

No evidence of phenotypic selection on large females leading to female-biased sexual size dimorphism in the frog *Polypedates megacephalus*

WEN BO LIAO^{1,2}, JUN MAO ZHONG², CHEN CHENG², LONG JIN² & ZHENG JUN WU¹

¹) Guangxi Key Laboratory of Rare and Endangered Animal Ecology, College of Life Science, Guangxi Normal University, Guilin, 541004, China

²) Key Laboratory of Southwest China Wildlife Resources Conservation (Ministry of Education), China West Normal University, Nanchong, 637009, China

Corresponding author: ZHENG JUN WU, e-mail: wu_zhengjun@aliyun.com

Manuscript received: 11 October 2015

Accepted: 7 January 2016 by ALEXANDER KUPFER

Abstract. Sexual size dimorphism (SSD), the difference in body size between males and females, is a widespread phenomenon and commonly attributed to variation in sex-specific patterns of selection. Using data from three populations of *Polypedates megacephalus*, we tested the hypotheses that sexual selection favoured large male body size and that fecundity selection favoured large female size. Females had a larger body size than males in all populations and thus exhibited a female-biased sexual size dimorphism. Standardized selection gradients showed that sexual selection for large male size was weak at best and hence unlikely to be an important driving force for SSD. As fecundity selection favouring large females was weak as well, it could not explain the female-biased SSD patterns found. However, a faster growth rate in females favoured a larger size, providing an explanation for female-biased SSD. Our findings suggest that female-biased SSD does not result from a phenotypic selection of female by size in *P. megacephalus*.

Key words. Amphibia, Anura, Rhacophoridae, fecundity selection, sexual selection, sexual size dimorphism.

Introduction

Sexual size dimorphism (SSD) is a widespread phenomenon among animals (DARWIN 1871). The occurrence of SSD has formerly been explained by several hypotheses. The sexual selection hypothesis predicts that intrasexual competition or intersexual mate choice favours a larger/smaller body size in one sex (ANDERSSON 1994). Alternatively, SSD may arise through the reproductive biology of the females, whereby a strong fecundity selection favours females that have an increased reproductive output due to their being larger (HERCZEG et al. 2010, HAN & HU 2013, MA et al. 2015). However, apart from these two evolutionary hypotheses, it is possible that SSD might simply arise as a consequence of sexual differences in age, an age-specific growth rate, or bimaturity between the sexes (for amphibians see HALLIDAY & VERRELL 1988, KUPFER 2007, ZHANG & LU 2013, LIAO et al. 2013, LIAO et al. 2015, LIAO et al. 2016) and ecology/niche divergence (SELANDER 1966, SERRANO-MENESES et al. 2006).

Thus far, most SSD studies have focused on interspecific patterns in amphibians (e.g., SHINE 1978, 1979, MONNET & CHERRY 2002, LIAO et al. 2013, ZHAO et al. 2016), whereas it was only during recent years that proximate mecha-

nisms resulting in SSD at intraspecific level were analysed in wild populations (LIAO & CHEN 2012, LIAO 2013, LIAO et al. 2015). Consequently, most of these studies have focused on taxa with female-biased SSD, which has indicated the positive selection on female body size to be stronger than that on male body size (LIAO 2013, LIAO et al. 2015). Females are larger than males in 90% of the species in anurans (e.g., SHINE 1979, KUPFER 2007, ZHANG & LU 2013). In most species, a larger female produces a larger clutch size and thus has a higher fecundity. Female-biased SSD in anurans is thought to result from a larger clutch size/fecundity, which favours a larger female size (MONNET & CHERRY 2002, HAN & HU 2013). However, studies on phenotypic selection on male and female sizes resulting in female-biased SSD by comparing the standardized selection gradients are rare in amphibians (LIAO et al. 2015).

The aim of this study was to investigate proximate mechanisms that may result in a female-biased SSD of the spotted treefrog (*Polypedates megacephalus*). We analysed male and female body sizes from three populations along an altitudinal gradient in Guizhou Province in China. We investigated whether female fecundity increases with increasing body size. We also compared the strength of selec-

tion acting on males and females for all populations with sufficient data on male mating success and female fecundity. Finally, we identified the age of all individuals to control for age-related differences in body size and SSD using skeletochronological methods. This allowed us to evaluate the observed SSD patterns as results of sex-specific differences in the age structure within populations.

Materials and methods

Study species

The spot-legged treefrog (*Polypedates megacephalus*) is a medium-sized anuran, which is widely distributed in China and lives at altitudes ranging from 520 to 2,200 m (FEI & YE 2001). Breeding activities begin in mid-April and continue until late July. It is a lekking species in which males congregate at ponds to wait for females, whereas females will only be present at these pools during individual nights for mating, and males will then be quick to approach arriving females (CHEN et al. 2016). Amplectant pairs move about at the edge of the ponds and will then produce foam on the ponds' water surface. This will then attract other males that come to join the pair and so form an amplecting group of two to five males and one female. In males, no direct physical competition for possession of the females can be observed during the spawning period.

Study sites

We visited three *P. megacephalus* populations located at different altitudes in Guizhou Province in western China during the 2014 and 2015 breeding seasons. The low-altitude population was located at 449 m in the Fanjing mountains (108°44.67' E, 27°46.33' N), where frogs reproduced in a farm pond (5.0×3.6×2.8 m; l×w×d) framed by a farmhouse. The mid-altitude population was located at 680 m in Shangzhong (108°43.38' E, 27°23.38' N), where the frogs likewise reproduced in a farm pond (3.0×4.2×3.8 m) near a small pig farm. The high-altitude population was located at 1,300 m in the Leigong mountains (108°10.27' E, 26°22.73' N), where frogs reproduced in two natural ponds (2.0×1.5×1.2 m and 12.0×4.0×0.3 m, respectively) framed by a farmhouse.

Sampling

Field observations were conducted at the three study sites during the breeding season in two successive years. After each female had deposited her eggs, we captured all males and females at the breeding sites and then estimated the clutch size of each nest. We collected a total of 209 tree frogs (Leigong: 28 unmated males, 20 mated males, and 20 females; Shangzhong: 27 unmated males, 21 mated males, and 21 females; Fanjing: 20 unmated males, 21 mated males, and 21 females) during the two breeding seasons. All individuals were confirmed to be adults by direct

observation of secondary sexual traits (presence of nuptial thumb pads in adult males and the inflated abdomen carrying developing eggs of adult females) and their breeding behaviour. Body size (snout–vent length: SVL in mm) of each individual was measured to the nearest 0.1 mm using dial callipers. The second phalange of the longest toe of the right hind limb of each treefrog was removed and stored in 4% neutral buffered formalin for age identification (see below). All treefrogs were then individually released at their original capture sites.

Age identification

Age was identified by means of skeletochronology, which is based on counting the number of lines of arrested growth (LAGs) in stained cross sections of the phalangeal bones (CASTANET & SMIRINA 1990). We used an improved method of paraffin-sectioning and Harris's haematoxylin-staining to produce histological sections for aging the adult animals. This method has been used in the skeletochronology of many Chinese anurans before (LIAO & LU 2010, LIAO & LU 2012, LI et al. 2013, HUANG et al. 2013, JIN et al. 2016). We selected cross-sections (13 µm thick) of the phalanx with the smallest medullar cavity for mounting them on glass slides. Digitalised photographs of cross-sections were taken using a Motic BA300 digital camera mounted on a MotiCam 2006 light microscope at 400× magnification. After this, the number of lines of arrested growth (LAG) was recorded by the same researcher (CHEN CHENG). We confirmed LAG endosteal resorption and double lines. Of 209 adult specimens, 207 (145 males and 62 females) exhibited clear LAGs in their bone cross sections. Growth was assessed by a non-linear regression in SPSS (21.0) statistical package (Statistical Product and Service Solutions Company, Chicago, USA) using VON BERTALANEFFY'S (1957) equation of $S_t = S_{\max} (1 - e^{-kt+b})$, where S_t is body size at age 't', S_{\max} is the estimated asymptotic maximum size, 'k' is a growth coefficient, and 'b' is a constant. The growth rate can then be calculated as $R = dS/dt = k(S_{\max} - S_t)$.

Clutch size

A total of 62 amplectant treefrogs were collected in two breeding seasons and transported to the laboratories that were close to the breeding sites. The pairs were kept separately in tanks (20×20×30 cm) filled with pond water to allow oviposition. We collected a total of 54 clutches and counted the total number of eggs in each clutch in a dish. After the experiments, all individuals and eggs were returned to the places where they had been collected.

Selection gradients

To compare strengths of selective forces on male and female size, linear standardized selection gradients were

Table 1. Mean body sizes (mm), age (years), and growth rates for three *Polypedates megacephalus* populations in Guizhou Province, China. (Specimens: Fanjin: males, n = 42; females, n = 21; Shangzhong: males, n = 48; females, n = 21; Leigong: males, n = 58; females, n = 20).

Population	Males					Females				
	Body size	Min. age	Average age	Max. age	Growth rate	Body size	Min. age	Average age	Max. age	Growth rate
Fanjin	43.6±3.7	2	2.6±2.0	4	1.47	59.3±3.1	2	2.8±0.8	4	2.61
Shangzhong	43.0±2.9	2	2.9±0.8	5	1.31	57.4±4.5	2	2.9±0.6	4	3.65
Leigong	44.0±3.2	2	3.1±0.8	5	1.94	58.4±5.4	2	3.0±0.8	4	2.54

estimated (LANDE & ARNOLD 1983) for each of the three populations from the data on male mating status and female fecundity. Following the methods of LANDE & ARNOLD (1983), body size was standardized (within each sex) by subtracting the population's mean from individual values and dividing them by the sample's standard deviation. Relative fitness was calculated by dividing the individual fitness (clutch size [females] or mating status [males]) by the mean fitness (i.e., mean clutch size or mating status) in the given population. We calculated the standardized linear selection gradients using a regression of relative fitness on standardized body size. Univariate linear selection gradients (β_1) were estimated from the model, relative fitness (w') = $c + \beta_1$ (standardized body size). We also calculated the non-linear selection gradients by applying a multiple regression of relative fitness on standardized body size and its square. Univariate non-linear selection gradients (γ_1) were estimated from the model, relative fitness (w') = $c + \beta_1$ (standardized body size) + β_2 (standardized body size)², where $\gamma_1 = 2\beta_2$.

Statistical analyses

All analyses were performed using the SPSS (21.0) statistical package. Body size and clutch volume were \log_{10} -transformed. To test for sex differences in mean body size or age between the three populations, we used a Generalized Linear Model (GLM) with 'log₁₀' (SVL) or 'age' as the dependent variable, 'sex' as a fixed factor, and 'population' as a random effect. We used a Generalized Linear Mixed Model (GLMM) with 'log₁₀' (SVL) as the dependent variable, 'sex' as a fixed factor, and 'population' as a random effect, 'age' and 'altitude' as covariates to test for sex differences in relative body size between populations. To assess the effect of female body size on clutch volume, another GLMM was used. Here, 'population' was included in the model as a random effect, 'year of collection' as a fixed factor, and 'female body size', 'female age', and 'altitude' as covariates. We tested for the variation of SSD among populations with 'age' being added to the model as a covariate together with 'sex × age' (fixed effect) and 'sex × population' (random effect) interactions. A significant sex × age interaction would be suggestive of sex differences in growth rates, whereas a significant sex × population value would provide evidence for between-population variation in SSD.

Results

Females had a larger body size than males (GLM: $F_{1, 203} = 1009.008$, $P < 0.001$; Table 1), but the average body size did not differ significantly between the three populations ($F_{2, 195} = 2.604$, $P = 0.277$). Likewise, there was a non-significant difference in average age between populations ($F_{2, 203} = 7.280$, $P = 0.121$) and between the sexes ($F_{1, 203} = 0.204$, $P = 0.696$; Table 1). Females always had a larger body size than males ($F_{1, 203, 006} = 70.602$, $P < 0.001$) when considering the effect of age on body size ($F_{1, 203, 182} = 16.089$, $P < 0.001$). Altitude did not affect average body size between the three populations (GLMM: altitude: $F_{1, 50.409} = 2.108$, $P = 0.153$; population: $Z = 0.560$, $P = 0.576$). The sex × age interaction revealed a non-significant difference in the relationship between body size and age (≈growth rate) between the sexes ($F_{1, 203, 013} = 4.467$, $P = 0.018$; Table 1). We also did not observe a significant sex × population variation between populations ($Z = 0.512$, $P = 0.609$).

The GLM revealed that clutch size differed significantly between populations ($F_{2, 53} = 95.859$, $P < 0.001$), but not relative to female body size ($F_{2, 53} = 2.442$, $P = 0.097$). Clutch size (286.4 ± 30.0) was highest in the high-altitude population and the natural ponds whereas it was lowest (192.4 ± 21.8) in the farmed frogs at the lowest altitude (Fig. 1). Clutch size did not increase with increasing female body size (GLMM: $F_{1, 50.100} = 1.039$, $P = 0.313$; Fig. 1), even when the age effect on body size was considered (body size: $F_{1, 49.098} = 1.171$, $P = 0.285$; age: $F_{1, 49.006} = 1.101$, $P = 0.299$).

The standardized linear or non-linear selection gradients demonstrated that sexual selection did not favour large males in the three populations, and the overall selection gradient estimated across all populations was non-significant. Meanwhile, the standardized linear or non-linear selection gradients on female size revealed that fecundity selection did not favour large females in all three populations, and the overall selection gradient was non-significant as well (Table 2).

Discussion

Our results uncovered significant differences in body size between males and females (i.e., sexual size dimorphism: SSD) for all the spot-legged treefrog (*P. megacephalus*) populations investigated, even after our correcting for age

effects. Furthermore, the differences in the growth rate caused by differences in altitude between populations and between the sexes exhibited a strong influence on body size. The patterns of SSD in the three populations can be explained as being a simple consequence of the populational variation of the growth rate. The standardized selection gradients from wild populations did not provide strong evidence of a positive selection favouring large male size. Hence, sexual selection in favour of larger males cannot explain SSD in *P. megacephalus*. As fecundity selection did not favour larger females, it failed to explain the female-biased SSD. This was supported by the discovery that female fecundity was not correlated with female body size both within and between populations.

There is some evidence from interspecific studies of patterns of SSD in vertebrates (FAIRBAIRN 1997), irrespective of whether females (as in most ectotherms) or males (as in most birds and mammals) are the larger sex (SZÉKELY et al. 2004), which needs to be looked at. The majority of studies suggest that sexual selection on male size is likely to explain male-biased SSD (ANDERSSON 1994). In a few cases, fecundity selection has been suggested to explain female-biased SSD (HERCZEG et al. 2010, LIAO et al. 2015). Female-biased SSD is the prevalent pattern in anurans (SHINE 1979), and this pattern was true also in the three *P. megacephalus* populations analysed. Selection gradients on both males and females could have produced SSD. In most cases, male-biased SSD is generally driven by the preferred selection on larger males as a consequence of sexual selection resulting from male–male competition or large-male-advantage (FAIRBAIRN & PREZIOSI 1994). In this study, we found that the male selection gradients were non-significant for all populations, thus demonstrating that sexual selection did not favour larger males in *P. megacephalus*. In contrast, sexual selection might in fact have favoured smaller males in taxa with female-biased SSD, because of the increased

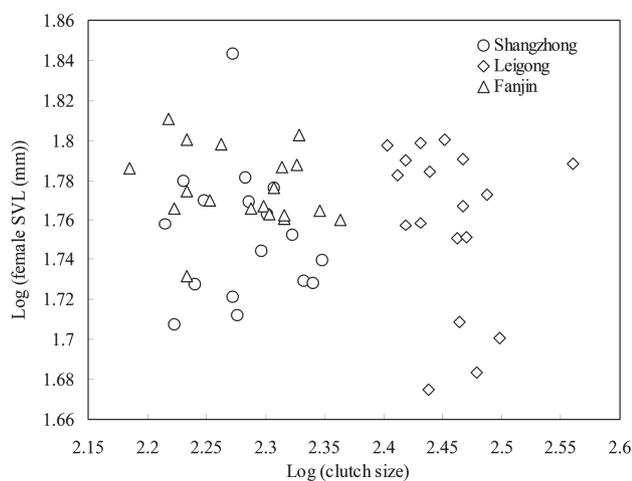


Figure 1. A non-significant relationship between female body size and clutch size in *Polypedates megacephalus* in the three populations investigated (female specimens: Fanjin, $n = 19$; Shangzhong, $n = 17$; Leigong, $n = 18$). Clutch size was largest in the Leigong Mountain population and smallest in the Fanjin Mountain population.

Table 2. Standardized selection gradients for sexual selection on male body size (dependent variable, mating status [mating or single]), and fecundity selection on female body size (dependent variable, reproductive fitness [clutch size/ mean clutch size]). Univariate linear selection gradients (β_1) were estimated from the model, relative fitness (w') = $c + \beta_1$ (standardized body size); Univariate nonlinear selection gradients (γ_1) were estimated from the model, relative fitness (w') = $c + \beta$ (standardized body size) + β_2 (standardized body size)², where $\gamma_1 = 2\beta_2$.

Population	Males		Females	
	β_1	γ_1	β_1	γ_1
Fanjin	-0.071	0.022	-0.003	-0.004
Shangzhong	-0.002	0.062	-0.001	0.002
Leigong	-0.079	0.080	-0.007	-0.032
Overall	-0.052	0.032	-0.006	0.006

mobility or agility of small males (see SZÉKELY et al. 2004 for birds). However, we did not observe any markedly improved mobility or agility in male *P. megacephalus*. Alternatively, fecundity selection has been suggested to explain female-biased SSD due to the increased reproductive investment of large females (e.g., HERCZEG et al. 2010, LIAO et al. 2015). We found that the standardized estimates of the strength of selection on females did not exhibit a positive selection, suggesting that fecundity selection did not favour large females, which is inconsistent with results that have previously been observed in other anurans (*Rhacophorus omeimontis*: MA et al. 2015; *Bufo andrewsi*: LIAO et al. 2015).

Intersexual differences in life-history traits, such as age, can also drive a female-biased SSD in anurans (MONNET & CHERRY 2002, ZHANG & LU 2013). In *P. megacephalus*, the higher average female age and longevity did not contribute to a female-biased SSD. However, previous studies in anurans suggested that age and growth rates can significantly influence body sizes within each sex (SHINE 1979, REINHARD et al. 2015). Consequently, differences in the growth rate and/or the time available for growth, as well as the two factors acting simultaneously, can result in SSD. As females have experienced a longer duration of growth than males, SSD will increasingly be biased towards females (ZHANG & LU 2013). In this study, we found that males and females did not exhibit differences in age at sexual maturity and longevity, but there were significant differences in growth rate (as an indicator of the sex \times age interaction on body size), demonstrating that females attained larger body sizes and grew faster towards the asymptotic body size than their male conspecifics. Consequently, faster growth results in more energy being devoted to somatic growth in order to achieve a larger body size, which leads to a female-biased SSD in this species, namely all amphibians faced the trade-off between reproduction and growth. Moreover, male and female growth are related to age and sexual maturity. As a result, males may even have the same growth rate, but may mature earlier than females, thus resulting in a smaller male size in some species (DUELLMAN & TRUEB

1986, MORRISON & HERO 2003). However, we found sex \times population to be non-significant between populations, suggesting that phenotypic selection on certain females did not result in variation in female-biased SSD selection.

In summary, our study suggests that sexual selection does not favour male body size in *P. megacephalus*, and cannot explain the occurrence of the female-biased SSD either. Meanwhile, fecundity selection does not favour a large female size, which is also unlikely to explain the female-biased SSD and an inference supported by the findings that female fecundity is not significantly correlated with female body size in *P. megacephalus*. However, faster female growth rates indicate that females apply more energy to growth and grow larger as a result (MORRISON & HERO 2003). Moreover, the predation risk in terms of diversity and density of predators in the different habitats (i.e., farm and natural ponds) at different altitudes impacts on growth rates in anurans (BECK et al. 2008). Hence, differences in growth rates (as an indicator of the sex \times age interaction on body size) between the sexes is a likely explanation for the female-biased SSD.

Acknowledgements

We thank two anonymous reviewers for their critical comments on an earlier draft of this manuscript. We appreciate the Guangxi Key Laboratory of Rare and Endangered Animal Ecology, Sichuan Province Outstanding Youth Academic Technology Leaders Program (2013JQ0016) and Sichuan Province Department of Education Innovation Team Project (15TD0019) for providing financial support. All experiments involving live animals were approved by the Animal Ethics Committee at the China West Normal University.

References

- ANDERSSON, M. (1994): Sexual Selection. – Princeton University Press, Princeton.
- BECK, E., I. KOTTKE, J. BENDIX, F. MAKESCHIN & R. MOSANDL (2008): Gradients in a tropical mountain ecosystem – a synthesis. – pp. 451–463 in: BECK, E., J. BENDIX, I. KOTTKE, F. MAKESCHIN & R. MOSANDL (eds): Gradients in a tropical mountain ecosystem of Ecuador, **198**.
- CASTANET, J. & E. M. SMIRINA (1990): Introduction to the skeleto-chronological method in amphibians and reptiles. – *Annales des sciences naturelles comprenant la zoologie*, **11**: 191–196.
- CHENG, C., Y. Y. HUANG & W. B. LIAO (2016): A comparison of testes size and sperm length in *Polypedates megacephalus* between two populations at different altitudes. – *Herpetological Journal*, **26**: 249–252.
- DARWIN, C. (1871): *The Descent of Man, and Selection in Relation to Sex*. – Murray, London.
- DUELLMAN, W. E. & D. L. TRUEB (1986): *Biology of Amphibians*. – McGraw-Hill Inc., New York.
- FAIRBAIRN, D. J. & R. F. PREZIOSI (1994): Sexual selection and the evolution of allometry for sexual size dimorphism in the water strider (*Aquarius remigis*). – *American Naturalist*, **144**: 101–118.
- FAIRBAIRN, D. J. (1997): Allometry for sexual size dimorphism: Pattern and process in the coevolution of body size in males and females. – *Annual Review of Ecology and Systematics*, **28**: 659–687.
- FEI, L. & C. Y. YE (2001): *The Colour Handbook of Amphibians of Sichuan*. – China Forestry Publishing House, Beijing.
- HALLIDAY, T. R. & P. A. VERRELL (1988): Body size and age in amphibians and reptiles. – *Journal of Herpetology*, **22**: 253–265.
- HAN, X. & J. Z. FU (2013): Does life history shape sexual size dimorphism in anurans? A comparative analysis. – *BMC Evolutionary Biology*, **13**: 27.
- HERCZEG, G., A. GONDA & J. MERILÄ (2010): Rensch's rule inverted female-driven gigantism in nine-spined stickleback *Pungitius pungitius*. – *Journal of Animal Ecology*, **79**: 581–588.
- HUANG, Y., H. Q. ZHU, Y. M. LIAO, L. JIN & W. B. LIAO (2013): Age structure, size and growth of a high-altitude bell toad in subtropical montane in southwestern China. – *Herpetological Journal*, **23**: 229–232.
- JIN, L., S. N. YANG, W. B. LIAO & S. LÜPOLD (2016): Altitude underlies variation in the mating system, somatic condition and investment in reproductive traits in male Asian grass frogs (*Fejervarya limnocharis*). – *Behavioral Ecology and Sociobiology*, **70**: 1197–1208.
- KUPFER, A. (2007): Sexual size dimorphism in amphibians: an overview. – pp. 50–59 in: FAIRBAIRN, D. J., W. U. BLANCKENHORN & T. SZÉKELY (eds): Sex, size and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press, Oxford.
- LANDE, R. & S. T. ARNOLD (1983): The measurement of selection on correlated characters. – *Evolution*, **37**: 1210–1216.
- LI, S. T., X. WU, D. Y. LI, S. L. LOU, Z. P. MI & W. B. LIAO (2013): Body size variation of Oorous Frog (*Odorrana grahami*) across altitudinal gradients. – *Herpetological Journal*, **23**: 187–192.
- LIAO, W. B. & W. CHEN (2012): Inverse Rensch-rule in a frog with female-biased sexual size dimorphism. – *Naturwissenschaften*, **99**: 427–431.
- LIAO, W. B. & X. LU (2010): Age structure and body size of the Chuanxi tree frog *Hyla annectans chuanxiensis* from two different elevations in Sichuan (China). – *Zoologischer Anzeiger*, **248**: 255–263.
- LIAO, W. B. & X. LU (2012): Adult body size = f (initial size + growth rate \times age): explaining the proximate cause of Bergman's cline in a toad along altitudinal gradients. – *Evolutionary Ecology*, **26**: 579–590.
- LIAO, W. B. (2013): Evolution of sexual size dimorphism in a frog obeys the inverse of Rensch's rule. – *Evolutionary Biology*, **40**: 293–299.
- LIAO, W. B., W. C. LIU & J. MERILÄ (2015): Andrew meets Rensch: Sexual size dimorphism and the inverse of Rensch's rule in Andrew's toad (*Bufo andrewsi*). – *Oecologia*, **177**: 389–399.
- LIAO, W. B., Y. ZENG, C. Q. ZHOU & R. JEHLE (2013): Sexual size dimorphism in anurans fails to obey Rensch's rule. – *Frontiers in Zoology*, **10**: 10.
- LIAO, W. B., Y. LUO, S. L. LOU, D. LU & R. JEHLE (2016): Geographic variation in life-history traits: growth season affects age structure, egg size and clutch size in Andrew's toad (*Bufo andrewsi*). – *Frontiers in Zoology*, **13**: 6.

- MA, X. H., L. ZHAO, X. LU, W. B. LIAO (2015): Female-biased sexual size dimorphism is driven by phenotypic selection on female in a treefrog. – *Herpetological Journal*, **25**: 123–126.
- MONNET, J. M. & M. I. CHERRY (2002): Sexual size dimorphism in anurans. – *Proceedings of the Royal Society B: Biology Science*, **269**: 2301–2307.
- MORRISON, F. C. & J. M. HERO (2003): Geographic variation in life-history characteristics of amphibians: a review. – *Journal of Animal Ecology*, **72**: 270–279.
- REINHARD, S., S. REINHARD & A. KUPFER (2015): Age and fecundity in *Salamandra algira*. – *Salamandra*, **51**: 19–24.
- SELANDER, R. K. (1966): Sexual dimorphism and differential niche utilization in birds. – *Condor*, **68**: 113–151.
- SERRANO-MENESES, M. A. & T. SZÉKELY (2006): Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation. – *Oikos*, **113**: 385–394.
- SHINE, R. (1978): Sexual size dimorphism and male combat in snakes. – *Oecologia*, **33**: 269–278.
- SHINE, R. (1979): Sexual selection and sexual dimorphism in the amphibia. – *Copeia*, **1979**: 297–306.
- SZÉKELY, T., R. P. FRECKLETON & J. D. REYNOLDS (2004): Sexual selection explains Rensch's rule of size dimorphism in shorebirds. – *Proceedings of the National Academy of Sciences of the USA*, **101**: 12224–12227.
- VON BERTALANFFY, L. (1957): Quantitative laws in metabolism and growth. – *Quarterly Review of Biology*, **32**: 217–231.
- ZHANG, L. X. & X. LU (2013): Sexual size dimorphism in anurans: ontogenetic determination revealed by an across-species comparison. – *Evolutionary Biology*, **40**: 84–91.
- ZHAO, L., Y. J. CHEN, S. L. LOU, Y. HUANG, R. JEHLER & W. B. LIAO (2016): Reciprocal sexual size dimorphism and Rensch's rule in toad-headed lizards (*Phrynocephalus vlangalii*). – *Salamandra*, **52**(3): 261–268.