



# Support for the thermal coadaptation hypothesis from the growth rates of *Sceloporus jarrovi* lizards

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## ABSTRACT

The thermal coadaptation hypothesis posits that ectotherms thermoregulate behaviorally to maintain body temperatures ( $T_b$ ) that maximize performance, such as net energy gain. Huey's (1982) energetics model describes how food availability and  $T_b$  interact to affect net energy gain. We tested the thermal coadaptation hypothesis and Huey's energetics model with growth rates of juvenile Yarrow's spiny lizards (*Sceloporus jarrovi*). We compared the preferred (selected)  $T_b$  range ( $T_{sel}$ ) of lizards in high and low energy states to their optimal temperature ( $T_o$ ) for growth over nine weeks, and determined whether the  $T_o$  for growth depended on food availability. We also measured the same lizards' resting metabolic rate at five  $T_b$ s to test the energetics model assumptions that metabolic cost increases exponentially with  $T_b$  and does not differ between energy states. The  $T_{sel}$  of lizards on both diets overlapped with the  $T_o$  for growth. The assumptions of the energetics model were verified, but the  $T_o$  for net energy gain did not depend on food availability. Therefore, we found support for the thermal coadaptation hypothesis. We did not find support for the energetics model, but this may have been due to low statistical power.

## 1. Introduction

Body temperature ( $T_b$ ) governs the behavioral and physiological capacities of ectotherms (e.g., Stevenson et al., 1985). Because ectotherms have limited physiological control over their  $T_b$ , most need to thermoregulate behaviorally to maintain  $T_b$ s that maximize performance and fitness (Huey and Kingsolver, 1989). Reptiles typically strive to maintain their  $T_b$  within a specific range ( $T_{sel}$ , here defined as the central 50% of  $T_b$ s selected in a thermal gradient) that can be achieved when circumstances (e.g., presence of predators) do not constrain temperature selection ( $T_{set}$  in Hertz et al. (1993)). The relationship between  $T_b$  and performance is described by thermal reaction norms, which are characterized by a gradual increase in performance as  $T_b$  increases to an optimal temperature ( $T_o$ ), followed by a rapid decline (Huey and Kingsolver, 1989). According to the thermal coadaptation hypothesis, thermal reaction norms have coevolved with thermal preference so that organisms attain optimal performance at  $T_b$ s within the temperature range normally experienced in the wild (Angilletta, 2009; Licht, 1967). One of the central predictions of this hypothesis is that  $T_o$  falls within  $T_{sel}$ .

While support for the thermal coadaptation hypothesis has been

found for performance measures such as locomotion (Blouin-Demers et al., 2003; Huey and Bennett, 1987; Lelièvre et al., 2010) and digestion (Angilletta et al., 2002; Dorcas et al., 1997), this support is mixed. The strength of support often depends on the species (Blouin-Demers et al., 2003; Halliday and Blouin-Demers, 2015; Huey and Bennett, 1987) or the trait under consideration (Angilletta et al., 2002; Dorcas et al., 1997; Lelièvre et al., 2010). One reason for this mixed support may be that the majority of studies use performance measures assumed to proxy fitness, whereas laboratory performance is often only loosely related to ecological performance and fitness (Irschick, 2003). Anderson et al. (2011) and Halliday and Blouin-Demers (2015) both found a strong association between preferred  $T_b$ s and more ultimate measures of fitness such as reproductive output, lifetime reproductive success, and population growth rate. Another reason for the lack of support may be that a preferred  $T_b$  range that is lower than  $T_o$  may in fact result in higher performance overall (Angilletta, 2009). Martin and Huey (2008) argued that preferred  $T_b$ s should not be centered on the  $T_o$ , but should instead be slightly below it due to the asymmetrical shape of thermal reaction norms and the imprecise nature of thermoregulation. In typical thermal reaction norms, performance increases slowly with  $T_b$  until  $T_o$  and then decreases sharply. Therefore,  $T_b$ s that are higher

Abbreviations: AICc, Akaike's Information Criterion corrected for small sample sizes; GAM, generalized additive model; GMM, generalized additive mixed model; LMM, linear mixed model; RMR, resting metabolic rate; SVL, snout-vent length;  $T_b$ , body temperature;  $T_o$ , optimal temperature;  $T_{sel}$ , preferred body temperature range;  $\dot{V}O_2$ , volume of oxygen consumed

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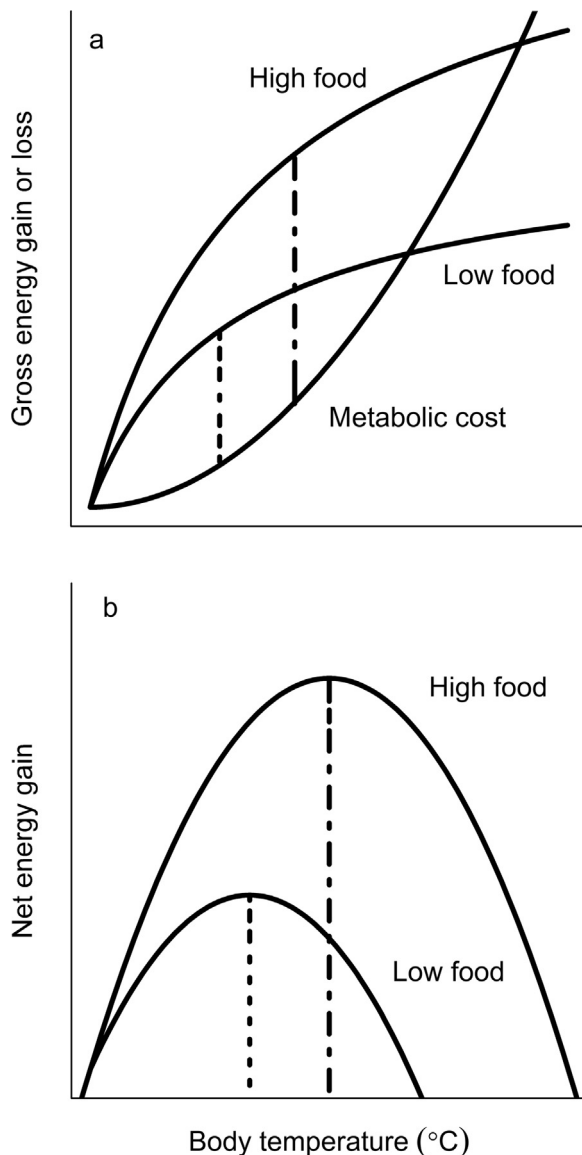


Fig. 1. A visual representation of Huey's (1982) energetics model. (a) Gross energy gain at high and low food availability and metabolic cost as functions of body temperature ( $T_b$ ). (b) Net energy gain (metabolic cost subtracted from gross energy gain) for high and low food availability as a function of  $T_b$ . The  $T_b$  that maximizes net energy gain for each food availability is indicated by a dotted line. Adapted from Huey (1982).

than  $T_o$  depress performance more than  $T_b$ s at an equivalent distance below  $T_o$ . Given that ectotherms thermoregulate imprecisely, an ectotherm preferring  $T_b$ s slightly below  $T_o$  would select fewer  $T_b$ s above  $T_o$  and would thus have a higher performance overall (Martin and Huey, 2008).

Individual growth rate is a more ultimate measure of fitness than the traits generally employed in tests of the thermal coadaptation hypothesis. Ectotherms may thermoregulate to maximize the rate of energy gain and growth. Many species raise their  $T_b$  after feeding (reviewed in Angilletta, 2009), optimize their digestive rate at their preferred  $T_b$  (e.g., Angilletta, 2001), or grow faster when allowed to thermoregulate (e.g., Sinervo and Adolph, 1989, 1994). Food availability also significantly affects energy gain and growth rate in ectotherms (e.g., Dunham, 1978). Based on previous work in salmonids (Brett, 1971), Huey (1982) proposed a model illustrating the relationship between food availability,  $T_b$ , and net energy gain. In this model, the rate at which food is processed (and thus the gross energy gain) increases with  $T_b$  until it reaches a plateau (Fig. 1A). Metabolic cost, in

contrast, increases exponentially with  $T_b$ . The net energy gain (gross energy gain – metabolic cost) therefore increases with  $T_b$  to a maximum and then rapidly decreases (Fig. 1B). At a given  $T_b$ , the gross energy gain increases with food availability, but the metabolic cost remains unchanged. Consequently, the net energy gain should be maximized at a higher  $T_b$  when food availability is higher. Ectotherms should therefore decrease their  $T_b$  when food is restricted to maximize net energy gain. Despite the proposal of Huey's (1982) model decades ago, few studies have tested the concurrent effects of food availability and temperature on energy gain (but see Brett, 1971; Elliott, 1982; Pilditch and Grant, 1999; Atkinson et al., 2006).

The goals of this study were two-fold. First, we tested the thermal coadaptation hypothesis with growth rates of juvenile Yarrow's spiny lizards, *Sceloporus jarrovi*. Growth rate has critical fitness consequences for juveniles of this species: larger juveniles are more likely to escape predators (Sinervo and Adolph, 1989), survive (Fox, 1978), and (in females) reproduce as yearlings (Ballinger, 1979). Thus, we predicted that the growth rate of *S. jarrovi* should be maximized within their  $T_{sel}$ . Second, we tested the central prediction of Huey's (1982) energetics model that the  $T_o$  for net energy gain at high food abundance should be higher than at lower food abundance, as well as two assumptions: (1) resting metabolic rate (RMR) increases exponentially over the  $T_b$  range typically experienced by the species, and (2) at a given  $T_b$ , RMR does not differ between energetic states. We used juvenile growth rate as a metric of net energy gain because juvenile ectotherms devote a significant proportion of their energy budget to growth (e.g., Niewiarowski, 2001; Peterson et al., 1999). We tested the assumptions concerning metabolic cost because RMR may plateau at high temperatures (Beaupré et al., 1993a). Furthermore, as the metabolic rate of many species is depressed during starvation (Wang et al., 2006), long-term food availability may reduce RMR.

We reared juvenile *S. jarrovi* under two food treatments and five temperatures, and measured their growth rate. We measured preferred  $T_b$ s of all the lizards before and after the growth experiment. Finally, we measured the oxygen consumed ( $\dot{V}O_2$ ) at the same temperatures as in the growth experiment, such that each lizard was tested at each temperature.

Although a decrease in the optimum temperature for net energy gain at reduced rations has been established in salmonids (Brett, 1971; Elliott, 1976), we believe our study is the first to test Huey's (1982) model with a terrestrial ectotherm. Furthermore,  $T_{sel}$  is often assumed to match the  $T_o$  for physiological processes such that it coincides with  $T_b$ s that maximize fitness, but this assumption has rarely been tested (Martin and Huey, 2008). We believe that growth rate is a better measure of fitness than those normally employed (Halliday and Blouin-Demers, 2015) and so provides a more stringent test of the thermal coadaptation hypothesis.

## 2. Materials and methods

### 2.1. Study site and species

*Sceloporus jarrovi* is a small lizard that is abundant in rocky habitats in southeastern Arizona and northern Mexico. On 30–31 July 2014, we captured 40 juvenile *S. jarrovi* (14 males, 26 females) by noose in the Chiricahua Mountains, Arizona, USA. We sexed the lizards with a secondary sexual character (enlarged post-anal scales in males), weighed them, and measured their snout-vent length (SVL) with callipers. The hatchlings measured on average ( $\pm$  SD)  $43.2 \pm 5.9$  mm in SVL and  $2.8 \pm 1.1$  g in mass. We estimated that the lizards were 3–9 weeks old upon capture because parturition occurs from late May to early July in this species (Ballinger, 1973). This research was conducted with a State of Arizona Scientific Collection Permit (SP675429), permission from the U.S. Forest Service, and approved by the University of Ottawa's Animal Care Committee (BL-1788).

## 2.2. Housing and lizard care

The lizards were transported to the University of Ottawa, Ottawa, Ontario, Canada, and housed in an environmental chamber. The lizards were housed individually in plastic terraria (30 × 17 × 11 cm) containing newspaper substrate, a water dish, and an opaque plastic tube for shelter. The lizards were provided with water ad libitum and ultraviolet light from 07:00 to 19:00. The environmental chamber operated on a 12 h light: 12 h dark cycle, and cycled between 28 °C during the day and 15 °C at night. Heat tape placed under one end of each terrarium produced a thermal gradient and allowed lizards to thermoregulate. We fed the lizards ad libitum with a 1:1 ratio of crickets (*Gryllos sigillatus*) and mealworms (*Tenebrio molitor*) dusted with a 1:1 mixture of calcium and vitamin powder. We recorded the number of both crickets and mealworms consumed by each lizard. Lizards were maintained in the laboratory for three weeks prior to experiments.

## 2.3. Food and thermal manipulations

We manipulated the diet and thermal environment of 30 lizards (11 males, 19 females) over a nine-week period. We semi-randomly assigned each lizard to a food treatment (high or low food) and temperature treatment (20, 25, 30, 35, or 38 °C), using a balanced study design such that each food × temperature treatment had three lizards, at least one of which was male. Individuals on the high food treatment were fed ad libitum, whereas those on the low food treatment alternated between being fed ad libitum for 48 h and fasted for 48 h (Sinervo and Adolph, 1994). Temperatures cycled between the assigned daytime (09:00 to 16:00) temperature and a night-time (20:00 to 6:00) temperature of 15 °C (Mathies and Andrews, 1997). A temperature data logger (Thermochron iButton D1S1921G-F5, Dallas Semiconductor, Sunnyvale, California) recorded the temperature of each terrarium every 15 min throughout the experiment. Terraria were shuffled periodically to avoid any positional effects (Hurlbert, 1984).

To determine how food consumption was related to temperature and diet, we ran a generalized additive mixed model (GAMM, Wood, 2011) with a negative binomial distribution. The dependent variable was the number of food items consumed weekly, the random effect was lizard ID, and the fixed effects were diet, experimental temperature (smoothed using a thin plate regression spline), mass, and sex. Experimental temperature was calculated as the mean daily high temperature (10:00 to 16:00) over the course of each week.

Given that crickets are higher in protein than mealworms (Bernard et al., 1997) and that the protein content of the diet may influence growth rate, body condition, and metabolic rate (e.g. Avery et al., 1993; Naya et al., 2007; Lee and Roh, 2010), we also determined whether the percentage of crickets consumed by the lizards differed by treatment. We ran a linear model (stats package, R Core Team, 2015) with experimental temperature (categorical) × food treatment as independent variables and the percentage of crickets consumed as the dependent variable. We sequentially removed non-significant variables and selected the most parsimonious model using AIC<sub>c</sub> (Akaike's Information Criterion corrected for small sample sizes, Burnham and Anderson, 2002).

## 2.4. Growth rate

We recorded the mass (± 0.1 g) of each lizard every week over the nine weeks of food and temperature manipulations using a digital scale. The growth rate over this time period was linear, so we calculated the growth rate (g/week) for each lizard from the slope of the linear regression between mass and week. To test the linearity of this relationship, we ran a linear mixed model (LMM, Pinheiro et al., 2015) fitted by maximizing the log-likelihood and with mass as the dependent variable, week as the fixed effect, and lizard ID as the random effect. Repeating our analyses with growth in snout-vent length instead of growth in mass

yielded qualitatively similar results.

## 2.5. Thermal reaction norms

We constructed thermal reaction norms by fitting several non-linear models to the growth data as a function of temperature (e.g., Bulté and Blouin-Demers, 2006, Table A.1). We incorporated the critical thermal maximum and minimum for growth (19.0 and 40.2 °C) into each model. We estimated 19.0 °C from our data because there was very little (if any) growth at 20 °C, and we used 40.2 °C because it is the mean critical thermal maximum value for juvenile *S. jarrovi* (Gilbert and Lattanzio, 2016) and no growth should occur above this temperature. We also ran a GAM with growth rate as the dependent variable and temperature (smoothed using a thin plate regression spline) as the independent variable and compared the AIC<sub>c</sub> of this GAM to the other non-linear models (Table A.1). We used the best nonlinear model (GAM) to predict the T<sub>o</sub> for growth for each diet. To determine the importance of initial lizard mass, sex, and diet on growth rate, we also ran a GAM with growth rate as the dependent variable and temperature (smoothed using a thin plate regression spline), diet, initial mass, and sex as the independent variables. We used model averaging (conditional average) on models with at least moderate support (AIC<sub>c</sub> < 7) to determine the importance of each linear variable (Barton, 2016).

## 2.6. Preferred body temperature

We measured the T<sub>sel</sub> of each lizard three times: twice before the growth experiment (once fed ad libitum and once fasted for 48 h, randomizing the order in which each individual was tested, and once after the growth experiment). We chose 48 h as a fasting period because it is consistent with previous studies of *S. jarrovi* (Beal et al., 2014; Schuler et al., 2011) and closely related species of lizards have been shown to pass food within 48 h of ingestion at preferred body temperatures (Angilletta, 2001; Beaupré et al., 1993b). We used a thermal gradient (Hertz et al., 1993) consisting of a particle board box (122 × 39 × 39 cm) with three laneways. We placed electric heating pads beneath one end to create a range of temperatures (~ 20–45 °C) within the thermal gradient. Lizards were placed individually into laneways at approximately 17:00 and allowed to habituate overnight. The next day, we measured the dorsal surface temperature of each lizard (Bakken, 1992) every 30 min from 08:00 to 16:30 using an infrared thermometer (Fluke 566 IR Thermometer). The thermometer was held in line with the lizard's body axis (Hare et al., 2007), approximately 2 cm above the surface immediately behind its pectoral girdle. We used this method instead of inserting a thermocouple into the cloaca (e.g., Brown and Griffin, 2005) or pressing an infrared thermometer to the cloaca (e.g., Beal et al., 2014) because of the small size of the lizards, and because repeated handling may increase stress and stress-induced increases in preferred T<sub>bs</sub> (Cabanac and Bernieri, 2000; Rey et al., 2015). Moreover, skin temperature is a good proxy for T<sub>b</sub> in other small lizard species (e.g., Bouazza et al., 2016; Hare et al., 2007; Herczeg et al., 2006).

To calculate T<sub>sel</sub>, we used the 25th and 75th percentiles of T<sub>bs</sub> selected by each lizard (Hertz et al., 1993) and averaged each percentile across lizards. To determine whether preferred T<sub>b</sub> depended on energetic state prior to the growth experiment (fed ad libitum vs. fasted for 48 h), we ran two LMMs fitted by maximizing the log-likelihood and with the 25th or 75th percentiles of preferred T<sub>bs</sub> as the dependent variable, lizard ID as the random effect, and energetic state, trial order, lane, and sex as fixed effects. For the post-growth experiment comparison (high vs. low food treatment), we ran linear models with food treatment, experimental temperature, lane, and sex as independent variables and the 25th or 75th percentiles of preferred T<sub>bs</sub> as the dependent variable. In all cases, we applied a 4th-power transformation to improve normality and homogeneity of variance, sequentially removed non-significant variables, and selected the most parsimonious model using AIC<sub>c</sub> (Table A.2).

## 2.7. Metabolic cost

Subsequent to the growth experiment, we quantified the same lizards' RMR at five temperatures using flow-through respirometry. We measured the  $\dot{V}O_2$  and the volume of carbon dioxide produced ( $\dot{V}CO_2$ ) in the following randomized order: 20, 30, 35, 25, and 38 °C. Every lizard was tested at all temperatures and fasted for 48 h prior to each trial to allow gut evacuation (e.g., Angilletta, 2001). There was a mean of 7.3 days (range = 4 to 21) between successive trials.

We placed the lizards in individual airtight respirometry chambers (310 ml) inside a programmable incubator. Incurrent air was scrubbed of  $H_2O$  using a Drierite column, pushed into a multiplexer (MUX-3, Sable Systems International, North Las Vegas, Nevada, USA), through a flow meter (Flow-Bar 8, Sable Systems International), and into one of six respirometry chambers. We dried the excurrent air and measured the  $CO_2$  using an LI-7000 differential analyzer (LI-COR® Biosciences), and the  $O_2$  using an OXZILLA II differential analyzer (Sable Systems International) after removing  $CO_2$  and  $H_2O$ . The flow rate into each container was determined by the lizard's mass and the incubator temperature (Table A.3). An empty reference chamber was measured before each lizard to monitor baseline values. We calibrated the  $O_2$  and  $CO_2$  analysers daily prior to trials.

For the first two hours after the lizards were placed in the respirometry chambers, the incubator temperature ramped from room temperature to the trial temperature and then was stable for one hour prior to measurements to allow the lizards to habituate to the trial temperature. We tested the lizards at two temperatures per night, except for the 38 °C trial. The temperature was ramped to the second temperature over an hour and the lizards were given an additional hour to habituate prior to measurements. All measurements were taken between 19:00 and 7:00 (during the scotophase), every second for 40 min (20, 25 and 30 °C), 60 min (35 °C) or 80 min (38 °C) for every lizard. Trials were longer at higher temperatures because the lizards moved more and longer trials increased the likelihood that RMR could be measured. Two temperature data loggers measured the incubator temperature every 15 min during respirometry trials.

We calculated the  $\dot{V}O_2$  for each temperature and lizard from the two-minute window with the lowest values over the measurement time period. The incubator temperature was calculated as the mean temperature recorded by the two data loggers from the beginning of the acclimation period to the end of the final trial at the given experimental temperature on that date.

To test whether the relationship was exponential, we ran a non-linear mixed model (Pinheiro et al., 2015) with  $\dot{V}O_2 = a \times (b)^{IT}$  as the formula (IT was the incubator temperature, and a and b were estimated to be 0.02 and 0.13, respectively, by the nlme() function) and lizard ID as the random effect. We compared the  $AIC_c$  of this model to that of the comparable LMM fitted by maximizing the log-likelihood. To test whether food treatment affected the RMR, we ran a LMM, fitted by maximizing log-likelihood, with  $\log_{10} \dot{V}O_2$  as the dependent variable, lizard ID as the random effect, and mass, temperature during the growth experiment, and incubator temperature  $\times$  diet as fixed effects. The  $\dot{V}O_2$  was  $\log_{10}$ -transformed to improve normality and homoscedasticity of residuals, but as it still did not meet assumptions, we removed four outliers (confirmed by the influence.measures() function, Fox and Weisberg, 2011). For both datasets (with and without outliers), we sequentially removed variables and selected the most parsimonious model using  $AIC_c$ . Statistical analyses were performed in R 3.2.2 (R Core Team, 2015). To test whether using minimum  $\dot{V}O_2$  values did not produce spurious results, we ran a Pearson correlation between the minimum and the mean of  $\dot{V}O_2$  values measured over the entire time period each lizard was sampled.

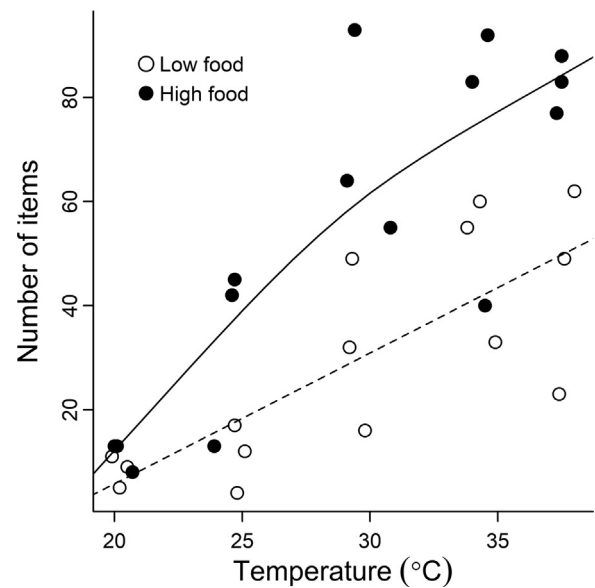


Fig. 2. The total number of food items consumed by *Sceloporus jarrovi* hatchlings ( $n = 30$ ) over nine weeks in relation to ambient temperature and diet. The relationship between items consumed and temperature for each diet, predicted from separate generalized additive models, is represented by a dotted (low food) or solid (high food) line.

## 3. Results

### 3.1. Food items consumed

Food consumption was highly influenced by both food treatment and temperature, and the GAMM model explained a good amount of the variation in the data (adjusted  $R^2 = 0.42$ , scale estimate = 0.3,  $N = 270$  within 30 groups). Lizards on the high food treatment consumed twice as much food (6 vs. 3 items per week) as those on the low food treatment, and ate more as temperature increased, but the quantity of food consumed was independent of mass and sex (Fig. 2, Table A.4). The percentage of the diet consisting of crickets for lizards at 30 °C was 27% higher than for lizards at 20 °C (estimate = 26.8, SE = 9.9,  $t = -2.72$ ,  $P = 0.01$ ). The percentage of crickets consumed did not differ between any other treatments (Table A.4). The model with temperature was more parsimonious ( $AIC_c = 265.7$ ) than either the temperature  $\times$  food treatment ( $AIC_c = 284.1$ ) or temperature + food treatment ( $AIC_c = 269.1$ ) models.

### 3.2. $T_o$ at high vs. low food availability

The prediction from Huey's (1982) model that the  $T_o$  for growth rate at high food availability should be higher than that at low food availability was not supported. Although lizards grew fastest at 32.0 °C and 31.6 °C on the high and low food diets, respectively, growth rate was independent of diet in the averaged GAM model (Table A.4). Growth rate increased to a maximum and then decreased with temperature, but initial mass and sex did not affect growth rate (Fig. 3, Table A.4). The assumption that growth rate over the nine week period was linear was verified because the "week" variable in the LMM between mass and week was highly significant (Table A.5), the  $AIC_c$  of this model (529.5) was smaller than the null model (631.2), and the residual plots showed no patterns indicating nonlinearity. The mean ( $\pm$  SE) growth rate across all temperature and food treatments was  $0.1 \pm 0.009$  g per week (Table A.5), which represents approximately a 2% increase in mass per week for a 4.6 g lizard.



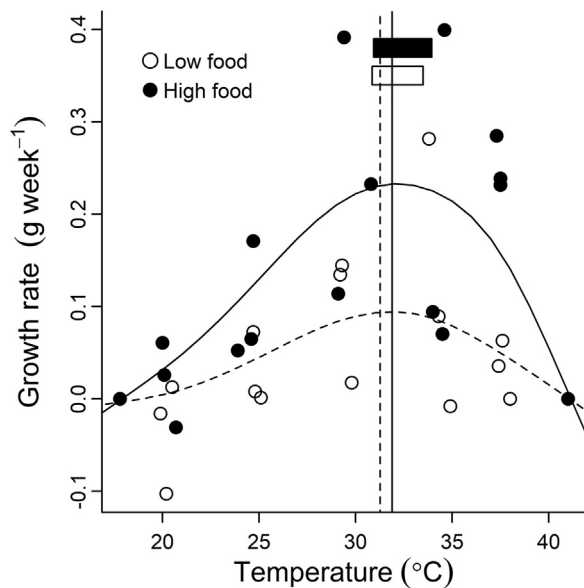


Fig. 3. The growth rate (g/week) of *Sceloporus jarrovi* hatchlings ( $n = 30$ ) in relation to ambient temperature and diet. Low food and high food diets are represented by dotted and solid lines, respectively. The relationship between temperature and each diet is predicted from a separate generalized additive model. The optimal temperature for growth for each diet is indicated by a vertical line. The preferred body temperature range ( $T_{sel}$ ) of lizards in each diet is illustrated as a filled (high food) or hollow (low food) rectangle.

### 3.3. $T_o$ overlap with $T_{sel}$

The prediction of the thermal coadaptation hypothesis that lizards should prefer  $T_b$ s that correspond to the  $T_o$  for growth rate was supported. The  $T_o$  for growth rate (32.0 °C and 31.6 °C for the high and low food diets, respectively: see previous section) fell within  $T_{sel}$  both prior to (lizards fed ad libitum: 30.6–33.2 °C, fasted for 48 h: 30.5–33.1 °C) and after (high food diet: 30.9–34.0 °C, low food diet: 30.9–33.5 °C) experimental manipulations (Fig. 3). Food availability did not affect the bounds of  $T_{sel}$  in either comparison (Tables A.2, A.5). Preferred  $T_b$ s increased with trial order in the short-term comparison, with the lower bound of  $T_{sel}$  increasing from 30.0 to 31.1 °C and the upper bound increasing from 32.5 to 33.9 °C between trials (Table A.5). After long-term exposure to different diets and temperatures, only the temperature manipulation significantly affected the lower bound of  $T_{sel}$ , with lizards who had been exposed to hotter temperatures during the growth experiment preferring cooler temperatures (Table A.5). Sex and lane did not significantly affect preferred  $T_b$  (Table A.2, A.5). Although there were some issues with the normality and homoscedasticity of residuals for all comparisons, we reached the same conclusions for the effect of food availability using non-parametric Kruskal-Wallis tests (lower bound, before manipulations:  $\chi^2 = 0.20$ ,  $DF = 1$ ,  $P = 0.76$ ; upper bound, before manipulations:  $\chi^2 = 0.16$ ,  $DF = 1$ ,  $P = 0.69$ ; lower bound, after manipulations:  $\chi^2 = 0.10$ ,  $DF = 1$ ,  $P = 0.76$ ; upper bound, after manipulations:  $\chi^2 = 0.15$ ,  $DF = 1$ ,  $P = 0.70$ ).

### 3.4. Metabolic cost assumptions

The assumption that the RMR increases exponentially with temperature was verified because the exponential model (30.6) had a lower AIC<sub>c</sub> value than the LMM (134.7) and the  $\log_{10} \dot{V}O_2$  increased linearly with incubator temperature (Fig. 4, Table A.6, A.7). The assumption that metabolic cost does not differ between diets was also verified because  $\dot{V}O_2$  was independent of diet (Table A.6) in the reduced dataset. Larger lizards had higher RMRs (Table A.7), but RMR was unaffected by the lizards' treatment temperature during the growth experiment. Diet and an incubator temperature  $\times$  diet interaction were both present in

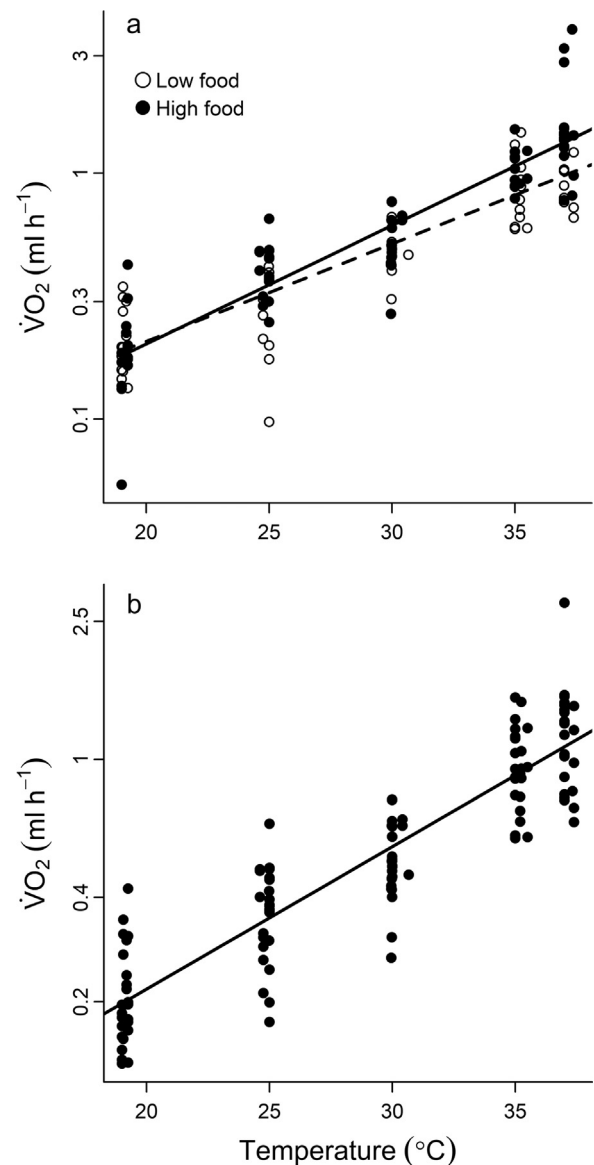


Fig. 4. The volume of oxygen produced ( $\dot{V}O_2$ , ml/hour) at rest by juvenile *Sceloporus jarrovi* ( $n = 27$ ) during respirometry trials at different ambient temperatures, with (a) the full dataset and (b) after removal of four outliers ( $r^2 = 0.82$ ). Note that the log scale is used on the y axis in both panels. In panel (a), the dotted and solid lines represent the slopes for the low ( $r^2 = 0.78$ ) and high ( $r^2 = 0.80$ ) food diets, respectively.

equally plausible models, but neither were significant (Table A.7). The full dataset indicated that the relationship between  $\dot{V}O_2$  and incubator temperature depended on diet (Table A.6, A.7), with  $\dot{V}O_2$  increasing with temperature at a faster rate in lizards on the high food diet (Fig. 4). As this model did not meet assumptions and the relationship disappeared when four outliers were removed, however, we considered the results from the reduced dataset to be more probable. The minimum and mean  $\dot{V}O_2$  values were strongly correlated ( $r = 0.96$ ), indicating that the minimum  $\dot{V}O_2$  values were a representative measure of resting metabolic rate.

## 4. Discussion

According to the thermal coadaptation hypothesis, ectotherms should choose  $T_b$ s that maximize performance and fitness (reviewed in Angilletta (2009)). In this experiment, we tested the thermal coadaptation hypothesis and Huey's (1982) energetics model with growth rates of juvenile *S. jarrovi*. The prediction that the  $T_o$  for growth rate

falls within  $T_{sel}$  (thermal coadaptation hypothesis) was supported, but the prediction that the  $T_o$  depends on food availability (energetics model) was not. Nevertheless, the assumptions that metabolic cost increases exponentially with temperature and is independent of diet (Huey, 1982) were verified.

Firstly, the prediction that the growth rate of *S. jarrovi* is maximized at the  $T_{sel}$  for their energetic state was supported. Both prior to and after thermal and diet manipulations, the  $T_{sel}$  of lizards overlapped with the  $T_o$  for growth rate in both energetic states. Moreover, lizards always preferred similar  $T_b$ s, regardless of their short- or long-term energetic state. Although many studies have found that preferred  $T_b$ s increase after feeding in reptiles (e.g., Blouin-Demers and Weatherhead, 2001; Brown and Griffin, 2005; Sievert and Andreadis, 1999), others found no effect (e.g., Mullens and Hutchison, 1992; Schuler et al., 2011). We also found no effect of energetic state on  $T_{sel}$ , which suggests that the benefit of lowering  $T_b$  in response to low food in our study was not great enough to warrant a change in behavior. In the thermal gradients before the growth experiment, it is possible that the lizards still had residual food in the gut after 48 h if the cool night temperatures slowed digestion (Angilletta, 2001). If the lizards were still digesting during the thermal gradient experiment, they may not have adjusted their  $T_{sel}$  while “fasting.” However, we obtained the same result once lizards were on high- and low-food diets for several weeks. Thus, we believe that the lizards failed to alter their  $T_{sel}$  when in a low energetic state because the  $T_o$  for net energy gain was only 0.4 °C lower on the low food diet, both  $T_o$  values fell within the  $T_{sel}$  of lizards fed ad libitum, and lizards often thermoregulate imprecisely (Martin and Huey, 2008). Indeed, Brown and Griffin (2005) argued that the decrease in  $T_b$  following food deprivation would only lead to a 3% decrease in metabolic rate in *Anolis carolinensis* and thus have negligible impacts on energy gain.

Martin and Huey (2008) predicted that preferred  $T_b$ s should be slightly below  $T_o$  due to the asymmetrical shape of the thermal reaction norm. However, our findings corroborated the original prediction of the thermal coadaptation hypothesis that  $T_o$  would fall within  $T_{sel}$  (Angilletta, 2009; Licht, 1967). High preferred  $T_b$ s and thermal tolerances may enable juvenile *S. jarrovi* to be active when it is too hot for adults. Juveniles of this species have a higher preferred  $T_b$ , critical thermal maximum, and  $T_o$  for stamina than adults (Gilbert and Lattanzio, 2016) and remain active later into the day (Simon and Middendorf, 1976). Since adults act aggressively towards juveniles (Ruby, 1978), it may be beneficial for juveniles to be active when there are few active adults. Juveniles are born during the hottest period of the year (May–August) and so they may need to remain active at higher temperatures to meet energetic demands for growth, even if these temperatures are close to their upper thermal limit. Furthermore, the relationship we found between temperature and growth rate does not appear strongly asymmetrical (Fig. 3), which Martin and Huey (2008) state as a scenario where organisms may not be expected to prefer  $T_b$ s below  $T_o$ .

We did not have the data to test another key prediction of the thermal coadaptation hypothesis, that the  $T_o$  for growth should fall within the range of commonly experienced field  $T_b$ s (Angilletta, 2009; Licht, 1967). A study on juvenile *S. jarrovi* from a nearby mountain chain found that the mean  $\pm$  SE of field  $T_b$ s was  $32.6 \pm 0.3$  °C (Gilbert and Lattanzio, 2016). Our  $T_o$  values (32.0 and 31.6 °C) are within 1 °C of this calculated mean field  $T_b$ . Given that ectotherms tend to thermoregulate imprecisely (Martin and Huey, 2008), the  $T_o$  for growth likely falls within the range of commonly experienced field  $T_b$ s. Although we cannot conclude that the  $T_o$  for growth falls within the range of commonly experienced field  $T_b$ s with the available evidence, we strongly suspect that this prediction of the thermal coadaptation hypothesis would also be supported.

Secondly, the central prediction of Huey's (1982) model that the  $T_o$  for net energy gain is higher at high food abundance was not supported. Although the  $T_o$  for growth rate at high food availability was 0.4 °C higher than the  $T_o$  at low food availability, lizards did not grow faster when more food was available, despite eating more. This contrasts with the finding

that the  $T_o$  for growth increases with food availability in salmonids (Brett, 1971; Elliott, 1976). Our results suggest either (1) that the difference in food consumption between diets was not large enough to incur a difference in growth rate in our experiment, (2) that the shapes of the gross energy gain or energy loss curves (Fig. 1A) are inaccurate for terrestrial ectotherms, or (3) that we had insufficient power to detect a difference. The difference in food consumption between diets may not have been large enough to incur a difference in growth rate. Lizards on the high food diet in our experiment consumed nearly twice more food on average than those on the low food diet. While it is possible that this difference was not large enough to cause differences in growth rate in *S. jarrovi*, the same food treatments incurred a difference in growth rate in other *Sceloporus* lizards (Sinervo and Adolf, 1994) allowed to thermoregulate nine hours per day. It is also possible that the lack of difference in  $T_o$  for growth between diets is due to a difference in energy loss curves (Fig. 1A) because the effect of incubator temperature on RMR depended on diet when we used the full dataset. This is an unlikely explanation, however, because the interaction was driven by four outliers and because RMR increased exponentially over the temperature range in both cases. It is more likely that the gross energy gain curves differ from Huey's (1982) model (Fig. 1A) due to acclimation to thermal or food manipulations, which would enable more efficient performance in response to food shortage or ambient temperature (Angilletta, 2009). In fact, it appears (qualitatively) that the food consumed by *S. jarrovi*, particularly at low food availability, does not plateau at higher temperatures (Fig. 2). We cannot rule out the possibility that our failure to detect a difference in growth rate between food treatments is due to a lack of statistical power. Although lizards on the high food diet consumed nearly twice as much food on average, the difference was smaller at low temperatures. The passage of food in the gut is slow at low temperatures (Angilletta, 2001) and the resulting convergence of growth rate between diets at low temperatures may have reduced our ability to detect an effect of diet on growth. Furthermore, the variation in growth rate among lizards within treatments was fairly high (Fig. 3). Further studies with larger sample sizes would increase the ability to detect a difference if it indeed exists.

Thirdly, the assumptions of Huey's (1982) energetics model were verified. The exponential increase in RMR confirmed the appropriateness of the temperature range used in our study (Beaupré et al., 1993a). Moreover, long-term food availability did not affect the RMR of the lizards in this study. The RMR of an ectotherm depends on food intake, as it increases after feeding (e.g., Wang et al., 2001), and is depressed during periods of starvation (Wang et al., 2006). The magnitude of the change in metabolic rate after feeding varies among species and correlates with meal size and hypertrophy of the gastrointestinal tract (Wang et al., 2001). This suggests that the fasting period (48 h) within each 4-day period in this study may not have been long enough to trigger significant physiological changes in *S. jarrovi*.

While it is possible that the ratio of crickets to mealworms consumed may also have contributed to the rapid growth rates of lizards in the 30 °C treatments (e.g., Avery et al., 1993), we believe its effect was negligible compared to the volume of food consumed. The only significant difference in the proportion of the diet consisting of crickets occurred between the lizards at 30 °C and 20 °C, and the effect of food volume (average of 52 food items at 30 °C vs. 10 at 20 °C) was likely more important at fueling growth than the protein content of the diet.

#### 4.1. Conclusions

In summary, we found strong support for the thermal coadaptation hypothesis, but none for Huey's (1982) energetics model. The support for the prediction that organisms prefer  $T_b$ s that coincide with the  $T_o$  for growth rate is consistent with other studies in which more ultimate measures of fitness were used (reviewed in Halliday and Blouin-Demers (2015)). Given that lizards thermoregulate imprecisely, they may not alter their  $T_{sel}$  to match a 0.4 °C decline in  $T_o$  for growth rate. Alternatively, juveniles may not lower their preferred  $T_b$ s in response to food

deprivation because they need to be active at suboptimal high temperatures to enhance growth prior to the onset of winter. More studies using ultimate measures of fitness to test the thermal coadaptation hypothesis are required to elucidate how thermal preference directly impacts fitness. We found no support for Huey's (1982) energetics model, which may be due to lack of power or to differences in the gross energy curves, if there was acclimation of digestive efficiency to thermal and/or dietary conditions (Angilletta, 2009). To determine whether the energetics model holds on a shorter timescale with less chance for acclimation, further studies with larger sample sizes should estimate the gross energy gain curves directly, for example by measuring metabolizable energy intake (Angilletta, 2001) of ectotherms on different diets and at multiple temperatures. A more complete

understanding of the interactions between temperature and food availability, thermoregulation, and growth rate may provide insights into the potential impacts of climate change on the fitness and persistence of ectotherms (e.g., Gilbert and Miles, 2016).

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### Appendix A. Model selection tables, parameter estimates for equally plausible models, and additional tables

(See Tables A1–A7).

**Table A.1**

Model selection for non-linear functions describing thermal reaction norms for growth rate in *Sceloporus jarrovi*, showing the Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) and the difference between the  $AIC_c$  of each model and the model with the lowest  $AIC_c$  ( $\Delta AIC_c$ ). The model with the lowest  $AIC_c$  is bolded.  $b_0$  to  $b_4$  are the parameters estimated in each model, and  $T$  is the experimental temperature.

Model	$AIC_c$	$\Delta AIC_c$
Quartic: $b_0 + b_1 T + b_2 T^2 + b_3 T^3 + b_4 T^4$ Stevenson et al. (1985):	– 48.05	14.64
Logistic $\times$ exponential decay: $b_0 \left( \frac{1}{1 + b_1 e^{-b_2(T-19.0)}} \right) (1 - e^{b_3(T-40.2)})$ Stevenson et al. (1985):	– 51.32	11.37
Exponential decay + exponential: $b_0 + (1 - e^{-b_1(T-19.0)}) + (1 + e^{b_2(T-40.2)})$ Ratkowsky et al. (1983):	– 51.09	11.6
Linear $\times$ exponential decay: $(b_0(T - 17.8))(1 - e^{b_1(T-41)})$	– 55.64	7.05
<b>Generalized Additive Model</b>	<b>– 62.69</b>	<b>0</b>

**Table A.2**

Model selection for the upper and lower limits of the preferred body temperature range of *Sceloporus jarrovi* in relation to energetic state (Food), sex, the lane of the thermal gradient, trial order (1 or 2), temperature ( $T$ ) and diet during the growth experiment; before and after the growth experiment. All models contained lizard ID as a random effect and were fit by maximizing the log-likelihood.  $AIC_c$  is the Akaike's Information Criterion corrected for small sample size for that model, and the  $\Delta AIC_c$  is the difference between the  $AIC_c$  of each model and the model with the lowest  $AIC_c$ . The bolded models have the lowest  $AIC_c$ .

Model independent variables	$AIC_c$	$\Delta AIC_c$
<b>Prior To, Lower:</b>		
Food + Sex + Lane + Trial	1863.4	5.7
Food + Lane + Trial	1860.8	3.1
Lane + Trial	1858.7	1.0
<b>Trial</b>	<b>1857.7</b>	<b>0</b>
<b>Prior To, Upper:</b>		
Food + Sex + Lane + Trial	1878.4	4.7
Food + Lane + Trial	1876.0	2.3
<b>Lane + Trial</b>	<b>1873.7</b>	<b>0</b>
Trial	1873.9	0.2
<b>After, Lower:</b>		
(Diet $\times$ T) + Sex + Lane	774.0	19.7
(Diet $\times$ T) + Lane	769.3	15.0
Diet + T + Lane	769.8	15.5
T + Lane	765.0	10.7
<b>T</b>	<b>754.3</b>	<b>0</b>
<b>After, Upper:</b>		
(Diet $\times$ T) + Sex + Lane	770.9	16.1
Diet + T + Sex + Lane	765.7	10.9
T + Sex + Lane	760.5	5.7
T + Lane	757.2	2.4
<b>T</b>	<b>754.8</b>	<b>0</b>
1	755.0	0.2

**Table A.3**

The air flow rate used for each lizard mass range and incubator temperature range during respirometry trials on *Sceloporus jarrovi*.

Mass (g)	Flow Rate (ml/min)	
	20–35 °C	38 °C
2.9–3.9	40	50
4.0–4.9	50	60
5.0–5.9	55	65
6.0–6.9	60	70
7.0–7.9	70	80
8.0–8.9	75	85
9.0–10.9	80	90

**Table A.4**

Parameter estimates for models for the lizards' growth rate, weekly number of food items consumed, and percentage of crickets in the diet, when subjected to different food and temperature treatments over nine weeks. Growth rate models are the most parsimonious (T) and averaged generalized additive models, as determined by AIC<sub>c</sub> comparison. The diet composition model is a linear model showing comparisons between all temperature treatments. The food items model is a generalized additive mixed model with a negative binomial distribution and lizard ID as a random effect. Experimental temperature is smoothed (s(T)) using a thin plate regression spline. Effective degrees of freedom (edf), estimated residual degrees of freedom (ref.df), and F-values are given for smoothed variables; and Estimate, standard error (SE) and t-values are given for parametric variables. Parameter estimates, SE and z-values are given for the averaged growth rate model.

Model	Variable	edf or Estimate	ref.df or SE	F, t or z	P
<b>Growth Rate</b>					
a) T	s(T)	2.96	3.57	9.19	< 0.0001
a) Averaged	s(T).1	−0.10	0.05	1.72	0.08
	s(T).2	0.06	0.13	0.49	0.62
	s(T).3	−0.05	0.06	0.82	0.41
	s(T).4	−0.03	0.09	0.31	0.76
	s(T).5	−0.02	0.02	0.83	0.40
	s(T).6	0.05	0.05	0.87	0.38
	s(T).7	0.02	0.02	0.88	0.38
	s(T).8	0.23	0.15	1.50	0.13
	s(T).9	−0.09	0.06	1.36	0.17
	Diet (Fasted)	−0.03	0.02	1.37	0.17
	Initial Mass	−0.001	0.02	0.09	0.92
	Sex (Male)	−0.003	0.04	0.07	0.94
<b>Food Items Consumed</b>	s(T)	1	1	53.05	< 0.0001
	Diet (Fasted)	−0.64	0.18	−3.52	0.0005
	Mass	0.02	0.05	0.45	0.65
	Sex	0.13	0.17	0.76	0.45
<b>Diet Composition</b>					
a) vs. 20 °C	T(25)	7.7	9.9	0.8	0.44
	T(30)	26.8	9.9	2.7	0.01
	T(35)	13.9	9.9	1.4	0.17
	T(38)	8.1	9.9	0.8	0.42
a) vs. 25 °C	T(30)	19.1	9.9	1.9	0.06
	T(35)	6.2	9.9	0.6	0.54
	T(38)	0.4	9.9	0.04	0.97
a) vs. 30 °C	T(35)	−1.3	9.9	−1.3	0.20
	T(38)	−18.7	9.9	−1.9	0.07
a) vs. 35 °C	T(38)	−5.8	9.9	−0.6	0.56

**Table A.5**

Parameter estimates for equally plausible linear models and linear mixed models for the determination of factors affecting lizards' mass over time and the preferred body temperature range, as determined through AIC<sub>c</sub> model comparison. All analyses (with mass or the bounds of the preferred body temperature range (Preferred T<sub>b</sub>, with a 4th-power transformation) as dependent variables) had the lizard ID as a random effect and were fitted by maximizing log-likelihood. Week is the number of weeks since the beginning of the growth experiment, T is the growth experimental temperature, and Trial is the trial order. For simplification, we show the ANOVA output for models including Lane.

Model	Variable	Value	SE	DF	T or F	P
<b>Mass</b>	Week	0.10	0.009	269	11.21	< 0.0001
<b>Preferred T<sub>b</sub></b>						
(Prior, Lower)						
a) Trial + Lane	Trial			1, 27	13.53	0.001
	Lane			5, 27	2.12	0.09
a) Trial	Trial	189907	532546	32	3.57	0.001

(continued on next page)



Table A.5 (continued)

Model	Variable	Value	SE	DF	T or F	P
<b>Preferred <math>T_b</math> (Prior, Upper)</b>						
a) Trial + Lane	Trial			1, 27	11.02	0.003
	Lane			5, 27	2.36	0.07
a) Trial	Trial	202792	64376	32	3.15	0.004
<b>Preferred <math>T_b</math> (After, Lower)</b>	T	−31588	14335	1, 24	−2.20	0.04
<b>Preferred <math>T_b</math> (After, Upper)</b>	T	−23739	14490	1, 24	−1.638	0.11

Table A.6

Model selection for the  $\log_{10}$ -transformed volume of oxygen consumed ( $\dot{V}O_2$ ) in relation to incubator temperature (IT), growth experiment treatment temperature (T), diet, and mass in *Sceloporus jarrovi*.

Model Independent Variables	AIC <sub>c</sub>	$\Delta AIC_c$
<b><math>\log_{10} \dot{V}O_2</math> (Full Dataset)</b>		
IT + Diet + Mass + T + (IT × Diet)	−135.12	1.07
IT + Diet + Mass + (IT × Diet)	<b>−136.27</b>	<b>0</b>
<b><math>\log_{10} \dot{V}O_2</math> (Reduced Dataset)</b>		
IT + Diet + Mass + T + (IT × Diet)	−196.26	3.56
IT + Diet + Mass + (IT × Diet)	−198.11	1.71
IT + Diet + Mass	−198.05	1.77
<b>IT + Mass</b>	<b>−199.82</b>	<b>0</b>

Table A.7

Parameter estimates for equally plausible linear mixed models for the determination of the factors affecting resting metabolic rate, as determined through AIC<sub>c</sub> model comparison. All analyses had the volume of oxygen consumed ( $\dot{V}O_2$ ) as a dependent variable, lizard ID as a random effect, and were fitted by maximizing log-likelihood. IT is the incubator temperature and T is the growth experimental temperature.

Model	Variable	Value	SE	DF	T or F	P
<b><math>\log_{10} \dot{V}O_2</math> (Full Dataset)</b>						
a) IT + Diet + Mass + T + (IT × Diet)	IT	0.05	0.002	101	19.04	< 0.0001
	Diet	0.24	0.107	23	2.25	0.03
	Mass	0.04	0.008	101	4.11	0.0001
	T	−0.003	0.003	23	−1.05	0.31
	IT × Diet	−0.008	0.003	101	−2.31	0.02
a) IT + Diet + Mass + (IT × Diet)	IT	0.05	0.002	101	19.17	< 0.0001
	Diet	0.24	0.107	24	2.20	0.04
	Mass	0.03	0.007	101	4.21	0.0001
	IT × Diet	−0.008	0.003	101	−2.33	0.02
<b><math>\log_{10} \dot{V}O_2</math> (Reduced Dataset)</b>						
a) IT + Diet + Mass + (IT × Diet)	IT	0.04	0.002	97	21.43	< 0.0001
	Diet	0.14	0.084	24	1.63	0.12
	Mass	0.03	0.005	97	5.78	< 0.0001
	IT × Diet	−0.004	0.003	97	−1.50	0.14
a) IT + Diet + Mass	IT	0.04	0.001	98	29.22	< 0.0001
	Diet	0.02	0.026	24	0.65	0.52
	Mass	0.03	0.005	98	5.87	< 0.0001
a) IT + Mass	IT	0.04	0.001	98	29.40	< 0.0001
	Mass	0.03	0.005	98	6.27	< 0.0001

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