Sexual dimorphism in the forelimb muscles of the Asiatic toad *Bufo gargarizans*

Zhi Ping Mi

College of Life Science, China West Normal University, Nanchong 637009, Sichuan Province, China

Theory predicts that sexual dimorphism evolves as a consequence of sexual selection. I studied sexual dimorphism in ten forelimb muscles used in the amplexus of *Bufo gargarizans* (deltoideus, pectoralis, coraco-humeralis longus, coraco-humeralis brevis, sterno-radialis, flexor carpi radialis, extensor carpi radialis, abductor indicus longus, extensor digitorum communis longus and flexor digitorum communis), and three forelimb muscles not involved in amplexus (infraspinatus, latissimus dorsi and triceps branchii). Muscle mass was higher in males for all muscles considered. Males found in amplexus had significantly larger forelimb muscles involved in amplexus than non-amplectant males (exceptions: coraco-humeralis longus and abductor indicus longus), whereas the mass of the three muscles not involved in amplexus did not differ between amplectant and non-amplectant males. My findings suggest that a male-mating advantage depends on the absolute mass of muscles involved in amplexus, in line with the assumption that sexual dimorphism in forelimb muscle mass has evolved under sexual selection.

Key words: Bufo gargarizans, forelimb muscle, sexual dimorphism, sexual selection

INTRODUCTION

Anurans exhibit a variety of secondary sexual dimorphisms such as body size, vocal apparatus, head dimensions and colouration (Duellman & Trueb, 1986). With regard to muscle dimorphisms, studies have focused on muscles mass (Kirby, 1983; Yekta & Blackburn, 1992; Lee, 2001; Lee & Corrales, 2002; Liao et al., 2012a, b), muscle fibre types and their sizes (Muller et al., 1969; Melichna et al., 1972; Oka et al., 1984; Dorlochter et al., 1994), and muscle isometric contractile properties (Peters & Aulner, 2000; Girgenrath & Marsh, 2003; Clark & Peters, 2006; Navas & James, 2007). Sexual dimorphisms of muscles can for example be associated with sound production (Schmidt, 1965; Kelley, 1986; Emerson & Boyd, 1999) or amplexus (Kirby, 1983), and have been interpreted as the result of sexual selection (Duellman, 1992; Lee, 2001).

 Previous studies have shown that forelimb muscles involved in amplexus, such as pectoralis series, coracobrachialis series, deltoideus, triceps branchii, extensor carpi radialis, flexor carpi radialis, sternoradialis and abductor indicus longus, are larger and heavier in males than in females. Larger forelimb muscles in males produce enhanced force for amplexing females, and to resist attempted take-overs by competing males (Kirby, 1983; Oka et al., 1984; Duellman, 1992; Yekta & Blackburn, 1992; Peters & Aulner, 2000; Lee, 2001; Clark & Peters, 2006; Navas & James, 2007; Liao et al., 2012a). These muscles are also less fatigable in males than in females, which may allow male frogs to maintain amplexus for prolonged periods (Peters & Aulner, 2000; Clark & Peters, 2006; Navas & James, 2007). However, forelimb muscles not involved in amplexus have not received much attention so far. In this study, I compared the mass of forelimb muscles between males and females depending on whether they are used during amplexus, considering amplectant and non-amplectant males.

 The Asiatic toad, *Bufo gargarizans*, is widely distributed in China, Russia and Korea (Fei & Ye, 2001). In Nanchong City, the species hibernates in mid-November, and reproduction takes place in December or January (Yu et al., 2009). It is an explosively breeding species, with a breeding season lasting 6–24 days (Yu & Lu, 2010). Males do not discriminate potential mates with respect to body size (Yu & Lu, 2010). The aims of the present study are to: (i) Quantify the differences in body size and mass of selected forelimb muscles between female and male *B. gargarizans*; (ii) Compare body size and selected forelimb muscles mass between amplectant and non-amplectant males.

MATERIALS AND METHODS

Bufo gargarizans were captured in a pond by hand at night between 24 January and 12 February 2011 in Shunqing County in Nanchong City, China (30°49′N, 106°03′E, 251 m elevation). Sixteen pairs in amplexus and 18 non-amplectant males were collected. All individuals were killed by pithing and stored in 10% neutral buffered formalin for dissection. Snout-vent lengths (SVL) were measured to the nearest 0.1 mm using electronic vernier calipers.

Dissections took place between 19 and 31 July 2011. I anatomized thirteen forelimb muscles on the right side of each specimen. Muscles were dried using a thermostat drier at 60°C, and then weighed to the nearest 0.1 mg using an electronic balance. The muscles analyzed in this paper are as follows: (1) deltoideus, pectoralis, coraco-humeralis longus, coraco-humeralis brevis, sterno-radialis, flexor carpi radialis, extensor carpi radialis, abductor indicus longus, extensor digitorum communis longus and flexor
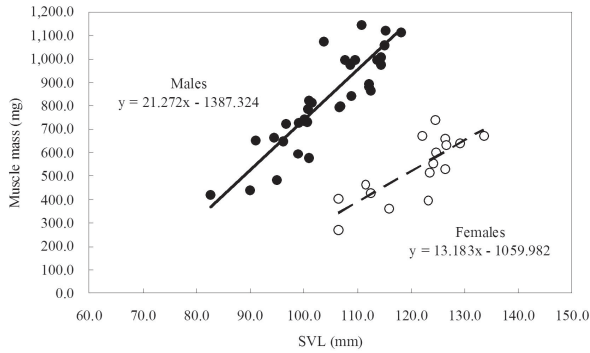
Correspondence: Zhi Ping Mi, College of Life Science, China West Normal University, Nanchong 637009, Sichuan Province, China; E-mail: mizhp@163.com; zhipingmi@126.com

Fig. 1. Linear regression of the total mass of forelimb muscles used in amplexus (deltoideus + pectoralis + coraco-humeralis longus + coraco-humeralis brevis + sterno-radialis etc.) on SVL for males (close circles, solid line) and females (open circles, broken line) of *Bufo gargarizans*.

Fig. 2. Linear regression of the total mass of forelimb muscles not used in amplexus (infraspinatus + latissimus dorsi + triceps branchii) on SVL for males (close circles, solid line) and females (open circles, broken line) of *Bufo gargarizans*.

digitorum communis, which participate directly in the axillary amplexus exhibited by *B. gargarizans* (defined here as muscles used in amplexus), controlling upper arm adduction, elbow flexion, wrist flexion and thumb extension (Feng, 1990; Yekta & Blackburn, 1992; Peters & Aulner, 2000; Lee, 2001); (2) infraspinatus, latissimus dorsi and triceps branchii which do not produce force during amplexus (defined here as muscles not used in amplexus); the three muscles can abduct upper arms for movements towards dorsally, and triceps branchii can extend the elbow (Feng, 1990).

Differences in SVL (males vs. females, amplectant vs. non-amplectant males) were tested by one-way ANOVA after testing data for normality. I regressed the muscle mass on SVL for each muscle, and compared regression coefficients between two groups with regression analysis for homogeneity. According to the regression equation, I calculated asymptotic muscle mass. Differences of adjusted means were tested for using analyses of covariance (ANCOVA), with SVL as the covariate. Means are given±1 SD.
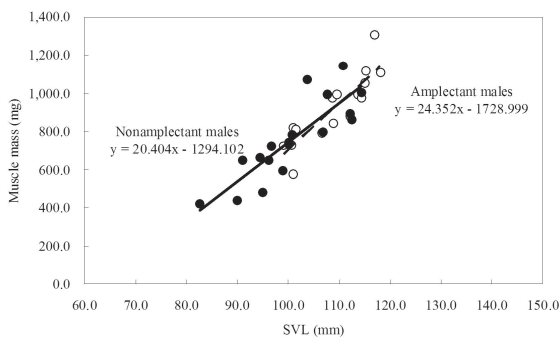
RESULTS

Comparison of males with females

On average, SVL of females was significantly larger than male SVL (ANOVA, $F_{1,49}$=40.70, $P<0.001$). SVL ranged from 82.5 to 118.0 mm (104.5±8.7 mm) in males, and from 106.4 to 133.5 mm (121±8.0 mm) in females.

For the thirteen forelimb muscles examined, the linear regression of muscle mass on SVL was highly significant ($P<0.01$), with 32.2–79.4% of variation in muscle mass being statistically explained by regression on SVL (Table 1). Slopes were homogeneous ($P>0.05$) for all comparison between the sexes except for flexor carpi radialis, extensor carpi radialis and abductor indicus longus ($P<0.01$). The adjusted mean of males always significantly exceeded that of females (Table 1). Independent of body size, all thirteen forelimb muscles in males were significantly heavier than in females (Table 1).

Linear regression of the total mass of the ten forelimb muscles used in amplexus correlated with SVL in both sexes (Fig. 1, Table 1), and the slopes were not homogenous ($P=0.034$). Total mass of the three forelimb muscles not

Fig. 3. Linear regression of the total mass of forelimb muscles used in amplexus (deltoideus + pectoralis + coraco-humeralis longus + coraco-humeralis brevis + sterno-radialis etc.) on SVL for non-amplectant males (close circles, solid line) and amplectant males (open circles, broken line) of *Bufo gargarizans*.
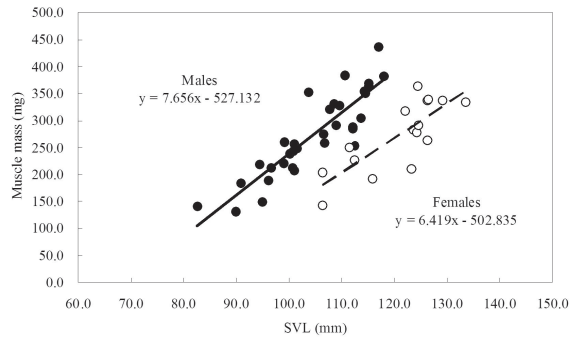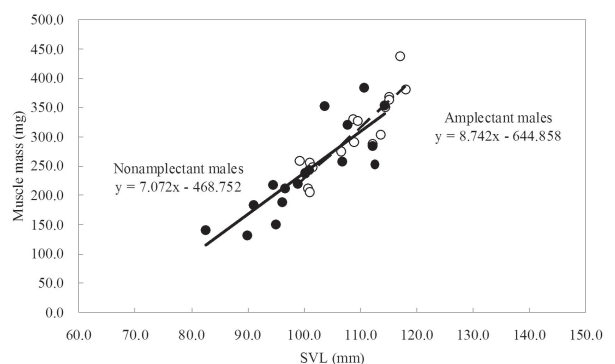

Fig. 4. Linear regression of the total mass of forelimb muscles not used in amplexus (infraspinatus + latissimus dorsi + triceps branchii) on SVL for non-amplectant males (close circles, solid line) and amplectant males (open circles, broken line) of *Bufo gargarizans*.

Table 1. Linear regression of muscle mass on SVL and results of ANCOVA comparing male and female of *Bufo gargarizans*. *P*<0.001 in all cases.

| Muscle | Males (*n*=34) | | | Females (*n*=16) | | | |
	Equation	R^2	Adj. mean	Equation	R^2	Adj. mean	F
Deltoideus	y=3.826x - 266.666	0.794	133.25±3.34	y=3.571x - 296.623	0.672	135.39±28.70	21734.81
Pectoralis	y=3.989x - 262.827	0.727	154.14±34.76	y=3.115x - 48.462	0.512	128.39±25.03	3965.36
Coraco-humeralis longus	y=1.133x - 79.258	0.666	39.17±9.88	y=0.669x - 52.128	0.324	28.81±5.38	1329.78
Coraco-humeralis brevis	y=0.729x - 51.699	0.733	24.51±6.35	y=0.572x - 46.080	0.495	23.12±4.59	2542.22
Sterno-radialis	y=1.540x - 105.441	0.743	55.52±13.42	y=1.274x - 111.732	0.592	42.38±10.23	7762.75
Flexor carpi radialis	y=3.023x - 187.387	0.713	128.60±26.34	y=0.426x - 25.585	0.381	25.96±3.44	1160.93
Extensor carpi radialis	y=3.528x - 216.340	0.644	152.44±30.75	y=1.423x - 106.798	0.491	65.36±11.44	1640.87
Abductor indicus longus	y=1.462x - 86.603	0.596	66.22±12.74	y=0.136x - 8.542	0.322	7.91±1.10	1312.65
Extensor digitorum communis longus	y=0.498x - 28.155	0.489	23.90±4.34	y=0.368x - 27.874	0.576	16.65±2.95	5061.10
Flexor digitorum communis	y=1.544x - 102.948	0.743	58.44±13.45	y=1.630x - 136.158	0.659	61.03±13.09	28754.99
Total	y=21.272x - 1387.324	0.771	836.19±185.35	y=13.183x - 1059.982	0.616	534.89±105.92	2285.24
Infraspinatus	y=2.217x - 149.573	0.703	82.17±19.32	y=2.029x - 161.424	0.589	84.04±16.30	12810.85
Latissimus dorsi	y=0.623x - 45.076	0.576	20.05±5.44	y=0.635x - 52.298	0.463	24.54±5.10	83329.37
Triceps branchii	y=4.816x - 332.382	0.791	170.93±41.96	y=3.755x - 289.114	0.658	165.16±30.18	2266.76
Total	y=7.656x - 527.132	0.781	273.14±66.71	y=6.419x - 502.835	0.641	273.73±51.58	3718.28

used in amplexus was also significantly correlated with SVL in both sexes (Fig. 2, Table 1), with homogenous slopes (*P*=0.383). The adjusted means of total mass between males and females significantly differed for both muscles used in amplexus (*P*<0.001) and muscles not used in amplexus (ANCOVA, *P*<0.001).

Comparison of amplectant males with non-amplectant males
Amplectant males were significantly larger than non-amplectant males (ANOVA, $F_{1,\,33}$=9.29, *P*=0.005). SVL ranged from 99.1 to 118.0 mm (mean=108.8±6.5 mm) in amplectant males and from 82.5 to 114.2 mm (mean=100.7±8.7 mm) in non-amplectant males. Muscle mass was correlated with SVL for both amplectant and

non-amplectant males(*P*<0.01, Table 2). The regression coefficients were homogeneous (*P*>0.05), and 31.5–81.3% of variation in muscle mass was explained through the regression. When controlling the influence of body size, the adjusted mean mass of muscles used in amplexus was significantly higher in amplectant males except for coraco-humeralis longus and abductor indicus longus. Differences in the adjusted mean mass of muscles not used in amplexus were not significant between amplectant and non-amplectant males (Table 2).

The total mass of the ten forelimb muscles used in amplexus was correlated with SVL in both amplectant and non-amplectant males (Table 2, Fig. 3), and the slopes were homogenous (*P*=0.44). The total mass of the three forelimb muscles not used in amplexus was

Table 2. Linear regression of muscle mass on SVL and results of ANCOVA comparing amplectant and nonamplectant males of *Bufo gargarizans*

Muscle	Nonamplectant males (*n*=18)			Amplectant males (*n*=16)			*F*	*P*
	Equation	R^2	Adj. mean	Equation	R^2	Adj. mean		
Deltoideus	y=3.689x - 250.575	0.775	120.87±32.26	y=4.628x - 356.511	0.786	147.22±30.24	21.06	0.000
Pectoralis	y=3.637x - 225.839	0.629	140.37±31.82	y=5.074x - 382.782	0.813	169.50±33.16	4.446	0.043
Coraco-humeralis longus	y=0.958x - 61.304	0.656	35.17±8.37	y=1.563x - 126.449	0.655	43.67±10.22	1.132	0.296
Coraco-humeralis brevis	y=0.651x - 44.159	0.658	21.40±5.70	y=0.819x - 61.186	0.703	27.96±5.35	10.534	0.003
Sterno-radialis	y=1.487x - 98.522	0.708	51.21±13.01	y=2.014x - 158.788	0.805	60.43±13.16	31.946	0.000
Flexor carpi radialis	y=3.168x - 200.868	0.721	118.11±27.72	y=2.995x - 185.698	0.586	140.29±19.57	159.362	0.000
Extensor carpi radialis	y=3.384x - 201.217	0.634	139.52±29.60	y=3.961x - 264.196	0.542	166.95±25.90	4.220	0.048
Abductor indicus longus	y=1.503x - 90.866	0.607	60.47±13.14	y=1.353x - 74.584	0.406	72.69±8.83	2.893	0.099
Extensor digitorum communis longus	y=0.398x - 19.025	0.424	21.04±3.48	y=0.48x - 25.069	0.315	27.18±3.14	485.558	0.000
Flexor digitorum communis	y=1.527x - 101.726	0.736	52.02±13.35	y=1.465x - 93.737	0.587	65.73±9.58	260.628	0.000
Total	y=20.404x - 1294.102	0.721	760.34±178.51	y=24.352x - 1728.999	0.762	921.63±159.16	7.579	0.010
Infraspinatus	y=2.061x - 133.947	0.658	73.57±18.04	y=2.521x - 182.594	0.670	91.81±16.47	0.073	0.789
Latissimus dorsi	y=0.484x - 31.096	0.465	17.63±4.23	y=0.903x - 75.583	0.643	22.71±5.90	0.000	0.988
Triceps branchii	y=4.527x - 303.708	0.736	152.11±39.60	y=5.318x - 386.681	0.767	192.16±34.75	0.755	0.392
Total	y=7.072x - 468.752	0.704	243.31±61.87	y=8.742x - 644.858	0.796	306.68±57.15	0.234	0.632

also correlated with SVL for both amplectant and non-amplectant males (Table 2, Fig. 4) at homogenous slopes (*P*=0.35). The ANCOVA showed that the differences in the adjusted means of total mass of the muscles used in amplexus significantly differed between amplectant and non-amplectant males (*P*=0.01, Table 2). However, there was no difference in the adjusted mean of total mass for muscles not used in amplexus between amplectant and non-amplectant males (*P*=0.632, Table 2).

DISCUSSION

Body sizes of female *B. gargarizans* significantly exceed that of adult males, consistently with previous studies on this species (Feng, 1990; Yu & Lu, 2010). Sexual size dimorphism is common in anurans (Shine, 1979; Liao et al., 2010; Li et al., 2010; Liao & Lu, 2010a, b; Liao et al., 2011; Liao & Lu 2011a; Liao, 2011; Liao & Lu, 2012). Fecundity selection suggests that there is a positive correlation between female fecundity and body size (Crump, 1974; Andersson, 1994; Liao & Lu 2009; Liao & Lu 2011b). For *B. gargarizans*, larger females lay more eggs than smaller females (Yu & Lu, 2010), which can be attributed to fecundity selection. Moreover, there are several hypotheses proposed to explain sexual size dimorphism, including physical combat (Shine, 1979), relative duration of the breeding period (Woolbright, 1983), intersexual difference in selection gradients (Arak,

1988), differences in life-history strategies (Halliday & Verrell, 1986), endocrine hormone differences (Regnier & Herrera, 1993) and sex differences in the age structure (Monnet & Cherry, 2002). These assumptions need to be further examined in *B. gargarizans*.

Previous studies largely used muscle mass and/or cross-sectional area to estimate muscle forces, with larger muscles exerting more force in amplexus (Oka et al., 1984; Lee, 1986, 2001; Peters & Aulner, 2000; Navas & James, 2007). My study reveals that not only the forelimb muscles involved in axillary amplexus,but also the forelimb muscles not involved in axillary amplexus are larger in males compared to females. Strong forelimb muscles involved in amplexus presumably can help males to retain their grasp of the female during attempted take-overs by competing males (Oka et al., 1984; Peters & Aulner, 2000; Lee, 2001). This size dimorphism in forelimb muscle mass has been previously attributed to sexual selection (Lee, 2001).

The mass of muscles not involved in amplexus do not differ between males and females, indicating that they are not involved in sexual selection (Duellman & Trueb, 1986). However, the present study showed that the infraspinatus, latissimus dorsi and triceps branchii muscles, despite not being involved in the amplexus, still exhibit sexual size dimorphism. How can this phenomenon be explained? Hindlimbs are in some species used to deter adversary males (Wells, 1979; Halliday, 1980). Lee & Corrales (2002) indeed revealed that male *Bufo marinus* possess higher hindlimb muscle mass than females as a result of of sexual selection. My results suggest that forelimb muscles not involved in amplexus might have co-evolved with the muscles targeted for sexual selection. However, a more detailed understanding of this phenomenon would benefit from comparative studies on the genetics, physiology and embryology of forelimb muscles.

Theory predicts that sexual selection favours the evolution of a large body size in males when male-male contest for physical possession of females result in a large male mating advantage (Yu & Lu, 2010; Liao & Lu, 2011c). In my study, amplectant males are significantly larger than non-amplectant males, suggesting that mating success is significantly non-random with respect to male body size. A large male-mating advantage may relate to muscle mass and forces. My data confirm that, independent of body size, eight out of ten forelimb muscles involved in amplexus are significantly heavier in amplectant males than in non-amplectant males (exceptions: coraco-humeralis longus and abductor indicus longus). I also found that total mass of the muscles used in amplexus of amplectant males exceeded that of non-amplectant males. Takeover attempts might have influenced the evolution of forelimb muscle traits in frogs (Navas & James, 2007). Strong muscles allow males to grip firmly on females during amplexus, and to resist take-over attempts by non-amplectant males (see also Lee, 2001 on *B. marinus,* and Liao et al., 2012a, b on *B. andrewsi*). The three forelimb muscles not involved in amplexus, on the other hand, did not differ between amplectant and non-amplectant males. It is possible that infraspinatus, latissimus dorsi and triceps branchii muscles do not play an important role

in amplexus. My results confirm that only the forelimb muscles involved in amplexus are related to male mating advantage in *B. gargarizans*. The significant differences in mass of the forelimb muscles involved in amplexus between amplectant and non-amplectant males may be the consequence of intra-sexual sexual selection expressed as male-male contest and environmental inducement (Lee, 2001).

ACKNOWLEDGEMENTS

REFERENCES

Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.

Arak, A. (1988). Sexual size dimorphism in body size: a model and a test. *Evolution* 42, 820–825.

Clark, D.L. & Peters, S.E. (2006). Isometric contractile properties of sexually dimorphic forelimb muscles in the marine toad *Bufo marinus* Linnaeus 1758: functional analysis and implications for amplexus. *Journal of Experimental Biology* 209, 3448–3456.

Crump, M.L. (1974). Reproductive strategies in a tropical anuran community. *Miscellaneous Publication of the Museum of Natural History, Univ. Kansas* 61, 1–68.

Dorlochter, M., Astrow, S.H. & Herrera, A.A. (1994). Effects of testosterone on a sexually dimorphic frog muscle: repeated *in vivo* observations and androgen receptor distribution. *Journal of Neurobiology* 25, 897–916.

Duellman, W.E. (1992). Reproductive strategies of frogs. *Scientific American* 267, 80–87.

Duellman, W.E. & Trueb, L. (1986). *Biology of Amphibians*. New York: McGraw-Hill.

Emerson, S.B. & Boyd, S. K. (1999). Mating Vocalizations of Female Frogs: Control and Evolutionary Mechanisms. *Brain, Behavior and Evolution* 53, 187–197.

Fei, L., Ye, C.Y. (2001). *The Colour Handbook of Amphibians of Sichuan*. Beijing: China Forestry Publishing House.

Feng, X.Y. (1990). *The Systematic Dissection of Bufo gargarizans*. Beijing: Higher Education Press.

Girgenrath, M. & Marsh, R.L. (2003). Season and testosterone affect contractile properties of fast calling muscles in the gray tree frog *Hyla chrysoscelis. American Journal of Physiology - Regulatory, Integrative and Comparative Physiology* 284, R1513–R1520.

Halliday, T. (1980). *Sexual strategy*. Chicago: University of Chicago Press.

Halliday, T. & Verrell, P.A. (1986). Review: sexual selection and body size in amphibians. *Journal of Herpetology* 1, 86–92.

Kelley, D. B. (1986). Neuroeffectors for vocalization in *Xenopus*

laevis: hormonal regulation of sexual dimorphism. *Journal of Neurobiology* 17, 231– 248.

Kirby, A.C. (1983). Physiology of the sternoradialis muscle: sexual dimorphism and role in amplexus in the leopard frog (*Rana pipiens*). *Comparative Biochemistry and Physiology A: Physiology* 74, 705–709.

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

Lee, J.C. (2001). Evolution of a secondary sexual dimorphism in the toad, *Bufo marinus*. *Copeia* 2001, 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*. *Journal of Herpetology* 36, 502–505.

Li, C., Liao, W.B., Yang, Z.S. & Zhou, C.Q. (2010). A skeletochronological estimation of age structure in a population of the Guenther's frog. *Hylarana guentheri*, from western China. *Acta Herpetologica* 5, 1–11.

Liao, W.B. & Lu, X. (2009). Male mate choice in the Andrew's toad *Bufo andrewsi*: a preference for larger females. *Journal of Ethology* 27, 413–417.

Liao, W.B. & Lu, X. (2010a). A skeletochronological estimation of age and body size by the Sichuan torrent frog (*Amolops mantzorum*) between two populations at different altitudes. *Animal Biology* 6, 479–489.

Liao, W.B. & Lu, X. (2010b). Age structure and body size of the Chuanxi tree toad *Hyla annectans chuanxiensis* from two different elevations (China). *Zoologischer Anzeiger* 248, 255–263.

Liao, W.B., Zhou, C.Q., Yang, Z.S. & Lu, X. (2010). Age, size and growth in two populations of the dark-spotted frog *Rana nigromaculata* at different altitudes in southwestern China. *Herpetological Journal* 20, 77–82.

Liao, W.B., Lu, X., Shen, Y.W. & Hu, J.C. (2011). Age structure and body size of two   populations of the rice frog *Rana limnocharis* from different altitudes. *Italian Journal of Zoology* 78, 215–228.

Liao, W.B. (2011). A skeletochronlogical estimate of age in a population of the Siberian Wood Frog, *Rana amurensis*, from northeastern China. *Acta Herpetologica* 6, 237–245.

Liao, W.B. & Lu, X. (2012). Adult body size = *f* (initial size + growth rate × age): explaining the proximate cause of Bergman's cline in a toad along altitudinal gradients. *Evolutionary Ecology* 26, 579–590.

Liao, W.B. & Lu, X. (2011a). Variation in body size, age and growth in the Omei Treefrog (*Rhacophorus omeimontis*) along an altitudinal gradient in western China. *Ethology, Ecology and Evolution* 23, 248–261.

Liao, W.B. & Lu, X. (2011b). A comparison of reproductive output of the Omei Treefrog (*Rhacophorus omeimontis*) between high and low elevations. *Animal Biology* 61, 263–276.

Liao, W.B. & Lu, X. (2011c). Proximate mechanisms leading to the large male-mating advantage in the Andrew's toad *Bufo andrewsi*. *Behaviour* 148, 1087–1102.

Liao, W.B., Wu, Q.G. & Barret, K. (2012a). Evolution of sexual dimorphism in the forelimb muscles of Andrew's toad (*Bufo andrewsi*) in response to putative sexual selection. *Animal Biology* 62, 83–93.

Liao, W.B., Liao, Y.M., Chen, W., Mi, Z.P. & Li, C. (2012b). Sexual dimorphism in hind limb muscle mass of the Andrew's Toad (*Bufo andrewsi*) in relation to sexual selection. *North-Western Journal of Zoology*, 8, 252–256.

Melichna, J., Gutmann, A.H. & Stichova, J. (1972). Sexual dimorphism in contraction properties and fibre pattern of the flexor carpi radialis muscle of the frog (*Rana temporaria* L.). *Experientia* 28, 89–91.

Monnet, J.M. & Cherry, M.I. (2002). Sexual size dimorphism in anurans. *Proceedings of the Royal Society of London B: Biological Sciences* 269, 2301–2307.

Muller, E.R.A., Galavazi, G. & Szirmai, J.A. (1969). Effect of castration and testosterone treatment on fiber width of the flexor carpi radialis muscle in the male frog (*Rana temporaria* L.). *General and Comparative Endocrinology* 13, 275–284.

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* Linnaeus 1758. *Journal of Experimental Biology* 210, 715–721.

Oka, Y., Ohtani, R., Satou, M. & Ueda, K. (1984). Sexually dimorphic muscles in the forelimb of the Japanese toad, *Bufo japonicus*. *Journal of Morphology* 180, 297–308.

Peters, S.E. & Aulner, D.A. (2000). Sexual dimorphism in forelimb muscles of the bullfrog, *Rana catesbeiana*: a functional analysis of isometric contractile properties. *Journal of Experimental Biology* 203, 3639–3654.

Regnier, M. & Herrera, A.A. (1993). Changes in contractile properties by androgen hormones in sexually dimorphic muscles of male frogs (*Xenopus laevis*). *Journal of Physiology* 461, 565–581.

Schmidt, R. S. (1965). Larynx control and call production in frogs. *Copeia* 1965, 143–147.

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

Wells, K.D. (1979). Reproductive behavior and male mating success in a Neotropical toad, *Bufo typhonius*. *Biotropica* 11, 301–307.

Woolbright, L.L. (1983). Sexual selection and size dimorphism in anuran Amphibia. *American Naturalist* 121, 110–119.

Yekta, N. & Blackburn, D. (1992). Sexual dimorphism in mass and protein content of the forelimb muscles of the northern leopard frog *Rana pipiens*. *Canadian Journal of Zoology* 70, 670–674.

Yu, T.L., Gu, Y.S., Du, J. & Lu, X. (2009). Seasonal variation and ontogenetic change in the diet of a population of *Bufo gargarizans* from the farmland, Sichuan, China. *Biharean Biologist* 3, 99–104.

Yu, T.L. & Lu, X. (2010). Sex recognition and mate choice lacking in male Asiatic toads (*Bufo gargarizans*). *Italian Journal of Zoology* 77, 476–480.