

RESEARCH ARTICLE

Trade-offs between burst performance and maximal exertion capacity in a wild amphibian, *Xenopus tropicalis*

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SUMMARY

Trade-offs are thought to impose barriers to phenotypic diversification and may limit the evolutionary responses of organisms to environmental changes. In particular, locomotor trade-offs between endurance or maximal exertion capacity and burst performance capacity have been observed in some species and may constrain the ability of organisms to disperse. Here, we tested for the presence of locomotor trade-offs between maximal exertion and burst performance capacity in an aquatic frog, the tropical clawed frog (*Xenopus tropicalis*). Given the importance of overland dispersal for this species, we focused on terrestrial exertion capacity (time and distance jumped until exhaustion) and tested whether it trades-off with aquatic burst performance capacity (maximum instantaneous velocity and acceleration), which is likely to be relevant in the context of predator escape and prey capture. Our data show that in both sexes, individuals with longer hindlimbs display higher endurance. Additionally, in females forelimb length was positively correlated with aquatic burst performance capacity and negatively correlated with terrestrial exertion. Trade-offs between endurance and burst performance capacity were detected, but were significant in males only. Finally, males and females differ in morphology and performance. Our data suggest that trade-offs are not universal and may be driven by sex-dependent selection on locomotor capacity. Moreover, our results suggest that locomotor trade-offs may result in sex-biased dispersal under selection for improved endurance capacity as is expected under habitat fragmentation scenarios.

Key words: trade-off, locomotion, maximal exertion capacity, burst performance, frog.

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INTRODUCTION

Phenotypic diversification can be constrained by trade-offs in the development or expression of phenotypic traits (Arnold, 1992; Schluter, 1996). Performance trade-offs are often thought of as imposing limits on phenotypic divergence and occur when different and conflicting functional demands are imposed on the same phenotypic trait (Arnold, 1992; Vanhooydonck et al., 2001; Levinton and Allen, 2005; Konuma and Chiba, 2007) (but see Herrel et al., 2009). For example, in lizards, selection on burst locomotion capacity can trade-off with endurance capacity in some clades (Vanhooydonck et al., 2001). Such a trade-off is likely caused by conflicting demands on the locomotor muscles to express either fast or slow muscle fiber types (Bonine et al., 2005). Yet, other studies have found limited evidence of a negative correlation between endurance and burst speed performance capacity, suggesting that such trade-offs may not be universal (Garland, 1988; Tsuji et al., 1989; Garland et al., 1990; Huey et al., 1990; Jayne and Bennett, 1990; Secor et al., 1992; Brodie and Garland, 1993; Garland, 1994; Sorci et al., 1995; Wilson et al., 2002). Interestingly, a study on the clawed frog *Xenopus laevis* identified trade-offs at the level of muscle physiology, yet none at the whole-animal level (Wilson et al., 2002), suggesting that speed–endurance performance trade-offs at the muscular level (e.g. Wilson and James, 2004; Wilson et al., 2004) may be masked by behavioral and morphological modifications at higher levels of organization.

If trade-offs between speed and endurance or maximal exertion capacity (*sensu* Bennett, 1980; Bennett, 1989; Cullum, 1997) exist,

these may impose important limitations on the ability of organisms to respond to habitat fragmentation. Indeed, habitat fragmentation is expected to select for organisms with a high dispersal ability, capable of high mobility and, specifically, high levels of maximal exertion capacity (Stevens et al., 2010; Morueta-Holme et al., 2010). Yet, burst performance capacity remains under constant selection as this determines an organism's ability to avoid predators and capture prey (Husak, 2006; James et al., 2007; Goodman, 2009). Increased habitat openness due to deforestation and fragmentation may even increase visibility and therefore predation risk. This leads to the potential conflicting situation where habitat fragmentation will select for individuals that display both high exertion capacity/stamina and high burst performance capacity, which may not be feasible (Goodman, 2009). Thus, it is important to investigate whether selection for endurance will come at the cost of burst speed and *vice versa* in a wide variety of organisms, and to identify the anatomical and physiological traits that are the basis of this trade-off.

Here, we used the tropical clawed frog, *Xenopus tropicalis*, as a model system to investigate trade-offs between endurance capacity and burst locomotor performance. *Xenopus tropicalis* is a predominantly aquatic frog that is distributed throughout the West African rainforest belt (Rödel, 2000). During periods of heavy rain, overland dispersal has been observed, suggesting an important role for terrestrial locomotion in dispersal (Rödel, 2000). The mature tropical forests in which this species lives are predicted to experience extreme climatic stress with average monthly temperatures rising

to more than 2 s.d. above the 1961–1990 baseline by 2070, possibly resulting in aridification and fragmentation of the intact, mature forests (Beaumont et al., 2011; Zelazowski et al., 2011). Locomotor trade-offs are particularly relevant in this context because selection on endurance capacity due to increased fragmentation may negatively affect the ability of an organism to escape from predators or to catch prey. Here, we decided to focus on both aquatic burst performance capacity, relevant to predator escape and prey capture, and terrestrial exertion capacity, relevant to the ability of animals to disperse away from unsuitable habitats. Indeed, the closely related also predominantly aquatic frog *Xenopus laevis* has been shown to carry out long-distance overland migrations in times of draught (Lobos and Jaksic, 2005). Habitat fragmentation may disrupt gene flow between the isolated ponds within which these animals live, ultimately leading to inbreeding and thus affecting the long-term survival of populations unless animals show increased dispersal and mobility. Selection on locomotor capacity and the resulting trade-offs may be exacerbated by the added effect of increased temperature due to global warming and habitat fragmentation. Indeed, thermal optima differ between burst performance and maximal exertion capacity (Herrel and Bonneaud, 2012) such that selection for the optimization of one performance trait may negatively affect the other.

Here, we tested whether trade-offs exist between burst performance and exertion capacity and whether these are identical for males and females given that the sexes are known to differ in limb morphology and performance capacity (Herrel et al., 2012). Finally, we explored correlations between morphology and performance traits to try to better understand the possible mechanisms underlying the observed trade-offs between endurance and burst performance capacity.

MATERIALS AND METHODS

Animals

Xenopus tropicalis Gray 1864 were caught in the wild in December 2009 in Cameroon, brought back to France and housed at the Station d'Ecologie Experimentale du CNRS at Moulis. Animals were housed in groups of 8–10 individuals in aquaria (60×30×30 cm) with the temperature set at 24°C, which is assumed to be close to the preferred and optimal temperature of *Xenopus* frogs (see Casterlin and Reynolds, 1980; Miller, 1982) and is similar to water temperatures measured in the field (22–26°C). Frogs were fed every other day with beef heart, earthworms or mosquito larvae *ad libitum*. All individuals were given 1 month to recover and were then pit-tagged (Nonatec, Rodange, Luxembourg) before the onset of the experiments, allowing unambiguous identification. A total of 126 individuals were included in the performance testing.

Morphometrics

All animals ($N=126$) were weighed (Ohaus, Brooklyn, NY, USA; precision ± 0.01 g) and measured using digital calipers (Mitutoyo, Kawasaki, Kanagawa, Japan; ± 0.01 mm). The following body dimensions were quantified: body length as the straight-line distance from the cloaca to the tip of the snout, the length, width and depth of the head, the length of the femur, the tibia, the foot, the longest toe, the humerus, the radius, the hand and the longest finger, the length of the ilium and the width across the top of the two ilia.

Performance

All performance traits were measured at 24°C. Before the onset of performance measurements, animals were placed for 1 h in an incubator set at 24°C in individual containers with some water. All

performance measurements were repeated three times over the course of 1 day for each individual (i.e. three filming sessions or endurance trials), with an inter-trial interval of at least 1 h during which animals were returned to the incubator and allowed to rest. At the end of the performance trials, animals were weighed and their pit tag numbers recorded; they were then returned to their home aquaria and fed. Animals were given at least 1 week to rest between the two different performance measurements.

Maximal exertion capacity was measured by chasing each individual down a 3 m long circular track until exhaustion, indicated by an unwillingness to move any further when touched and the lack of a righting response (inability to turn when animals are placed on their backs). The floor of the endurance track was covered with cork to improve traction. For each individual, we recorded both the total distance covered and time spent moving until exhaustion. Data for two individuals were removed from the dataset as they were more than 3 s.d. away from the mean. Burst performance capacity was quantified by measuring maximal instantaneous swimming speed and acceleration. Animals were filmed in dorsal view using a Redlake MotionPro high speed camera (Tallahassee, FL, USA) set at 500 Hz. Illumination was provided by two custom-made arrays of eight ultra-bright LEDs. A scale was filmed at the onset of each trial and used to convert measurements in pixels to metric units. Only video clips of good contrast and in which the frog swam continuously and in a straight line were retained. Next, video clips were saved, cropped to include at least two locomotor cycles (i.e. two complete flexion–extension cycles) and analyzed using ProAnalyst (Xcitex, Cambridge, MA, USA) software. For each frame, the snout tip was digitized either manually or using the auto-tracking routine implemented in ProAnalyst. Raw coordinates were exported to Excel 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, 2005), with a cutoff frequency set at 30 Hz. 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).

Analyses

All data were \log_{10} -transformed before analyses to fulfill assumptions of normality and homoscedascity. To investigate the existence of performance trade-offs (i.e. a negative correlation between maximal exertion and burst performance capacity), Pearson's product-moment correlations were calculated between each performance trait for all individuals combined as well as for each sex separately. Next, a factor analysis with varimax rotation was performed on the morphological data to reduce the dimensionality of the dataset (for males and females separately). Factors with eigenvalues greater than one were retained. A second factor analysis with varimax rotation was performed on performance data for males and females separately, and factors with eigenvalues greater than one were extracted. Factor scores were saved as new variables and used in subsequent correlation analyses. To explore the correlation between morphology and performance, Pearson's product-moment correlations were calculated between performance and morphological factors. To further investigate the relationships between morphology and performance, correlations were also calculated between raw performance traits and morphological factors. All analyses were performed using SPSS v. 15.0.

RESULTS

Both measures of burst performance (instantaneous velocity and acceleration) were significantly and positively correlated across all individuals ($r=0.46$, $P<0.001$, $N=126$). Both measures of exertion capacity (time and distance jumped until exhaustion) were also positively correlated across all individuals ($r=0.71$, $P<0.001$, $N=124$). A trade-off between time until exhaustion and maximal instantaneous velocity was observed when pooling data from all individuals ($r=-0.28$, $P=0.002$, $N=124$; Fig. 1A). No significant trade-offs were observed between the distance jumped until exhaustion and either measure of burst performance, nor between maximal acceleration capacity and either of the measures of exertion capacity. Yet, a negative trend was observed between the time until

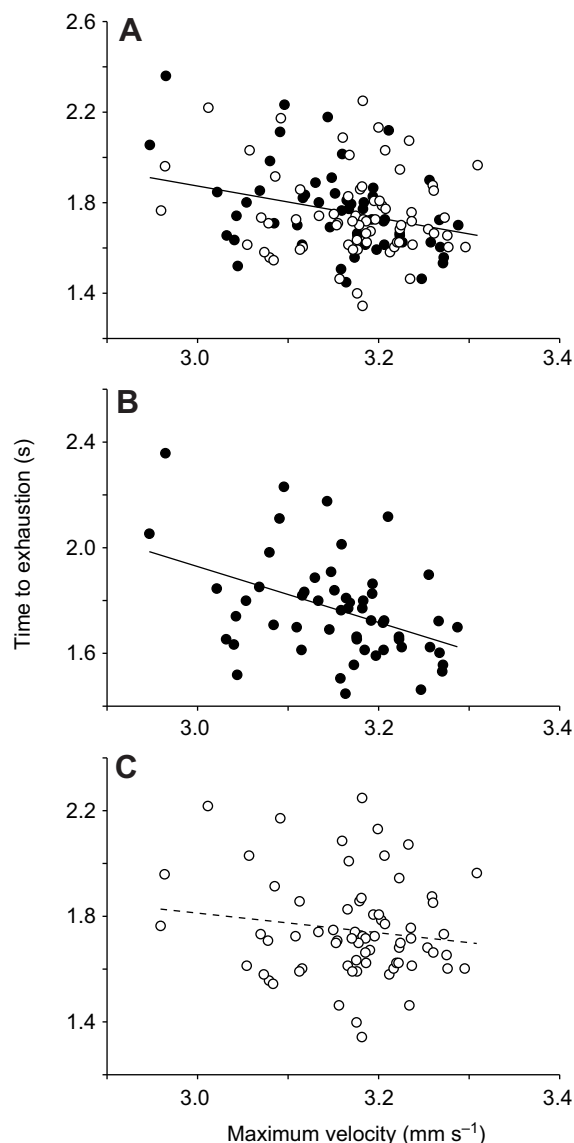


Fig. 1. Performance trade-off between exertion capacity and burst speed in *Xenopus tropicalis*. Data are \log_{10} -transformed maximum time until fatigue (exertion capacity) plotted against \log_{10} -transformed maximum instantaneous velocity (burst speed) for (A) all individuals, (B) males and (C) females. Males are represented as filled circles, females as open circles. Significant correlations are indicated by solid lines; the non-significant negative trend observed in females in C appears as a dashed line.

exhaustion and maximal instantaneous acceleration when pooling data for males and females ($r=-0.15$, $P=0.10$, $N=124$).

When analyzing data separately for the two sexes, a significant trade-off was observed in males between time jumped until exhaustion and maximal instantaneous velocity ($r=-0.43$, $P=0.001$, $N=55$) and the distance covered until exhaustion and the maximal instantaneous velocity ($r=-0.39$, $P=0.003$, $N=55$; Fig. 1B). Acceleration capacity was not correlated with either measure of exertion in males (time jumped until exhaustion: $r=-0.07$, $P=0.60$, $N=55$; distance covered: $r=-0.16$, $P=0.26$, $N=55$). In females, no significant trade-off between either measure of exertion capacity and maximal velocity was observed. However, a non-significant trend was observed between the time until exhaustion and maximal instantaneous velocity ($r=-0.14$, $P=0.24$, $N=69$; Fig. 1C). Finally, acceleration capacity was not correlated with either measure of exertion in females (time jumped until exhaustion: $r=0.01$, $P=0.97$, $N=69$; distance covered: $r=0.10$, $P=0.42$, $N=69$).

A factor analysis with varimax rotation performed on the limb and body dimensions retained two axes, which explained 73.2% of morphological variation for males and 90.7% of the variation for females. For both sexes, the first factor was positively correlated with body size, hindlimb length and ilium size. The second factor was positively correlated with forelimb length (Table 1). From here on, the first morphological factor will be referred to as 'body size/hindlimb' and the second morphological factor as 'forelimb'. Performance variation was summarized on two factors that explained 84.4% of the variance in males and 76.6% in females. The first factor was positively correlated with both measures of exertion capacity (i.e. time until exhaustion and distance until exhaustion), while the second was determined by the two measures of burst performance (i.e. maximal velocity and maximal acceleration; see Table 2). From here onwards, the first performance factor will be referred to as 'overall exertion' and the second as 'overall burst performance'.

In males, body size/hindlimb was significantly and positively correlated with overall exertion ($r=0.54$, $P<0.001$, $N=55$), but no other significant correlations between morphology and performance were observed in males (Fig. 2). Correlations between the raw measures of endurance and morphology confirmed this result and

Table 1. Results of a factor analysis performed on the morphological data for male and female *Xenopus tropicalis* separately

	Males		Females	
	1	2	1	2
Eigenvalue	7.65	2.60	7.26	5.44
% variation explained	54.64	18.60	51.86	38.88
Snout-vent length (mm)	0.84	0.30	0.80	0.56
Mass (g)	0.95	0.18	0.84	0.52
Femur length (mm)	0.81	0.16	0.74	0.63
Tibia length (mm)	0.92	0.22	0.82	0.55
Foot length (mm)	0.93	0.17	0.85	0.48
Toe length (mm)	0.74	0.33	0.65	0.66
Hindlimb length (mm)	0.95	0.25	0.79	0.60
Humerus length (mm)	0.12	0.64	0.64	0.72
Radius length (mm)	0.78	0.26	0.71	0.80
Hand length (mm)	0.08	0.59	0.32	0.80
Finger length (mm)	0.07	0.78	0.40	0.84
Forelimb length (mm)	0.45	0.86	0.61	0.78
Ilium length (mm)	0.89	0.16	0.82	0.51
Ilium width (mm)	0.78	-0.10	0.85	0.28

Values in bold represent loadings greater than 0.7.

Table 2. Results of a factor analysis performed on performance data for male and female *X. tropicalis* separately

	Males		Females	
	1	2	1	2
Eigenvalue	1.98	1.40	1.56	1.51
% variation explained	49.57	34.92	39.00	37.63
Maximum velocity (mm s ⁻¹)	-0.42	0.73	-0.04	0.87
Maximum acceleration (mm s ⁻²)	0.05	0.92	0.06	0.84
Maximum time (s)	0.96	-0.09	0.89	-0.14
Maximum distance (cm)	0.94	-0.14	0.87	0.17

Values in bold represent loadings greater than 0.7.

showed a positive correlation between both measures of exertion and variation in body size/hindlimb (time until exhaustion: $r=0.52$, $P<0.001$; distance until exhaustion: $r=0.61$, $P<0.001$, $N=55$).

In females, body size/hindlimb was also positively correlated with exertion capacity ($r=0.31$, $P=0.009$, $N=69$). Forelimb length was positively correlated with overall burst performance ($r=0.32$, $P=0.008$, $N=69$), yet negatively correlated with overall exertion ($r=-0.33$, $P=0.005$, $N=69$; Fig. 2). Correlations between the raw measures of performance and body size/hindlimb confirmed these results (distance until exhaustion: $r=0.49$, $P<0.001$, $N=69$; maximal velocity: $r=0.26$, $P=0.029$, $N=70$). A non-significant positive trend was also observed between forelimb length and maximal acceleration ($r=0.21$, $P=0.08$, $N=70$). A significant negative correlation was observed between forelimb length and the time moved until exhaustion ($r=-0.50$, $P<0.001$, $N=69$).

DISCUSSION

A significant trade-off between exertion capacity and burst speed was detected across all individuals. However, significant sex-related differences were observed. In males, a trade-off exists between time jumped until exhaustion (exertion capacity) and both measures of burst performance: maximal instantaneous velocity and maximum instantaneous acceleration. In females, a negative, but non-significant trend between time jumped until exhaustion and maximal instantaneous velocity was observed.

Previous studies of vertebrate locomotion have found equivocal evidence of endurance or exertion capacity *versus* burst performance trade-offs (Garland, 1988; Tsuji et al., 1989; Huey et al., 1984; Huey et al., 1990; Jayne and Bennett, 1990; Garland, 1994; Sorci et al., 1995; Vanhooydonck et al., 2001; Wilson et al., 2002). Interestingly, Wilson and co-authors (Wilson et al., 2002) identified trade-offs at the level of muscle physiology, but not whole-organism performance in the closely related species *X. laevis*. The difference between our results for *X. tropicalis* and those reported for *X. laevis* (Wilson et al., 2002) may be due to the use of endurance *versus* exertion capacity. Indeed, whereas Wilson and co-authors (Wilson et al., 2002) tested endurance capacity in an aquatic environment, we quantified terrestrial exertion capacity. As the functional demands of aquatic and terrestrial locomotion are very different, this may play a role in explaining the observed locomotor trade-off. Yet, no trade-off between aquatic and terrestrial burst performance was observed in the semi-aquatic frog *Rana esculenta*, suggesting that constraints on burst performance are similar in the two media (Nauwelaerts et al., 2007). Although *X. tropicalis* has a primarily aquatic lifestyle, it must use overland dispersal to reach suitable

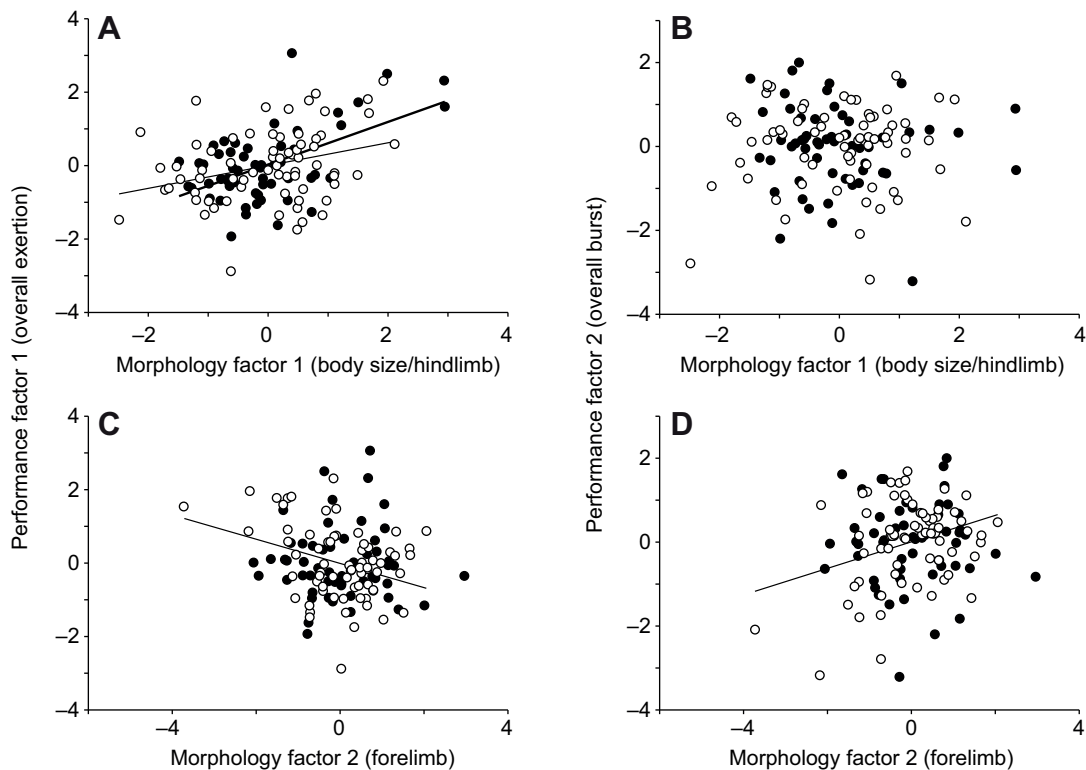


Fig. 2. Correlations between morphology and performance in *X. tropicalis*. (A,B) Scatter plot of the effects of body size/hindlimb length on overall exertion capacity (A) and overall burst speed (B). (C,D) Scatter plots displaying the correlations between forelimb length and overall exertion capacity (C) and overall burst speed (D). Males are represented as filled circles, females as open circles. Lines represent significant correlations for females. The bold line in A represents a significant correlation for males.

aquatic habitats, as shallow pools are dispersed across the landscape. Moreover, while moving from one water body to the next, animals are exposed and vulnerable to predation, likely imposing selection for them to move as fast as possible over medium to long distances. Thus, terrestrial exertion capacity may be an ecologically important trait that is under strong selection in the wild. Moreover, studies on the closely related *X. laevis* have identified terrestrial locomotion as the primary mode of dispersal in introduced populations of this species (Measey and Tinsley, 1998; Lobos and Jaksic, 2005; Eggert and Fouquet, 2006; Faraone et al., 2008). In addition to selection on increased exertion capacity, selection on increased terrestrial burst performance may also occur. Given that the same morphological traits are important in driving both terrestrial and aquatic burst performance (Nauwelaerts et al., 2007) this could trade-off directly with selection on exertion capacity, at least in males. However, as *Xenopus* frogs typically move over land at night (Rödel, 2000) this may offset some of the potential increased predation pressure.

Despite the considerable number of studies on performance trade-offs, to our knowledge none have examined sex differences in such trade-offs. Yet, sexual dimorphism in performance capacity has been observed in a wide array of taxa including humans, horses, dogs, albatross, fleas, lizards and recently also *Xenopus* frogs (Cullum, 1998; Shaffer et al., 2001; Krasnov et al., 2003; Lailvaux et al., 2003; Lailvaux, 2007; Van Damme et al., 2008; Kaliontzopoulou et al., 2010; Herrel et al., 2012). Proximal causes for performance differences between the sexes have been attributed to differences in body size, body fat, muscle composition and distribution, and cardiovascular and respiratory differences, which alter oxygen-carrying capacity. *Xenopus tropicalis* males are smaller than females, yet perform equally well, suggesting that male morphology (i.e. their relatively long hindlimbs) may compensate for their smaller body size (Herrel et al., 2012). Ecological studies on *X. tropicalis* are, however, needed to provide the ecological context that may help explain sex-dependent differences in locomotion and dispersal.

In both male and female *X. tropicalis*, body size and hindlimb length were positively correlated with terrestrial exertion capacity. Moreover, in females, forelimb length was positively correlated with aquatic burst performance, yet negatively correlated with terrestrial exertion capacity. Although this inverse correlation of forelimb length with the two performance traits would be expected to give rise to a trade-off in females as well, this was not observed. Physiological traits such as an increased cardiovascular capacity may override the effect of external anatomy on performance, thus masking the trade-off between exertion capacity and burst performance in females. As no correlation between forelimb length and burst performance was detected in males, sex-specific differences in locomotor kinematics likely exist. Previous studies have explored the physiological basis of inter-individual variation in performance at the muscular and enzymatic level (Wilson and Franklin, 2000; James et al., 2005; James et al., 2007; Nauwelaerts et al., 2007) and have demonstrated that body size is generally the best predictor of performance (Wilson and Franklin, 2000; Nauwelaerts et al., 2007). Many vertebrates compensate for small body size with increased relative hindlimb length or relative mass of propulsive muscles to gain elevated levels of locomotor performance (James et al., 2007; Herrel et al., 2012). Additionally, differences in the proportion of different muscle fiber types have also been demonstrated to affect performance ability (Komi, 1984; Garland, 1988; Gleeson and Harrison, 1988). Indeed, while type one fast-twitch fibers maximize burst performance, type two slow oxidative fibers are beneficial for endurance and endurance capacity

(Wilson et al., 2002). Given the observed lack of correlation between external morphological traits and performance in males, the proximal cause of the trade-off observed between exertion capacity and burst speed is likely physiological. Indeed, based on our results we predict the presence of differences in fiber type composition of the limb muscles in both sexes.

In summary, our data suggest that trade-offs are not universal and may be driven by sex-dependent selection on locomotor capacity. Moreover, our results suggest that locomotor trade-offs may result in sex-biased dispersal under selection for improved exertion capacity, as is expected under habitat fragmentation scenarios. Characterizing the proximal causes of trade-offs may help elucidate physiological constraints on evolutionary divergence (Angilletta et al., 2003) and may be of crucial importance in the context of the ongoing fragmentation of natural habitats. Although many-to-one mapping of morphology to function may provide ways to circumvent trade-offs, investment in improved performance due to strong selection on locomotor capacity will likely trade-off with other traits such as, for example, reproductive output, longevity and immunity. How the effect of increased selection on locomotor capacity plays out in the long run remains to be tested using long-term monitoring of natural populations or lab-based artificial selection experiments. Although involving a considerable investment of time and effort, these types of studies are essential to fully understand the consequences of altered selective pressures due to anthropogenic disturbances such as habitat fragmentation or global warming.

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REFERENCES

- Angilletta, M., Jr, Wilson, R., Navas, C. and James, R. (2003). Tradeoffs and the evolution of thermal reaction norms. *Trends Rev. Ecol. Evol.* **18**, 234-240.
- Arnold, S. J. (1992). Constraints on phenotypic evolution. *Am. Nat.* **140**, S85-S107.
- Beaumont, L. J., Pitman, A., Perkins, S., Zimmermann, N. E., Yoccoz, N. G. and Thuiller, W. (2011). Impacts of climate change on the world's most exceptional ecoregions. *Proc. Natl. Acad. Sci. USA* **108**, 2306-2311.
- Bennett, A. F. (1980). The thermal dependence of lizard behavior. *Anim. Behav.* **28**, 752-762.
- Bennett, A. F. (1989). Integrated studies of locomotor performance. In *Complex Organismal Functions: Integration and Evolution in Vertebrates* (ed. D. B. Wake and G. Roth), pp. 191-202. Chichester, UK: John Wiley and Sons.
- Bonine, K. E., Gleeson, T. T. and Garland, T., Jr (2005). Muscle fiber-type variation in lizards (Squamata) and phylogenetic reconstruction of hypothesized ancestral states. *J. Exp. Biol.* **208**, 4529-4547.
- Brodie, E. D., III and Garland, T., Jr (1993). Quantitative genetics of snake populations. In *Snakes: Ecology and Behavior* (ed. R. A. Seigel and J. T. Collins), pp. 315-362. New York, NY: McGraw-Hill.
- Casterlin, M. E. and Reynolds, W. W. (1980). Diel activity and thermoregulation behavior of a fully aquatic frog: *Xenopus laevis*. *Hydrobiologia* **75**, 189-191.
- Cullum, A. J. (1997). Comparisons of physiological performance in sexual and asexual whiptail lizards (genus *Cnemidophorus*): implications for the role of heterozygosity. *Am. Nat.* **150**, 24-47.
- Cullum, A. J. (1998). Sexual dimorphism in physiological performance of whiptail lizards (genus *Cnemidophorus*). *Physiol. Zool.* **71**, 541-552.
- Eggert, C. and Fouquet, A. (2006). A preliminary biotelemetry study of a feral invasive *Xenopus laevis* population in France. *Alytes* **23**, 144-149.
- Faraone, F., Lillo, F., Giacalone, G. and Lo Valvo, M. (2008). The large invasive population of *Xenopus laevis* in Sicily, Italy. *Amphib.-reptil.* **29**, 405-412.

- Garland, T., Jr (1988). Genetic basis of activity metabolism. I. Inheritance of speed, stamina and antipredator displays in the garter snake *Thamnophis sirtalis*. *Evolution* **42**, 335-350.
- Garland, T., Jr (1994). Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. In *Lizard Ecology: Historical and Experimental Perspectives* (ed. L. J. Vitt and E. R. Pianka), pp. 237-259. Princeton, NJ: Princeton University Press.
- Garland, T., Jr, Bennett, A. F. and Daniels, C. B. (1990). Heritability of locomotor performance and its correlates in a natural population. *Experientia* **46**, 530-533.
- Gleeson, T. T. and Harrison, J. M. (1988). Muscle composition and its relation to sprint running in the lizard *Dipsosaurus dorsalis*. *Am. J. Physiol.* **255**, R470-R477.
- Goodman, B. A. (2009). Nowhere to run: the role of habitat openness and refuge use in defining patterns of morphological and performance evolution in tropical lizards. *J. Evol. Biol.* **22**, 1535-1544.
- Herrel, A. and Bonneaud, C. (2012). Temperature dependence of locomotor performance in the tropical clawed frog, *Xenopus tropicalis*. *J. Exp. Biol.* **215**, 2465-2470.
- Herrel, A., Podos, J., Vanhooydonck, B. and Hendry, A. P. (2009). Force-velocity trade-off in Darwin's finch jaw function: a biomechanical basis for ecological speciation? *Funct. Ecol.* **23**, 119-125.
- Herrel, A., Gonwouo, L. N., Fokam, E. B., Ngundu, W. I. and Bonneaud, C. (2012). Inter-sexual differences in body shape and locomotor performance in the aquatic frog, *Xenopus tropicalis*. *J. Zool.* **287**, 311-316.
- Huey, R., Dunham, A. E., Overall, K. L. and Newman, R. A. (1990). Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*. *Physiol. Zool.* **63**, 845-872.
- Huey, R. B., Bennett, A. A., John-Alder, H. and Nagy, K. (1984). Locomotor capacity and foraging behavior of Kalahari lacertid lizards. *Anim. Behav.* **32**, 41-50.
- Husak, J. F. (2006). Does survival depend on how fast you can run or how fast you do run? *Funct. Ecol.* **20**, 1080-1086.
- James, R. S., Wilson, R. S., de Carvalho, J. E., Kohlsdorf, T., Gomes, F. R. and Navas, C. A. (2005). Interindividual differences in leg muscle mass and pyruvate kinase activity correlate with interindividual differences in jumping performance of *Hyla multilineata*. *Physiol. Biochem. Zool.* **78**, 857-867.
- James, R. S., Navas, C. A. and Herrel, A. (2007). How important are skeletal muscle mechanics in setting limits on jumping performance? *J. Exp. Biol.* **210**, 923-933.
- Jayne, B. C. and Bennett, A. F. (1990). Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* **44**, 1204-1229.
- Kaliontzopoulou, A., Carretero, M. and Llorente, G. (2010). Sexual dimorphism in traits related to locomotion: ontogenetic patterns of variation in *Podarcis* wall lizards. *Biol. J. Linn. Soc. Lond.* **99**, 530-543.
- Komi, P. V. (1984). Physiological and biomechanical correlates of muscle function: effects of muscle structure and stretch-shortening cycle on force and speed. *Exerc. Sport Sci. Rev.* **12**, 81-121.
- Konuma, J. and Chiba, S. (2007). Trade-offs between force and fit: extreme morphologies associated with feeding behavior in carabid beetles. *Am. Nat.* **170**, 90-100.
- Krasnov, B. R., Burdelov, S. A., Khokhlova, I. S. and Burdelova, N. V. (2003). Sexual size dimorphism, morphological traits and jump performance in seven species of desert fleas (Siphonaptera). *J. Zool.* **261**, 181-189.
- Lailvaux, S. P. (2007). Interactive effects of sex and temperature on locomotion in reptiles. *Integr. Comp. Biol.* **47**, 189-199.
- Lailvaux, S. P., Alexander, G. J. and Whiting, M. J. (2003). Sex-based differences and similarities in locomotor performance, thermal preferences, and escape behaviour in the lizard *Platysaurus intermedius wilhelmi*. *Physiol. Biochem. Zool.* **76**, 511-521.
- Levinton, J. S. and Allen, B. J. (2005). The paradox of the weakening combatant: trade-off between closing force and gripping speed in a sexually selected combat structure. *Funct. Ecol.* **19**, 159-165.
- Lobos, G. and Jaksic, F. M. (2005). The ongoing invasion of African clawed frogs (*Xenopus laevis*) in Chile: causes of concern. *Biodiv. Cons.* **14**, 429-439.
- Measey, G. J. and Tinsley, R. C. (1998). Feral *Xenopus laevis* in South Wales. *Herpetol. J.* **8**, 23-27.
- Miller, K. (1982). Effect of temperature on sprint performance in the frog *Xenopus laevis* and the salamander *Necturus maculosus*. *Copeia* **1982**, 695-698.
- Morueta-Holme, N., Flojgaard, C. and Svenning, J. C. (2010). Climate change risks and conservation implications for a threatened small-range mammal species. *PLoS ONE* **5**, e10360.
- Nauwelaerts, S., Ramsay, J. and Aerts, P. (2007). Morphological correlates of aquatic and terrestrial locomotion in a semi-aquatic frog, *Rana esculenta*: no evidence for a design conflict. *J. Anat.* **210**, 304-317.
- Rödel, M. (2000). *Herpetofauna of West Africa*, Vol. 1, *Amphibians of the Western Savannah*. Frankfurt, Germany: Chimaira.
- Schluter, D. (1996). Adaptive radiation along genetic lines of least resistance. *Evolution* **50**, 1766-1774.
- Secor, S. M., Jayne, B. C. and Bennett, A. F. (1992). Locomotor performance and energetic cost of sidewinding by the snake *Crotalus cerastes*. *J. Exp. Biol.* **163**, 1-14.
- Shaffer, S. A., Weimerskirch, H. and Costa, D. P. (2001). Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. *Funct. Ecol.* **15**, 203-210.
- Sorci, G., Swallow, J. G., Garland, T., Jr and Clobert, J. (1995). Quantitative genetics of locomotor speed and endurance in the lizard *Lacerta vivipara*. *Physiol. Zool.* **68**, 698-720.
- Stevens, V. M., Pavoine, S. and Baguette, M. (2010). Variation within and between closely related species uncovers high intra-specific variability in dispersal. *PLoS ONE* **5**, e11123.
- Tsuji, J. S., Huey, R. B., Van Berkum, F. H., Garland, T. and Shaw, R. G. (1989). Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphometric correlates. *Evol. Ecol.* **3**, 240-252.
- Van Damme, R., Entin, P., Vanhooydonck, B. and Herrel, A. (2008). Causes of sexual dimorphism in performance traits: a comparative approach. *Evol. Ecol. Res.* **10**, 229-250.
- Vanhooydonck, B., Van Damme, R. and Aerts, P. (2001). Speed and stamina trade-off in lacertid lizards. *Evolution* **55**, 1040-1048.
- Wilson, R. S. and Franklin, C. E. (2000). Absence of thermal acclimatory capacity of locomotor performance in adults of the frog *Limnodynastes peronii*. *Comp. Biochem. Physiol.* **127A**, 21-28.
- Wilson, R. S. and James, R. S. (2004). Constraints on muscular performance: trade-offs between power output and fatigue resistance. *Proc. Biol. Sci.* **271** Suppl. **4**, S222-S225.
- Wilson, R. S., James, R. S. and Van Damme, R. (2002). Trade-offs between speed and endurance in the frog *Xenopus laevis*: a multi-level approach. *J. Exp. Biol.* **205**, 1145-1152.
- Wilson, R. S., James, R. S., Kohlsdorf, T. and Cox, V. M. (2004). Interindividual variation of isolated muscle performance and fibre-type composition in the toad *Bufo viridus*. *J. Comp. Physiol. B* **174**, 453-459.
- Winter, D. (2005). *Biomechanics and Motor Control of Human Movement*. New York, NY: John Wiley and Sons.
- Zelazowski, P., Malhi, Y., Huntingford, C., Sitch, S. and Fisher, J. B. (2011). Changes in the potential distribution of humid tropical forests on a warmer planet. *Philos. Transact. A* **369**, 137-160.