Intersexual differences in body shape and locomotor performance in the aquatic frog, *Xenopus tropicalis*

A. Herrel[1], L. N. Gonwouo[2], E. B. Fokam[3], W. I. Ngundu[3] & C. Bonneaud[4]

1 Département d'Ecologie et de Gestion de la Biodiversité, Paris, France
2 Faculty of Science, Laboratory of Zoology, University of Yaoundé I, Yaoundé, Cameroon
3 Department of Plant and Animal Sciences, University of Buea, Buea, Cameroon
4 Station d'Ecologie Expérimentale du CNRS à Moulis, Saint-Girons, France

Abstract

Dimorphisms between the sexes are common in vertebrates and may reflect the divergent selective pressures operating on each sex. For example, in species where males do not show territory defense or pronounced male–male combat, females are typically larger than males as fecundity selection will favor large female body size. This is often the case in frogs where male–male competition is limited to calling behavior. Yet, whether differences in reproductive strategies between the two sexes are reflected in shape dimorphisms, and how those differences in shape may affect relevant whole-organism performance traits, remains poorly studied. Here we use *Xenopus tropicalis* frogs to test for intersexual differences in body size, body shape and locomotor performance traits. Our results show that females are larger than males, but that males have relatively longer limbs and heads than females. In absolute terms, males and females perform equally well at different locomotor tasks (burst performance and maximal exertion capacity). Yet, for a given body size, males have a higher exertion capacity than females. Increased exertion capacity in males is likely the consequence of their relatively longer limbs and may reflect selection on locomotor capacity in males to compensate for their smaller absolute body size.

Introduction

Differences in body size between the sexes are common in vertebrates and are thought to reflect the divergent selective pressures operating on each sex associated with differences in life-history strategies (Shine, 1990; Monnet & Cherry, 2002). For example, in species where males do not show territory defense or pronounced male–male combat such as some frogs or snakes, females are under fecundity selection for large body size and are hence typically larger than males (Shine, 1979). In many frogs, male–male competition is limited to calling behavior and, as expected, frogs predominantly show a female-biased sexual size dimorphism (Shine, 1979; but see Halliday & Verrell, 1986). However, in some frogs a male-biased size and shape dimorphism exists and is thought to be associated with physical male–male combat in some populations (Schauble, 2004).

However, differences in reproductive, life-history or ecological strategies between the two sexes may be reflected in differences in body shape in addition to differences in overall size (i.e. size-independent differences in morphology; Lee, 1986, 2001; Lee & Corrales, 2002; Schauble, 2004). Shape dimorphism in traits related to locomotion (Gomes *et al.*, 2009), may allow one sex to maximize performance when it is

pertinent to its reproductive strategy; for example, male lizards have longer legs and higher sprint speeds allowing them to defend territories (Lailvaux, Alexander & Whiting, 2003; Husak *et al.*, 2006; Lailvaux, 2007). Although some data exist on sex-specific differences in locomotor performance in ectotherms, these studies are few (see review in Lailvaux, 2007). Yet, sex-based differences in performance are potentially important modifiers of male and female behavioral strategies and overall fitness, and therefore deserve to be investigated in greater detail (Lee & Corrales, 2002; Lailvaux, 2007).

Despite the many papers devoted to locomotion in frogs (e.g. Zug, 1972, 1978; Emerson, 1978; Marsh, 1994; Wilson, Franklin & James, 2000; Nauwelaerts & Aerts, 2006; Nauwelaerts, Ramsay & Aerts, 2007; Gomes *et al.*, 2009), hardly anything is known about sex-specific differences in locomotor performance, or performance in general in this group. Yet, sex-based differences in morphology and performance may be more common than typically assumed. For example, males of many species are known to develop hypertrophied forearm muscles during the breeding season, allowing them to generate larger forces, which help them to hold on to females during the breeding season (Lee, 2001; Navas & James, 2007). Here we use *Xenopus (Silurana) tropicalis* frogs

to test for intersexual differences in body size, body shape, and locomotor performance traits. Despite being a model organism in developmental biology and genetics (Cannatella & De Sa, 1993; Segerdell *et al.*, 2008; Berg, Gyllenhammar & Kvarnryd, 2009; Hellsten *et al.*, 2010), surprisingly little is known about the ecology and natural history of these animals. *Xenopus tropicalis* are small, principally aquatic pipid frogs (Kobel, Loumont & Tinsley, 1996) that inhabit tropical areas of western Africa (Rödel, 2000). *Xenopus tropicalis* lives in small, isolated puddles in tropical forests and sometimes has mass migrations during the rainy season, which coincides with the reproductive season (Rödel, 2000). Frogs of the genus *Xenopus* are known to be dimorphic in body size, with females being larger than males (Cannatella & De Sa, 1993). Moreover, males have different calls than females and the associated larynx morphology also differs between the sexes (Tobias *et al.*, 2004; Baur, Nasipak & Kelley, 2008). Yet, hardly anything is known about differences in body shape that may be pertinent to ecologically relevant performance traits such as locomotion or feeding. Here we test for differences in body shape and locomotor performance between the sexes in an aquatic frog (*X. tropicalis*). Given that females are known to be larger than males in most pipids, their larger body size will provide them with a performance advantage as a larger distance is covered for every stride taken. During overland migrations to suitable new ponds during the rainy season, males will thus be at a performance disadvantage because of their smaller body size. Consequently, we predict shape differences between the sexes allowing males to perform equally well as females for traits relevant to dispersal.

Materials and methods

Animals

Xenopus tropicalis were caught at a single locality in the wild in December 2009 in Western Cameroon, brought back to France and were housed at the Station d'Ecologie Experimentale du Centre National de la Recherche Scientifique at Moulis. Animals were exported with the authorization for export from the Cameroonian Ministry of Forestry and Wildlife (MINFOF). Animals were housed in groups of 8–10 individuals in aquaria at 24°C and fed every other day with beef heart, earthworms or mosquito larvae *ad libitum*. All individuals were pit-tagged (NONATEC, Lutronic International, Rodange, Luxembourg) before the onset of the experiments allowing further unambiguous identification. Morphological measurements were taken on a total of 127 individuals, and 124 of those were used in subsequent performance trials.

Morphometrics

All animals ($n = 127$) were weighed (Ohaus, Brooklyn, NY, USA; precision ± 0.01 g) and measured using digital calipers (Mitutoyo, Kawasaki, Kanagawa, Japan; $\pm$ 0.01 mm). The following body dimensions were quantified: body length as the straight-line distance from the posterior margin of 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 (Fig. 1).

Performance

Performance traits were measured for 124 individuals at a fixed temperature of 24°C, which is assumed to be close to the preferred and optimal temperature of *Xenopus* frogs (see Casterlin & Reynolds, 1980; Miller, 1982) and is close to temperatures measured in the field. The animals were placed in individual containers with some water for 1 h in an incubator set at 24°C prior to each measurement. Between trials, animals were returned to the incubator and allowed to rest for 1 h. At the end of the performance trials, animals were weighed, their pit-tag numbers recorded, and they were returned to their home aquaria and fed. Animals were given at least a 1-week rest between different performance measures (burst performance capacity vs. maximal exertion capacity). All performance measurements were repeated three times for each individual, and the best measure was retained for analysis.

Maximal exertion capacity was measured by chasing each individual down a 3-m long circular terrestrial track until exhaustion, indicated by the lack of a righting response. Note that individuals recovered quickly from these trials and were immediately ready to eat when placed back in their home aquaria. The floor of the track was covered with cork to improve traction. For each individual, we recorded both the total distance covered and time spent moving until exhaustion. Burst performance capacity was quantified by measuring maximal instantaneous swimming speed and acceleration. Animals were filmed in dorsal view using a Redlake Motion-Pro high-speed camera set at 500 Hz. Illumination was provided by two custom-made arrays of eight ultra bright 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 analyzed using ProAnalyst (Xcitex Inc., 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 a spreadsheet 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 meet assumptions of normality and homoscedascity. To test for
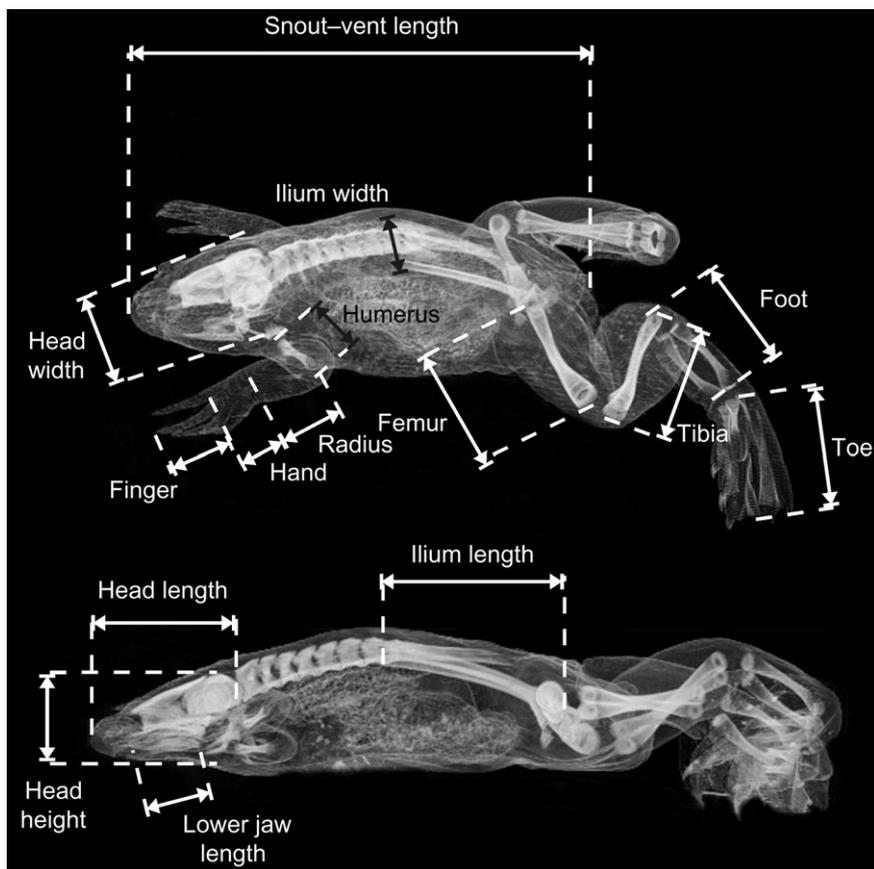
Figure 1 Morphological measurements taken on each individual of *Xenopus tropicalis*. Measurements illustrated using an image derived from a computed tomography-scan courtesy of Renaud Boistel (Université de Poitiers).

differences in size between the sexes, we ran a multivariate analysis of variance (MANOVA) coupled to univariate analyses of variance on snout–vent length (SVL) and body mass (further referred to as 'body size'). Next, we tested for size-independent differences between the sexes in head, body, and limb dimensions using a multivariate analysis of covariance (MANCOVA) with both SVL and body mass as covariates. Finally, we used a MANOVA to test for differences between the sexes in absolute, and MANCOVAs with both SVL and mass as covariates to test for differences between the sexes in relative locomotor performance capacity. All analyses were performed using the Statistical Package for the Social Sciences (SPSS) V. 15.0 (SPSS Inc., Chicago, IL, USA).

Results

Body size was significantly different between males and females (Wilks's lambda = 0.83, $F_{2, 124}$ = 13.09, P < 0.001) with females being larger than males in both SVL ($F_{1,125}$ = 17.71, P < 0.001) and body mass ($F_{1,125}$ = 23.54, P < 0.001; Table 1). Size-corrected limb and body dimensions were also significantly different between males and females (Wilks's lambda = 0.62, $F_{16,108}$ = 4.21, P < 0.001). All morphological traits except for head width, head height, ilium length and ilium width displayed significant differences between the sexes, with males having relatively longer heads and limbs for a given SVL and mass (Table 1; Fig. 2).

No significant differences in locomotor performance were observed between sexes in absolute terms despite the smaller male body size (Wilks's lambda = 0.98, $F_{4,119}$ = 0.64, P = 0.64). However, when correcting for body size, performance differences between sexes became significant (Wilks's lambda = 0.90, $F_{4,117}$ = 3.41, P = 0.01) with males exhibiting higher maximal exertion capacity in terms of the distance run until exhaustion than females for a given body size ($F_{1,120}$ = 10.14, P = 0.002). Burst performance capacity was not different between the sexes, after correcting for differences in overall size (Table 1).

Discussion

Our results show that, as has been observed for most frogs as well as other species of *Xenopus*, females are larger than males (Shine, 1979, 1990; Halliday & Verrell, 1986; Measey & Tinsley, 1998). However, male *X. tropicalis* have relatively longer fore and hind-limbs and heads than females. Whereas in absolute terms, males and females perform equally well at different locomotor tasks (burst performance and maximal exertion capacity), males have a higher maximal exertion capacity than females for a given body size. Our data suggest that this may potentially be explained by their relatively longer hind-limbs. Indeed, on average, frogs with longer hind-limbs are better jumpers and jump longer distances (Zug, 1972, 1978; Gomes *et al.*, 2009). If the number of jumps an indi-

Table 1 Table summarizing the morphometric and performance data

	Males ($n = 56$)	Females ($n = 71$)
Snout–vent length (mm)	36.12 ± 2.94	40.81 ± 7.08
Mass (g)	4.93 ± 1.27	7.49 ± 3.22
Head length (mm)	10.35 ± 0.71	10.88 ± 1.59
Head width (mm)	11.67 ± 0.73	12.61 ± 1.75
Head height (mm)	6.11 ± 0.78	6.74 ± 0.99
Lower jaw length (mm)	8.93 ± 0.76	9.51 ± 1.53
Femur length (mm)	16.44 ± 1.13	17.51 ± 2.58
Tibia length (mm)	16.31 ± 1.28	17.59 ± 2.56
Foot length (mm)	11.16 ± 1.00	12.08 ± 1.85
Toe length (mm)	12.79 ± 1.30	13.62 ± 2.35
Hind-limb length (mm)	56.70 ± 4.25	60.81 ± 9.01
Humerus length (mm)	8.04 ± 0.63	8.48 ± 1.32
Radius length (mm)	7.63 ± 0.69	7.96 ± 1.25
Hand length (mm)	1.78 ± 0.21	1.82 ± 0.43
Finger length (mm)	5.81 ± 0.80	5.95 ± 1.25
Forelimb length (mm)	23.26 ± 1.54	24.22 ± 3.92
Ilium length (mm)	18.79 ± 1.67	21.75 ± 4.15
Ilium width (mm)	8.10 ± 0.96	8.65 ± 1.18
Maximal velocity (m s^{-1})	1.44 ± 0.25	1.50 ± 0.24
Maximal acceleration (m s^{-2})	50.09 ± 8.46	52.22 ± 7.94
Maximal time (s)	80.66 ± 121.92	61.88 ± 31.96
Maximal distance (m)	1.03 ± 1.34	0.80 ± 0.23

Table entries are means ± standard deviations. Note that only 70 females were included in measurements of burst performance and 69 females for endurance measurements.
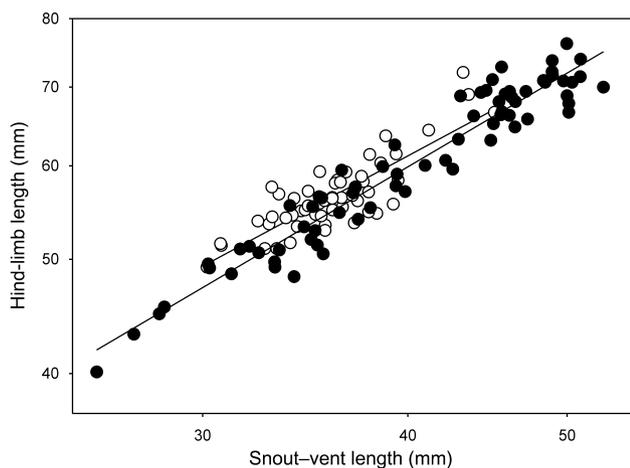
Figure 2 Sex differences in hind-limb length as a function of body size (snout–vent length) in wild-caught *Xenopus tropicalis* illustrating how males have longer hind-limbs than females for a given body size. Males are indicated with open circles and female with closed circles.

vidual can perform is limited by the energy stores available (Miller & Camilliere, 1981), then longer hind-limbs should translate into a greater maximal exertion capacity. This would be true only when the maximal exertion capacity is measured as the distance jumped, but not as the length of time jumped, as any single jump will be greater for individuals with longer limbs. This is exactly what is observed in our data, suggesting a proximate mechanism to explain the observed difference in relative exertion capacity between males and females. Although differences in hind-limb length are also expected to be related to a greater aquatic burst performance capacity (see Nauwelaerts *et al.*, 2007), in fully aquatic pipids like *X. tropicalis*, swimming performance is determined not only by limb length, but also by the sliding of the urostyle across the pelvis (Videler & Jorna, 1985). This renders the relationships between morphology and performance more complex and may explain the lack of differences in aquatic burst performance capacity between males and females.

The observed differences in relative hind-limb length and maximal exertion capacity in males relative to females suggest selection on maximal exertion capacity in males relative to females, which may be the consequence of the smaller absolute body size in males. Exertion capacity is likely under selection in *X. tropicalis*, as individuals of both sexes need to disperse between pools and ponds to colonize different bodies of water. Indeed, another aquatic frog, *X. laevis*, has been shown to show long-distance overland migrations in time of draught (Lobos & Jaksic, 2005) and during torrential rains (Rödel, 2000). Given that *X. tropicalis* males are smaller than females yet have to travel similar distances, they may experience increased selection for long hind-limbs to allow them to reach similar levels of absolute performance. Yet, this hypothesis remains to be tested.

Differences in head dimensions are unlikely to be related to differences in locomotor performance, however. Indeed, although head shape may affect streamlining of the animal in an aquatic environment and thus the drag on the body, the difference between the sexes was observed for terrestrial locomotion only (i.e. endurance), where drag has a negligible effect on locomotor performance. Differences in head dimensions may instead be related to differences in diet between the two sexes. As *Xenopus* are fully aquatic suction feeders (but see Measey, 1998a), differences in head shape between the two sexes may result in differences in suction-feeding performance and thus in diet. Unfortunately, no data are available on sexual differences in diet and thus, this hypothesis remains to be tested. Yet, for a feral population of *X. laevis*, no difference in diet was observed between the sexes (Measey, 1998b).

Alternatively, differences in head shape may be related to vocalization or other forms of male–male competition. In *Limnodynastes peronii* frogs, a sexual dimorphism in head shape was observed with males having wider heads than females (Schauble, 2004). In this species, the wider heads in males were suggested to be related to physical aggression among males. However, in *X. tropicalis*, males have longer, relatively narrower heads than females, which is unlikely to be related to direct physical aggression among males. Finally, the longer forelimbs in males relative to females may be related to the use of the forelimb during amplexus in *Xenopus* frogs. As males hold on to females during breeding, longer forelimbs may provide a better grip (Lee, 1986; Measey & Tinsley, 1997). In explosive breeding anurans, it was demonstrated that amplectant males have longer forelimbs and greater forelimb muscle mass than non-amplectant males and females

of the same species (Lee, 1986, 2001). Indeed, longer forelimbs and stronger muscles may allow males to hold on to a female during mating struggles where other males are trying to displace the amplectant male from the female. However, as *Xenopus* are not explosive breeders and males do not 'fight' over females, it remains unsure whether the difference in forelimb length between the sexes can be explained by selection on mate-holding capacity. Clearly, more data on the ecology and natural history of these animals are needed to explore the ecological and evolutionary factors underlying the observed differences in morphology and performance between the sexes.

Acknowledgements

References

Baur, L.A., Nasipak, B.T. & Kelley, D.B. (2008). Sexually differentiated, androgen-regulated, larynx-specific myosin heavy-chain isoforms in *Xenopus tropicalis*; comparison to *Xenopus laevis*. *Dev. Genes Evol.* **218**, 371–379.

Berg, C., Gyllenhammar, I. & Kvarnryd, M. (2009). *Xenopus tropicalis* as a test system for developmental and reproductive toxicity. *J. Toxicol. Environ. Health A* **72**, 219–225.

Cannatella, D.C. & De Sa, R.O. (1993). *Xenopus laevis* as a model organism. *Syst. Biol.* **42**, 476–507.

Casterlin, M.E. & Reynolds, W.W. (1980). Diel activity and thermoregulatory behavior of a fully aquatic frog: *Xenopus laevis*. *Hydrobiologia* **75**, 189–191.

Emerson, S.B. (1978). Allometry and jumping in frogs: helping the twain to meet. *Evolution* **32**, 551–564.

Gomes, F.R., Rezende, E.L., Grizante, M.B. & Navas, C.A. (2009). The evolution of jumping performance in anurans: morphological correlates and ecological implications. *J. Evol. Biol.* **22**, 1088–1097.

Halliday, T.R. & Verrell, P.R. (1986). Review: sexual selection and body size in amphibians. *Herpetol. J.* **1**, 86–92.

Hellsten, U., Harland, R.M., Gilchrist, M.J., Hendrix, D., Jurka, J., Kapitonov, V., Ovcharenko, I., Putnam, N.H., Shu, S., Taher, L., Blitz, I.L., Blumberg, B., Dichmann, D.S., Dubchak, I., Amaya, E., Detter, J.C., Fletcher, R., Gerhard, D.S., Goodstein, D., Graves, T., Grigoriev, I.V., Grimwood, J., Kawashima, T., Lindquist, E., Lucas, S.M., Mead, P.E., Mitros, T., Ogino, H., Ohta, Y., Poliakov, A.V., Pollet, N., Robert, R., Salamov, A., Sater, A.K., Schmutz, J., Terry, A., Vize, P.D., Warren, W.C., Wells,

D., Wills, A., Wilson, R.K., Zimmerman, L.B., Zorn, A.M., Grainger, R., Grammer, T., Khokha, M.K., Richardson, P.M. & Rokhsar, D.S. (2010). The genome of the Western Clawed Frog *Xenopus tropicalis*. *Science* **328**, 633–636.

Husak, J.F., Fox, S.F., Lovern, M.B. & Van Den Busche, R.A. (2006). Faster lizards sire more offspring: sexual selection on whole-animal performance. *Evolution* **60**, 2122–2130.

Kobel, H.R., Loumont, C. & Tinsley, R.C. (1996). The extant species. In *The biology of* Xenopus: 9–34. (eds. Tinsley, R.C. & Kobel, H.R. (Eds). Oxford: Oxford University Press.

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. & 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.

Lee, J.C. (1986). Is the large-male mating advantage in anurans an epiphenomenon? *Oecologia* **69**, 207–212.

Lee, J.C. (2001). Evolution of secondary sexual dimorphism in the toad, *Bufo marinus*. *Copeia* **2000**, 928–935.

Lee, J.C. & Corrales, A.D. (2002). Sexual dimorphism in hind-limb muscle mass is associated with male reproductive success in *Bufo marinus*. *J. Herpetol.* **36**, 502–505.

Lobos, G. & Jaksic, F.M. (2005). The ongoing invasion of African clawed frogs (*Xenopus laevis*) in Chile: causes of concern. *Biodivers. Conserv.* **14**, 429–439.

Marsh, R.L. (1994). Jumping ability of anuran amphibians. In *Advances in veterinary science and comparative medicine*: Vol. **38** 51–111. Jones, J.H. (Ed.). New York: Academic Press.

Measey, G.J. (1998a). Terrestrial prey capture in *Xenopus laevis*. *Copeia* **1998**, 787–791.

Measey, G.J. (1998b). Diet of feral *Xenopus laevis* (Daudin) in South Wales, UK. *J. Zool.* **246**, 287–298.

Measey, G.J. & Tinsley, R. (1997). Mating Behavior of *Xenopus wittei* (Anura: Pipidae). *Copeia* **1997**, 601–609.

Measey, G.J. & Tinsley, R. (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.

Miller, K. & Camilliere, J.J. (1981). Physical training improves swimming performance of the African clawed frog *Xenopus laevis*. *Herpetologica* **37**, 1–10.

Monnet, J.-M. & Cherry, M.I. (2002). Sexual size dimorphism in anurans. *Proc. R. Soc. B* **269**, 2301–2307.

Nauwelaerts, S. & Aerts, P. (2006). Take-off and landing forces in jumping frogs. *J. Exp. Biol.* **209**, 66–77.

Nauwelaerts, S., Ramsay, J. & Aerts, P. (2007). Morphological correlates of aquatic and terrestrial locomotion in a semi-aquatic forg, *Rana esculenta*: no evidence for a design conflict. *J. Anat.* **210**, 304–317.

Navas, C.A. & James, R.S. (2007). Sexual dimorphism of extensor carpi radialis muscle size, isometric force, relaxation rate and stamina during the breeding season of the frog *Rana temporaria* Linneaeus 1758. *J. Exp. Biol.* **210**, 715–721.

Rödel, M. (2000). *Herpetofauna of West Africa*. Vol. **1**. Chimaira: Amphibians of the Western Savanah.

Schauble, C.S. (2004). Variation in body size and sexual dimorphism across geographical and environmental space in the frogs *Limnodynastes tasmaniensis* and *L. peronii*. *Biol. J. Linn. Soc.* **82**, 39–56.

Segerdell, E., Bowes, J.B., Pollet, N. & Vize, P.D. (2008). An ontology for *Xenopus* anatomy and development. *BMC Dev. Biol.* **8**, 92. doi:10.1186/1471-213X-8-92.

Shine, R. (1979). Sexual selection and sexual dimorphism in the Amphibia. *Copeia* **1979**, 297–306.

Shine, R. (1990). Proximate determinants of sexual differences in adult body size. *Am. Nat.* **135**, 278–283.

Tobias, M.L., Barnard, C., O'Hagan, R., Horng, S.H., Rand, M. & Kelly, D.B. (2004). Vocal communication between male *Xenopus laevis*. *Anim. Behav.* **67**, 353–365.

Videler, J.J. & Jorna, J.T. (1985). Function of the sliding pelvis in *Xenopus laevis*. *Copeia* **1985**, 254–257.

Wilson, R.S., Franklin, C.E. & James, R.S. (2000). Allometric scaling relationships of jumping performance in the striped marsh frog *Limnodynastes peronii*. *J. Exp. Biol.* **203**, 1937–1946.

Winter, D. (2005). *Biomechanics and motor control of human movement*. New York: John Wiley and Sons.

Zug, G.R. (1972). Anuran locomotion: structure and function I. preliminary observations on the relation between jumping and osteometrics of appendicular and postaxial skeleton. *Copeia* **1972**, 613–624.

Zug, G.R. (1978). Anuran locomotion: structure and function 2. Jumping performance of semiaquatic, terrestrial, and arboreal frogs. *Smithson. Contrib. Zool.* **276**, 1–31.