cost-benefit model that accounted for the high cost of failing to thermoregulate. I also extended the model to high-temperature environments (e.g., tropical savannahs, deserts), which are centres of global biodiversity and abundance of lizards.

A conceptual cost-benefit model provides a framework for understanding the relative effort invested in behavioural thermoregulation, but measuring the actual costs and benefits experienced by individual organisms is difficult. Rather than measuring the effects of thermoregulation directly, most studies have inferred costs by examining the difference between a null-model and a real thermoregulating organism (Hertz 1992; Meek 2005; Anderson *et al.* 2007). Thermal null models address the question of how we should quantify thermoregulation given different available environmental conditions. Initially, researchers compared lizard body temperatures to environmental temperatures, directly (Cowles & Bogert 1944; Ruibal 1961). This early version of a null model comparison was used widely until a seminal paper that demonstrated that any item with thermal inertia (e.g., a liquid-filled beer can) appears to thermoregulate by having a "body" temperature that is different from ambient temperature (Heath 1964). Hertz, Huey & Stevenson (1993) extended this null model to encompass three ideas: (1) objects with mass have thermal inertia that must be included in environmental temperature measurements; (2) rather than being different from their environment, thermoregulators are trying to achieve a particular body temperature; and (3) null model temperatures must be a random sample of temperatures from the environment (Hertz et al). This method revolutionized thermoregulatory studies, providing simple indices that scored habitat thermal quality, and quality and effectiveness of thermoregulation.

The approach of Hertz et al. (1993) requires three datasets: (1) an estimate of optimal body temperature (T_{opt}, e.g. preferred, set-point or optimal) measured in the laboratory; (2) field-active body temperature (T_b), and (3) operative environmental temperature (T_e) measured using models placed in the field. This results in three different metrics. Thermal quality of the habitat is estimated as the mean absolute difference between T_e and $T_{opt.}$ The quality of thermoregulation is the mean absolute difference between T_b and T_{opt}. The effectiveness of thermoregulation is 1 minus the ratio of the two, with 0 representing a perfect thermoconformer (i.e., T_b deviated from T_{opt} the same amount as T_e deviated from T_{opt}) and 1 representing a perfect thermoregulator (i.e., T_b never deviates from $T_{opt,}$ even though T_e does deviate).

Hertz, Huey & Stevenson's (1993) null model represented a major conceptual advance in studying thermoregulation, but is limited in several ways. There is a difference between the structure of the indices of Hertz et al. (1993) and the thermal performance curve: the thermal performance curve is asymmetric whereas the thermoregulatory indices d_e, d_b, and E are symmetrical. The consequence of an asymmetric thermal performance curve is that overheating has a stronger effect on performance or fitness than overcooling (Figure 4-1). This is not captured by metrics that measure mean absolute deviation. Secondly, operative environmental temperatures are measured using models of lizards (to account for the thermal inertia of the lizard) placed around the habitat. These static models assume that the organism reaches thermal equilibrium at each point. However, field data show that many organisms move around in their habitat (Huey & Pianka 1980), and do not necessarily reach equilibrium temperature with any particular site (e.g., Seebacher & Shine 2004; Christian & Tracy 2006).

In the third chapter of my thesis, I developed a new null model for behavioural thermoregulation that was not constrained by the limiting assumptions incumbent upon the original method of (Hertz *et al.* 1993). The null model samples environmental temperature by making a random walk through a detailed, spatio-temporally realistic thermal map. These temperatures were transformed into null-model body temperatures (operative temperatures) by a differential equation that includes parameters for organism size and rate of movement (which was calibrated using real lizards, Chapter 4). Finally, both the temperature estimated for the non-thermoregulating null model and actual, measured, lizard body temperatures are transformed using the thermal performance curve to create a fitness-based metric called thermal benefit. Using this null model, I aimed to describe habitat thermal quality available to lizards in fine detail, and measure the benefit gained by, and effort invested in, behavioural thermoregulation of the black-throated rainbow skink, *Carlia sexdentata*.

My new null model, once developed, lent itself to examining the effects of particular environmental parameters and scenarios on lizards. By modeling changing temperature in the thermal landscape, I could measure the shift in habitat thermal quality throughout the day (Chapter 3). I demonstrated another use of the null model in the fourth chapter of my thesis. The trajectory of global temperatures into the near future has been modeled thoroughly, and the clear consensus is that global temperatures are increasing (Stocker *et al.* 2013). Other environmental phenomena are not necessarily as well understood, particularly if those phenomena have many inputs and parameters influencing them. One such phenomenon is cloud cover. Cloud cover is not static, and as the climate changes, there is reason to expect levels of cloud cover to change (Clusella-Trullas *et al.* 2011; Leahy *et al.* 2013). There are predictions that the effect of increasing temperatures on lizards will be dire, but increasing cloud cover may interact with solar radiation reaching the ground and ameliorate the effect of climate change to some extent. In Chapter 5, I used the random walk null model to explore how predicted shifts in cloud cover with climate change could influence behavioural thermoregulation in lizards.

Increasing temperatures may impact the fitness of organisms negatively, and ultimately some ectotherms may not persist, particularly those living in environments near their thermal optimum (Colwell *et al.* 2008; Sinervo *et al.* 2010; but see Kearney, Shine & Porter 2009). Tropical ectotherms are the ones most often living in environments near their thermal optimum (Tewksbury *et al.* 2008; Somero 2010). Yet, tropical ectotherms may not be as strongly impacted as some predictions imply. In chapter 6, I argued that the high, stable environments found across much of the tropics, that promote the evolution of thermal specialisation also demand increased behavioural thermoregulatory ability and precision, particularly at high temperature. Increased thermoregulatory ability in a hot environment should increase variability in individual survival of extreme events, reinforcing the strength of natural selection on thermoregulation (Chown *et al.* 2010). Thus, the very factor predicted to cause large-scale extinction (high environmental temperatures) may, in fact, cause species to increase thermoregulatory precision, and predispose them to rapid adaptation, improving their chance for survival. While this mechanism is unlikely to save all tropical ectotherms from the effects of climate change, it may provide a buffer from the environment that allows physiological adaptation and evolution to occur, which could reduce the number of extinctions caused by climate change.

Thesis structure and overview

Initially, I set out to examine claims that tropical ectotherms are “toast” (Huey *et al.* 2010). This idea stemmed from (Sinervo *et al.* 2010) theory, which predicted large scale extinctions of reptiles under climate change. While Sinervo *et al.*’s (2010) paper was compelling, my own observations of tropical skinks indicated that they lived in areas where extinction should have happened: how were they still present in the environment? I began by examining the thermal literature, and found that many basic premises supporting the thinking in thermal ecology were based in cool and stable environments, which didn’t apply to the lizards I was observing in tropical savannahs. The first step I took to remedy the situation was to provide a conceptual advance to the theory of the costs and benefits of thermoregulation (Chapter 2, Vickers *et al.* 2011). Ultimately this model generated predictions consistent with the existing theory in cool environments, but including radically different predictions when individuals experienced high temperatures. My new predictions for behaviour in high temperature environments had been empirically supported by studies that contradicted the original model (Blouin-Demers & Nadeau 2005), and continue to be supported by my findings (though I am probably positively predisposed).

Building on the cost benefit model, and focusing on the properties of the thermal performance curve and discussions in the literature on the importance of thermal transience (Christian & Tracy 2006), I developed a new null model for behavioural thermoregulation. This required a thorough understanding of null model theory in ecology, and I spent some time studying the controversy about null models that raged in the ecological literature of the 1980s. I made an effort to create a new null model that was much closer to reality than the previous model, and did not commit the Narcisisstic fallacy of including processes of interest (i.e., behavioural thermoregulation, for example necessarily reaching equilibrium temperature, or deliberately selecting microhabitat, Colwell & Winkler 1984), and actually allowed a detailed examination of behavioural plasticity and daily shifts in the thermal regime experienced by organisms. The phenomenon of changes in behaviour in response to changing environmental temperatures is well known to any natural historian of reptiles, but I think I provide the first real quantification of it. Precise quantification of behavioural thermoregulation is important, because it allows us to predict the changes in behaviour that should occur in response to changes in environmental temperatures, which is critical in the face of climate change.

I spent some time calibrating my predictions of reptile body temperatures, to those of real organisms, which is required to achieve accurate model fitting, and then applied my new null model to an old idea: that cloud cover influences ectotherms thermoregulation by influencing environmental temperatures. Cloud cover is difficult to predict, so I extrapolated recent observed shifts in cloud cover into the future, and found that increasing cloud cover may ameliorate climate effects on ectotherms.

My penultimate chapter brings the body of theory together, and finally addresses my original question: Are tropical ectotherms actually toast?

Chapter 2 Extending the cost-benefit model of thermoregulation: Thermoregulation in high temperature environments

Mathew Vickers[1, 2], Carryn Manicom[1], and Lin Schwarzkopf[1]

[1]School of Marine and Tropical Biology, James Cook University, Townsville Q
4811 Australia

[2] Corresponding Author

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Abstract

The classic cost-benefit model of ectothermic thermoregulation compared energetic costs and benefits, providing a critical framework for understanding this process (Huey & Slatkin 1976). It considered the case where environmental temperature (T_e) was less than selected temperature of the organism (T_{sel}), predicting that to minimise increasing energetic costs of thermoregulation as habitat thermal quality declined, thermoregulatory effort should decrease until the lizard thermoconformed. We extended this model to include the case where Te exceeds T_{sel}, and redefined costs and benefits in terms of fitness, to include effects of body temperature (T_b) on performance and survival. Our extended model predicts lizards will *increase* thermoregulatory effort as habitat thermal quality declines, gaining the fitness benefits of optimal T_b and maximising the net benefit of activity. Further, to offset the disproportionately high fitness costs of high T_e compared to low T_e, we predicted lizards would thermoregulate more effectively at high T_e than at low. We tested our predictions on three sympatric skink species (*Carlia rostralis*, *C. rubrigularis*, and *C. storri*) in hot savannah woodlands and found thermoregulatory effort increased as thermal quality declined, and that lizards thermoregulated most effectively at high T_e.

Introduction

Ectotherms derive their body temperature from their environment, but many ectotherms can optimise metabolism and performance via behavioural thermoregulation. The extent to which ectotherms can control their body temperature, and what factors influence their probability of doing so, are classic ecological questions (e.g., Cowles & Bogert 1944). Also, thermoregulation in ectotherms influences many large macroecological patterns (Soininen *et al.* 2007). Recent anthropogenic effects such as climate change threaten ectotherms, and increase the need to understand this critical aspect of their biology (Huey *et al.* 2009; Sinervo *et al.* 2010).

The probability that an ectotherm will engage in behavioural thermoregulation is dependent on a trade-off of associated costs and benefits, first modelled by Huey & Slatkin (1976) for reptiles. Their model made the fundamental prediction that as the energetic cost of thermoregulation increased, thermoregulatory effort should decrease, and individuals should thermoconform. Whereas some studies have supported predictions of the cost-benefit model, both experimentally (Herczeg *et al.* 2006) and with field observations (Ruibal 1961; Huey & Webster 1976; Hertz *et al.* 1993; Shine & Madsen 1996), others have not (e.g., Blouin-Demers & Weatherhead 2002; Blouin-Demers & Nadeau 2005).

The original Huey & Slatkin (1976) considered only the case where operative environmental temperature (T_e) was below optimal or selected body temperature (T_{sel}). For many reptiles in temperate or sub-tropical environments, T_e is frequently below T_{sel} (Van Damme *et al.* 1987; Grbac & Bauwens 2001). However, most reptiles live in the tropics (Pianka & Schall 1981; Pianka & Vitt 2003), in highly thermally heterogeneous habitats, such as open woodland and savannah(Woinarski *et al.* 2007). In addition, most reptiles are small-bodied for at least part of their lives. Highly thermally heterogeneous environments are characterised by high variation in T_e, which can cause rapid shifts in T_b for a small reptile moving through the environment (Herczeg *et al.* 2007). Consequently, behavioural thermoregulation is needed by most reptiles to avoid dangerously high T_b (Cowles & Bogert 1944; modelled by Kearney *et al.* 2009). Therefore, an extension of the original model that accounts for temperatures higher than selected temperatures is required for a thorough understanding of thermoregulation in most reptiles.

The original cost-benefit model for thermoregulation (Huey & Slatkin 1976) measured costs and benefits in terms of energy, and suggested that thermoconforming, or 'passivity', was a low-cost alternative to thermoregulation in the absence of appropriate environmental temperatures (T_e), or if appropriate T_e was too energetically costly to access. However, risk or perceived risk of mortality is a cost to fitness, and in some environments, the risks of thermoconforming may be high. For example, at high T_e, the risk of thermoconforming for an ectotherm, even for a very short period of time, may include death (Herczeg *et al.* 2007; Kearney & Porter 2009). Even at low T_e, there is a direct risk of thermoconforming that includes increased probability of mortality caused by exposure to inappropriate temperatures (Gilchrist 1995). Thermoconforming at suboptimal T_e also causes decrements in performance (benefits) associated with suboptimal T_b that can lead to an increase in the risk of predation (Bennett 1980; Christian & Tracy 1981), reduced prey capture success (Greenwald 1974), or reduced mating success (Willmer 1991). In sum, the net benefit to fitness of thermoconforming may be lower than its low energetic cost indicates. Several recent studies have found that in poor thermal quality (cold) environments, reptiles increase (rather than decrease) thermoregulatory effort (Blouin-Demers & Weatherhead 2002; Blouin-Demers & Nadeau 2005). These studies suggested that avoiding the risks and disadvantages of thermoconforming are an impetus for increased thermoregulatory effort, and that the net benefit of thermoregulation may have been underestimated by the original cost-benefit model (Blouin-Demers & Weatherhead 2002; Blouin-Demers & Nadeau 2005). Avoiding the risks of thermoconforming is a critical benefit of thermoregulation, at least under certain circumstances, which could be reflected in an extended model of thermoregulation.

We have extended the classic cost-benefit model of Huey & Slatkin (1976), to explain the dynamics of thermoregulation for a wider range of species and environments. Our extended model makes three key changes to the original. First, we measure the costs and benefits of thermoregulation in terms of fitness (for example, lifetime reproductive output), rather than in terms of energy/time, as in the original formulation. Using some measure of fitness as currency allows us to explicitly include costs to fitness such as increased probability of mortality, performance decrements, and reduced mating success (Figure 2-1). Secondly, we suggest that the benefit of precise thermoregulation is constant, and independent of T_e. Metabolic and performance benefits gained when $T_b = T_{sel}$ are the same for any T_e. Third, we extend both the costs and benefits into ranges of environmental temperatures warmer than the preferred temperature (Figure 2-1, unshaded area). The key prediction from our new model is that to maintain the benefits of optimal T_b ($T_b = T_{sel}$), animals will thermoregulate with more effort as T_e deviates from T_{sel}.

Reptiles manage the risk of mortality from high body temperature by retreating to shelter once T_e exceeds a certain limit (Cowles & Bogert 1944), but until they are in shelter, the only risk-mitigation measure available to them is to increase the precision, accuracy, and effectiveness of their thermoregulation to avoid extreme T_bs. Thus, the second prediction of our extended cost-benefit model for thermoregulation is that lizards will thermoregulate more effectively at high T_e than low.

We test the predictions of our extended model using thermoregulatory data from three species of small sympatric skinks in the genus *Carlia,* which occur in tropical savanna woodlands of northern Australia*.* We measured body temperatures during activity (T_b), available thermal microclimates (T_e) in the habitat they used, and selected temperatures in a thermal gradient (T_{sel}) in summer and winter.

Methods

Species and Study Site

This study was conducted on 64 summer and 94 winter days from August 2003 to August 2005 at Ramsay Bay, Hinchinbrook Island, Queensland, Australia (18°24'S, 146°17'E). All sampling took place on sunny days between 0700 and 1800. The site was mostly open *Melaleuca* spp. woodland, and included some vine forest with *Eucalyptus* spp. The understorey was typically shrubs

(*Terminalia* spp.) and grasses, and the ground was uniformly covered in leaf litter. The canopy provided a thermally heterogeneous environment, with about 50% of the substrate shaded at midday. Sun and shade spots were similar in size, and were in the order of tens of square centimeters to square meters in area. The area was monsoonal with mild, relatively dry conditions in April - September (Austral winter), and hot, humid, and wet weather from October - March (Austral summer).

We studied the three most abundant diurnal lizard species, which represented more than 85% of observed lizards (Manicom 2010), *Carlia rostralis* (n = 1032, mean adult SVL = 54 mm ± 7.3 SD, mean adult mass = 4.8 g ± 2.4 SD), *C. rubrigularis* (n = 856, mean adult SVL = 45.5 mm ± 5.1 SD, mean adult mass = 2.7 g ± 1.6 SD), *C. storri* (n = 566, mean adult SVL = 41.4 mm ± 3.8 SD, mean adult mass = 2.0 g ± 1.4 SD). These skinks were ground-dwelling, cursorial predators, with overlapping habitat and activity times, and competed directly for food and space (Manicom 2010).

Thermal Indices

We used thermal indices developed by Hertz *et al.* (1993) (Table 2-1). Thermal quality (d_e) of the habitat is typically regarded as high when $d_e < 3$, and a low when $d_e > 5$ (Hertz *et al.* 1993; Diaz & Cabezas-Diaz 2004), and thermoregulation is expected to require less effort (and therefore be more precise) when thermal quality is highest (i.e., < 3). Apparent high precision of thermoregulation (low d_b) can be an artefact of large body size and high thermal inertia, or of living in a thermally congenial habitat where thermoregulation is unnecessary (Seebacher

& Shine 2004), or can indicate that thermoregulation is a high priority to the animal (Blouin-Demers & Nadeau 2005). Conversely, high d_b can indicate that thermoregulation is a low priority, or that poor habitat thermal quality impedes precise thermoregulation. A thermoconformer scores $E = 0$, a perfect thermoregulator scores $E = 1$, and $E < 0$ implies that the animal's body temperature is farther from T_{sel} than the available environmental temperature.

Available environmental temperatures (T_e) were not normally distributed, so we present median temperature, which provided a better measure of the temperature of the average location (Zar 1974), though calculations of standard indices (d_e, d_b, E) were based on mean values for consistency with other published works.

Table 2-1. Definitions of indices of thermoregulation (from Hertz et al. 1993).

Index	Definition
T_{sel}	Selected body temperature. Central 50% of body temperatures measured in thermal gradient
T_e	Operative environmental temperature
d_e	Thermal quality of habitat, measured as mean absolute deviation of T_e from T_{sel}
T_b	Field active cloacal temperature
d_b	Accuracy of thermoregulation, measured as mean absolute deviation of T_b from T_{sel}
E	Effectiveness of thermoregulation, $E = 1 - d_b/d_e$

Analysis of thermoregulatory effort was conducted using a linear regression of d_b and d_e (Blouin-Demers & Nadeau 2005). The model tested was that the slope of the regression was equal to zero (m = 0). A slope of 1 (m = 1) implies that thermoregulatory effort remains constant as thermal quality of the habitat decreases (i.e. as d_e increases). Slope > 1 suggests that effort declines as thermal quality declines, and m < 1 indicates thermoregulatory effort increases as thermal quality decreases. Confidence intervals were constructed from the t-distribution as t x SE of the slope for a two tailed distribution at $\alpha = 0.05$ (Zar 1974) around m to determine the possible range of values of m relative to 0 and 1.

Estimates of selected temperatures (T_{sel})

The range of preferred body temperatures (T_{sel}) of the three skink species was determined in the laboratory using thermal gradients (Licht *et al.* 1966; Hertz *et al.* 1993). Skinks were individually housed in large containers (600 L x 500 W x 450 H mm) with a 75-W light bulb at one end creating a photothermal gradient, offering a range of available operative temperatures (22° to 50° C) between 0800 and 1700. A photothermal gradient was a realistic method of heat provision for these heliothermic skinks. Food (a domestic cricket, *Acheta domestica*) was available once daily and water was always available in the middle of the gradient, and lizards were held in thermal gradients for 3 days before temperature measurements commenced. Over a 20-day period, T_b was recorded once per day at different times between 0800 and 1700. Temperature was never measured within 1 hour of feeding, to reduce the effects of metabolic heat production associated with digestion on T_b.

A quick-reading digital thermocouple thermometer [Type T, Model 90000] was used to measure cloacal T_b to the nearest 0.1° C. Lizards were held by the upper body to reduce heat transfer from researchers' hands to lizards, and readings were finalised within 10s of capture. T_{sel} was measured in the laboratory in summer (October/November) and in winter (July) for all three skink species. The central 50% of the observed range of T_b was used to estimate T_{sel} (Hertz *et al.* 1993; Christian & Weavers 1996).

Estimates of operative environmental temperatures (T_e)

In the field, available environmental operative temperatures (T_e) were measured hourly to the nearest 0.1° C using digital temperature recorders (Thermochron iButtons™ , n = 42), while lizards were active and being sampled. iButtons™ provide a suitable model of operative environmental temperatures available to small (< 10 g) skinks (Vitt & Sartorius 1999). iButtons™ were placed on the substrate in the open at regular intervals over the entire site. We targeted areas used by skinks, avoiding very large areas (>20m across) that received full sunlight for the entire day. iButtons™ were moved every two months to new locations, while maintaining a similar distribution of iButtons™ across the site.

Estimates of body or active temperature (T_b)

The study area was searched actively, and adult lizards were captured by hand. We recorded cloacal temperature (T_b) of active lizards, not disturbed from retreat sites or under cover, and chased for less than 30s, within 30s of capture, using the same digital thermometer used in the laboratory.

Statistical methods

Statistical analyses were conducted using R 2.9.1, and calculations of de, db, and E followed definitions in Hertz et al. (1993) (Table 2-1). Confidence intervals around E were calculated by bootstrapping with replacement (n = 5000). The relationship between d_b and d_e was determined using least-squares regression.

Results

Selected Temperatures in Thermal Gradients (T_{sel})

Selected body temperatures (T_{sel}) for the *Carlia spp.* were within the range of 25.5 to 32.3° C and were lower in winter than in summer for all species (Figure 2-2, Table 2-2). The highest T_b reached by lizards in either the laboratory or field ranged from 38.5° to 40° C among the species. The highest critical thermal maximum recorded for a *Carlia* by Greer (1980) was 43.6° C.

Table 2-2. Thermoregulation indices recorded for summer and winter for three *Carlia* species. Selected body temperature (T_{sel}, °C) was higher in summer than winter, presumably to allow better exploitation of higher environmental temperatures encountered in summer. Habitat thermal quality (mean d_e) was similar in summer and winter, though the SD (in parentheses) of d_e was greater in summer than in winter, and environmental temperature (T_e) was significantly more variable in summer than in winter (see text). Precision of thermoregulation (d_b) was higher in summer than winter, a reflection of the high cost of thermoregulating under extreme conditions.

Species	Season	T_{sel}	d_e	d_b
C. rostralis	Winter	26.4 - 29.3	3.62 (3.09)	1.40 (1.43)
	Summer	28.0 - 32.0	3.37 (5.04)	0.65 (1.18)
C. rubrigularis	Winter	25.4 - 28.3	2.95 (3.01)	1.67 (0.99)
	Summer	28.2 - 31.4	3.66 (5.17)	0.71 (0.99)
C. storri	Winter	25.5 - 29.0	2.94 (2.92)	1.66 (1.74)
	Summer	29.4 - 32.3	3.93 (4.89)	0.62 (1.96)

Operative Environmental Temperatures (T_e)

In both seasons, mean d_e was approximately 3°C, indicative of high thermal quality of the habitat (Table 2-2). Despite similar d_e values, the different thermal regimes in summer and winter produced habitats of very different thermal quality. Variability in T_e was significantly different between summer and winter (Bartlett's K-squared = 12666.44, df = 1, p-value < 0.01, winter [median ± Median Absolute Deviation] 23.5° C ± 2.97, summer 29° C ± 5.19, Figure 2-2).

The higher variability of T_e in summer meant that a greater proportion of available temperatures were high enough to be dangerous to skinks (Figure 2-3).

During winter, environmental thermal quality was high. From 1000 to 1600, median T_e was within the bounds of T_{sel} for all species (Figure 2-2). Typically, T_e was less than T_{sel} (Figure 2-3), though there were many sites where T_e was greater than T_{sel}, and even some greater than the highest CT_{max} for *Carlia* spp. (Greer 1980, Figure 2-3). Summer had similar morning temperatures to winter, and most T_e were less than T_{sel} (Figure 2-3), however from 1000 to 1500, median T_e was above T_{sel} for all species (Figure 2-2), and up to 40% of T_e were above CT_{max} recorded for *Carlia* spp. (Greer 1980, Figure 2-3). Thus, although mean d_e was around 3°C, a putative "average location" during summer was too hot. This, combined with the prevalence of dangerously high T_e, indicated that in summer the environment was of low thermal quality.

Active T_b and Thermoregulatory Precision (d_b and E)

We collected body temperatures from 289 *Carlia rostralis* (88 summer, 201 winter), 259 *C. rubrigularis* (71 summer, 188 winter), and 192 *C. storri* (97 summer, 95 winter). In winter, the three species thermoregulated with intermediate effectiveness ($E \approx 0.5$). In summer, however, all species were significantly more effective at thermoregulation ($E \approx 0.8$, Figure 2-3) despite the lower thermal quality of the habitat. The effectiveness of thermoregulation was mostly driven by the precision of thermoregulation (d_b). In winter, all species were within the top 30% of all literature-reported d_b values ($d_b < 1.7$°C, Table 2-2, Blouin-Demers & Nadeau 2005), but in summer, they were within the top

10% of reported values ($d_b < 0.8°C$, Table 2-2). Thermoregulatory effort increased as thermal quality of the environment decreased (d_e increased) for all species (Figure 2-4) across both seasons

(*C. rostralis* [$d_b = 0.3173*de + 0.3477$, $R^2 = 0.31$, $p < 0.01$, $0.19 < m < 0.44$]

C. rubrigularis [$d_b = 0.2301*d_e + 0.9158$, $R^2 = 0.08$, $p = 0.03$, $0.02 < m < 0.44$]

C. storri [$d_b = 0.5305*d_e - 0.0919$, $R^2 = 0.25$, $p < 0.01$, $0.27 < m < 0.79$]).

In winter, T_b was often above T_{sel} (Figure 2-6), despite the distribution of T_e, where median T_e was often within T_{sel} (Figure 2-2), and most T_e were below T_{sel} (Figure 2-3). By comparison, in summer, median T_e was often above T_{sel} (Figure 2-2), yet summer T_b were distributed similarly to winter T_b. The reason for this difference was that lizards were inactive during the middle of the summer day, when T_{sel} was presumably unattainable due to very high T_e (Figure 2-6). Maintaining T_b above T_{sel} in summer may be an uncontrollable side effect of high T_e; lizards seek refuge at midday rather than risking still higher T_b. In winter, the lizards had greater access to low T_e, and the lower variation in T_e in winter meant available T_e were nearer T_{sel} than in summer (Figure 2-2, Figure 2-3), implying a deliberate choice to maintain high T_b, (e.g., DeWitt 1967), or that precise thermoregulation in winter was relatively less important than other activities.

Discussion

The tropical lizard species studied here behaved as predicted by our extended cost-benefit model of thermoregulation (Figure 2-1). Thermoregulatory accuracy (Table 2-2) and effort (Figure 2-3) were highest in summer, when T_e was highest and thermal quality of habitat lowest. Despite apparent high thermal quality of the habitat determined from mean values, inspection of T_e distributions (Figure 2-2, Figure 2-3) confirmed that thermoregulation was critical to ensure lizard survival. In summer, lizards thermoregulated precisely, and maintained T_b above T_{sel}, possibly to extend available activity time and space (DeWitt 1967; Grant & Dunham 1990), until the T_e of this tropical woodland became high enough to force lizards to retreat. There is evidence that these lizards continue to thermoregulate even in retreats (Andersson *et al.* 2010). Overall, lizard thermoregulation was highly accurate.

Median environmental temperature (T_e) was congenial to skink thermoregulatory needs throughout the year (Figure 2-2); often within selected body temperature (T_{sel}) for these skinks. Thermal quality was high ($2.9 < d_e < 3.9$, Table 2-2), as commonly reported for tropical environments (e.g., Shine & Madsen 1996; Luiselli & Akani 2002). Under these conditions, deliberate, active thermoregulation seems unnecessary. However, midday T_e exceeded 60° C in both seasons, high enough to kill a thermoconformer, and exceeding *Carlia* spp. critical thermal maximum (CT_{max}, Greer 1980) by up to 5% of the day in winter and 40% of the day in summer (Figure 2-3). The distribution of available temperatures is particularly important for animals with low thermal inertia and high susceptibility to small-scale perturbations in T_e (Seebacher & Shine 2004), and who heat very quickly under moderately hot conditions (Herczeg et al. 2007). Clearly, in this environment, T_e was often too high to allow an ectotherm to thermoconform. This reaffirms that mean d_e cannot be used alone to describe thermal quality, and cannot account for the disproportionate costs of an environment that is too hot versus too cold, in terms of thermoregulatory strategies (Figure 2-3; Hertz *et al.* 1993; Huey & Kingsolver 1993).

These skinks showed high precision and accuracy of thermoregulation throughout the year (Figure 2-4, Table 2-2), although thermoregulation was both less accurate (higher d_b, Table 2-2) and less effective (lower E, Figure 2-3) in winter than summer. Furthermore, less effort was invested in thermoregulation in winter, when thermal quality was higher (low d_e, Figure 2-4). If skinks were thermoconforming, body temperature (T_b) and T_e distributions would have been similar, but they did not thermoconform in either season. Indeed, the comparatively low effectiveness and accuracy of thermoregulation in winter occurred because T_b was above T_{sel} even though T_e was typically below T_{sel} (Figure 2-2). The implication is that lizards actively raised their T_b above T_{sel}, although it is unknown whether T_b was deliberately increased by the skinks for performance benefits, hence increasing foraging success and predator avoidance, or whether T_b was increased as a necessary side effect of foraging in the too-hot habitat of their prey (DeWitt 1967; Kohlsdorf & Navas 2006). A recent model suggested that predators of ectothermic prey should spend more time in hotter areas, which would increase reptile T_b as we observed (Mitchell & Angilletta 2009). Invertebrate prey availability, and, therefore, the potential for high skink foraging success, appears to increase at warmer times of day (M. Vickers unpublished data). DeWitt (1967 and Grant & Dunham (1990) also observed lizards in hot environments (deserts) active at T_b much higher than T_{sel}, and attributed this to the lizards' lack of time to complete daily activities (foraging) without spending some time at T_b higher than T_{sel}.

Habitat thermal quality was lower in summer than winter, and as our model predicted (Figure 2-1), skinks invested more effort in thermoregulation in summer (Figure 2-4), resulting in increased thermoregulatory precision (Table 2-2) and effectiveness (Figure 2-3). Skink T_{sel} was higher in summer than winter, which is common (e.g., Van Damme et al. 1987), increasing the availability of optimal T_e in the hotter summer environment and extending activity time, but resulting in a reduced margin of error for thermoregulation, since T_{sel} was closer to CT_{max} (Greer 1980). At the moderately high temperature of 50°C, small (< 12g) reptiles heat up at 4° C per minute (Herczeg et al. 2007). Temperatures at our study site were regularly higher than 50° C (Figure 2-2). Accordingly, in summer, skinks had to avoid increasing T_b beyond the point of "no return" (i.e., loss of righting ability or CT_{max}), which may have been quite difficult, or even impossible, in such extreme conditions. Thus, skinks retreated to shelter sites during the middle of summer days (Figure 2-6). Note that retreating to shelter was not necessarily abandoning thermoregulation (thermoconforming). In the tropics, shelter sites were often within preferred temperature ranges for *Carlia* (Andersson et al. 2010), and thermoregulation in shelter sites is common to many reptiles (Huey et al. 1989), including Carlia (Andersson et al. 2010).

The distribution of environmental temperatures in summer (T_e) was positively skewed, and T_e was frequently higher than T_{sel}. Despite the increased effort and precision of thermoregulation in summer, T_b was also often above T_{sel}. As with winter, this may have been deliberate, to improve performance and foraging success, however, the distribution of T_b and T_e were more similar in summer than winter (Figure 2-3, Figure 2-6), suggesting that skinks may not have been able to lower T_b to T_{sel} and still have enough time and space to complete required activities in winter (Grant & Dunham 1990). The combination of a reduced margin of error for thermoregulation, poor thermal quality, and highly skewed summer T_e necessarily resulted in significantly more precise thermoregulation (Figure 2-3) due to the high cost or cost in terms of risk of thermoconforming (death). Had the cost in terms of risk of thermoconforming increased but not been lethal, as in cool climates, thermoregulatory precision may have decreased as occurs in the low-temperature cost-benefit model of Huey & Slatkin (1976) (e.g., Hertz et al. 1993; Sartorius et al. 2002; Herczeg et al. 2006).

Here we present an extension of the cost-benefit model of thermoregulation, designed to include the case where T_e exceeds T_{sel}. This new model acknowledges the high cost of thermoconforming (Blouin-Demers & Nadeau 2005) rather than just the cost of thermoregulating, especially in extreme environments. Future work needs to consider the disproportionate cost of high versus low T_e (Huey & Kingsolver 1993) on thermoregulation when describing habitat thermal quality. Also, particularly for small animals, which are especially susceptible (Seebacher & Shine 2004), variation in, and extreme values of $T_{e,}$ are more likely play a more important role in determining habitat thermal quality, and hence thermoregulatory behaviour, than mean or median temperatures. This will be especially important under increasingly variable temperature regimes predicted by climate change models (Deutsch et al. 2008; Huey et al. 2009; Sinervo et al. 2010).

Figures

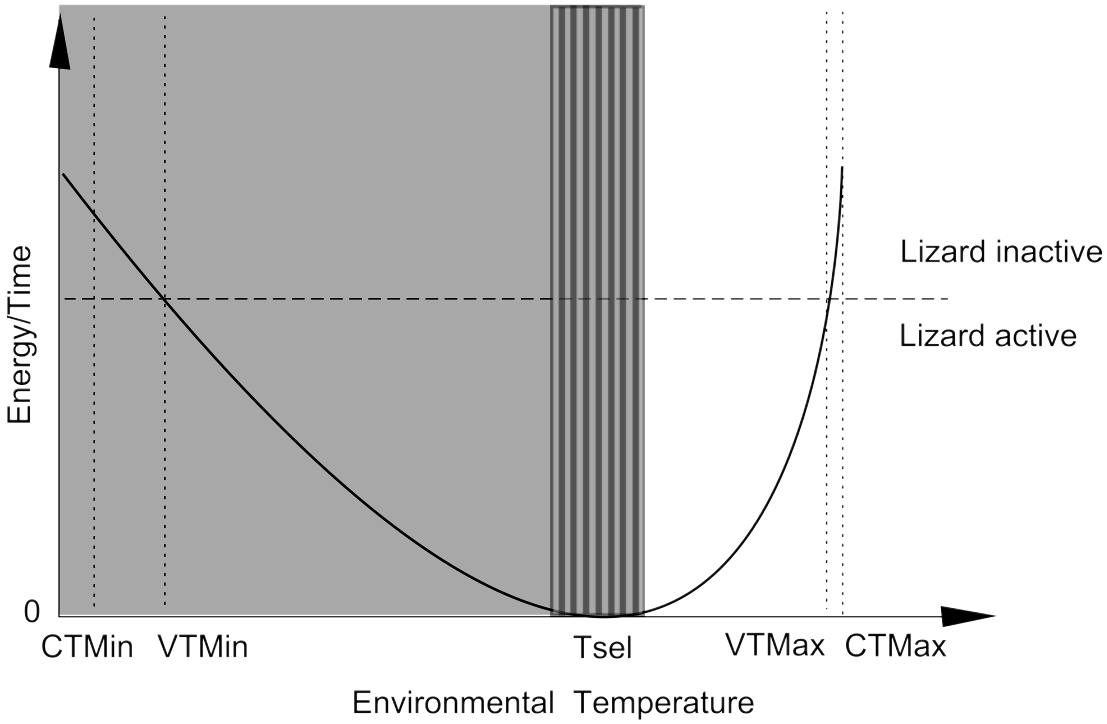

Figure 2-1. Fitness cost and benefit of thermoregulatory activity. The solid curve indicates the fitness cost of attaining $T_b = T_{sel}$; the dashed horizontal line is the benefit (constant, and independent of T_e). The area between the curves is the net fitness benefit of perfect thermoregulation. The voluntary thermal maximum (VT_{Max}) and minimum (VT_{Min}) occur when net benefit is zero, at the intersection of cost and benefit. Here, lizards will become inactive, seeking refuge to avoid more extreme temperatures such as critical thermal maximum (CT_{max}) and minimum (CT_{min}). As T_e deviates further from T_{sel}, a thermoregulator must invest more effort in thermoregulation to remain active and achieve the benefit of $T_b = T_{sel}$. The asymmetrical curve is consistent with thermal-energetic relationships and also accounts for the cost in terms of risk of thermoconforming at high T_e. The shaded side, $T_e < T_{sel}$, is consistent with the original cost-benefit model for

thermoregulation (Huey & Slatkin 1976); here we extend the model to include the unshaded side, in which $T_e > T_{sel}$, which needs to be incorporated into cost-benefit model for thermoregulation.

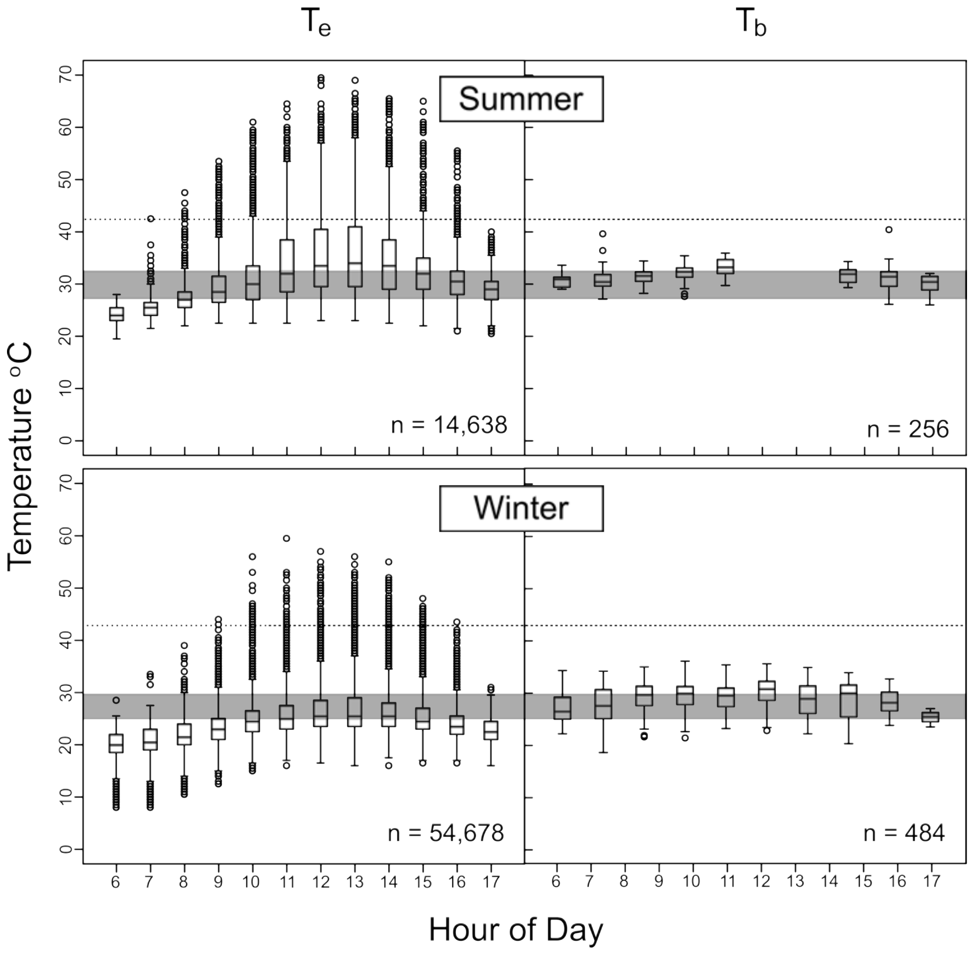

Figure 2-2. Hourly available operative environmental temperatures (T_e) and body temperatures (T_b) of skinks at Hinchinbrook Island in winter and summer. Open circles are 'outliers' (estimated as 1.5*[inter-quartile range] outside the 1st and 3rd quartiles). We have included them here because of the critical nature, in terms of biological significance, of occasional high temperatures in the environment. The dashed line illustrates the highest CT_{max} measured for any *Carlia* spp. (Greer 1980), the shaded zone represents the maximum T_{sel} range for three species of *Carlia* skinks. The left side of the figure is T_e, right side is T_b pooled across species. Median T_e is typically within T_{sel} in winter, and below T_{sel} in the early morning and afternoon. Compared to this, summer has very hot days with early and late median T_e within T_{sel}, but through the middle of the day

median T_e is above T_{sel}. In both seasons, T_b is near the upper limit of T_{sel}, and toward the middle of the day, exceeds T_{sel}.

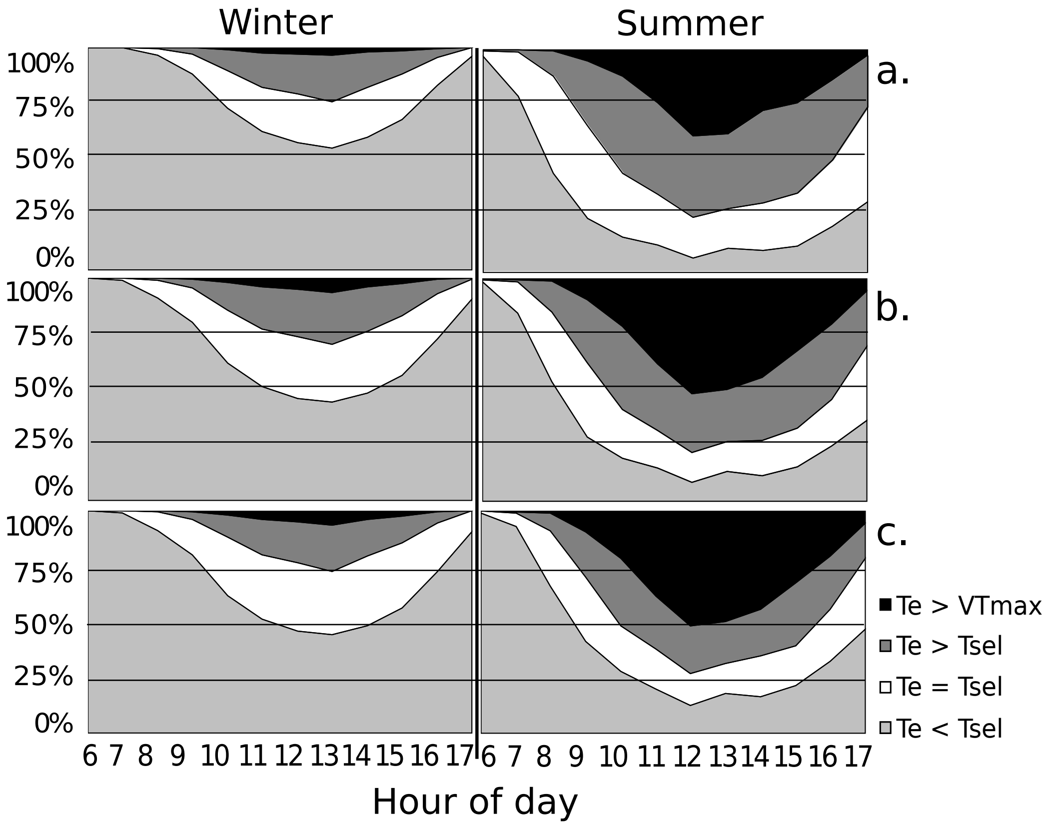

Figure 2-3. Proportion of environmental temperature (T_e) measurements that were less (light grey), equal (white), or greater than selected body temperature (T_{sel}), as well as the proportion of T_e measurements less than the critical thermal maximum (CT_{max}) reached for any *Carlia* species (Greer 1890, dark grey) for winter (left hand panels) and summer (right hand panels) throughout the day (winter n = 163 days, summer n = 70 days). Although habitat thermal quality (d_e) is similar in both seasons, the thermal profile was quite different. T_e was mostly less than T_{sel} during winter, though up to 5% of T_e was above CT_{max}. At least 50% of T_e in winter were high enough to allow individuals to raise body temperature (T_b) to at least T_{sel}. In summer, T_e was typically above T_{sel}, and up to 40% of T_e were above CT_{max}. For most of the day in summer, T_e low enough to allow a lizard to cool to T_{sel} were scarce, as little as 15% of the day.

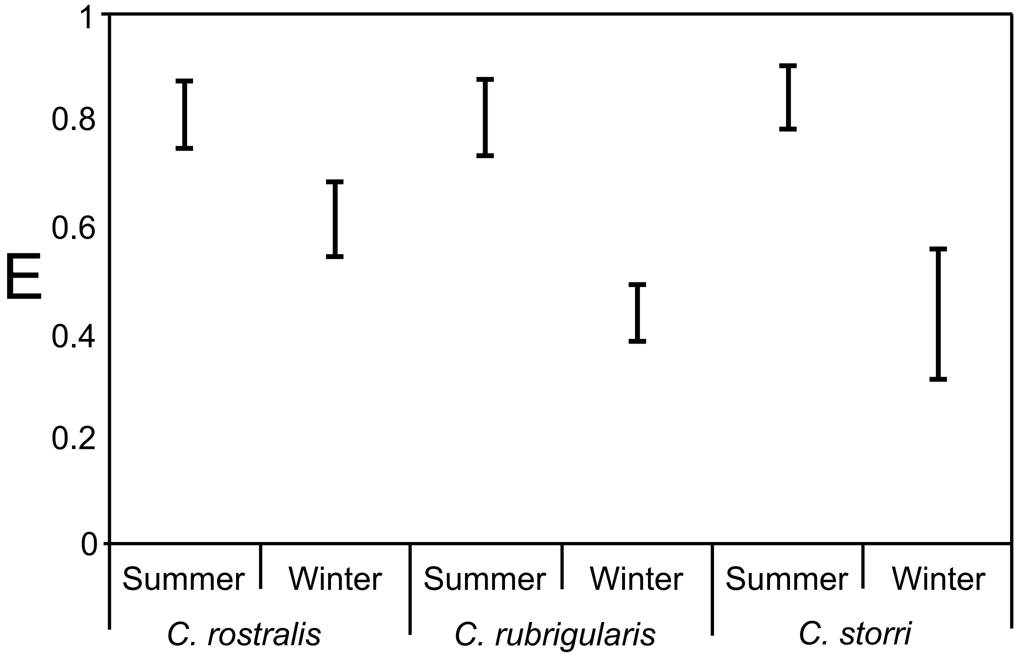

Figure 2-4. Effectiveness of thermoregulation (E ± 95%CI) for active lizards in summer and winter. E was significantly higher in summer than winter for all species.

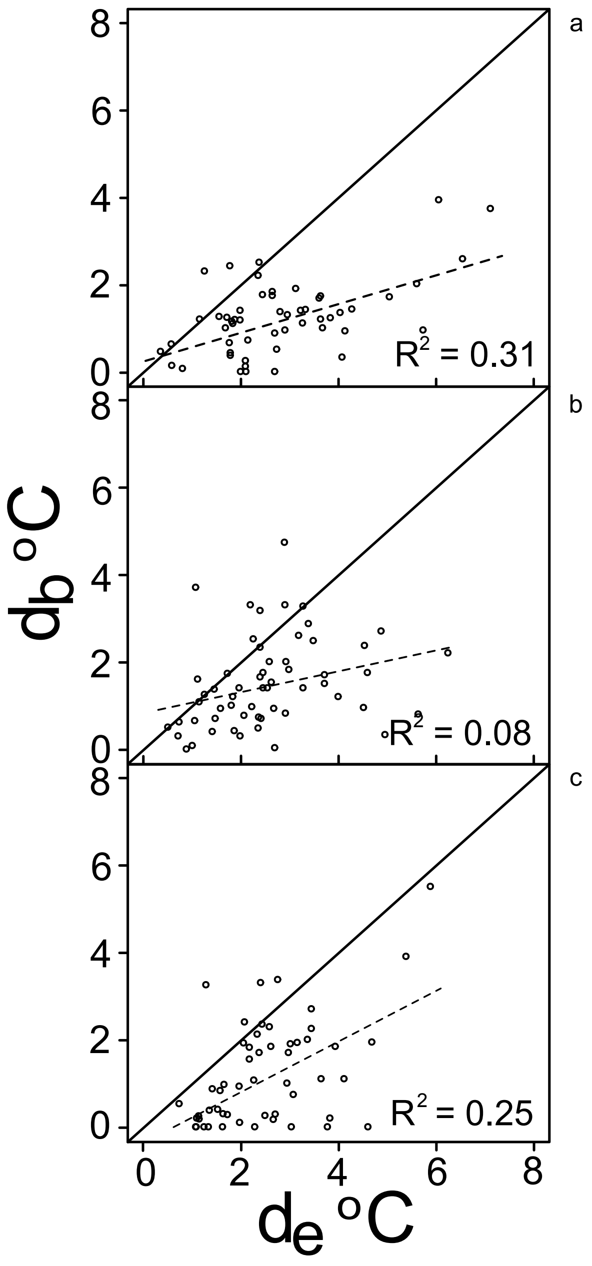

Figure 2-5. Mean accuracy of thermoregulation (d_b) and mean thermal quality of the habitat (d_e) measured per hour across the study period for a. *Carlia rostralis*, b. *C. rubrigularis*, c. *C. storri*. Dashed lines are linear regressions, solid lines are a reference line for m = 1. Hyopthesis tested: m = 0. In all cases, m < 1 (see text), hence as thermal quality decreased (or d_e increased), thermoregulatory effort increased.

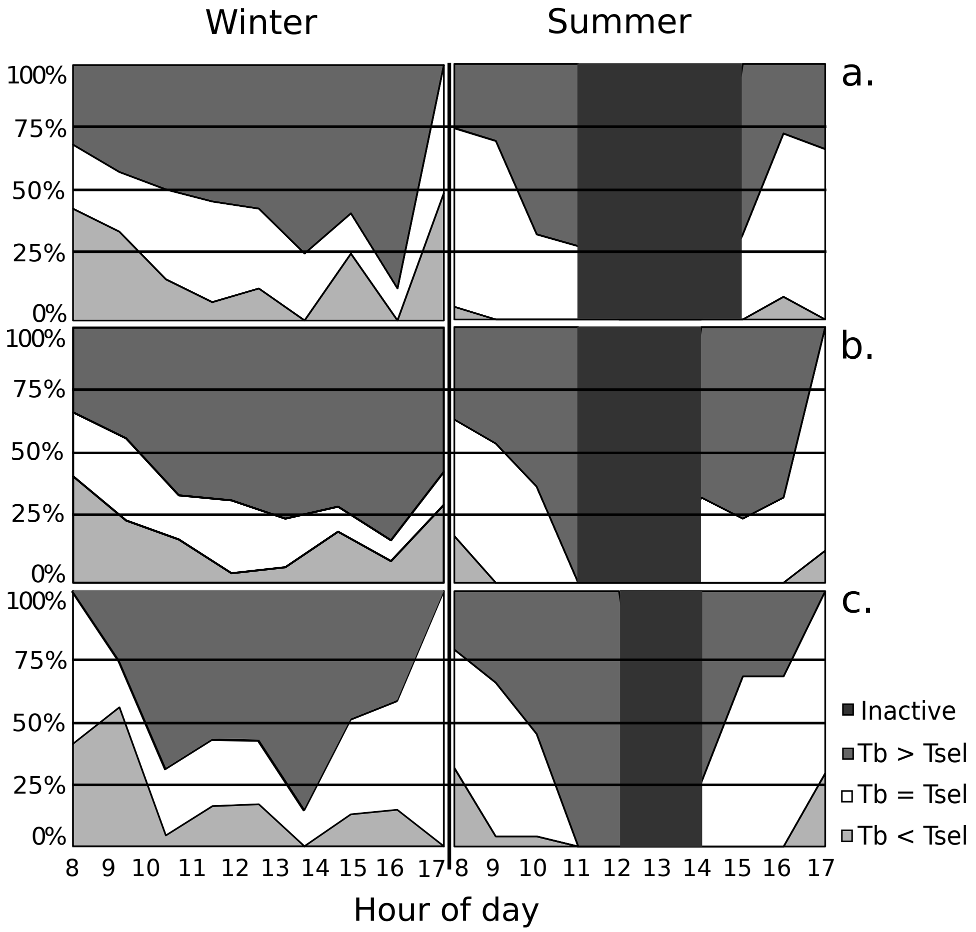

Figure 2-6. Proportion of body temperature (T_b) measurements that were less (grey), equal (white), or greater (dark grey) than selected temperature (T_{sel}) for three *Carlia spp*. in winter (left) and summer (right) throughout the day. Light grey in the middle of the summer day is when lizards were inactive so unavailable for T_b measurement, but were likely to be thermoregulating in retreat sites. Lizards maintained T_b above T_{sel} for most of the day in both seasons even though the environmental thermal profile through the day was quite different. This may be deliberate, with lizards capitalising on the performance benefits associated with increased T_b, or a side effect of foraging in too hot areas where prey are active.

Chapter 3 Using iButtons™, copper models, and small temperature sensors to estimate lizard field body temperature

Abstract

Classically, behavioural thermoregulation is studied by contrasting operative environmental temperature with animal body temperature. Operative environmental temperature is usually the measured body temperature of a copper-model replicate of the animal. Copper models can be costly or difficult to construct, which can prohibit their use in extensive documentation of environmental temperature. I describe a method to estimate operative environmental temperature of lizards using three different temperature loggers: iButtons™, copper models, and simple, tiny DS18B20 sensors. I transform temperatures using a simple differential equation, scalable to lizard body size. My results show that with appropriate calibration, either method is equally useful in estimating rate of body temperature change and equilibrium temperature for skinks, which allows wide use of cheap, simple data loggers for collecting environmental temperature. This method is particularly applicable to estimating body temperature of an organism moving through the habitat.

Introduction

Studying thermoregulation in ectotherms relies on comparing their body temperature with predicted temperatures from a null model (Hertz *et al.* 1993). Null model temperatures are referred to as ‘operative environmental temperatures’, and represent the temperature the organism would reach at equilibrium if it were in the sample location. In lizards, operative environmental temperatures are typically collected by measuring the temperature of calibrated cast copper models of the lizard distributed randomly through the habitat (Hertz *et al.* 1993; Bakken & Angilletta 2013). Copper models are tried-and-tested, but they are limited in a number of ways (i) they can be costly and time consuming to design and construct, and so limit the number samples, or the spatial extent of the study; (ii) static copper models carry the assumption that the lizard necessarily reaches thermal equilibrium at each site it encounters; this is not always the case, especially for wide-foraging (Huey & Pianka 1980), fast-moving, or large-bodied organisms (Seebacher & Shine 2004; Christian & Tracy 2006; Vickers & Schwarzkopf 2013, Chapter 3).

An alternative method to using copper models to estimate operative environmental temperature is estimating lizard body temperature from first principles. Body temperature is the sum of previous body temperature and heat gained (or lost). Heat can be gained or lost by conduction, convection, radiation, and evaporation, although evaporative heat loss is low in small organisms (Porter *et al.* 1973). The effect of radiation, conduction, or convection is dependent upon the surface area to volume ratio of the organism and the temperature gradient experienced, for example, the difference between body temperature now and body temperature at the next time step, divided by the length of the time step. Thermal gradients can be steep, for example, a in lizard shuttling between sun and shade sites (Dzialowski & O'Connor 2001), or very shallow, for example, for a large python moving about in habitat at night (Shine & Madsen 1996). Estimating lizard body temperature has been attempted in many ways (Florides 1999; Shine & Kearney 2001; Fei *et al.* 2012a), requiring many temperature measurements and an understanding of energy-mass balance, and a thermal constant for the organism on many surface types, and so is not necessarily convenient for field ecologists.

Recently, inexpensive small (iButton™) and tiny (DS18B20 sensors) temperature data loggers have become available, which can allow researchers to collect data on habitat temperatures in far more locations than are possible using traditional cast copper models. Data loggers, such as iButtons™, record the temperature at the internal digital thermometer imbedded in the device. An iButton™ is acted on by similar heat sources as a lizard would be in the same location (convection, conduction, and radiation), and so rather than assessing each component of the heat model to estimate lizard body temperatures, I measured temperatures using iButtons™ and scaled those to operative environmental temperature using a simple differential equation. The digital thermometer was a DS18B20 thermal probe, and I compare operative environmental temperature from the iButton™ to that of a copper model fitted with a DS18B20 probe, and with the probe itself. For each of the three logger types I optimise the parameters for estimating operative temperature for rainbow skinks *(Carlia spp.)*, and compare the efficacy of the three logger types for dynamically estimating lizard body temperature.

Methods

Study species

The experiments were conducted at two separate locations in Queensland, Australia: Lizard Island (September 2013, 14.66°S, 145.55°E), and Wambiana (October 2013, 20.55°S, 146.10°). At Lizard Island, the body temperatures of sandy rainbow skinks (*Carlia dogare*, n =4, SVL 48 mm, mass 4.8 g) were compared to those of iButtons™. At Wambiana, the body temperatures of shaded-litter rainbow skinks (*Carlia munda*, n=3, 45mm, 4.1g) were compared with temperatures reached by DS18B20 sensors, and copper models fitted with DS18B20 sensors. In both locations, lizards were captured by hand and returned to the laboratory, where experiments were conducted immediately. Lizards were returned to their point of capture within an hour.

Experimental design

Lizards were taped to an unstained wooden block (300 mm L x 50 mm H x 100 mm W) using Millipore tape, and a logger was placed immediately adjacent to them. The logger was either an iButton™ in a 3 x 3 cm 'calico' (equal weft and warp plain weave fabric in unbleached cotton) cloth bag to reduce the effect of direct radiation or both sensor (DS18B20) and copper model fitted with a sensor. The wooden block, equipped with a live lizard, recorder, and sensors was placed approximately 30 cm below a 60W light bulb at the start of the experiment, and the block was kept under the light bulb until the lizard showed signs of distress (struggling, and high body temperature, <38°C, approximately 3-4 minutes), and was then removed from under the light bulb to allow cooling. I continued recording body and sensor temperature for another 3-5 minutes. The experiment took place in a room cooled to approximately 23 °C.

Temperature measurement

The iButton™ was tasked to record temperature every minute, and the sensor and copper model were tasked to record temperature approximately every 40 seconds.

The sensors were attached to a RaspberryPi™ computer by a 10-m Category 5 Ethernet cable. There were 20 sensors positioned at equal distances along the cable, data from only two were used for each experiment (one naked, one in a copper model). The sensors were soldered in parallel along the data cable such that they received parasite power from the RaspberryPi™, and were controlled by a purpose-written script that polled the sensors in order. Polling the unused 18 sensors meant sample rate was limited to intervals of approximately 40 sec. Copper models were a hollow tube of 2mm thick copper sheet, a similar length and diameter as a Carlia (~90mm long, 15mm diameter).

A probe (a 3-mm gauge metal type K thermocouple) was inserted in the lizard's cloaca, and attached to a quick reading digital thermometer (Comark KM-C28K), and body temperature was recorded to the nearest 0.1 °C every minute. For each lizard, a GAM was fitted to temperatures recorded over time using a cubic regression spline smoother, using function MGCV in R (Wood 2011; R Core Team

2013). The GAM was used to predict lizard body temperature every second, and all GAMs had near-perfect fit, with total deviance explained > 99.5%. There was minor heterogeneity of variance in the models, which was unlikely to cause errors in interpretation. GAMs were fitted following Zuur *et al.* (2009) and Wood (2011).

Modeling and optimisation

Logger data were used in Equation 1 (adapted from Mitchell 1976; Angilletta 2009) to estimate environmental temperature, equivalent to null model body temperature, or the temperature a lizard should obtain under the same circumstances, given no behavioural or physiological processes to control body temperature.

Equation 1 evaluates body temperature, dT_b, and requires knowledge of body temperature at time *i*, $T_{b(i)}$, environmental temperature (T_e) at time *i*, and *i*+1, and a parameter, K, that incorporates body size and a thermal time constant. Final body temperature is then used as $T_{b(i)}$ in the next iteration. In this way, body temperature is integrated over time, and would only reach equilibrium with the site if it remained in place long enough and/or the site temperature remained constant for long enough.

Equation 1.

$$T_{b(i)} = Tb_{(i-1)} - Te_{(i)} * \exp(K-t) + T_{e(i)}$$

From the literature, the range of K for a 4.5g skink, standing approximately 1.5 cm above the substrate (similar to the *Carlia* species, studied in Chapters 2, 3, 5) is in the range of 0.02 – 0.7 (Mitchell 1976). The model here stopped at 0.2, as the small size of the lizard didn't require further testing. To determine the value of K that best estimated environmental operative temperature for *Carlia* skinks, I ran the equation using all K values in a sequence from 0.02, to 0.2, incremented by 0.01, the results of which were used for comparison with the real lizard paired with the logger.

Sum of squared differences between operative environmental temperature estimates and the lizard GAM model determined the "best" K value (lowest SS) for closest model fit. Visual inspection of plots was also used in conjunction with sum of squared differences to determine the "best" K value for estimating equilibrium temperature and rate of increase or decrease of body temperature, which were not necessarily the same as the K values that optimised sums of squares.

Results

Lizard Island - iButtons™

K values that produced model outputs that best approximated the lizard temperature differed slightly among the four *C. dogare* studied at Lizard Island (Figure 3-1). Model operative temperature estimated lizard body temperature best for two of the lizards (1, 4), and less closely, but still reasonably well for the other two (2, 3). The parameter (K) producing the lowest sum of squared differences between operative temperature and real lizards ranged among lizards from 0.003 to 0.006 (Figure 3-1). However, particular aspects of lizard body temperature were optimised at slightly different, overlapping, K values: best estimation of maximum temperature was for K = 0.003 - 0.009 (closest match between model and lizard maximum, Figure 3-2); closest estimation of increasing body temperature (increasing slope) was near K = 0.005; closest estimation of decreasing body temperature (decreasing slope) was higher, near 0.01 – 0.015 (Figure 3-1).

Wambiana Station – copper models and thermal sensors

Model outputs for both the copper models and the sensor models (Figure 3-3) was as variable as model outputs from iButtons™ (Figure 3-1). For the copper models, the size parameter (K) with lowest sum of squared differences between copper-model operative temperature and lizard (*C. munda*) body temperature varied amongst lizards from 0.004 – 0.008 amongst the four lizards, while for the sensor, lowest sum of squares was for K from 0.004 to 0.005 (Figure 3-4). As with the iButton™ model outputs, particular aspects of lizard body temperature were best estimated using different K parameters, though in general there was less variability in the range of copper/sensor K values than for iButtons™. Best estimate of maximum, increasing and decreasing body temperature was similar to lowest sum of squares, approximately K = 0.005 – 0.008 (Figure 3-3).

Discussion

iButtons™, sensors, and copper models equipped with a sensor all provided excellent estimates of the operative temperature of *Carlia* skinks. Operative temperatures calculated from the iButtons™ estimated the rate of lizard body temperature change better, but were more variable in the accuracy of predicted maximum temperature than were either of the other sensors (Figure 3-1, Figure 3-3). For estimating body temperature in a dynamic model, in which 'body temperature' is updated every second (e.g. Rodriguez-Girones 2002; Fei *et al.* 2012; Vickers & Schwarzkopf 2013, Chapter 3), iButtons™ performed slightly better. However, for studies in which equilibrium temperature is required (Hertz *et al.* 1993; Blouin-Demers & Weatherhead 2002; Herczeg *et al.* 2003), the best estimates were obtained using copper models and sensors. Importantly the methods of the original null-model of thermoregulation (Hertz *et al.* 1993) rely on equilibrium temperatures of copper models for operative environmental temperature. While steady state temperature is important for studying thermoregulation, the shortcomings of relying on equilibrium temperature have been discussed (Seebacher & Shine 2004), and the importance of thermal transience has been recognised for large organisms (Christian & Tracy 2006), and must be considered in small ones, as while very small organisms have a small lag (Stevenson 1985b), even a small lag may be ecologically relevant due to the strong thermal dependence of traits such as locomotion (Full & Tullis 1990).

For *Carlia* skinks, for best estimation of all four aspects of body temperature from iButtons™: rate of increase and decrease, maximum temperature, and best overall fit, I recommend a value of K between 0.005 – 0.008. For best estimation of all four aspects of body temperature from sensors and copper models, I recommend a value of K near 0.005. AAmongst all lizards for each logger type, values of K that best estimated these four aspects overlapped, although there was some variability. Decreasing K slowed the rate of temperature increase and underestimated maximum body temperature; in all, decreasing K increases the ‘body size’ and decreases the thermal constant (heat exchange rate) for the model: estimating operative environmental temperature for larger organisms required a slightly smaller K value. The smaller K value required to estimate body temperature from the sensors and copper models is probably caused by their lower thermal inertia compared with iButtons™. This model was formulated under laboratory conditions; artificial heat/light source, no wind, which are factors to consider when applying this model to real-world ecological studies. The K value that was the best fit (~0.005) was at the low end of K values from Mitchell (1976), which is due to the small body size of the lizards used, and the mass of the logger used. It is important to test any given temperature logging method against the organism being studied.

The copper models I used were simply constructed, and did not match scalation and details of body appearance of the lizards perfectly, so their results may be less accurate compared to other cast models (Hertz 1992; Bakken & Angilletta 2013), however, the usefulness of increasing degrees of model accuracy is unclear (Shine & Kearney 2001). Despite the simple construction of my models, operative temperature calculated from copper models was a good estimator of lizard body temperature. Interestingly, the sensor without a copper model surrounding was as accurate in terms of both maximum body temperature and rate of temperature change. Precise copper models have been used for important work describing microclimates (Grant & Dunham 1988; Huey 1991) and for determining the physiological impacts of body temperature on lizards (Diaz 1997; Gvoždík 2002). My results show that using sensors without copper models may be a better, cheaper and easier method to obtain similar results, especially if many locations must be sampled, which is good news for field ecologists, as the cost and effort involved in creating copper models can be prohibitive. The most portable method I tested for recording environmental temperature was iButtons™. They operate independently and can be placed easily around any terrain, while the sensors, which must be tethered to a data recorder with an external power supply, were more cumbersome and difficult to use in remote areas. On the other hand, the sensors can be better than iButtons™ in other ways, because their data are recorded and stored directly into a database, whereas iButtons™ must be distributed, collected, connected to a computer and downloaded, a tedious process vulnerable to human error, especially if there are many iButtons™. Using cheaper data loggers will facilitate more thorough sampling of the thermal environment: more sites at the cost of detailed description of microclimate. An organism can alter its posture at a particular site, controlling its body temperature by presenting more or less surface area to various heat sources (radiation, convection and conductance). Simple loggers cannot capture this, but many simple loggers can sample more locations. The trade off in information quality obtained by measuring small adjustments in posture versus measuring many sites should be examined in more detail.

Ultimately, which logger is used to estimate operative temperature doesn’t really matter, provided it is calibrated to the organism in question, and there is no systematic bias in the operative temperature estimated (Bakken & Angilletta 2013). I found no evidence of systematic bias among the predictions made from the sensors, although particular aspects of the body temperature were slightly better estimated if different values of K were used. Variability of K among individuals may be caused by a number of things. As K is sometimes called a 'body size' parameter, the most obvious source of variation may have been lizard body size. Another source of variability in precision of operative temperature estimates is that lizards use physiological methods to alter their rate of body temperature change compared to a non-living model (Seebacher & Franklin 2005).

I have presented a new and simple method that can be used to predict lizard body temperature change and thermal equilibrium from temperature data loggers, that is particularly applicable to estimating temperature of a lizard moving dynamically through a habitat. Further development of equation 1 will include comparing the performance of temperatures measured by iButtons™ and models with lizards tethered in the environment to account for more sources of heat than just radiation from a light bulb, and further experimentation involving larger and smaller organisms.

Figures

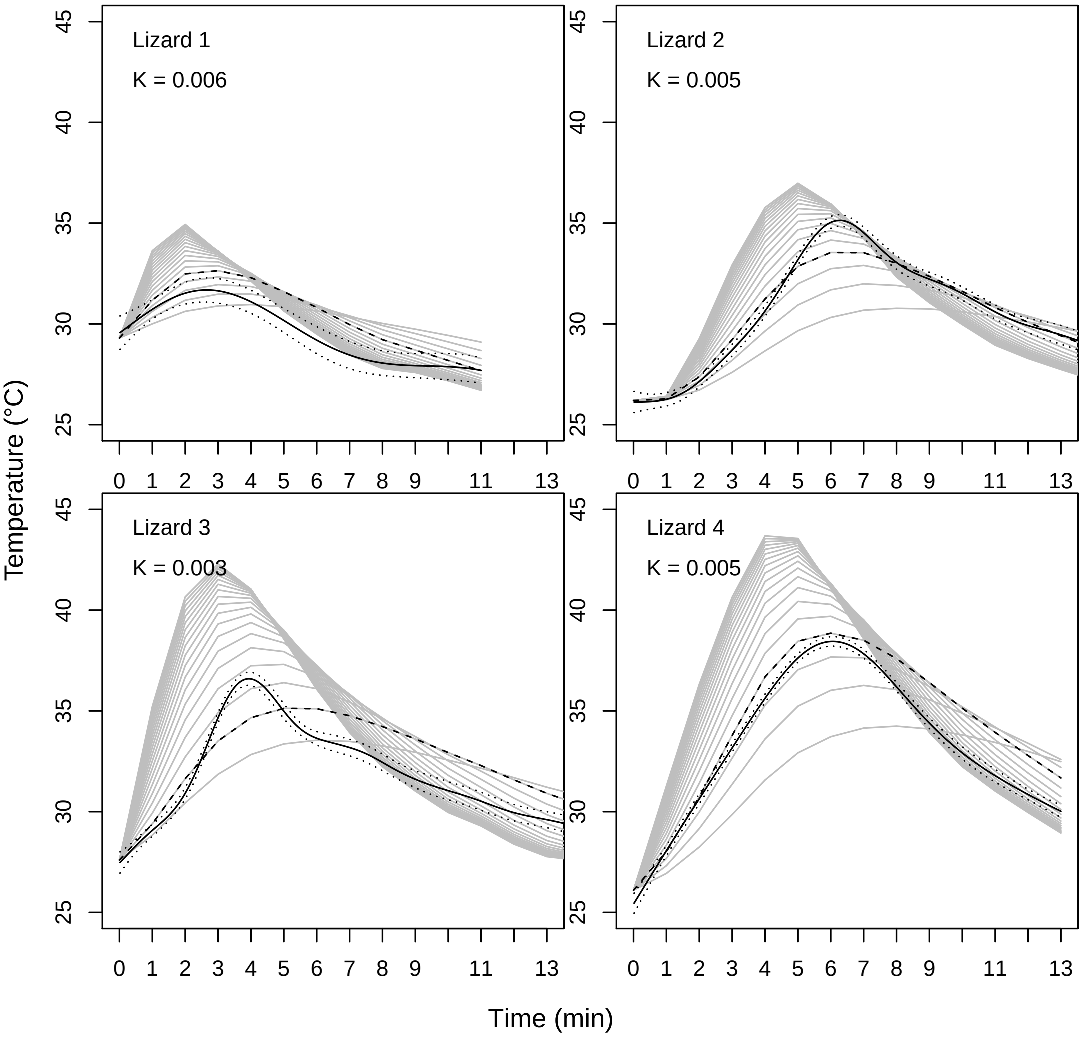

Figure 3-1. Operative temperatures predicted from iButton™ temperature loggers at Lizard Island; each plot represents a different lizard (*Carlia dogare*) with paired iButton™ experiment. For each plot the topmost grey line is an iButton™ temperature. Successive grey lines moving downward (getting flatter) are operative temperatures estimated by increasing K values (from 0.002 – 0.02), each line is one K value. Lizard body temperature is shown (black line), with GAM prediction intervals (dotted, +-2xSE). The K value with the lowest sum

of squared differences between operative temperature estimate and lizard body temperature is indicated on the plot, and its prediction is drawn as a dotted line. The best estimation of maximum temperature occurred when operative temperature peaked at the same temperature as the real lizard. The best estimation of rate of change occurs when the slope of the model is most similar to the slope of the lizard temperature.

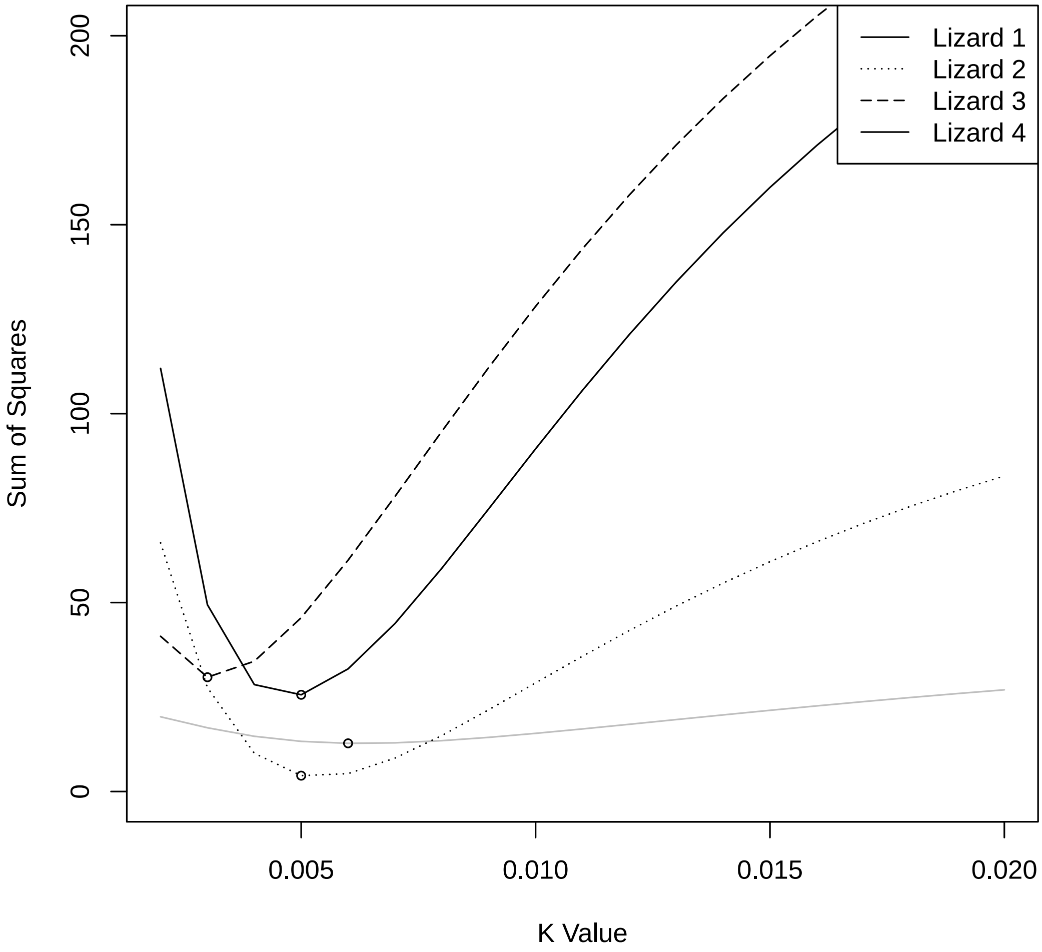

Figure 3-2. Response of sum of squared differences between lizard body temperature and model outputs (shown in Figure 1) to variations in the K value. Points on line indicate the K value with the lowest sum of squares. For example, total SS for lizard 2 begins at ~75 (K = 0.001), decreases to ~5 (K = 0.05), and then increases as K increases to 0.02.

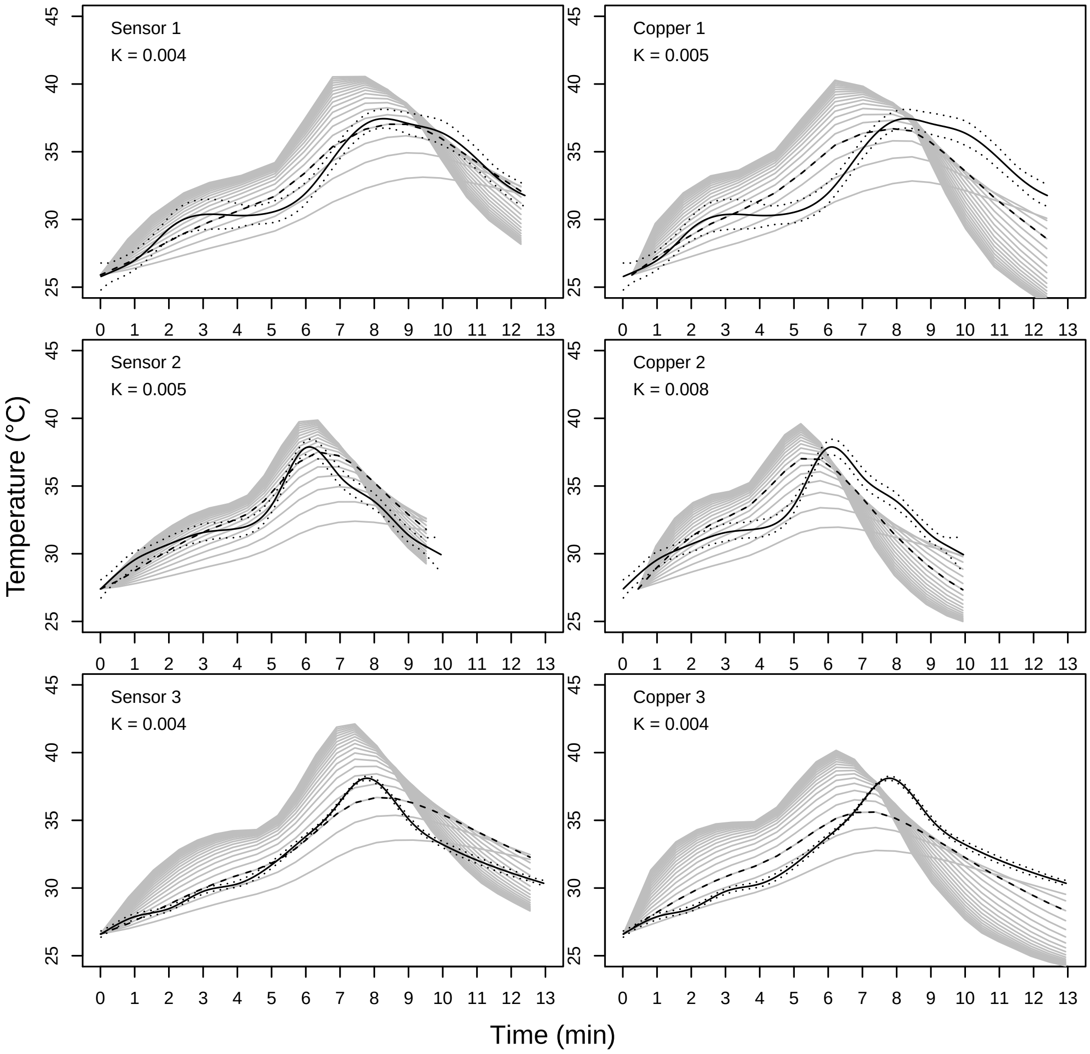

Figure 3-3. Operative temperature predicted from copper models (left) and sensors (right), each row is the same lizard (*Carlia munda*) and copper model pair at Wambiana Station. Logger temperature is the topmost grey line, successive grey lines moving downward are for increasing K values (from 0.002 – 0.02), each line is one K value. The black line is lizard body temperature, dotted lines are GAM predictions intervals (+- 2*SE). K value with lowest sum of squares compared with lizard body temperature given, and plotted as dotted black line. The K value with the lowest sum of squared differences between operative temperature estimate and lizard body temperature is indicated on the plot, and

its prediction is drawn as a dotted line. The best estimation of maximum temperature occurs when operative temperature peaks at the same temperature as the real lizard. The best estimation of rate of change occurs when the slope of the model is most similar to the slope of the lizard temperature.

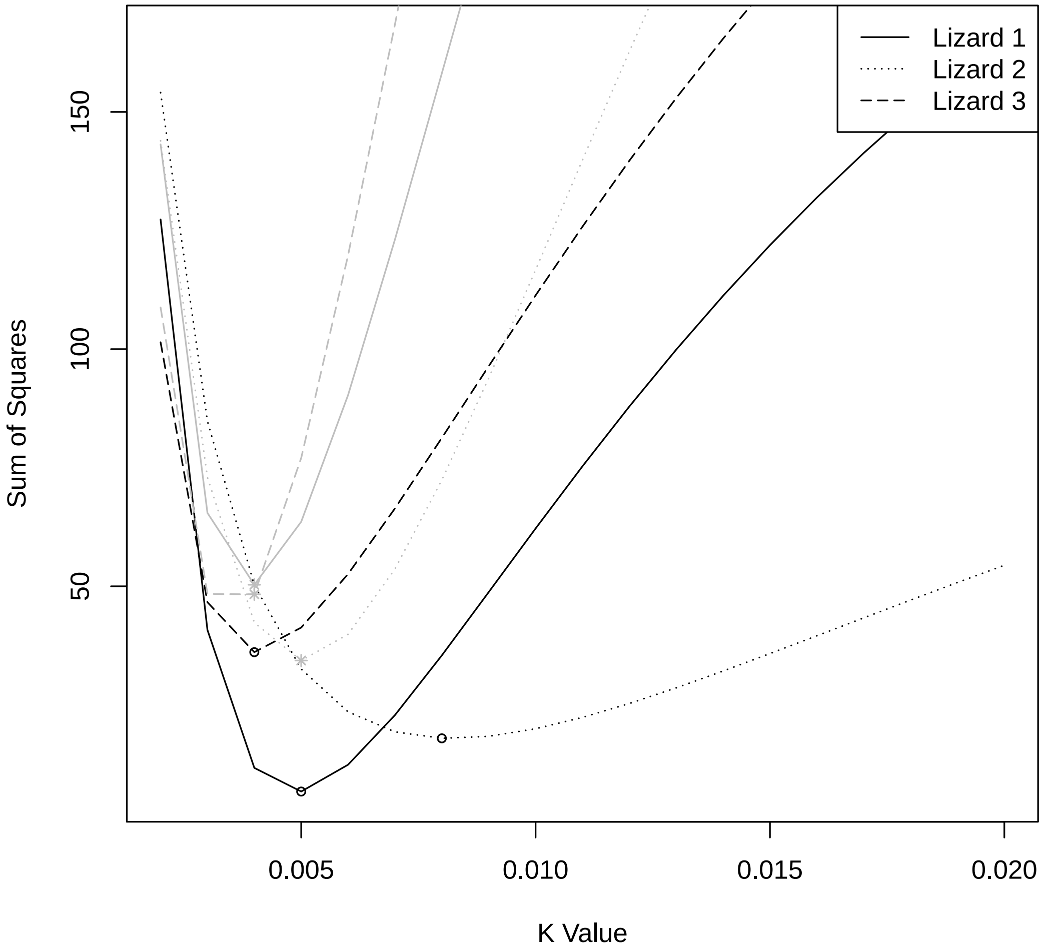

Figure 3-4. Response of sum of squares between lizard body temperature and model outputs (shown in Figure 3) to K value. Points on line indicate K values with lowest sum of squares. For example, total SS for lizard 1 begins at ~125 (K = 0.001), decreases to ~10 (K = 0.05), and then increases as K increases to 0.02.

Chapter 4 A random walk in the park: an individual-based null model for behavioural thermoregulation.

Mathew Vickers[1, 2*], Lin Schwarzkopf[1]

1. School of Marine and Tropical Biology, James Cook University, Townsville, Australia
2. CSIRO Sustainable Ecosystems, Ecology Program, PMB PO, Aitkenvale, Queensland 4814

* Corresponding author Vickers.mathew@gmail.com

In review, Functional Ecology

Summary

1. Behavioural thermoregulators leverage their environment to control body temperature. Habitat thermal quality dictates the difficulty of precise thermoregulation, the quality of behavioural thermoregulation in turn impacts organism fitness through the effect of body temperature on performance traits.
2. Comparing the body temperature of a thermoregulator with expectations from a null model allows us to estimate both habitat thermal quality and the effect of behavioural thermoregulation on body temperature.
3. Available null models rely on static physical models of the organism to generate an index of thermal quality and thermoregulator effectiveness. Such null models account for neither movement through the environment, a primary method of thermoregulation, nor the spatial and temporal distribution of environmental temperature.
4. We present a new null model based on a random walk through a spatially and temporally consistent reconstruction of the thermal environment, to estimate a temporally integrated distribution of null body temperatures for comparison with a real thermoregulator.
5. Body temperature of the null model was estimated from environmental temperature using a simple differential equation with parameters for body size and movement rate.
6. We determined a fitness-based metric that dynamically described habitat thermal quality through the day. The metric was calculated by mapping body temperature to the thermal performance curve, such that body

temperature could be translated to a ‘Thermal Benefit’ between 0 (mortality) and 1 (highest performance). Thermal Benefit was calculated for the null model and a real organism (lizard), and the difference between the real animal’s Thermal Benefit and null model’s Thermal Benefit indicated the benefit of behavioural thermoregulation.

7. We demonstrated our model using a skink in an Australian tropical open woodland and described a shift in habitat thermal quality through the day, and a compensatory shift in thermoregulatory effort, and hence benefit of behavioural thermoregulation, as thermal quality deteriorated in the middle of the day.
8. Our new null model provides a temporally integrated, realistic estimate of habitat thermal quality and thermoregulatory effort and benefit. Our metric, Thermal Benefit, summarises these in the evolutionarily relevant context of organism fitness.

Key-words body, ectotherm, habitat, reptile, skink, thermal quality, temperature

Introduction

In ecology, null models are most useful when experiments cannot easily be used to isolate the mechanism underlying a pattern or process (Pianka 1986; Gotelli & Graves 1996). In ecological studies, null models are often created using randomised observations of the environment, such as the ideal free distribution (Gotelli & Graves 1996). However, this type of model can be insensitive to sources of random variation arising from the behaviour of individuals (Ulrich & Gotelli, 2013). In such cases, individual-based modeling, or simulations, can be useful. Increasingly, the influence of individual-level experience on population-level processes is being recognized, for example in species distributions, speciation rates and behavioural syndromes (Sih *et al.* 2004). Individual-based modeling has been instrumental in understanding the thermal physiology of the roundworm, *Caenorhabditus elegans* (Anderson *et al.* 2007) and here, we propose an individual-based null model to assess behavioural thermoregulation in vertebrate ectotherms.

Ectotherm body temperatures often differ from environmental temperatures, a phenomenon first described by Cowles & Bogert (1944). They used differences between air temperature and ectotherm body temperatures to demonstrate that ectotherms were thermoregulating. This method was used until (Heath 1964), demonstrated that any object with mass (e.g., a fluid-filled can of beer) also appears to thermoregulate if air and “body” temperatures are compared. A more explicit null model was required to demonstrate thermoregulation, specifically one that included behavioural observations in addition to air temperatures and body temperatures (Heath 1964). Accordingly, a null model for behavioural thermoregulation was developed that was contingent upon three primary assumptions (Hertz *et al.* 1993): (i) an individual strives to attain a particular set-point, or selected, temperature (optimum T_b; T_{set} or T_{sel}) rather than simply being different from available environmental temperatures; (ii) body temperature (T_b) must be compared to a null-distribution of available operative environmental temperatures (T_e), determined using temperatures of a non-thermoregulating model placed in a similar environment; and (iii) the null distribution of available T_b could be estimated as a random sample of T_e. This null model for behavioural thermoregulation has three components: (i) a sample of T_e experienced by the focal organism; (ii) a physical model intended to accurately estimate available T_b in the environment while accounting for thermal inertia; and (iii) a quantification of the quality of T_b control given the available T_e within that habitat (i.e., the habitat thermal quality). Sampling the environment to estimate operative T_e must be done with caution since the proportions of 'good' and 'bad' sites in the habitat can easily be misrepresented (Hertz et al. 1993). The model, often constructed of hollow copper, provides an estimate of the thermal energy balance that would be experienced by the organism (e.g., a lizard), integrating solar radiation, convection, conductance, and other sources of heat exchange (e.g., (Bakken & Angilletta 2013). Habitat thermal quality (or d_e) measures the deviation between the operative environmental temperatures estimated by the non-thermoregulating model (T_e) and the preferred temperature for the lizard (T_{sel}), while the deviation between actual body temperatures achieved (T_b) and T_{sel} is an estimate of thermoregulator ability, or d_b (Hertz et al, 1993). The thermoregulatory ability of an animal was, thus, defined relative to the available distribution of T_e, and relative to the preferred body temperature, T_{sel}. These indices have been used and reworked extensively (Sartorius et al. 2002; Christian & Weavers 1996; Blouin-Demers & Nadeau 2005), and have been central to analyses quantifying trends in thermoregulation across habitats, latitudinal gradients and clades (Grant & Dunham 1988; Sinervo *et al.* 2010). However, this null model has been criticized, because the static distribution of operative T_e fails to provide a null distribution for animals that move through the habitat without necessarily equilibrating to each site they pass through (Seebacher & Shine 2004). Thus, this null model represents a sit-and-wait mode forager, or sessile organism. Ultimately, this means the predictions of this null distribution are necessarily shaped by the behaviour of immobility in the environment (Harvey *et al.* 1983), and is an example of the Narcissus effect, where the process of interest is present and erroneously uncontrolled in the null model (Colwell & Winkler 1984).

The null model created by Hertz *et al.* (1993) for a non-thermoregulator is a total randomization, analogous to an ideal free distribution. Effectively, totally randomized distributions like this assume that good and bad sites are arranged evenly throughout the environment in both space and time, and individuals have knowledge of this and act accordingly, moving without cost to appropriate temperatures when they are available. Real ectotherms, however, cannot move cost-free between locations. In addition, the null model by Hertz *et al.* (1993) does not take into account the temporal or spatial distribution of available temperatures, to which actual thermoregulators are subject. The middle of the day is usually hotter than dusk or dawn, and sun and shade are not necessarily arranged randomly or evenly. Accordingly, a random sample of T_e is a relatively unrepresentative null distribution of temperatures for a thermoregulator in real time and space, because a landscape is a structured entity, and time moves forward only. Thus, a better null model for behavioural thermoregulation should experience spatially and temporally consistent T_e sampled in a random order, or a random walk through a realistic thermal landscape. That a random walk through a thermal landscape would be the next major advance in null model for behavioural thermoregulation was predicted by (Hertz *et al.* 1993), and discussed by Seebacher & Shine (2004), but, to our knowledge, such a null model has never yet been implemented. A random walk produces a sample of available T_e chosen without reference to preferred T_b, as might be experienced by a non-thermoregulator moving through the landscape. The thermal landscape can be mapped on a fine scale using data-loggers, and random walks can be plotted through that landscape. Then, the T_b of our putative non-thermoregulator, or null model, can be estimated using any of a number of biophysical models, accounting for any amount of thermal mass, physiological characteristics, postures, stances or behaviours, including speed of movement (Stevenson 1985a; Kearney & Porter 2009). The T_b achieved by the null model can then be mapped directly on to a thermal performance curve for the species of interest, to provide a score for Thermal Benefit (range: 0-1, Figure 4-1 d), which provides an estimate of the thermal quality of the habitat. The same score applied to *in situ* real lizard T_b estimates the quality of thermoregulation. The thermal performance curve could be estimated using running speed, metabolic rate, digestion rate, or any process of interest, provided it can be mapped to T_b.

For the purposes of demonstrating the value of including movement in the null model, and mapping body temperatures to the thermal performance curve, we make some simplifying assumptions. The first is that the thermal balance of the organism being modeled (a lizard) is encapsulated by the thermal balance of a data logger (in this case an iButton™), and the calibration of the null model body temperature estimate includes heat exchange parameters. That is to say, the iButton™ is subjected to the many sources of heat transfer that would ultimately act on an organism in the same location, and so these do not need to be explicitly added to the model. This reduces complexity of calculation, and making fewer measurements of environmental parameters reduces sources of error. The second is that we interpolate the thermal performance curve as a trapezoid with straight lines connecting the upper and lower thermal optima to the upper and lower critical thermal limits (Figure 4-1 d). We feel that these assumptions do not reduce the power or quality of inference from our results, as our body temperature estimation model is highly accurate at predicting the body temperatures of real organisms in similar locations (Chapter 4), and the thermal performance curve based on a trapezoidal estimation is not very different from a real, 'generalised' thermal performance curve. This method for producing a null model integrates body temperature across time, at any chosen level of precision, and provides a dynamic representation of habitat thermal quality and thermoregulation quality, addressing a point first made by Hertz *et al.* (1993), that a single metric cannot describe the complexity of thermoregulation.

We demonstrate our new null model for behavioural thermoregulation using as a model system black-throated rainbow skinks (*Carlia sexdentata*) in the wild. We compare the Thermal Benefit (*sensu stricto* – see definition above) obtained by the null model with that obtained by individual, real lizards in the same environment. The null model begins at a randomly chosen point in a discrete reconstruction of an actual spatially and temporally explicit thermal landscape, and plots a random walk through the landscape, moving forward in time. The sample of available operative environmental temperatures experienced by the null model is transformed to a putative lizard's body temperature using a simple biophysical model (Mitchell 1976; Roughgarden 1998), and we then use a thermal performance curve to estimate the Thermal Benefit, integrated across time, achieved by our null model. Examination of the Thermal Benefit gained by the null model reveals the thermal quality of the environment, which we use to infer potential lizard activity time for comparison with empirical activity data. Comparison of the Thermal Benefit of the null model with Thermal Benefit obtained by real lizards in the natural habitat allows us to estimate the relative effort invested in thermoregulation, and the benefit of thermoregulating.

Methods

Field site Te recording

The thermal landscape was measured in an open tropical woodland at Pormpuraaw Aboriginal Community on the Cape York Peninsula (CYP) in North Queensland, Australia (14°53'34.23"S, 141°37'25.36"E), on a sunny day in July 2011. Spinifex and other grasses dominated the landscape to a height of approximately 1 m. Patches of relatively shady vine thicket between 10 and 100 m in diameter occurred in the landscape, spaced approximately 20 to 50 m apart. The study species, *Carlia sexdentata*, is a ground-dwelling skink and, while locally abundant, was restricted to patches of vine thicket. The weather was typical for CYP in March through September: hot, dry and sunny. Mean air temperature was 29.9 °C.

Calibrated temperature-monitoring data-loggers (Thermochron iButtons™), were placed in a 10 x 10 m grid of 100 iButtons™, set to record surface temperature in °C ± 0.5 every 2 min in the vine thickets. Data loggers were wrapped in a neutral coloured 3 x 3 cm cotton and were placed directly on the ground. Concurrently, T_b of hand-captured active *C. sexdentata* (*n* = 36) were recorded throughout the day using a calibrated Digitech QM-7223 infra-red thermometer within 10 s of capture. Temperature of the dorsal surface between the hind legs was read from a distance of 3 cm from the aperture, which had a distance:spot ratio of 8:1. All recorded T_b were measured within 30 s of sighting the lizard. A continuous survey of *C. sexdentata* was conducted through the day by a practised observer who walked at a constant speed through the study site from 6:00 to 18:00, and recorded lizard activity as the number of lizards sighted/min.

T_{sel} estimation

T_{sel} was estimated, using a thermal gradient, from a population of *C. sexdentata* near Wathaniin, CYP in 2012. The gradient was an aluminium slab (2 x 0.15 x 0.018 m). At each end, under the gradient and connected by heat-paste, was a Peltier plate: one tasked to cold, the other to hot. The plates were turned on and temperature allowed to stabilise for at least one hour, creating a thermal gradient ranging from 20 to 45 °C. The skinks, therefore, had access to a gradient of temperatures that averaged 12.5 °C/m. A skink was introduced to the gradient and allowed to habituate for 40 min, and then T_b (cloacal temperature) was measured every 20 min using a quick-reading digital thermocouple, 10 times (a total of 3 h 20 min). T_{sel} was defined as the central 50% of T_b determined under these conditions, which was 31.4-33.8 °C.

Model

A 3-dimensional matrix of T_e was constructed from the data-logger measurements. The spatial component was represented as an X-Y plane, with time on a Z-axis. At the first time step in the simulation, a random start location was chosen on the X-Y plane using a random number generator. After this, time in the simulation always advanced in increments of 1 s. Each simulation had a predetermined movement rate (the probability of moving in space), and if a step was taken, it was taken in a random direction in the Moore Neighborhood (into one of the 8 cells surrounding the central cell). Random walks were conducted at 10 movement rates to assess the effect of moment rate on thermoregulation. Rates were defined as the probability of taking a step each second, from 0 probability (stationary model), 0.5, 0.25, 0.125, 0.0625, 0.03125, 0.015625, 0.007813, 0.003906, 0.001953 equating to approximately one step every 0, 2, 4, 8, 16, 32, 64, 128, 256, 512 seconds respectively. Random walks (n = 100 at each walk rate) were conducted through the matrix (Figure 4-1 a,b). Each walk yielded a vector of T_e sampled every second for its duration, from which T_b were calculated (Equation 1, Figure 4-1 c). The equation we used was as simple as possible, while still adequately predicting body temperature, to illustrate the use of the null model without a complex biophysical model including water balance, multiple sources of heat transfer, and convection. The heat lost by evaporative water loss cancels directly with heat gained by metabolism in reptiles (Porter *et* *al.* 1973). The iButtons™ used to collect T_e themselves were subject to many forces determining temperature, including convection, conduction, solar radiation etc., and so these variables did not need to be expressly added to the model. Importantly, we found the model to be a precise and accurate fit to lizard body temperatures in the same habitat, with no consistent biases (Chapter 4).

Calculated body temperature was transformed into a Thermal Benefit by inserting body temperature (T_b) into the thermal performance curve (TPC) equation, and solving for performance on a scale of 0-1 (Figure 4-1 d). We used a trapezoidal approximation of the TPC for simplicity, as it made little difference to the result.

Equation 1.

$$T_{b(i)} = Tb_{(i-1)} - Te_{(i)} * \exp(K-t) + T_{e(i)}$$

where
$T_{b(i)}$ = body temperature at time i-1
$T_{e(i)}$ = environmental point temperature at time i
t = time (s)
K = body size constant

This is a standard heat transfer equation that includes a body size parameter, K, from Mitchell (1976), which assumes the lizard is prone on the substrate, and is a cylinder 1-cm in diameter, 15-cm long, and assuming no special poses or direction with respect to wind.

Statistical methods:

The model was written using the R language (R Core Team 2013), using the packages deSolve (Soetaert & Petzoldt 2010) and plyr (Wickham 2011).

Results:

The null model was essentially immortal, in that, when body temperature exceeded critical thermal limits, the benefit obtained was zero, rather than causing death or termination of the walk. If a death-limit had been imposed, no simulation would have survived past 11:30, i.e., every null model's estimated T_b exceeded critical thermal maximum (CT_{max} =44.5 °C) by 11:30 on the first day. Thermal Benefit at 6:00 was around 50%, and increased steadily to near 100% at about 10:00. Benefit then dropped to zero around midday, after which it rose again to near 100% around 16:00 and decreased to about 90% by 17:00 (Figure 4-2). The primary effect of increasing movement rate was an increase in variability of Thermal Benefit with movement rate (Figure 4-2, top panel). The faster a model lizard moved, the wider the variety of thermal habitat that became available to it.

Carlia sexdentata achieved high (60-100%), Thermal Benefit through the day (Figure 4-2). The lowest and most variable Thermal Benefit occurred in the morning until 10:00, but throughout the middle of the day, Thermal Benefit was uniformly above 80%. The difference between the Thermal Benefit obtained by real *C. sexdentata* and the null model indicates the effort invested in thermoregulation. As the day progressed, and T_e increased (Figure 4-3), *C. sexdentata* invested more effort in thermoregulation, as this difference increased from 0 to near 1 (Figure 4-2, bottom panel). Low, or variable, effort was invested in the morning period, from 8:00 through 10:00, when Thermal Benefit obtained by real *C. sexdentata* were within the Inter-Quartile Range of the null model (Figure 4-2, bottom panel). In general, *Carlia sexdentata* activity aligned well with periods of high Thermal Benefit for the null model: highest activity was in the morning around 8:30, with a secondary peak at about midday, and a smaller peak at around 15:30pm (Figure 4-2).

Discussion

The null model presented here provides a more realistic null model for thermoregulation than did previous models because we have added two more realistic aspects: (i) the model moves forward in time; and (ii) the landscape is a structured entity. Our null model allows T_b at time (t) to depend on T_b at time (t-1), and on T_e at time (t) and (t-1). Operative environmental temperatures (T_e) experienced are the result of the order in which the environment is sampled, which is a function of the spatial and temporal distribution of T_e. Any real organism must exist within these constraints; even an organism that does not thermoregulate, and moves without regard to its T_b. Ultimately, our null model generates a continuous expected distribution of T_b for a non-thermoregulator, which, converted to Thermal Benefit (a score of relative thermal performance), is indicative of thermal quality of the habitat, and the thermoregulatory challenges posed to its inhabitants. Our proposed metric, Thermal Benefit, is also used to assess the quality of the thermoregulator. Our index (Thermal Benefit) recognizes that the effect of T_b on the fitness of an organism is not symmetrical about the optimum (Huey & Stevenson 1979). By using high temporal resolution in the null model, the shift in habitat thermal quality through the day becomes apparent, and the associated shift in thermoregulatory effort by lizards is also clear (Figure 4-2), better describing ectotherm (lizard) biology and the plasticity of thermoregulatory behaviour not captured by existing metrics, such as d_e, and d_b, and E.

Theory suggests that thermoregulation should occur when the net benefit to fitness is positive (Huey & Slatkin 1976; Vickers *et al.* 2011, Chapter 2) and that thermoregulatory effort should increase as thermal quality declines (Blouin-Demers & Nadeau 2005; Besson & Cree 2010; Vickers *et al.* 2011, Chapter 2). There are two ways to increase the net benefit of thermoregulation: increasing gross benefit, or decreasing cost. The intrinsic Thermal Benefit of the environment is estimated by the Thermal Benefit of the null model. The Thermal Benefit obtained by real lizards can be estimated if T_b is known, and the difference between the real lizard and null-model benefit is the benefit gained by behavioural thermoregulation, plus some residual benefit.

Where ε is the benefit gained or lost as the by-product of other activities, for example, foraging in a thermally beneficial site. Benefit of thermoregulation is the currency of reward for thermoregulatory effort, and is a function of effort invested: more effort invested means more benefit gained. This framework can be used to study thermoregulatory behaviour. Contrasting lizard and null model Thermal Benefit shows the effort invested in thermoregulation: when the null model achieves low benefit, but the lizard achieves high benefit, effort invested must be high. On the other hand, if the null model and real lizard achieve similar Thermal Benefit, thermoregulatory effort is low. Effort here is not energetic cost, but implies careful, deliberate, or non-random site selection. Energetic cost of thermoregulation depends on the spatial configuration of environmental temperature, and the movement required by the lizard to find the sites it occupies for thermoregulation.

The dynamic nature of habitat thermal quality at Pormpuraaw can be clearly seen by the shift in median Thermal Benefit experienced by the null model. Pormpuraaw is tropical woodland; typically considered one of the more thermally homogeneous and congenial habitats available to reptiles (Hertz 1974; Shine & Madsen 1996). There were, however, clear peaks in thermal quality at 10:00 and 16:00, with a trough between these times when thermal quality dropped to zero (Figure 4-2). Increasing movement rate increased variability in Thermal Benefit (Figure 4-2, top panel). This increase in variability occurred because randomly moving individuals who move faster experience more habitats. Every simulated null model suffered mortality by 11:30, that is: T_b exceeded critical thermal maximum. Mortality occurs at this time because 50% of the habitat is hotter than the critical thermal maximum, and an individual moving randomly through such a habitat interacts with these high temperatures sufficiently often to raise body temperature above the CT_{max}.

Compared to the null model, *Carlia sexdentata* achieved high, stable Thermal Benefit throughout the day (Figure 4-2, bottom panel). The constant Thermal Benefit obtained in such a variable environment indicated a dramatic shift in thermoregulatory effort throughout the day that compensated for the variability in thermal quality of the habitat. The lizards avoided dangerously high temperature, and even sub-optimal temperatures, by such behaviours as keeping to shaded areas, going under cover, or going underground. Animals we measured in the field were all active, not flushed from refugia, so refugia were not included in the null model. Indeed, including such behaviour as retreating to cover would be adding thermoregulatory behaviour into the null model, which would be inappropriate.

Behavioural and effort shifts have been undetectable in previous null models. When our null model achieved high Thermal Benefit, it was less costly for lizards to achieve high Thermal Benefit (10:00 and 16:00), yet morning was precisely when the Thermal Benefit obtained by wild *C. sexdentata* was poorest and most variable (Figure 4-2, bottom panel). This suggests that thermoregulatory effort was lowest while thermal quality was highest, agreeing with recent theory (Blouin-Demers & Nadeau 2005; Vickers *et al.* 2011, Chapter 2). Although it seems paradoxical, investing little effort when the benefit from the environment is already high may be the best strategy to maximise net Thermal Benefit. Minimising thermoregulatory effort may increase time available for other activities, such as foraging, mate-finding, reproduction, home-range maintenance etcetera (for an exhaustive list, see Brattstrom ,1965). After 10:00, Thermal Benefit obtained by real *C. sexdentata* was still uniformly above 0.8, despite very low scores for the null model. This suggests that lizards invested a lot of effort into thermoregulation, most likely due to the dire consequences of failing to thermoregulate: all null model simulations (n=100) 'died' by 11:30 because their body temperature exceeded critical thermal limits.

Thermal Benefit ranged from 0 – 1, and at almost all times of the day between 6:00 and 18:00, there were locations where the Thermal Benefit associated with available environmental temperature was 1. With careful site selection it may have been possible to for a lizard to attain perfect Thermal Benefit throughout the day, but real lizards rarely, if ever, did. This could have been an artefact of either our sampling of field-active lizards or our assumptions: a few lizards were chased up to 30 s, which likely affected their body temperature, and our estimate of the thermal performance curve may have been too coarse. We assumed all lizards strived to reach their thermal optimum at all times, but a benefit of 80% may be good enough. Additionally, there may be a diminishing rate of return with increased effort above 80% benefit, particularly when Thermal Benefit of the null model is low. Recent theory also suggests that rather than strive to attain perfect Thermal Benefit, active lizards ought to err, maintaining T_b below optimal, to buffer slight imprecision, accidents or emergencies (Martin & Huey 2008). *Carlia sexdentata* activity was highest in the early morning when Thermal Benefit obtained by the null model was highest, and effort invested in thermoregulation by the lizards at this time was low. In his analysis of thermoregulatory behaviour, (Stevenson 1985a) predicted that constraining activity time has the greatest impact on body temperature, and our model suggests that this evaluation is reasonable. Thus, while additional effort invested in thermoregulation in the morning before 10:00 was low, simply maximizing activity during periods when thermoregulation is low cost is a cheap and highly effective thermoregulatory behaviour. *Carlia sexdentata* activity declined as Thermal Benefit of the null model decreased through the middle of the day, to a minimum activity level at about 14:00, with a later, smaller peak at about 16:00. Many studies have observed that reptile activity peaks in the morning, sometimes with a smaller peak in the afternoon (e.g., Schwarzkopf & Brooks 1985; Bauwens *et al.* 1996; Firth & Belan 1998)). Curiously, *C. sexdentata* appeared to have two peaks in morning activity, which may indicate that there is an intersection of bimodal (early and late) and unimodal (middle of the day) activity periods by different individuals in the population. At times when most available environmental temperatures were lethally high, *C. sexdentata* activity ceased, as the lizards probably retreated to shelter sites (harmonic radar tracking data corroborates this for other, similar species, pers. obs.). The small afternoon peak in activity and high Thermal Benefit obtained by the null model implies that, at least thermally, there is a window of opportunity available for increased activity in the afternoon for these lizards. Such an increase influences predictions of lizard (Sinervo *et al.* 2010) and ectotherm (Deutsch *et al.* 2008) extinction rates under climate change: without needing to invoke acclimation, adaptation, or spatial range shift, the afternoon becomes a period that could be exploited, increasing potential activity time.

The system in which we tested our new null model for thermoregulation was limited by: our small landscape size relative to the distribution of *C. sexdentata*; discretisation of the landscape; and our relatively coarse estimate of the thermal performance curve. However, our new framework should be applicable to a wide range of systems and scales from coarse-grained to completely continuous in both space and time. Choice of spatial and temporal scale will depend on the body size and thermal inertia of each species being examined, and by using different biophysical models, the same data could be used to assess the thermal habitat from the perspective of many organisms, from tiny invertebrates to large vertebrates, and even endotherms, such as mammals. Appropriate parameterisation of a biophysical model for estimating T_b from T_e accounts for thermal inertia, and, while we have used a simple model, other environmental variables may be included as required by the investigator (e.g. Kearney & Porter 2009). Our null model provides a framework in which to quantify the benefit of thermoregulation, and the effort invested in it. It will be possible to establish rules for the model to make the model more realistic, and more appropriate to describe the likely behaviour of a thermoregulator. Systematic removal of such rules could indicate the contribution of each behaviour to the benefit of thermoregulation, or even behaviours that are deleterious to optimum body temperature. The null model is the perfect thermoconformer, and an obvious next step may be to create a “perfectly thermoregulating” or Panglossus model (Huey – pers. comm.): the perfect walk (e.g. Fei *et al.* 2012b). Combined, these models could provide a thermal-benefit envelope for our behavioural thermoregulator to predict the likely behaviour of real organisms in a changing world.

Figures

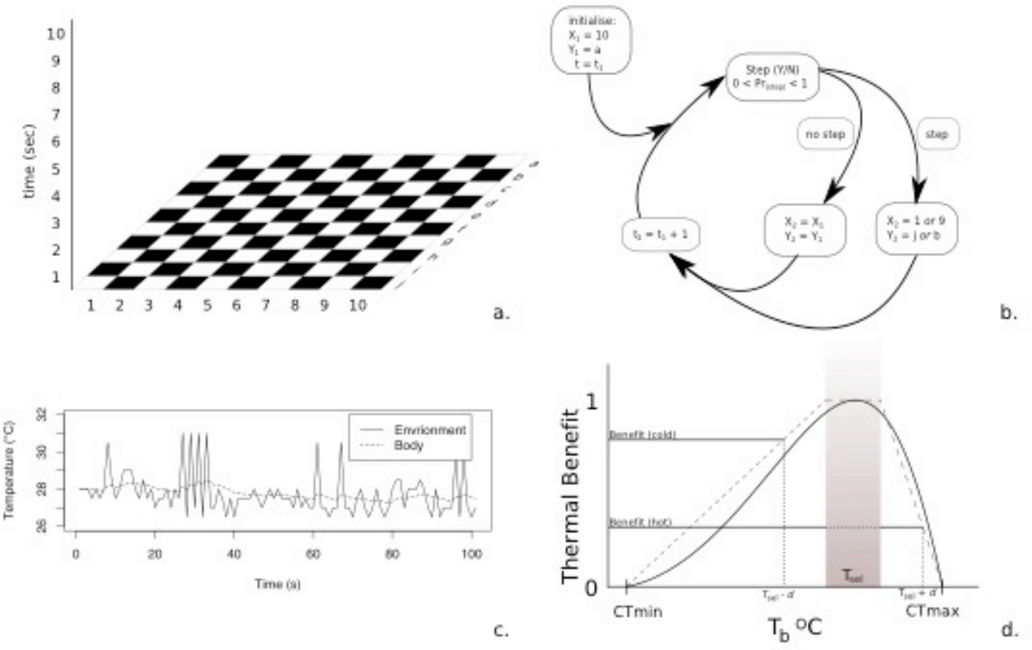

Figure 4-1. (a) Temperature was measured in each cell on the toroidal X-Y plane at 2-min intervals (time on the Z-axis). A random walk through the temperature matrix, conducted as shown in (b), was used to sample environmental temperature as a non-thermoregulating lizard might. (c) Environmental temperature (solid line) was integrated through time according to movement rate and lizard size to estimate body temperature of a lizard (dashed line) according to equation 1. (d). A theoretical thermal performance curve (solid curve) with the trapezoidal approximation we used such that when body temperature (Tb) equaled selected or optimal body temperature (Tsel, shaded), Thermal Benefit = 1. Straight line interpolations to critical thermal limits (CT_{max}, CT_{min}, from literature), which scored Thermal Benefit = 0. The asymmetry of the

effects of overly warm body temperatures versus overly cool body temperatures were accounted for by Thermal Benefit: a given deviation d of T_b below T_{sel} (T_{sel} – d, cold) scores a higher Thermal Benefit than the same deviation above (T_{sel} + d, hot).

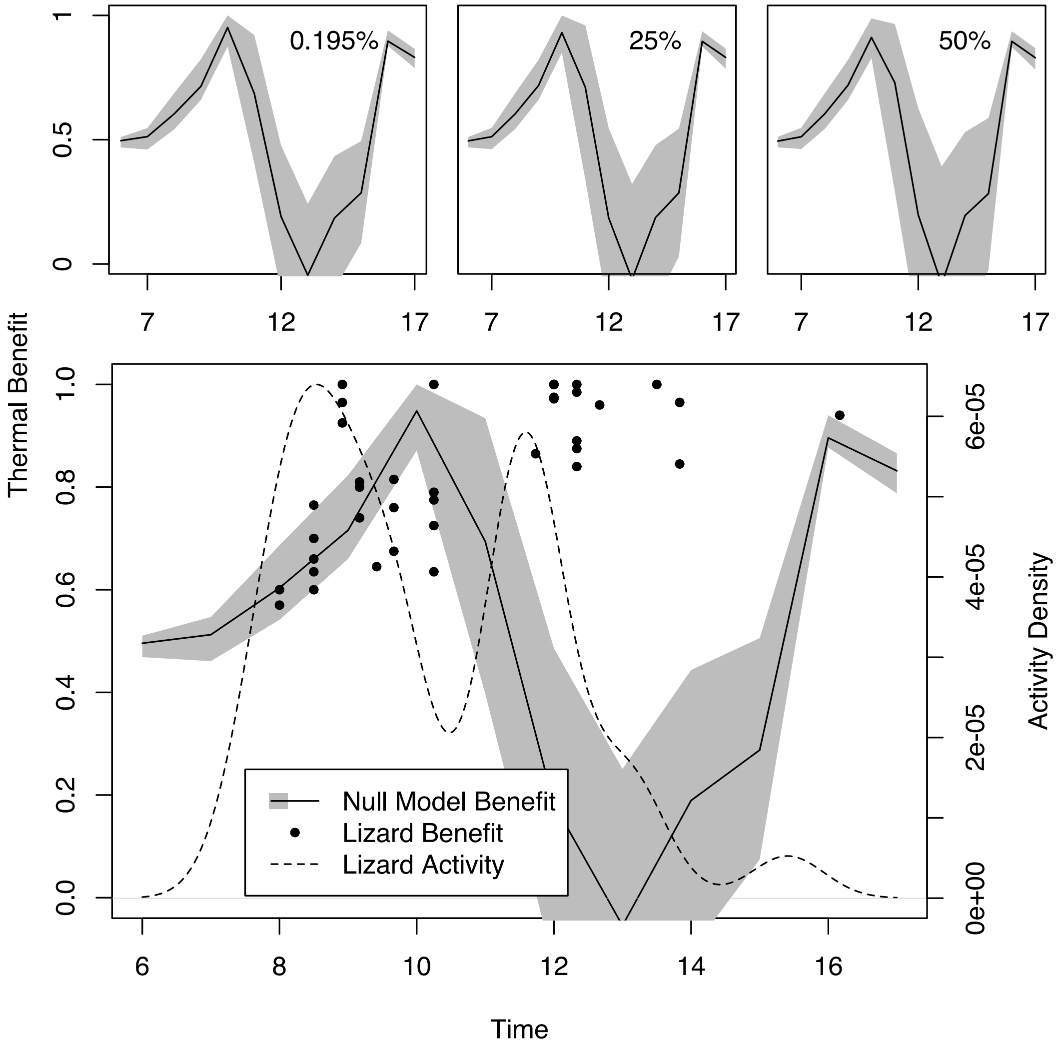

Figure 4-2. Top panel: median Thermal benefit (+- IQR, shaded) of null model with different probability of movement. Bottom Panel: median Thermal Benefit obtained by the null model (solid line) with Inter Quartile Range (shaded), Thermal Benefit (points) and kernel density estimate of activity (dashed line) of *Carlia sexdentata* (Gaussian kernel, bandwidth = 2000).

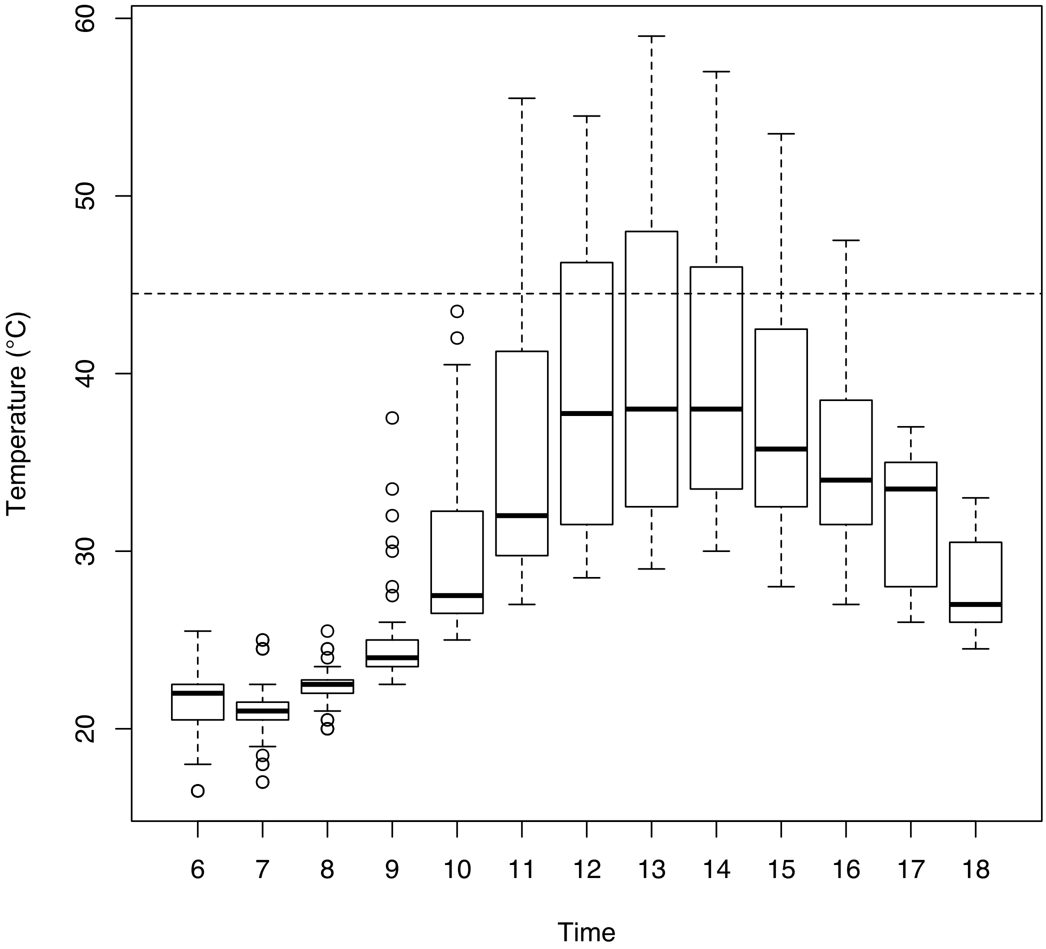

Figure 4-3. Environmental temperature (T_e) through the day measured by 100 data loggers over over 3 days at Pormpuraaw. Line in boxplots represents median, box is central 50% of data, whiskers include up to 2 standard deviations, with outliers beyond, dashed line represents CT_{max} for *Carlia sexdentata* (44.5 °C).

Chapter 5 Cloud cover will influence the effect of climate change on species: a fair-weather forecast

Running head: The effect of clouds and climate change on ectotherms

Mathew Vickers[1,2,3], Ross A Alford[2], Lin Schwarzkopf[2]

1. Corresponding Author
   E: vickers.mathew@gmail.com
   P: +61 400 815 990
2. School of Marine and Tropical Biology, James Cook University, Townsville.
3. CSIRO Sustainable Ecosystems, Ecology Program, PMB PO, Aitkenvale, Queensland 4814

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Abstract

Changing environmental temperatures are likely to disrupt a number of natural systems, and to cause population declines and extinctions, but few studies have considered the effects of variation in cloud cover on organisms in conjunction with temperature change. Ectotherms are strongly influenced by their thermal habitat, and the thermal habitat is strongly influenced by cloudiness. We used a new, spatially explicit null model for behavioural thermoregulation to describe the influence of habitat thermal quality on lizard potential activity time both under cloudy and sunny conditions in winter and summer, given the current climate, and given a 3 °C temperature increase, to determine whether the frequency of cloudy days will have major effects on the persistence of small ectotherms. We found that thermal quality in summer was more variable than winter, and that in summer, cloudy days had the highest thermal quality, while in winter, sunny days had the highest thermal quality. Given 3°C of climate warming, the thermal quality of summer decreased, but the thermal quality of winter days increased so much that the total thermal quality over the year was higher given climate change than in the current climate. Increasing cloud cover increased thermal quality given climate warming, but never increased the thermal quality of summer enough to compensate for climate change.

Introduction

Climate change predictions are clear: global average temperatures are increasing (Stocker *et al.* 2013). Rising temperatures are likely to have a range of effects on many species. The most alarming predictions include species range reductions (Parmesan & Yohe 2003) and extensive extinctions (e.g., Sinervo *et al.*, 2010). Ectotherms rely on environmental temperature to control their body temperature, and this, in association with the strong influence of temperature on performance (Huey & Kingsolver 1993; Vickers *et al.* 2011, Chapter 2), means ectotherms are likely to be severely impacted by increasing global temperatures (Deutsch *et al.* 2008). Ectotherms perform best at their thermal optimum, which is typically near their thermal maximum (Huey & Kingsolver 1993), and they have a higher rate of performance reduction per degree at body temperatures above their thermal optimum than below: overheating is more costly than overcooling (Huey & Kingsolver 1993; Vickers *et al.* 2011, Chapter 2). Climate warming brings an increased likelihood of overheating, which can be fatal to organisms that live near their thermal maximum (Huey *et al.* 2010). While ectotherms will likely increase their thermoregulatory effort to offset the increased threat of hotter conditions (Blouin-Demers & Nadeau 2005; Vickers *et al.* 2011, Chapter 2), there is a limit to the capacity of behavioural thermoregulation to buffer high environmental temperatures (Huey *et al.* 2010), and when it is reached, ectotherms are forced to retreat to shelter (Grant & Dunham 1988), thereby losing potential activity time. Even when they are active, the increased risk of high environmental temperatures must be offset by increased effort in thermoregulation (Vickers *et al.* 2011, Chapter 2), which may reduce time available for foraging and other essential activities, potentially reducing reproductive capacity (Adolph & Porter 1993) and eventually causing extinction (Sinervo *et al.* 2010). For many species, it is not the increase in mean temperatures that will cause problems, it is an increase in the range and temporal extent of high temperatures (Kearney *et al.* 2009). However, it is possible that these effects may buffered and therefore mitigated, by other environmental phenomena, such as cloud cover (Leahy *et al.* 2013).

All else being equal, increasing global temperatures will reduce the total activity period available to tropical ectotherms, in particular during summer (Adolph & Porter 1993; Sinervo *et al.* 2010). Total activity period across the season is of paramount importance, as dynamic energy budget models demonstrate; particular resources, for example food, can be stored and used at a later date, buffering diel or short term stochastic events (Adolph & Porter 1993; Kearney & Porter 2009). However, the direction of change in other environmental variables is less certain. For instance, the processes underlying cloud formation are sufficiently complex (Henderson-Sellers 1986) that predictions of future cloud cover and distribution remain elusive. Remotely sensed data show that global patterns of cloud cover have changed over the last 30 years: in the Americas and Europe, cloud cover has diminished, while in much of Africa, Asia and, to some extent, Australia, cloud cover has increased (Figure 3 in Herman *et al.*, 2013). Bonebrake & Mastrandrea (2010) use IPCC data to predict an increase in rainfall in the next 100 years in the tropics and high northern hemisphere latitudes, but a decrease in high southern hemisphere and mid northern hemisphere latitudes.

While not predicting cloud cover *per se*, these changes in rainfall would probably be accompanied by changes in cloud cover.

Through its effect on ambient temperature, cloud cover influences reptile activity periods (Huey 1974) and through its effects on physiology it can affect the evolution of ectotherms (Clusella-Trullas *et al.* 2009; Andrews & Schwarzkopf 2012). In temperate and high-elevation environments, many species' activity levels are reduced during cloudy periods (Huey 1974; Hare & Cree 2010), but under a warmer climate scenario, the effect of clouds may be different.

Cloud cover may reduce ambient temperature in the hottest parts of the day or year by reducing solar radiation, cooling the environment to a level where activity is possible in habitats that otherwise would be too warm. Therefore, while increased temperatures threaten ectotherms by curtailing available activity time (Sinervo *et al.* 2010), it is possible that cloudy days could provide a buffer against extreme heat caused by solar radiation, offsetting some of the risk to ectotherms of overheating. Indeed, increasing cloud cover and precipitation increases the variability in ectotherm thermal performance, which may improve survival in a climate that is too warm (Clusella-Trullas *et al.* 2011). If observed cloud cover shifts continue, increased cloud cover in Africa, Asia, and parts of Australia may shelter ectotherms from the effects of climate change, while in the Americas and Europe, the opposite effect can be expected: decreased cloudiness may mean increased solar radiation, exacerbating the effects of climate change on ectotherms.

Using a spatially explicit null-model for behavioural thermoregulation (Chapter 3, Vickers & Schwarzkopf 2013) we examine the difference in habitat thermal quality between cloudy and sunny days, and the potential influence of this on behaviour. We use as a model system small (ca. 5 g) black-throated rainbow skinks (*Carlia rostralis*) in low-elevation vine thicket on a tropical island. We assess the potential activity period of this species on cloudy and sunny days in present environments and under a scenario of climate change, using a 3˚C increase in average temperature. We use our results to examine the hypothesis that the frequency of cloudy days may have major effects on the persistence of small ectotherms as the climate changes.

Methods

Measures of Environmental Temperatures

Operative environmental temperatures (T_e) were recorded between August 2003 and August 2005 at Ramsay Bay, Hinchinbrook Island, Australia (18˚24'S, 146˚17'E). The site is low-lying dune scrub and vine thicket with patches of *Melaleuca* swamp, and the lizard population is numerically dominated by the black-throated rainbow skink, *Carlia rostralis*. T_e were collected using Thermochron iButtons™ wrapped in neutral-coloured cloth, which recorded T_e every hour for over 30 days per sample, yielding >100,000 total temperature recordings. Eighty iButtons™ were distributed randomly throughout the habitat, over approximately 2 ha. iButtons™ were initialized at random times such that, on average, any given minute was sampled, and many were sampled twice at different locations. iButtons™ were deployed for a total of 184 days in the summer and 237 in the winter (Figure 5-1).

Measures of Preferred Temperature of Skinks

Adult *Carlia rostralis* were taken to our laboratory at James Cook University in summer (October/November, n = 10) and in winter (July, n = 11), where we measured preferred (or selected) temperatures. Skinks were individually housed in large containers (600 mm x length x 500 mm width x 450 mm height), with a 75-W light bulb at one end creating a photothermal gradient, offering a range of available operative temperatures (22–50°C) between 0800 and 1700 hours. A photothermal gradient was a realistic method of heat provision for these heliothermic skinks. Food (a domestic cricket, *Acheta domestica*) was available once daily, and water was always available in the middle of the gradient. Lizards were held in thermal gradients for 3 days before temperature measurements commenced. The central 50% of these data were used to represent the selected body temperatures (T_{sel}, Figure 5-1, Hertz *et al.*, 1993) for *C. rostralis*; we used this measure as a proxy for optimal performance temperature.

Measures of Activity

Lizard activity was scored as the number of lizards seen per observer per minute by trained observers dressed similarly and moving at a rate of approximately $2km \bullet h^{-1}$ through the habitat. Activity observations were conducted between 6:00 and 18:00 daily. We recorded only those lizards that were visible moving or sitting still; none were counted if they were flushed from under cover.

Null Model

The null model was produced in the programming language R (R Core Team 2013), and consisted of a point taking a random walk through a 10 x 10 x time matrix. Time advanced every second, and every time-step the model decides whether to move, and if so, where. The null model had a probability of stepping 0.03125 times per second, or about once every 32s, similar to real black-throated rainbow skinks (pers. obs.). We found that changing movement rate in the simulation only increased the variability of experienced T_e to a small extent, and did not strongly influence the outcome of the model (Vickers & Schwarzkopf 2013, Chapter 3).

The matrix was generated uniquely for each model run, and was a 10 x 10 pseudo-realistic thermal map of the area. We call it pseudo-realistic in that it was constructed from iButtons™ randomly selected from those available by season and level of cloudiness. When the model "stepped" onto an iButton™, an iButton™ temperature was sampled from the total pool for that iButton™ for that hour. Due to the nature of iButton™ sampling, we treat iButton™ location in the model as a random factor. This means null model outputs are indicative of a wider range of habitat, increasing the generality of the results across the habitat, but decreasing precision of predictions about particular locations in the habitat. One limitation of this pseudo-realistic map is that it fails to replicate any spatial autocorrelation that may exist in a real habitat.

Model lizard body temperature was estimated every second as an integral through time, assuming the lizard was a cylinder with dimensions 10mm x 120mm, weighing 4.8g, 1 cm above the substrate, which is quite representative of rainbow skinks (*Carlia rostralis* = 4.8g, SVL 54mm). Body temperature was mapped to the thermal performance curve, to yield a Thermal Benefit index from 0 to 1 where 0 = no performance, and 1 = maximum performance. To simplify calculation and the complexities of dealing with many individual curves, the thermal performance curve was interpolated using a polygonal approximation (as described by Vickers & Schwarzkopf 2013, Chapter 3), using T_{sel} for *Carlia rostralis* from (Chapter 3, Vickers *et al.*, 2011; Figure 5-1), and CT_{max} and CT_{min} from (Greer 1980). A more detailed description of the null model used in this paper is provided by (Chapter 3, Vickers & Schwarzkopf 2013).

Cloudy days, Sunny Days, and Seasons

Hinchinbrook Island experiences two distinct seasons: summer (the wet season) occurs in November through March, and winter (the dry season) occurs in May through September (Figure 5-1). Throughout the study period, cloud cover was recorded up to 10 times per day on a scale from 0-10 (0% – 100% cloud cover, estimated as percent of sky covered by heavy cloud). Cloudy days were defined as any day with an average cloud cover exceeding 60%. This threshold was selected to maximise both the number of cloudy days in the winter and the number of sunny days in the summer available to the model. The scenarios we tested were current conditions, climate change of +3 °C, with normal cloud cover (based on current conditions) and climate change with number of cloud covered days altered by: -40%, -30%, -20%, -10%, 0%, 10%, 20%, 30%, 40%.

Thermal Benefit, and its interaction with Activity

The energetic benefit of foraging depends on body temperature *via* body temperature's influence on processes such as foraging success and digestive efficiency (Adolph & Porter 1993). This influence can be modeled by an index we have called Thermal Benefit: Thermal Benefit ranges from 0-1, where 0 = no performance (i.e., a critical thermal limit was exceeded, causing death), and 1 = the best possible performance, achieved at optimal body temperature (T_{sel}). For a given body temperature, the energetic benefit of foraging scales linearly with time spent foraging (Adolph & Porter 1993). To estimate the benefit derived by a lizard from activity at different body temperatures, we multiply activity and thermal benefit to create a score "Activity x Benefit". For example, a lizard, active 20% of the time at a 100% Thermal Benefit would score 0.2 units. One active for 20% of the time at 50% benefit scores 0.1 units. Multiplying activity rate by benefit yielded an internally consistent, dimensionless index. The index was summed across the day to estimate the gross benefit of activity for an individual for one day, which we used to estimate and compare the effects of season and cloudiness on fitness.

We calculated the Activity x Benefit index as follows: for every lizard activity measurement made, a Thermal Benefit was randomly sampled from the null model at the same time, season, and cloudiness. These two values were multiplied. The process was bootstrapped with replacement of benefit value (n=1000) to provide a distribution of Activity x Benefit for summer-, and winter-, cloudy-, and sunny-, days. Total Activity x Benefit for a season was estimated by summing daily Activity x Benefit per season and cloud treatment (n= number of days in the season/cloud level). This was repeated for contemporary and climate change conditions, and the effect of increased cloud cover was calculated by increasing or decreasing the number of cloudy days sampled.

We did not change phenology, activity rate or time, physiology or size of model skinks, so we could focus on how skinks with present-day physiological tolerances and behaviour might respond to a different climate. Our estimates are, therefore, a worst-case scenario, and do not include the fact that skink biology may be plastic enough to accommodate predicted changes (Goodman *et al.* 2013).

Results

Thermal benefit – contemporary thermal regime

The median Thermal Benefit obtained by the model on both cloudy and sunny days in winter ranged from ca. 0.6 – 0.8, starting low in the morning and increasing towards the middle of the day (Figure 5-2). The variation in Thermal Benefit was somewhat lower on cloudy days, probably due to the buffering effect of clouds on incident solar radiation. During summer, median Thermal Benefit ranged from ca. 0.8 – 1 on cloudy days, and 0.6 – 1 on sunny days (Figure 5-2). On cloudy summer days, Thermal Benefit started around 0.8, increased towards 1 by 11:00, and then decreased throughout the hot middle of the day. The midday decline in Thermal Benefit was more noticeable on sunny days in summer, due to the high temperature of open, sunny areas. Similarly, the increased variability in benefit on sunny days probably occurred because increased incident solar radiation made loggers struck directly by the sun especially hot. At times, the 50% prediction limit included zero, indicating a very hot (lethal) environment (Figure 5-2).

Thermal benefit assuming 3°C climate warming

Assuming 3°C climate warming, Thermal Benefit in winter uniformly increased, particularly on cloudy days. Thermal Benefit hovered around 1 (i.e., conditions were optimal) for most of the day in winter. In summer, under climate change, Thermal Benefit did not shift uniformly throughout the day. In the mornings and late afternoon, Thermal Benefit improved under climate change. In the middle of the day, however, Thermal Benefit decreased on both cloudy and sunny days, increasing the proportion of lethal time (i.e., times when Thermal Benefit = 0). The greatest impact occurred on sunny days, when the median benefit dropped as low as 0.4, and the 50% prediction limit included zero from about 12:00 to 14:00 (Figure 5-2).

Activity

Real black-throated rainbow skinks had different activity patterns on cloudy than on sunny days, and in winter versus summer. In winter, lizards were most active in the middle of the day on cloudy days, probably compensating for the lower thermal quality of the habitat in the morning and evening, and capitalizing on the high and less variable thermal quality habitat available around midday (Figure 5-2). On sunny days, the activity profile was much flatter and less variable, reflecting the availability of high thermal quality habitat throughout the day: the high thermal quality in the morning meant there was no need to compensate with elevated activity levels at midday (Figure 5-2).

In summer, on cloudy days, activity started high, decreased, and then increased towards the middle of the day, peaking at around 13:00, before decreasing again (Figure 5-2). Variability in activity period was low on cloudy summer days, indicating that most lizards followed this activity regime. On sunny days in summer, activity had a more variable profile, with a peak before the hottest period of the day. Activity steadily decreased towards the afternoon (Figure 5-2).

Activity x Thermal Benefit scores under the present thermal regime

Activity x Benefit scores in both seasons were more variable at the beginning and end of the day, in part aligning with increases in variability of activity at those times (Figure 5-2, Figure 5-3). In summer, there was also a marked depression of Activity x Benefit in the middle of the day when Thermal Benefit was low, particularly on sunny days. Winter had a much flatter profile, and in both seasons, cloudy days had higher Activity x Benefit scores than did sunny days.

Activity x Benefit scores assuming 3°C climate warming

In winter, the Activity x Benefit score was uniformly higher given climate change than under the present climate regime (Figure 5-3), a reflection of availability of high-quality operative temperatures in the climate change scenario.

In summer, Activity x Benefit scores given climate change were lower through the middle of the day than under present day conditions, though the morning and afternoon periods showed similar scores (Figure 5-3). Consistent with the idea that high temperatures are dangerous, the decreases in Activity x Benefit scores were greater on sunny compared to cloudy days.

Total Activity x Benefit Scores

Summing Activity x Benefit scores across seasons, and across the year, revealed that under climate change, our model skinks may, overall, be somewhat better off (Figure 5-4). This was primarily due to the large increase in Activity x Benefit scores in winter compared to the smaller decrement in these scores in summer (Figure 5-4). Under contemporary conditions, overall Activity x Benefit scores were very similar in winter and summer (Figure 5-3, Figure 5-4), but as the climate warms, although there is a total increase in Activity x Benefit scores throughout the year, the difference in scores between summer and winter became more highly pronounced (Figure 5-4).

Varying Cloudiness

Under shifts in cloudiness from 40% fewer cloudy days to 40% more, Activity x Benefit scores shifted linearly (Figure 5-4). Total Activity x Benefit scores were greater under climate change for all scenarios in which cloud cover was greater than or equal to 10% less than current cover. Decreasing cloud cover meant there were uniform decreases in Activity x Benefit scores in summer and winter, and therefore overall. Under no level of cloudiness were Activity x Benefit scores in summer given climate change as high as in the current day, though the opposite was true for winter: climate change lead to higher Activity x Benefit scores in winter.

Discussion

We used a null model for behavioural thermoregulation to describe the presently available thermal environment for tropical woodland lizards, and then to predict complex effects of climate change and varying cloudiness on habitat thermal quality in summer and winter. We found that thermal quality of habitat was higher in winter than in summer, and tended to be higher on cloudy days than sunny. Empirically measured lizard activity matched our estimates of thermal quality, such that lizards tended to be active when thermal quality was high. Assuming that lizard activity continued to follow the same pattern observed today, we added a 3˚C increase to average temperature to simulate climate change, and predicted that black-throated rainbow skinks (*Carlia rostralis*) will ultimately gain in total annual Activity x Benefit scores under climate change, even given scenarios with altered cloudiness. An improvement in overall thermal quality of the environment contrasts with many of the estimates for tropical lizards suggesting that temperatures will become so warm that lizards will become extinct (Huey *et al.* 2010; Sinervo *et al.* 2010). The devil is in the detail, however, as close scrutiny of seasonal effects clearly demonstrated that given 3°C of climate warming, summer will have a substantially lower habitat thermal quality than it does at present. The thermal quality of habitat available in summer was strongly influenced by cloudiness: fewer clouds meant even lower summer thermal quality, whereas increased cloudiness somewhat ameliorated the effect of increased temperature. It appears increased cloudiness may provide limited respite in cases where the likelihood of extinction due to climate change is otherwise very high.

If we assume the cumulative effect of thermal quality is simply the sum of thermal quality across the year, it appears climate change will improve the outlook for rainbow skinks (*C. rostralis*; Figure 5-4). Unhappily, however, different seasons are unlikely to have equal impact throughout the life history of this species, and those of ectotherms in general (Adolph & Porter 1993). The increase in the total Activity x Benefit score we observed was driven by an increased Thermal Benefit obtained in winter given 3°C of climate warming. In comparison to contemporary conditions, a 3˚C increase in environmental temperatures caused a gross reduction in Thermal Benefit (Figure 5-2), and Activity x Benefit scores (Figure 5-4) in summer. Summer and winter have different patterns of Activity x Benefit scores because in summer, the hot temperatures are pushed high above the thermal optimum (e.g., Huey *et al.*, 2010), while in winter increasing temperatures often approach the thermal optimum. Many species are altering their phenology along with climate change, performing activities earlier or later in the seasons as necessary, capitalizing on the novel thermal regime (Walther *et al.* 2002). A trade off in Activity x Benefit scores between summer (worse) and winter (better, Figure 5-4) in tropical ectotherms may buffer the impact of climate change for individuals that can store extra energy (or 'benefit') from winter to help survive the summer (Drent & Daan 1980) but not for those that cannot. For many species, including rainbow skinks (*Carlia* spp.), eggs hatch (or young are born) in early summer (Greer 1980), so hatchlings or juveniles will not have the opportunity to store resources if they enter very difficult conditions, for example very short available activity periods.

If, on the other hand, we examine diel patterns, it is clear that Thermal Benefit is not static throughout the day (Figure 5-2), nor would we expect it to be (Grant & Dunham 1988; Adolph & Porter 1993). Variation in diel patterns of Thermal Benefit seemed particularly important in summer (especially given 3°C of warming), when Thermal Benefit in the middle of the day dropped substantially. In the summer mornings and afternoons, benefit was clearly higher given 3°C of climate warming compared to contemporary conditions (Figure 5-2). Our predictions of Activity x Benefit in summer, which showed a sharp reduction given climate change (Figure 5-4), assumed no compensatory shift in lizard activity rate or period as the climate changes. Clearly, reptiles have the capacity to alter their behaviour on cloudy and sunny days (Figure 5-2) (e.g., Huey & Kingsolver, 1993), and across latitudes and elevations (Clusella-Trullas *et al.* 2009). Depending on the relative importance of thermoregulation, such plasticity in their behaviour might allow lizards to compensate for the reduced thermal quality of the habitat at midday by increasing crepuscular activity rates, thereby offsetting some of the effects of climate change (e.g., Kearney *et al.*, 2009). Shifting activity period depends strongly on many external factors (e.g., Abom *et al.*, 2012), for example availability of prey and predators. At least one study suggests thermal regimes may be appropriate, but prey availability may determine activity levels in large tropical lizards (Christian *et al.* 1995). Another suggests that predator avoidance maybe more important than thermoregulation (Downes & Shine 1998), though the outcome might have been different if the thermal threat was as deadly as the predator.

In recent years, cloud cover has shifted measurably (Herman *et al.* 2013), and as climate continues to change, it seems likely that the distribution of cloud cover will not remain static. Already, there are reports of recent significant cloud cover change (Middleton *et al.* 2001; Qian *et al.* 2006; Herman *et al.* 2013). It is not likely, however, that cloud cover will be reduced everywhere, and so predictions of the effect of climate change on species must consider the effects of cloud cover on temperature and apparent solar radiation. In addition, such predictions should take into account flow-on effects of temperature and cloud cover change to potential activity time and behaviour, and then onto survivorship and fitness. Cloud cover adversely affects reproduction in one cool-temperate ectotherm species (Hare & Cree 2010), but there is no evidence the effect will be similar in warmer tropical climates. Although some predictions, using increased mean temperature modeled in isolation, suggest activity period will be curtailed causing species decline and extinctions (Sinervo *et al.* 2010), increased temperature with a simultaneous increase in cloud cover may, in fact, improve thermal quality of the habitat (Figure 5-2), and increase the Activity x Benefit score profile through both winter and summer (Figure 5-4). The variable effect of increased temperature among seasons (winter becomes a better thermal environment), and within the day (mornings and afternoons in summer improve) means we should reexamine climate envelope models, for example including more detail such as variable cloud cover. Increased temperature with a simultaneous decrease in cloud cover, as has occurred in much of Europe, eastern Africa, and the Americas, is more likely to compound the effect of increasing temperature, further decreasing thermal quality of the habitat and the Activity x Benefit profile in summer. Systematic changes in thermal quality of habitat will have pronounced effects on things like reproduction and offspring quality (Hare & Cree 2010). In addition, flow-on effects to food sources and habitat will have profound effects on species.

We have attempted to isolate the effects of temperature and cloud cover on a population of black-throated rainbow skinks, and assumed that factors such as behaviour and habitat structure remained constant, although they may change. Much behaviour may be constrained by, for example, high quality foraging time: when are prey available? Theory suggests that ectothermic prey should escape their predators by using habitat that is too hot for them (Mitchell & Angilletta 2009). Both ectothermic predators and their prey must alter their thermoregulatory behaviour under climate change, possibly in similar ways. Of course, most prey for ectotherms are themselves ectotherms, and ultimately, most ectotherms are prey, painting a ‘Red Queen’ scenario of organisms exposed to hotter and hotter environments, and never quite able to adapt. Our model should be applicable to any ectotherm if appropriate biophysical equations are used for body temperature estimation, and if the habitat temperature variation is measured on a scale appropriate to body size.

In conclusion, from this model, it appears that thermal benefit for black-throated rainbow skinks in winter will be much better under climate change, although thermal benefit in the summer will be worse, even if the number of cloudy days increases by 40%. If summer is a limiting factor due to high temperature, and reduced thermal quality interrupts breeding or other key activities, increased cloud cover may not offset the effect of 3 °C warming, and climate change will be have a negative effect. If summer is not so limiting, or if there exists enough behavioural plasticity to alter diel activity patterns, black-throated rainbow skinks may find the annual total thermal quality to be better than today.

Figures

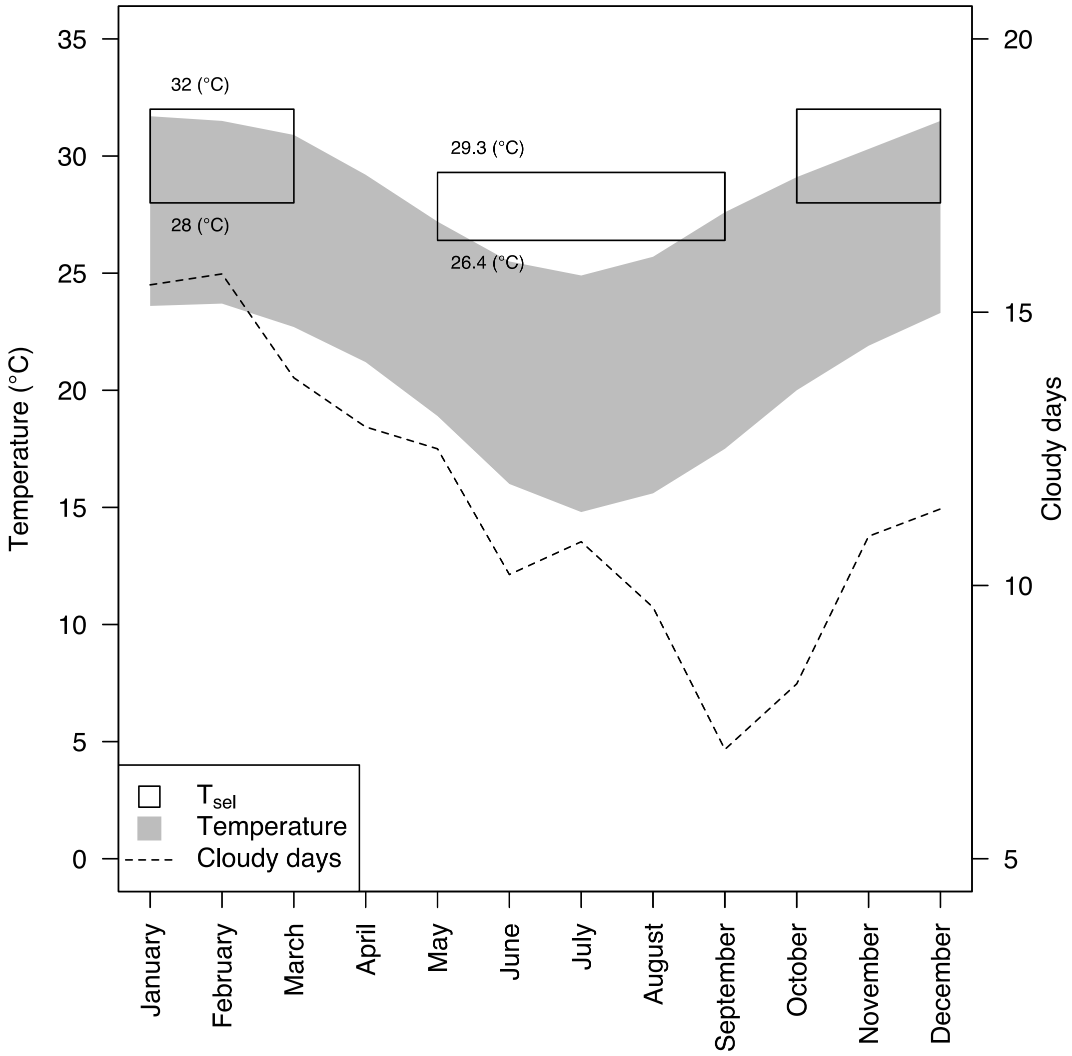

Figure 5-1. Range of mean maximum and minimum air temperature (grey area), and mean number of cloudy days (dashed line) at Lucinda weather station near Hinchinbrook Island 1981- 2010 (data from www.bom.gov.au); rectangles show selected temperature ranges for *Carlia rostralis* in the Austral summer and winter.

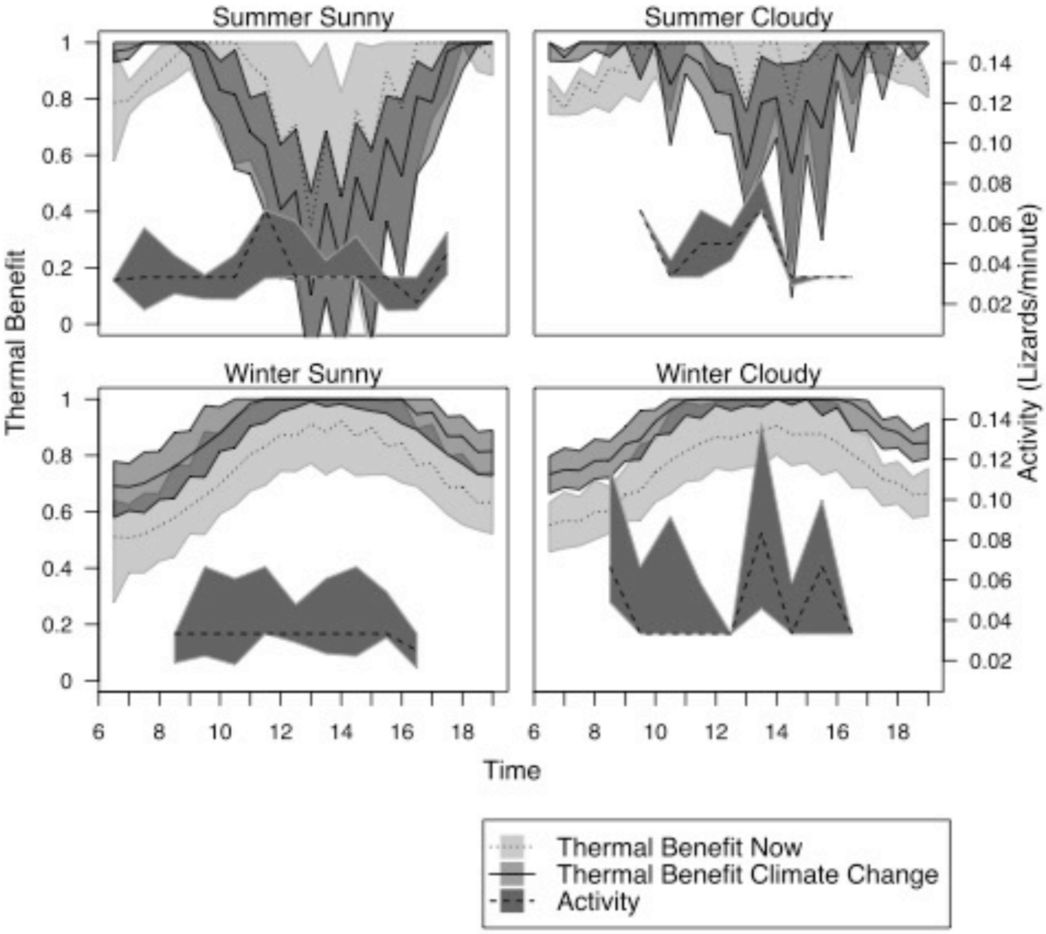

Figure 5-2. Median Thermal Benefit (+- 50% prediction limit) of contemporary thermal habitat (lightest grey, dotted line), and projected 3˚C temperature increase (medium grey, solid line), and empirically determined mean activity (+- 50%CI, dark grey, dashed line) for rainbow skinks (*Carlia rostralis*) at Hinchinbrook Island in Summer (top) and Winter (bottom) on Cloudy (left) and Sunny (right) days.

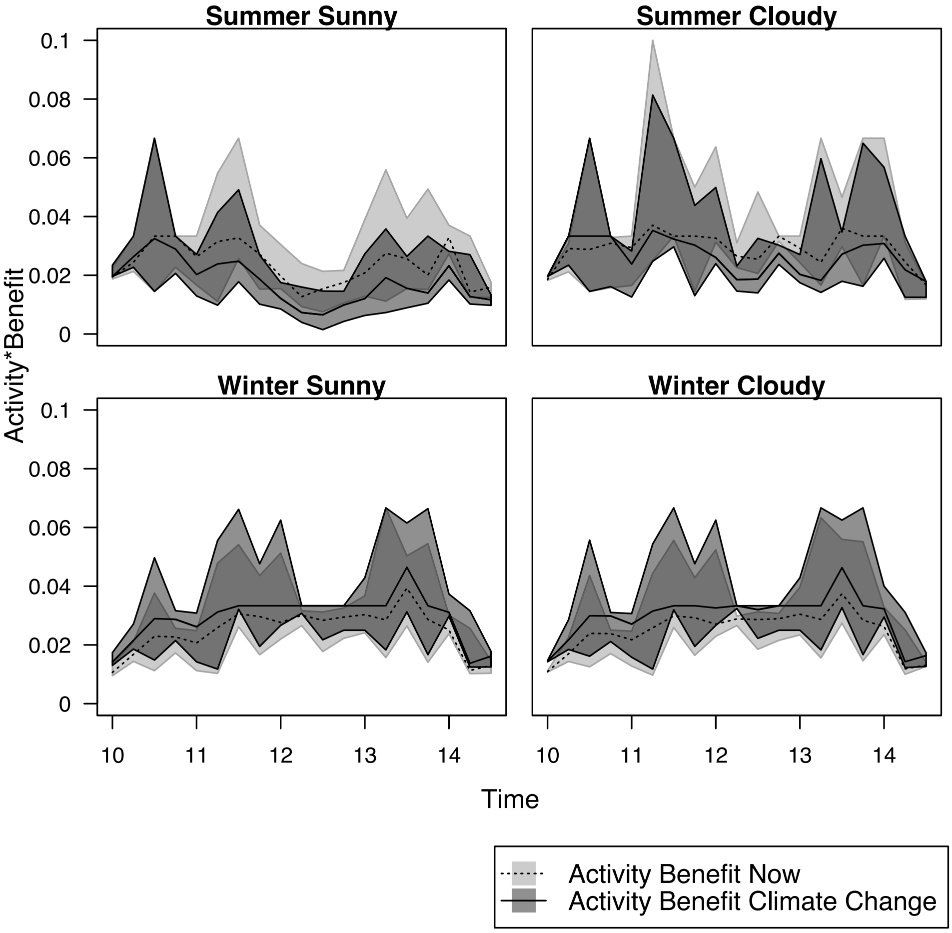

Figure 5-3. Mean Activity x Benefit scores (+-50% bootstrapped CI, n=1000) profile for contemporary thermal habitat (light grey, dotted line) and predicted 3˚C temperature increase (medium grey, solid line) in Summer (top) and Winter (bottom) on Cloudy (left) and Sunny (Right) days for *Carlia rostralis* on Hinchinbrook Island.

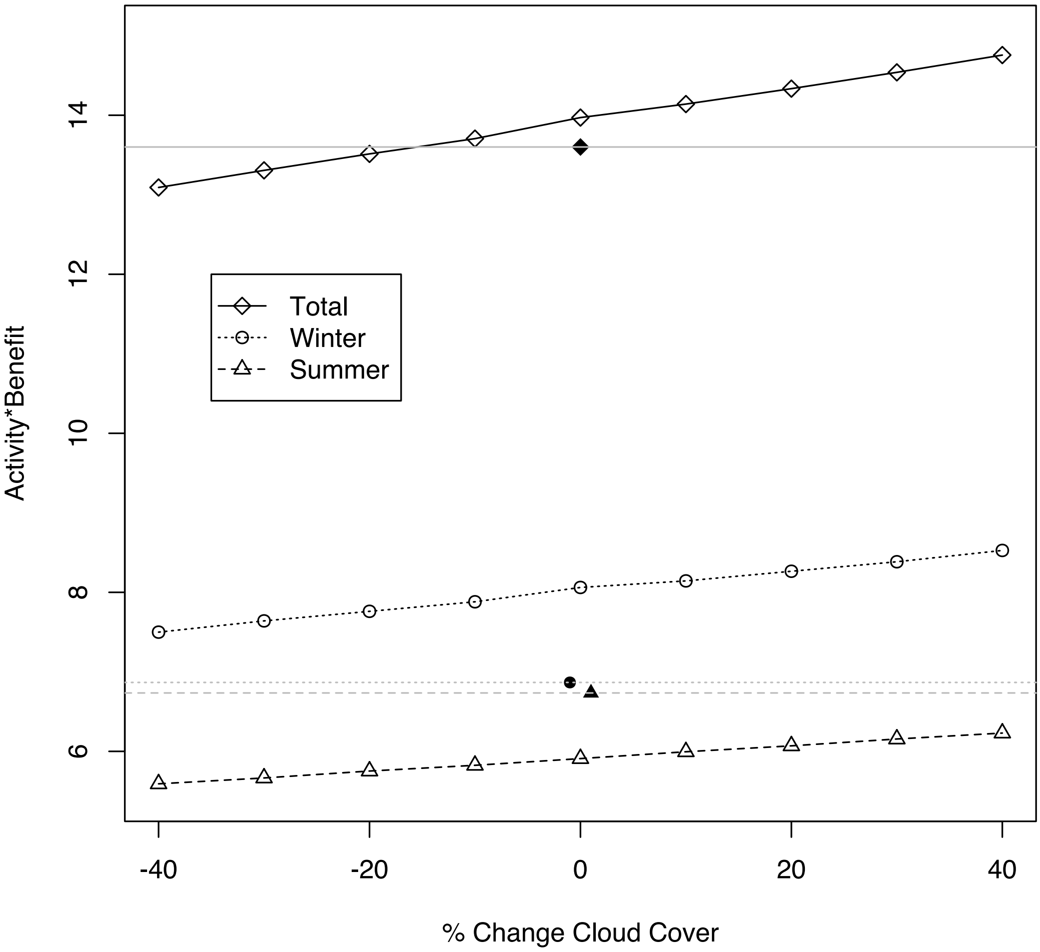

Figure 5-4. Activity*Benefit scores under contemporary conditions (filled points, grey lines) and under climate change with shifting cloud coverage in the different seasons (open points, black lines, one point per model scenario).

Chapter 6 Are tropical ectotherms harder to toast?

Mathew Vickers[1,2] and Ben L Phillips[3]

1. School of Marine and Tropical Biology, James Cook University.
2. CSIRO Sustainable Ecosystems, Ecology Program, PMB PO, Aitkenvale, Queensland 4814
3. Department of Zoology, University of Melbourne

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Abstract

There is a prevailing view that tropical ectotherms might be at particular risk from anthropogenic climate change. The argument for this flows from the observation that temperatures tend to be more stable in the tropics; consequently, tropical ectotherms tend to be thermal specialists relative to their temperate counterparts. If all else is equal, a given shift in environmental temperature will impart a greater fitness cost to the thermal specialist. Thus, as the world warms, the current expectation is that tropical ectotherms will pay a higher fitness cost than temperate ectotherms. Although this argument is persuasive, we argue here that the tropics, in addition to favouring thermal specialization, will also favour the evolution of highly precise behavioural thermoregulation. Because of this, tropical species may be preadapted to avoid excessively high environmental temperatures and may also, because of this, experience stronger selection on physiological traits in a changing climate. As a consequence, tropical species may, in fact, be both demographically buffered, and more likely to show rapid adaptation than their temperate counterparts. It is clear that before we can make generalisations about where the worst impacts of climate change will fall, we need to account for behaviour.

Introduction

The majority of terrestrial ectothermic animals (terrestrial ectotherms) live in the tropics, and as anthropogenic climate change progresses, there is deep concern that these tropical ectotherms will be particularly hard hit by the projected increase in temperature (Deutsch *et al.* 2008; Huey *et al.* 2009). The reason for this concern is that the high and narrow thermal performance optima of tropical ectotherms are near to their upper critical thermal limit (T_{opt} is near CT_{max}, Figure 1). As a result, a two-degree increase in the average temperature is predicted to “toast” tropical ectotherms. That is, habitat temperature will increase such that it more often exceeds their thermal optimum, and possibly their thermal maximum, reducing activity times (Sinervo *et al.* 2010) and fitness, and ultimately causing declines and extinctions. Conversely, due to the relatively broader and flatter thermal performance curve of temperate species, the same two degree shift is predicted to see far fewer temperate species exceeding their tolerances (Fig. 1, Deutsch *et al.* 2008). We argue that, rather than condemning them, the narrow thermal tolerance limits and associated thermal specialisation of many tropical ectotherms instead provides a mechanism for the increased behavioural thermoregulatory capacity that will buffer tropical ectotherms from climate change.

Why do tropical species have narrow thermal limits? The tropics is a thermally stable place: although mean environmental temperature increases towards the equator, temperature variability decreases (Janzen 1967; Vázquez & Stevens 2004). Because of this thermal stability, tropical ectotherms have evolved to specialize on a relatively narrow range of temperatures (Deutsch *et al.* 2008). In line with the low-variance and high mean of environmental temperatures, the optimal body temperatures of tropical ectotherms are typically higher, narrower, and nearer to their critical thermal maxima than those of their temperate counterparts (Huey *et al.* 2010).

The argument that thermal specialization places tropical terrestrial ectotherms at particular risk from climate change is persuasive, but we argue here that it may be misleading, because it misses a vital factor: behaviour. Behavioural thermoregulation filters the local environment; it allows individuals to choose the parts of their environments that optimize their body temperature reducing selection pressure (the “Bogert Effect”). It has long been established that most ectotherms capable of movement employ behavioural thermoregulation (Cowles & Bogert 1944). Although many ectotherms thermoregulate, they vary in the precision to which they do so – some species are highly precise thermoregulators, others less so (Hertz *et al.* 1993; Row & Blouin-Demers 2006), and still others are thermoconformers (Huey *et al.* 2009). If thermoregulating ectotherms in the tropics tend to be better at behavioural thermoregulation (i.e., they are more precise thermoregulators, Vickers *et al.* 2011), their behavioural capacity may ameliorate the predicted heightened physiological impact of climate change (e.g., Kearney et al., 2009). We argue here that tropical ectotherms should be particularly precise thermoregulators. Our argument centers on a basic consideration of the selective forces operating on behavioural thermoregulation in the tropics. To understand these basic forces, we first need to understand the thermal performance curve.

The thermal performance curve, and thermal specialization in the tropics

The dependence of organismal processes on temperature is well described (Gilchrist 1995). The sum total of the responses of an organism to temperature results in the thermal performance curve for that organism (Figure 1), which, in its idealized form, captures the relationship between body temperature and fitness (Arnold 1983). The thermal performance curve has a characteristic hump-shape (Huey & Kingsolver 1989) where fitness is maximised at some intermediate temperature (thermal optimum) and declines as body temperature deviates from the optimum. Moreover, the curve is asymmetric so the thermal optimum is closer to the thermal maximum than the thermal minimum so fitness decreases slowly with decreasing temperatures (colder), but decreases rapidly with increasing temperature (hotter; Figure 1). Therefore a warmer deviation from the optimum body temperature is more costly than the same deviation in the cold direction. Because of this asymmetry, most organisms should have a strong behavioural sensitivity to high temperatures, where a degree above the thermal optimum is much more dangerous than a degree below it (e.g., Vickers *et al.* 2011).

Thermal performance curves vary greatly among species, and one obvious axis of variation is in their degree of thermal specialization (Izem & Kingsolver 2005). The argument that terrestrial tropical ectotherms are toast (Tewksbury *et al.* 2008; Huey *et al.* 2010; Sinervo *et al.* 2010) relies heavily on the observation that tropical ectotherms tend to have narrower thermal performance curves (i.e., they are thermal specialists) relative to their temperate counterparts. Why does thermal specialization scale with latitude? Our current understanding is that organisms that operate at high temperature typically perform better than those operating at low temperature (Huey & Kingsolver 1993). That is, maximum fitness (driven by rates of metabolism, energy uptake etc.) is higher for species that can operate at higher temperatures (Frazier *et al.* 2006). This “hotter-is-better” hypothesis explains why thermal performance curves tend to be asymmetric, with high performance closer to the critical thermal maximum than the critical thermal minimum (Huey & Kingsolver 1989), and it has clear support at the broad evolutionary scale (Clarke 2003; Frazier *et al.* 2006). Conversely, support becomes more ambiguous within species (Huey & Kingsolver 1993; Clarke 2003; Latimer *et al.* 2011). Nonetheless, it seems clear that most species have thermal optima close to the upper end of their thermal tolerances. The critical thermal maximum, however, appears to be highly constrained (Clarke 2003). This is less true for the critical thermal minimum (Huey & Kingsolver 1989; Clusella-Trullas *et al.* 2011). Thus, at higher latitudes, the capacity to perform at lower temperature has evolved but with no associated decrease in critical thermal maximum (Addo-Bediako *et al.* 2000), which has resulted in a broadening (Latimer *et al.* 2011) and flattening of the thermal performance curve farther away from the tropics (Tewksbury *et al.* 2008). Therefore, compared to their temperate relatives (thermal generalists), tropical species tend to have narrow thermal performance curves, often with a higher peak fitness (thermal specialists) (Frazier *et al.* 2006; Tewksbury *et al.* 2008).

Importantly, the reason we currently expect tropical ectotherms to be harder hit by climate change is exactly because tropical ectotherms tend to be thermal specialists (Deutsch *et al.* 2008). The argument goes that, all else being equal, a shift in environmental temperature will have a greater impact on specialist species with their narrower thermal performance curves. However, behavioural differences, stemming from differing selective forces between tropical and temperate zones, mean that all else may, in fact, not be equal. Tropical species should be better behavioural thermoregulators since (1) Hot, thermally stable, habitat begets thermal specialisation, and (2) Thermal specialisation demands precise thermoregulation, and (3) Precise thermoregulation may lead to heightened selection on physiology.

1. Stability begets specialisation

The tropics tend to be hot. Such tropical habitats as rain- or cloud-forests are relatively warm and stable, facilitating thermoconformation (Hertz *et al.* 1993). However, vastly more area in the tropics is occupied by habitats such as savannah or open woodland that are more thermally heterogeneous, with higher mean and maximum temperatures that often exceed the critical thermal maxima of the species that live there (Christian & Bedford 1995; Kearney *et al.* 2009). Thus, poor thermoregulation, particularly with regard to high temperatures, can be extremely dangerous in much of the tropics (Vickers and Schwarzkopf, 2013, Chapter 3). The very real risk of being killed outright by high temperatures in open woodlands, deserts, and savannahs must create a strong selection force on tropical ectotherms to be very precise behavioural thermoregulators, maintaining boy temperature near their preferred range (Vickers *et al.* 2011). For example, without careful attention a desert lizard could be killed if it strays too far from cool microhabitat (Grant & Dunham 1988). Thus, in places where microhabitat temperatures are regularly antagonistic to life (e.g., > 45°C), thermoconforming should be a rare strategy; tropical thermoregulators need to be good at thermoregulation simply to survive. This has not been widely recognized because the thermoregulation they are good at is not the traditionally considered form, acquiring heat in cold environments, instead it is the ability to regulate activity to avoid the lethal temperatures that are already common in tropical habitats (Vickers and Schwarzkopf 2013, Chapter 3).

2. Thermal specialists should be better thermoregulators

Thermal specialists by definition have steep, narrow thermal performance curves, while generalists have flat, broad thermal performance curves. When an individual's thermal performance curve is narrow (thermal specialist), the change in fitness it experiences per degree body temperature deviation from optimum is large (Huey & Kingsolver 1989; Tewksbury *et al.* 2008). Conversely, when an individual's thermal performance curve is broad (thermal generalist), the change in fitness it experiences per degree deviation from optimum is small (Figure 1). Another way of capturing this idea is that a specialist incurs a greater cost than a generalist for errors in thermoregulation, so a specialist should be a better thermoregulator (e.g. Gilchrist, 1995). Accordingly, in any given environment we would expect the specialist to be under stronger selection for precise thermoregulation than the generalist.

The relatively warm, stable, environment of the tropics should produce an evolutionary ratchet on thermoregulatory behaviour. Warm, stable conditions favour thermal specialization (Janzen 1967), but thermal specialization, in turn, creates strong evolutionary pressure for precise thermoregulation. The ability to precisely thermoregulate drives further specialization, and so on (Ghalambor *et al.* 2006). The heightened cost of thermoregulatory errors for thermal specialists means we have every reason to suspect that tropical ectotherms are highly precise thermoregulators with strategies for avoiding excessively hot conditions.

3. Precise thermoregulation may lead to stronger selection on physiology

Thus, we might expect tropical ectotherms to be particularly precise thermoregulators, and so capable of buffering themselves from acute episodes of extreme climate. There is, however, a view that precise behavioural thermoregulation, because it buffers individuals from the extremes of the environment, causes reduced selection on physiology (Huey *et al.* 2012; Buckley *et al.* 2013). As a consequence, it is argued, thermoregulators will be less evolutionarily labile than thermoconformers when the environment changes.

Although appealingly intuitive, and probably true when selection is soft, the broader truth is more complex (Phillips & Shine 2014). To illustrate this point, it is useful to consider a very extreme event, where mean environmental temperature exceeds the critical thermal maximum for a population. If our population is composed of non-thermoregulators, the population is obliterated, there are no survivors and, because of this, no selection can occur. If the population were composed of careful thermoregulators, on the other hand, more individuals would survive in the micro-refugia they select, and selection can occur. Behaviour, by increasing survival in extreme situations, can lead to much higher selection strength.

Why does this happen? It comes about as a consequence of the non-linear relationships between phenotype and survival probability. A phenotype that doubles survival probability from 0.01 to 0.02 in an extreme event may increase survival probability five-fold (or more) when mean survival is slightly higher (or the event is less extreme). That is, the same trait can be under stronger selection when the demographic impact is weaker compared with the situation of a strong demographic impact (Phillips & Shine 2014). Thermoregulation, by weakening the demographic impact of an extreme event, can actually lead to stronger selection.

Given that many of the biological consequences of climate change will be manifest as extreme events (Parmesan *et al.* 2000; Wellbergen *et al.* 2008), it is worth considering such a situation carefully. Thermoregulation, (and more broadly, phenotypic plasticity) may act to increase the evolutionary potential of populations under extreme scenarios (Phillips & Shine 2014). Thus, as well as creating an evolutionary ratchet for increasing physiological specialization in a constant environment, a capacity to thermoregulate potentially also acts to increase selection on physiology in a changing environment. Tropical ectotherms may not only be good at avoiding the worst excesses of environmental change (because they are particularly good thermoregulators), but they may also face stronger selection on thermal physiology as a consequence.

Synthesis

Many species will meet unprecedented challenges as climate change progresses, and in a static scenario, where mechanisms such as individual behaviour are not invoked, species declines often seem inevitable. The prevailing view is that the major impacts of climate change may fall on tropical ectotherms, but this view does not adequately account for behaviour. We have presented arguments that suggest that 1) behavioural thermoregulation is likely to be more precise in many tropical ectotherms; 2) this behavioural capacity will buffer individuals and populations from climate change, and in doing so 3) it may actually increase the strength of selection on physiology. Thus, incorporating consideration of behavioural thermoregulation calls into question the prevailing view that tropical ectotherms are toast, because it suggests that they may in fact be more resilient in both ecological and evolutionary senses.

It is, of course, possible that we are wrong. But the heightened requirement for behavioural thermoregulation in many tropical ectotherms is clear, and it also is clear that this may help protect them from predicted negative effects of climate change. Somewhat paradoxically, behavioural thermoregulation is most precise in the very high temperature areas of the tropics: the deserts, savannahs and open woodlands. As such, behaviour may provide the strongest buffer to species in these areas, while species that thermoconform, or are from less extreme environments such as rainforests, may be hardest hit. This possibility warrants much greater consideration. To assess this possibility requires a much stronger focus on the behavioural aspects of thermal physiology: as a first step it requires a focus on geographic variation in thermoregulatory behaviour, particularly around behaviour under extreme conditions. Appropriate data on this front are currently sorely lacking.

While survival and fitness result from a complex interplay of behaviour, physiology, and adaptation (Huey *et al.* 2012), the question becomes: is the behavioural toolkit currently possessed by tropical ectotherms enough to buffer them from impending change? The consensus prediction is that the change in absolute temperature is likely to be smaller in the tropics than in temperate regions (Stocker *et al.*, 2013). So this smaller shift, coupled with the more precise thermoregulatory capacity of tropical species, might mean that tropical species are, in fact, less impacted by climate change than their temperate counterparts. Certainly, the lower extinction rates of tropical species during episodes of past climate change might give us pause for thought (e.g., Liow et al., 2008; Rolland et al., 2014). Although the rate of past climate change may not be the same as we are currently experiencing, the fact remains that tropical species appear to have survived these fluctuations better than their temperate counterparts.

How do we go about testing the possibility that behaviour may protect tropical species from climate change? Essentially, we need to know which limit is likely to be encountered first, the limit to behaviour or the limit to physiological tolerance in ectotherms across a cline of habitat varying in its degree of thermal heterogeneity. In reality, it is the interaction, or combination, of physiology and behaviour that determines a species' performance, though it may be initially more instructive to explore these effects in isolation. Many studies test the physiological costs and limits of body temperature, but we require data on the behavioural mechanisms behind thermoregulation, their rules, limits, and plasticity. Further, we need to thoroughly understand the cost of thermoregulation, not only in terms of energy, but in terms of fitness as well. For example, the fitness cost of maintaining thermoregulatory strategies and the cognitive ability to execute them. Answering these questions is a challenge, and may require new approaches. But if we are to be clear about the impact of climate change on the majority of the world's species, the question is vital, and well worth the effort.

Figures

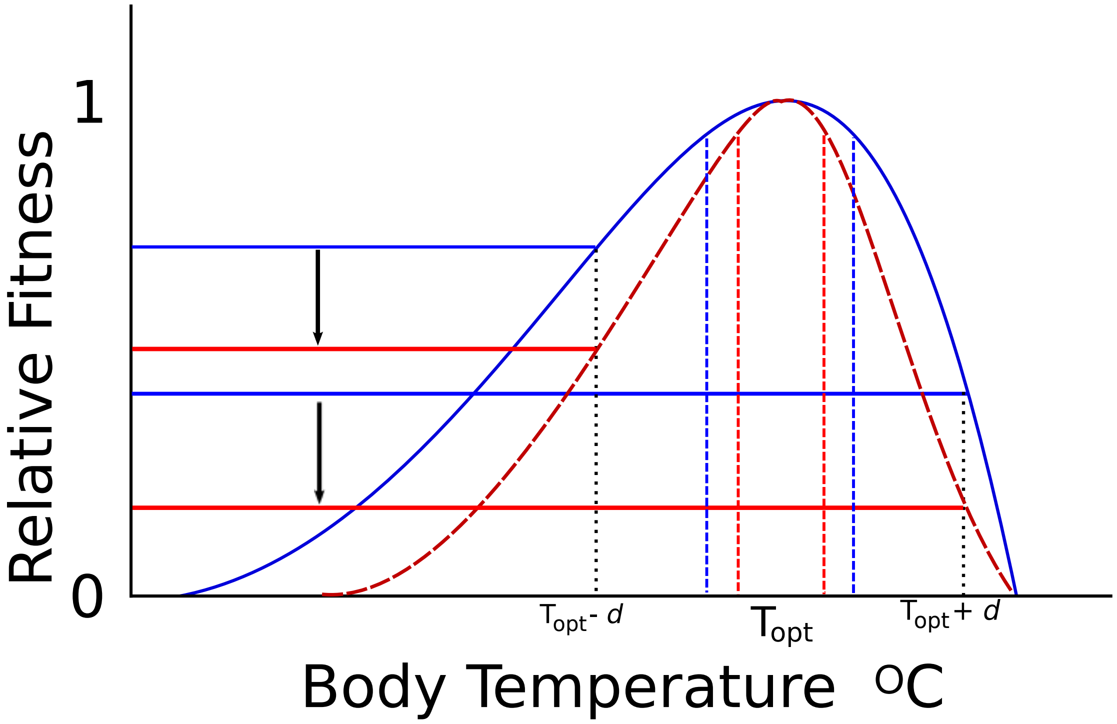

Figure 6-1. Comparison of relative fitness as a function of body temperature between temperate (blue) and tropical (red) ectotherms. Vertical dashed blue and red lines show thermal optimum range. The fitness functions have been overlaid so optimal body temperatures overlap (in reality, the tropical species would likely have a higher optimum). The Tropical species has a narrower curve relative to the temperate species. As a result of the narrower, steeper, curve the tropical species suffers higher fitness consequences for a given shift (*d*) in body temperature away from optimal (size of difference between tropical and temperate shown by black arrows). The asymmetry of the curve means that any shift (*d*) in body temperature above the optimal ($T_{opt}+d$) incurs a higher fitness cost than the same shift below optimal ($T_{opt}-d$).

Chapter 7. Discussion

I provide a conceptual advance to the cost-benefit model for behavioural thermoregulation, which produces two novel, distinct, and testable hypotheses that distinguish this cost-benefit model from the original (Huey & Slatkin 1976). The first hypothesis is that ectotherms should increase thermoregulatory effort as temperatures deviate from optimal, and the second hypothesis is that specifically, ectotherms ought to be especially effective at thermoregulating in high temperatures. I found support for these predictions using empirical data collected from three sympatric *Carlia* skinks (Vickers *et al.* 2011, Chapter 2), and data from previous studies are also supportive (Blouin-Demers & Nadeau 2005). These findings are somewhat intuitive when accounting for the cost of not thermoregulating. In an optimal habitat, the cost of not thermoregulating is likely to be very low: with little or no effort, body temperature should be at or near the thermal optimum. Thus, the impetus to thermoregulate will be low. Conversely, as environmental temperature moves away from thermal optimum, the penalty for thermoconforming (being the same temperature of the environment) increases, which should increase thermoregulatory effort. Consider an environment with a thermal cline that ranges from lethally cold to optimal to lethally hot. With little effort, an individual can easily occupy the optimal environment, but the individual must behaviourally thermoregulate with more effort and precision to avoid dangerous temperatures to occupy sites further from the optimal. This example can be restated in terms of shifting geographic distributions in terms of altitude or latitude. The idea that hot environments will produce increased effort in thermoregulation stems from the asymmetrical shape of the thermal performance curve: as temperature increases, performance increases until the optimum, and then performance decreases very sharply toward the critical thermal maximum. A higher rate of cost for failing to thermoregulate at high temperature means more effort should be invested to offset the risk; species in hotter environments must necessarily be good at performing in them.

One way to examine the cost of failing to thermoregulate is by analyzing thermal habitat quality, which is estimated using a null model. My novel random walk null model for behavioural thermoregulation (developed in Chapter 3) is an alternative to the original null model of (Hertz *et al.* 1993). My new model incorporates advances made by (Christian & Tracy 2006) and thermal transients and thermal inertia discussed in the literature (e.g., Seebacher & Shine 2004). I make use of modern data collection and analysis techniques to estimate thermal quality (thermal benefit), integrated over time, of the habitat. This allowed examination of the spatial and temporal aspects of the habitat thermal quality as well as the benefit of behavioural thermoregulation. Using this model highlighted an obvious shift in the benefits of behavioural thermoregulation throughout the day, which implies that there is strong plasticity in the thermoregulatory capacity for individual *Carlia sexdentata* (Vickers & Schwarzkopf 2013, Chapter 3). Such plasticity in thermoregulatory behaviour is not surprising, but has not been rigorously demonstrated previously.

I then applied my new null model to examine the differences in thermal habitat quality between cloudy and sunny days, and to predict the effects of climate change on lizards under a wide range of cloud cover regimes (Chapter 4). My results demonstrate that the thermal quality of the environment, averaged over the year, was improved by climate warming. This pattern is due to an increase in thermal quality in winter offsetting the decrease in summer. Increases in the number of cloudy days will further improve the thermal benefits accrued by ectotherms under climate change, most importantly by improving thermal benefit in summer. By contrast, decreases in the number of cloudy days decreased the thermal benefits accrued under climate change. The fates of lizards under these regimes are strongly dependent on the interaction between behavioural plasticity, phenology, and adaptation to a changing climate.

Tropical ectotherms are at particular risk of climate warming (Deutsch *et al.* 2008; Somero 2010; Huey, Losos & Moritz 2010; Sinervo *et al.* 2010; Chapperon & Seuront 2011; but see Overgaard *et al.* 2014). The idea stems from the relative shapes of the thermal performance curve for tropical versus temperature species. Tropical species have steep and narrow curves while temperate species have broader, flatter curves. Tropical species live near their thermal optimum, while temperate species live below. These combined mean that an increase in temperature will cause a larger fitness decrease to tropical species than to temperate, and may even cause a fitness increase to temperate species (Deutsch *et al.* 2008). Fitness is related to the thermal habitat via temperature's influence on the thermal performance curve summarized in as thermal benefit. The total thermal benefit that a lizard acquires at any time can be described by the equation from (Chapter 3, Vickers & Schwarzkopf 2013).

Thermal Benefit obtained by real Lizard = Thermal Benefit of the habitat + Thermal Benefit of Thermoregulation + ε

If the thermal benefit of behavioural thermoregulation remains constant, decreasing thermal benefit (quality) of the habitat will decrease the total thermal benefit obtained by the lizard. Summarizing habitat thermal quality for use in correlative predictions of species persistence typically relies on behavioural thermoregulation remaining constant (Sinervo *et al.* 2010). However, thermoregulatory ability varies within and among species along habitat thermal gradients (Chapter 6), and the benefit from thermoregulation can vary throughout the day for individuals (Chapter 3, Vickers & Schwarzkopf 2013), implying that the effort invested in thermoregulation is highly plastic, and context dependent. It seems reasonable to expect that this lability will be capitalized upon to offset the decrease in thermal benefit of the habitat caused by warming climate. More precise predictions will come with the development of aid mechanistic models informed by behavioural thermoregulation (Kearney 2006; Kearney & Porter 2009).

To survive or escape the effects of climate change, species must take one of a very few options: acclimation, adaptation, relocation, or extirpation. Extirpation is entirely undesirable. Evidence is mounting for relocation to be unfeasible, at least for terrestrial ectotherms (Buckley *et al.* 2013), and adaptation alone is likely to take too long (Colwell *et al.* 2008; Buckley *et al.* 2013), which leaves acclimation. While it may not be the final solution, acclimation has the potential to provide a hiatus to the threat of climate change, giving time for species to adapt, and an obvious axis for acclimation is behavioural thermoregulation.

Behavioural thermoregulation provides a mechanism for organisms to filter environmental temperature and thereby limit the impact of unfavourable temperatures on physiology and survival. The heightened capacity for behavioural thermoregulation in tropical ectotherms may help buffer animals so that they have time to acclimatize, relocate, or adapt to new thermal challenges (Kearney *et al.* 2009). The idea that tropical ectotherms will leverage their ability to behaviourally thermoregulate to cope with increasing temperature can be derived from the extended cost-benefit model for behavioural thermoregulation (Chapter 2, Vickers *et al.* 2011).

The idea that behavioural thermoregulation will buffer climate change is speculative, and has been discussed (Kearney *et al.* 2009), but I posit that rather than relying on increases in shade or ground cover, terrestrial ectotherms, in particular in the tropics, may already have the toolkit necessary, and predictions of extinctions and survival should be reconsidered in this light. The good news is that the future might not be as bleak as current predictions suggest.

Future directions

Focused study is required to determine whether a shift in behaviour enough to buffer the effect of changing climate, and allow time for adaptation, acclimation, migration, or climate temperature reversal. The degree of behavioural buffer available might be examined using a model incorporating the plasticity available in behavioural thermoregulation with the rule set a lizard uses to control body temperature, and empirically testing ideas that a fluctuating environment, with varying levels of survival dependent on behavioural trait values, increases selective pressure and rate of adaptation. Updating the cost-benefit model, and developing the null model for behavioural thermoregulation was the first step in this challenge.

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