Asian Herpetological Research 2015, 6(4): 298–304
DOI: 10.16373/j.cnki.ahr.150025

ORIGINAL ARTICLE

Significant Male Biased Sexual Size Dimorphism in *Leptobrachium leishanensis*

Yingying QI, Wei ZHANG, Li HUANG, Zhenhua LUO, Mian ZHAO and Hua WU*

Institute of Evolution and Ecology, *International Research Centre of Ecology and Environment*, *School of Life Sciences*, *Central China Normal University*, *Wuhan* 430079, *Hubei*, *China*

Abstract Sexual size dimorphism (SSD) is a widespread phenomenon among animals, and whose evolution and maintenance has been a central topic in evolutionary biology since Darwin's time. SSD varies in direction among the major taxonomic groups of animals and even within the same groups. In anurans, female biased SSD is the rule in many lineages, whereas male biased SSD is a rare phenomenon. In this paper, we analyze whether SSD exists in *Leptobrachium leishanensis* by comparing morphological characteristics between the sexes. Our results show that all six morphological characteristics measured are significantly different between the sexes. Males are significantly larger than females, indicating that the male biased SSD of this species is apparent. The size of the nuptial spines, a special secondary sex trait of males, is significantly and positively correlated with body size. We suggest that the resource defense polygyny mating system and parental care behavior may be explanations for the evolution of male biased SSD and nuptial spine development in this species.

Keywords Sexual size dimorphism, *Leptobrachium leishanensis*, mating system, parental care, evolution

1. Introduction

Sexual size dimorphism (SSD) refers to the difference in body size between the sexes and is widespread among animals (Short and Balaban, 1994; Nie *et al*., 2012). SSD is highly variable in magnitude and direction among the major taxonomic groups: in birds, lizards and most mammals, males tend to be the larger sex (Selander, 1972; Temeles, 1985; Crook, 1972); whereas in fish and anurans, female biased SSD is the rule in many lineages. Females are larger than males in up to 90% of anuran species (Shine, 1979; Monnet and Cherry, 2002). However, in species in which males engage in physical combat with each other, males are larger than females; this is very rare and only occurs in 5% of anuran species (Shine, 1979; Schauble, 2004).

The evolution and maintenance of SSD has puzzled evolutionary biologists since Darwin (Darwin, 1871; Fairbairn, 1997; Fairbairn *et al*., 2007). Darwin considered that most SSD was a result of sexual selection whereby evolutionary forces acted separately on the sexes. However, with the development of evolutionary theory, key hypotheses have been proposed for the evolution of SSD: (1) natural selection for ecological resource divergence (Preest, 1994; Herrel *et al*., 1999; Butler *et al*., 2000; Bolnick and Doebeli, 2003), in which SSD evolution produces different optimal ecological niches to reduce the inter-sexual competition when body size is relative to resource use (Weatherhead, 1980; Shine, 1991; Butler *et al*., 2007); (2) fecundity selection (Wiklund and Karlsson, 1988; Fairbairn and Shine, 1993), which favors larger females that have increased reproductive output through greater allocation to individual offspring, greater numbers of offspring, or the ability to reproduce more frequently; and (3) sexual selection (Berry and Shine, 1980; Abouheif and Fairbairn, 1997; Cox *et al*., 2003), which favors a large size in one sex to improve intra-sexual competition or inter-sexual mate choice success (Parker, 1992; Johnstone *et al*., 1996). SSD is often used as an indicator of the intensity of sexual selection

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* Corresponding author: Prof. Hua WU, from Central China Normal University, Wuhan, China, with his research focusing on animal behavior and evolutionary biology.
E-mail: wuhua@mail.ccnu.edu.cn
Received: 7 April 2015 Accepted: 11 August 2015

in animals and that selection intensity promotes SSD variation among species (Moore and Wilson, 2002). Additionally, the mating system of a species is associated with the intensity of sexual selection (Selander, 1972) as polygynous and polyandrous species naturally have more intensive competition than monogamous species. Consequently, the mating system can mediate the evolution of SSD. However, these hypotheses remain controversial and still require additional experiments to test the relationship between SSD and sexual selection in different species (Darwin, 1871; Fairbairn and Preziosi, 1994).

Leptobrachium leishanensis is an endemic species of China and is only distributed in the southeastern areas of Guizhou Province. During the breeding season (late October to December), males grow four nuptial spines on the upper jaw and the forearms become enlarged, whereas females do not exhibit this phenotype (Figure 1). *L. leishanensis* exhibits a resource defense polygyny mating system in which males provide parental care after mating (Zheng *et al.*, 2010). In the early breeding season, males enter streams and construct nests under flat rocks. Here, they vocalize underwater to attract females for mating. Males hollow out space underneath the nest rock to provide space during amplexus. Females leave after laying eggs, whereas most males remain underwater for more mating opportunities or to care for the eggs and embryos until the larvae emerge from the egg mass.

In recent years, studies of *L. leishanensis* have increased and have mainly focused on observations of reproductive behaviors as well as the development of eggs, genetic diversity, and phylogenetic studies (Zheng, 2008; Rao and Wilkinson, 2008; Zhang *et al.*, 2015). To our knowledge, a survey regarding SSD has not been published for *L. leishanensis*. Furthermore, studies have demonstrated that some species of the genus *Leptobrachium* exhibit significantly male biased size differences (Hudson and Fu, 2013). For example, the body length of male *L. boringii* may be 20 mm larger than females (Liu and Hu, 1961). This type of SSD is rare among anurans. Thus, we aimed to determine whether SSD exists in *L. leishanensis*, which sex is larger, and the potential explanations for the evolution of SSD in this species. Therefore, we conducted this study to determine the role of SSD in *L. leishanensis*, which not only helps improve our understanding of the characteristics of this species and the genus *Leptobrachium* but is also an important contribution to systematic and evolutionary research on anurans.

Figure 1 The male (left) and female (right) of the species *L. leishanensis*. The numbering of the nuptial spines on the male is shown.

2. Materials and Methods

A field survey was conducted in Leigongshan National Nature Reserve (26°15′–26°32′ N, 108°05′–108°24′ E, Guizhou Province, China) from 30 October to 2 December 2012 and 26 October to 24 November 2013. The study site has several streams with an elevation of ~1400–1500 m above sea level (a.s.l.). During this time of year, the local temperature is relatively low (mean air temperature: 8.5°C) and *L. leishanensis* begins to enter the rocky stream to breed. We monitored the streams and searched for *L. leishanensis* specimens. When toads were captured, we marked them using colored lines. Specifically, we tied the waist of each toad using four circle lines of different colors (red, green, pink, yellow, blue, orange, purple, etc.) and distinguished the individuals based on different color combinations of the lines to ensure that no individual was measured twice. In addition, the specimens were sexed based on the presence or absence of nuptial spines. For each individual, the following body dimensions were quantified: mass (M), snout-vent length (SVL, from the tip of the nose to the anus), head width (HW, across the base of the head at its widest point), head length (HL, from the tip of the snout to the base of the skull), forearm length (FL, from the elbow to the tip of the third toe), and forearm width (FW, recording the widest part of forearm). Bilateral characteristics were measured on the right side only. For males, we also measured the bottom diameter and height of each nuptial spine. All of the measurements were performed using a digital caliper to the nearest 0.01 mm and a set of digital scales to the nearest 0.01 g. Each morphometric characteristic was measured three times and we used the mean value for the final data analysis.

The specimens were released at the capture sites as soon as possible after the measurements were collected.

We used the Kolmogorov-Smirnov tests and Levene's tests to assess the normality and homogeneity of variances of the data before further analyses. Using linear regressions, the relationship between SVL and other body dimension indexes were analyzed. We used independent samples *t* tests to analyze the inter-sexual differences of dimorphic characteristics. Then, we used a principal component analysis (PCA) to establish integrated variables for males (PCm) and females (PCf). For males and females, respectively, to test intra-sexual body size variation, we randomly selected 50 individuals and conducted one sample *t* test between PCm (or PCf) for the selected group and PCm (or PCf) for all the individuals. We repeated the test 20 times for each sex. Finally, a linear regression was conducted to check the relationship between SVL and the bottom diameter of nuptial spines of the males. All statistical analyses were performed using SPSS Version 17.0 and at the significance level of 0.05.

3. Results

3.1 Inter-sexual comparison of *L. leishanensis* characteristics A total of 893 specimens (732♂ and 161♀) were successfully recorded. The comparison for body size variables are presented in Table 1. The M, HL, HW, FL and FW characteristics all displayed significant positive correlations with SVL in both males and females (Table 1). In addition, the six characteristics all differed significantly between sexes (all $P<0.001$; Table 1), and each characteristic was greater in males than in females (Table 1). For example, the mean SVL of males was 11.34 mm larger than that of females (males: 78.64±9.23 mm; females: 67.30±8.40 mm; independent samples *t* test: $t=-17.739$, $df=891$, $P<0.001$; Table 1; Figure 1). Thus, we demonstrate that there is a significant SSD between males and females of *L. leishanensis.*

We extracted two principal components explaining 92.24% of the variation within the model (Table 1). Principal component one (PC1) accounted for 81.15% of the variation, and variables M, SVL, HW, FL and FW were the most sexually dimorphic characteristics (Table 1). Principal component two (PC2) explained 11.09% of the total variation, and HL played an important role in PC2 (Table 1). Thus, PC1 and PC2 represent the size information of individuals. Figure 2 shows that, although the values do overlap to a small extent, the relative degree of isolation between males and females is clear.

3.2 Intra-sexual comparisons of body size We extracted one principal component in males (PCm) and one principal component in females (PCf) (Table 2). PCm explained 79.51% of the male characteristics, and PCf explained 81.60% of the female characteristics.

Based on the histogram (Figure 3) of variation of intra-sexual body size, male PCms varied from 28.19 to 68.11 (mean: 45.73; median: 44.57), with individuals with PCms of 37.00–54.00 accounting for 79.23%, of the total male population, meaning that medium-sized individuals occupied a large proportion of our toad population. For females, the PCfs varied from 21.58 to 44.26 (mean: 35.17; median: 36.05). Individuals within the range of 31.00 to 41.00 accounted for 76.00% of the female population. Therefore, the female median body size tended toward the larger side of their body size range compared to the median body size of the males (Figure 3). Furthermore, our one sample *t* tests between PCms (or PCfs) of the randomly selected groups and all the individuals for male (or females) showed significantly intrasexual variations in body size for both sexes (male: $P=0.027\pm0.049$; female: $P=0.019\pm0.033$).

Table 1 Comparison of morphometric traits (Mean ± SD) between males and females (SD: standard deviation. **: significant difference at the level of 0.01 as tested by independent samples *t* test. *r*: correlation to SVL) and the extraction of principal components (PC1 and PC2) using the component matrix (variables loading strongly on each principal component are in bold) of *L. leishanensis*.

Variables	Males		Females		*t*-value	*P*-value	PC1	PC2
	Mean±SD (*n*=732)	*r*	Mean±SD (*n*=161)	*r*				
SVL**	78.64±9.23	–	67.30±8.40	–	–17.739	<0.001	**0.952**	–0.063
HW**	33.98±4.06	0.911	27.58±3.04	0.909	–15.354	<0.001	**0.974**	–0.068
HL**	21.49±3.39	0.492	19.67±2.46	0.695	–9.652	<0.001	0.638	**0.767**
FL**	43.70±4.45	0.835	37.25±4.15	0.849	–18.324	<0.001	**0.938**	–0.090
FW**	14.11±2.57	0.832	7.38±1.34	0.701	–21.391	<0.001	**0.902**	–0.217
M**	47.22±17.13	0.919	27.15±9.91	0.901	–17.991	<0.001	**0.956**	–0.088
Eigenvalue							4.869	0.66
% variation explained							81.15	11.092

Table 2 Extraction of principal components PCm on males and PCf on females using a component matrix.

Variables	PCm	PCf
M	0.955	0.944
SVL	0.948	0.938
HW	0.964	0.966
HL	0.596	0.795
FL	0.918	0.942
FW	0.912	0.821
Eigenvalue	4.77	4.896
% variation explained	79.506	81.598

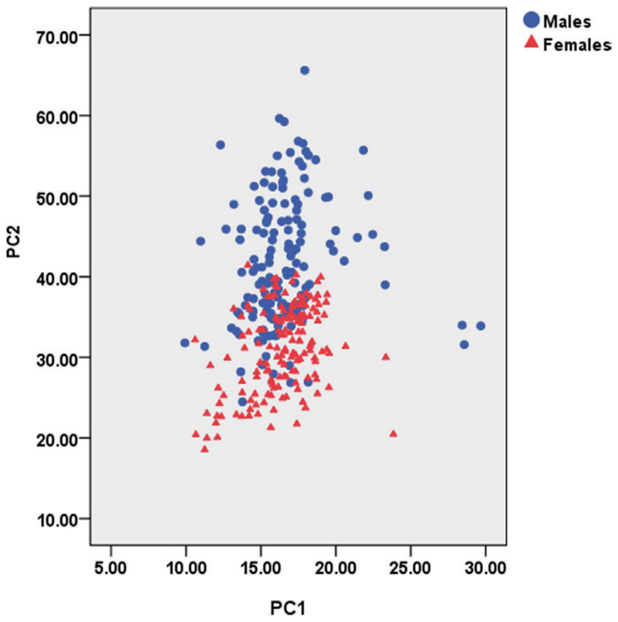

Figure 2 Orientation of individual males and females of *L. leishanensis* on the two principal components. Note the degree of separation between males and females.

3.3 The difference in nuptial spines on males Males grow four nuptial spines on their upper jaw during the breeding seasons. We numbered the nuptial spines as shown in Figure 1. Our results showed a significantly positive correlation between the bottom diameter and the height of nuptial spines (correlation analysis: r=0.925, n=2890, P<0.001; a total of 732 males were measured with most of them had 4 nuptial spines, and a small number of the males had 2 or none spine); that is, nuptial spine height increases with the increase of its bottom diameter. Furthermore, there was no significant difference on bottom diameter or height between nuptial spine 1 and 4 and between spine 2 and 3 in males (P>0.05). Therefore, we divided the nuptial spines into two groups. Nuptial spines 1 and 4 (bottom diameter: 4.34±0.91 mm, height: 4.17±0.91 mm) were significantly larger than nuptial spines 2 and 3 (bottom diameter: 3.43±0.76 mm, height: 3.26±0.84 mm) (P<0.05). Using linear analysis between PCm and the bottom diameter of nuptial spine 1, we determined that the bottom diameter of nuptial spine 1 has a significant positive correlation with PCm (Figure 4). The result suggests that larger males are more likely to possess larger nuptial spines.

4. Discussion

Our results show that male biased SSD is evident in *L. leishanensis*, with males being larger than females. This phenomenon was consistent with some species of the genus *Leptobrachium* (Liu and Hu, 1961; Hudson and Fu, 2013). In addition, the size of the nuptial spines was positively correlated with the body size of males. Evolution of this male biased SSD and the development of nuptial spines might be explained by the resource

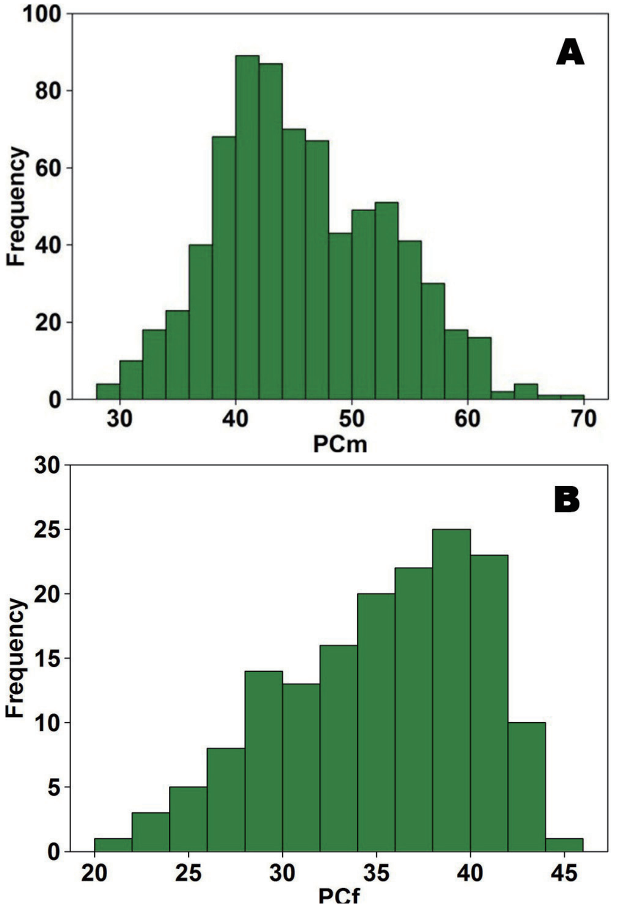

Figure 3 The histogram showing the variation in PCm in males (A) and PCf in females (B). A larger PCm value indicates a larger body size in males, and a larger PCf value indicates a larger body size in females.

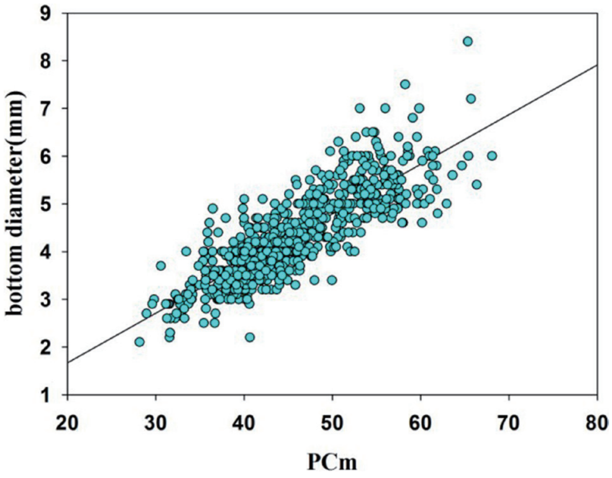

Figure 4 Variation in the bottom diameter (mm) of nuptial spine 1 relative to PCm in *L. leishanensis* (Pearson correlation coefficient: 0.095).

defense polygyny mating system and parental care behaviors of this species (Trivers, 1971; Emlen and Oring, 1977).

4.1 The inter-sexual difference in body size In species with the resource defense polygyny mating system, males indirectly access females by occupying food and territory that are necessary for reproductive success (Emlen and Oring, 1977). Studies on other species, such as *L. boringii*, indicated that larger males are stronger in physical combats to get higher quality territories, and females prefer larger males to obtain higher breeding success (Andersson, 1994; Semlitsch, 1994; Smith, 1987; Reading, 2001; Hudson and Fu, 2013). Thus, sexual selection might favor larger males by male-male competition and female choice (Reading, 2001). Although this study did not illustrate quantitative relationships among male body size, female mating rate, and breeding success, our field observations found that there were more egg masses under the territory stones of larger *L. leishanensis* males, which might suggest that females prefer larger males and larger male could attain more mating chances.

Parental care behaviors of males might be another mechanism contributing to evolution of the male biased SSD (Mc Diarmid, 1978; Wells, 2007; Han and Fu, 2013). As larger males are stronger and have higher quality territories to provide better cares for their offspring, they might be preferred by females and could have higher offspring survival rates. Our field observations of *L. leishanensis* found possible evidence of male parental care (they stayed beside the nests after females left, performed nest cleaning and protected the eggs against predators). Because parental care is an energy costly task, the advantages of larger males on offering better parental care might lead to higher reproductive success for them and lead to male-biased body size dimorphism in this species. Furthermore, Katsikaros and Shine (1997) and Han and Fu (2013) demonstrated that body sizes are positively correlated to ages among anuran species (e.g., *Adelotus brevis*, *Rana kuhlii*, *Bufo melanostictus*) and considered that the variations in age at sexual maturity might lead to various forms of sexual dimorphism and have important impacts on SSD evolution.

4.2 The evolution of nuptial spines on males Nuptial spines are an important secondary sexual characteristic in males that only appears during the breeding season and falls off after the breeding season has ended. Previous studies indicated that nuptial spines could be weapons to ward off conspecifics or predators (Cameron *et al*, 2011), or a trait revealing sexual vigor or strength of a male (Clutton-Brock, 1982; Cameron *et al*, 2011). Although functions of nuptial spines in the breeding of *L. leishanensis* are not presently clear, we considered they might be important physical tools in defeating rivals during male-male combats, which was observed in some anuran species (Kluge, 1981; Katsikaros and Shine, 1997; Tsuji and Matsui, 2002), including the congeneric species *L. boringii* (Hudson *et al*., 2011), and during our field surveys. Our study found a positive relationship between nuptial spine size and male body length. Large males with strong nuptial spines should be favored by sexual selection, which might drive the development of nuptial spines in males and evolution of male biased SSD in *L. leishanensis*.

4.3 The intra-sex variation in body size Medium-sized males were observed more in number in our *L. leishanensis* population during breeding seasons. We consider this phenomenon might be caused by a balance among multiple selective pressures (Blanckenhorn, 2005). Although larger males have advantages on viability and breeding success, they face a higher predation risk and need to reduce locomotion to stay in the limited space under the breeding rock and protect the eggs for nearly two months during breeding seasons. However, as each female lays only one mass of eggs within approximately one week each breeding season and then leaves the mating site, their predation risk would be much lower than that of males. Sexual selection might favor larger females with higher fecundity and they might have higher reproductive success. Thus, sexual selection could lead to a relatively high proportion of large females within the population.

In summary, *L. leishanensis* exhibits significant sexual dimorphism in body size. The male biased SSD may be a result of sexual selection, which is related to the special polygyny mating system in this species and parental care behaviors in males.

Acknowledgements This research was supported by National Natural Science Foundation of China (No. 31270425, No. 31470442). We thank Jian Chen for his help in field investigations and data collection.

Our studies were conducted under an animal ethics approval granted by Central China Normal University. All study animals were treated ethically following the "Guidelines for the Use of Animals in Research" published in Animal Behavior and the laws of China.

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