Current Zoology 58 (2): 236–243, 2012

Sexual size dimorphism and female reproduction in the white-striped grass lizard *Takydromus wolteri*

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Abstract Sexual size dimorphism (SSD) has long attracted the attention of biologists, and life-history variation is thought to play an important role in the evolution of SSD. Here we quantified SSD and female reproductive traits to identify potential associations between SSD and female reproduction in the white-striped grass lizard *Takydromus wolteri*. In a population from Chuzhou, China, the largest male and female were 53.0 mm and 57.5 mm in snout-vent length (SVL), respectively. Females were larger in SVL and abdomen length, whereas males were larger in head size and tail length. Females produced up to five clutches of eggs during the breeding season, with large females producing more clutches and more eggs per clutch than small ones. As a result, large females had a higher annual fecundity and reproductive output. Egg size was positively correlated with maternal SVL in the first clutch, but not in subsequent clutches. These results suggest that *T. wolteri* is a species with female-biased SSD, and that fecundity selection, in which large females have higher fecundity due to their higher capacity for laying eggs, is likely correlated with the evolution of SSD in this species [*Current Zoology* 58 (2): 236–243, 2012].

Keywords Reptilia, Lacertidae, *Takydromus wolteri*, Sexual size dimorphism, Female reproduction

Sexual size dimorphism (SSD) is a body size difference between males and females of the same species. This phenomenon is widespread in reptiles, but types of SSD vary greatly among taxa and populations (Andersson, 1994; Cox et al., 2003; Fairbairn et al., 2007). Studies have offered many hypotheses to explain the ultimate causes of SSD, and SSD is determined by many selective pressures that often differ between the sexes in strength and direction (Darwin, 1871). Sexual selection acting through female choice or intra-sexual competition in males and fecundity selection in females is now widely accepted to be the major evolutionary force favoring larger body sizes in either male or female reptiles (Olsson et al., 2002).

For male-biased SSD, a large body size often increases male mating success due to intra-sexual competition or female choice (Darwin, 1871; Andersson, 1994; Cox et al., 2003). For female-biased SSD, a large body size means greater reproductive output, often expressed as clutch size and egg or litter (in ovoviviparous species) size, because female fecundity is positively correlated to maternal body size (Darwin, 1871; Shine, 1988; Cox et al., 2007; Stephens and Wiens, 2009; Pincheira-Donoso and Tregenza, 2011).

Natural selection acting to reduce intersexual resource competition and differential mortality between the sexes can also cause SSD in reptiles (Slatkin, 1984; Shine, 1989; Hews, 1990; Cox et al., 2007). In this scenario, ecological factors such as dietary partitioning and ecomorph differences have been demonstrated to act as selective forces driving the evolution of SSD in some species (Shine, 1989; Stamps et al., 1997; Butler et al., 2000; Butler and King, 2004). These explanations for SSD are not mutually exclusive, because a sexually dimorphic trait initially induced by sexual selection may have a secondary role in reducing intersexual resource competition and thus intra-specific competition (Shine, 1991; Vincent et al., 2004).

Recently, studies on SSD have integrated most disciplines of evolutionary biology and provide an excellent opportunity to examine the putative selective basis for divergence in morphological traits (Vitt and Cooper, 1985; Shine et al., 1998). One such selective basis is the role of life-history variation in the evolution of SSD. Organisms differing in SSD may have different life history traits regarding growth and development, age at maturity and lifespan. Some of these life history traits are difficult to examine quantitatively, but the morphological traits of the two sexes and the female reproductive output can be easily measured. Numerous studies have shown that reproductive output is associated with morphological traits in reptiles (Cooper and Vitt, 1989;

Received June. 28, 2011; accepted Oct. 23, 2011.

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Shine et al., 1998; Stephens and Wiens, 2009; Pincheira-Donoso and Tregenza, 2011), thus, data on female reproduction can be crucial to understanding the evolutionary causes of SSD.

The white-striped grass lizard *Takydromus wolteri* ranges from east-northeast China (Anhui, Jiangsu, Liaoning, Jilin and Heilongjiang) to North Korea and the eastern Russia (Zhao and Adler, 1993; Arnold, 1997). Although *T. wolteri* is widely distributed, no quantitative data on sexual size dimorphism and female reproduction has been published. Here, we report on sexual size dimorphism and female reproduction in a population of *T. wolteri* in Chuzhou, Anhui, eastern China. Our aims are as follows: (1) to test sexual dimorphism in ecologically-important morphological features, such as body size, head size, abdomen length and tail length; (2) to investigate relationships among egg size, clutch size, reproductive output and female size; and (3) to identify potential associations between sexual dimorphism and female reproductive output.

1 Materials and Methods

1.1 Animal collection and care

Lizards were collected by noose or hand in March 2010 from a population at Chuzhou, Anhui, eastern China. A total of 185 white-striped lizards were collected, of which 82 were female and 103 were male. We transported the lizards to our laboratory in Chuzhou University, measured (to the nearest 0.1 mm) snout-vent length (SVL), tail length (TL), abdomen length (AL, from the posterior base of the forelimb to the anterior base of the hind limb), head length (HL, from the snout to the posterior end of the skull), and head width (HW, taken at the posterior end of mandible) using the same calipers (Qu et al., 2011). We marked each animal via unique combinations of clipped toes. We noted whether the lizards had a full tail or not, and removed data for the tail-less lizards from later morphological analyses.

Lizards were raised in an outdoor enclosure (4 × 3 m). The enclosure contained a substrate of sand (~15 cm depth), with grasses and pieces of clay tile provided as shelter and basking sites. Water and mealworms (larvae of *Tenebrio molitor*) and house crickets *Achetus domesticus* dusted with multivitamins and minerals were provided daily, so that excess food was always available in the enclosure.

We checked the lizards every three days. Females with shelled oviductal eggs were brought back to the laboratory from the enclosure and housed individually in 20 × 15 × 20 cm egg-laying cages with 4 cm depth moist soil and a 20-W spotlight mounted in each cage to allow thermoregulation.

Eggs were collected and weighed (to the nearest 0.001 g) on a Sartorius balance (Goettingen, Germany) within three hours of oviposition, thereby minimizing any uncertainty about the egg mass due to the loss or gain of water (Hao et al., 2006). Post-oviposition females has SVL measured and were weighed before they were returned to the outdoor enclosure for subsequent reproduction. Clutch size was counted as the total number of eggs in a clutch. Clutch mass was calculated as the total mass of eggs in a clutch. Mean egg mass of a clutch was calculated as clutch mass divided by clutch size. *Takydromus wolteri* females produce more than one clutch of eggs in a breeding season. Clutch interval was calculated as the time interval between sequential clutches for each female (to the nearest 0.1 d). The experiment was terminated for each female two weeks (a time interval long enough to know whether a female would become gravid again) after the last clutch was laid. Annual fecundity of each female was calculated as the total number of eggs produced in the breeding season, annual reproductive output of each female was calculated as the total mass of eggs produced in the breeding season, and mean annual egg mass was calculated as annual reproductive output divided by annual fecundity.

1.2 Statistical analyses

Statistical analyses were performed with Statistica v6.0 for PC (StatSoft, Tulsa, USA). All data were tested for normality using the Kolmogorov-Smirnov test and for homogeneity of variances using Bartlett's test. Log_e transformation was performed when necessary to satisfy the assumptions for parametric tests. We used the *t*-test to examine whether mean values for adult SVL differed between sexes. HL, HW, AL and TL were positively correlated with SVL in each sex (Fig. 1). We used One-Way analysis of covariance (ANCOVA) with SVL as the covariate and sex as the factor to examine the effects of the sex on morphological traits. Prior to this analysis the assumption of homogeneity of slopes was tested. When the parallelism assumption was not met, we used the separate-slope model to test the difference between slopes (García-Berthou, 2001). One-Way ANOVA with clutch frequency as the factor was used to examine differences between female SVL among clutch frequencies. Data on clutch size, egg mass, and clutch mass were analyzed using ANCOVA with female SVL as the covariate and clutch frequency as the factor to examine differences in female reproductive parameters

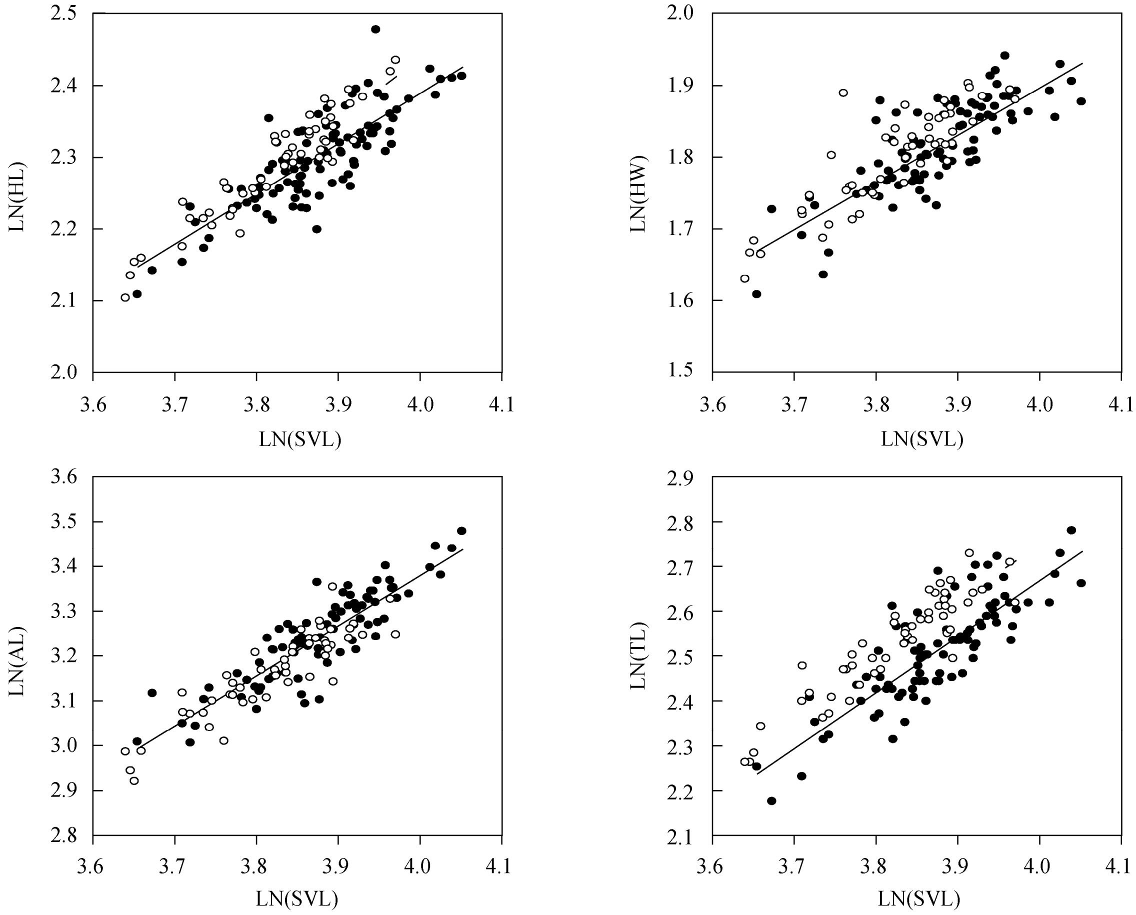

Fig. 1 Linear regressions of head length, head width, abdomen length and tail length on snout-vent length in white-striped grass lizards *Takydromus wolteri*

Females: solid circle and solid line; males: open circle and dashed line.

among clutch frequencies. Tukey's test was used to examine differences between all groups of this factor. Simple linear regression was used to analyze the relationship between female reproductive parameters and female body size. Partial correlation analyses were used to examine relationships between egg mass and clutch size, while holding female SVL constant. Because homogeneity of variances was not met, we used the Kruskal-Wallis test to examine the difference in time intervals among clutch frequencies. Values are presented as mean ± standard error, and the significance level was set at $\alpha = 0.05$.

2 Results

2.1 Sexual dimorphism

A total of 66 females and 72 males out of 185 lizards had a full tail. The largest male had a SVL of 53.0 mm and the largest female was 57.5 mm. Mean SVL was greater in adult females than adult males (*t*-test, $t = 3.67$, $df = 136$, $P < 0.001$) (Table 1).

Table 1 Descriptive statistics of morphological traits of adult *Takydromus wolteri*

Morphological traits	Female (*n* = 66)	Male (*n* = 72)
Snout-vent length (mm)	48.7 ± 0.5, 38.7–57.5	46.3 ± 0.4, 38.1–53.0
Abdomen length (mm)	26.3 ± 0.3, 20.2–32.4	23.7 ± 0.2, 18.5–28.6
Head length (mm)	9.9 ± 0.1, 8.2–11.3	10.0 ± 0.1, 8.2–11.9
Head width (mm)	6.1 ± 0.05, 5.0–7.0	6.1 ± 0.05, 5.1–6.8
Tail length (cm)	12.3 ± 0.2, 8.8–16.1	12.7 ± 0.2, 9.6–15.3

Data are expressed as mean ± standard error and range.

Head size (HL and HW), AL and TL increased with SVL in both sexes (simple linear regression, all $P < 0.0001$) (Fig. 1). The rates at which HL increased with SVL differed significantly between the sexes ($F_{1,\ 134} = 5.60$, $P < 0.02$); the slope of the regression was larger for males than females (Tukey's test, $P < 0.05$) (Fig. 1). Males had larger heads (both HL and HW) as well as longer tails than females of the same SVL (Tukey's test, all $P < 0.05$) but had shorter AL ($P < 0.001$) (Table 1 and Fig. 1).

2.2 Female reproduction

The egg-laying season was from early May to the end of July. Most of the females (~ 96%) produced more than one clutch of eggs during the breeding season. A total of 231 clutches were collected from 76 females in 2010 (Table 2 and 3), and the smallest reproductive female was 45.1 mm in SVL. Females with different clutch frequencies differed in mean SVL (One-Way ANOVA, $F_{4,\ 71} = 7.17$, $P < 0.0001$), with large females producing more clutches than small ones. Single-clutched females were smaller in mean SVL than those producing two or more clutches (Tukey's test, $P < 0.03$), but females producing three or more clutches did not differ in SVL (Tukey's test, $P > 0.86$) (Table 3). The mean clutch interval was slightly longer in females producing two clutches than those producing three or more clutches, but the difference was not statistically significant (Kruskal-Wallis test, $H_3 = 5.11$, $n = 155$, $P = 0.16$) (Table 2).

Clutch size varied from 1–5 eggs for the first clutch, 1– 4 eggs for the second to fourth clutches, and 1– 3 eggs for the fifth clutch (Table 2). Clutch size was positively related to female SVL in the first to fourth clutches (all $P < 0.02$), but not in the fifth clutch ($r^2 = 0.69$, $F_{1,\ 1} = 2.27$, $P = 0.37$) because of small sample sizes (Table 2). An ANCOVA on the linear relationship between clutch size and female SVL showed homogeneous slopes ($F_{3,\ 220} = 1.33$, $P = 0.27$) but different intercepts ($F_{3,\ 223} = 14.96$, $P < 0.0001$) among the first four clutches. Mean clutch size was larger in the first clutch than that in the three subsequent clutches (Tukey's test, all $P < 0.007$), but clutch size did not differ among these three subsequent clutches (Tukey's test, all $P > 0.31$) (Table 2). Clutch size was positively related to female AL in the first three clutches (all $P < 0.007$) but not in the fourth clutch ($F_{1,\ 22} = 3.44$, $P < 0.07$).

Clutch mass was positively related to female SVL in the first four clutches (all $P < 0.007$) but not in the fifth clutch ($r^2 = 0.50$, $F_{1,\ 1} = 1.02$, $P = 0.50$) (Table 2). The ANCOVA on the linear relationship between clutch mass and female SVL revealed homogeneous slopes ($F_{3,\ 220} = 2.67$, $P > 0.05$) but different intercepts ($F_{3,\ 223} = 23.20$, $P < 0.0001$) among the first four clutches: the first clutch had the largest clutch mass (Tukey's test, all $P < 0.001$), then the second and the fourth clutches, and

Table 2 Descriptive statistics of reproductive traits of female *Takydromus wolteri*

	First clutch ($n = 76$)	Second clutch ($n = 73$)	Third clutch ($n = 55$)	Fourth clutch ($n = 24$)	Fifth clutch ($n = 3$)
Snout-vent length (mm)	51.9 ± 0.3, 45.1–59.4	52.6 ± 0.3, 45.1–60.1	53.2 ± 0.3, 48.7–59.3	53.3 ± 0.4, 50.3–58.9	52.2 ± 1.3, 50.8–54.8
Clutch interval (days)		20.9 ± 1.0, 11.2–60.9	20.8 ± 1.3, 9.9–55.0	17.3 ± 0.8, 13.0–28.4	18.4 ± 5.3, 12.0–29.0
Clutch size (eggs)	2.8 ± 0.1, 1–5	2.4 ± 0.1, 1–4	2.2 ± 0.1, 1–4	2.3 ± 0.1, 1–4	2.0 ± 0.6, 1–3
Clutch mean egg mass (g)	0.20 ± 0.003, 0.15–0.26	0.20 ± 0.003, 0.12–0.36	0.19 ± 0.004, 0.16–0.26	0.18 ± 0.003, 0.15–0.24	0.19 ± 0.02, 0.16–0.24
Clutch mass (g)	0.55 ± 0.02, 0.19–1.03	0.47 ± 0.01, 0.12–0.75	0.41 ± 0.02, 0.16—0.69	0.42 ± 0.03, 0.17–0.82	0.36 ± 0.08, 0.24–0.51

Data are expressed as mean ± standard error and range.

Table 3 Annual fecundity, annual mean egg mass, and annual reproductive output of female *Takydromus wolteri*

	Single-clutched ($n = 3$)	Two-clutched ($n = 18$)	Three-clutched ($n = 31$)	Four-clutched ($n = 21$)	Five-clutched ($n = 3$)
Snout-vent length (mm)	46.2 ± 0.8, 45.1–47.7	51.1 ± 0.6, 45.4–54.6	52.9 ± 0.5, 48.4–60.1	53.6 ± 0.5, 50.1–58.9	52.2 ± 1.2, 51.0–54.2
Annual fecundity (eggs)	1.7 ± 0.7, 1– 3	4.6 ± 0.3, 2–6	7.5 ± 0.3, 5–11	10.1 ± 0.4, 7–13	12.0 ± 0.6, 11–13
Annual mean egg mass (g)	0.19 ± 0.02, 0.16–0.21	0.20 ± 0.01, 0.16–0.29	0.19 ± 0.002, 0.17–0.21	0.20 ± 0.003, 0.17–0.23	0.19 ± 0.01, 0.18–0.21
Annual reproductive output (g)	0.30 ± 0.09, 0.19–0.48	0.90 ± 0.05, 0.57–1.22	1.43 ± 0.05, 0.93–2.26	1.99 ± 0.06, 1.53–2.72	2.27 ± 0.22, 1.96–2.70

Data are expressed as mean ± standard error and range.

finally the third clutch (Table 2). Clutch mass was positively related to female AL in the first four clutches (all $P < 0.04$).

Clutch mean egg mass was positively related to female SVL in the first clutch ($F_{1,74} = 4.13$, $P < 0.05$), but not in subsequent clutches (all $P > 0.05$) (Table 2). When holding female SVL constant using a partial correlation analysis, clutch mean egg size was negatively related to clutch size in the first (r = -0.45, t = -4.32, df = 73, $P < 0.0001$) and second clutches (r = -0.37, t = -3.31, df = 70, $P < 0.002$), but not in subsequent clutches (all $P > 0.24$); however, clutch mass was not related to clutch mean egg size. Partial correlation analysis with female SVL and clutch size as predictor variables and clutch mass as a dependent variable showed that clutch mass was positively related to clutch size in all reproductive events (all $P < 0.0001$).

Annual fecundity (the total number of eggs produced in the breeding season) varied from 1–13 eggs (Table 3), and was positively related to female SVL ($r^2 = 0.40$, $F_{1,74} = 50.35$, $P < 0.0001$) (Fig. 2). Annual reproductive output (the total mass of eggs produced in the breeding season) varied from 0.19– 2.70 g (Table 3) and was also positively related to female SVL ($r^2 = 0.44$, $F_{1,74} = 58.49$, $P < 0.0001$) (Fig. 2). Females that were distinct in clutch frequency did not differ in annual mean egg mass (ANCOVA, $F_{4,70} = 0.67$, $P = 0.61$), but they did differ in annual fecundity ($F_{4,70} = 46.05$, $P < 0.0001$) and annual reproductive output ($F_{4,70} = 46.05$, $P < 0.0001$). Females that produced more clutches had greater annual fecundity and reproductive output (Table 3). When holding female SVL constant using a partial correlation analysis, annual mean egg size was independent of annual fecundity (r = -0.21, t = -0.16, df= 73, $P = 0.07$).

3 Discussion

T. wolteri is a female-biased SSD species (Table 1). Fecundity selection for large size has been proposed to explain female-biased SSD (Andersson, 1994; Cox et al., 2007). Large females may have higher fecundity due to their high capacity for laying eggs (Cooper and Vitt, 1989; Mouton and Van Wyk, 1993; Du et al., 2005a), because maternal body volume, represented as female body size or female abdomen length, is one of the constraints that may limit reproductive output (Du and Lü, 2010). *T. wolteri* is an oviparous species in which females produce multiple clutches (up to five in this study) in the breeding season. Compared to single-clutch species, *T. wolteri* can achieve higher reproductive output by increasing egg number in each clutch and/or increasing reproductive frequencies.

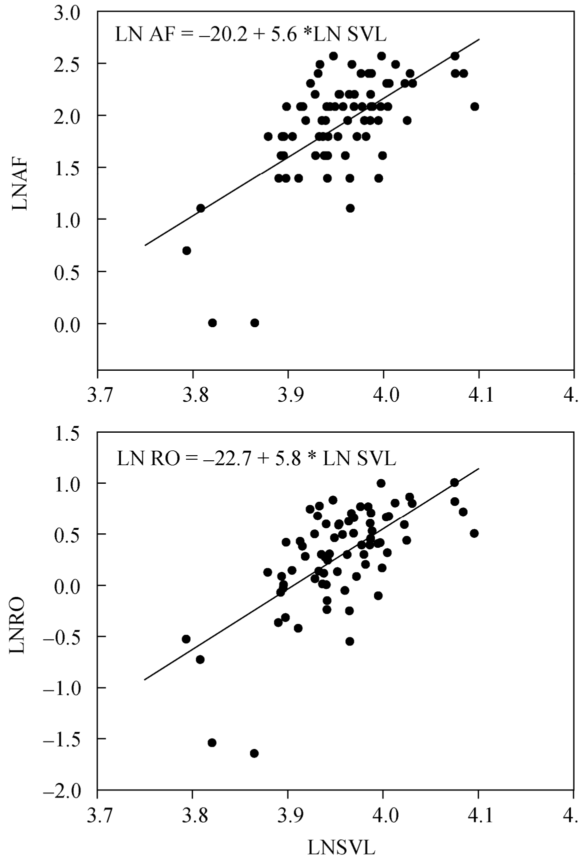

Fig. 2 Relationship between annual fecundity (total number of eggs produced per breeding season), annual reproductive output (total mass of eggs produced per breeding season) and female snout-vent length

Regression equations are indicated in the figure.

In our study, larger females not only produced more eggs (and clutch mass) in each clutch, but also produced more clutches in the breeding season (Table 2 and 3). Consequently, larger females have higher annual fecundity and annual reproductive output. Selection acting to increase fecundity or clutch mass via increasing female size has been seen in other female-biased SSD lizard species such as *Sphenomorphus indicus* (Ji and Du, 2000), *Phrynocephalus vlangalii* (Zhang et al., 2005) and *Gekko japonicus* (Ji et al., 1991). However, indicators of fecundity selection are not consistently associated with female-biased SSD. For example, higher fecundity associated with larger female size was observed in *Takydromus septentrionalis* (Du et al., 2005b, 2006; Ji et al., 2007) and *T. hsuehshanensis* (Huang, 1998), but adult *T. septentrionalis* and *T. hsuehshanensis* are sexually monomorphic (Ji et al., 1998; Huang, 1998).

The trade-off between size and number of eggs may differ from clutch to clutch in *Takydromus wolteri*. A longer period (from mid-March to early May) for preparation could explain why females produced more and bigger eggs in the first clutch. Compared to the first clutch, the interval between subsequent clutches was relatively short in *T. wolteri* (Table 2). A shorter clutch interval probably means less net energy gain for reproduction, and might result in females of *T. wolteri* producing subsequent clutches of a smaller size. Here, neither clutch size nor clutch interval changed significantly during the breeding season (Table 2). This reproductive strategy has also been observed in the grass lizard (*T. septentrionalis*, Luo et al., 2010).

Female *T. wolteri* with larger bodies are explained well by fecundity selection, but why do males have smaller bodies in this species? Several hypotheses have been proposed to explain sexual selection for small male size (reviewed in Blanckenhorn, 2005), such as time budget advantages, energy budget advantages and agility advantages. The time and/or energy budget advantage hypothesis argues that smaller individuals require less food to function and maintain themselves; therefore, small males could have surplus energy and time for activities that increase their mating and reproductive success, especially in food-limited environments (Anderssson, 1994; Blanckenhorn et al., 1995; Hakkarainen et al., 1996; Bisazza and Pilastro, 1997; Yasuda and Dixon, 2002). The agility advantage hypothesis predicts that small males may be more agile and maneuverable when courting, mate searching and defending mating territories, ultimately resulting in increased mating and reproductive success (Blanckenhorn, 2005 and references therein).

We could not directly test these hypotheses here; however, female *T. wolteri* had a long breeding season and produced multiple clutches and this may require males to mate several times during the breeding season to ensure egg fertilization. Female *T. wolteri* often mated readily after oviposition, and the maximum number of male mating records in our experiment was five (data not shown). However, male mating success is sensitive to female encounter rates in the wild. We infer that males would need to expend more time and energy searching for mates in the wild than in our enclosures, which might favor smaller males in *T. wolteri*. Time and energy budget and agility advantages for smaller males coupled with fecundity selection for larger females have likely increased body-size differences between the sexes and caused the evolution of female-biased SSD in *T. wolteri*.

Male *T. wolteri* had bigger heads and longer tails than females (Table 1 and Fig. 1). The longer tails in males could be due to physiological differences between sexes as males need additional tail space to accommodate hemipenes (Arnold, 1986). Unfortunately, did not collect data on the size of hemipenes to address this hypothesis for sexual dimorphism in TL. In addition to this explanation, there might be ecological causes driving longer tails in males. Males actively search for mates which may increase the rate of exposure to predators in the wild. Many lizard species use caudal autotomy to escape from predators (Arnold, 1984). In our study, the proportion of partially tail-less males (31 of 103, or 30.1%) was larger than for females (16 of 82, or 19.5%). Therefore, a longer tail may be beneficial for male *T. wolteri*.

Adult males having larger heads than females is a widespread pattern in lizards, including in male-biased SSD species (*Eumeces chinensis*, Lin and Ji, 2000; *E. elegans*, Du and Ji, 2001; *Podarcis melisellensis* and *Lacerta oxycephala*, Verwaigen et al., 2002; *Gallotia caesaris*, Molina-Borja et al., 2010), female-biased SSD species (*Sphenomorphus indicus*, Ji and Du, 2000; *Phrynocephalus vlangalii*, Zhang et al., 2005; *Takydromus sauteri*, Huang, 2006), and monomorphic species (*Takydromus septentrionalis*, Ji et al., 1998; *Eremias brenchleyi*, Xu and Ji, 2003; *E. multiocellata*, Li et al., 2006; *Eulamprus leuaensis*, Dubey et al., 2011). Large male heads have been attributed to the advantages of a larger gape and more powerful jaws in battles with rival males or in retaining a grip on females during mating (*Podarcis melisellensis* and *Lacerta oxycephala*, Verwaigen et al., 2002; *Lacerta vivipara*, Gvozdík and Van Damme, 2003; *Anolis carolinensis*, Lailvaux et al., 2004; *Gallotia galloti*, Huyghe et al., 2005; *Eulamprus leuaensis*, Dubey et al., 2011). Given the lack of pronounced male-male competition in *T. wolteri*, intra-sexual competition is unlikely to be the cause of sexual dimorphism in head size. Instead, larger heads in male *T. wolteri* may be associated with their mating success because males must hold on to the female's abdomen in order to mate successfully.

Acknowledgements The work was carried out in compliance with laws of China. Financial support for this research was provided by the local government of Anhui Province to XF Xu (KJ2010A249) and Anhui Province Natural Science Foundation to LG Luo (10040606Q46). Thanks to Cheng-Feng Tang, Li Ma, Yong-Long Chen, Xian-Yu Tian and Yong Jin for help with this research.

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