Linking Thermal Environments, Body Condition, and Thermoregulatory Behavior to Predict the Performance of Lizards

by

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ABSTRACT

Environmental variation impacts physiological performance in animals. As a result, many animals thermoregulate to buffer unfavorable thermal variation in their environments. Animals are only expected to thermoregulate when the benefits outweigh the costs, although both are difficult to quantify. I examined how habitats and organismal factors shape thermoregulation and physiological performance in lizards. I found that habitat structure shapes opportunities for thermoregulation in two species of Anolis lizards. In dense tropical rainforests where there is low habitat heterogeneity, the range of available microclimates is narrow. Consequently, lizards in the tropics tend to be thermal specialists – performing best over a narrow range of temperatures. This phenotype should lead to decreased performance under climate warming. I then investigated the relationship between body condition, feeding, and thermoregulation in Yarrow's spiny lizards (*Sceloporus jarrovii*) using lab- and field-based experiments. In the lab experiment, when lizards were observed in an artificial thermal gradient, neither body condition nor feeding status influenced the mean body temperature. When simulated costs of thermoregulation were higher, all lizards reduced thermoregulation similarly. However, when lizards were observed in an outdoor thermal arena, individuals with lower body condition decreased thermoregulatory performance, resulting in a lower mean body temperature. Animals with poor body condition may face greater risk of predation when thermoregulating. Finally, I conducted a comparative analysis to quantify relationships between the potential for thermoregulatory performance and empirical measures of productivity (i.e., growth rates and reproductive output) in lizard populations. A model that assumes lizards are active whenever preferred temperatures were available overestimated the duration that a lizard could maintain a preferred body temperature. As such, studies equating predicted thermoregulatory performance with fitness in the context of climate change should be interpreted cautiously. Overall, environmental factors and organismal traits shape the thermoregulatory behavior of animals, ultimately affecting their physiological performance and fitness. Biologists should consider these relationships when modeling the impacts of climate change on future performance.

DEDICATION

To my loving parents, for their unwavering support. And to my partner in science and in life. Everything is sweeter with you, Jake.

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CHAPTER 1

HABITAT STRUCTURE MEDIATES VULNERABILITY TO CLIMATE CHANGE THROUGH ITS EFFECTS ON THERMOREGULATORY BEHAVIORS

Abstract

Tropical ectotherms are thought to be especially vulnerable to climate change because they are thermal specialists, having evolved in aseasonal thermal environments. However, even within the tropics, habitat structure can influence opportunities for behavioral thermoregulation. Open (and edge) habitats likely promote more effective thermoregulation due to the high spatial heterogeneity of the thermal landscape, while forests are thermally homogenous and may constrain opportunities for behavioral buffering of environmental temperatures. Nevertheless, the ways in which behavior and physiology interact at local scales to influence the response to climate change are rarely investigated. I examined the thermal ecology and physiology of two lizard species that occupy distinct environments in the tropics. The brown anole lizard (*Anolis sagrei*) lives along forest edges in The Bahamas, whereas the Panamanian slender anole (*Anolis apletophallus*) lives under the canopy of mature forests in Panama. I combined detailed estimates of environmental variation, thermoregulatory behavior, and physiology to model the vulnerability of each of these species. My projections suggest that forest-dwelling slender anoles will experience severely reduced locomotor performance, activity time, and energy budgets as the climate warms over the coming century. Conversely, the forest-edge dwelling brown anoles may use behavioral compensation in the face of warming, maintaining population viability for many decades. These results indicate that local habitat variation, through its effects on behavior and physiology, is a major

determinant of vulnerability to climate change. When attempting to predict the impacts of climate change on a given population, broad-scale characteristics such as latitude may have limited predictive power.

Introduction

Several global and regional-scale analyses have suggested that tropical ectotherms are more vulnerable to the effects of anthropogenic climate change than species at higher latitudes (Deutsch et al. 2008, Tewksbury et al. 2008, Huey et al. 2009, Kearney et al. 2009, Sinervo et al. 2010, Sunday et al. 2010, Urban et al. 2012, Sunday et al. 2014). Tropical species are projected to experience greater restrictions in activity (Sinervo et al. 2010), physiological performance (Huey et al. 2009, Sunday et al. 2010, Sunday et al. 2014), and energy budgets (Kearney et al. 2009), and greater declines in population growth rates (Deutsch et al. 2008) relative to temperate species. These predictions are based on the observation that the seasonally stable nature of tropical thermal environments has led to the evolution of narrow thermal niches, or thermal specialization (Deutsch et al. 2008, Tewksbury et al. 2008, Huey et al. 2009, Kearney et al. 2009, Sinervo et al. 2010, Sunday et al. 2010, Urban et al. 2012, Sunday et al. 2014).

The prediction that tropical species may be more vulnerable to thermal change is reasonable, because, as with any niche specialist, thermal specialists should have limited capacity to maintain fitness when their environment shifts. Nevertheless, to encompass many species over vast geographic areas, global-scale studies often rely on coarse-scale climatic data (e.g., low-resolution temperature layers from WorldClim.org), simplistic measures of thermal physiology (e.g., critical thermal limits), and an assumption of thermoconformity (i.e., equating organismal body temperature with average air temperature). Moreover, global-scale analyses focus on macroecological variables and rarely consider the potential for *in situ* responses (e.g., plasticity and genetic adaptation). This approach, which has undoubtedly been useful in generating global-scale hypotheses, may mask substantial local variation in the vulnerability of populations (Sears and Angilletta 2011, Gunderson and Leal 2012, Potter et al. 2013, Gunderson and Leal 2016, Fey et al. 2019).

The tropics contain a diverse array of terrestrial habitat types that can favor alternative behavioral strategies for maintaining optimal body temperatures (Kaspari 1993, Gunderson and Leal 2012, Logan et al. 2015). Many tropical species live in open or edge habitats that provide high levels of thermal heterogeneity (Gunderson and Leal 2012, Logan et al. 2013). These habitats favor the behavioral strategy of thermoregulation, whereby individuals can shuttle between microclimates to maintain narrow body temperature distributions (Huey 1974a). Thermoregulators maintain stable internal body temperatures even as the ambient environment fluctuates (Huey 1974a, Huey and Slatkin 1976, Huey and Kingsolver 1989, Hertz 1993). In contrast, there are also many tropical species that live under the shade of dense forest canopies. In these spatially homogenous thermal environments, behavioral thermoregulation is costly because the large distances between sunny and shady microhabitat patches increase the energetic cost of behavioral shuttling (Huey et al. 2009). The thermal environments of closed-canopy tropical forests favor thermoconformity, whereby individuals allow their body temperatures to track ambient variation (Huey 1974a, Huey and Slatkin 1976, Sears and Angilletta 2015, Sears et al. 2016). For any ectothermic species in any habitat, body temperature distributions ultimately depend on the interaction between thermoregulatory effort (i.e., where they fall on the continuum between perfect thermoconformity and perfect thermoregulation) and spatiotemporal variation in environmental temperature (Angilletta 2009, Fey et al. 2019).

Local habitat structure, through its effects on behavior, should also affect the breadth of the thermal niche, and the populations with the broadest thermal niches should be the least vulnerable to climate change. Theory suggests that the breadth of a given population's thermal niche should correspond to that population's body temperature distribution, which is constrained by the environment (Lynch and Gabriel 1987, Gabriel and Lynch 1992). Populations that thermoregulate precisely should have narrow body temperature distributions and therefore narrow thermal niches. Indeed, many higher-latitude species are remarkably efficient at maintaining preferred body temperatures during activity (e.g. Agamid lizards from the southern tip of Africa (Logan et al. 2019) and Liolaemid lizards from the Andes of Argentina (Valdecantos et al. 2013) suggesting that narrow thermal niches may be common in temperate and high-elevation regions despite broad intra-annual variation in environmental temperature.

Although behavioral strategies interact with thermal landscapes to determine the thermal niches of populations, individuals also use behavior as their first line of defense when thermal environments change (Huey et al. 2003, Muñoz and Bodensteiner 2019). Thus, the vulnerability of populations to climate change ultimately depends on the capacity to compensate for changes in temperature with behavioral adjustments, and this occurs in the context of the thermal niche (the same degree of behavioral thermoregulation has a greater compensatory effect on an organism with a narrow thermal niche; (Kearney et al. 2009, Buckley et al. 2013, Buckley and Huey 2016). Without explicitly considering the interactions among thermoregulatory behavior, local thermal variation, and the breadth of the thermal niche, it is not possible to fully predict the vulnerability of ectotherm populations to climate change.

In this study, I evaluated the extent to which local habitat structure influences the predicted response to climate change in two species of tropical lizard. The brown anole (*Anolis sagrei*) lives in open and forest-edge habitat in The Bahamas (Losos et al. 2004) whereas the Panamanian slender anole (*Anolis apletophallus*; hereafter the "slender anole") occurs in closed-canopy tropical forest in Panama (Andrews and Sexton 1981). First, I monitored field-active body temperatures in the context of the spatiotemporal structure of the thermal landscape to evaluate the thermoregulatory strategy employed by each population. Second, I examined the thermal performance breadth of each population by measuring both sprint speed and resting metabolic rate as a function of body temperature. Finally, I used these data to model the effects of rising environmental temperatures on locomotor performance, activity time, and energetics while explicitly considering the potential for behavioral buffering. I hypothesized that the physiological and behavioral phenotypes of each species would primarily be dictated by local habitat structure, and that the species with the broadest thermal performance breadth and the greatest capacity for behavioral thermoregulation would be the least vulnerable to climate change.

Methods

Study System and Experimental Design

I sampled a population of adult (male SVL > 35 mm; female SVL > 30 mm) brown anoles on the island of Great Exuma in The Bahamas (23.5333° N, 75.8333° W) and a population of adult (male and female SVL > 38 mm) slender anoles from Soberanía National Park, Panama (9.1165° N, 79.6965° W). Both species are generalist arthropod-predators that perch at similar heights in their respective habitats (~ 0.5 - 1.5 m; (Schoener 1968, Scott et al. 1976). Both species maintain small territories (Sexton et al. 1963, Tokarz 1998), store sperm (Calsbeek et al. 2007, Stapley 2018), have short (< 1 year) generation times (Andrews and Rand 1974), and reach peak reproduction during northern hemisphere summers (~ May – October) (Andrews and Rand 1974, Andrews 1979, Logan et al. 2014). Nevertheless, they occur in very different structural environments. The brown anole lives in scrubby vegetation or along the edges of coppice forest (Fig 1.6.), whereas the slender anole lives in the understory of lowland, closed-canopy forests (Fig 1.7.).

Environmental and Field-Active Body Temperatures

I used temperature data loggers to quantify variation in the local thermal environments available to lizards (Bakken and Gates 1975, Bakken 1992). I built these loggers in different ways for each species to account for the primary avenue of heat transfer in each habitat type. For brown anoles, which live in a habitat where heat transfer is dominated by solar radiation, I followed the method used by Logan et al. (Logan et al. 2014, Logan et al. 2016, Logan et al. 2018). Brown anole data loggers were built from thin-walled, cylindrical copper piping, sized and painted to approximate the physical characteristics of an adult brown anole, and equipped with iButtons (Maxim Integrated, San Jose, CA) to record temperature. For slender anoles, which live in a habitat where heat transfer is dominated by convection, I coated iButtons in PlastiDip (PlastiDip International, Blaine, MN) for waterproofing, and then glued each to a small (10 cm) length of pine wood. To deploy data loggers (brown anole, N = 24; slender anole, N = 34), I haphazardly chose locations along linear transects meant to cover a large portion of each habitat type at our field sites. At each initially chosen location, I picked a random side of the transect (left or right), then walked a random distance from the transect (0 – 3 m in 1 m intervals) and placed the data logger at a random height in the vegetation (0.5 – 2 m in 0.5 m intervals) and orientation on the branch or tree trunk (facing upwards, facing downwards, or on the side of the branch). I programmed brown anole data loggers to record temperatures from April 17 to June 19, 2018 (every 60 minutes), whereas I programmed slender anole data loggers to record temperatures from July 11 to November 7, 2017 (every 100 minutes). Although these data sets were collected in different years, I verified that weather conditions were not anomalous at either location with respect to mean ambient conditions by examining historical weather station data (Bahamas: www.weatherunderground.com; Panama: Smithsonian Lutz Watershed Meteorological Station on Barro Colorado Island). Historical weather data is not available for the island of Great Exuma in The Bahamas, so I used data from a nearby island (New Providence). Mean annual temperatures differed by less than 1°C among years at each location and as such I treat our data logger measurements as capturing representative thermal profiles of the two different habitats. Hereafter, I refer to the temperatures recorded by these data loggers as “environmental temperatures” rather than “operative temperatures” because the latter require precise calibration with live animals. From 2018 onwards, I use data from a weather station I set up close to the field site on Great Exuma, The Bahamas (HOBO RX3000 Station, Onset Computer Co., MA, USA) and the same weather station that I used to examine historical temperatures on Barro Colorado Island, Panama (Vaisala HMP60), to monitor monthly changes in ambient air temperatures at each of the field sites. I used general linear models to compare daily (0700 – 1800 h) and nightly (1800 – 0700 h) average environmental temperature (T_e), minimum T_e, and maximum T_e between sites.

At each site, as data loggers were recording environmental temperatures, I captured lizards by hand or slip noose and measured their field-active body temperatures (T_b) with an Omega HH147U type K thermocouple thermometer (brown anole, N = 107; slender anole, N = 577). I avoided pseudoreplication in The Bahamas by toe clipping individuals (two toes clipped per individual). If I captured an individual and found that it had been previously marked, it was immediately released, and no body temperature was recorded. In Panama, pseudoreplication was impossible as all captured individuals were subsequently transplanted to islands in the Panama Canal as part of a separate study. To compare thermoregulatory strategies, I fit general linear models with T_b as the dependent variable. The independent variables were mean environmental temperature (T_e) at the time of capture, species, body mass, and an interaction between T_e and species. Model comparisons were conducted with the MUMIN package in R version 3.6.2 (R Core Team 2020). I used Akaike’s Information Criterion (AIC) scores to identify the best model (Akaike 1987).

Thermal Sensitivity of Locomotor Performance

I measured lizard sprint speed following Logan et al. (2014, 2016, 2018) by sprinting lizards at five body temperatures that span their thermal tolerance range (Logan et al. 2014, Logan et al. 2016, Logan et al. 2018). Sprint speeds were measured on a group of brown anoles captured in 2011 for a previous study (Logan et al. 2014), and no other physiological trait was measured on these individuals. Similarly, sprint speed was measured in a subset of slender anoles in 2018, and no other physiological trait was measured in those individuals. Because these species achieve different body temperature ranges in nature (see Results), I measured sprint speed at different sets of temperatures for each. I measured sprint speed at 15°, 22°, 28°, 35°, and 42°C in brown anoles (N = 38; data available only for males), and 15°, 20°, 25°, 30°, and 34°C in slender anoles (N = 26; males and females). The sprint track consisted of a wooden dowel (diameter = 2.5 cm, length = 1 m) that was demarcated every 10 cm and placed at a 20° angle (to discourage hopping) in a rectangular plastic bin. I brought individuals to the desired temperature by placing them in an incubator prior to each set of trials. Typically, I left individuals in the incubator for 15 – 20 minutes to reach the target temperature for a given trial, although they were never left in the incubator for more than five minutes at the warmest trial temperature due to the risk of death from overheating. I confirmed that lizards were at the desired temperature by measuring cloacal body temperatures with an Omega HH147U type K thermocouple thermometer prior to each set of trials. I motivated lizards to run 3-4 times in quick succession at each trial temperature. I recorded each set of trials with a high-speed digital video camera (GoPro set to 120 frames per second), and videos were analyzed in the motion analysis program Kinovea (www.kinovea.org). I did not include trials in statistical analyses if they occurred more than 30 seconds after the lizard had been removed from the incubator due to the rapid rate at which the body temperature of small ectotherms can equilibrate to ambient conditions. I considered a lizard's sprint speed to be 0 m/s if the individual was unable to run 10 cm continuously, or if it was unable to remain on the vertical surface of the dowel without falling off. All individuals were given at least two hours' rest between trials, and no individual was sprinted at more than three temperatures per day. Lizards included in sprint speed trials were never kept in captivity for more than 72 hours and they were eventually released back to their original spot of capture.

The thermal performance curve (TPC) of each individual lizard was estimated by fitting the full set of asymmetric parabolic equations built into the program TableCurve 2D (Systat Software, Inc.) to the raw sprint data (Angilletta 2006, Logan et al. 2014, Logan et al. 2016, Logan et al. 2018, Neel and McBrayer 2018, Neel et al. 2020). The optimal model for each individual was selected using AIC (Akaike 1987). From the best-fit TPC for each individual, I extracted several thermal performance traits: maximum sprint speed (P_{max}), the thermal optimum (T_{opt}), and the performance breadth (the range of temperatures over which the individual can achieve at least 80% of maximum performance; T_{br}; Huey and Stevenson 1979). To accurately compare T_{opt} and T_{br} between populations, I first converted raw sprint speeds to relative sprint speeds by dividing each sprint speed value by each individual's P_{max}. I analyzed relative instead of absolute sprint speed because the species were measured at different sets of temperatures and it is not clear how similar values of P_{max} in different species translate into differences in fitness. To visualize the population-average TPC, I calculated each individual's mean relative sprint speed at each trial temperature and followed the same curve-fitting procedure as described above. To test for differences in thermal performance traits between populations, I used general linear models with either 'T_{opt}' or 'T_{br}' as dependent variables and 'species' and 'body mass' (measured with a digital balance) as independent variables.

Thermal Sensitivity of Resting Metabolic Rate

I quantified resting metabolic rates using PreSens (PreSens Precision Sensing, Regensburg, Germany) fiberoptic closed-system respirometry. I measured oxygen consumption (VO_2) at the ecologically relevant body temperatures of 25° and 35°C for brown anoles (N = 32; males and females), and 20° and 30°C for slender anoles (N = 40; males and females), randomizing the order of temperatures for batches of three to six individuals. In brown anoles, lizards that were assessed for RMR were also included in thermal tolerance trials (see below), but the trial order was randomized to eliminate potential order effects, and I never exposed individuals to both types of assay in the same day. In slender anoles, RMR was assessed for a subset of lizards caught in 2018, and these lizards were not exposed to any other physiological assay. No individual of either species was kept in captivity for more than 72 hours during these experiments. All individuals of both species were given a minimum of 16 hours in captivity prior to measurements to ensure that they were not in peak digestion, and all lizards were measured at times of the day during which they are typically active. I first placed lizards inside airtight jars (240 ml), then placed the jars inside of an incubator set to the desired trial temperature. I gave each lizard at least one hour to acclimate to the incubator, and then measured O_2 every two seconds for 30 minutes thereafter. I calculated VO_2 (ml/g/hr) as the mass-specific slope of O_2 depletion per unit time. To compare the thermal sensitivity of metabolic rates between populations, I calculated slopes and temperature coefficients (Q_{10}) for each individual. Q_{10} was calculated using the following standard formula:

$$Q_{10} = \frac{R_2}{R_1}^{\frac{10℃}{(T_2 - T_1)}} \qquad [1.1]$$

Where R_1 is the VO_2 (ml/g/hr) at the lower trial temperature (T_1; °C) and R_2 is the VO_2 (ml/g/hr) at the upper trial temperature (T_2; °C). I used a general linear model to compare mean Q_{10} and slope values among populations. Neither the thermal sensitivity (Q_{10}) or total oxygen consumption differed between the sexes for either species, so I pooled the sexes for climate change projections (see below).

Thermal Preference

I used laboratory thermal gradients to quantify each species' preferred temperatures (Bennett and Johnalder 1984, Bauwens et al. 1995). Gradients were built from rectangular plastic bins (0.9 m long x 0.4 m wide x 0.3 m deep), with 250 W infrared heat bulbs suspended over one end of each bin. The temperature range in the gradients differed between species based on their respective field-active body temperature distributions and critical thermal limits (see Results). Thermal gradient temperatures spanned from 20°- 45°C for brown anoles (N = 63; males and females) and 22°- 38°C for slender anoles (N = 55; males and females). To record body temperatures, I inserted a Type T thermocouple into each individual's cloaca and fixed it in place with a small piece of medical tape (Neel and McBrayer 2018). I placed individuals of both species in the gradient for one hour prior to the start of each trial to acclimate them to the unfamiliar conditions. I then measured internal body temperatures every 30 seconds, continuously, for one hour thereafter. The individuals of both species that were assessed for T_{pref} were not assessed for any other physiological trait, nor were they kept in captivity for more than 72 hours before being released to their original spot of capture. I decomposed the body temperature data for each individual into several different thermoregulatory traits, including the mean, minimum, maximum, standard deviation, and interquartile range (middle 50%) of temperatures selected in the gradient. To test for differences between populations, I used general linear models with each thermoregulatory trait as the dependent variable and 'body mass' and 'species' as independent variables.

Thermal Tolerance

I measured two proxies for upper and lower thermal tolerance limits. To measure critical thermal minima (CT_{min}), I cooled lizards (brown anoles, N = 807; slender anoles, N = 813; males and females of both species) in an incubator set to 2°C. I allowed each lizard to cool to body temperatures below the point at which they lost their righting response (established with pilot trials) and then removed the animal from the incubator and allowed it to heat back up towards room temperature. As the lizard warmed back up, I checked for a righting response every 5-10 seconds by gently flipping it onto its back and observing whether it could regain an upright position. I scored CT_{min} as the body temperature (measured with an Omega HH147U type K thermocouple thermometer) at which the individual regained its righting response. If a lizard failed to right itself, I gave that individual a minimum break of 30 minutes at room temperature before placing the lizard back in the incubator and conducting a second trial. If the lizard failed to achieve its righting response for a second time, I did not include it in the final data set.

I also quantified the voluntary thermal maximum (VT_{max}) for each individual (brown anoles, N = 812; slender anole, N = 843; males and females of both species). VT_{max} is the upper body temperature where an animal displays fleeing behavior, and it may manifest in nature as the seeking of cooler microhabitats or thermal refugia when body temperatures reach a critical upper set-point (Weese 1917, Cameron and Rusch 2017). To measure VT_{max}, I placed lizards that had been maintained at room temperature (22°C) inside small plastic containers within an incubator set to 50°C. I continuously observed lizards until they exhibited obvious fleeing behavior, which occurs abruptly at a threshold temperature and is easily distinguishable from normal exploratory movement around the container. Lizards typically took ~3-7 minutes to reach $VT_{max.}$ Once an individual exhibited escape or fleeing behavior, I removed it from the incubator and recorded its body temperature with an Omega HH147U type K thermocouple thermometer. This body temperature was scored as the individual's VT_{max}. Brown anoles that were assayed for CT_{min} and VT_{max} were also assayed for RMR (see above). Slender anoles that were assayed for these two traits, on the other hand, were not subjected to any other physiological or behavioral experiment. I randomized the order of exposure to different physiological assays in both species to eliminate potential order effects, and all lizards were given a minimum of 90 minutes rest between experiments. After no more than 72 hours, lizards were either released back to their spot of capture or transplanted to experimental islands as part of a separate, ongoing experimental evolution study. I compared thermal tolerance limits between populations using general linear models with either CT_{min} or VT_{max} as dependent variables and 'body mass' and 'species' as independent variables.

Projecting the Impact of Climate Warming

I projected the effects of future climate warming on activity time, locomotor performance, and resting metabolic expenditure for each species. To do this, I first used field-based measurements of thermoregulatory behavior to convert future environmental temperatures to future body temperatures of lizards in each habitat. As a result, all projections explicitly include the effects of behavioral buffering. I modeled thermoregulatory behavior by fitting a linear model (regression) relating field-active body temperature to mean environmental temperature (estimated as the average environmental temperature logged within 30 minutes of each body temperature measurement) for each species. The slope of this relationship can vary between zero and one, with a slope of zero defining perfect thermoregulation (if it overlaps with mean T_{pref}) and a slope of one defining perfect thermoconformity (Hertz 1993). I retained the slope and y-intercept from these functions to predict lizard body temperatures under a range of environmental temperatures assuming that behavioral responses to warming remain consistent through the end of the century. My projections are based on a warming scenario of a 3°C increase by the year 2100, which aligns with the IPCC's warming predictions for Central America and the Caribbean if there are no changes in global policies that limit CO_2 emissions (IPCC 2018). I assume a uniform increase in temperature each year (+0.0365°C/year).

To project future activity levels, I assumed that lizards were active if predicted mean body temperature for the population was below the average VT_{max} for that population. I projected changes in activity time relative to present day (thus, activity time was set at 100% in the year 2019). To project changes in locomotor performance, I integrated the thermoregulatory model that predicts future body temperatures for each species with polynomial functions that describe the relationship between body temperature and sprint performance. Again, as with activity time, I projected changes in sprint performance relative to present day. Thus, I set sprint performance for each species in 2019 to 100%. To project changes in resting metabolic expenditure I used standard indirect calorimetry methods (Lighton 2008) to convert oxygen consumed (VO_2) to annual energy expenditure (kcal). I used the linear function describing the relationship between body temperature and oxygen consumption to predict energetic requirements under future climate conditions. I converted projected oxygen consumption at the annual (daytime) average environmental temperature to resting metabolic energy expenditure, assuming that both species remain active during an average of 12 hours per day over the year. I used measures of resting metabolic rates to make inferences about energy expenditure during activity because both species are sit-and-wait predators, and as such they spend large amounts of time being sedentary, even during activity hours. For example, Talbot (1979) reported that slender anoles spend over 80% of their day sitting still and scanning their environment for food (Talbot 1979). My projections assume evolutionary stasis in thermoregulatory behavior and thermal tolerance, as well as limited potential for physiological plasticity.

Results

Thermal heterogeneity and thermoregulatory strategy

Mean environmental temperature between 0700 and 1800 h and the daily maximal environmental temperature in edge habitat in The Bahamas exceeded those in forest habitat in Panama (ANOVA: mean: $F_{1, 58} = 551.90$, $P < 0.0001$; maximum: $F_{1, 58} = 306.08$, $P < 0.0001$; Fig 1.1). By contrast, the daily minimal environmental temperature in Panama exceeded that in The Bahamas (ANOVA: minimum: $F_{1, 58} = 836.73$, $P < 0.0001$). Average daily environmental temperature was 29.4 ± 0.1°C for brown anoles in The Bahamas and 25.9 ± 0.1°C for slender anoles in Panama. The range of average daily environmental temperatures spanned 21.0°– 40.7°C in brown anole habitat in The Bahamas and 22.9°– 29.6°C in slender anole habitat in Panama. Mean nighttime environmental temperature (between 1800 and 0700 h) was also higher in The Bahamas than in Panama but means differed much less than daytime environmental temperatures (ANOVA: average T_e: $F_{1, 58} = 127.61$, $P < 0.0001$; maximum T_e: $F_{1, 58} = 94.06$, $P < 0.0001$). Minimum nighttime environmental temperature was lower in The Bahamas than in Panama (ANOVA: minimum T_e : $F_{1, 58} = 541.269$, $P < 0.0001$). The average nighttime minimum and maximum environmental temperatures spanned 19.7° – 29.6°C in The Bahamas and 22.3° – 26.6°C in Panama.

Field-active body temperatures (T_b) were higher in brown anoles ($\overline{x} = 31.86 \pm 0.20$°C) than slender anoles ($\overline{x} = 28.15 \pm 0.04$°C; ANCOVA: $F_{2, 674} = 442.4$, $P < 0.0001$).

Mass did not affect brown anole body temperatures (ANCOVA: $F_{2, 85}$= 1.25, P = 0.60), but did affect slender anole body temperatures, with heavier lizards having slightly lower field-active body temperatures ($F_{2, 495}$ = 230.8, P < 0.0001). Environmental temperatures describe much of the variation in field-active body temperatures in Panama (R^2 = 0.48, $F_{2, 495}$ = 230.8, P < 0.0001), but not in The Bahamas (R^2 = 0.03, $F_{2, 85}$= 1.25, P = 0.28), and the slopes of the linear regressions between mean environmental temperature and mean field-active body temperature differed between species (ANCOVA: $F_{3, 680}$= 732.1, P < 0.0001, Fig. 2). The body temperatures of slender anoles in Panama closely tracked environmental temperatures (M = 0.77), whereas body temperatures of brown anoles in The Bahamas were relatively independent of environmental temperatures (M = 0.23).

Thermal physiology

In a thermal gradient, brown anoles selected warmer mean (brown: $\bar{x}$ = 31.11 ± 0.6°C; slender: $\bar{x}$ = 27.05 ± 0.3°C; ANCOVA: $F_{2,112}$ = 34.34, P < 0.0001), minimum (brown: $\bar{x}$ = 28.60 ± 0.6°C; slender: $\bar{x}$ = 25.49 ± 0.3°C; $F_{2,112}$ = 19.69, P < 0.0001) and maximum (brown: $\bar{x}$ = 33.36 ± 0.6°C; slender: $\bar{x}$ = 29.30 ± 0.3°C; $F_{2,112}$ = 31.59, P < 0.0001) temperatures, compared to slender anoles. The standard deviation of body temperatures chosen in a thermal gradient did not differ between species ($F_{2,112}$ = 0.68, P = 0.4). The interquartile range of body temperatures chosen was 30.22° – 32.09°C for brown anoles and 26.16° – 27.86°C for slender anoles. Mass did not affect the mean (ANCOVA: $F_{2,112}$ = 34.34, P=0.34) or range (ANCOVA: $F_{2,112}$ = 1.883, P=0.45) of preferred temperatures selected in the thermal gradient.

The thermal optimum (T_{opt}) for sprint performance was higher in brown anoles ($\bar{x}$ = 32.23 ± 0.76°C) than in slender anoles ($\bar{x}$ = 27.85 ± 0.51°C; ANCOVA: $F_{2, 58}$ = 10.58, P = 0.0001; Fig 1.3). Thermal performance breadth (T_{br}) was nearly two-fold larger in brown anoles (T_{br} = 12.99 ± 0.98), compared to slender anoles (T_{br} = 6.94 ± 0.53; ANCOVA: $F_{2, 58}$ = 12.05, P < 0.0001, Fig 1.3). Mass did not affect T_{opt} or T_{br} in either species (T_{opt}: ANCOVA: $F_{2, 58}$ = 10.58, P = 0.72; T_{br}: ANCOVA: $F_{2, 58}$ = 12.05, P = 0.92). The critical thermal minimum (CT_{min}) was lower in slender anoles ($\bar{x}$ = 13.74 ± 0.08°C) than brown anoles ($\bar{x}$ = 15.00 ± 0.09°C; ANCOVA: $F_{3, 1521}$ = 60.1, P = 0.0001). Mass affected CT_{min}, with smaller individuals having lower CT_{min} in both species (ANCOVA: $F_{3, 1521}$ = 60.1, P < 0.0001). Maximum voluntary temperatures (VT_{max}) were higher in brown anoles ($\bar{x}$ = 35.78 ± 0.08°C) than in slender anoles ($\bar{x}$ = 29.62 ± 0.06°C; ANCOVA: $F_{3, 1552}$ = 1225, P < 0.0001). Mass did not affect VT_{max} in either species (ANCOVA: $F_{3, 1552}$ = 1225, P= 0.062). There was no interaction between body mass and species for either CT_{min} (ANCOVA: $F_{3, 1521}$= 60.1, P = 0.67) or VT_{max} (ANCOVA: $F_{3, 1552}$= 1225, P = 0.32). The thermal sensitivity of resting metabolic rate was greater in slender anoles than in brown anoles (ANCOVA: $F_{1,70}$ = 19.22, P < 0.0001, Fig 1.4). The slope of the relationship between oxygen consumption (VO_2; ml/g/hr) and body temperature was greater for slender anoles ($\bar{x}$ = 0.076 ± 0.009) than for brown anoles ($\bar{x}$ = 0.030 ± 0.004). Temperature coefficients (Q_{10}) for resting metabolic rates were also higher in slender anoles (Q_{10} = 5.81 ± 0.60) compared to brown anoles (Q_{10} = 2.88 ± 0.67; ANOVA: $F_{1,71}$ = 10.61, P = 0.0017).

Projected effects of climate warming

We projected larger declines in performance across all metrics in slender anoles compared to brown anoles (Fig 1.5). Annual activity levels were unaffected in both species until about the year 2045, at which point projected body temperatures for slender anoles began to rise above the species' maximum voluntary temperature (VT_{max}) for an increasing portion of the day, and their activity time begins to decline precipitously (Fig 1.5A). Similarly, after several decades of steady increases in environmental temperature, I project a sharp decline in locomotor performance in slender anoles, while brown anoles remained relatively unaffected (Fig 1.5B). My model suggests a 32.1% decrease in relative locomotor performance for the slender anole by the year 2100, while brown anoles should experience a mere 2.7% decrease in locomotor performance. My models suggest that resting metabolic expenditure (kJ/year) will increase steadily in slender anoles while remained relatively unchanged in brown anoles through the year 2100 (Fig 1.5C). Whereas annual resting metabolic expenditure is predicted to increase by 18.9 kJ in slender anoles over the next century, it is predicted to increase by only 1.8 kJ in brown anoles.

Discussion

I integrated detailed measurements of local thermal environments, behavior, and physiology to test whether two closely related species of tropical ectotherm are likely to respond to climate change in the same way. Congruent with the hypotheses, I found that slender anoles from lowland tropical forest in Panama live in a spatially homogenous thermal environment. On average, slender anole habitat provides only 25% of the range of midday environmental temperatures compared to brown anole habitat. As a result, slender anoles thermoconform, experiencing the full temporal range of temperatures in their habitat during activity. Despite their lack of thermoregulation, the low temporal variation in temperature experienced by slender anoles in Panama (Figs 1.1 and 1.8) has led to a narrow thermal niche in that species. By contrast, the forest-edge dwelling brown anole lives in a spatially heterogenous environment (Figs 1.1 and 1.9). As a result, they actively thermoregulate and maintain a narrow range of body temperatures relative to the wide range of temperatures available during activity (Fig 1.2). Compared to slender anoles, brown anoles had a much broader thermal niche (possibly due to the greater variation in nocturnal temperature distributions in The Bahamas). By explicitly modeling behavioral thermoregulation in the context of each populations' current thermal niche, I showed that slender anoles may experience significant declines in activity and performance, while brown anoles may only be minimally impacted by future climate warming (Fig 1.5, A-C).

My study populations differed in thermal physiology. Brown anoles had higher thermal optima, broader performance breadths, higher thermal preferences, and higher voluntary thermal maxima, relative to slender anoles. Generally, differences in thermal physiology between populations matched differences in body temperature distributions, but the thermal physiology of my study species did not always follow *a priori* predictions. For example, the slender anole had a lower CT_{min} than the brown anole despite living in a much more temporally stable thermal environment. Nighttime temperatures under the forest canopy in Soberanía National Park rarely drop below 21°C, yet this species has a CT_{min} of less than 14°C. It is unclear why this would be the case because slender anoles must only very rarely, if ever, experience temperatures this cold in lowland Panama. It seems that the abnormally low CT_{min} of this species may be linked (via pleiotropy, genetic linkage, or physical constraint) to some other physiological function that is not directly related to environmental temperature but nevertheless permits them to maintain the righting response at extremely low body temperatures (Hochachka and Somero 2002). Regardless, the CT_{min} of slender anoles is so far outside their thermal performance breadth that it had little impact on the climate change projections for that species. Also note that body size affected some thermal traits, including field-active body temperatures in slender anoles and CT_{min} in both species, but the main effect of 'species' was still significant, implying that thermal traits have adapted to local environments independent of the effects of body size.

The thermal sensitivity of resting metabolic rate was higher in slender anoles than in brown anoles. Because brown anoles experience far more thermal variation between nighttime lows and daytime highs, selection may favor a reduced thermal sensitivity of metabolic rate to help reduce the energetic burden of large temperature swings (Dillon et al. 2010, Buckley et al. 2013, Logan et al. 2019). The higher thermal sensitivity of metabolism in the slender anole, in combination with its thermoconforming behavioral strategy, has large implications for their energetic demands under climate warming. I predict that slender anole energetic demands will increase steadily over the coming century, and this increase may lead to population declines if less energy becomes available for reproduction.

My climate-impact models, which explicitly include the effects of behavior, suggest that slender anoles will experience substantial declines in locomotor performance and activity time. These predictions occur not only because slender anoles are thermal specialists, but also because they do not have the capacity to buffer themselves against changing conditions using thermoregulatory behavior. Interestingly, a recent analysis of 40 years' worth of slender anole abundance data demonstrated that a population on Barro Colorado Island, Panama, has been declining steadily for many years, and that this decline was associated with historic climate patterns (Stapley et al. 2015). My results suggest that population declines are likely to continue. By contrast, my projections suggest that brown anoles will experience almost no change in locomotor performance, activity time, and energetic expenditure, even when mean environmental temperatures exceed their tolerance limits. This insensitivity to global warming occurs because brown anoles actively thermoregulate, seeking out cooler microsites when the broader habitat becomes too warm.

Previous global analyses have suggested that tropical species are especially vulnerable to rapid climate change (Deutsch et al. 2008, Tewksbury et al. 2008, Huey et al. 2009, Kearney et al. 2009, Dillon et al. 2010, Sinervo et al. 2010, Sunday et al. 2010, Huey et al. 2012, Sunday et al. 2014). My climate-impact projections that incorporated empirical measures of thermoregulatory behavior and thermal physiology generated contrasting predictions for how two low-latitude congeners will respond to climate warming (Figs. 5A-C). Some of these differences were dramatic. For example, I predict that the activity time of brown anoles will be virtually unaffected by warming through the end of the century. In sharp contrast, as temperatures continue to rise, the proportion of the day where slender anoles could be active (i.e., when predicted $T_b < VT_{max}$) should begin to decrease rapidly after the year 2045. By the year 2100, if average environmental temperature has increased by 3°C, potential activity time for slender anoles is projected to decrease by more than 83% relative to present day (Fig. 5A), and the slender anole would likely experience local extirpation in Soberanía National Park. Restricted windows for activity have been linked to lizard extinctions in previous studies (Sinervo et al. 2010) and may represent a critical determinant of population viability. Taken together, my fine-scale ecological, physiological, and behavioral data support the results of prior studies that suggested tropical forest ectotherms are particularly vulnerable to anthropogenic climate change (Huey et al. 2009, Huey et al. 2012).

Although I studied different species, an important role of habitat structure in determining behavioral strategy and physiology has also been found among populations within individual species. For example, Huey (1974) found that a population of Puerto Rican crested anoles (*Anolis cristatellus*) living in open habitat in a public park actively thermoregulated while an adjacent population living in closed-canopy forest thermoconformed (Huey 1974a). Gunderson and Leal (2012) found a similar pattern in the same species by comparing populations living in xeric and mesic forest habitat (Gunderson and Leal 2012). Neel and McBrayer (2018) discovered different patterns of thermoregulation and thermal physiology in populations of the Florida scrub lizard (*Sceloporus woodi*) occupying managed and unmanaged habitat (Neel and McBrayer 2018). These patterns of intraspecific variation suggest that local habitat variation can give rise to divergent behavioral strategies, and by extension, extinction probabilities, on short temporal and fine geographic scales.

It is important to note that our analysis ignores potential avenues of *in situ* adaptation such as acclimation (plasticity) and genetic adaptation. A number of recent studies have suggested that thermal physiology may have the capacity to both acclimate and evolve rapidly under changing environmental conditions (Leal and Gunderson 2012, Logan et al. 2014, Gilbert and Miles 2017), and these processes have the potential to significantly alter climate-impact predictions (but see (Logan et al. 2018, Logan et al. 2019, Martins et al. 2019) which found low heritability of the thermal niche). Slender anoles are forced to experience the diel variation in their thermal environments during activity. Thus, in the event of climate warming, heat-intolerant individuals should be rapidly removed by selection and baseline thermal physiology could evolve relatively quickly (Lynch and Walsh 1996). Indeed, I measured mean VT_{max} and T_b values for slender anoles that were about 1°C and 0.5°C higher, respectively, than the values for these traits measured 50 years ago by Ballinger et al. (1970), although the experimental procedure for VT_{max} differed slightly between these two studies and cannot be ruled out as the source of the difference in that trait (Ballinger et al. 1970). Regardless, this pattern suggests that thermal tolerance may have already evolved (or changed via plasticity) as a result of recent climate warming. Because my climate-impact projections do not include the potentially mitigating effects of plasticity and genetic adaptation, they should be seen as likely overestimating the vulnerability of the slender anole. Additionally, tropical forests may buffer changes in temperature to some extent, reducing the magnitude of change experienced by slender anoles relative to brown anoles (De Frenne et al. 2019). My analyses also ignore other variables that are likely to change as a result of climate change, including precipitation, cloud cover, wind dynamics, and the frequency of extreme weather events (Bonebrake and Mastrandrea 2010, Clusella-Trullas et al. 2011, Bonebrake and Deutsch 2012, Campbell-Staton et al. 2017, Grant et al. 2017). Finally, although I used an integrative, data-rich approach, my study consisted of a comparison of only two species, and as such the results should be interpreted with caution. Next-generation climate-impact models should not only include estimates of local thermal environments, physiology, and behavior, but should also consider how these factors interact to constrain or facilitate *in situ* adaptation to multi-modal environmental change across a diverse range of species.

I found that a tropical forest lizard may be substantially more vulnerable to climate change than a closely related species living in forest-edge habitat. This pattern is likely driven by the way in which habitat structure constrains thermoregulatory buffering of suboptimal environmental temperatures (Neel and McBrayer 2018). Tropical lowland forests are thermally homogenous in space, and forest lizards are forced to thermoconform in these environments. Despite the thermoconforming behavior of slender anoles, the temporal stability of the thermal environment experienced by this species has resulted in a narrow thermal niche. The projections suggest that the combination of the slender anole's narrow thermal niche with their thermoconforming behavior may reduce population sizes over the next several decades. By contrast, the edge-dwelling brown anole can shuttle between microclimates to maintain body temperatures that deviate from mean environmental temperatures. Because the brown anole has a broader thermal niche and is able to use behavior to compensate for changes in the thermal environment, they should experience minimal, if any, declines in population size. Contrary to previous studies that treat tropical organisms as uniformly vulnerable, my study suggests that local habitat structure is probably the primary factor driving variation in vulnerability. Indeed, it is likely that many temperate species are at risk under climate change, while many tropical species are not, and that data on local thermal environments are necessary for accurate climate-impact forecasts.

Fig 1.1. Variation in thermal environments among sites. (A) Monthly average ambient air temperature from local weather stations in Great Exuma, The Bahamas (closed circles) and Barro Colorado Island, Panama (open circles). Means ± 1 S. D. are shown. (B) Frequency distributions of the average midday (1200) environmental temperatures available to lizards in Soberanía National Park, Panama and (C) Great Exuma, The Bahamas, as measured via data loggers distributed randomly in the habitat of each species.

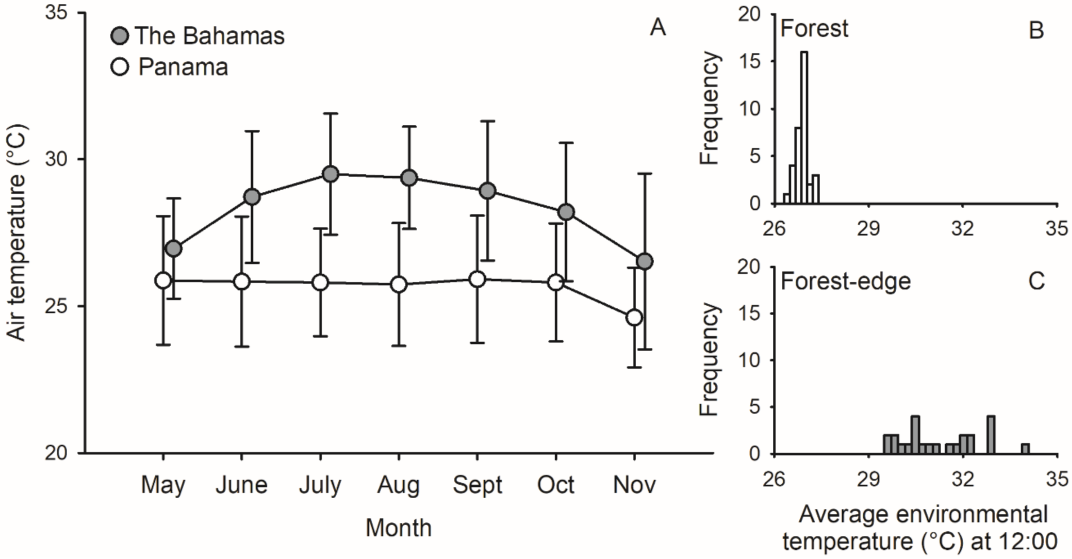


Fig 1.2. Body temperatures of slender anoles in Panama (left) and brown anoles in The Bahamas (right) as a function of mean environmental temperature (averaged across all data loggers) during the time the lizard was captured. Dashed lines represent a slope of one (perfect thermoconformity). Horizontal grey rectangles show the middle 50% of preferred temperatures selected in a thermal gradient (T_{pref}). The mean voluntary thermal maximum (VT_{max}) for each species is shown with dotted horizontal lines in each panel.

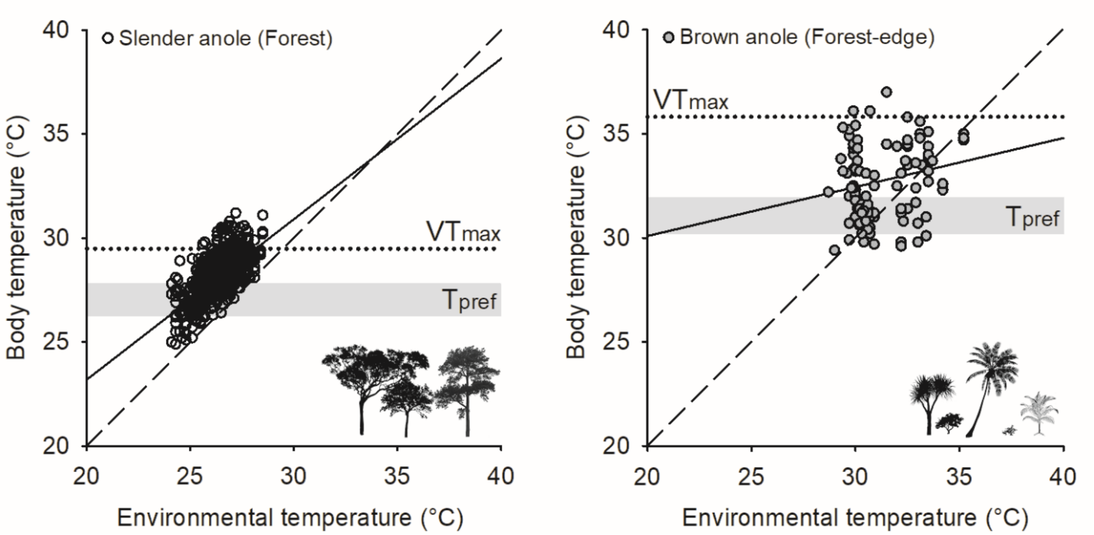


Fig 1.3. Thermal sensitivity of sprint performance in Panamanian slender anoles (dashed line) and Bahamian brown anoles (solid line). The 80% thermal performance breadths for the slender anole (dashed bracket) and brown anole (solid bracket) are also shown.

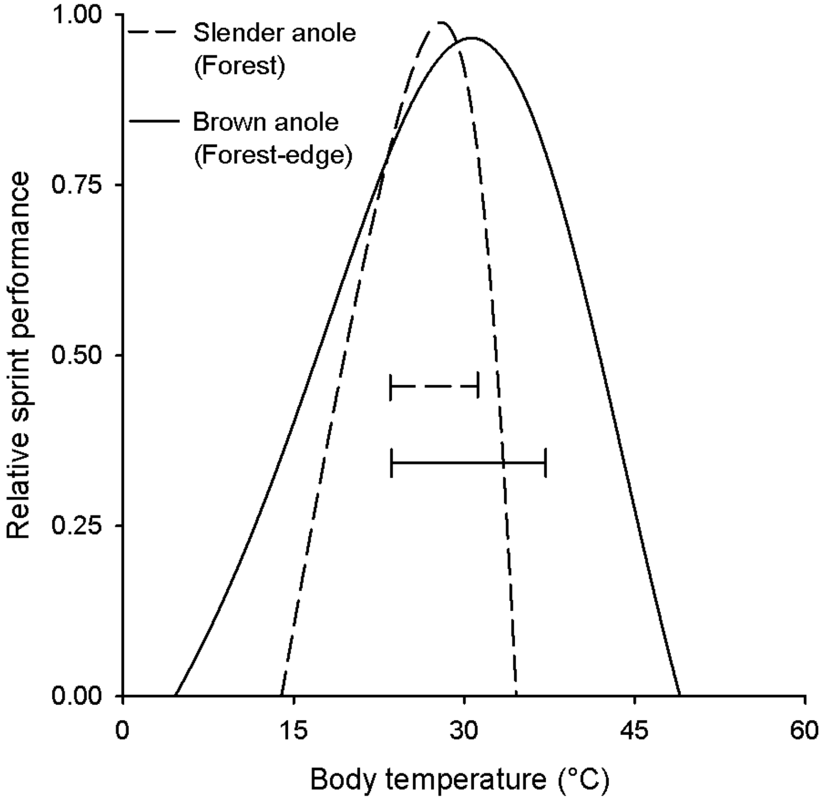


Fig 1.4. Thermal sensitivity of resting metabolic rate in Panamanian slender anoles (open circles) and Bahamian brown anoles (closed circles).

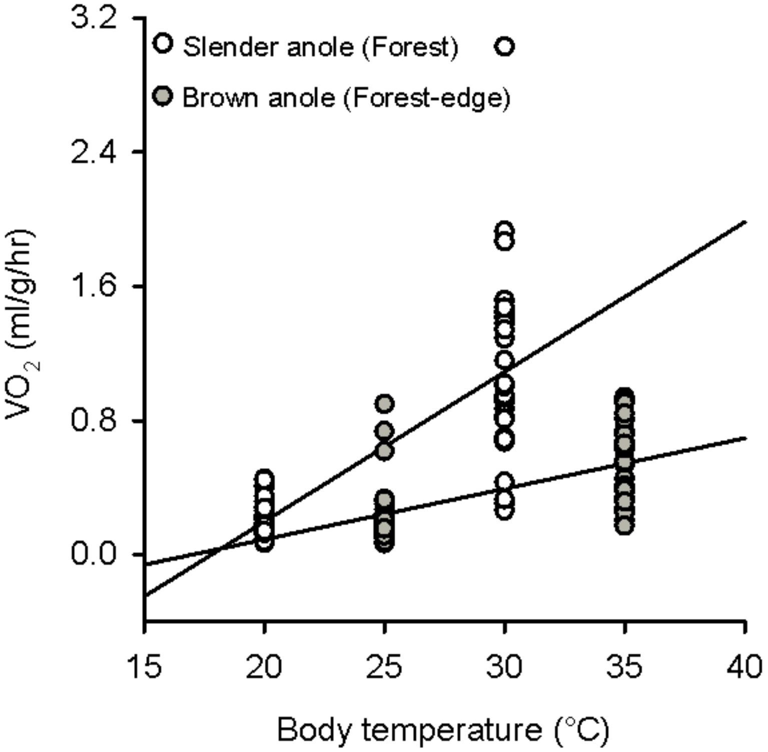


Fig 1.5. Projected changes in (A) potential activity time (assuming that lizards become inactive when predicted body temperatures exceed voluntary thermal maxima), (B) relative locomotor performance, and (C) annual energy expenditure. The projections in (A) and (B) are all relative to present day, assuming that activity and locomotor performance are currently maximized. I assumed a uniform 3°C increase in average (daytime) environmental temperature through the end of the century (+0.0365°C/year for 80 years).

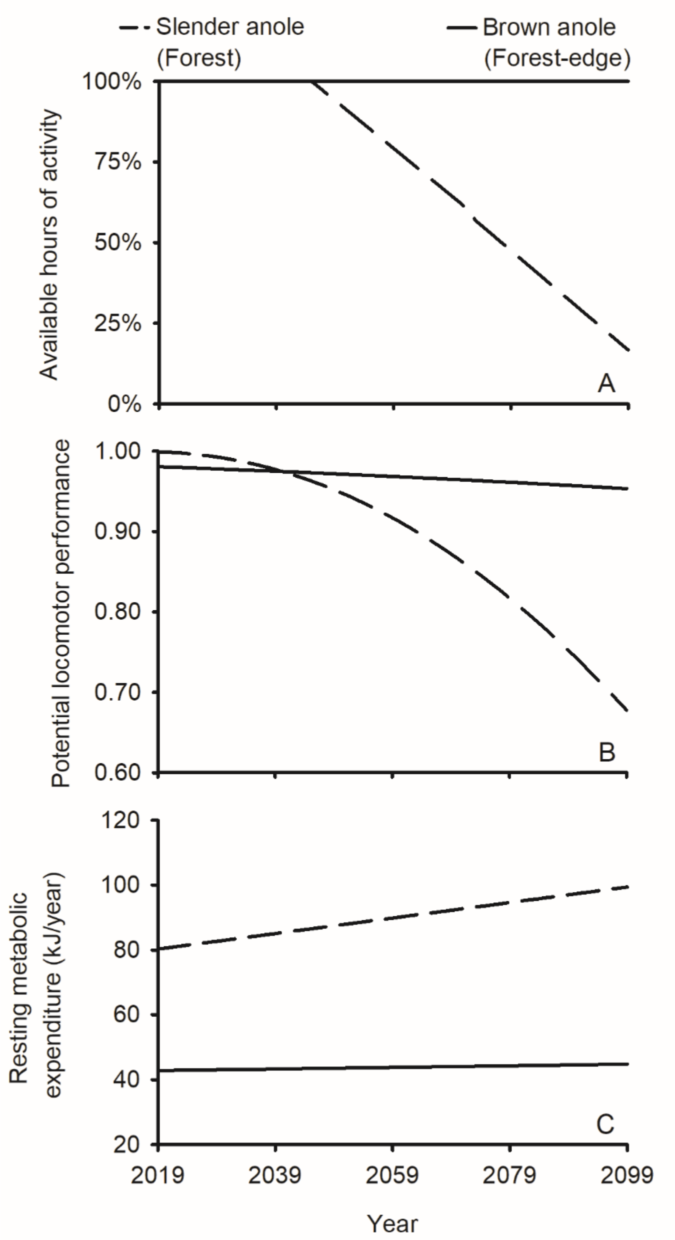


Fig 1.6. Brown anole habitat in Great Exuma, The Bahamas.

Fig 1.7. Slender anole habitat in Soberanía National Park, Panama.

Fig 1.8. Distribution of hourly environmental temperatures collected from data loggers distributed randomly in the habitat of brown anoles in The Bahamas (A) and slender anoles in Panama (B). Black data points show the average hourly temperature for each data logger. Horizontal shaded rectangles show the average interquartile range of temperatures selected in a laboratory thermal gradient (T_{pref}). Dashed lines represent average voluntary thermal maxima (VT_{max}). Critical thermal minima (CT_{min}) are not shown because they were far below typical environmental temperatures in both habitats.

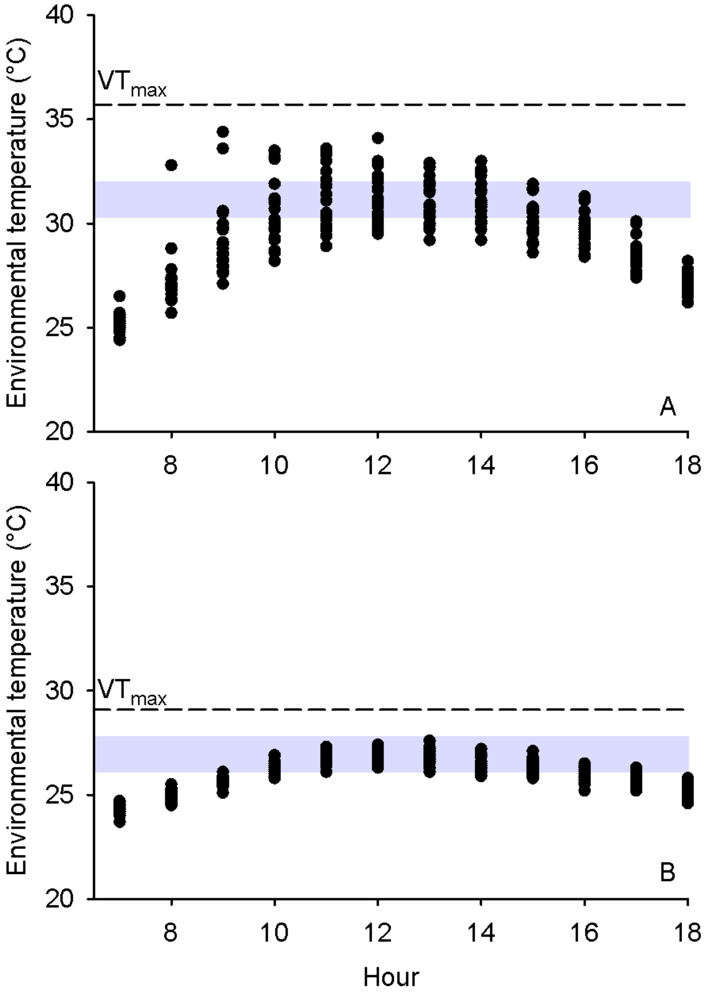
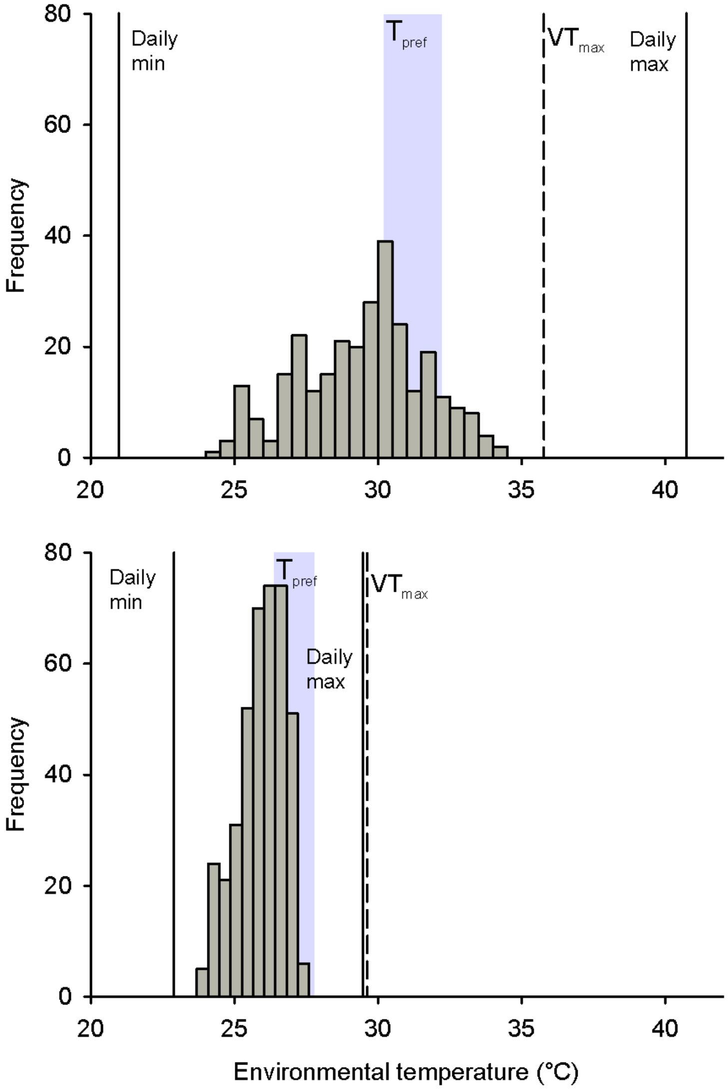


Fig 1.9. Frequency distribution of average hourly environmental temperatures collected from data loggers distributed randomly in the habitat of brown anoles in The Bahamas (top) and slender anoles in Panama (bottom). Solid lines show average daily minimum and maximum environmental temperatures, respectively. Dashed lines show average upper voluntary temperature (VT_{max}). Vertical shaded rectangles show the interquartile range of preferred temperatures (T_{pref}).



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CHAPTER 2

THE EFFECTS OF BODY CONDITION ON THE THERMAL PHYSIOLOGY OF A MONTANE LIZARD

Abstract

Thermoregulatory decisions are influenced by a variety of factors, including the interplay between an animal's physiological state and surrounding environment. Classic optimality models propose that animals should thermoregulate only when the benefits outweigh the energetic costs. However, quantifying the actual benefits can be challenging as many physiological and ecological processes scale non-linearly with time or energy availability, such as foraging and digestion. Additionally, estimating the costs can also be complicated as the physiological state of the animal may affect the mortality risk associated with thermoregulation. Here, I present data from a series of lab-based experiments where I investigate the relationship between body condition and thermal physiology in Yarrow's spiny lizards (*Sceloporus jarrovii*). First, I quantified the effects of body condition and feeding status on thermal preference. Second, I quantified the accuracy of thermoregulation upon experimentally manipulating the energetic cost of shuttling between microclimates. When lizards were observed in an artificial thermal gradient, neither body condition nor feeding status influenced the mean body temperature. When simulated costs of thermoregulation were higher, all lizards reduced thermoregulation similarly. However, the non-natural conditions in the lab may have influenced the behavior observed as behavioral experiments are especially susceptible to influence form the environment in which they are performed. Body condition and the optimal level of thermoregulation are likely linked in natural populations as both directly

impact energy availability and usage. To understand how an animal’s physiological state may shape the optimal level of thermoregulation, future work must consider the diverse ecological and physiological interactions that can constrain behavior in natural environments.

Introduction

Thermoregulatory behaviors depend on the relative costs and benefits associated with thermoregulation (Huey and Slatkin 1976). The optimal level of thermoregulation is shaped by complex interactions between the physiological state of the organism and their environment, among numerous other factors. Costs and benefits can be both energetic or nonenergetic, although energetic factors are particularly important as they proximately mediate the effects of body temperature on survivorship and fecundity. Ectotherms perform best within a narrow range of body temperatures (Huey 1982). If the energetic costs of thermoregulation (e.g., movement costs when shuttling or searching for preferred microclimates) outweigh the physiological benefit of being active at a preferred body temperature, fitness should be maximized when an organism thermoregulates imperfectly. However, perfect thermoregulation should be favored when the net energetic benefit outweighs the energetic cost and mortality risk of thermoregulating in a given environment.

The amount of stored energy an animal has available should influence decisions about energy gain. Rates of feeding and digestion are maximized within a narrow range of temperatures (Waldschmidt et al. 1986, McConnachie and Alexander 2004, Fontaine et al. 2018, Volkoff and Rønnestad 2020). Thus, an animal in an energy-deficient state, with a higher utility for energy gain, should maintain a body temperature that speeds the rate of energy gain. However, animals with little stored energy may experience a greater cost of thermoregulation. For example, if low body condition has reduced the performance of muscles, an animal would be slower when encountering predators. Elevated predation risk may deter an animal from actively shuttling between sunny and shaded microclimates – as it may increase exposure or attract the attention of a predator. Food availability would likely also shape the thermoregulatory decisions made in an animal with low body condition. In environments with high food availability, investing energy in thermoregulation could eventually yield a greater energetic return. When food is scarce, investing in thermoregulation would yield little energetic return on investment. Because body condition might promote or suppress thermoregulation, depending on one's assumptions, we need experiments that confirm these theoretical ideas and distinguish the net effect of body condition on thermoregulatory behavior.

To evaluate these competing models, I studied the thermoregulation of lizards (*Sceloporus jarrovii*) in a series of lab-based experiments. I quantified the effects of body condition and feeding status on thermal preference, and the accuracy of thermoregulation upon experimentally manipulating the energetic cost of shuttling between microclimates. The goal of the lab experiments was to answer two questions. First, how does body condition and feeding status change thermal preference? Second, how does body condition and the relative costs of thermoregulation influence thermoregulatory behavior? I hypothesized that if lowered body condition resulted in a greater net cost of thermoregulation, that lizards will decrease thermoregulation and let body temperatures conform with that of their environment. Conversely, if lower body condition resulted in a greater net benefit of thermoregulation, I expect that lizards will increase thermoregulation.

Methods

Experimental Design

I collected male *Sceloporus jarrovii* lizards in the Chiricahua Mountains of Arizona (1500-2500 m). Lizards were transported to a laboratory at Arizona State University, where they were weighed and toe-clipped for identification. While in the lab, lizards were individually housed in plastic terraria (46 × 30 × 17 cm) in between measurements. Terraria were stored in incubators (DR-36VL; Percival Scientific, Perry, Iowa, USA) programmed on a diel cycle, with daytime temperatures approximating the species' known preferred temperature (33°C, Rusch and Angilletta 2017), and night time temperatures 10°C cooler. All methods were approved by the Arizona State University Institutional Animal Care and Use Committee (protocol 19-1718R), US Forest Service (permit # SUP-2105/2167), and a Scientific Collecting License from Arizona Game and Fish Department (# SP407021).

I quantified the thermal preference of each lizard in a thermal gradient within five days of capture. After which, lizards were randomly assigned to one of two treatments: 1) food-restricted treatment in which lizards were fasted, and 2) a fed treatment, in which lizards were fed adult crickets (*Acheta domestica*) coated with a vitamin powder (Rep-Cal, Los Gatos, CA, USA) every other day. All lizards were given water and were weighed daily. Lizards were kept in their respective treatment groups for a similar amount of time as in the following arena experiment (10 days; 2-8% mass loss in food restricted treatment group), and were then randomly assigned to be either be fed or fasted immediately before re-measuring thermal preference. Lizards that were fed were offered five adult crickets (*Acheta domestica*) coated with a vitamin powder (Rep-Cal, Los Gatos, CA, USA) 15 minutes prior to being transferred to the thermal gradient. An observer checked each lizard to ensure that all had consumed at least one cricket prior to data collection. After each lizard's thermal preference was quantified (protocol described below), lizards were returned to their terreraria and given two days to allow food consumed to be passed. Then, lizards were flipped to the opposite fed/fasted group and thermal preference was again quantified for a third time.

To determine how body condition and the relative costs of thermoregulation affect thermal preference, I manipulated the energetic cost of thermoregulation in a thermal gradient (Fig 2.4). The "costly" treatment was created by suspending a heat lamp over the longituidnal sides of a rectangular gradient. Each heat lamp was connected to a timer, programmed to turn on for 15 minutes, and remain off for 10 minutes prior to turning back on. This resulted in a gradient where one heat lamp would be on for 10 minutes, then both heat lamps would be on together for 5 minutes, repeating this throughout the trial. The resultant gradient had preferred temperatures available continuously throughout the trial. The thermal range in the "costly" gradient spanned 20°- 36°C. However, a lizard would be forced to constantly shuttle between the illuminated/deluminated heat lamps to attain preferred temperatures. All lizards were fed in the 15 minutes prior to data collection. As during previous thermal preference trials, data were collected using a thermocouple inserted into the lizard's cloaca that recorded body temperatures 2 minutes. Each trial lasted 3 hours (1 hour acclimation; 2 hours data collection). I kept the lizards in their same body condition treatment groups (food-restricted or fed) that were randomly assigned at the beginning of the experiment. All lizards had thermoregulation quantified in both a costly thermal gradient and a non-costly thermal gradient (the latter being identical to gradients used to measure preferred body temperature, described above; N = 31). The order of trials was randomized. Lizards were given 4 days between trials. I fed all lizards five crickets prior to data collection in both "costly" and"non-costly" gradients. Lizards with low body condition may have more to gain energetically from thermoregulating while foraging or digesting, especially when predation is low. I predicted that control lizards would decrease thermoregulation in the "costly" gradient, but that lizards in the low body condition treatment group would maintain relatively high levels of thermoregulation regardless of the costs.

Thermal preference

The preferred body temperatures of each lizard (N = 31) were measured within two days of returning from the field. I used laboratory thermal gradients to quantify each individual's preferred temperatures (Bennett and Johnalder 1984, Bauwens et al. 1995). Gradients were built from rectangular plastic bins (0.9 m long x 0.4 m wide x 0.3 m deep), with 250 W heat bulbs suspended over one end of each bin. The thermal range in the gradient spanned 20°- 40°C. To record body temperatures, I inserted a Type T thermocouple into each individual's cloaca and fixed it in place with a small portion of medical tape (Neel and McBrayer 2018). I placed individuals in the gradient for one hour prior to the start of each trial to acclimate them to the unfamiliar conditions. I then measured internal body temperatures every 2 minutes for one hour using a MadgeTech

OctTCTemp -200V2 data logger (Warner, New Hampshire, USA). I decomposed the body temperature data for each individual into several different thermoregulatory traits, including the mean, minimum, maximum, standard deviation, and interquartile range (middle 50%) of temperatures selected in the gradient. Average preferred temperatures (33.7 ± 1.5 °C) align with previously published preferred temperatures for the species (~33-34°C), suggesting our methods are appropriate and able to be replicated (Schuler et al. 2011, Rusch and Angilletta 2017).

Body Condition

Body condition was calculated using three common indices, based on relationships between body mass and length. For the first index, I divided a lizard's mass by its snout-vent length (SVL). For the second index (R_i), I calculated the residual of log-transformed mass after regression onto log-transformed SVL. Regressions were performed separately for each sex. For the third index (M_i), I used the following standard equation:

$$M_i = M \times (SVL_0/SVL)^{b_{SMA}} \qquad [2.1]$$

Where M and SVL are the body mass and the snout-vent length of the individual. SVL_0 is the mean snout-vent length of the population, and b_{SMA} is the standardized major axis slope from the ordinary least squares (OLS) regression of log-transformed body mass on log-transformed SVL divided by Pearson's correlation coefficient (Peig and Green 2009, Warner et al. 2016).

Statistical Analysis

I conducted all statistical analyses using the *nlme* (Pinheiro et al. 2012) and *MuMIn* libraries (Barton 2010) in R statistical software (version 4.2.2; R Core Team, 2022). I used generalized additive mixed modeling (GAMM) to detect patterns in body temperatures selected in lab-based thermal gradients. To obtain a single variable that described an animal's body condition, I used a PCA to generate a linear combination of three body condition indices. The three body condition indices were calculated by: 1) dividing an animal's mass by its weight, 2) calculating ordinary least squares (OLS) regressions of log-transformed body mass on log-transformed snout-vent length (SVL), and 3) scaled mass index was calculated by solving equation 2.1. I then used GAMM to estimate the effects of the first principle component, feeding status, and gradient type (i.e., non-costly/control or costly) on body temperatures selected in thermal gradiens. I included individual as a random factor.

After fitting the statistical models, I used multimodel averaging to estimate the most probable parameters of each model. Multimodel averaging is related to a model-selection approach, where one uses Akaike's Information Criterion (AIC) or a similar index to rank models on their likelihoods of describing the data (Burnham 1998). However, when there is uncertainty about the best model, using a model-selection approach can bias parameter estimates (Harrison et al. 2018). I accounted for this uncertainty by considering all probable models as opposed to one model with less than 100% likelihood, using multimodel averaging. I weighted each model's parameter estimates by that model's likelihood of describing the data, and then averaged the weighted paramesters across all probable models to estimate the magnitude of the effects.

I used the *dredge* function to fit a set of models representing all possible subsets of the fixed factors and their interactions. I then calculaed the Akaike weight for each model, which is the probability that the model describes the data better than the other models. I used the Akaike weights to compute a weighted average of each parameter, and averaged the weighted parameters across the most probable models to determine the most probable relationship between $PC1_{BCI}$, feeding status, and gradient type (i.e., non-costly/control or costly) and the body temperatures selected in lab-based thermal gradients. I plotted the most likely models over raw data to interpret effect sizes, model fit, and biological relevance (Fig 2.5).

Results

The principle component analysis of body condition revealed that the three indices loaded in the same direction and similar magnitude, suggesting that all indices covary positively. The first principle component ($PC1_{BCI}$) captured 94% of the variation in the three indices of body condition (Tables 2.3 and 2.4).

Neither the body condition nor feeding status of lizards (i.e., whether a lizard was fed or fasted immediately prior to data collection) explained variation in thermal preference in a standard thermal gradient (Table 2.1). I was interested in seeing if the relationship between body condition and body temperatures selected in the gradient differed when the relative costs of thermoregulation were elevated. Lizards selected body temperatures within their preferred range (IQR = 33.8 – 36.1°C) only when the simulated costs of thermoregulation were low (i.e., in the ‘non-costly’ gradient; Figs 2.2 and 2.5). When lizards were forced to continuously shuttle to maintain a body temperature within their preferred range (i.e., in the ‘costly’ gradient; Fig 2.4), all lizards decreased thermoregulation, regardless of body condition (Table 2.2; Figs 2.2 and 2.5). The first principal component generated from the three body condition indices ($PC1_{BCI}$) captured 94% of the cumulative variation in the three body condition indices (Table 2.4).

Discussion

Animals are expected to optimize performance according to the pressures and constraints posed by both their environment, and their physiological state. Indeed, the weight of abiotic constraints in shaping behavioral thermoregulation is well documented, especially in lizards (Huey 1974b, Huey and Slatkin 1976, Herczeg et al. 2006, Sears and Angilletta 2011, 2015, Sears et al. 2016, Basson et al. 2017). However, the impacts of other factors, such as competition (Žagar et al. 2015, Rusch and Angilletta 2017), predation (Amo et al. 2007b), and physiological state (Herczeg et al. 2008), remain less understood.

Ectothermic animals stand to gain the most energetically when processing food at optimal body temperatures (Huey 1982, Waldschmidt et al. 1987). Given the deaccelerating relationship between energy assimilation and the time spent at the optimal body temperature (Levy et al. 2017), animals should be motivated to thermoregulate immediately after eating. I hypothesized that lizards with low body condition might have an inherently greater utility for energy, and may therefore benefit more from increasing thermoregulation while processing food, regardless of the costs (Fig 2.1). However, I found that all lizards decreased thermoregulation in the lab similarly when simulated costs were higher, regardless of body condition (Table 2.2; Figs 2.2 and 2.5). Our results suggest that poor body condition may not increase energy gain enough to offset the cost of thermoregulation, or alternatively, poor body condition may not translate to consequential effects on fitness.

Many animals have been found to decrease preferred temperatures when fasted, versus when fed (Slip and Shine 1988, Lutterschmidt and Reinert 1990, Blouin-Demers and Weatherhead 2001, Gvoždík 2003, Minoli and Lazzari 2003, Tsai and Tu 2005, Wallman and Bennett 2006). However, I observed no difference in thermal preference between fed and fasted individuals (Table 2.1). Animals that decrease thermal preference when fasted may be rapidly responding to changes in their thermal sensitivity of performance, with thermal optima shifting to lower body temperatures as the rate of feeding decreases (Elliott 1982). Our study system, *Sceloporus jarrovii,* spans an impressive ~1500 m altitudinal gradient, and subsequently experiences high thermal variation across their range. A recent niche modelling study found that the distribution of *S. jarrovii* is limited to higher elevations not because of the high summer temperatures in the lowlands, but surprisingly because of the scarcity of days below freezing temperatures in the winter (Wiens et al. 2019). Perhaps the high thermal variation experienced by *S. jarrovii* in their montane environments leads this cold-adapted species to possess a wide thermal performance breadth (Huey and Stevenson 1979b), which would further reduce the benefits of increased thermoregulation in a costly environment (Huey and Slatkin 1976). Integrating both abiotic, and biotic constraints, into optimal models of thermoregulation will be critical in accurately predicting how novel variation in climates and food availability will impact future performance.

Climate change affects the body conditions of organisms as well as their thermal environments. As temperatures warm, many animals will be forced to restrict activity to times when low body temperatures are feasible (Sinervo et al. 2010, Sunday et al. 2014, Gunderson and Leal 2016, Huey and Kingsolver 2019), which will likely reduce foraging activity. Other organisms will exhibit range shifts to reduce novel variation in their thermal environment (Lavergne et al. 2010, Chen et al. 2011, Pardi and Smith 2012, Corlett and Westcott 2013), which may also disrupt food webs (Moya-Laraño et al. 2012, du Pontavice et al. 2020, Barbour and Gibert 2021) and contribute to food shortages (Coley 1998, Laws 2017). When food is scarce, animals likely experience periods of low body conditions (Kitaysky et al. 1999), which should influence how they use stored energy and attempt to acquire more (Cooper et al. 2015). Moreover, ectothermic animals experience higher metabolic demands at warmer body temperatures, compounding the impacts of potential reduced activity times and food scarcity (Huey and Kingsolver 2019).

In natural environments, higher mortality risk may shift the optimal level of thermoregulation towards thermoconformity for an animal with poor body condition. However, in lab settings that are free from predators, the relative costs and benefits shaping thermoregulatory decisions may be similar for all animals, regardless of body condition. To predict thermoregulation and subsequent performance consequences in changing environments, we need to understand the complex interactions between the environment, and physiological factors, such as an animal's body condition, to estimate the diverse costs that shape the optimal thermoregulatory strategy in natural populations.

Table 2.1. A ranking of mean thermal preference models based on the likelihood of being the best model. For each model, I provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed. Feeding status (i.e., whether lizard was fed or fasted during trial) nor body condition influenced thermal preference. The null model was therefore most likely. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	AIC_c	ΔAIC_c	*Weight*
1. null model	35	-885.5	1842.5	0.00	0.46
2. feeding status	36	-885.01	1843.5	1.04	0.27
3. $PC1_{BCI}$	36	-885.58	1844.7	2.18	0.15
4. feeding status + $PC1_{BCI}$	37	-885.00	1845.6	3.11	0.10
5. feeding status + $PC1_{BCI}$ + (feeding status · $PC1_{BCI}$)	38	-885.60	1848.9	6.39	0.02

Table 2.2. A ranking of mean thermal preference models based on the likelihood of being the best model. For each model, I provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed. The 'cost' of thermoregulation (i.e., gradient type was 'costly' or 'non-costly') shaped thermal preference. Individual mean thermal preference, body condition, and all interaction effects were not included in the most likely model. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	*AIC_c*	*ΔAIC_c*	*Weight*
1. cost	66	-2038.5	4211.5	0.00	0.38
2. cost + individual T_{pref}	67	-2038.2	4212.9	1.40	0.19
3. cost + individual T_{pref} + (cost · individual T_{pref})	68	-2037.6	4213.9	2.41	0.11
4. $PC1_{BCI}$ + cost + ($PC1_{BCI}$ · cost)	68	-2037.9	4214.4	2.92	0.09
5. $PC1_{BCI}$ + cost	67	-2039.3	4215.1	3.56	0.06
6. $PC1_{BCI}$ + cost + individual T_{pref} + ($PC1_{BCI}$ · cost)	69	-2037.5	4215.8	4.26	0.04
7. $PC1_{BCI}$ + cost + individual T_{pref}	68	-2038.9	4216.4	4.88	0.03
8. $PC1_{BCI}$ + cost + individual T_{pref} + ($PC1_{BCI}$ · cost) + (cost · individual T_{pref})	70	-2036.9	4216.6	5.12	0.03
9. $PC1_{BCI}$ + cost + individual T_{pref} + (cost · individual T_{pref})	69	-2039.0	4217.4	5.89	0.02
10. $PC1_{BCI}$ + cost + individual T_{pref} + ($PC1_{BCI}$ · cost) + ($PC1_{BCI}$ · individual T_{pref})	70	-2037.7	4218.2	6.68	0.01

Table 2.3. Factor loadings describing how much each of our three body condition indices contributes to the principal components. I calculated three body condition indices by: 1) dividing an animal's mass by its length, 2) calculating ordinary least squares (OLS) regressions of log-transformed body mass on log-transformed snout-vent length (SVL), and 3) scaled mass index was calculated by solving equation 2.1.

Body condition index	*Comp 1*	*Comp 2*	*Comp 3*
Mass (g) / SVL (mm)	0.5600356	0.8284473	0.005935925
OLS regression	0.5856294	-0.4009368	0.704477035
Scaled mass index, M_i	0.5860020	-0.3910560	-0.709701960

Table 2.4. The eigen values and proportions of variance explained by body condition principal components.

	Comp 1	*Comp 2*	*Comp 3*
Eigen value	2.8370334	0.16055532	0.002411232
Standard deviation	1.6843496	0.40069356	0.049104294
Proportion of variance	0.9456778	0.05351844	0.000803743
Cumulative proportion	0.9456778	0.99919626	1.000000000

Fig 2.1. A graphical model describing the asymptotic relationship between an animal's stored energy and survival probability. An animal with little stored energy has a high utility for additional energy derived from foraging and thermoregulation, whereas an animal with more stored energy has a low utility for additional energy. In this way, the amount of energy an animal has stored shapes the relative payoff for thermoregulatory behavior.

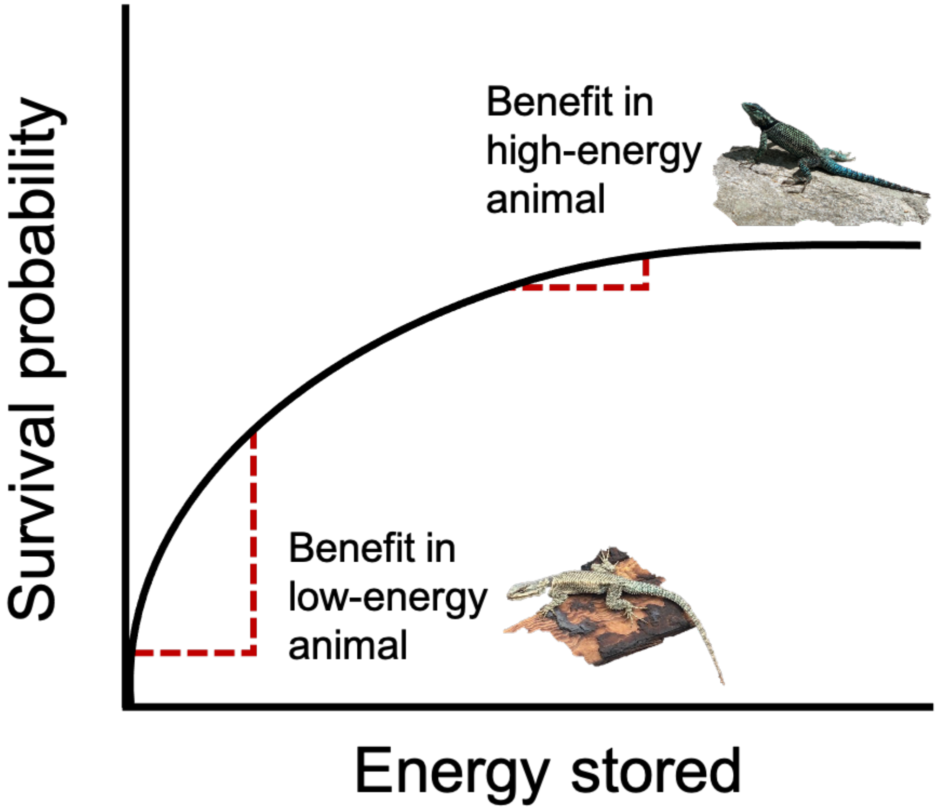


Fig 2.2. Body temperatures selected in a thermal gradient in the lab were dependent on the simulated costs of thermoregulation, but not a lizard's body condition. Observed data are shown for lizards (N = 31) in the "costly" and "non-costly" or control gradient. Available operative temperatures spanned ~22 – 36 °C in the "costly" gradient and ~22 – 40 °C in the "non-costly" gradient. The red bars show the upper range of available temperatures in each gradient. The grey shaded area shows the middle 50% of preferred body temperatures.

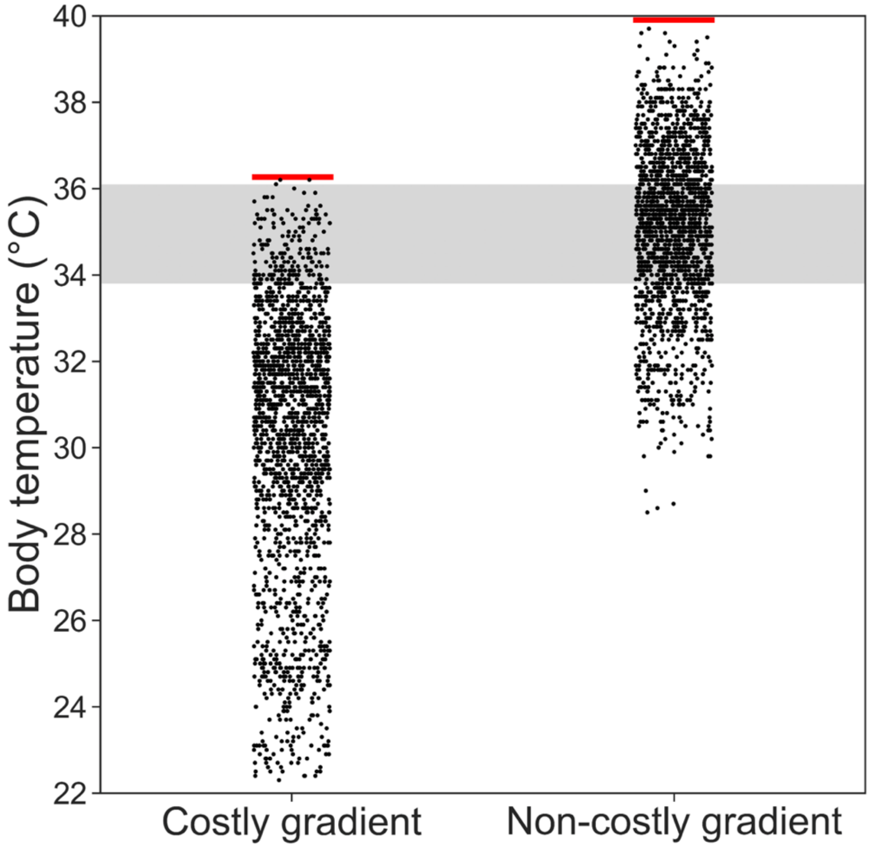


Fig 2.3. Neither body condition, nor feeding status, significantly shaped body temperatures selected in a thermal gradient in the lab. Observed data are shown for lizards (N = 31) that were either fed (blue) or fasted (orange) immediately prior to data collection. Body temperatures selected are plotted each lizard's body condition, using the simplest body condition index—mass divided by length. Available operative temperatures spanned ~22 – 40 °C in the thermal gradient.

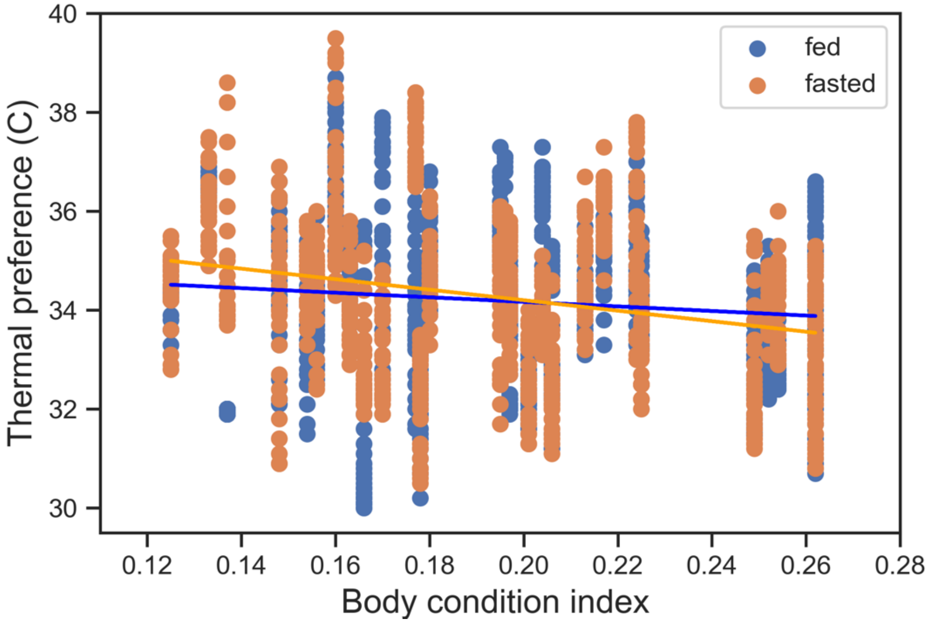


Fig 2.4. Schematic showing design of the costly thermal gradient. Heat lamps were connected to timers programmed to turn on/off at set intervals, forcing lizards to shuttle continuously to maintain a temperature within the known preferred range.

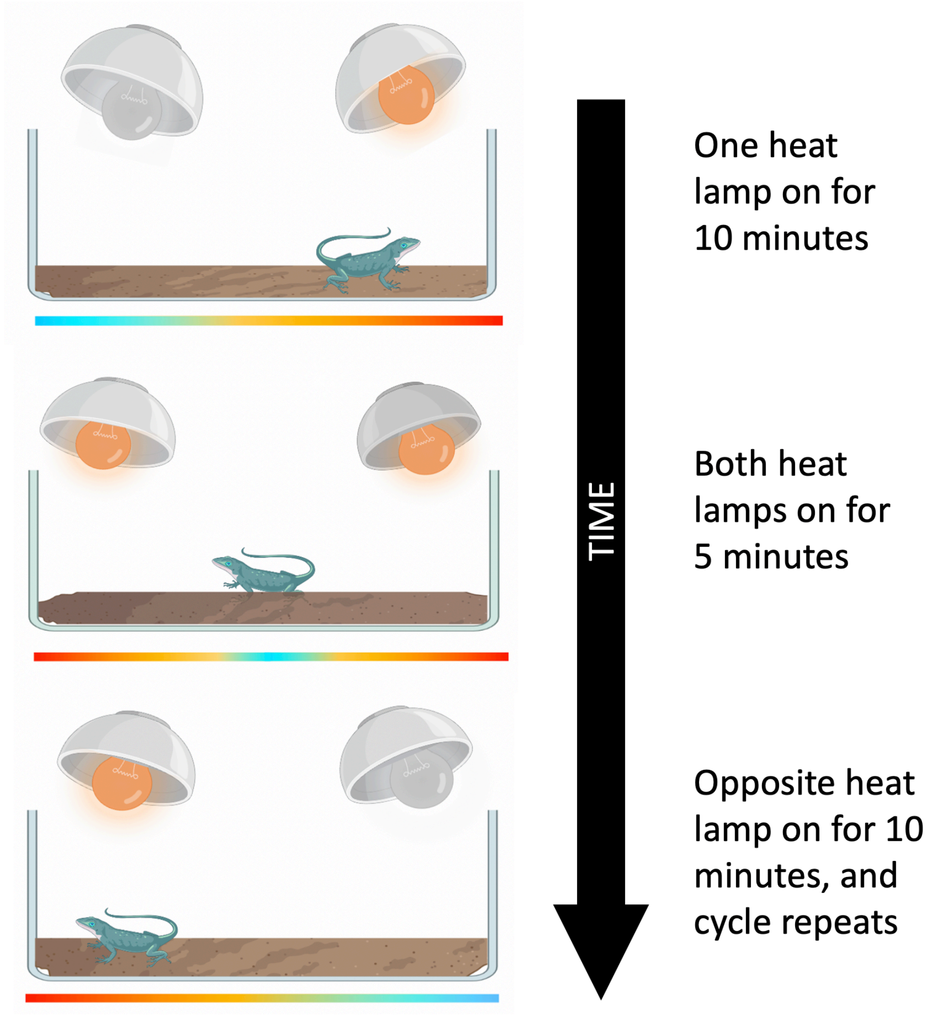
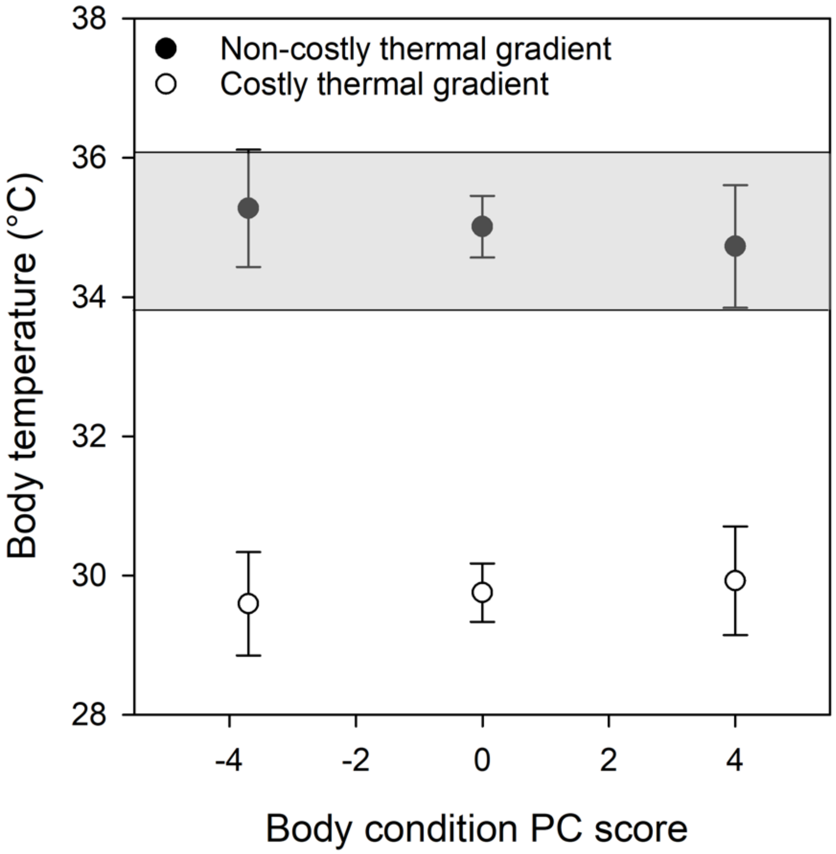


Fig 2.5. Body temperatures selected in a thermal gradient in the lab were dependent on the simulated costs of thermoregulation, but not a lizard's body condition. Symbol and error bars show the most likely relationship between body temperatures, body condition, and the simulated costs of thermoregulation, calculated from multimodel averaging. The grey shaded area shows the middle 50% of preferred body temperatures. As the body condition PC score increases, so does animal body condition. Three body condition indices were calculated by: 1) dividing an animal's mass by its weight, 2) calculating ordinary least squares (OLS) regressions of log-transformed body mass on log-transformed snout-vent length (SVL), and 3) scaled mass index was calculated by solving equation 2.1. These indices were loaded on the principal component. The body condition PC1 captured 94% of the variation in body condition.



CHAPTER 3

THE IMPACTS OF BODY CONDITION ON THE THERMOREGULATORY BEHAVIOR OF A MONTANE LIZARD

Abstract

Thermoregulatory decisions are shaped by numerous factors, including interactions between an animal's physiological state and their environment. According to classic optimality models describing thermoregulation, an animal should thermoregulate only when the energetic costs outweigh the benefits. However, estimating the associated costs is difficult, because physiological state may influence the relative mortality risk associated with thermoregulation (via variation in vulnerability to predation). I investigated the relationship between body condition and thermoregulation in Yarrow's spiny lizards (*Sceloporus jarrovii*). I manipulated body condition and habitat heterogeneity and quantified thermoregulation in outdoor arenas. I hypothesized that if lowered body condition resulted in a greater net cost of thermoregulation, that lizards will decrease thermoregulation and let body temperatures conform with that of their environment. Indeed, when lizards were observed in an outdoor thermal arena, individuals with lower body condition decreased thermoregulation and had a lower mean body temperature. Surprisingly, I did not observe a clear effect of spatial heterogeneity on thermoregulation, regardless of body condition. Body condition and the optimal level of thermoregulation are likely linked as both directly impact energy availability and usage. Animals with poor body condition may face greater survivorship costs when thermoregulating due to increased vulnerability to predation. To understand how an animal's physiological state may shape the optimal level of thermoregulation, future

work must consider the diverse ecological and physiological interactions that can constrain behavior in natural environments.

Introduction

Thermoregulation should only be favored in environments where the relative benefits of thermoregulating outweigh the costs (Huey and Slatkin 1976). Accurately quantifying these costs and benefits is a difficult, as it requires an understanding of the physiological state of the organism and its interactions with the environment, among other factors. Energetic costs and benefits are particularly important, as they can have a significant impact on survivorship and fecundity. Organisms perform best within a narrow range of body temperatures (Huey 1982). When the energetic costs of thermoregulation, such as movement costs when searching for preferred microclimates, outweigh the physiological benefits of maintaining a preferred body temperature, it may be advantageous for the organism to thermoregulate imperfectly to maximize fitness. On the other hand, if the net energetic benefit of thermoregulation outweighs the energetic cost and mortality risk, perfect thermoregulation should be favored. Accurately determining the optimal degree of thermoregulation is essential for understanding the trade-offs between costs and benefits and predicting how thermoregulatory behaviors may evolve in different environments.

An animal's available stored energy levels should play a crucial role in determining their decisions pertaining to energy gain. Rates of feeding and digestion are maximized within a narrow range of temperatures (Waldschmidt et al. 1986, McConnachie and Alexander 2004, Fontaine et al. 2018, Volkoff and Rønnestad 2020).

Therefore, an energy-deficient animal should maintain a body temperature that promotes the rate of energy gain, even if it comes at a greater cost of thermoregulation. However, animals with little stored energy may experience reduced muscle performance, making them slower and more vulnerable to predators. As a result, thermoregulatory decisions may be influenced by the risk of predation and food availability. In environments with high food availability, investing in thermoregulation may lead to a greater return on investment, whereas in low food availability environments, it may yield little benefit. Therefore, it is important to understand the role of body condition in shaping thermoregulatory decisions.

I manipulated body condition and habitat heterogeneity and quantified thermoregulation in *Sceloporus jarrovii* lizards in outdoor arenas. I hypothesized that if lowered body condition resulted in a greater net cost of thermoregulation, that lizards will decrease thermoregulation and let body temperatures conform with that of their environment. Conversely, if lower body condition resulted in a greater net benefit of thermoregulation, I expect that lizards will increase thermoregulation.

Methods

Arena Experiment Design

In October of 2020 and March of 2021, I collected male *Sceloporus jarrovii* lizards (N =22) in the Chiricahua Mountains of Arizona (1500-2500 m). Lizards were transported to a laboratory at Arizona State University, where they were weighed and toe-clipped for identification. While in the lab, lizards were individually housed in plastic terraria (46 × 30 × 17 cm) in between measurements. Terraria were stored in incubators (DR-36VL;

Percival Scientific, Perry, Iowa, USA) programmed on a diel cycle, with daytime temperatures approximating the species' known preferred temperature (33°C, Rusch and Angilletta 2017), and night time temperatures 10°C cooler. All methods were approved by the Arizona State University Institutional Animal Care and Use Committee (protocol 19-1718R), US Forest Service (permit # SUP-2105/2167), and a Scientific Collecting License from Arizona Game and Fish Department (# SP407021).

Outdoor arenas located ~25 miles east of main campus, at ASU's polytechnic campus, were designed to quantify thermoregulation. There, six 83.5 m^2 arenas were prepped with 30% shade cloth covering the entire arenas, and one of two spatial distributions of 85% shade cloth creating distinct levels of heterogeneity (Figure S3). The low-heterogeneity arenas had shaded microclimates aggregated in one corner of the arena. The low-heterogeneity arenas were created using one piece of shade cloth (5.5 × 5.5 m) suspended over the corner of the arena. The high-heterogeneity arenas had shaded microclimates uniformly dispersed throughout the arena. The high-heterogeneity arenas were created using 16 patches of 1.4 × 1.4 m shade cloth (similar to methods described by Sears et al. 2016). Each arena had four shelters available that were placed in a uniform, grid-like pattern throughout each (Fig 3.3).

After measuring preferred temperatures in the lab using the protocol described above, lizards were randomly assigned to one of two treatments: 1) food-restricted treatment in which lizards were fasted, and 2) a fed treatment, in which lizards were fed adult crickets (Acheta domestica) coated with a vitamin powder (Rep-Cal, Los Gatos, CA, USA) every other day. All lizards were given water and were weighed daily. Lizards in the food-restricted treatment group were not fed until the day they were transferred to arenas. The sampled lizards (N = 22) varied in their SVL (85.4 ± 2.8 mm) and body mass (19.0 ± 2.3 g) at the time of capture in the field. By manipulating food availability in the lab, lizard masses decreased in the treatment group (18.2 ± 2.6 g) and increased in the control group (20.8 ± 2.8 g). Lizards were kept in treatment groups for 7-11 days, then offered five crickets and immediately transferred to outdoor arenas. Ihad six arenas, therefore I collected data from six animals per day in the arenas. During this portion of the experiment, each day, three randomly selected control group lizards were sampled in the arenas, and three food restricted treatment group lizards were sampled. The three food restricted treatment group lizards were selected based on their body condition. The individuals that had experienced the largest decrease in body condition were selected from the food restricted treatment group. Lizards in the treatment group lost 2-8% body mass prior to being sampled in the arenas.

Lizards were kept in arenas from 10:00 to 17:00, which aligns with observed activity times at the tail ends of their activity season in March – April and October – November (Neel per obs). Given our sample size, I needed a five-day window to observe all lizards in the arenas. Once a lizard was returned to the lab from the arenas, it was immediately switched to the other treatment, and the experiment was replicated. I predicted that all lizards would thermoregulate more accurately in the high-heterogeneity arenas given the lower energetic costs of thermoregulation. I furthermore predicted that lizards with poorer body condition would increase thermoregulation regardless of arena type if the benefits of digesting food at optimal temperatures outweighed the energetic movement costs and potential predation risk associated with thermoregulation.

Quantifying thermoregulation in arenas

Body temperatures selected in arenas were measured using a temperature logger (mass = 1.6 ± 0.07 g), surgically implanted in the abdominal cavity of each lizard. I miniaturized DS1921 iButtons (Maxim Integrated, San Jose, CA) following protocol described by Robert and Thompson (2003). Each logger was programmed to record temperature at a 15-min interval for the duration of the experiment. To waterproof the loggers, they were first coated with a plastic sealant (Plasti Dip, Plasti Dip International, Blaine, MN, USA), and then with paraffin wax (Gulf Wax, Kalton, Ohio, USA). Surgical procedures followed those of Sears et al. (2016) and Rusch and Angilletta (2017). In a pilot experiment, surgically implantating a temperature logger did not effect the body temperatures of lizards (Fig 3.4).

To quantify thermoregulation, I needed to estimate operative temperatures available in the arenas during each trial. Hollow copper models, electroformed to match the size of the focal animal would typically be used to measure operative temperatures. However, since competition impacts preferred temperatures in our study system (Rusch and Angilletta 2017), I did not want to place lizard models in the arenas during the experiment. Instead, I placed temperature loggers (DS1921 iButtons; Maxim Integrated, San Jose, CA) under each combination of shade cloth in the arenas. The loggers were painted white to alter their reflective properties. I also placed two copper electroformed lizard models under each shade level (30% and 85%), each equipped with a temperature logger inside (DS1921 iButtons; Maxim Integrated, San Jose, CA). I also placed a temperature logger ~10 cm from each electroformed lizard model (Figure S5) and regressed the electroformed lizard model temperature against the logger temperature to estimate operative temperatures under all combinations of shade. Lizard body temperatures selected in arenas will be compared to preferred temperatures and operative temperatures under each shade level to quantify differences in thermoregulation and activity, similar to methods described by Davis et al. (2008).

Statistical analyses

I conducted all statistical analyses using the *nlme* (Pinheiro et al. 2012) and *MuMIn* libraries (Barton 2010) in R statistical software (version 4.2.2; R Core Team, 2022). I used generalized additive mixed modeling (GAMM) to detect patterns in body temperatures selected in arenas. To obtain a single variable that described the thermal environment of the arenas at each point in time, I used a principal component analysis (PCA) to generate a linear combination of two highly correlated variables: maximum operative temperature and the range of available operative temperatures. To obtain a single variable that described an animal's body condition, I used a PCA to generate a linear combination of three body condition indices. The three body condition indices were calculated by: 1) dividing an animal's mass by its weight, 2) calculating ordinary least squares (OLS) regressions of log-transformed body mass on log-transformed snout-vent length (SVL), and 3) scaled mass index was calculated by solving equation 2.1. I then used GAMM to estimate the effects $PC1_{ENV}$, $PC1_{BCI}$, and arena type (low- or high-heterogeneity) on body temperatures selected in arenas. I included individual as a random factor. I added a correlation structure to describe variation in body temperature within and among days.

After fitting the statistical models, I used multimodel averaging to estimate the most probable parameters of each model. Multimodel averaging is related to a model-selection approach, where one uses Akaike's Information Criterion (AIC) or a similar index to rank models on their likelihoods of describing the data (Burnham 1998). However, when there is uncertainty about the best model, using a model-selection approach can bias parameter estimates (Harrison et al. 2018). I accounted for this uncertainty by considering all probable models as opposed to one model with less than 100% likelihood, using multimodel averaging. I weighted each model's parameter estimates by that model's likelihood of describing the data, and then averaged the weighted paramesters across all probable models to estimate the magnitude of the effects. I used the *dredge* function to fit a set of models representing all possible subsets of the fixed factors and their interactions. I then calculaed the Akaike weight for each model, which is the probability that the model describes the data better than the other models. I used the Akaike weights to compute a weighted average of each parameter, and averaged the weighted parameters across the most probable models to determine the most probable relationship between $PC1_{ENV,}$ $PC1_{BCI}$, arena type (e.g., low- or high-heterogeneity), and the body temperatures selected in the arenas. I plotted the most likely models over raw data to interpret effect sizes, model fit, and biological relevance (Figs 3.1-3.2).

Results

The principle component analyses yielded informative principles components for our subsequent analysis. For the PCA of environmental temperatures, the two variables—maximum operative temperature and the range of operative temperatures—loaded in the same direction and similar magnitude, indicating that the variables were positively correlated. The first principle component ($PC1_{Env}$) captured 95% of the variation in environment temperatures (see Tables 3.2 and 3.3). For the PCA of body condition indices, the three indices loaded in the same direction and similar magnitude, indicating that the variables were positively correlated. The first principle component ($PC1_{BCI}$) captured 93% of the variation in body condition (see Tables 3.4 and 3.5).

Both environmental temperature and body condition determined the body temperature selected in the arenas. The most likely model of body temperature included the first principal component of environmental temperature and the first principal component of body condition (see Table 3.3). A lizard in poorer condition selected a lower mean body temperature (Figs 3.1 and 3.2). However, the spatial distribution of microclimates, determined by the distribution of shade patches in the arena, did not shape selected body temperatures (Table 3.3). Animal body conditions decreased by 12.0 – 12.8% on average between the control and experimental treatment groups. On average, lizards with low body condition ($PC1_{BCI} = -3.7$) selected body temperatures that were 1.2°C cooler than did lizards with high body condition ($PC1_{BCI} = 4$). Although, regardless of body condition, all lizards thermoregulated to temperatures within the preferred range (IQR = 33.8 – 36.1°C; Fig 3.1).

Discussion

Ectotherms must achieve preferred body temperatures during activity to optimize physiological performance. However, many abiotic and biotic factors interact to influence the relative costs and benefits associated with thermoregulation (Huey and Slatkin 1976). The relationship between habitat heterogeneity and reduced costs of thermoregulation in lizards is well established (Sears and Angilletta 2011, Goller et al. 2014, Sears and Angilletta 2015, Sears et al. 2016, Basson et al. 2017, Neel et al. 2021). Yet, our data interestingly did not support this well-documented phenomenon (Table 3; Figure 2). It is possible that low sample sizes ('low-heterogeneity' spatial distribution, N = 10 lizards; 'high-heterogeneity' spatial distribution, N = 12 lizards) prevented us from observing this effect. Or alternatively, perhaps the relative costs of thermoregulation were similarly low in both high- and low-heterogeneity arenas due to the lack of predators or competing lizards in the arenas (Rusch and Angilletta 2017), or because available operative temperatures in the arenas were similar, or slightly above, preferred temperatures during the experiment which may have reduced pressure to actively shuttle to maintain a preferred body temperature. Congruent with classic cost-benefit models, if preferred microclimates could be easily reached in both high- and low-heterogeneity arenas, active thermoregulation should be favored by all lizards (Huey and Slatkin 1976, Herczeg et al. 2006).

Physiological factors, such as animal body condition, are also important to consider when studying thermoregulation. I found that lizards in poor condition had body temperatures that were 1.2°C cooler than control lizards in semi-natural, outdoor arenas (Figure 2). Body condition and the optimal level of thermoregulation are likely linked as both directly impact energy availability and usage, although the causal relationship remains under studied in many animals. In Southern Yellow-billed Hornbills (*Tockus leucomelas*), high environmental temperatures lead to increased rates of evaporative cooling which decreases animal body condition via a reduction in foraging efficiency (van de Ven et al. 2019). When environmental temperatures approach an animal's lethal limits, there is inevitably strong selective pressure to increase thermoregulation, regardless of costs, to avoid overheating (Vickers et al. 2011, Neel and McBrayer 2018). However, under benign environmental conditions, where thermoregulation isn't required to avoid death, low energy stores may lower the optimal level of thermoregulation if there is greater pressure to conserve energy. Decreasing thermoregulatory efforts may conserve energy via two pathways: reduced energetic expenditure on shuttling between microclimates, and maintaining a lower metabolic rate. Shuttling between sunny and shaded microclimates comes at a high energetic, and also survivorship cost via increased predation (Huey 1974a, Huey and Slatkin 1976, Martín and López 1999, Downes 2001, Sears et al. 2016). Additionally, reduced activity levels and increased time spent in cool refuges would lead to lower oxygen utilization (Bennett and Nagy 1977, Bennett 1978, Kooijman 2000). Indeed, many animals have been shown to decrease metabolic rates during periods of low food availability (O'Connor et al. 2000, Auer et al. 2015), or when conserving energy for reproduction (Sparling et al. 2006). Furthermore, animals in an energy-deficient state may be especially susceptible to predation (Murray 2002), however, findings on this topic are mixed (Wirsing et al. 2002, Amo et al. 2007a).

Lizards with poorer body condition selected cooler body temperatures when thermoregulating in outdoor arenas (Table 3.1). However, in lab-based experiments, body condition did not impact the body temperatures lizards selected, regardless of the simulated costs of thermoregulation (Table 2.2). In the lab, animals do not experience all aspects of their environment. For example, in the lab, an animal does not experience predation or the pressure to forage since food is provided (depending on the logistics of the experiment). Furthermore, animals are typically housed individually, eliminating any inter- or intraspecific interactions that can influence behavioral decisions, like competition for territories or mates. Whereas, in an animal's natural environment, there are numerous uncontrollable physical and socio-environmental factors.

Any number of interacting factors could shape behavior observed in lab settings, as behavioral experiments are especially susceptible to influence from the environment in which they are performed (Calisi and Bentley 2009). Perhaps in the outdoor arenas, lizards with poor body condition were less active overall in response to the elevated predation risk, relative to in the lab. Indeed, our outdoor arenas were fully enclosed around the base but were open on top (Fig 3.3), allowing for any potential avian predators to swoop in during the experiment; in fact, I did lose one lizard during the arena experiment to a likely avian predator. Furthermore, *S. jarrovii* has been shown to decrease activity in response to avian predators (Rusch, unpublished data). Thermoregulatory activity likely increases the risk of being killed by a predator in natural environments. Moreover, an animal in an energy-deficient state may be worse at evading predators (Murray 2002, Wirsing et al. 2002). In natural environments, higher mortality risk may shift the optimal level of thermoregulation towards thermoconformity for an animal with poor body condition. However, in lab settings that are free from predators, the relative costs and benefits shaping thermoregulatory decisions may be similar for all animals, regardless of body condition. To predict thermoregulation and subsequent performance consequences in changing environments, we need to understand the complex interactions between the environment, and physiological factors, such as an animal's body condition, to estimate the diverse costs that shape the optimal thermoregulatory strategy in natural populations. Recent advances in biologging have greatly improved our ability to estimate thermoregulation in complex environments (Heithaus et al. 2006, Hays et al. 2007, Carfagno and Weatherhead 2008, Rutz and Hays 2009, Sequeira et al. 2021). Biologging technology should be used to investigate the interactions between animal body condition, predation, and thermoregulation in natural populations of free-moving animals. Future research should be conducted to determine whether body condition lowers the optimal level of thermoregulation in natural populations experiencing some level of predation risk.

Table 3.1. A ranking of mean body temperature models selected in arenas based on the likelihood of being the best model. For each model, I provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed. The most likely model included effects of a principal component of environmental temperatures ($PC1_{Env}$) and of lizard body condition ($PC1_{BCI}$). For body condition, I generated a PC score from three body condition indices. Each model also contained an intercept and a random term associated with individual lizards.

Model	*K*	*logLik*	*AIC$_c$*	*Δ AIC$_c$*	*Weight*
1. $PC1_{Env} + PC1_{BCI}$	10	-2196.5	4413.3	0.00	0.47
2. $PC1_{Env}$	8	-2199.1	4414.5	1.16	0.26
3. $PC1_{Env}$ + (patches · $PC1_{BCI}$)	10	-2198.3	4416.9	3.58	0.07
4. $PC1_{Env} + PC1_{BCI}$ + (patches · $PC1_{BCI}$)	12	-2196.5	4417.4	4.11	0.06
5. $PC1_{Env}$ + ($PC1_{Env}$ · patches) + $PC1_{BCI}$	12	-2196.5	4417.4	4.11	0.06
6. $PC1_{Env}$ + ($PC1_{Env}$ · patches)	10	-2199.1	4418.6	5.25	0.03
7. $PC1_{Env}$ + ($PC1_{Env}$ · patches) + ($PC1_{BCI}$ · patches)	12	-2198.3	4421.0	7.69	0.01

Table 3.2. Factor loadings describing how much the maximum operative temperature and range of operative temperatures contribute to the principal components. Operative temperatures were estimated using hollow, electroformed copper lizard models and thermal data loggers (Fig 3.4).

Environmental temperature variable	*Comp 1*	*Comp 2*
Maximum operative temperature	0.7071068	0.7071068
Range of operative temperatures	0.7071068	- 0.7071068

Table 3.3. The eigen values and proportions of variance explained by thermal environment principal components.

	Comp 1	*Comp 2*
Eigen value	1.9108503	0.08914964
Standard deviation	1.3823351	0.29857938
Proportion of variance	0.9554252	0.04457482
Cumulative proportion	0.9554252	0.99904453

Table 3.4. Factor loadings describing how much each of our three body condition indices contributes to the principal components. I calculated three body condition indices by: 1) dividing an animal's mass by its length, 2) calculating ordinary least squares (OLS) regressions of log-transformed body mass on log-transformed snout-vent length (SVL), and 3) scaled mass index was calculated by solving equation 2.1.

Body condition index	*Comp 1*	*Comp 2*	*Comp 3*
Mass (g) / SVL (mm)	0.5562454	0.8309754	0.008425525
OLS regression	0.5873064	-0.4002688	0.703460089
Scaled mass index, M_i	0.5879305	- 0.3863481	- 0.710684820

Table 3.5. The eigen values and proportions of variance explained by body condition principal components.

	Comp 1	*Comp 2*	*Comp 3*
Eigen value	2.8064808	0.19065275	0.002866395
Standard deviation	1.6752555	0.43663802	0.0535387268
Proportion of variance	0.9354936	0.06355092	0.0009554651
Cumulative proportion	0.9354936	0.99904453	1.0000000000

Fig 3.1. Body temperatures of lizards in outdoor arenas are plotted against a principal component of environmental temperatures ($PC1_{ENV}$). Lines denote the most likely relationship between body temperatures, $PC1_{ENV}$, and body condition, calculated from multimodel averaging. Observed data points for lizards in the experimental (open symbol) and control (closed symbol) body condition treatment groups are shown overlaid. Grey bar shows thermal preference range (mean ± se) measured in the lab. Body temperatures selected in outdoor arenas depended on animal body condition, with poorer body condition animals selecting lower body temperatures. As $PC1_{ENV}$ increases, so does the maximum operative temperature and the range of temperatures between sun and shade, which are the two variables that load on the principal component. $PC1_{ENV}$ captured 95% of the cumulative variation in the maximal and range of available operative temperatures in the arenas.

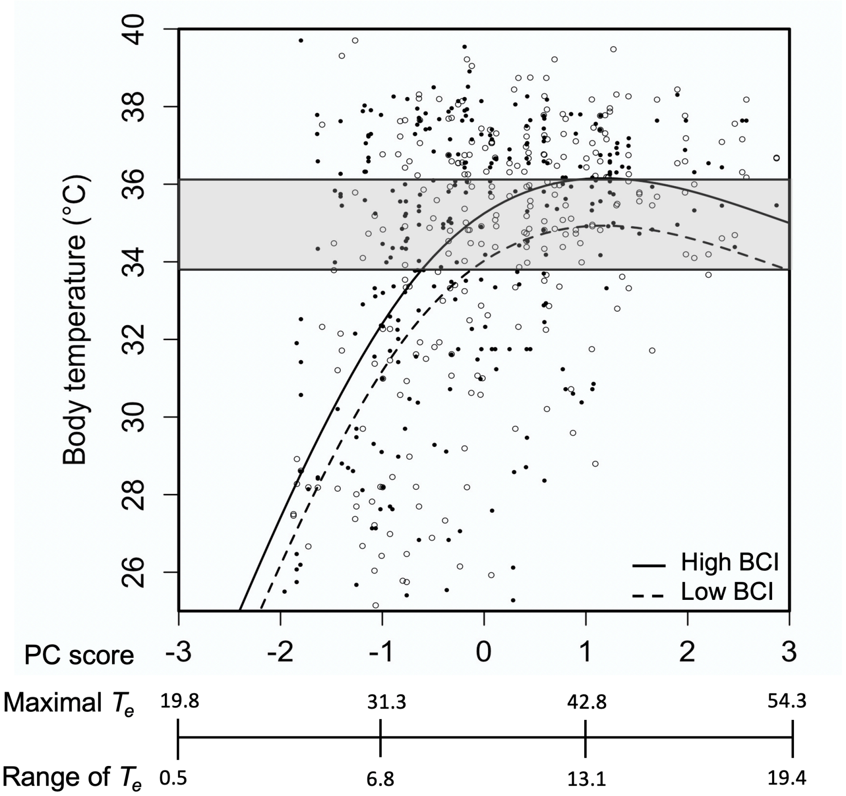


Fig 3.2. Body temperatures of lizards in outdoor arenas are plotted against a principal component of environmental temperatures ($PC1_{ENV}$) and a principal component of animal body condition ($PC1_{BCI}$). Area shows the most likely relationship between body temperatures, $PC1_{ENV}$, and $PC1_{BCI}$, calculated from multimodel averaging. Observed data points are shown overlaid. As $PC1_{ENV}$ increases, so does the maximum operative temperature and the range of temperatures between sun and shade, which are the two variables that load on the principal component. $PC1_{ENV}$ captured 95% of the cumulative variation in the maximal and range of available operative temperatures in the arenas. As $PC1_{BCI}$ increases, so does animal body condition. The three body condition indices were calculated by: 1) dividing an animal's mass by its weight, 2) calculating ordinary least squares (OLS) regressions of log-transformed body mass on log-transformed snout-vent length (SVL), and 3) scaled mass index was calculated by solving equation 2.1. These indices were loaded on the principal component. $PC1_{BCI}$ captured 93% of the variation in body condition.

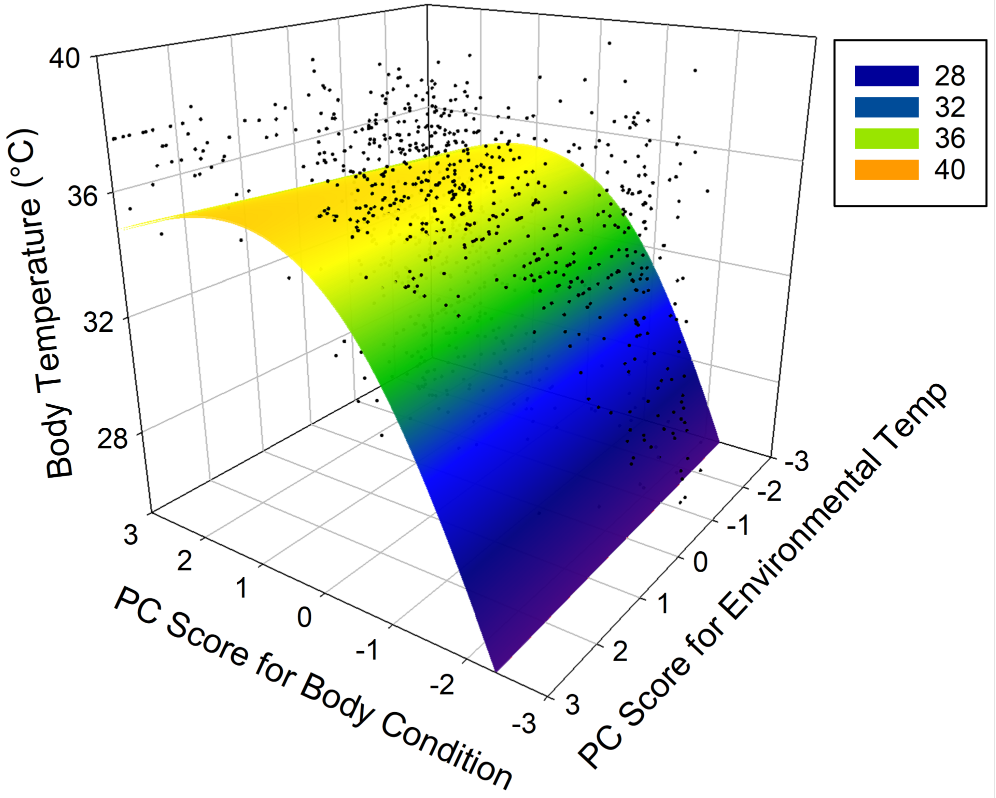


Fig 3.3. Outdoor arenas (83.6 m^2) were used to quantify variation in lizard thermoregulation. Arenas were designed to represent either a high-heterogeneity (left) or a low-heterogeneity spatial distribution of microclimates (right). All arenas were covered in 30% shade cloth. Then, 36% of the arena was additionally covered with 85% shade cloth, distributed in either 16 patches in the high spatial heterogeneity arenas, or 1 patch in the low spatial heterogeneity arenas.

Fig 3.4. Preferred body temperatures selected in a thermal gradient were not impacted by logger implantation surgery ($t_{2,49}$ = -1.49, P = 0.13). Lizards had thermal preference measured in the lab prior to logger implantation surgery, and then again, the day following the surgery (N = 50).

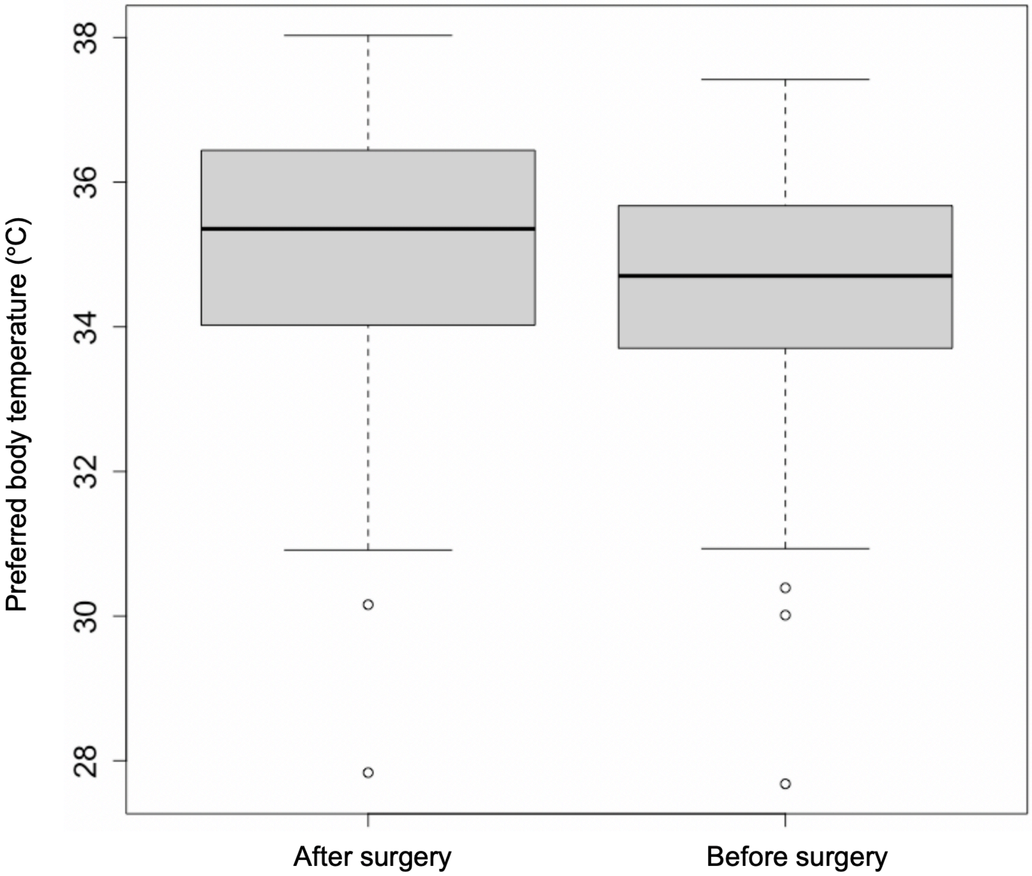


Fig 3.5. Hollow electroformed copper lizard operative temperature model, equipped with a temperature logger inside, next to a bare temperature logger. The relationships between these two temperatures, under each shade combination, were used to estimate animal operative temperatures under all shade combinations in the arenas.

CHAPTER 4

THE EFFECTS OF ACTIVITY ON POPULATION-LEVEL MEASURES OF PRODUCTIVITY IN LIZARDS: A COMPARATIVE ANALYSIS

Abstract

Ectotherm performance is highest within a relatively narrow range of body temperatures. As climates warm, organisms are expected to achieve their preferred body temperatures less frequently, constraining the time available for foraging, mate acquisition, territory defense, and thermoregulation. To understand how climate change will impact the persistence of ectotherms, it is important to understand how thermal constraints on activity impact the productivity of ectotherms in different environments. Still, the impact of restricted activity on organismal productivity are difficult to quantify for myriad reasons. Here, I used a population-level comparative analysis to examine relationships between potential activity time and three measures of organismal productivity: 1) growth rates, 2) relative clutch mass, or 3) reproductive output. Data for relative clutch mass and reproductive output ($\bar{x} \pm se$) were taken directly from the literature. Growth rate data were collected from growth trajectory figures in the literature and processed using the freeware, WebPlotDigitizer. Then, I integrated estimates of heat flux from complex environments using the approach developed by Campbell and Norman (1988) and Bakken (1980), with downscaled microclimate data from NicheMapR, to model hourly body temperatures throughout the year for each population sampled. I use preferred temperatures to predict activity restrictions. I compare predicted annual activity times to population-level measures of organismal growth and reproduction using computation modeling and pre-existing productivity data for N = 58 lizard species across N = 126

populations. While there was substantial variation in the potential annual time for activity, this variation did not explain variation in growth or reproduction of lizards among populations.

Introduction

Life-history traits vary widely among species and populations. Scientists have often correlated life-history traits with population survivorship (Tinkle 1972, Tinkle and Ballinger 1972) or performance curves (Stearns 1976) to describe life-history patterns and evolution. However, there are drawbacks to both these approaches as one must assume knowledge regarding the ecological factors shaping life histories, and those traits' genetic underpinnings. Life-history phenotypes in natural populations are affected by numerous environmental factors and interactions (Ballinger 1979, Berven and Gill 1983, Werner 1986, Adolph and Porter 1993). Factors such as temperature, food availability, and predation risk are known to directly impact lizard life histories (Tinkle and Ballinger 1972, Dunham 1978, Ballinger 1979, Sinervo 1990, Tinkle et al. 1993). Physiological performance is constrained by temperature (Huey and Stevenson 1979a, Huey 1982, Hertz et al. 1983, Congdon 1989, Grant 1990, Angilletta et al. 2010). Performances such as energy assimilation directly shape the evolution of life-history traits, including the age and size at maturity, the timing of reproduction, and the number and size of offspring – which are directly linked to fitness (Stearns 1977, McGraw and Caswell 1996). As a result, thermal heterogeneity favors the evolution of plastic life histories.

Climate change is expected to impact the fitness of organisms and dynamics of populations by altering the availability of preferred microclimates. As climate change reshapes thermal landscapes, biologists are eager to quantify the link between novel thermal variation in environments and physiological performance to predict the impact on fitness. Ectotherms at lower latitudes and altitudes are expected to have less time for activity, while lizards at higher latitudes and altitudes are expected to have more time (Deutch et al. 2008, Tewksbury et al. 2008, Sinervo et al. 2010, Kearney 2013, Kingsolver et al. 2013, Lara-Reséndiz et al. 2015, Pontes-da-Silva et al. 2018, Herrando-Pérez et al. 2019, Huey and Kingsolver 2019). However, given that much of the global biodiversity is concentrated in lower latitudes and altitudes, potential activity time is expected to decrease for most organisms as climates warm, constraining the time available for activities such as searching for mates and foraging. Recent studies have linked available activity windows—the duration of time when expected body temperatures fall within known preferred thermal ranges—with potential extinction risk inherently assume that available activity times and fitness are linearly related (Jiang et al. , Buckley 2008, Deutsch et al. 2008, Kearney et al. 2009, Sinervo et al. 2010, Caldwell et al. 2015, Laspiur et al. 2021, Anderson et al. 2022). However, activity times are shaped not only by thermal conditions, but also by factors such as predation risk (Van Buskirk and Arioli 2002), food availability (Abrams 1991, Mikolajewski et al. 2005), and energetic demands (Rock et al. 2002, Paranjpe et al. 2013).

Activity requirements are determined by numerous factors, such as seasonal variation in energy requirements (such as during reproductive seasons), and also short-term variation in expected energy returns. Energy assimilation varies with body temperature (Angilletta 2001) and with the amount of time previously spent at preferred temperatures (i.e., thermal opportunity; Levy et al. 2017). For example, in environments with high thermal opportunity, lizards can maintain an optimal energy budget at lower activity durations due to the diminishing returns of time spent at preferred temperatures on energy assimilation rates (Levy et al. 2017). Despite these diminishing returns, current models assume that energy assimilation increases linearly with thermal opportunity.

Here, I propose to use comparative analysis techniques and computational modeling to investigate the effects of activity on population-level measures of productivity in widespread lizard taxa to address the following questions: 1) Do computational estimates of potential activity (when predicted body temperatures are within preferred ranges) align with available empirical estimates of activity?, 2) How do activity levels correlate with two productivity measures; growth rates and reproductive output?, and 3) How does productivity and performance vary across latitudes and altitudes? Specifically, I hypothesize that lizards in warmer climates (i.e., lower latitudes and altitudes) will have higher body temperatures and wider windows for annual potential activity under current climatic conditions. Furthermore, because time spent at preferred temperatures influences energy assimilation with diminishing returns, I predict that lizards will have lower empirical activity levels than what would be expected if lizards are active whenever preferred temperatures are available.

Methods

Literature search and data digitalization

I searched the literature for primary, peer-reviewed studies reporting one or more of the following productivity measures: growth rates, relative clutch mass, and reproductive output. I searched the terms “growth rates AND lizards”, “growth trajectories AND lizards", "relative clutch mass AND lizards", and "reproductive output AND lizards" in Google Scholar in the spring and summer of 2020. Studies reporting one or more of the foci productivity measures for populations in nature (i.e., not lab-reared) were retained for data digitization.

Data for relative clutch mass and reproductive output ($\overline{x} \pm$ se) were taken directly from the publications. I defined relative clutch mass as the ratio of the clutch mass to the total maternal mass using the following standard formula:

$$\frac{clutch/neonate\ wet\ mass\ (g)}{total\ body\ mass\ (g) - clutch/neonate\ wet\ mass\ (g)} \quad [4.1]$$

I defined annual reproductive output as the number of eggs or neonates per year, calculated from clutch size and clutch frequency. I only included data from studies that provided wet mass. Growth rates were determined from figures relating individual growth by age, using the freeware WebPlotDigitizer version 4.4 (Rohatgi 2020). Publications were excluded from the search if they quantified productivity differently than how I defined the productivity measures above, or if authors did not provide sufficient geographical information describing where populations were sampled.

Activity time estimates

I started by integrating estimates of heat flux from complex environments using the approach developed by Campbell and Norman (1988) and Bakken (1980) and later refined by Sears et al. (2016). I used downscaled microclimate data from NicheMapR (Kearney and Porter 2017) to model hourly body temperatures throughout the year in full sun and full shade, assuming lizards were on the ground and experiencing a wind speed of 0.1 m/s. Except for temperatures, altitudes, latitudes, and longitudes, I assumed all study sites were equivalent in their meteorological characteristics (e.g., wind speed, cloud cover, soil thermal conductivity) because locally specific information was unavailable. I calculated operative temperatures (T_e) by solving a series of heat flux equations that integrate sources of radiation from the air, ground, and sun for each hour of the day. I then calculated hourly body temperatures (T_b) assuming the lizard experienced a given T_e for 5 minutes. Computed body temperatures represent steady-state temperatures since small lizards have a thermal time constant of approximately 5 minutes (Sears et al. 2016). Next, I used species-level data on thermal preferences from the literature to estimate activity windows when predicted body temperatures fell within preferred thermal ranges. When species-level data could not be found, I used genus-level estimates of thermal preference. To evaluate the robustness of the results, I calculated activity windows assuming two preference ranges: mean preferred temperature ± 2.5°C, and mean preferred temperature ± 5°C. I considered a lizard to be inactive if the estimated body temperatures in full sun and full shade were both outside of the preferred range. If predicted body temperature in the sun or shade was within the preferred range, I assumed an animal could remain active (Fig 4.1). The current Python script for these simulations can be found at https://github.com/laurenneel/comparative-analysis.

Statistical analyses

I conducted all statistical analyses using the *nlme* (Pinheiro et al. 2012) and *MuMIn* libraries (Barton 2010) in R statistical software (version 4.2.2; R Core Team, 2022).

Growth data for each population were fit to two functions, the von Bertalanffy function (Bertalanffy 1960; Fig 4.2) and logistic by size function (SVL; Blumberg 1968; Fig 4.3). Then, Akaike's Information Criterion was used to determine the model of best fit (Akaike 1987). The growth model with the lowest AIC score was then fit to the size at age data for each population sampled and growth rate parameters were retained (Fig 4.4).

I used general linear mixed effects models to determine the effects of geographic and ecological factors in shaping projected annual activity windows and population-level productivity. I used the *lme* function to fit a generalized linear mixed effects model with a Gaussian distribution of error and fixed effects of altitude, the absolute value of latitude, animal length (i.e., SVL), reproductive mode (i.e., oviparous or viviparous), and diet (i.e., herbivore, omnivore, or carnivore). Population was included as a random effect. Identical statistical analyses were carried out using both narrower ($T_{pref} \pm 2.5°C$) and broader ($T_{pref} \pm 5°C$) thermal preference ranges to estimate activity times, and results did not differ. Reported results reflect projected activity times assuming activity whenever body temperatures within ± 5°C of mean preferred temperatures were available.

For each of our dependent productivity variables (relative clutch mass, reproductive output, growth rate, and asymptotic size), I fit general linear mixed effects models with fixed effects of altitude, the absolute value of latitude, animal length (i.e., SVL), reproductive mode (i.e., oviparous or viviparous), diet (i.e., herbivore, omnivore, or carnivore), and annual activity window. Population was included as a random effect.

After fitting the statistical models, I used model selection for every analysis. First, I used the dredge function to fit a set of models representing all possible subsets of the fixed factors and their interactions. For each model in the set, I calculated the Akaike weight, which is the probability that the model describes the data better than the other models. I reported all models with an Akaike weight of at least 3% in statistics tables (Tables 4.1-4.5).

Results

I modeled body temperatures for 126 populations of lizards and estimated available activity windows under current climates, and also under a 3°C uniform warming scenario. The most-likely model included fixed effects of latitude, SVL, season, and interactive effects of latitude, SVL, and season (Table 5.1). Annual activity windows were similar when constraining activity to narrower ($T_{pref} \pm 2.5$°C) and wider thermal preference ranges ($T_{pref} \pm 5$°C; Fig 4.5). A 3°C warming scenario increased available activity windows in all populations besides at tropical latitudes, where potential activity windows declined when activity was restricted to within 2.5°C of a species' mean thermal preference (Fig 4.5). Available annual activity time was not in the most likely model for any of the productivity measures (Tables 4.1-4.5; Fig 4.6).

To validate the activity model, I compared model predictions to a small sample of lizards that were surgically implanted with body temperature loggers. I compared activity model predictions to hourly field-active body temperatures recorded for *Sceloporus jarrovii* (N=2) lizards in a single population. My model predicted activity with 64% accuracy overall (Figs 4.8-4.9). When model predictions were incorrect, they were more frequently over-estimating activity times, rather than underestimating them. When model predictions were inaccurate (36% of model predictions), activity was being overestimated 96% of the time and was only being underestimated 4% of the time.

Discussion

Adolph and Porter (1993) were among the first to empirically link predicted activity times to life-history traits of lizards. They estimated the relationships between activity time and energy assimilation, reproductive investment, and survival rate–and empirically supported their theoretical predictions with data collected from populations of *Sceloporus undulatus* (Adolph and Porter 1993). They showed that populations with higher annual activity times had increased egg mass and annual fecundity, as well as decreased survivorship (Grant and Porter 1992, Adolph and Porter 1993, Adolph and Porter 1996). Given this seminal work, it's often been taken as true that activity directly translates to population dynamics. However, decades of advances in ecological methods and statistical standards should lead current biologists to reevaluate these assumptions—indeed Porter et al. excluded outlier populations in some of these seminal works (Grant and Porter 1992, Adolph and Porter 1996), which may have unintentionally increased the supposed generalizability of their models. Here, I present a biophysical model linking potential activity windows with population-level measures of productivity. I show while there is substantial variation in potential annual diurnal activity windows (range: 1272 – 2760 hours), this variation does not explain differences in population level growth or reproduction (Fig 4.7).

Early life-history research in lizards (Tinkle and Woodward 1967, Tinkle 1969, Tinkle et al. 1970, Ballinger 1973, Tinkle and Hadley 1975, Adolph and Porter 1993, Tinkle et al. 1993) provided the necessary framework used by biologists studying life-histories, population dynamics and demography today. The idea – demonstrated by Adolph and Porter (1993) – that increasing available activity time directly translates to productivity has been used as the basis for numerous studies evaluating the vulnerability of lizard populations to climate change (Jiang et al. , Buckley 2008, Deutsch et al. 2008, Kearney et al. 2009, Sinervo et al. 2010, Caldwell et al. 2015, Laspiur et al. 2021, Anderson et al. 2022). In general, activity times are computationally modeled and then transformed into energy or fitness. Broad studies linking thermal environments to fitness may be useful in illuminating general trends in vulnerability to climate change, such as tropical species being especially at risk (Tewksbury et al. 2008, Huey et al. 2009). However, the application of this simplified framework to predict impacts on specific populations should be exercised cautiously.

The impacts of climate change on organisms depends not only on the shift in environmental temperatures, but also on the behavior, morphology, physiology, and ecology of the focal organism – and the varying capacities organisms have for exhibiting plasticity or adaptive responses. I predicted available activity times for N= 58 species of lizards across N = 126 populations. I modeled body temperatures using population-specific downscaled microclimate input data and species-specific morphological (e.g., mass and length), physiological (e.g., thermal preference), and ecological (e.g., reproductive mode (e.g., oviparous versus viviparous) and diet (e.g., carnivore, omnivore, herbivore)) data. I assumed that a lizard would be active if a body temperature within the species' preferred range (activity window 10°C = T_{pref} $\bar{x} \pm 5$°C ; activity window 5°C = T_{pref} $\bar{x} \pm 2.5$°C) was available between full shade and full sun microclimates. The model showed that while there is substantial variation in potential annual diurnal activity windows (range: 1272 – 2760 hours), this variation does not explain differences in population level growth or reproduction (Fig 4.7). Activity and energetics are undoubtedly related in nature (Adolph and Porter 1993, Angilletta 2001, Niewiarowski 2001, Sears 2005). However, the data suggests that various noise introduced from complex physiological and ecological factors break up this correlation large-scale (Fig 4.7).

Numerous other factors besides thermal environments affect activity, such as predation risk (Van Buskirk and Arioli 2002), food availability (Abrams 1991, Mikolajewski et al. 2005), reproductive status (Rock et al. 2002, Paranjpe et al. 2013), and recent past activity (Levy et al. 2017). Hormones have been known to influence thermoregulation (Rusch and Angilletta 2017, Rusch et al. 2018) and activity (DeNardo and Sinervo 1994, John-Alder et al. 2009) in lizards. For example, DeNardo and Sinervo (1994) observed contrasting effects of testosterone and corticosterone on the activity and home-range size of side-blotched lizards (*Uta stansburiana*). In addition, Levy et al. (2017) computationally and empirically demonstrated that lizard activity depends on past opportunities for thermoregulation. If these diverse physiological and ecological factors interact to shape the relationship between activity and energetics in complex ways, large-scale correlations may be difficult to observe.

Biophysical models are valuable tools for coarsely estimating the vulnerability of species to climate change. However, such models represent the upper bounds on activity and should be interpreted conservatively. To validate the model, I compared predicted activity times with empirical data from a small subset of lizards surgically implanted with thermal loggers that tracked internal body temperatures *in situ* (*Sceloporus jarrovii*, N =2). My model accurately predicted activity 64% of the time. When model predictions were incorrect, they were more frequently over-estimating activity times when lizards were likely in burrows or other thermal refugia despite preferred microclimates being available. Activity models that assume animals are active whenever preferred microclimates are available, undoubtedly overestimate actual activity times in natural populations. Activity and energetics are indisputably related in natural populations (Adolph and Porter 1993, Angilletta 2001, Niewiarowski 2001, Sears 2005). However, many ecological and physiological factors also interact to shape the relationship between activity and fitness. Broad geographic- and taxonomic-scale studies should exercise caution and avoid assuming that activity directly correlates with fitness when predicting the effects of climate change at the population-level. The minimum activity times required to avoid population declines in the context of climate change – will vary based on the physiologies and ecologies of each population. Future studies should examine the proximate mechanisms shaping activity decisions in natural populations.

Table 4.1. A ranking of activity window models based on the likelihood of being the best model. For each model, I provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed. The most likely model included effects of latitude, SVL, season, and the following interaction terms: latitude · SVL, latitude · season, and latitude · SVL · season.

Model	*K*	*logLik*	*AIC_c*	*ΔAIC_c*	*Weight*
1. latitude + SVL + season + (latitude · SVL) + (latitude · season) + (SVL · season) + (latitude · SVL · season)	18	-2427.9	4893.7	0.00	0.61
2. latitude + altitude + SVL + season + (latitude · SVL) + (latitude · season) + (SVL · altitude) + (SVL · season) + (latitude · SVL · season)	20	-2426.7	4895.7	1.95	0.22
3. latitude + altitude + SVL + season + (latitude · altitude) + (latitude · SVL) + (latitude · season) + (SVL · altitude) + (SVL · season) + (latitude · SVL · season)	21	-2426.5	4897.6	3.90	0.08
4. latitude + altitude + SVL + season + (latitude · altitude) + (latitude · SVL) + (latitude · season) + (SVL · season) + (latitude · SVL · season)	20	-2427.9	4898.2	4.44	0.06
5. latitude + altitude + SVL + season + (latitude · SVL) + (latitude · season) + (SVL · season) + (latitude · SVL · season)	19	-2431.1	4902.2	8.50	0.01

Table 4.2. A ranking of relative clutch mass models based on the likelihood of being the best model. For each model, I provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 1% are listed. The most likely model was the null model.

Model	*K*	*logLik*	*AIC$_c$*	*ΔAIC$_c$*	*Weight*
1. null model	3	51.35	-96.3	0.00	0.51
2. latitude + SVL + season + (latitude · SVL)	6	54.34	-95.1	1.16	0.29
3. SVL	4	51.47	-94.2	2.06	0.18
4. latitude	4	47.78	-86.9	9.44	0.01

Table 4.3. A ranking of reproductive output models based on the likelihood of being the best model. For each model, I provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 3% are listed. The most likely model was the null model.

Model	*K*	*logLik*	AIC_c	ΔAIC_c	*Weight*
1. altitude	3	-116.77	240.2	0.00	0.05
2. altitude + SVL	4	-115.73	240.7	0.42	0.04
3. latitude + activity time + altitude + (latitude · altitude)	6	-113.21	241.1	0.90	0.03

Table 4.4. A ranking of growth rate (*r*) models based on the likelihood of being the best model. For each model, I provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 3% are listed. The most likely model included only reproductive mode.

Model	*K*	*logLik*	AIC_c	ΔAIC_c	*Weight*
1. reproductive mode	4	52.12	-92.2	0.00	0.57
2. altitude + reproductive mode	5	52.23	-87.8	4.44	0.06
3. diet + reproductive mode	5	52.14	-87.6	4.63	0.05
4. diet + reproductive mode + (diet · reproductive mode)	5	52.14	-87.6	4.63	0.05
5. activity time + reproductive mode	5	52.12	-87.6	4.66	0.05
6. latitude + reproductive mode	5	52.12	-87.6	4.67	0.05
7. null model	2	45.91	-86.8	5.41	0.03

Table 4.5. A ranking of asymptotic size ($L\infty$) based on the likelihood of being the best model. For each model, I provide the Akaike weight, which equals the probability that the model describes the data better than other models. Only models with an Akaike weight of at least 3% are listed. The most likely model was the null model.

Model	*K*	*logLik*	*AIC_c*	*ΔAIC_c*	*Weight*
1. null model	2	-59.49	124.0	0.00	0.37
2. diet	3	-59.25	126.8	2.70	0.09
3. activity time	3	-59.32	126.8	2.85	0.09
4. latitude	3	-59.45	127.1	3.11	0.07

Table 4.6. Productivity data, population location, literature citations, and thermal preference data used in comparative analysis.

Species	Productivity data collected	Pop. latitude	Pop. altitude	Study citation	Mean preferred Tb (°C)	Tpref citation(s)
Acanthodactylus boskianus	growth	30.67	35	Darwish and H.K. Hussein, 2000. Ecological Significance of Geographic Differences in Growth Rate of The Sand Lizard, Acanthodactylus boskianus. *Pakistan Journal of Biological Sciences, 3: 2154-2158.*	36.2	Meiri, S., Bauer, A., Chirio, L., Colli, G., Das, I., Doan, T., Feldman, A., Herrera, F., Nosovolov, M., Pafilis, P., Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P., Van Damme, R. 2013. Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. 22: 834-845.
Acanthodactylus boskianus	growth	30.67	-5	Darwish and H.K. Hussein, 2000. Ecological Significance of Geographic Differences in Growth Rate of The Sand Lizard, Acanthodactylus boskianus. *Pakistan Journal of Biological Sciences, 3: 2154-2158.*	36.2	Meiri, S., Bauer, A., Chirio, L., Colli, G., Das, I., Doan, T., Feldman, A., Herrera, F., Nosovolov, M., Pafilis, P., Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P., Van Damme, R. 2013. Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. 22: 834-845.
Acanthodactylus erythrurus	reproductive output	40.48	600	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	33.1	Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.
Anotis maccoyi	relative clutch mass	-35.30	1200	Shine, R. 1980. "Costs" of reproduction in reptiles. Oecologia, 46(1), 92-100.	17.8	Shine, R. 1983. Reptilian viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. Oecologia 57: 397-405.

Basiliscus vittatus	relative clutch mass	18.26	170	Gabriel Suárez-Varón, Orlando Suárez-Rodríguez, Gisela Granados-González, Maricela Villagrán-Santa Cruz, Kevin M. Gribbins, Diego Cortez-Quezada, & Oswaldo Hernández-Gallegos. 2019. Relative clutch mass of Basiliscus vittatus Wiegmann, 1828 (Squamata, Corytophanidae): Female morphological constraints. Herpetozoa, 32(3), 211-219.	36.2	Hirth, H. F. 1965. Temperature preferences of five species of Neotropical lizards. Herpetologica, 20: 273-276.
Callisaurus draconoides	relative clutch mass	33.19	400	Vitt, L. J., and Congdon, J. D. 1978. Body Shape, Reproductive Effort, and Relative Clutch Mass in Lizards: Resolution of a Paradox. The American Naturalist 1978 112:985, 595-608	39.3	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422
Carlia rubrigularis	relative clutch mass	16.80	50	Goodman, B.A. 2006. Costs of reproduction in a tropical invariant-clutch producing lizard (*Carlia rubrigularis*). Journal of Zoology, 270: 236-243	29.8	Vickers, M., Manicom, C., and Schwarzkopf, L. 2011. Extending the cost-benefit model of thermoreuglation: high-temperature environments. The American Naturalist. 177(4): 452- 461.
Cophosaurus texanus	relative clutch mass	32.14	1220	Vitt, L. J., and Congdon, J. D. 1978. Body Shape, Reproductive Effort, and Relative Clutch Mass in Lizards: Resolution of a Paradox. The American Naturalist 1978 112:985, 595-608	36.8	Meiri, S., Bauer, A., Chirio, L., Colli, G., Das, I., Doan, T., Feldman, A., Herrera, F., Nosovolov, M., Pafilis, P., Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P., Van Damme, R. 2013. Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. 22: 834-845.
Cophosaurus texanus scitulus	growth	33.11	1371	Sugg, D. W., Fitzgerald, L. A., & Snell, H. L. 1995. Growth rate, timing of reproduction, and size dimorphism in the southwestern earless lizard (Cophosaurus texanus scitulus). *The Southwestern Naturalist*, *40*(2), 193–202.	36.8	Meiri, S., Bauer, A., Chirio, L., Colli, G., Das, I., Doan, T., Feldman, A., Herrera, F., Nosovolov, M., Pafilis, P., Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P., Van Damme, R. 2013. Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. 22: 834-845.

Ctenosaura pectinata	relative clutch mass	18.40	930	Castro-Franco, Rubén & Zagal, María Guadalupe & Méndez-de-la-Cruz, Fausto. 2011. Variation in parental investment and relative clutch mass of the spiny-tail iguana, Ctenosaura pectinata (Squamata: Iguanidae) in central México. Revista Mexicana de Biodiversidad. 82. 10.22201/ib.20078706e.2011.1.454.	32.1	Gadsden, H., Ruiz, S., Castañeda, G., & Lara-Reséndiz, R. A. (2018). Selected body temperature in Mexican lizard species. Global Journal of Ecology, 3, 1-4.
Eumeces okadae	reproductive output	35.05	40	Hasegawa, M. Density effects on life-history traits of an island lizard population. 1997. *Ecol. Res*. **12**, 111–118.	29.8	Sinervo, B., Mendez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz, M., Lara-Resendiz, R., Martinez-Mendez, N., Calderon-Espinosa, M. L., Meza-Lazaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Sepulveda, P. V., Rocha, C. F. D., Ibarguengoytia, N., Puntriano, C. A., Massot, M., Lep
Gambelia wislizeni	relative clutch mass	37.10	1280	Vitt, L. J., and Congdon, J. D. 1978. Body Shape, Reproductive Effort, and Relative Clutch Mass in Lizards: Resolution of a Paradox. The American Naturalist 1978 112:985, 595-608	38.1	Cunningham, J. D. 1966. Additional observations on the body temperatures of reptiles. Herpetologica, 22: 184-189; Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422.
Holbrookia maculata	growth	41.36	1160	Jones, S., & Ballinger, R. (1987). Comparative Life Histories of Holbrookia Maculata and Sceloporus Undulatus in Western Nebraska. Ecology, 68(6), 1828-1838.	36.3	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Meiri, S., Bauer, A., Chirio, L., Colli, G., Das, I., Doan, T., Feldman, A., Herrera, F., Nosovolov, M., Pafilis, P., Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P., Van Damme, R. 2013. Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. 22: 834-845.

Holbrookia maculata	relative clutch mass	32.14	1220	Vitt, L. J., and Congdon, J. D. 1978. Body Shape, Reproductive Effort, and Relative Clutch Mass in Lizards: Resolution of a Paradox. The American Naturalist 1978 112:985, 595-608	36.3	Degenhardt, W. G., Painter, C. W. and Price, A. H. 1996. Amphibians and reptiles of New Mexico. University of New Mexico Press, Albuquerque; Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422
Lacerta agilis	reproductive output	51.24	320	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	32.2	Tertyshnikov, M. F. 1976. Influence of weather and climate on activity of sand and varicoloured lizards. Ekologiya 3: 57-61; Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.
Lacerta lepida	reproductive output	38.98	628	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	30.4	Busack, S. D. and Visnaw, J. A. 1989. Observations on the natural history of Lacerta lepida in. Cadiz province, Spain. Amphibia-Reptilia, 10: 201-213.
Lacerta monticola	relative clutch mass	43.15	85	Galán, P., & Rúa, M. 2003. Reproductive characteristics of a lowland population of an alpine lizard: Lacerta monticola (Squamata, Lacertidae) in north-west Spain. Animal Biology, 53(4), 347-366.	31.5	Arnold, E. N. 1987. Resource partition among lacertid lizards in southern Europe. Journal of Zoology B. 1: 739ñ782; Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.
Lacerta monticola cantabrica	reproductive output	43.24	800	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	31.5	Arnold, E. N. 1987. Resource partition among lacertid lizards in southern Europe. Journal of Zoology B. 1: 739ñ782; Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.

Lacerta monticola cyreni	reproductive output	40.65	1000	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	28.2	Monasterio, C., Salvador, A., Iraeta, P. and D?az, J. A. 2009. The effects of thermal biology and refuge availability on the restricted distribution of an alpine lizard. Journal of Biogeography 36: 1673-1684.
Lacerta schreiberi	reproductive output	40.96	800	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	31.1	Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.
Lacerta viridis	reproductive output	47.51	20	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	33.9	Arnold, E. N. 1987. Resource partition among lacertid lizards in southern Europe. Journal of Zoology B. 1: 739ñ782; Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.
Lacerta vivipara	reproductive output	43.24	800	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	30.5	Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.
Lacerta vivipara	reproductive output	51.26	15	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	30.5	Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.
Lampropholis guichenoti	relative clutch mass	-35.30	1200	Shine, R. 1980. “Costs” of reproduction in reptiles. Oecologia, 46(1), 92-100.	30.3	Shine, R. 1983. Reptilian viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. Oecologia 57: 397-405.

Leiolopisma coventryi	relative clutch mass	-35.30	1200	Shine, R. 1980. "Costs" of reproduction in reptiles. Oecologia, 46(1), 92-100.	27	Greer, A. E. 1989. The biology and evolution of Australian lizards. Surrey Beatty and Sons, Chipping Norton, NSW; Shine, R. 1983. Reptilian viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. Oecologia 57: 397-405.
Leiolopisma extrecasteauxii	relative clutch mass	-35.30	1200	Shine, R. 1980. "Costs" of reproduction in reptiles. Oecologia, 46(1), 92-100.	31.9	Greer, A. E. 1989. The biology and evolution of Australian lizards. Surrey Beatty and Sons, Chipping Norton, NSW; Shine, R. 1983. Reptilian viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. Oecologia 57: 397-405.
Microlophus occipitalis	growth	-2.10	200	Watkins, G. 1996. Proximate Causes of Sexual Size Dimorphism in the Iguanian Lizard Microlophus Occipitalis. Ecology, 77(5), 1473-1482.	38.3	Rowe, J., Clark, D., Martin, C., and Valle, C. 2020. Diel and seasonal variations in the thermal biology of San Cristobal Lava Lizards (Microlophus bivittatus). Journal of Thermal Biology. 88:102518
Phrynocephalus przewalskii	relative clutch mass	38.50	1400	Zeng, Z., Zhao, J., & Sun, B. 2013. Life history variation among geographically close populations of the toad-headed lizard (Phrynocephalus przewalskii): Exploring environmental and physiological associations. Acta Oecologica, 51(C), 28-33.	33.5	Xu, H. and Yang, F. 1995. Simulation model of activity of Phrynocephalus przewalskii. Ecological Modelling 77: 197-204.
Phrynocephalus przewalskii	relative clutch mass	39.13	1400	Zeng, Z., Zhao, J., & Sun, B. 2013. Life history variation among geographically close populations of the toad-headed lizard (Phrynocephalus przewalskii): Exploring environmental and physiological associations. Acta Oecologica, 51(C), 28-33.	33.5	Xu, H. and Yang, F. 1995. Simulation model of activity of Phrynocephalus przewalskii. Ecological Modelling 77: 197-204.

Phrynocephalus przewalskii	relative clutch mass	38.35	2500	Zeng, Z., Zhao, J., & Sun, B. 2013. Life history variation among geographically close populations of the toad-headed lizard (Phrynocephalus przewalskii): Exploring environmental and physiological associations. Acta Oecologica, 51(C), 28-33.	33.5	Xu, H. and Yang, F. 1995. Simulation model of activity of Phrynocephalus przewalskii. Ecological Modelling 77: 197-204.
Phrynosoma asio	relative clutch mass	29.54	20	Pianka, E., & Parker, W. 1975. Ecology of Horned Lizards: A Review with Special Reference to Phrynosoma platyrhinos. Copeia, 1975(1), 141-162.	32.4	Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76; Woolrich-Pina, G. A., Lemos-Espinal, J. A., Smith, G. R., Oliver-Lopez, L., Correa-Sanchez, F., Altamirano-Alvarez, T. A. and Montoya-Ayala, R. 2012. Thermal ecology of the lizard Sceloporus gadoviae (Squamata: Phrynosomatidae) in a semiarid region of southern Puebla, Mexico. Phyllomedusa 11: 21-27.
Phrynosoma braconnieri	relative clutch mass	29.54	20	Pianka, E., & Parker, W. 1975. Ecology of Horned Lizards: A Review with Special Reference to Phrynosoma platyrhinos. Copeia, 1975(1), 141-162.	35.9	Zamudio, K. R., Parra-Olea, G. 2000. Reproductive mode and female reproductive cycles of 2 endemic Mexican horned lizards (Phrynosoma taurus and Phrynosoma braconnieri). Copeia. 222-229.
Phrynosoma cornutum	relative clutch mass	32.14	1220	Vitt, L. J., and Congdon, J. D. 1978. Body Shape, Reproductive Effort, and Relative Clutch Mass in Lizards: Resolution of a Paradox. The American Naturalist 1978 112:985, 595-608	37.1	Degenhardt, W. G., Painter, C. W. and Price, A. H. 1996. Amphibians and reptiles of New Mexico. University of New Mexico Press, Albuquerque.; Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422

Phrynosoma cornutum	relative clutch mass	31.94	1675	Pianka, E., & Parker, W. 1975. Ecology of Horned Lizards: A Review with Special Reference to Phrynosoma platyrhinos. Copeia, 1975(1), 141-162.	37.1	Degenhardt, W. G., Painter, C. W. and Price, A. H. 1996. Amphibians and reptiles of New Mexico. University of New Mexico Press, Albuquerque.; Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422
Phrynosoma coronatum	relative clutch mass	32.47	800	Pianka, E., & Parker, W. 1975. Ecology of Horned Lizards: A Review with Special Reference to Phrynosoma platyrhinos. Copeia, 1975(1), 141-162.	35.5	Cunningham, J. D. 1966. Additional observations on the body temperatures of reptiles. Herpetologica, 22: 184-189; Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422.
Phrynosoma douglassi	relative clutch mass	40.60	1400	Pianka, E., & Parker, W. 1975. Ecology of Horned Lizards: A Review with Special Reference to Phrynosoma platyrhinos. Copeia, 1975(1), 141-162.	33.8	Degenhardt, W. G., Painter, C. W. and Price, A. H. 1996. Amphibians and reptiles of New Mexico. University of New Mexico Press, Albuquerque; Woolrich-Pina, G. A., Lemos-Espinal, J. A., Smith, G. R., Oliver-Lopez, L., Correa-Sanchez, F., Altamirano-Alvarez, T. A. and Montoya-Ayala, R. 2012. Thermal ecology of the lizard Sceloporus gadoviae (Squamata: Phrynosomatidae) in a semiarid region of southern Puebla, Mexico. Phyllomedusa 11: 21-27.
Phrynosoma mcalli	relative clutch mass	34.08	900	Pianka, E., & Parker, W. 1975. Ecology of Horned Lizards: A Review with Special Reference to Phrynosoma platyrhinos. Copeia, 1975(1), 141-162.	37.4	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422
Phrynosoma modestum	relative clutch mass	32.14	1220	Vitt, L. J., and Congdon, J. D. 1978. Body Shape, Reproductive Effort, and Relative Clutch Mass in Lizards: Resolution of a Paradox. The American Naturalist 1978 112:985, 595-608	28.7	Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76

Phrynosoma modestum	relative clutch mass	32.03	1675	Pianka, E., & Parker, W. 1975. Ecology of Horned Lizards: A Review with Special Reference to Phrynosoma platyrhinos. Copeia, 1975(1), 141-162.	28.7	Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Phrynosoma orbiculare	relative clutch mass	19.54	20	Pianka, E., & Parker, W. 1975. Ecology of Horned Lizards: A Review with Special Reference to Phrynosoma platyrhinos. Copeia, 1975(1), 141-162.	37.9	Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76; Woolrich-Pina, G. A., Lemos-Espinal, J. A., Smith, G. R., Oliver-Lopez, L., Correa-Sanchez, F., Altamirano-Alvarez, T. A. and Montoya-Ayala, R. 2012. Thermal ecology of the lizard Sceloporus gadoviae (Squamata: Phrynosomatidae) in a semiarid region of southern Puebla, Mexico. Phyllomedusa 11: 21-27.
Phrynosoma platyrhinos	relative clutch mass	40.12	1800	Pianka, E., & Parker, W. 1975. Ecology of Horned Lizards: A Review with Special Reference to Phrynosoma platyrhinos. Copeia, 1975(1), 141-162.	35.5	Pianka, E. R. 1986. Ecology and natural history of desert lizards. Princeton University Press, Princeton.; Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Woolrich-Pina, G. A., Lemos-Espinal, J. A., Smith, G. R., Oliver-Lopez, L., Correa-Sanchez, F., Altamirano-Alvarez, T. A. and Montoya-Ayala, R. 2012. Thermal ecology of the lizard Sceloporus gadoviae (Squamata: Phrynosomatidae) in a semiarid region of southern Puebla, Mexico. Phyllomedusa 11: 21-27.

Phrynosoma platyrhinos	relative clutch mass	40.60	1400	Pianka, E., & Parker, W. 1975. Ecology of Horned Lizards: A Review with Special Reference to Phrynosoma platyrhinos. Copeia, 1975(1), 141-162.	35.5	Pianka, E. R. 1986. Ecology and natural history of desert lizards. Princeton University Press, Princeton.; Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Woolrich-Pina, G. A., Lemos-Espinal, J. A., Smith, G. R., Oliver-Lopez, L., Correa-Sanchez, F., Altamirano-Alvarez, T. A. and Montoya-Ayala, R. 2012. Thermal ecology of the lizard Sceloporus gadoviae (Squamata: Phrynosomatidae) in a semiarid region of southern Puebla, Mexico. Phyllomedusa 11: 21-27.
Phrynosoma platyrhinos	relative clutch mass	35.06	760	Pianka, E., & Parker, W. 1975. Ecology of Horned Lizards: A Review with Special Reference to Phrynosoma platyrhinos. Copeia, 1975(1), 141-162.	35.5	Pianka, E. R. 1986. Ecology and natural history of desert lizards. Princeton University Press, Princeton.; Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Woolrich-Pina, G. A., Lemos-Espinal, J. A., Smith, G. R., Oliver-Lopez, L., Correa-Sanchez, F., Altamirano-Alvarez, T. A. and Montoya-Ayala, R. 2012. Thermal ecology of the lizard Sceloporus gadoviae (Squamata: Phrynosomatidae) in a semiarid region of southern Puebla, Mexico. Phyllomedusa 11: 21-27.

Phrynosoma platyrhinos	relative clutch mass	40.60	1400	Pianka, E., & Parker, W. 1975. Ecology of Horned Lizards: A Review with Special Reference to Phrynosoma platyrhinos. Copeia, 1975(1), 141-162.	35.5	Pianka, E. R. 1986. Ecology and natural history of desert lizards. Princeton University Press, Princeton.; Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Woolrich-Pina, G. A., Lemos-Espinal, J. A., Smith, G. R., Oliver-Lopez, L., Correa-Sanchez, F., Altamirano-Alvarez, T. A. and Montoya-Ayala, R. 2012. Thermal ecology of the lizard Sceloporus gadoviae (Squamata: Phrynosomatidae) in a semiarid region of southern Puebla, Mexico. Phyllomedusa 11: 21-27.
Phrynosoma solare	relative clutch mass	32.57	480	Pianka, E., & Parker, W. 1975. Ecology of Horned Lizards: A Review with Special Reference to Phrynosoma platyrhinos. Copeia, 1975(1), 141-162.	34.7	Degenhardt, W. G., Painter, C. W. and Price, A. H. 1996. Amphibians and reptiles of New Mexico. University of New Mexico Press, Albuquerque
Podacris hispanica	reproductive output	40.96	800	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	31.9	Arnold, E. N. 1987. Resource partition among lacertid lizards in southern Europe. Journal of Zoology B. 1: 739ñ782; Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.
Podacris hispanica	reproductive output	43.24	800	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	31.9	Arnold, E. N. 1987. Resource partition among lacertid lizards in southern Europe. Journal of Zoology B. 1: 739ñ782; Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.

Podacris hispanica atrata	reproductive output	39.89	67	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	31.9	Arnold, E. N. 1987. Resource partition among lacertid lizards in southern Europe. Journal of Zoology B. 1: 739ñ782; Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.
Podacris lilfordi	relative clutch mass	22.09	100	Castilla, A. M., & Bauwens, D. 2000. Reproductive Characteristics of the Island Lacertid Lizard Podarcis lilfordi. *Journal of Herpetology*, *34*(3), 390–396.	32.3	Salvador, A. 2008. Lagartija balear – Podarcis lilfordi (Günther, 1874). Version 4-02-2008. Enciclopedia virtual de los vertebrados Espanoles.
Podacris muralis	reproductive output	43.24	800	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	32.2	Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.
Podarcis hispanicus	relative clutch mass	40.47	1750	Ortega, J., López, P., & Martín, J. 2015. Altitudinally divergent adult phenotypes in Iberian wall lizards are not driven by egg differences or hatchling growth rates. Oecologia, 177(2), 357-366.	31.9	Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.
Podarcis hispanicus	relative clutch mass	40.44	1250	Ortega, J., López, P., & Martín, J. 2015. Altitudinally divergent adult phenotypes in Iberian wall lizards are not driven by egg differences or hatchling growth rates. Oecologia, 177(2), 357-366.	31.9	Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.
Psammodromus algirus	reproductive output	40.96	800	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	32.8	Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395; Salvador, A. 2010. Lagartija colilarga Psammodromus algirus. Version 25-06-2010. En: Enciclopedia Virtual de los Vertebrados Espanoles. Salvador, A., Marco, A. (Eds.).

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Psammodromus hispanicus	reproductive output	40.96	800	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	31.4	Verwaijen, D. and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. Journal of Thermal Biology 32: 388-395.
Sceloporus clarki	growth	33.86	1077	Tinkle, D., & Dunham, A. 1986. Comparative life histories of two syntopic sceloporine lizards. Copeia, (1), 1-18.	34	Jones, L. and Lovich, R. 2009. Lizards of the American southwest: a photographic field guide. Rio Nuevo Publishers, Tuscon.; Woolrich-Pina, G. A., Lemos-Espinal, J. A., Smith, G. R., Oliver-Lopez, L., Correa-Sanchez, F., Altamirano-Alvarez, T. A. and Montoya-Ayala, R. 2012. Thermal ecology of the lizard Sceloporus gadoviae (Squamata: Phrynosomatidae) in a semiarid region of southern Puebla, Mexico. Phyllomedusa 11: 21-27.
Sceloporus graciosus	growth	37.20	1950	Tinkle, D., Dunham, A., & Congdon, J. 1993. Life History and Demographic Variation in the Lizard Sceloporus Graciosus: A Long-Term Study. Ecology, 74(8), 2413-2429.	36.6	Huey, R. B. and Pianka, E. R. 2007. Lizard thermal biology: do genders differ? American Naturalist 170: 473-478; Pianka, E. R. 1986. Ecology and natural history of desert lizards. Princeton University Press, Princeton.
Sceloporus graciosus	growth	37.50	2040	Tinkle, D., Dunham, A., & Congdon, J. 1993. Life History and Demographic Variation in the Lizard Sceloporus Graciosus: A Long-Term Study. Ecology, 74(8), 2413-2429.	36.6	Huey, R. B. and Pianka, E. R. 2007. Lizard thermal biology: do genders differ? American Naturalist 170: 473-478; Pianka, E. R. 1986. Ecology and natural history of desert lizards. Princeton University Press, Princeton.
Sceloporus grammicus	growth	19.41	3200	Méndez-de La Cruz, F., Cuellar, O., & Zúñiga-Vega, J. (2008). Body growth in one montane population of Sceloporus grammicus (Sauria, Phrynosomatidae) in Central México.	32.4	Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico.

				Amphibia-Reptilia, 29(1), 127-134.		Herpetological Journal 7: 74-76
Sceloporus grammicus	growth	19.10	3700	Lemos-Espinal, J., & Ballinger, Royce E. (1992). Ecology and Comparative Demography of the Lizard Sceloporus Grammicus: Life History of an Altitudinal Generalists on the Eastern Slope of the Iztaccihuatl Volcano, Puebla, Mexico, ProQuest Dissertations and Theses.	32.4	Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus grammicus	growth	19.10	4400	Lemos-Espinal, J., & Ballinger, Royce E. (1992). Ecology and Comparative Demography of the Lizard Sceloporus Grammicus: Life History of an Altitudinal Generalists on the Eastern Slope of the Iztaccihuatl Volcano, Puebla, Mexico, ProQuest Dissertations and Theses.	32.4	Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus jarrovi	growth	31.53	1685	Cox, R., & John-Alder, H. (2007). Growing Apart Together: The Development of Contrasting Sexual Size Dimorphisms in Sympatric Sceloporus Lizards. Herpetologica, 63(3), 245-257.	32.4	Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76; Huey, R. B. and Pianka, E. R. 2007. Lizard thermal biology: do genders differ? American Naturalist 170: 473-478; Pianka, E. R. 1986. Ecology and natural history of desert lizards. Princeton University Press, Princeton.
Sceloporus merriami	growth	29.23	1036	Ballinger, R., Droge, D., & Jones, S. (1981). Reproduction in a Nebraska Sandhills Population of the Northern Prairie Lizard Sceloporus undulatus garmani. The American Midland Naturalist, 106(1), 157-164.	34.6	Meiri, S., Bauer, A., Chirio, L., Colli, G., Das, I., Doan, T., Feldman, A., Herrera, F., Nosovolov, M., Pafilis, P., Donoso, D., Powney, G., Torres-Carvajal, O., Uetz, P., Van Damme, R. 2013. Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. 22: 834-845.

Sceloporus mucronatus	growth	33.11	1371	Ortega-León, A., Smith, E., Zúñiga-Vega, J., & Méndez-De La Cruz, F. 2007. Growth and demography of one population of the lizard Sceloporus mucronatus. Western North American Naturalist, 67(4), 492-502.	30.3	Sinervo, B., Mendez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz, M., Lara-Resendiz, R., Martinez-Mendez, N., Calderon-Espinosa, M. L., Meza-Lazaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Sepulveda, P. V., Rocha, C. F. D., Ibarguengoytia, N., Puntriano, C. A., Massot, M., Lep; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76; Woolrich-Pina, G. A., Lemos-Espinal, J. A., Smith, G. R., Oliver-Lopez, L., Correa-Sanchez, F., Altamirano-Alvarez, T. A. and Montoya-Ayala, R. 2012. Thermal ecology of the lizard Sceloporus gadoviae (Squamata: Phrynosomatidae) in a semiarid region of southern Puebla, Mexico. Phyllomedusa 11: 21-27.
Sceloporus undulatus	reproductive output	37.27	1220	Tinkle, D. 1972. The Dynamics of a Utah Population of Sceloporus undulatus. Herpetologica, 28(4), 351-359.	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76.

Sceloporus undulatus	growth	33.86	1077	Tinkle, D., & Dunham, A. 1986. Comparative life histories of two syntopic sceloporine lizards. Copeia, (1), 1-18.	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76.
Sceloporus undulatus	growth	41.36	1160	Jones, S., & Ballinger, R. (1987). Comparative Life Histories of Holbrookia Maculata and Sceloporus Undulatus in Western Nebraska. Ecology, 68(6), 1828-1838.	32.8	Angilletta, M.J., Jr. 2001. Thermal and physiological constraints on energy assimilation in a widespread lizard (Sceloporus undulatus). Ecology, 82: 3044-3056.
Sceloporus undulatus	growth	40.00	20	Haenel, G., & John-Alder, H. (2002). Experimental and demographic analyses of growth rate and sexual size dimorphism in a lizard, Sceloporus undulatus. Oikos, 96(1), 70-81.	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus undulatus	relative clutch mass	32.14	1220	Vitt, L. J., and Congdon, J. D. 1978. Body Shape, Reproductive Effort, and Relative Clutch Mass in Lizards: Resolution of a Paradox. The American Naturalist 1978 112:985, 595-608	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus undulatus	relative clutch mass	34.13	790	Vitt, L. J., and Congdon, J. D. 1978. Body Shape, Reproductive Effort, and Relative Clutch Mass in Lizards: Resolution of a Paradox. The American Naturalist 1978 112:985, 595-608	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus

						ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus undulatus	relative clutch mass	33.24	60	Tinkle, D. 1972. The Dynamics of a Utah Population of Sceloporus undulatus. Herpetologica, 28(4), 351-359.	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus undulatus	relative clutch mass	30.88	731	Tinkle, D. 1972. The Dynamics of a Utah Population of Sceloporus undulatus. Herpetologica, 28(4), 351-359.	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus undulatus	relative clutch mass	39.57	213	Tinkle, D. 1972. The Dynamics of a Utah Population of Sceloporus undulatus. Herpetologica, 28(4), 351-359.	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus undulatus	relative clutch mass	38.86	2377	Tinkle, D. 1972. The Dynamics of a Utah Population of Sceloporus undulatus. Herpetologica, 28(4), 351-359.	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body

						temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus undulatus	relative clutch mass	39.20	292	Ferguson, G., Bohlen, C., & Woolley, H. 1980. Sceloporus Undulatus: Comparative Life History and Regulation of a Kansas Population. Ecology, 61(2), 313-322.	32.8	Angilletta, M.J., Jr. 2001. Thermal and physiological constraints on energy assimilation in a widespread lizard (Sceloporus undulatus). Ecology, 82: 3044-3056.
Sceloporus undulatus	relative clutch mass	31.30	49	Crenshaw, J. 1955. The Life History of the Southern Spiny Lizard, Sceloporus undulatus undulatus Latreille. The American Midland Naturalist, 54(2), 257-298.	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus undulatus	relative clutch mass	41.47	1110	Ballinger, R., Droge, D., & Jones, S. 1981. Reproduction in a Nebraska Sandhills Population of the Northern Prairie Lizard Sceloporus undulatus garmani. The American Midland Naturalist, 106(1), 157-164.	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus undulatus	relative clutch mass	40.00	20	Ballinger, R., Droge, D., & Jones, S. 1981. Reproduction in a Nebraska Sandhills Population of the Northern Prairie Lizard Sceloporus undulatus garmani. The American Midland Naturalist, 106(1), 157-164.	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76

Sceloporus undulatus consobrinus	relative clutch mass	32.46	1200	Vinegar, M. B. 1975. Life History Phenomena in Two Populations of the Lizard Sceloporus undulatus in Southwestern New Mexico. *The American Midland Naturalist*, *93*(2), 388–402.	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus undulatus garmani	relative clutch mass	41.38	1097	Ballinger, R., Droge, D., & Jones, S. 1981. Reproduction in a Nebraska Sandhills Population of the Northern Prairie Lizard Sceloporus undulatus garmani. The American Midland Naturalist, 106(1), 157-164.	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus undulatus tristichus	relative clutch mass	32.87	2057	Vinegar, M. B. 1975. Life History Phenomena in Two Populations of the Lizard Sceloporus undulatus in Southwestern New Mexico. The American Midland Naturalist, 93(2), 388–402.	32.5	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76
Sceloporus virgatus	growth	31.53	1685	Cox, R., & John-Alder, H. (2007). Growing Apart Together: The Development of Contrasting Sexual Size Dimorphisms in Sympatric Sceloporus Lizards. Herpetologica, 63(3), 245-257.	34	Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76; Andrews, R. M. 1998. Geographic variation in field body temperature of Sceloporus lizards. Journal of Thermal Biology 23: 329-334.; Brattstrom, B. H. 1965. Body temperatures of

						reptiles. American Midland Naturalist, 73: 376-422
Sphenomorphus tympanum	relative clutch mass	-35.30	1200	Shine, R. 1980. “Costs” of reproduction in reptiles. Oecologia, 46(1), 92-100.	28.8	Greer, A. E. 1989. The biology and evolution of Australian lizards. Surrey Beatty and Sons, Chipping Norton, NSW; Shine, R. 1983. Reptilian viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. Oecologia 57: 397-405.
Takydromus septentrionalis	relative clutch mass	32.18	100	Du, W., Ji, X., Zhang, Y., Xu, X., & Shine, R. 2005. Identifying sources of variation in reproductive and life-history traits among five populations of a Chinese lizard (*Takydromus septentrionalis* Lacertidae), *Biological Journal of the Linnean Society. 85(4):443-453*	30.4	Xiang, J., Weiguo, D. and Pingyue, S. 1996. Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards, Takydromus septentrionalis. Journal of Thermal Biology 21: 155-161.
Takydromus septentrionalis	relative clutch mass	29.50	45	Du, W., Ji, X., Zhang, Y., Xu, X., & Shine, R. 2005. Identifying sources of variation in reproductive and life-history traits among five populations of a Chinese lizard (Takydromus septentrionalis Lacertidae), Biological Journal of the Linnean Society. 85(4):443-453	30.4	Xiang, J., Weiguo, D. and Pingyue, S. 1996. Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards, Takydromus septentrionalis. Journal of Thermal Biology 21: 155-161.
Takydromus septentrionalis	relative clutch mass	28.26	70	Du, W., Ji, X., Zhang, Y., Xu, X., & Shine, R. 2005. Identifying sources of variation in reproductive and life-history traits among five populations of a Chinese lizard (Takydromus septentrionalis Lacertidae), Biological	30.4	Xiang, J., Weiguo, D. and Pingyue, S. 1996. Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards,

				Journal of the Linnean Society. 85(4):443-453		Takydromus septentrionalis. Journal of Thermal Biology 21: 155-161.
Takydromus septentrionalis	relative clutch mass	26.40	50	Du, W., Ji, X., Zhang, Y., Xu, X., & Shine, R. 2005. Identifying sources of variation in reproductive and life-history traits among five populations of a Chinese lizard (Takydromus septentrionalis Lacertidae), Biological Journal of the Linnean Society. 85(4):443-453	30.4	Xiang, J., Weiguo, D. and Pingyue, S. 1996. Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards, Takydromus septentrionalis. Journal of Thermal Biology 21: 155-161.
Takydromus septentrionalis	relative clutch mass	26.30	270	Du, W., Ji, X., Zhang, Y., Xu, X., & Shine, R. 2005. Identifying sources of variation in reproductive and life-history traits among five populations of a Chinese lizard (Takydromus septentrionalis Lacertidae), Biological Journal of the Linnean Society. 85(4):443-453	30.4	Xiang, J., Weiguo, D. and Pingyue, S. 1996. Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards, Takydromus septentrionalis. Journal of Thermal Biology 21: 155-161.
Takydromus tachydromoides	reproductive output	36.16	1600	Bauwens, D., & Diaz-Uriarte, R. (1997). Covariation of Life-History Traits in Lacertid Lizards: A Comparative Study. The American Naturalist, 149(1), 91-111.	32.9	Koji Mochida, Takahide Sasai, Yohei Kadota, Mari Nishikawa, Makoto M. Itou, Mamoru Toda. 2018. Thermal Reaction Norms of Locomotor Performance in Lacertid Lizards of the Genus Takydromus. Current Herpetology, 37(2), 114-123.
Tropidurus nanuzae	relative clutch mass	-18.25	800	Conrado A. B Galdino, & Monique Van Sluys. 2011. Clutch size in the small-sized lizard Eurolophosaurus nanuzae (Tropiduridae): Does it vary along the geographic distribution of the species? Iheringia: Série Zoologia, 101(1-2), 61-64.	34.1	Kiefer, M. C., Van Sluys, M. and Rocha, C. F. D. 2008. Clutch and egg size of the tropical lizard Tropidurus torquatus (Tropiduridae) along its geographic range in coastal eastern Brazil. Canadian Journal of Zoology 86: 1376-1388.

Urosaurus ornatus	growth	33.27	1220	Tinkle, D., & Dunham, A. 1983. Demography of the Tree Lizard, Urosaurus ornatus, in Central Arizona. Copeia, 1983(3), 585-598.	35.8	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422; Lemos-Espinal, J. A., Smith, G. R. and Ballinger, R. E. 1997. Body temperatures of Sceloporus ochoteranae from two populations in Guerrero, Mexico. Herpetological Journal 7: 74-76.
Urosaurus ornatus	relative clutch mass	33.19	400	Vitt, L. J., and Congdon, J. D. 1978. Body Shape, Reproductive Effort, and Relative Clutch Mass in Lizards: Resolution of a Paradox. The American Naturalist 1978 112:985, 595-608	35.8	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422
Urosaurus ornatus	relative clutch mass	32.14	1220	Vitt, L. J., and Congdon, J. D. 1978. Body Shape, Reproductive Effort, and Relative Clutch Mass in Lizards: Resolution of a Paradox. The American Naturalist 1978 112:985, 595-608	35.8	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422
Urosaurus ornatus	relative clutch mass	32.80	100	Vitt, L. J., and Congdon, J. D. 1978. Body Shape, Reproductive Effort, and Relative Clutch Mass in Lizards: Resolution of a Paradox. The American Naturalist 1978 112:985, 595-608	35.8	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422
Urosaurus ornatus	relative clutch mass	29.40	975	Dunham, A. 1982. Demographic and Life-History Variation among Populations of the Iguanid Lizard Urosaurus ornatus: Implications for the Study of Life-History Phenomena in Lizards. Herpetologica, 38(1), 208-221.	35.8	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422
Urosaurus ornatus	relative clutch mass	31.56	1340	Dunham, A. 1982. Demographic and Life-History Variation among Populations of the Iguanid Lizard Urosaurus ornatus: Implications for the Study of Life-History Phenomena in Lizards. Herpetologica, 38(1), 208-221.	35.8	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422
Urosaurus ornatus	relative clutch mass	31.93	1950	Dunham, A. 1982. Demographic and Life-History Variation among Populations of the Iguanid Lizard Urosaurus ornatus: Implications for the Study of Life-History Phenomena in Lizards. Herpetologica, 38(1), 208-221.	35.8	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422

Urosaurus ornatus	relative clutch mass	33.86	1095	Dunham, A. 1982. Demographic and Life-History Variation among Populations of the Iguanid Lizard Urosaurus ornatus: Implications for the Study of Life-History Phenomena in Lizards. Herpetologica, 38(1), 208-221.	35.8	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422
Uta stanburiana	reproductive output	26.52	1129	Gadsden, H., & Castañeda, G. (2012). Demography of the side-blotched lizard, Uta stansburiana, in sand dunes of the central chihuahuan desert. The Southwestern Naturalist, 57(3), 292-303.	35.4	Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist, 73: 376-422

Fig 4.1. Flow diagram of heat flux simulation. The flow diagram illustrates inputs of data (rhombuses), data estimated from literature (hexagons), decisions for the model (diamonds), calculations (rectangles), and the beginning of the heat flux simulation (oval). Flow diagram figure adapted from Fig. S8 in Riddell et al. (2019).

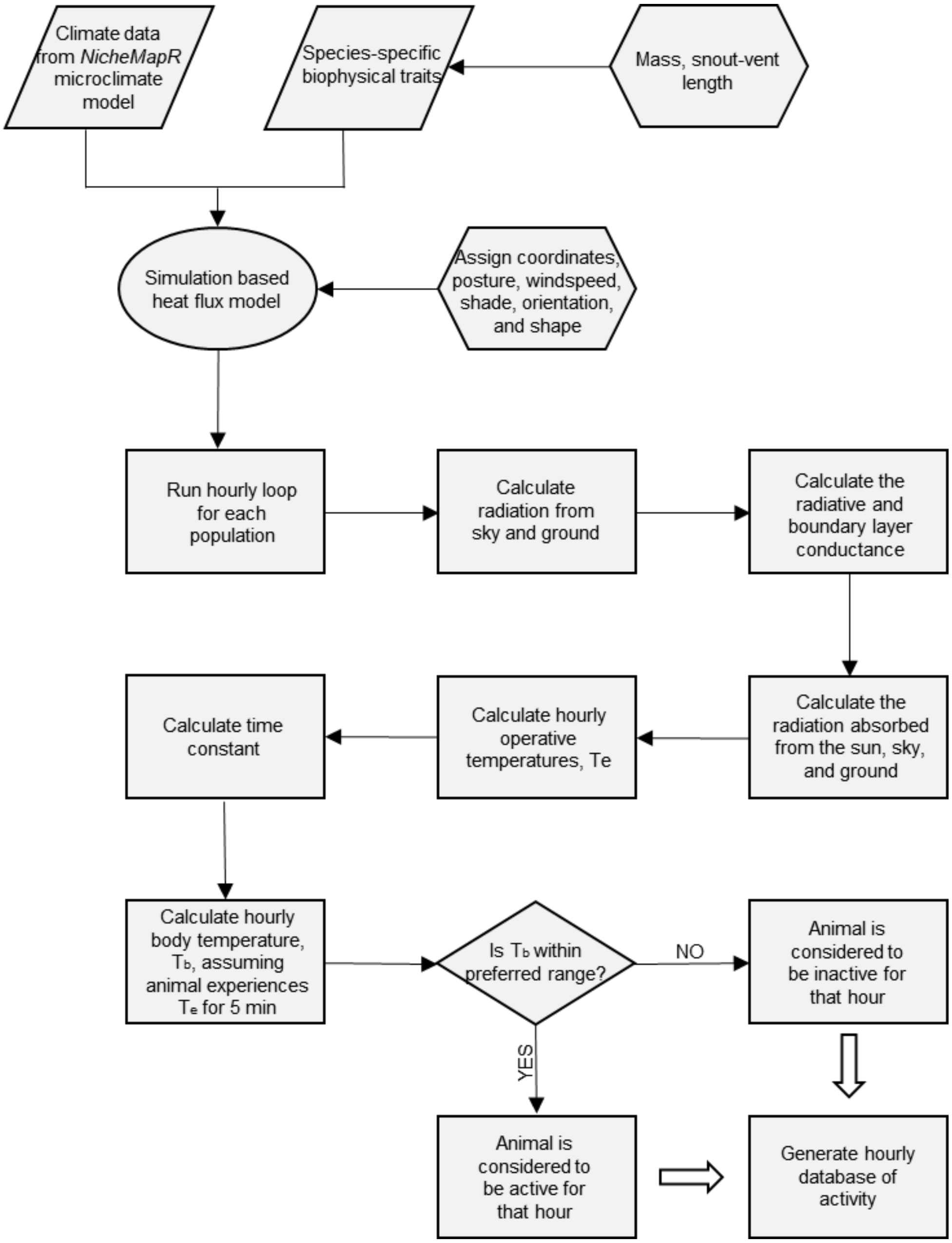


Fig 4.2. Growth data from each population were fit to the logistic by size function (SVL; Blumberg 1968), and the von Bertalanffy function (Bertalanffy 1960). AIC was used to determine that the logistic growth function had the best fit (Akaike 1987). The logistic growth model was then fit to the size at age data for each population sampled and growth rate parameters were retained.

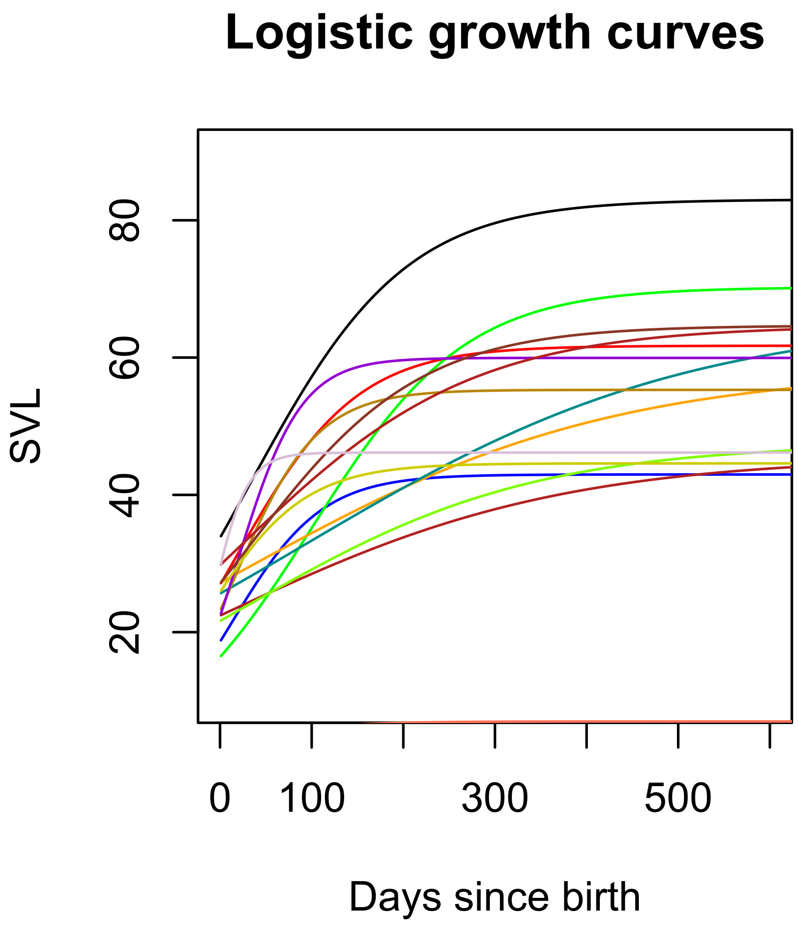


Fig 4.3. Growth data from each population were fit to the logistic by size function (SVL; Blumberg 1968), and the von Bertalanffy function (Bertalanffy 1960). AIC was used to determine that the logistic growth function had the best fit (Akaike 1987). The logistic growth model was then fit to the size at age data for each population sampled and growth rate parameters were retained.

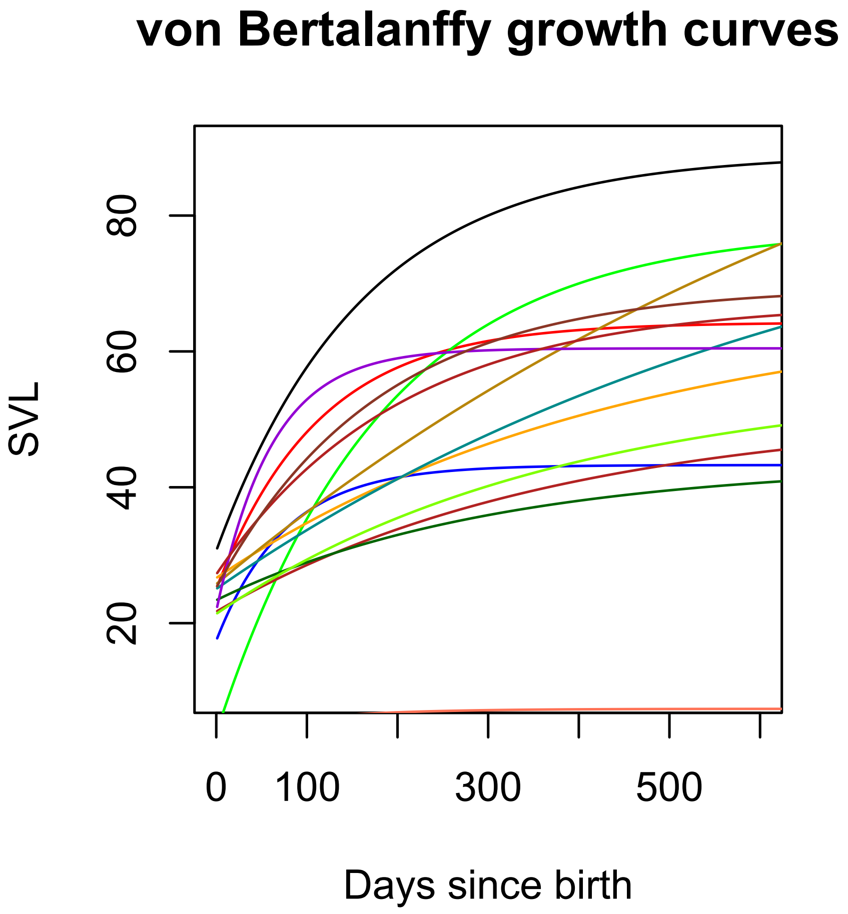


Fig 4.4. Growth data from each population were fit to the logistic by size function (SVL; Blumberg 1968), and the von Bertalanffy function (Bertalanffy 1960). AIC was used to determine that the logistic growth function had the best fit (Akaike 1987). The logistic growth model was then fit to the size at age data for each population sampled and growth rate parameters were retained. Here I show the predicted logistic growth curve (blue line) for all growth trajectory data sampled (red symbols).

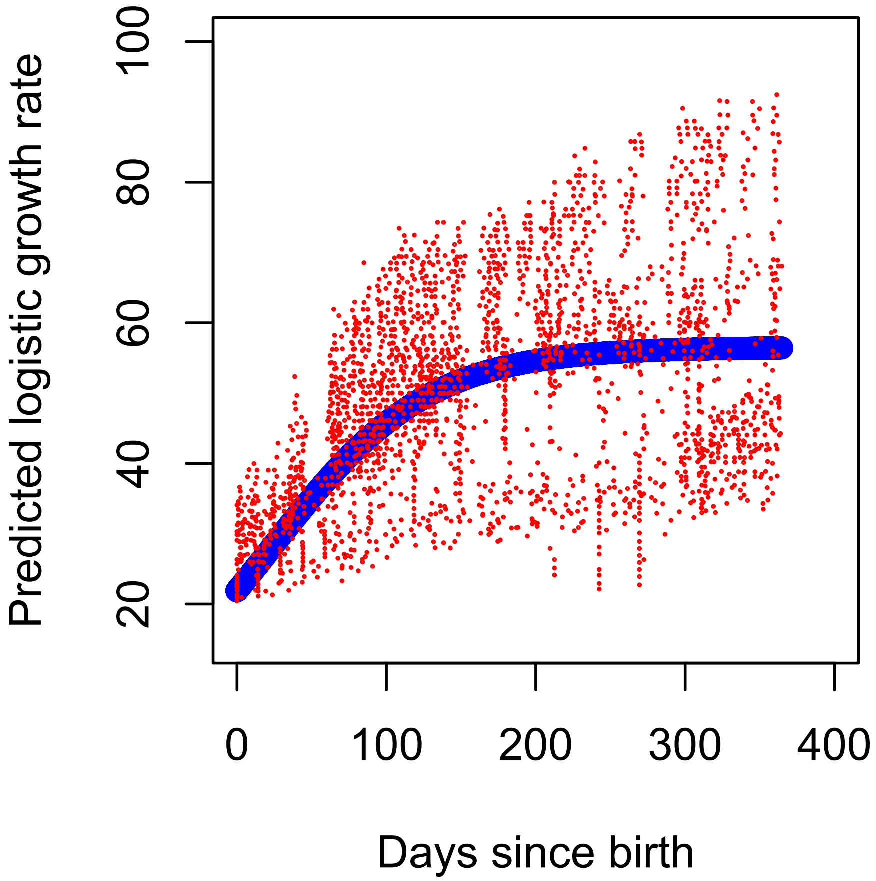


Fig 4.5. Annual activity hours, where computational estimates of lizard body temperatures fell within a species known preferred temperature range (T_{pref} $\bar{x}$ ± 5°C) under current climatic conditions (blue) and under a 3°C uniform warming scenario (red). Under both current conditions and future climates, in lower latitudes (A) and altitudes (C) lizards have larger annual activity windows where preferred body temperatures are available.

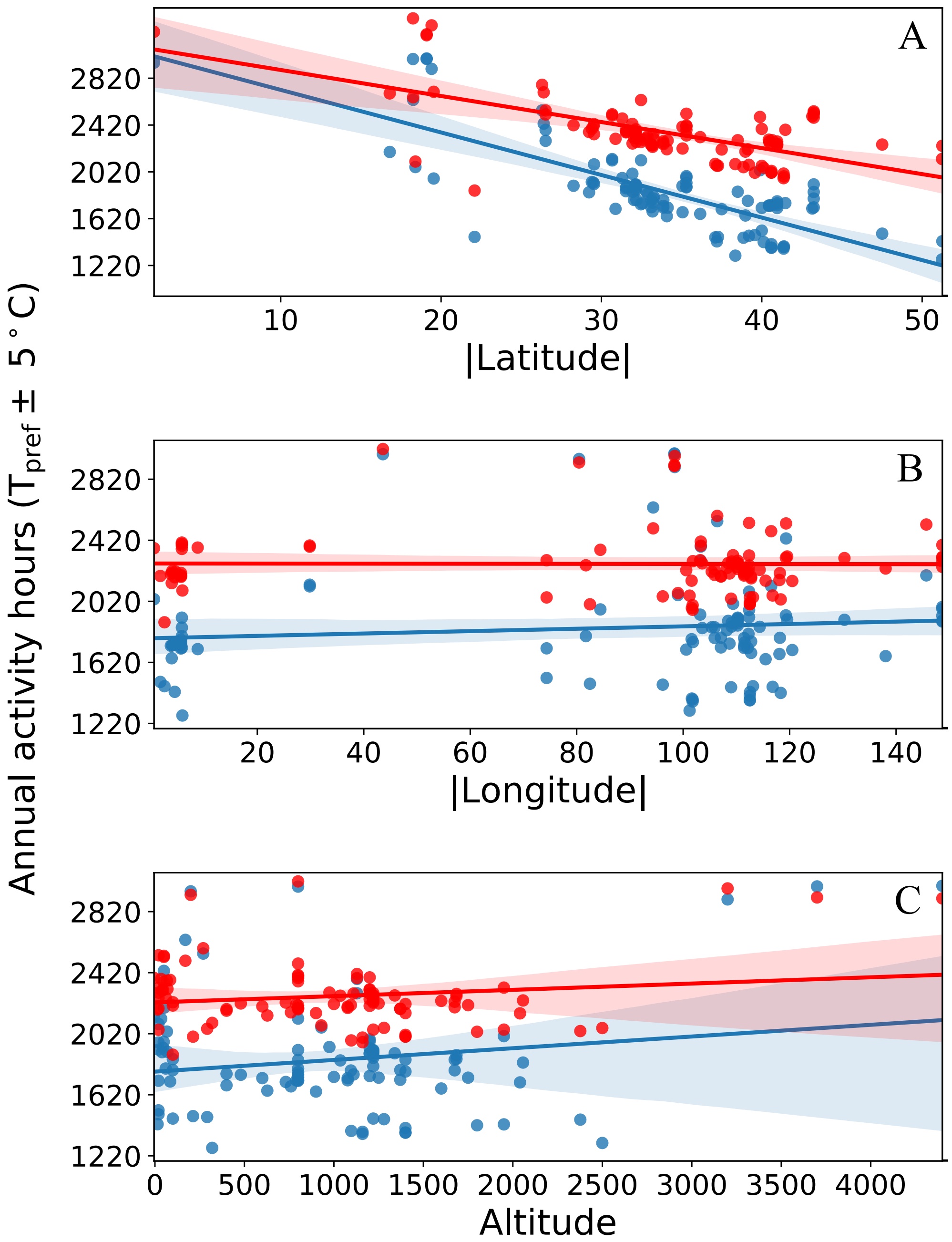


Fig 4.6. Annual activity hours, where computational estimates of lizard body temperatures fell within a species known preferred temperature range (T_{pref} $\bar{x}$ ± 2.5°C) under current climatic conditions (blue) and under a 3°C uniform warming scenario (red). Under both current conditions and future climates, in lower latitudes (A) and altitudes (C) lizards have larger annual activity windows where preferred body temperatures are available. In future climates, lizard populations in lower latitudes are expected to experience a decrease in annual activity times (A).

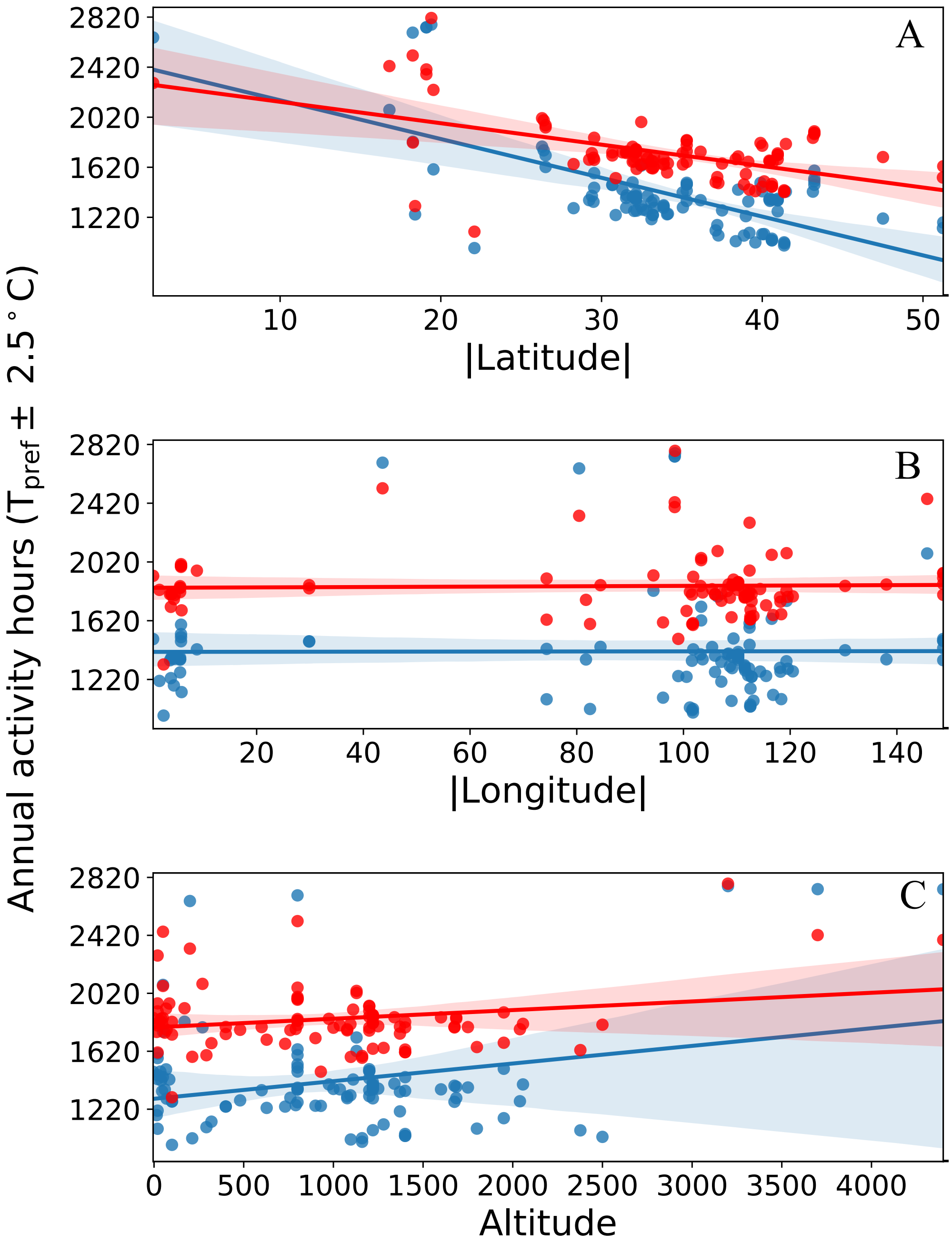


Fig 4.7. Computational estimates of available activity windows did not explain variation in lizard growth rates (A), asymptotic snout-vent length (B), relative clutch mass (C), or reproductive output (D).

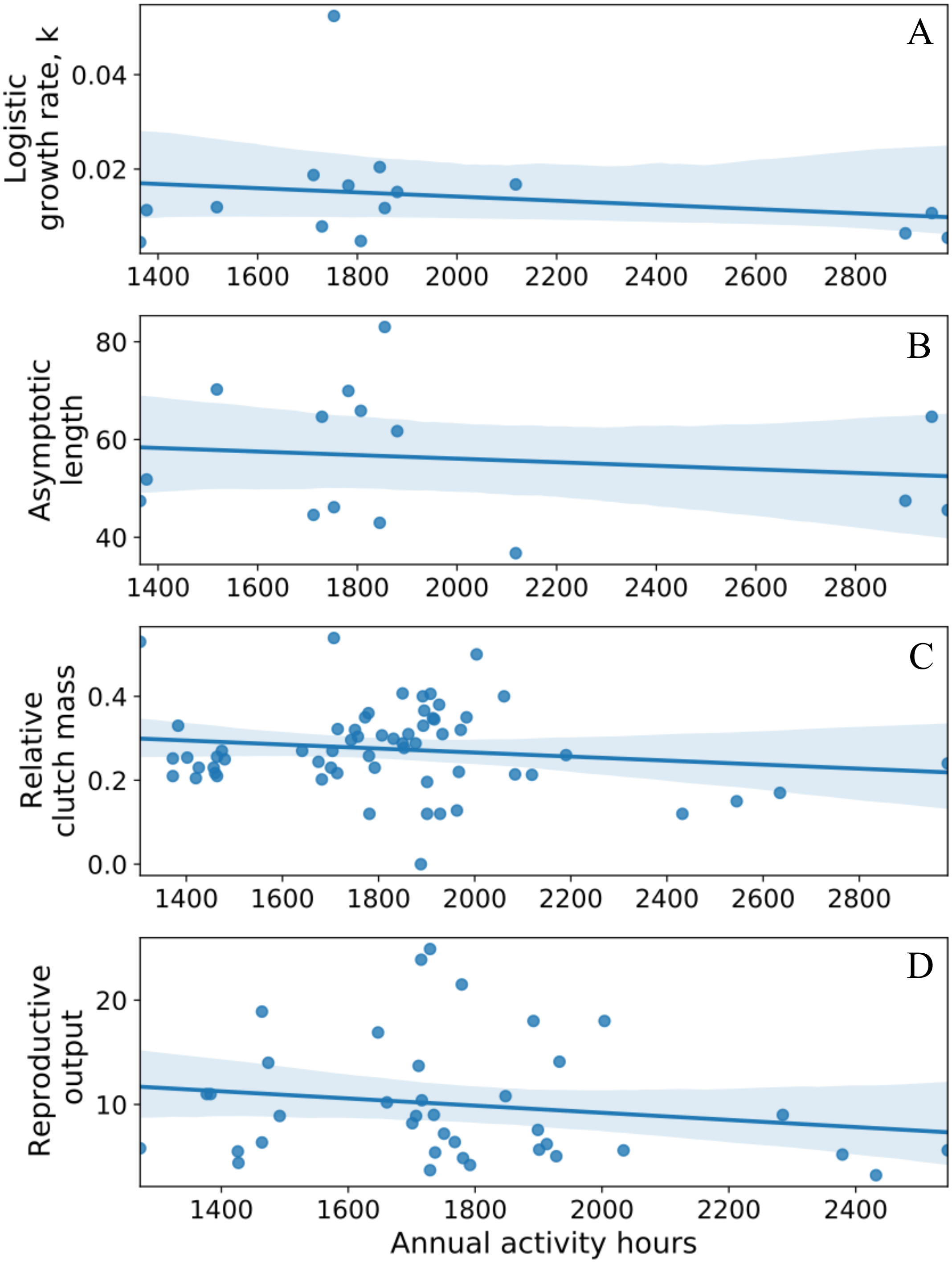


Fig 4.8. The model predicted activity with 64% accuracy in a population of *Sceloporus jarrovii.* The biophysical model predicted activity (blue line) during the day when a body temperature within each species thermal preference range (respective T_{pref} x̅ ± 5°C) was available in either full sun (light red line) or full shade (light blue line). Grey bars denote show thermal preference ranges for each group (T_{pref} x̅ ± 2.5°C).

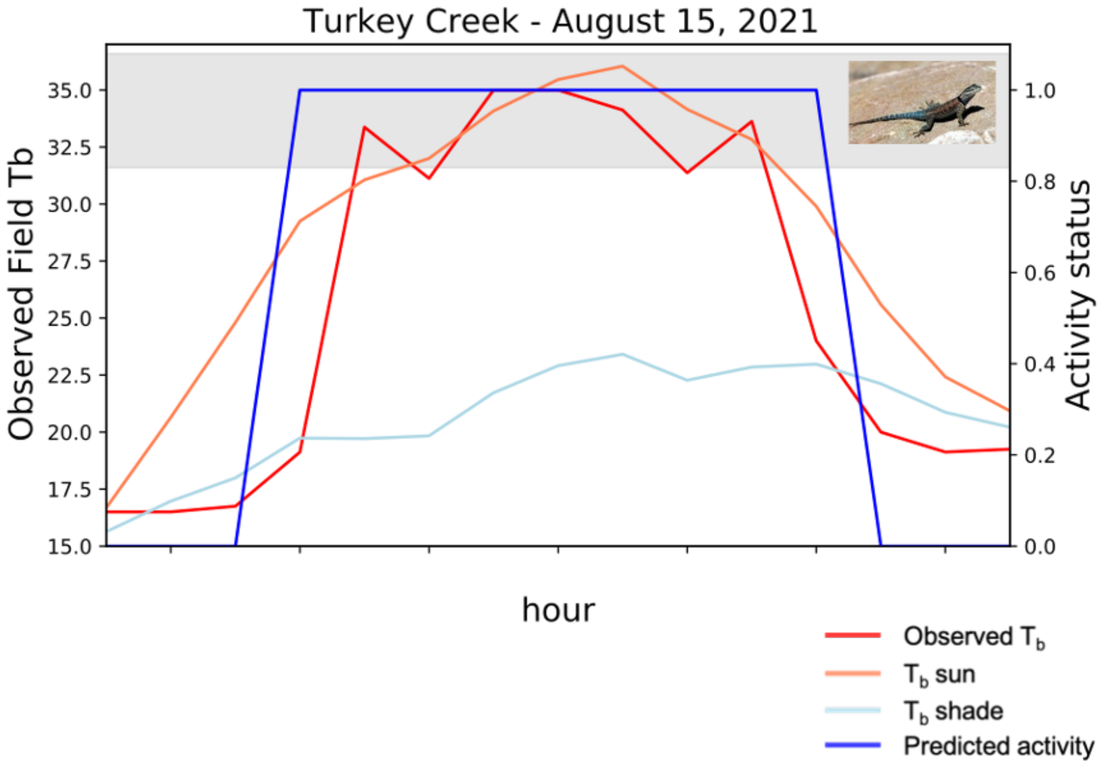
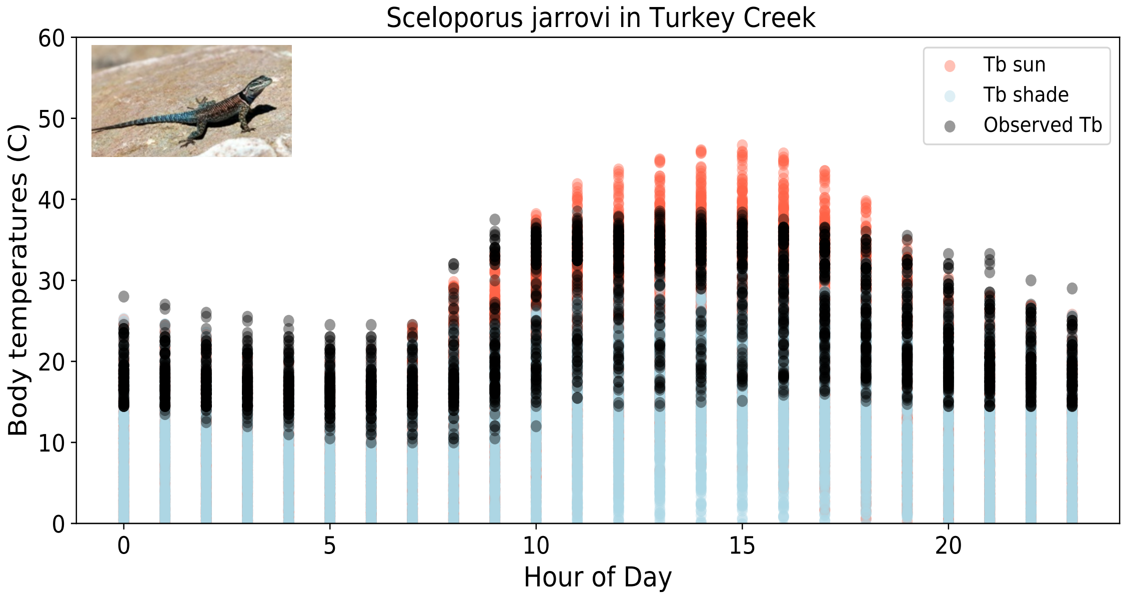


Fig 4.9. Computational estimates of lizard body temperatures in full sun (red symbol) and shade (blue symbol), and observed field-active body temperatures (black symbol) for *Sceloporus jarrovii* lizards from a single population in Turkey Creek, Arizona.



CONCLUSIONS

My dissertation revealed the importance of considering both environmental and organismal factors when studying variation in thermoregulation and subsequent performance to inform predictive models. In chapter one, I found that habitat structure shapes opportunities for thermoregulation in two species of *Anolis* lizards. Lizards living in dense tropical rainforests had high physiological performance over a relatively narrow range of temperatures, due to the low-heterogeneity and subsequently low variation in available microclimates. However, lizards in open patchy environments with high-heterogeneity had access to a wider range of temperatures throughout time, leading to relatively high performance over a broader thermal range. Thermal specialists will likely have reduced performance under climate warming, as low-heterogeneity environments make it more difficult to buffer unfavorable thermal variation via thermoregulation. In chapters two and three I investigated the relationship between body condition, feeding, and thermoregulation in Yarrow's spiny lizards (*Sceloporus jarrovii*) using a combination of lab- and field-based approaches. In the lab experiments, the thermoregulation and thermal preference of lizards was unaffected by both feeding status and animal body condition. When the simulated costs of thermoregulation were elevated, all lizards decreased thermoregulation similarly. However, when lizards were observed in a semi-natural, outdoor thermal arenas, individuals with lower body condition decreased thermoregulation and had a lower mean body temperature. Based on this research, animals with poor body condition may face reduced chances of survival when thermoregulating, because of increased vulnerability to predation. Finally, for chapter four, I conducted a large-scale comparative analysis to quantify relationships between the potential for thermoregulatory performance and empirical measures of productivity (i.e., growth and reproduction) in lizard populations spanning diverse taxonomic groups. Past research has assumed a linear relationship between available activity time—when preferred microclimates are available—and fitness. However, many factors besides thermal conditions shape activity as well, including factors such as predation risk, food availability, and energetic demands. A model that assumes lizards are active whenever preferred temperatures were available vastly overestimated empirical activity times. Studies equating predicted thermoregulatory performance with fitness should be interpreted cautiously, because the minimum activity times required to avoid population declines in the context of climate change will vary based on the physiologies and behaviors of the organisms within each population. Overall, environments and trait impact the thermoregulatory behavior of animals, which ultimately affects their physiological performance and fitness. It is crucial for biologists to consider these complex relationships when modeling the potential impacts of climate change on the future persistence of animal populations.

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APPENDIX A

CO-AUTHOR APPROVAL

All coauthors of published chapters granted permission to use those chapters in this dissertation.