PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Individual variation in thermal performance curves: swimming burst speed and jumping endurance in wild-caught tropical clawed frogs

Vincent Careau · Peter A. Biro · Camille Bonneaud · Eric B. Fokam · Anthony Herrel

Abstract The importance of studying individual variation in locomotor performance has long been recognized as it may determine the ability of an organism to escape from predators, catch prey or disperse. In ectotherms, locomotor performance is highly influenced by ambient temperature (T_a), yet several studies have showed that individual differences are usually retained across a T_a gradient. Less is known, however, about individual differences in thermal sensitivity of performance, despite the fact that it could represent adaptive sources of phenotypic variation and/or additional substrate for selection to act upon. We quantified swimming and jumping performance in 18 wild-caught tropical clawed frogs (*Xenopus tropicalis*) across a T_a gradient. Maximum swimming velocity and acceleration were not repeatable and individuals did not differ in how their swimming performance varied across T_a. By contrast, time and distance jumped until exhaustion were repeatable across the T_a gradient, indicating that individuals that perform best at a given T_a also perform best at another T_a. Moreover, thermal sensitivity of jumping endurance significantly differed among individuals, with individuals of high performance at low T_a displaying the highest sensitivity to T_a. Individual differences in terrestrial performance increased with decreasing T_a, which is opposite to results obtained in lizards at the inter-specific and among-individual levels. To verify the generality of these patterns, we need more studies on individual variation in thermal reaction norms for locomotor performance in lizards and frogs.

Keywords Anura · Climate change · Random regression · Repeatability · *Silurana*

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Introduction

Locomotor performance, such as sprint speed and endurance, may determine an individual's ability to escape from predators, catch prey, and disperse to new habitats (Arnold 1983; Irschick and Garland 2001). Several studies have reported that locomotor performance significantly differs among individuals (Djawdan and Garland 1988; Friedman et al. 1992; Garland and Losos 1994) which constitutes the 'raw material' upon which natural selection can act directly (Arnold and Bennett 1984; Garland 1988; Boake 1989; Brodie and Russell 1999). Because locomotor performance is highly dependent on ambient temperature (T_a)

in ectotherms (Bennett 1980), a crucial step when studying their performance is to evaluate the extent to which individual differences hold across a T_a gradient (termed thermal repeatability; R_T). Significant R_T for aspects of locomotor performance has been reported in several species of lizards and amphibians (Bennett 1980; Putnam and Bennett 1981; Huey and Hertz 1984; Huey and Dunham 1987; Preest and Pough 1989; Van Berkum et al. 1989).

Although R_T indicates that, on average, individuals roughly maintain their rank order across a T_a gradient, it does not necessarily exclude the possibility that individuals also differ in their sensitivity to T_a. For example, if individuals with the highest overall performance are also the most sensitive to T_a, then the amount of variation among individuals will change across the T_a gradient, but the rank order is maintained. The way in which performance traits vary as a function of T_a is referred to as thermal performance curves (Huey and Stevenson 1979; Stinchcombe et al. 2012). Several quantitative-genetic studies have showed that thermal performance curves have an underlying genetic basis in insects and bacteriophages (Gilchrist 1996; Izem and Kingsolver 2005; Knies et al. 2009; Latimer et al. 2011; Stinchcombe et al. 2012). However, little is known in vertebrate species as to whether individuals differ in their thermal sensitivity of performance (Preest and Pough 1989; Artacho et al. 2013), despite the fact that this form of variation could contain additional substrate for selection to act upon and/or represent sources of adaptive phenotypic variation.

We can test for individual differences in thermal performance curves whenever performance has been measured in a set of individuals across a T_a gradient. In fact, such data sets have been collected many times in the past (e.g. Bennett 1980; Putnam and Bennett 1981; Huey and Dunham 1987; Van Berkum et al. 1989; Brodie and Russell 1999; Herrel and Bonneaud 2012), yet individual differences in thermal sensitivity have rarely been explicitly evaluated in a performance trait (but see Preest and Pough 1989; Artacho et al. 2013). In general, individual differences in sensitivity to a variety of biotic and abiotic factors are thought to be an adaptive response to variability (Brommer 2013). A promising step toward identifying constraints on the evolution of thermal physiology is thus to analyse performance curves as infinite-dimensional traits (Angilletta et al. 2002).

Anurans (frogs, toads) have long been—and continue to be—a great model system to study the evolution of thermal dependence of locomotor performance. Anurans employ a variety of locomotor forms such as walking, hopping, jumping, and swimming to capture prey, escape predators, search for mates, and disperse to novel habitats during migration to breeding sites. Numerous studies on anurans revealed that thermal sensitivity of locomotor performance is highly variable among species (Huey and Stevenson 1979; Putnam and Bennett 1981; Miller 1982; John-Alder

et al. 1988; Londos and Brooks 1988; Preest and Pough 1989; Whitehead et al. 1989; Knowles and Weigl 1990; Wilson et al. 2000; Niehaus et al. 2011). However, little is known about differences in thermal sensitivity among populations within a given species (Wilson 2001) and among individuals within populations (Preest and Pough 1989).

Here, we test for the presence of individual variation in thermal performance curves of both aquatic burst swimming performance and terrestrial endurance capacity in wild-caught male tropical clawed frogs, *Xenopus* (*Silurana*) *tropicalis* (Wagler 1827). *X. tropicalis* is distributed throughout the West African tropical rainforest, which is a highly stable habitat with relatively little seasonal T_a fluctuation. As predicted for aquatic ectotherm species adapted to such thermally stable environments (Wilson et al. 2000; Navas et al. 2008), locomotor performance in *X. tropicalis* is highly sensitive to changes in T_a (Herrel and Bonneaud 2012). Although the initial objective in Herrel and Bonneaud (2012) was to measure performance breadth to verify whether it conforms to the general trend among amphibians (i.e. that *X. tropicalis* has a narrow performance breadth compared to temperate species), their repeated measures data provided us with an ideal opportunity to re-analyse them from the perspective of individual variation in thermal sensitivity. Our objective was, first, to estimate R_T in aquatic burst swimming performance and terrestrial endurance capacity and, second, to test for the presence of significant individual variation in thermal sensitivity of these performance traits.

Materials and methods

Animals

Xenopus tropicalis is a nearly fully aquatic amphibian, spending the rainy season in pools and puddles of gallery forests and the dry season under rocks and roots of riverbanks (Rödel 2000). However, during periods of heavy rain, overland dispersal from the forests to nearby savannah ponds has been observed (Rödel 2000). As in many *Xenopus* species, females are larger than males in *X. tropicalis* (Herrel et al. 2012), but male *X. tropicalis* have relatively longer fore- and hind limbs than females. As a result, males have a higher maximal exertion capacity than females for a given body size (Herrel et al. 2012). Since males disperse to find females which remain generally more stationary, selection on mobility is likely greater in males than females. Therefore, we restricted this study to males, for which both aquatic and terrestrial performance measures should represent ecologically relevant measures that affect fitness in this species, the former being mostly relevant to predator escape and prey capture and the latter to the ability

of animals to find mates and colonize novel habitats during migration to breeding sites (Herrel and Bonneaud 2012).

Individuals were caught in the wild in December 2009 in Cameroon, brought back to France and housed at the Station d'Ecologie Expérimentale du CNRS at Moulis. Animals were housed in groups of eight to ten individuals in aquaria of $60 \times 30 \times 30$ cm and kept at a T_a of 24 °C. This T_a is similar to those experienced by individuals living in stagnant pools and ponds in undisturbed forests (A. H., personal observation) and close to the optimal (25 °C) and preferred (22.4 °C) body temperature in a closely related species [*Xenopus laevis* (Casterlin and Reynolds 1980; Miller 1982)]. Animals were fed every other day with beef heart, earthworms or mosquito larvae. All individuals were pittagged (Nonatec, Rodange, Luxembourg) before the onset of the experiments, allowing unambiguous identification of each individual. Animals were kept in the laboratory for 3 months before the onset of the performance trials. Performance capacity at 24 °C did not decline with time spent in captivity, as frogs measured 9 months later did not differ in their maximal exertion or burst performance capacity and burst performance traits measured in the laboratory did not differ from measurements on animals in the field (A. H., unpublished data).

Temperature testing

Performance traits (burst performance and maximal exertion capacity) were measured for the same 18 males at six different T_a (15, 20, 24, 27, 30 and 32 °C). The highest and lowest T_a, despite being potentially outside the range of ecologically relevant T_a (see Fig. S1) and close to the critical thermal maximal and minimal for that species, were selected to establish a temperature performance curve [i.e. breadth and optimum (Herrel and Bonneaud 2012)]. Removing burst performance data for the lowest T_a did not change our conclusions. Removing data for the highest T_a did not change our conclusions for maximum swimming acceleration and time jumped until exhaustion (we could not verify this for maximum swimming velocity and distance jumped until exhaustion because the random regression models did not converge for these traits). Before the onset of performance measurements, animals were placed for 1 h in individual containers with water in an incubator set at the target T_a. All performance measurements were repeated three times for each individual with an inter-trial interval of at least 1 h during which animals were returned to the incubator and allowed to rest. Immediately after the trials we checked body T_a. Animals never deviated more than ~0.5 °C from the desired T_a except for endurance trials at the lowest T_a (see below). At the end of the performance trials, animals were weighed, their pit tag numbers were recorded and they were returned to their home aquaria and fed ad libitum. Animals

were given at least 1 week to rest between measurement of different performance parameters (burst performance capacity vs endurance) and at least 1 day between trials at different T_a. The order of the trial T_a was assigned using a random table. Animals were never tested on the same day that they were fed, such that the time elapsed between last feeding and testing ranged from 1 to 2 days.

Burst swimming

Burst performance capacity was quantified by measuring maximal instantaneous swimming speed and acceleration during escape, locomotion events provoked by gently probing the frog with a stick. Animals were filmed in dorsal view using a Redlake MotionPro high-speed camera (Tallahassee, FL) set at 500 Hz [see Fig. 1 in Herrel and Bonneaud (2012)]. Illumination was provided by two custom-made arrays of eight ultra-bright red light-emitting diodes. A scale was filmed at the onset of each trial and used to scale measurements in pixels to metric units. Only video clips of good contrast and where the frog swam continuously and in a straight line were retained. Next, video clips were saved, cropped to include at least two locomotor cycles and analysed using ProAnalyst software (Xcitex, Cambridge, MA). For each frame, the snout tip was digitized using the auto-tracking routine implemented in ProAnalyst; this was done manually when video quality was low (both methods yielded identical results). Raw coordinates were exported to Excel (Microsoft, Redmond, WA) and the displacement of the individual along its path was calculated. Next, the raw displacement profile was smoothed using a zero phase shift low-pass Butterworth filter (Winter 2004) with the cut-off frequency set at 30 Hz [see Fig. 1 in Herrel and Bonneaud (2012)]. Velocities and accelerations were calculated by numerical differentiation of the smoothed displacement profiles. For each individual, we extracted the single highest instantaneous velocity and acceleration across all swimming sequences recorded (i.e. the fastest velocity and acceleration may thus come from different sequences). All swimming trials were conducted over two consecutive days (1 and 2 March 2010) following the same T_a order for each individual (20, 28, 15, 30, and 32 °C).

Jumping endurance

Maximal exertion capacity was measured by manually chasing each individual down a 3-m-long circular track until it was exhausted. Animals were considered exhausted if they were no longer able to right themselves after having been placed on their back. The floor of the endurance track was covered with cork to improve traction. For each individual, we recorded both the total distance covered and the time spent moving until exhaustion. As above, we extracted the single highest time and

distance spent moving until exhaustion across all chasing trials. All endurance trials for a given T_a were conducted on the same day for all individuals, with 1–14 days between successive T_a. Note that we were did not record exertion capacity at 15 °C because we were unable to sufficiently cool down the room, causing the animals to heat up during the trials.

Statistical analysis

All analyses were conducted in ASReml-R (Butler et al. 2009) on $\log_{10}$-transformed data to help model convergence and meet assumptions of normality. We began by fitting a mixed model with individual identity fitted as a random effect (intercept) to test if individuals differ significantly in their overall level of performance across the entire T_a gradient. All models included fixed effects of T_a and body mass. We also included a second-order polynomial effect of T_a (T_a^2) to account for the non-linearity observed in the data as suggested by a loess curve fitted to the data (not shown). As body mass was highly repeatable across T_a [$R_T = 0.98 \pm 0.01$; likelihood ratio test (LRT) $\chi^2 = 247.63$; $P < 0.0001$], we assigned the individual mean values to each performance measure (doing so could "rescue" some performance measurements where body mass was not recorded). Significance of fixed effects was tested with a conditional Wald F-statistic and the denominator df were determined following Kenward and Roger (1997).

The extent to which individuals consistently differ from each other across the entire T_a gradient is captured by thermal repeatability (R_T), calculated as the ratio of among-individual variance (V_I) to total phenotypic variance (V_P). V_I is quantified as the variance attributed to individual identity as a random effect and V_P as the sum of V_I and residual variance (V_R; conditioned on fixed effects). We tested for the statistical significance of V_I using a LRT comparing the log-likelihoods of a full model that included V_I and a reduced model that excluded it. The LRT statistic is equal to twice the difference in log-likelihoods between the two nested models and is assumed to follow a χ^2-distribution with df equal to the difference in the number of parameters estimated. However, when testing a single component against a boundary of its parameter space (e.g. $V_I > 0$), the χ^2-statistic is distributed as an equally weighted mixture of χ^2-distributions with 1 and 0 df ($\chi^2_{0:1}$). In practice, this is equivalent to halving P-values obtained from a χ^2-distribution with 1 df (Dominicus et al. 2006). We calculated the marginal and conditional R^2 for linear mixed models (R^2_{GLMM}) following Nakagawa and Schielzeth (2013). While the marginal R^2 represents the amount of variance explained by fixed effects, the conditional R^2 can be interpreted as the variance explained by the entire model, with the difference between the two reflecting how much variability is in random effects (Nakagawa and Schielzeth 2013).

In a second step, we used random regressions (Henderson 1982) to estimate the amount of among-individual variance in the slope of the (within-individual) relationship between performance traits and T_a. Random slope models describe the pattern of among-individual variation over an environmental gradient by estimating the variance in elevation (intercept; V_I), the variance in slope (V_S), and the covariance between elevation and slope (COV_{I-S}). Note that V_I, V_S, and V_R are not comparable because they are expressed in different units of the response variable (Y) and the environmental covariate (X): V_I and V_R are expressed in units of Y^2, but V_S is expressed in units of $Y^2 \cdot X^{-2}$ (Martin et al. 2011). Unfortunately, we cannot calculate the marginal and conditional R^2 for random slope models (Nakagawa and Schielzeth 2013). To give an overall idea of the variance explained by the random slopes, we calculated the 'total R^2' as the R^2 of the linear regression of the observed values against the predicted values by the model.

Evidence for the presence of random slopes was assessed by comparing a model that included V_I, V_S, and COV_{I-S} against a model that included V_I only. Since V_S is bounded to zero, but COV_{I-S} is not, the χ^2-statistic is distributed as a mixture of χ^2-distributions with 1 and 2 df ($\chi^2_{1:2}$), which is obtained by adding half the P-value obtained for a χ^2_1 distribution and half the P-value obtained for a χ^2_2 distribution. We also included non-linear random effects to test whether individuals differ in the curvature of their thermal reaction norm, but doing so either yielded convergence problems or did not significantly increase the likelihood of the models (results not shown).

Significant V_S and COV_{I-S} indicate that individuals differ in their responses to T_a (i.e. individual slopes are not parallel) and that variation across individuals changes with T_a. We calculated the T_a-specific repeatability following the model of summing variance as presented by Singer and Willett (2003):

$$T_a - \text{specific } R = [V_I + (2 \times COV_{I-S} \times T_a) + (V_S \times T_a^2)]$$
$$/[V_I + (2 \times COV_{I-S} \times T_a)$$
$$+ (V_S \times T_a^2) + V_R].$$

where V_I is the random intercept variance, V_S is random slope variance, COV_{I-S} is the covariance between intercepts and slopes, and V_R is the residual variance (assumed to remain constant across T_a). Approximate SEs for all repeatability estimates were obtained using the delta method [see Appendix 1 in Lynch and Walsh (1998)].

Results

Body mass had a positive and significant effect on maximum swimming velocity and maximum jumping distance, but not on other performance measures (Table 1).

Fig. 1 Individual variation in locomotor performance in 18 wild-caught male tropical clawed frogs (*Xenopus tropicalis*). Observed variation (*circles*) in **a** maximum swimming velocity, **b** maximum swimming acceleration, **c** time jumped until exhaustion, and **d** distance jumped until exhaustion as function of temperature. *Lines* represent predicted individual trajectories from the random regression models in Table 2. See Tables S1 and S2 for results after excluding the individual Xt121, which appeared as an outlier in **c** and **d**
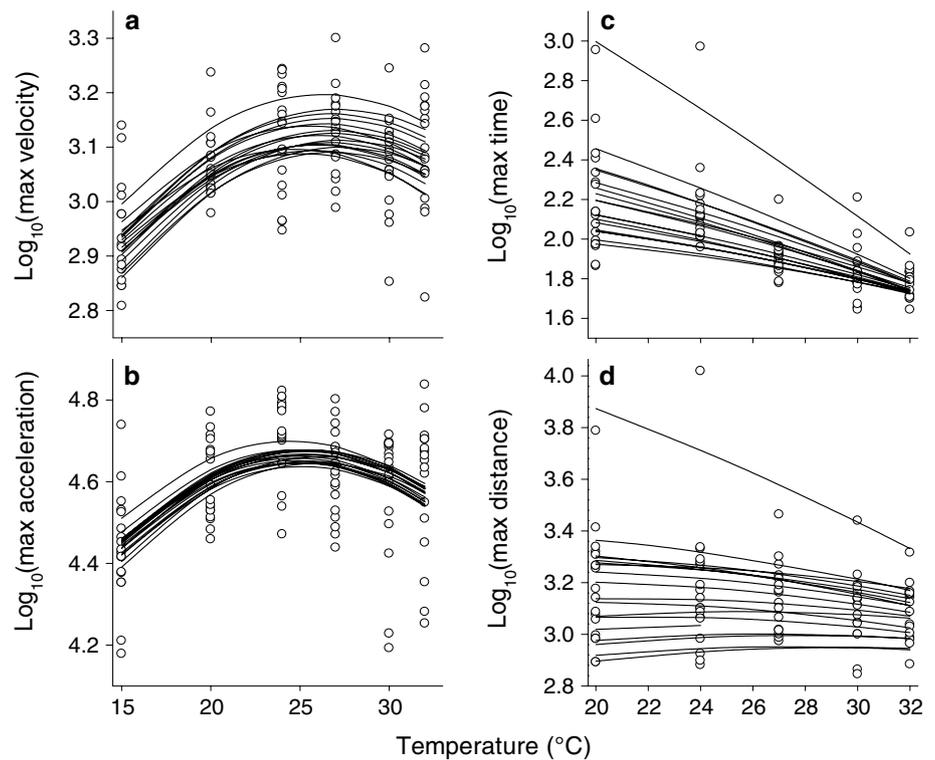
The linear term for T_a had a significant effect on all performance measures (Table 1), with an overall positive effect on aquatic burst performance measures (Fig. 1a, b) and a negative effect on terrestrial endurance measures (Fig. 1c, d). The second-order polynomial for T_a had a significant effect on burst performance measures (Table 1; Fig. 1a, b), but not on endurance measures (Table 1; Fig. 1c, d).

At the individual level, the V_I component did not differ from zero in the two aquatic burst speed measures, but was significant for the two terrestrial endurance measures (Table 1). In other words, there was no evidence that individuals differed in aquatic performance, but there were individual differences in terrestrial thermal performance that held across the T_a gradient (Table 1). By comparing the marginal and conditional R^2 (Table 1), we estimated that the V_I component accounted for 24 and 37 % of the variance in the maximum time and distance jumped until exhaustion, respectively (see also total R^2 estimates in Fig. 2).

We considered whether individuals differed in thermal sensitivity by adding a random slope effect (V_S) and a covariance between V_I and V_S (COV_{I-S}), which did not improve model fit for the two aquatic burst performance measures, but did improve model fit for the two terrestrial endurance performance measures (Table 2). In other words, individuals differed in how their terrestrial thermal performance changed across the T_a-gradient (Fig. 3). The total R^2 increased from 0.76 to 0.86 and 0.80 to 0.88 for maximum

time and distance jumped until exhaustion, respectively (Fig. 2).

Moreover, individuals with high overall terrestrial performance were also more sensitive to T_a (Fig. 1c, d), as indicated by the negative COV_{I-S} for both time and distance jumped until exhaustion (Table 1). Finally, the negative COV_{I-S} (Table 2) also indicates that differences among individuals and T_a-specific repeatability tended to decrease as T_a increased (Fig. 3).

Discussion

In our sample of 18 wild-caught male tropical clawed frogs, we did not find evidence that individuals consistently differed in aquatic burst speed performance (maximum swimming velocity and acceleration) when tested across a T_a gradient of 17 °C. By contrast, terrestrial endurance performance (time and distance jumped until exhaustion) was repeatable across a T_a gradient of 12 °C. Moreover, we found significant individual variation in thermal sensitivity of terrestrial endurance performance. Note, however, that random slopes accounted for a relatively low proportion of the variance (i.e. ~8–10 %) compared to that accounted by random intercepts alone (i.e. 24–37 %). The intercepts and slopes of the thermal performance curves were negatively correlated across individuals, such that the rankings of individuals remained relatively constant across the T_a gradient,
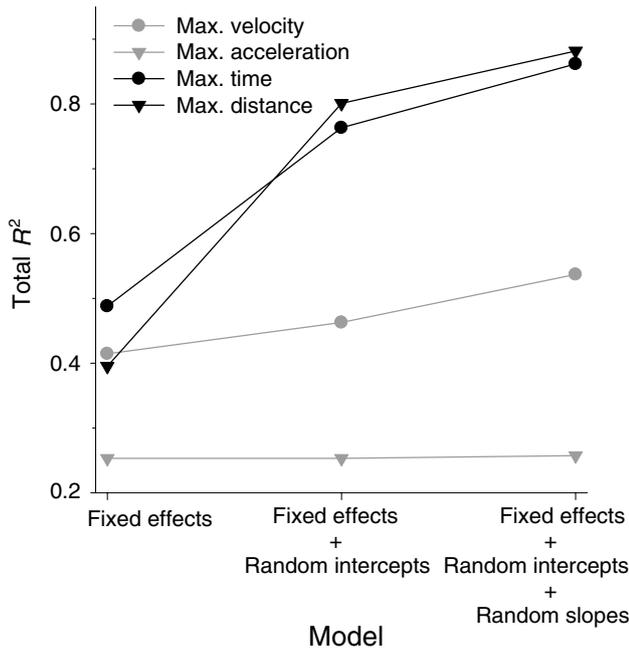
Fig. 2 Total R^2 in various models of locomotory performance quantified in the aquatic environment (maximum swimming velocity and acceleration; *grey symbols*) and the terrestrial environment (time and distance jumped until exhaustion; *black symbols*)

but individuals with high terrestrial performance at low T_a were those whose performance declined more rapidly with increases in T_a.

Our study, combined with previous studies reporting significant R_T for terrestrial locomotor performance traits in anurans [*Bufo boreas*, $R_T = 0.51$; *Bufo americanus*, $R_T = 0.53$; *Rana pipiens*, $R_T = 0.51$ (Putnam and Bennett 1981; Preest and Pough 1989)], indicate that individuals that have the highest terrestrial performance at a given T_a also have the highest terrestrial performance at another T_a. By contrast, we could not find any estimate of R_T for aquatic swimming performance in anurans. This prevents us from assessing whether the absence of among-individual variation in swimming performance is specific to *X. tropicalis* and our protocol, or if it is a general property of anurans. Interestingly, in juvenile turtles, terrestrial burst speed performance was repeatable over 30 weeks ($R = 0.45$), whereas aquatic burst speed performance traits was not ($R = 0.16$) (Elnitsky and Claussen 2006). By contrast, short-term repeatability was significant in both swimming and running burst speed ($R = 0.51$ and 0.56, respectively) in adult alpine newts [*Ichthyosaura alpestris* (Šamajová and Gvoždík 2010)]. An interesting avenue for future research would be to compare R_T for burst and endurance performance measures taken in both the aquatic and terrestrial environments.

Our results suggest that individual differences in thermal sensitivity of jumping performance could represent

Table 1 Parameters from univariate mixed-effect models with fixed effects of temperature (T_a), T_a^2, and body mass and a random intercept effect for two aquatic burst speed measures [maximum (*Max.*) swimming velocity and acceleration] and two terrestrial endurance capacity measures (time jumped until exhaustion and distance jumped until exhaustion) in 18 wild-caught male tropical clawed frogs (*Xenopus tropicalis*)

Trait	Fixed effects									Random effects						
	T_a			T_a^2			Body mass			Intercept			Residual	Repeatability	(R^2_{GLMM})	
	df	F	P	df	F	P	df	F	P	$V_I \pm$ SE	($\chi^2_{0:1}$)	P	$V_R \pm$ SE	$R_T \pm$ SE	Marg.	Cond.
Aquatic swimming performance																
Max. velocity	88.0	37.44	<0.0001	88	29.75	<0.0001	16	7.61	0.0140	0.0397 ± 0.0620	0.53	0.2329	0.7629 ± 0.1150	0.049 ± 0.076	0.408	0.408
Max. acceleration	104.0	10.38	0.0017	104	23.27	<0.0001	104	1.59	0.2102	0.0000 ± 0.0000	0.00	0.5000	1.6992 ± 0.2356	0.000 ± 0.000	0.248	0.248
Terrestrial jumping performance																
Max. time	67.2	124.70	<0.0001	66.4	0.42	0.5179	15.9	3.21	0.0922	1.5249 ± 0.6761	22.87	<0.0001	1.8145 ± 0.3153	0.457 ± 0.122	0.476	0.715
Max. distance	66.8	14.95	0.0003	66.2	0.87	0.3541	15.9	14.28	0.0016	1.2969 ± 0.5218	40.80	<0.0001	0.8308 ± 0.1445	0.610 ± 0.107	0.388	0.761

Estimates of between- (V_I) and within-individual variances (V_R) and thermal repeatability (R_T) are reported ±SE

The significance of V_I was tested using a log-likelihood ratio (LRT) test with a χ^2-statistic distributed as an equally weighted mixture of χ^2-distributions with 1 and 0 df ($\chi^2_{0:1}$). Variance components were multiplied by 100. Also shown are the marginal (*Marg.*) and conditional (*Cond.*) R^2 estimated for general linear mixed models (R^2_{GLMM})

Table 2 Parameters from univariate random regression models with fixed effects of temperature (T_a), T_a2, and body mass and random effects of intercept (V_I), slope (V_S), and the covariance between intercept and slope ($COV_{I–S}$) for two burst speed measures (max velocity and max acceleration) and two endurance capacity measures (time jumped until exhaustion and distance jumped until exhaustion) in 18 wild-caught male tropical clawed frogs (*Xenopus tropicalis*)

Trait	Variance components				Vs intercept model	
	$V_I \pm SE$	$V_S \pm SE$	$COV_{I–S} \pm SE$	$V_R \pm SE$	$(\chi^2_{1:2})$	P
Aquatic swimming performance						
Max. velocity	0.7532 ± 1.0877	0.0015 ± 0.0018	-0.0332 ± 0.0436	0.7026 ± 0.1179	1.45	0.3574
Max. acceleration	0.0072 ± 1.9260	0.0000 ± 0.0030	-0.0003 ± 0.0741	1.6940 ± 0.2772	0.00	0.9999
Terrestrial jumping performance						
Max. time	35.685 ± 15.661	0.0294 ± 0.0149	-1.0228 ± 0.4786	1.1240 ± 0.2209	21.97	<0.0001
Max. distance	19.316 ± 8.2377	0.0138 ± 0.0070	-0.5156 ± 0.2376	0.5119 ± 0.0995	24.35	<0.0001

The significance of V_S and $COV_{I–S}$ was tested using a log-likelihood ratio test by comparing the full model vs a model that included a random intercept only (Table 1), with a χ^2 statistic distributed as an equally weighted mixture of χ^2-distributions with one and two *df* ($\chi^2_{1:2}$). Variance components were multiplied by 100

additional substrate for natural selection to act upon (Brodie and Russell 1999). We are aware of few other studies that tested for and reported individual differences in thermal sensitivity of performance in ectotherms. In *B. americanus*, Preest and Pough (1989) found significant individual variation in sensitivity to T_a, but the statistical method used to support this claim is obscure. Supposedly, the balanced sampling design with four measures per individual

Fig. 3 Temperature-specific repeatability ($R \pm$ SE) in performance across a temperature gradient in wild-caught male tropical clawed frogs (*X. tropicalis*). Locomotory performance was quantified at 15, 20, 24, 27, 30 and 32 °C in the aquatic environment (maximum swimming velocity and acceleration; *grey symbols*) and at 20, 24, 27, 30 and 32 °C in the terrestrial environment (time and distance jumped until exhaustion; *black symbols*)

allowed the authors to include an interaction (as a fixed effect) between individual identity and T_a to test for individual variation in the thermal sensitivity. In another study conducted on common lizards (*Zootoca vivipara*), Artacho et al. (2013) used random regression and reported significant individual variation in thermal sensitivity of sprint speed. Careau et al. (2014) also used random regression to reveal significant individual differences in thermal sensitivity of both standard and maximal metabolic rates in wild-caught slimy salamanders (*Plethodon albagula*).

It is noteworthy that the individuals with the highest performance, despite showing the highest thermal sensitivity, largely retained their rank across the T_a gradient (Fig. 3c, d). Results from Artacho et al. (2013) also suggest that individuals with high overall performance did so across the T_a gradient. These observations are contrary to a central tenet of evolutionary biology that specialization for one task curtails the ability to perform a variety of tasks [i.e. 'a jack-of-all-trades is a master of none'; see also Huey and Hertz (1984); Angilletta et al. (2003)]. Instead, our findings are consistent with a whole body of literature on intraspecific, local adaptation in ectotherms across climate gradients. For example, many fish populations from high latitudes show physiological thermal reaction norms that exceed those of low-latitude populations across the entire T_a range (Conover et al. 2009). This evolutionary principle, termed 'countergradient variation', stipulates that local adaptation across environmental gradients involves change in thermal sensitivity, leading to increases in trait expression over the entire environmental gradient but no difference in the thermal optimum (Baumann and Conover 2011).

The random regression may also be used to analyse differences in thermal sensitivity across populations or species. Using data reported in Bennett (1980) on burst speed and distance running capacity in six species of lizards, one may use the same modeling approach as in Table 2 to reveal
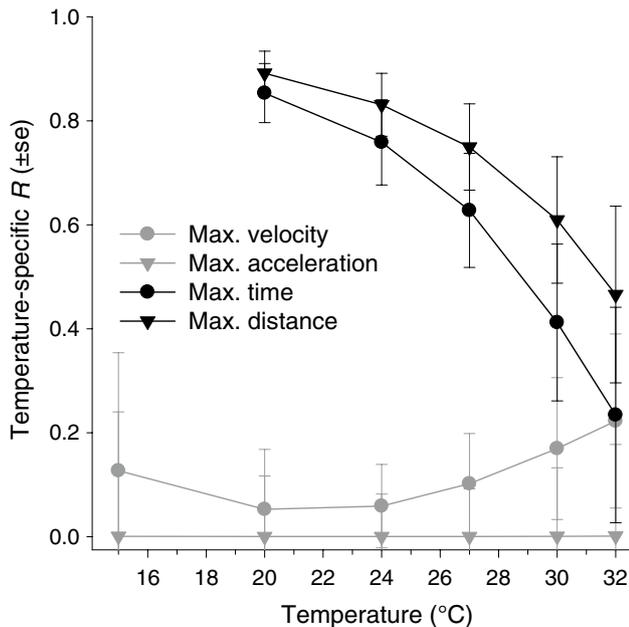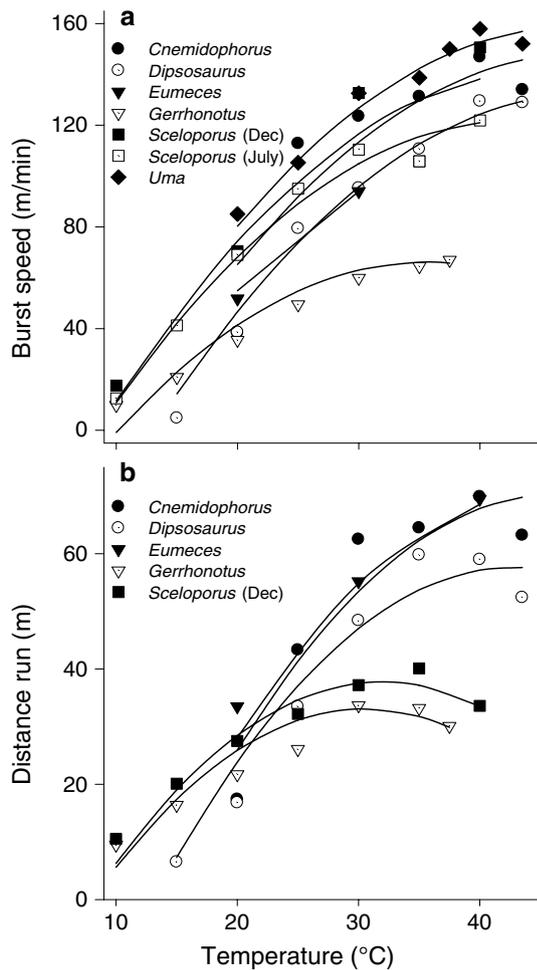
Fig. 4 Interspecific variation in locomotor performance in six lizard species. Data from Bennett (1980) Table 6 for **a** burst speed and Table 8 for **b** distance run during a 2-min trial. Burst speed was measured in December and July in *Sceloporus*. Random regression models were fitted to the data with fixed effects of temperature (T_a) and T_a^2 and random intercepts and slopes for species (with a covariance between the two) were included. In both cases, the random regression significantly increased the likelihoods of the models (compared to a model with species as the sole random effect; for burst speed, $\chi^2_{1:2} = 11.68$, $P = 0.002$; for distance run, $\chi^2_{1:2} = 23.58$, $P < 0.001$) and the covariance between intercept and slope was positive (interspecific variation increases with T_a)

significant species differences in thermal sensitivity of performance (Fig. 4). Although solid conclusions on interspecific differences in thermal sensitivity await a bigger sample size and an analysis that incorporates phylogeny [i.e. phylogenetic mixed models (Hadfield and Nakagawa 2010)], we can see that inter-specific differences in sprint speed across lizards are higher as T_a increases (Fig. 4). This is consistent with the intra-specific results in Artacho et al. (2013), who found a positive covariance between the intercepts and slopes of thermal reaction norms in the common lizard (COV$_{I-S}$; hence among-individual variation increased with increasing

T_a). By contrast, our data showed the opposite pattern as we obtained a negative COV$_{I-S}$ (hence among-individual variation increased with decreasing T_a; Fig. 3). These results support the hypothesis that the 'thermal sensitivities of anuran jumping and lizard sprinting have apparently evolved under different sets of physiological constraints. Lizards vary primarily in their adaptations for high-temperature performance, whereas frogs vary mostly in their low-temperature performance' (John-Alder et al. 1988). An interesting avenue for future research would be to quantify COV$_{I-S}$ for performance curves in a variety of anurans and squamates and test whether it correlates with preferred or optimal body temperatures.

Reporting significant individual and interspecific differences in thermal sensitivity are just two of several steps required to reach a cohesive understanding of how evolution shapes complex phenotypes (Careau and Garland 2012). For example, we need to test whether individual differences in thermal sensitivity have an underlying genetic basis [for studies on invertebrates, see Gilchrist (1996); Izem and Kingsolver (2005); Latimer et al. (2011)]. We also need to know whether performance in the laboratory is closely related to performance under natural conditions and potentially under selection in the wild (Irschick 2003). In lizards, for example, many studies have shown that individuals in the field often do not use their maximum locomotor capacity during such activities as (simulated) predator avoidance and foraging (Irschick and Garland 2001; Braña 2003; Irschick et al. 2005; Husak 2006; Husak and Fox 2006). In the Fowler's toad (*Bufo woodhousei fowleri*), Walton (1988) found that sprinting and sustained jumping performance measured in the laboratory were negatively correlated with activity and number of beetles eaten in the field. Therefore, both quantitative genetics and field studies of *X. tropicalis* are needed to reveal whether among-individual differences in endurance are heritable and under selection.

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