



Interindividual Variation in Thermal Sensitivity of Maximal Sprint Speed, Thermal Behavior, and Resting Metabolic Rate in a Lizard

Author(s): Paulina Artacho, Isabelle Jouanneau, and Jean-François Le Galliard

Source: *Physiological and Biochemical Zoology*, Vol. 86, No. 4 (July/August 2013), pp. 458-469

Published by: [The University of Chicago Press](#)

Stable URL: <http://www.jstor.org/stable/10.1086/671376>

Accessed: 11/10/2013 22:19

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press is collaborating with JSTOR to digitize, preserve and extend access to *Physiological and Biochemical Zoology*.

<http://www.jstor.org>

Interindividual Variation in Thermal Sensitivity of Maximal Sprint Speed, Thermal Behavior, and Resting Metabolic Rate in a Lizard

Paulina Artacho^{1,2,*}

Isabelle Jouanneau²

Jean-François Le Galliard^{2,3}

¹Instituto de Ciencias Ambientales y Evolutivas, Campus Isla Teja, Universidad Austral de Chile, Valdivia, Chile; ²Centre de Recherche en Ecologie Expérimentale et Prédictive (CEREEP)—Ecotron IleDeFrance, Unité Mixte de Service 3194, École Normale Supérieure, Centre National de la Recherche Scientifique (CNRS), 78 rue du Château, 77140 St-Pierre-lès-Nemours, France; ³Laboratoire Ecologie et Evolution, CNRS, Université Pierre et Marie Curie, Unité Mixte de Recherche 7625, 7 Quai St. Bernard, 75005 Paris, France

Accepted 5/1/2013; Electronically Published 6/13/2013

ABSTRACT

Studies of the relationship of performance and behavioral traits with environmental factors have tended to neglect interindividual variation even though quantification of this variation is fundamental to understanding how phenotypic traits can evolve. In ectotherms, functional integration of locomotor performance, thermal behavior, and energy metabolism is of special interest because of the potential for coadaptation among these traits. For this reason, we analyzed interindividual variation, covariation, and repeatability of the thermal sensitivity of maximal sprint speed, preferred body temperature, thermal precision, and resting metabolic rate measured in ca. 200 common lizards (*Zootoca vivipara*) that varied by sex, age, and body size. We found significant interindividual variation in selected body temperatures and in the thermal performance curve of maximal sprint speed for both the intercept (expected trait value at the average temperature) and the slope (measure of thermal sensitivity). Interindividual differences in maximal sprint speed across temperatures, preferred body temperature, and thermal precision were significantly repeatable. A positive relationship existed between preferred body temperature and thermal precision, implying that individuals selecting higher temperatures were more precise. The resting metabolic rate was highly variable but was not related to thermal sensitivity of maximal sprint speed or thermal behavior. Thus, locomotor

performance, thermal behavior, and energy metabolism were not directly functionally linked in the common lizard.

Introduction

The study of variation and functional integration of suites of ecologically important traits, such as whole-organism performance, behavior, and physiology, is crucial to understanding how complex phenotypes have evolved (Ghalambor et al. 2003). If the evolution of particular combinations of phenotypic traits is driven by natural selection, then coadaptation could emerge between them (Angilletta et al. 2006). Thus, our understanding of the ecology and evolution of performance, energy metabolism, and behavior could be improved if patterns of individual variation and covariation are taken into account (Careau and Garland 2012). In ectotherms, functional integration of locomotor performance, thermal behavior, and metabolic rates is of special interest because of their potential coadaptation (Huey and Bennett 1987; Huey and Kingsolver 1989; Garland et al. 1991; Angilletta et al. 2006). However, previous studies have focused more on phylogenetic and interpopulation comparisons and have paid little attention to patterns of interindividual variation and covariation among these traits (but see Huey and Dunham 1987; Austin and Shaffer 1992; Clusella-Trullas et al. 2007; Nespolo and Franco 2007).

Some of the best-studied traits from an individual perspective in ectotherms have been locomotor performances (e.g., sprint speed or endurance), which are involved in predator escape, capture of prey, and acquisition of mates (e.g., Irschick and Garland 2001). Locomotor performances vary substantially among individuals and show significant repeatability and heritability (Garland 1988; Tsuji et al. 1989). In addition, variation in locomotor performance has been linked to morphology, reproductive status, and age (e.g., Bonine and Garland 1999). However, one of the most influential determinants of variation in locomotor performances in ectotherms is temperature (Angilletta et al. 2002*b*). The effect of this environmental variable on performance—that is, the thermal sensitivity of the trait—can be visualized and quantified through a thermal performance curve. This curve relates individual values of performance to individual values of body temperature and has a bell shape with a steep performance decline as temperature gets close to the critical thermal maximum (Huey and Bennett 1987; Huey and Kingsolver 1989). Much information has accumulated about the thermal sensitivity of locomotor performance comparing species and populations, but relatively little is avail-

* Corresponding author; e-mail: paulinaartacho@gmail.com.

able to describe interindividual variation in performance curves (e.g., Angilletta 2006; Angilletta et al. 2010). Another physiological property of ectotherms that is also intimately linked to temperature is energy metabolism, in particular the maintenance cost represented by the resting or standard metabolic rate (Careau and Garland 2012). The resting metabolic rate in diurnal ectotherms can be defined as the energy expended by an individual at rest, fasted, and in a nonreproductive state (Sears 2005). Variation in this trait is often consistent among individuals (Nespolo and Franco 2007), being also importantly influenced by body mass, reproductive status, and sex (e.g., Niewiarowski and Waldschmidt 1992).

Both thermal performance curves and metabolic rates could covary with thermoregulatory behavior, with which ectotherms may buffer the variation in their body temperatures imposed by the thermal environment. In fact, one central tenet of thermal adaptation theory is that thermoregulation behavior is shaped by a coadaptive process among preferred body temperature, optimal temperature for locomotor performances, and metabolic expenditure (Huey and Bennett 1987; Brown et al. 2004; Angilletta 2009). Yet to our knowledge no study has examined covariation among the thermal sensitivity of locomotor performance, thermal preferences, and resting metabolic rate within a population. Theoretical models and some empirical studies conducted across populations or across species have indicated that performance traits and thermal behavior should coevolve, such that populations or species are selected to match their body temperatures to the optimum for their performances (Huey and Bennett 1987; Huey and Kingsolver 1989; Angilletta et al. 2002a). For example, analysis of performance curves in the genus *Drosophila* demonstrates that species that experience high body temperatures in nature have evolved high optimal temperature for sprinting (Huey and Kingsolver 1993). Yet other empirical studies failed to provide strong evidence of coadaptation among these traits and suggested that thermal behavior is an evolutionary rigid trait (Angilletta et al. 2006). Instead, much less attention has been paid to exploring covariation among the thermal performance curve, thermal behavior, and energy metabolism. Although most ectotherms do not use metabolism to regulate their body temperature, higher energy expenditure could be functionally linked to preferences for lower body temperatures, as has been shown for fruit flies (Ueno et al. 2012), and to higher thermal sensitivity, as has been shown for grasshoppers (Chappell 1983). Selection could also maintain a positive correlation between whole-organism performances and maintenance metabolism because the two traits contribute positively to production (growth and reproduction) at the expense of survival and longevity (Careau and Garland 2012).

Here, we analyzed interindividual variation and covariation of the thermal sensitivity of maximal sprint speed, thermal behavior (selected body temperatures and thermal precision), and resting metabolic rate within one population of the common lizard (*Zootoca vivipara*). We focused on such variation among individuals within the same population because the thermal environment that animals experience is commonly spa-

tially and temporally heterogeneous (Sears et al. 2011), and thermoregulation in terrestrial reptiles of temperate climates is the key factor influencing thermal habitat selection (Blouin-Demers and Weatherhead 2001). We quantified the thermal performance curve of maximal sprint speed by means of the individual reaction norm approach fitted through a mixed-effects statistical model (Nussey et al. 2007). We used a linear reaction norm approach to quantify the individual variation in the intercept (the expected trait value at the mean body temperature) and the slope (the change in maximal sprint speed across the thermal gradient) of the thermal performance curve. The slope in particular gives a measure of the thermal sensitivity of maximal sprint speed for each individual (Nussey et al. 2007). We also quantified selected body temperatures and the resting metabolic rate at a given temperature. We tested for the effects of sex, age, and body mass on all traits and also estimated their repeatability. In general, we expected significant and consistent between-individual variation in all traits. Finally, we surveyed the phenotypic relationships between thermal sensitivity of maximal sprint speed, preferred body temperature, thermal precision, and resting metabolic rate.

Significant correlations between these traits are predicted by the following hypotheses. First, the compensation hypothesis predicts a negative correlation between resting metabolic rate and preferred body temperature under the assumption that individuals with high maintenance energetic costs could compensate by selecting lower body temperatures during activity (Tsuji 1988; Ligon et al. 2012). Second, Careau et al. (2008) proposed a production model where a more productive lifestyle (faster growth and reproduction) has higher maintenance costs. For lizards, a more productive lifestyle would require active and accurate thermoregulation at high body temperatures, as well as high values and a stronger thermal sensitivity of locomotor performances (Careau and Garland 2012). Thus, this production model predicts a positive correlation among resting metabolic rate, preferred body temperature, and thermal sensitivity of maximal sprint speed and a positive correlation between preferred body temperature and thermal precision. Finally, if thermal coadaptation exists, preferred body temperature and thermal precision should correlate positively with the thermal sensitivity of maximal sprint speed (Angilletta et al. 2006).

Material and Methods

Study Sample

The common lizard is a viviparous lacertid (adult snout-vent length = 50–70 mm) of diurnal habits living in peat bogs and heathland in large parts of Eurasia. Two hundred individuals (females and males of each three known ages: 1 yr old, 2 yr old, and older) were captured by hand during June 2010 in enclosed, seminatural populations located in a meadow at the Centre de Recherche en Ecologie Expérimentale et Prédictive, France (48°17'N, 2°41'E). Then, animals were measured for snout-vent length (mm) and maintained under standard conditions in individual terraria heated on one side with an in-

candescent bulb (25 W). Animals were fed ad lib. every second day with crickets (*Acheta domestica*). All animals were measured in the postbreeding period, and specifically females were evaluated approximately 1 mo after parturition.

Measurement of Preferred Body Temperature and Estimation of Thermal Precision

Selected body temperatures were measured in a thermal gradient. Because *Zootoca vivipara* is heliothermic, heat sources were provided by an incandescent bulb (40 W) placed at one end of a terrarium (41 cm × 55 cm × 77 cm) from 0900 to 1700 hours local time. The thermal gradient ranged from room temperature (21°–22°C) at the end of the terrarium to 40°–42°C under the bulb. All individuals were fed the day before the measurements, and water was provided ad lib. during each trial. Lizards were placed in the gradient the evening before measurements to allow acclimation. The measurements of selected body temperatures were obtained with an infrared thermometer every 30 min from 1030 to 1700 hours local time. Given the large quantity of measurements per individual, we preferred to record the surface temperature rather than the cloacal body temperature because the latter would have required frequently handling the lizards and possibly altering their behavior. Body surface temperature and cloacal temperature were highly but not perfectly correlated (the calibration curve was performed with some animals not included in this study; $R^2 = 0.96$, slope = 1.73 ± 0.07 SE, $P < 0.001$), whereby we transform the surface body temperature using the calibration curve. Then, readings of surface body temperature calibrated by the cloacal temperature were considered estimates of behaviorally selected body temperatures.

We recorded the location of each lizard in the terrarium as follows: position 1, near the heat source and above the substrate; position 2, near the heat source and hidden in the soil; position 3, far from the heat source and above the substrate; and position 4, far from the heat source and hidden in the soil. As we were interested in measuring activity body temperature, we eliminated records when the lizards were hidden in the soil far from the heat source (Herczeg et al. 2006). However, results remained qualitatively unchanged when we included all records in the analysis. Preferred body temperature was calculated as the daily average of body temperatures, and thermal precision was estimated as the variance in body temperatures around the preferred body temperature calculated for each individual. High variance around the preferred body temperature means that thermal precision is low. In addition, we measured preferred body temperature and estimated the thermal precision a second time in a sample of 22 males 1 mo after the initial measurement. We calculated the repeatability of both variables using the intraclass correlation coefficient (see below).

Measurement of Maximal Sprint Speed

To determine the thermal sensitivity of a measure of locomotor performance, we characterized sprint speed at five temperatures

(20°, 24°, 28°, 32°, and 36°C) normally experienced by common lizards during the activity season. Lizards were raced on a 2.5-m-long linear racetrack covered with a cork floor and equipped with photoelectric cells spaced by 25 cm. Individuals were randomly assigned to groups of approximately 12 individuals, and the sequence of temperatures for each group was also established in a random fashion. Each lizard was run at all temperatures on two consecutive days. First, lizards were kept individually in an environmental chamber to the test temperature for at least 1 h before the measurements were obtained, which is enough time to reach the temperature desired (e.g., Le Galliard et al. 2003). Then, each lizard was placed on one end of the racetrack and chased along the track by gently tapping the tail with a soft brush. The total number of taps was recorded as an index of stimulation. Sprint speed values (cm s^{-1}) were estimated over a 25-cm interval from three repeated trials per temperature spaced by 30 min. The fastest speed of the three trials for each temperature tested was considered the estimate of maximal sprint speed. The corresponding number of stimulations was also included in the analysis. Animals that had a broken tail, had some evident physical default (e.g., broken legs or tail loss during the trials), or were extremely unmotivated were excluded from the analysis ($n = 14$ individuals). Body mass was measured before and after all trials, and we did not find a significant decrease in body mass between the first and second day of measurements. In addition, we calculated the repeatability of maximal sprint speed through the temperature range and short-term repeatability through the three trials using the intraclass correlation coefficient obtained from variance components after the best model in table 1 (see below).

Measurement of Resting Metabolic Rate

The resting metabolic rate—or standard metabolic rate for ectotherms—is the minimum energetic cost of maintenance estimated in fasting individuals at rest and at a given temperature during the time period when the animals are normally active (Angilletta 2001). Metabolic rates were estimated with a multiple-channel flowthrough respirometry system (Qubit Systems, Kingston, ON) composed of a differential oxygen analyzer (DOX; S104 Differential Oxygen Analyzer) and a CO₂ analyzer (S157) connected to respirometry software (QS Research). The O₂ analyzer was used in differential mode—that is, set to measure differential oxygen concentration between homogeneous gas from the atmosphere (compressed in a bank and used as the DOX reference) and from the gas line from the chamber—because it is more precise than the absolute setting. Incoming air flowed through columns of soda lime and Drierite to remove CO₂ and H₂O, respectively. After passing through the absorbent columns, air was pushed through an eight-channel multiplexer at 140 mL min⁻¹. Six channels were used for measuring lizards, one channel was used for the CO₂ and O₂ reference, and another channel was used for the DOX reference. Outgoing air was split into two parts: one part entered the CO₂ analyzer at 50 mL min⁻¹, and another part was scrubbed of water and entered the O₂ analyzer at 25 mL min⁻¹. Metabolic records were pro-

Table 1: Best selected model describing thermal sensitivity of maximal sprint speed according to sex, age, and number of stimulations (stimulation index) in common lizards (*Zootoca vivipara*)

	Estimate \pm SE	$F_{[ndf, ddf]}$	P
Fixed effects:			
Intercept (female, >2 yr old)	.979 \pm .019	2,636.88 _[1, 689]	<.0001
Body temperature ($^{\circ}\text{C}$)	.026 \pm .001	934.68 _[1, 689]	<.0001
Body temperature ² ($^{\circ}\text{C}$)	-.0004 \pm .0001	10.63 _[1, 689]	.001
Age		10.03 _[2, 169]	.0001
1 yr old	.059 \pm .018		
2 yr old	.111 \pm .026		
Sex (male)	.077 \pm .015	26.71 _[1, 169]	<.0001
Stimulation index	-.020 \pm .001	289.43 _[1, 689]	<.0001
	Estimate of SD (95% CI)		
Random effects:			
Intercept (m s^{-1})	.094 (.081–.100)		
Slope ($\text{m s}^{-1} \text{ }^{\circ}\text{C}^{-1}$)	.007 (.005–.009)		
Correlation between intercept and slope	.707 (.413–.868)		
Residual (within individual)	.1037 (.097–.110)		

Note. The stimulation index was calculated by counting the number of taps needed to motivate the lizard to run on the racetrack. Body temperature was standardized after subtracting the temperature mean. The intercept was estimated for a female lizard that was more than 2 yr old at the mean body temperature. ndf = numerator degree of freedom, ddf = denominator degree of freedom.

cessed by a macro program recorded in ExpeData software (Sable Systems) to transform the measure from parts per million to milliliters of CO_2 and O_2 per hour, taking into account the flow rate passing through the chambers with the animals (140 mL min^{-1}).

The metabolic rate of each lizard was measured at 20°C after a period of fasting of 72 h to ensure a postabsorptive state (Le Galliard et al. 2013). Individuals were maintained the evening before measurements in a controlled temperature cabinet at 20°C . At 0900 hours, six lizards were weighed to the nearest 0.1 mg and sealed in respirometry chambers (60 mL) installed in another temperature cabinet at 20°C . Lizards were then allowed to acclimate to chambers for 1 h, and we measured outgoing CO_2 and O_2 concentrations for half an hour. Individuals were weighed after removal from the chambers, and new lizards were placed in the chambers. In total, we measured 14 individuals per day from 0900 to 1800 hours. Baselines of CO_2 and O_2 concentrations were recorded every 1 h of recording. The respiratory quotient was used to convert CO_2 production values (mL h^{-1}) to energy expenditure (J h^{-1}). We took the average of each complete record as the estimation of resting metabolic rate. Although we measured both CO_2 production and O_2 consumption, we choose the former for estimating energy expenditure because this measure can produce more precise estimates when the respiratory quotient is known (Walsberg and Wolf 1995). Measures of CO_2 production have a greater signal-to-noise ratio with respect to O_2 consumption given that the air entering the chambers was scrubbed of CO_2 .

Statistical Analyses

All variables were analyzed using R software (ver. 2.10; <http://www.r-project.org/>). Repeated measurements of maximal sprint speed and selected body temperatures were analyzed with mixed-effects linear models using the statistical package *lme* (Pinheiro and Bates 2002). This methodology provides estimates of individual differences in intercept (value of the trait in the mean environment) and slope (change in the trait value with the environment) and best linear unbiased predictions for each individual. For maximal sprint speed, we used temperature, sex, age, body mass, and stimulation index as fixed effects. Intercept and slope of the regression between maximal sprint speed and temperatures were used as random effects. The temperature range was standardized by subtracting the mean temperature (28°C). First, we constructed a full model including all fixed and random effects. Then, we fitted the random effects using a restricted maximum likelihood approach and tested for the significance of random effects using likelihood ratio tests (LRTs). Subsequently, we fitted the fixed effects using the maximum likelihood approach, and comparison between models was performed using the Akaike Information Criterion. Reported parameter estimates for both fixed and random effects were obtained with restricted maximum likelihood. The significance of the fixed effects was tested by F statistics. Post hoc tests were performed to determine which temperatures yielded significantly different maximal sprint speed values.

To analyze thermoregulation, we first evaluated the effects of individual traits on daily variation in selected body temperatures; however, we obtained similar qualitative results when we analyzed preferred body temperature (mean value of the

day). We used repeated measurements of body temperatures and evaluated the fixed effects of sex, age, body mass, time of day, and position in box. The random effect tested was the variation among individuals in the intercept of the regression line between body temperatures and time of day. We followed the same procedure mentioned above to fit the fixed and random effects. To analyze thermal precision, we used a linear model implemented with *lm* (Crawley 2013). We analyzed the effects of preferred body temperature, age, sex, and body mass. Before this analysis, preferred body temperature and body mass were log transformed to meet the normality and variance homogeneity assumptions. In addition, we analyzed the effects of body mass (log transformed), age, and sex on resting metabolic rate (log transformed) by means of linear models implemented with *lm* (Crawley 2013). We began with a full model to test the main effects and two-way interactions, and we reduced the model by deleting nonsignificant terms one by one.

We estimated repeatability for maximal sprint speed, preferred body temperature, and thermal precision (i.e., the consistent individual differences) by means of the intraclass correlation coefficient, τ (Falconer and Mackay 1996). The intraclass correlation coefficient measures the fraction of variation in a phenotypic trait that is due to differences among individuals, and it can be calculated from variance components of the linear models as $\tau = \sigma(\text{between})/[\sigma(\text{between}) + \sigma(\text{within})]$. In brief, the logic behind this metric is that traits that show relatively low within-individual variance compared with high between-individual variance are more repeatable. Finally, we analyzed the relationship between the intercept and slope of the thermal sensitivity of maximal sprint speed, preferred body temperature, thermal precision, and resting metabolic rate using Pearson pairwise correlations. We used individual estimates of the intercept and slope of individual thermal sensitivity of maximal sprint speed from the mixed-effects model previously explained to quantify variation in mean sprint speed and thermal sensitivity (Nussey et al. 2007). Table A1 summarizes the raw data.

Results

Variation in maximal sprint speed was influenced by a positive linear and a negative quadratic effect of body temperature (table 1). The maximal sprint speed increased relatively by approximately 100% from 20° to 36°C, and pairwise Tukey post hoc tests showed that maximal sprint speed means were all significantly different between body temperatures (see fig. 1). The average maximal sprint speed at 20°C was 0.65 cm s⁻¹ and reached 1.13 cm s⁻¹ at 36°C. The significant negative concavity indicates a slowing down of the increase in maximal sprint speed when temperature increases. In addition, variation in maximal sprint speed was explained by additive effects of sex and age, with males running faster than females on average and with 2-yr-old individuals running faster than older and 1-yr-old individuals independent of body size (fig. 1). By means of an LRT, we found that both slopes (LRT = 51.4, $P < 0.0001$) and intercepts (LRT = 178.6, df =

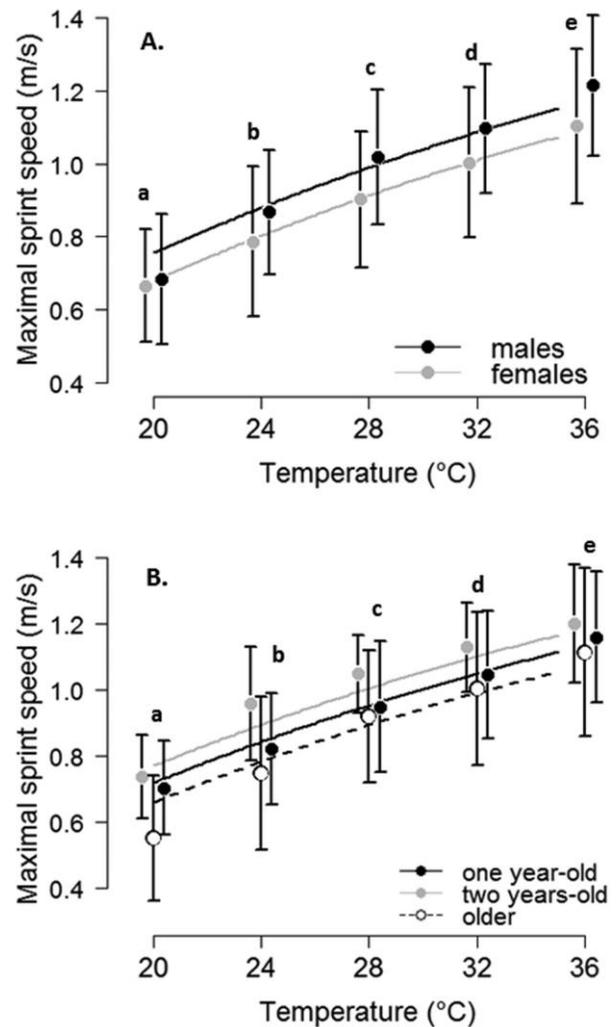


Figure 1. Thermal sensitivity of maximal sprint speed according to the best selected model summarized in table 1. A shows mean values (\pm SD) by sex per temperature and B shows mean values (\pm SD) by age per temperature in common lizards (*Zootoca vivipara*). Curves are predicted regressions from the best selected models. Different letters indicate significant differences after pairwise Tukey post hoc tests.

1, $P < 0.0001$; see table 1) of the thermal performance curve were significant in the model. The variance for the intercept ($\sigma^2 = 0.01$, 17.2%) explained almost five times more variation in maximal sprint speed than did the variance for the slope ($\sigma^2 = 0.002$, 3%) of the thermal performance curve. Moreover, we found a strong positive correlation between the intercept and slope ($\sigma^2 = 0.03$, 58.6%). On the other hand, the repeatability (τ) of maximal sprint speed across temperatures was weak but significant ($\tau = 0.38$, $P < 0.0001$; fig. A1). The short-term repeatability of maximal sprint speed calculated across the three trials within each temperature group was in all cases significant (all $P < 0.001$) but changed depending on body temperature (20°C: $\tau = 0.50$; 24°C: $\tau = 0.52$; 28°C: $\tau = 0.50$; 32°C: $\tau = 0.38$; 36°C: $\tau = 0.35$; see fig. A1).

Selected body temperatures decreased slightly throughout the

Table 2: Best selected model describing daily variation in selected body temperatures according to sex, age, and position in the terrarium in common lizards (*Zootoca vivipara*)

	Estimate \pm SE	$F_{[ndf, ddf]}$	P
Fixed effects:			
Intercept (female, >2 yr old)	34.956 \pm .125	78,524.29 _[1, 1967]	<.0001
Time of day (h)	-.004 \pm .0003	202.65 _[1, 1967]	<.0001
Position in terrarium		247.74 _[1, 1967]	<.0001
2	-1.374 \pm .069		
3	-1.729 \pm .124		
Age		5.32 _[2, 191]	.006
1 yr old	.402 \pm .125		
2 yr old	.378 \pm .177		
Sex (male)	.463 \pm .101	20.85 _[1, 191]	<.0001
	Estimate of SD (95% CI)		
Random effects:			
Intercept ($^{\circ}\text{C min}^{-1}$)	.589 (.502–.672)		
Residual (within individual)	1.266 (1.226–1.306)		

Note. See "Material and Methods" for an explanation of position. The intercept was estimated for a female lizard that was more than 2 yr old at the beginning of the daily measurement.

day, and males had higher selected body temperatures than females (table 2; fig. 2A). Age also had an effect on selected body temperatures, and after a Tukey post hoc test, 1- and 2-yr-old individuals had slightly higher selected body temperatures (0.4°C) than older individuals. We tested the significance of the random effect (i.e., intercept) using an LRT, which showed that dropping the intercept had a significant effect (LRT = 168.751, df = 1, $P < 0.001$; see table 2). Although the intercept explained an important part of the variation in selected body temperatures among individuals ($\sigma^2 = 0.35$, 17%), the variation within individuals was even larger ($\sigma^2 = 1.60$, 82%). The temporal repeatability of preferred body temperature over a period of 1 mo was high ($\tau = 0.60$, $P = 0.001$; fig. A2). In addition, thermal precision increased (i.e., less variation around the mean) with the increase in the preferred body temperature (estimate = -10.466 , $t = 5.992$, $P < 0.0001$). Finally, the temporal repeatability of thermal precision was low but significant ($\tau = 0.37$, $P = 0.04$; fig. A2).

The model describing individual variation in resting metabolic rate retained only body mass ($P = 0.016$) but explained a very small proportion of the variation in that trait ($r^2 = 0.03$). The correlation matrix (table 3; fig. A3) further showed no significant pairwise correlation between the individual intercept and thermal sensitivity of maximal sprint speed (i.e., slope), preferred body temperature, and resting metabolic rate (all $P > 0.19$). The exceptions were the negative correlations between preferred body temperature and thermal precision and the positive correlation between the intercept and slope of the thermal performance curve of maximal sprint speed.

Discussion

Although interindividual variation is common in many locomotor, physiological, and behavioral traits, most studies of ther-

mal physiology and behavior have focused on species or population means and tended to neglect this important source of variation (Sinervo et al. 1991; Iraeta et al. 2011). This trend implies that conspecifics are treated as if they were equivalent and respond the same to their thermal environment. Yet individual variation does not merely represent the raw material on which selection can act (Bennett 1987)—its study can also help us understand the functional integration, coadaptation, and genetic constraints among traits (e.g., Huey and Dunham 1987; Careau and Garland 2012). With that idea in mind, we surveyed interindividual variation in the thermal sensitivity of maximal sprint speed, selected body temperatures, thermal precision, and resting metabolic rate, as well as the phenotypic covariation among these traits, in common lizards.

We detected significant interindividual differences in the mean (i.e., intercept) and thermal sensitivity (i.e., slope) of maximal sprint speed. Furthermore, more variation was caused by individual differences in the mean performance than in thermal sensitivity, and the two traits were positively correlated. The latter means that individuals that were faster at average body temperature (i.e., 28°C) also more strongly increased their maximal sprint speed with their body temperature. This implies that interindividual differences in maximal sprint speed increased when temperatures increased above the mean. Between-individual variation in maximal sprint speed was consistent across temperatures, but the repeatability was somewhat lower ($\tau = 0.38$) than other values previously reported. For instance, the repeatability reported for *Zootoca vivipara* at 30°C was 0.49 (Vandamme et al. 1990) and varied between 0.62 and 0.85 for hatchlings of *Sceloporus occidentalis* across a thermal range of 28° – 37°C (Vanberkum et al. 1989). The lower repeatability detected in our study could be due to the inclusion of low temperatures that impair locomotion (Angilletta et al. 2002a) and

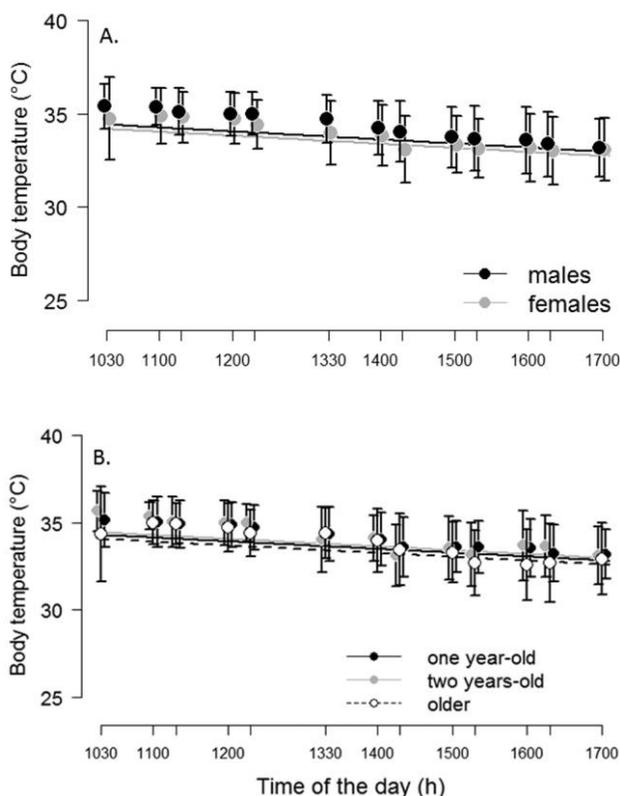


Figure 2. Daily variation in selected body temperatures according to the best selected model summarized in table 2. *A* shows mean values (\pm SD) by sex and *B* shows mean values (\pm SD) by age in common lizards (*Zootoca vivipara*). Curves are predicted regressions from the best selected models.

to the occurrence of individual variation in thermal sensitivity. On average, maximal sprint speed increased significantly over the entire array of tested body temperatures, but we were not able to estimate accurately the optimum temperature since we did not test individuals very close to their critical thermal maximum (Angilletta et al. 2002a). This regular increase in maximal sprint speed with body temperature partially contrasts with the relative thermal insensitivity of locomotor performance in other lizards tested at temperatures normally experienced during the activity period (Hertz et al. 1983; Angilletta et al. 2002a). In addition, males were faster than females, and 2-yr-old individuals were faster than 1-yr-old and older individuals. Evidence for sex-based differences in running speed appear to be mixed (e.g., Vanberkum et al. 1989; Peterson and Husak 2006) and not completely explained by sexual size dimorphism, which suggests that more complex interactions among sex, thermal sensitivity, and behavior take place (Lailvaux 2007). The observed sexual difference could also come from stronger sexual selection on sprint speed in male than in female common lizards, but this issue has not yet been addressed in this species.

Our investigation of interindividual variation in thermoregulation behavior adds to a growing list of rare studies of this topic (Carretero et al. 2005; Stapley 2006; Clusella-Trullas et

al. 2007). We detected interindividual differences in the selected body temperature measured in the laboratory in an environment free of ecological costs of thermoregulation or thermal constraints. Moreover, lizards selected higher body temperatures in the morning after emergence and decreased body temperatures progressively during the day, which parallels findings in natural populations of common lizards (Carretero et al. 2005). We estimated temporal repeatability of preferred body temperature over a month and found high estimates of repeatability ($\tau = 0.60$) relative to the few studies previously performed over shorter time periods. For instance, in a study performed in four species of cordylid lizards, repeatability of preferred body temperature over three consecutive days ranged between almost 0 to 0.48 (Clusella-Trullas et al. 2007). In addition, Le Galliard et al. (2003) found high repeatability ($\tau = 0.66$) for preferred body temperature in female common lizards over two successive days, and Stapley (2006) reported values between 0.5 and 0.6 in individuals of *Pseudomoia entrecasteauxii* measured across 3 d. It is possible that we obtained high values of repeatability because we minimally disturbed the animals, habituated all lizards to the thermal gradient, and eliminated the values when lizards were inactive. In addition, thermal precision showed a significant but low repeatability over a month. To our knowledge, this is the first report of repeatability in some index that describes the precision of thermoregulation, providing evidence that this trait might respond to selection, although probably slowly given the low repeatability. Overall, the evidence that both preferred body temperature and thermal precision are repeatable support the view that *Z. vivipara* is an active and accurate thermoregulator.

Resting metabolic rate was measured only at one relatively low body temperature (20°C), given that lizards are generally not active at night or in the shade, to obtain an accurate estimate of the maintenance energetic costs (no individual had a preferred body temperature of 20°C in our data [range = 31°–35.6°C], and the mean body temperatures of inactive lizards during the day was 29.6°C). Yet resting metabolism varied as high as 10-fold among individuals (see also Le Galliard et al. 2013). Some of this interindividual variation was explained solely by variation in body mass, but considerable residual variation remained irrespective of age and sex. This large variation in maintenance metabolism is not unique to the common lizard because maintenance metabolic rates are highly variable both within and between species. Body mass has been found to be a significant predictor of resting or standard metabolic rate in other lizards and snakes, as in the common lizard, but age and sex were also influential in other species (e.g., Angilletta 2001).

Contrary to our predictions (see “Introduction”), we found only one significant relationship when we analyzed the correlations between individual estimates of the mean and thermal sensitivity of maximal sprint speed, preferred body temperature, thermal precision, and resting metabolic rate, despite the large sample size included in the analysis. More specifically, individuals that selected higher body temperatures showed higher thermal precision, that is, lower variance around preferred body temperature. A suitable control of the body tem-

Table 3: Matrix correlation between individual estimates of the intercept and slope of the thermal performance curve of maximal sprint speed (intercept MSS and slope MSS), preferred body temperature (PBT), thermal precision, and resting metabolic rate (RMR)

Variable	Intercept MSS	Slope MSS	PBT	Thermal precision	RMR
Intercept MSS89	.04	-.01	.03
Slope MSS	<.00102	-.03	-.04
PBT	.37	.61	...	-.44	-.11
Thermal precision	.94	.83	<.00114
RMR	.91	.28	.19	.08	...

Note. Pairwise Spearman correlation coefficients (above the diagonal) and *P* values (below the diagonal) are given. Boldface type indicates significant values.

perature around the preferred body temperature enables appropriate exploitation of the thermal niche and could increase fitness (Huey and Slatkin 1976; Angilletta et al. 2006). Individuals with higher preferred body temperatures closer to the critical thermal maximum are at greater risk of exceeding the optimal temperature, which is expected to generate a quick drop in fitness (Martin and Huey 2008). Thus, individuals that select higher body temperatures should thermoregulate more accurately around their preferred body temperature if it matches the optimal temperature for fitness. On the other hand, the association between high preferred body temperature and high thermal precision partially agrees with the expectation of the production model (see “Introduction”), where a more productive lifestyle would require active and accurate thermoregulation at high body temperatures (Careau et al. 2008; Careau and Garland 2012). In general, the lack of an association between the majorities of the traits involved in this study was contrary to our expectations but is in agreement with the findings of three other studies of this topic (Garland et al. 1987; Dohm et al. 1998; Le Galliard et al. 2013). For example, a recent study also executed in the common lizard analyzed the association between exploratory behavior, resting metabolic rate, and locomotor performance (endurance capacity and maximal sprint speed) in juveniles. This study showed a weak positive relationship among exploration score, maximal sprint speed, and endurance in individuals of 1-yr-old lizards but no relationship with resting metabolic rate (Le Galliard et al. 2013). Our analysis demonstrates further that this conclusion holds when maximal sprint speed is analyzed across a range of body temperatures rather than at the optimal body temperature (as in Le Galliard et al. 2013) and that thermal behavior is unrelated to metabolism and performance. Thus, interindividual relationships among performance traits, activity behavior, and metabolism remain elusive in this species.

With respect to the relationship between resting metabolic rate and preferred body temperature, none of our predictions were supported, in particular the hypothesis that higher basal metabolic rate could be compensated with low body temper-

atures. This result may imply that thermoregulation to high body temperature does not entail higher energy costs in the common lizard. Very few attempts have been made to test whether energy expenditure is coadapted with thermal preferences or thermal niche (Angilletta 2001, 2009). Rogowitz (2003) analyzed whether the standard metabolic rate could covary with the thermal and habitat niche in *Anolis* lizards and found that lizards occupying cooler thermal niches had relatively low mass-independent energy costs. This finding seems to run against the classical but somewhat controversial metabolic cold adaptation hypothesis (Addo-Bediako et al. 2002) and points out that other factors (e.g., type of habitat) of the thermal niche could influence energy costs. Another study performed recently in a fossorial skink (*Saiphos equalis*) showed that individual values of the metabolic rate increased with body temperature, as expected in ectotherms, but no relationship was found between the selected body temperature of individuals and their metabolic rates (Wu et al. 2009). More field and laboratory studies should be conducted to understand the significance of high interindividual variation in thermal physiology traits as a key element in the functional integration of thermal behavior and performance curve, its role in shaping intrapopulation thermal specializations, and its relationship with fitness.

Acknowledgments

We are thankful to B. Decenci re, S. Perret, M. Gallardo Ruiz, and J. Saravia for their kind help. This study was funded by the Centre National de la Recherche Scientifique (CNRS), the Agence Nationale de la Recherche (ANR; grant 07-JCJC-0120), and a postdoctoral fellowship (Becas Chile) from the Comisi n Nacional de Investigaci n Cient fica y Tecnol gica de Chile (CONICYT) to P. Artacho. All protocols were approved by the regional ethics committee in animal experiment 3 of the R gion  le-de-France (file p3/2009/007).

APPENDIX

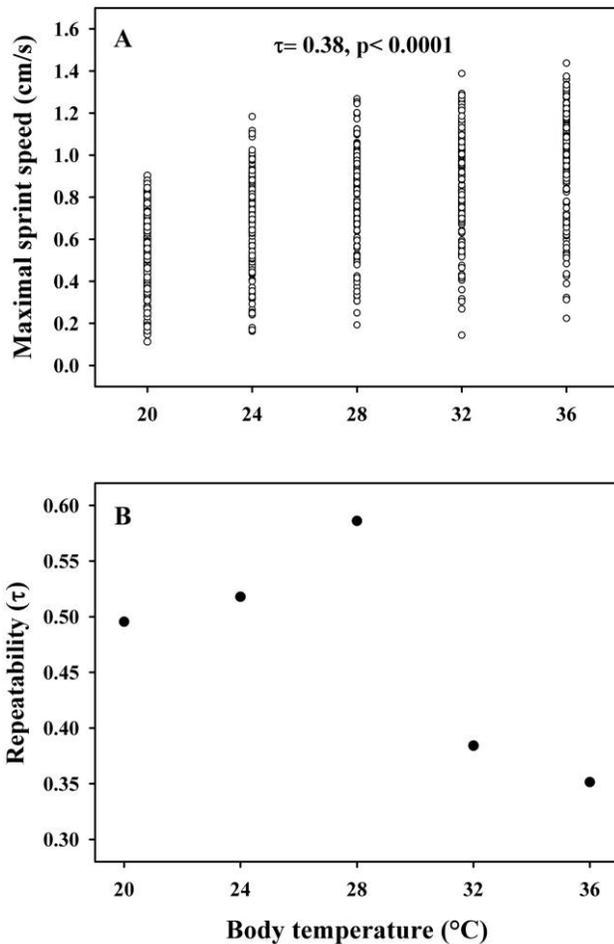


Figure A1. A, Maximal sprint speed (cm/s) across body temperatures (°C). τ is the intraclass correlation coefficient whereby repeatability was evaluated. Each circle represents a new individual, but they are repeated across temperatures. B, Short-term repeatability (τ) per temperature among three trials of sprint speed performed with a 1-h interval between each.

Table A1: Descriptive statistics for morphological traits (snout-vent length [SVL] and body mass), maximal sprint speed (MSS), preferred body temperature (PBT), and resting metabolic rate (RMR) in common lizards (*Zootoca vivipara*)

Age, variable	Females	Males
1 yr old:		
SVL (mm)	56.42 ± 2.23	53.74 ± 1.86
Body mass (g)	3.19 ± .38	3.21 ± .33
MSS (cm s ⁻¹)	.89 ± .24	.99 ± .24
PBT (°C)	33.28 ± 1.16	34.22 ± .68
RMR (J h ⁻¹)	9.81 ± 5.96	10.27 ± 6.71
2 yr old:		
SVL (mm)	66.25 ± 2.94	59.20 ± 2.63
Body mass (g)	4.23 ± .48	3.94 ± .45
MSS (cm s ⁻¹)	.97 ± .20	1.06 ± .23
PBT (°C)	33.12 ± 1.11	33.48 ± 1.07
RMR (J h ⁻¹)	14.62 ± 7.44	9.65 ± 3.93
More than 2 yr old:		
LMA (mm)	67.83 ± 2.93	59.56 ± 1.28
Body mass (g)	4.65 ± .48	4.26 ± .35
MSS (cm s ⁻¹)	.85 ± .28	.89 ± .31
PBT (°C)	33.01 ± 1.16	33.18 ± 1.19
RMR (J h ⁻¹)	11.85 ± 6.56	13.09 ± 7.01

Note. Data are mean ± SD.

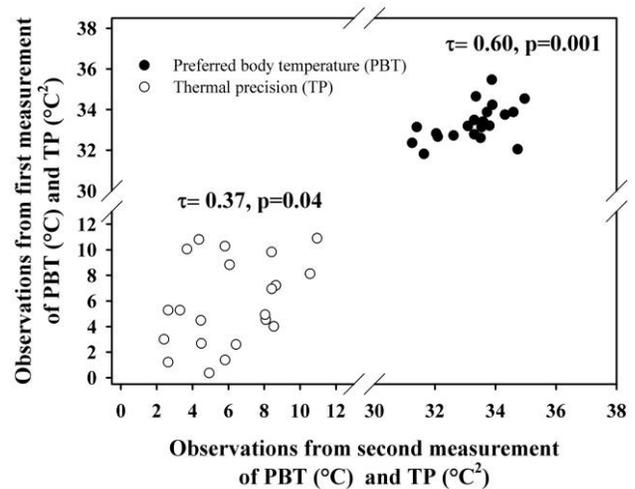


Figure A2. Repeatability of preferred body temperature and thermal precision among 22 males measured before and after a 1-mo interval. τ , the intraclass correlation coefficient, is reported for both traits.

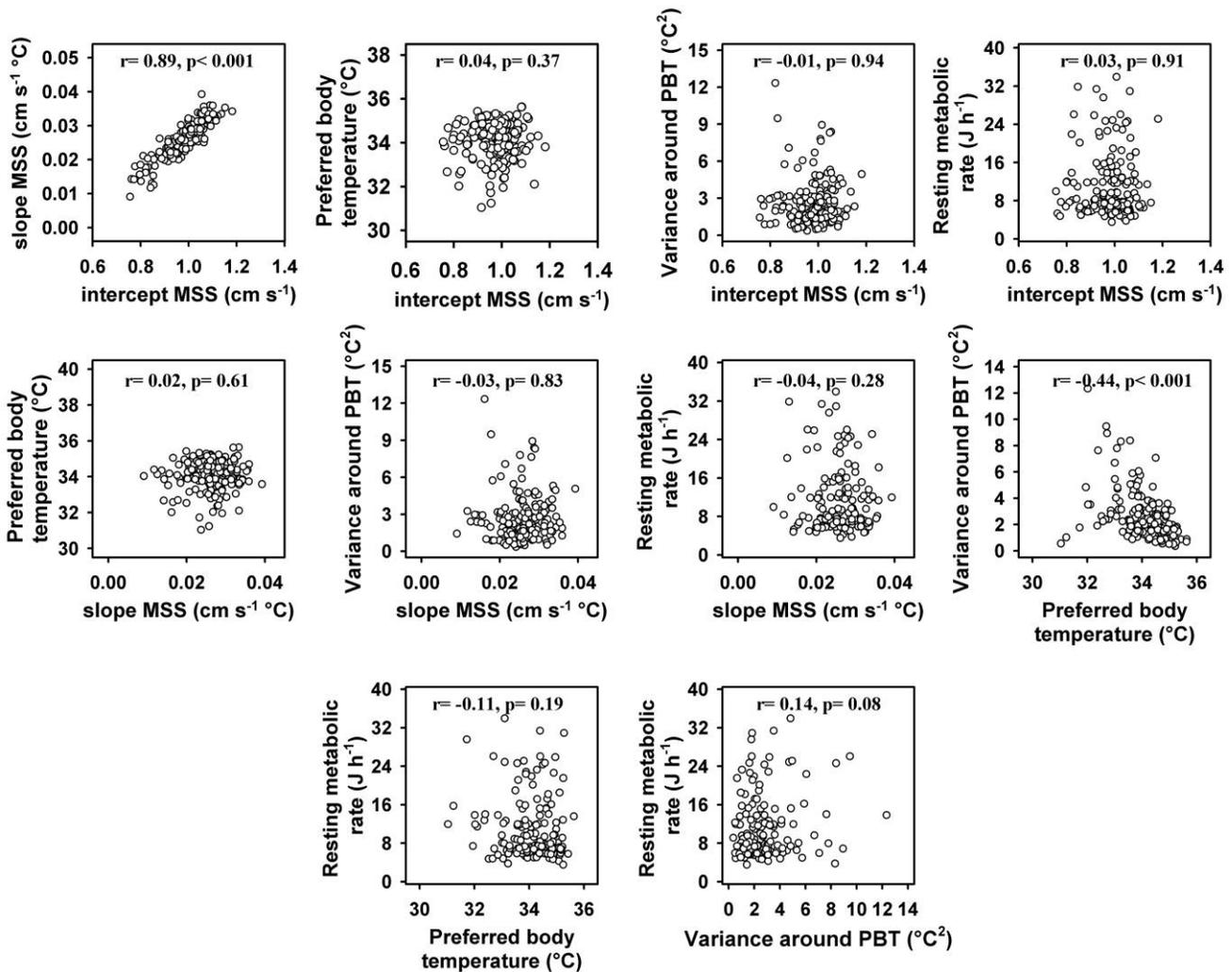


Figure A3. Bivariate plots between all traits measured, that is, the intercept and slope of the thermal performance curve of maximal sprint speed (MSS), preferred body temperature (PBT), variance around PBT (i.e., thermal precision), and resting metabolic rate. In each plot the result of the Pearson pairwise correlations is shown.

Literature Cited

- Addo-Bediako A., S.L. Chown, and K.J. Gaston. 2002. Metabolic cold adaptation in insects: a large-scale perspective. *Funct Ecol* 16:332–338.
- Angilletta M.J., Jr. 2001. Variation in metabolic rate between populations of a geographically widespread lizard. *Physiol Biochem Zool* 74:11–21.
- . 2006. Estimating and comparing thermal performance curves. *J Therm Biol* 31:541–545.
- . 2009. *Thermal adaptation: a theoretical and empirical synthesis*. Oxford University Press, Oxford.
- Angilletta M.J., Jr., A.F. Bennett, H. Guderley, C.A. Navas, F. Seebacher, and R.S. Wilson. 2006. Coadaptation: a unifying principle in evolutionary thermal biology. *Physiol Biochem Zool* 79:282–294.
- Angilletta M.J., Jr., T. Hill, and M.A. Robson. 2002a. Is physiological performance optimized by thermoregulatory behavior? a case study of the eastern fence lizard, *Sceloporus undulatus*. *J Therm Biol* 27:199–204.
- Angilletta M.J., Jr., R.B. Huey, and M.R. Frazier. 2010. Thermodynamic effects on organismal performance: is hotter better? *Physiol Biochem Zool* 83:197–206.
- Angilletta M.J., Jr., P.H. Niewiarowski, and C.A. Navas. 2002b. The evolution of thermal physiology in ectotherms. *J Therm Biol* 27:249–268.
- Austin C.C. and H.B. Shaffer. 1992. Short-term, medium-term, and long-term repeatability of locomotor performance in the tiger salamander *Ambystoma californiense*. *Funct Ecol* 6:145–153.
- Bennett A.F. 1987. *Interindividual variability: an underutilized resource*. Cambridge University Press, Cambridge.
- Blouin-Demers G. and P.J. Weatherhead. 2001. An experimental test of the link between foraging, habitat selection and ther-

- moregulation in black rat snakes *Elaphe obsoleta obsoleta*. *J Anim Ecol* 70:1006–1013.
- Bonine K.E. and T. Garland. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *J Zool* 248:255–265.
- Brown J.H., J.F. Gillooly, A.P. Allen, V.M. Savage, and G.B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Careau V. and T. Garland. 2012. Performance, personality and energetics: correlation, causation and mechanism. *Physiol Biochem Zool* 85:543–571.
- Careau V., D. Thomas, M.M. Humphries, and D. Reale. 2008. Energy metabolism and animal personality. *Oikos* 117:641–653.
- Carretero M.A., J.M. Roig, and G.A. Llorente. 2005. Variation in preferred body temperature in an oviparous population of *Lacerta (Zootoca) vivipara*. *Herpetol J* 15:51–55.
- Chappell M.A. 1983. Metabolism and thermoregulation in desert and montane grasshoppers. *Oecologia* 56:126–131.
- Clusella-Trullas S., J.S. Terblanche, J.H. van Wyk, and J.R. Spotila. 2007. Low repeatability of preferred body temperature in four species of cordylid lizards: temporal variation and implications for adaptive significance. *Evol Ecol* 21:63–79.
- Crawley M.J. 2013. *The R book*. Wiley, Chichester.
- Dohm M.R., T. Garland, C.J. Cole, and C.R. Townsend. 1998. Physiological variation and allometry in western whiptail lizards (*Cnemidophorus tigris*) from a transect across a persistent hybrid zone. *Copeia* 1998:1–13.
- Falconer D.S. and T.F.C. Mackay. 1996. *Introduction to quantitative genetics*. Longman, Edinburgh.
- Garland T. 1988. Genetic basis of activity metabolism. 1. Inheritance of speed, stamina, and antipredator displays in the garter snake *Thamnophis sirtalis*. *Evolution* 42:335–350.
- Garland T., P.L. Else, A.J. Hulbert, and P. Tap. 1987. Effects of endurance training and captivity on activity metabolism of lizards. *Am J Physiol* 252:R450–R456.
- Garland T., R.B. Huey, and A.F. Bennett. 1991. Phylogeny and coadaptation of thermal physiology in lizards: a reanalysis. *Evolution* 45:1969–1975.
- Ghalambor C.K., J.A. Walker, and D.N. Reznick. 2003. Multi-trait selection, adaptation, and constraints on the evolution of burst swimming performance. *Integr Comp Biol* 43:431–438.
- Herczeg G., A. Gonda, J. Saarikivi, and J. Merila. 2006. Experimental support for the cost-benefit model of lizard thermoregulation. *Behav Ecol Sociobiol* 60:405–414.
- Hertz P.E., R.B. Huey, and E. Nevo. 1983. Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. *Evolution* 37:1075–1084.
- Huey R.B. and A.F. Bennett. 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. *Evolution* 41:1098–1115.
- Huey R.B. and A.E. Dunham. 1987. Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami*. *Evolution* 41:1116–1120.
- Huey R.B. and J.G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol Evol* 4:131–135.
- . 1993. Evolution of resistance to high temperature in ectotherms. *Am Nat* 142:S21–S46.
- Huey R.B. and M. Slatkin. 1976. Cost and benefits of lizard thermoregulation. *Q Rev Biol* 51:363–384.
- Iraeta P., C. Monasterio, A. Salvador, and J.A. Diaz. 2011. Sexual dimorphism and interpopulation differences in lizard hind limb length: locomotor performance or chemical signalling? *Biol J Linn Soc* 104:318–329.
- Irschick D.J. and T. Garland. 2001. Integrating function and ecology in studies of adaptation: investigations of locomotor capacity as a model system. *Annu Rev Ecol Syst* 32:367–396.
- Lailvaux S.P. 2007. Interactive effects of sex and temperature on locomotion in reptiles. *Integr Comp Biol* 47:189–199.
- Le Galliard J.-F., M. Le Bris, and J. Clobert. 2003. Timing of locomotor impairment and shift in thermal preferences during gravidity in a viviparous lizard. *Funct Ecol* 17:877–885.
- Le Galliard J.-F., M. Paquet, M. Cisel, and L. Montes-Poloni. 2013. Personality and the pace-of-life syndrome: variation and selection on exploration, metabolism and locomotor performances. *Funct Ecol* 27:136–144.
- Ligon D.B., C.C. Peterson, and M.B. Lovern. 2012. Acute and persistent effects of pre- and posthatching thermal environments on growth and metabolism in the red-eared slider turtle, *Trachemys scripta elegans*. *J Exp Zool* 317:227–235.
- Martin T.L. and R.B. Huey. 2008. Why “suboptimal” is optimal: Jensen’s inequality and ectotherm thermal preferences. *Am Nat* 171:E102–E118.
- Nespolo R.F. and M. Franco. 2007. Whole-animal metabolic rate is a repeatable trait: a meta-analysis. *J Exp Biol* 210:2000–2005.
- Niewiarowski P.H. and S.R. Waldschmidt. 1992. Variation in metabolic rates of a lizard: use of SMR in ecological contexts. *Funct Ecol* 6:15–22.
- Nussey D.H., A.J. Wilson, and J.E. Brommer. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. *J Evol Biol* 20:831–844.
- Peterson C.C. and J.F. Husak. 2006. Locomotor performance and sexual selection: individual variation in sprint speed of collared lizards (*Crotaphytus collaris*). *Copeia* 2006:216–224.
- Pinheiro J.C. and D.M. Bates. 2002. *Mixed-effect models in S and S-plus*. Springer, New York.
- Rogowitz G.L. 2003. Analysis of energy expenditure of *Anolis* lizards in relation to thermal and structural niches: phylogenetically independent comparisons. *J Herpetol* 37:82–91.
- Sears M.W. 2005. Resting metabolic expenditure as a potential source of variation in growth rates of the sagebrush lizard. *Comp Biochem Physiol A* 140:171–177.
- Sears M.W., E. Raskin, and M.J. Angilletta Jr. 2011. The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integr Comp Biol* 51:666–675.
- Sinervo B., R. Hedges, and S.C. Adolph. 1991. Decreased sprint speed as a cost of reproduction in the lizard *Sceloporus occidentalis*: variation among populations. *J Exp Biol* 155:323–336.
- Stapley J. 2006. Individual variation in preferred body temperature covaries with social behaviours and colour in male lizards. *J Therm Biol* 31:362–369.

- Tsuji J.S. 1988. Seasonal profiles of standard metabolic rate of lizards (*Sceloporus occidentalis*) in relation to latitude. *Physiol Zool* 61:230–240.
- Tsuji J.S., R.B. Huey, F.H. Vanberkum, T. Garland, and R.G. Shaw. 1989. Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphometric correlates. *Evol Ecol* 3:240–252.
- Ueno T., J. Tomita, S. Kume, and K. Kume. 2012. Dopamine modulates metabolic rate and temperature sensitivity in *Drosophila melanogaster*. *PLoS ONE* 7:e31513.
- Vanberkum F.H., R.B. Huey, J.S. Tsuji, and T. Garland. 1989. Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard *Sceloporus occidentalis* (Baird and Girard). *Funct Ecol* 3:97–105.
- Vandamme R., D. Bauwens, and R.F. Verheyen. 1990. Evolutionary rigidity of thermal physiology: the case of the cool temperate lizard *Lacerta vivipara*. *Oikos* 57:61–67.
- Walsberg G.E. and B.O. Wolf. 1995. Variation in the respiratory quotient of birds and implications for indirect calorimetry using measurements of carbon dioxide production. *J Exp Biol* 198:213–219.
- Wu Q., S.L. Parker, and M.B. Thompson. 2009. Selected body temperature, metabolic rate and activity pattern of the Australian fossorial skink, *Saiphos equalis*. *Herpetol J* 19:127–133.