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Article

Sexual size monomorphism may evolve in lizards with a body size maximizing reproductive performance for both sexes

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Abstract

We used *Takydromus septentrionalis*, a sexually size-monomorphic lacertid lizard, as a model system to test the hypothesis that sexual size monomorphism may evolve in lizards where reproductive performance is maximized at a similar body size for both sexes. We allowed lizards housed in laboratory enclosures to lay as many clutches (for females) as they could or to mate as many times (for males) as they could in a breeding season. Size-assortative mating was weak but evident in *T. septentrionalis*, as revealed by the fact that male and female snout–vent lengths (SVLs) in mating pairs were significantly and positively correlated. Mating frequency (indicative of male reproductive performance) varied from 1 to 8 per breeding season, generally increasing as SVL increased in adult males smaller than 67.4 mm SVL. Clutch frequency varied from 1 to 7 per breeding season, with female reproductive performance (determined by clutch frequency, annual fecundity, and annual reproductive output) maximized in females with a SVL of 68.0 mm. Accordingly to our hypothesis, the reproductive performance was maximized in the intermediate sized rather than the largest individuals in both sexes, and the body size maximizing reproductive performance was similar for both sexes. Future work could usefully investigate other lineages of lizards with sexually monomorphic species in a phylogenetic context to corroborate the hypothesis of this study.

Key words: annual fecundity, annual reproductive output, clutch frequency, mating frequency, *Takydromus septentrionalis*.

Body size affects many aspects of animal biology and ecology (Roff 2002; Shine 2005). Sexual differences in behavior, activity, diet, habitat use, energy allocation strategy, and reproductive investment can lead to sexually divergent growth trajectories, and the differences or similarities in direction and magnitude of natural and sexual selection between males and females can favor larger males or larger females, or sexual size monomorphism (Fairbairn 1997; Fairbairn et al. 2007; Dunham and Rudolf 2009; Corl et al. 2010). The direction and magnitude of sexual size dimorphism (SSD) vary among taxa (Cox et al. 2003, 2007; Stillwell et al. 2010). For example, males are often the larger sex in birds and mammals (Fairbairn 2007) and females are often the larger sex in insects and amphibians (Monnet and Cherry 2002; Cueva del Castillo and Núñez-Farfán 2008; Stillwell et al. 2010). Within reptiles, more species display female-biased SSD in snakes and turtles and more species display male-biased SSD in lizards and crocodilians (Cox et al. 2007). In species with evident male–male competition, large males often have an enhanced ability to fight against small ones for access to resources and mates (López et al. 2002; Sacchi et al. 2009). Intrasexual selection leading to increased male size is therefore often cited to explain male-biased SSD (Cox et al. 2007; Corl et al. 2010). On the other side, female fecundity (as measured by the number of offspring produced per reproductive episode or season) or reproductive output (as measured by the total mass of offspring produced per reproductive episode or season) generally increases with female size (Cox et al. 2007; Pincheira-Donoso and Tregenza 2011). Fecundity selection leading to increased female size is therefore a hypothesis often cited to explain female-biased SSD (Andersson 1994; Bonnet et al. 2000; Cox et al. 2003). Nonetheless, species with strong male–male competition do not always have male-biased SSD, and species with strong size-related fecundity or reproductive output do not always have female-biased SSD (Cox et al. 2007; Dunham and Rudolf 2009; Odreitz and Sefc 2015; McCullough and Simmons 2016). Actually, the selective forces driving the evolution of SSD are not exclusive and, in a given species or population, SSD can evolve by the interplay between natural (fecundity) selection and sexual selection (Cueva del Castillo and Núñez-Farfán 2008; Corl et al. 2010; Jiménez-Arcos et al. 2017).

The intensity of sexual selection on male body size can be estimated by measuring mating success. Past studies on reptiles generally show that mating success is enhanced in large males (Olsson and Madsen 1998; Shine and Mason 2005; Fischer et al. 2008; Keogh et al. 2012). However, the increase in mating success in large males can be constrained by the energetic costs associated to a high mobility, defense of territories, and escape from predators (Abell 2000; Ancona et al. 2010). Moreover, mating success is not always maximized in the largest males. In the common lizard *Zootoca* (*Lacerta*) *vivipara*, for example, mating success is maximized in intermediate-sized males (Richard et al. 2005). The intensity of sexual selection and the degree of male-biased SSD are also linked to mating systems. For example, polygynous species where 1 male has exclusive access to multiple females often display extremely strong male–male competition, highly skewed mating success, and strong male-biased SSD (Rivas and Burghardt 2005; Pyron et al. 2013). Other male characteristics such as color patterns and head dimensions that are associated with male–male competition and female mate preference may also affect the link between body size and mating success, which has been generally explained in the rock–paper–scissors model system (Sinervo and Lively 1996; San-Jose et al. 2014). The links between male body size and mating success have been examined in several species of reptiles, but in none of these species was the body size maximizing mating success examined.

The intensity of fecundity selection on female body size is associated with reproductive output (Cox et al. 2003; Pincheira-Donoso and Tregenza 2011). Fecundity selection primarily acts to maximize clutch or litter size in species reproducing infrequently, or to increase reproductive frequency per breeding season in species reproducing frequently (Cox et al. 2003). Under this selective pressure, species reproducing frequently should exhibit a positive relationship between reproductive frequency and female size, and a small female-biased SSD relative to species reproducing infrequently. However, empirical evidence supporting this prediction is sparse. Interestingly, interspecific comparisons have revealed a negative relationship between reproductive frequency and body size in lizards (Clobert et al. 1998; Cox et al. 2003). Moreover, increased fecundity can be constrained by female body size or reproductive investment, and different reproductive parameters are actually interrelated and interact with each other (Roff 2002).

Male-biased SSD is a predominant pattern of SSD in lizards, although female-biased SSD or sexual size monomorphism can be found in nearly all families (Cox et al. 2007). Researchers often attribute size monomorphism to the lack of male–male competition, rarely considering the role of fecundity selection (Li et al. 2006; Dashevsky et al. 2013). In fact, male–male competition or sexual selection is not necessarily missing in species lacking SSD (Kratochvíl and Frynta 2002; Cox et al. 2007) and it can be expected a bias in SSD toward the sex under stronger positive selective pressure (Cueva del Castillo and Núñez-Farfán 2008). Theoretical studies hypothesize that size monomorphism can occur in species where sexual selection leading to increased male size is equal to fecundity selection leading to increased female size (Cooper and Vitt 1989; Siepielski et al. 2011), but empirical studies testing this hypothesis are sparse.

The northern grass lizard *Takydromus septentrionalis* is a multiple-clutched oviparous lacertid species endemic to China, occurring in the central and southern provinces of the country (Liu 1999; Cai et al. 2012). Adults are sexually dimorphic in head size but not in body size (Ji et al. 1998). Male–male combat is rare even if existing in *T. septentrionalis*, females reproduce frequently and can lay up to 9 clutches per breeding season from early April to late August, and larger females generally produce more and heavier clutches than smaller ones (Ji et al. 1994; Du et al. 2005; Ji et al. 2007; Luo et al. 2010; Guo et al. 2020). Here, we used *T. septentrionalis* as a model animal to test the hypothesis that sexual size monomorphism may evolve in species where reproductive performance is maximized at a similar body size in both sexes. We predicted that the body size maximizing reproductive performance should be similar for both sexes of *T. septentrionalis*.

Materials and Methods

We collected 253 lizards (122 males and 131 females) larger than 50 mm snout–vent length (SVL) in early April 2017 from a previous studied population (Ji et al. 2007; Cai et al. 2012; Guo et al. 2020) in Lishui (28°46′N, 119°92′E), East China. Lizards were transported to our laboratory in Hangzhou, where they were weighed, measured (for SVL and tail length), and numbered via unique combinations of clipped toes. Between 25 and 27 individuals (11–13 males and 12–14 females) were randomly housed in each of 10 2 × 1.5 × 0.6 m (length × width × height) enclosures in the backyard of our laboratory. Each enclosure was filled with a soil substrate (150 mm depth), pieces of clay tiles and grasses, and subjected to 24 h monitoring. Lizards exposed to a natural light cycle could regulate body temperature behaviorally during the daytime. Food (mealworms [*Tenebrio molitor*] and house crickets [*Achetus domesticus*]) and water enriched with vitamins and minerals were provided *ad libitum*. We individually moved mating lizards into 450 × 300 × 300 mm terraria to record their identity number, body size, and copulation duration (time from the beginning to the end of copulation). After copulation, lizards were returned to their own enclosure.

We palpated females at 5-day intervals to check their reproductive status. Females with shelled oviductal eggs were individually moved into 200 × 150 × 200 mm egg-laying terraria with a soil substrate (40 mm depth) and a 20-W spotlight for thermoregulation. Females remaining in the egg-laying terraria laid a clutch of eggs often within 3 days. Eggs were collected and weighed always less than 6 h post-laying. Post-laying females were measured and weighed before they were returned to the enclosures where they remained until they again carried shelled oviductal eggs or mated with males. Females were allowed to produce as many clutches as they could. For the 7 females that laid abnormal eggs (with condensed yolk or retained for an unusually long period) once or twice throughout the breeding season, we only recorded their clutch size. We ended the experiment 2 weeks (an interval long enough to know if a female can get gravid again; Luo et al. 2010) after the last female laid eggs, and then released all lizards at their sites of capture. We defined clutch frequency as the number of clutches produced per season, annual fecundity as the total number of eggs produced per season, and annual reproductive output as the total mass of eggs produced per season.

We used correlation analysis to examine whether and how female SVL was correlated with male SVL in mating pairs. We used a series of linear regression analysis to examine whether mating frequency, copulation duration, the time interval between 2 consecutive copulations, clutch mean egg mass, clutch frequency, annual fecundity, or annual reproductive output were related to male or female SVL. We used one-way ANOVA to examine whether SVL, tail length, and body mass differed between females with different clutch frequencies and between males with different mating frequencies. Prior to ANOVA, data were tested for normality using the Kolmogorov–Smirnov test and for homogeneity of variances using the Bartlett's test. We used Tukey's *post hoc* test to find means that differed significantly from each other. We used a principal components analysis (PCA) to identify variables with main contributions to female reproductive performance and then used PCA scores to show how it varied with SVL. We also estimated the relative fitness for both sexes through standardizing reproductive performance data of males (mating frequency) and females (clutch frequency and annual fecundity) according to Arnold and Wade (1984), and used one-way ANCOVA with ln-transformed male or female SVL as the covariate to compare the relative impact of selection on reproductive traits in both sexes. Throughout this paper, values are presented as mean ± standard error and the significance level is set at $\alpha = 0.05$.

Results

Of the 122 males, 117 mated at least once per breeding season, with mating frequency varying from 1 to 8 (Table 1). The smallest mating male was 53.3 mm SVL and the smallest reproductive female was 55.1 mm SVL.

One-way ANOVAs revealed that males with different mating frequencies differed in mean values for SVL ($F_{7,109} = 4.74$, $P < 0.001$) and body mass ($F_{7,109} = 2.21$, $P < 0.05$), but not in mean tail length ($F_{7,109} = 0.81$, $P = 0.580$) (Table 1). Size-assortative mating was weak but statistically evident, as revealed by the fact that large males generally tended to mate with large females (Figure 1). Mating frequency generally increased as male SVL increased ($r^2 = 0.17$, $F_{1,115} = 24.31$, $P < 0.001$), whereas neither copulation duration ($r^2 = 0.02$, $F_{1,89} = 1.61$, $P = 0.208$) nor the time interval between 2 consecutive copulations ($r^2 = 0.02$, $F_{1,65} = 1.21$, $P = 0.275$) was related to male SVL. The curve depicting the nonlinear relationship between mating frequency and male SVL showed that mating frequency was maximized in males with a body size of 67.4 mm SVL (Figure 2).

Females laid eggs between April and August. One-way ANOVAs revealed that females with different clutch frequencies differed in mean values for SVL ($F_{6,117} = 29.36$, $P < 0.001$) and body mass ($F_{6,117} = 11.31$, $P < 0.001$), but not in mean tail length ($F_{6,117} = 0.81$, $P = 0.562$) (Table 2). Single-clutched females were on average smaller than those producing 3 or more clutches (Tukey's test, all $P < 0.01$), females producing 3 or fewer clutches were on average smaller than those laying more clutches (Tukey's test, all $P < 0.003$), and females producing 4–7 clutches did not differ from each other in mean SVL (Tukey's test, all $P > 0.442$). Clutch mean egg mass ($r^2 = 0.05$, $F_{1,122} = 5.86$, $P = 0.017$), clutch frequency ($r^2 = 0.53$, $F_{1,122} = 139.97$, $P < 0.001$), annual fecundity ($r^2 = 0.62$, $F_{1,122} = 200.46$, $P < 0.001$), and annual reproductive output ($r^2 = 0.63$, $F_{1,122} = 206.51$, $P < 0.001$) were positively related to female SVL, whereas clutch interval (the time interval between 2 successive clutches) was independent of female SVL ($r^2 = 0.04$, $F_{1,85} = 3.54$, $P = 0.063$). PCA on clutch mean egg size, clutch frequency, annual fecundity, and annual reproductive output resolved one component (PC1) with eigenvalues ≥ 1, which had high positive loadings for clutch frequency, annual fecundity, and annual reproductive output and accounted for 72.4% of the total variance (Supplementary Table S1). The curve depicting the nonlinear relationship between PC1 score and female SVL showed that female reproductive performance (largely determined by clutch frequency, annual fecundity, and annual reproductive output; Supplementary Table S1) was maximized in females with a body size of 68.0 mm SVL (Figure 2). ANCOVA revealed that there were no significant differences in selection gradients for reproductive traits between the sexes (estimation with female reproductive frequency, $F_{1,237} = 0.09$, $P = 0.769$; estimation with female annual fecundity, $F_{1,237} = 3.51$, $P = 0.062$).

Discussion

Male mating success can be affected by differences in sizes or ages (Richard et al. 2005; Han et al. 2010). Male mating success is related

Table 1. Descriptive statistics for body size, copulation duration and time interval between copulations of male *T. septentrionalis* that mated at least once during the breeding season

	Mating frequency							
	Once	Twice	Thrice	4 times	5 times	6 times	7 times	8 times
N	50	26	18	11	5	3	3	1
SVL (mm)	62.8 ± 0.5 53.3–70.3	64.5 ± 0.6 58.1–70.2	66.0 ± 0.6 62.3–69.8	67.3 ± 0.3 65.9–69.5	66.4 ± 0.6 65.0–68.6	65.6 ± 0.3 64.9–65.9	66.8 ± 0.7 65.3–67.6	67.5
Tail length (mm)	172.9 ± 6.7 44.3–258.0	182.3 ± 7.8 99.5–238.5	173.7 ± 10.7 85.8–231.2	158.9 ± 12.3 104.5–226.6	176.2 ± 12.7 144.8–218.3	178.9 ± 11.4 165.6–201.6	219.8 ± 3.7 213.3–226.1	167.0
Body mass (g)	5.5 ± 0.1 3.5–7.7	6.0 ± 0.2 4.7–7.4	6.1 ± 0.2 4.8–7.9	6.1 ± 0.2 5.4–7.7	6.5 ± 0.2 6.0–7.4	6.1 ± 0.4 5.7–6.9	6.5 ± 0.2 6.1–6.7	6.3
Copulation duration (min)	158.0 ± 8.3 75–230	155.7 ± 6.2 90–235	159.6 ± 9.2 74–260	153.0 ± 9.3 60–267	170.6 ± 15.7 64–267	127.1 ± 15.1 65–285	135.3 ± 12.7 80–236	186.2 ± 31.2 95–288
Time interval between copulations (d)	—	35.8 ± 3.9 5–80	25.6 ± 2.3 5–47	15.2 ± 1.4 1–32	14.6 ± 2.2 1–37	15.3 ± 3.0 2–43	15.9 ± 2.7 2–38	11.4 ± 1.6 7–17

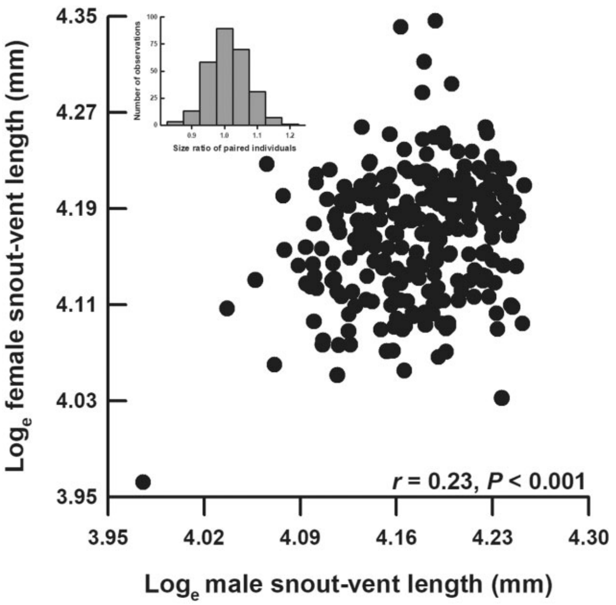

Figure 1. A scatter plot showing the degree and direction of the correlation between female and male SVLs in 272 mating pairs. The small plot shows frequency distributions of the size ratio of paired individuals.

to body size in diverse animal taxa (Olsson and Madsen 1998; Shine and Mason 2005; Fischer et al. 2008; Dubey et al. 2009; Keogh et al. 2012). Usually, larger males attain more mating opportunities and potentially higher mating success, and this is especially true for species where male–male competition is evident (Shine and Mason 2005; Shetty and Shine 2002; Dubey et al. 2009). However, in *T. septentrionalis*, mating frequency was maximized in males with a medium body size (Figure 2). This finding is consistent with the pattern of size-dependence of mating success reported for the damselfly *Enallagma hageni* (Fincke 1982), *Z. vivipara* (Richard et al. 2005), and the gray seal *Halichoerus grypus* (Lidgard et al. 2005).

Takydromus septentrionalis is not among lizard species displaying evident male–male agonistic behavior (Ji et al. 1994; Du and Yao 2007; Guo et al. 2020). Evidence from field observations reveals that northern grass lizards are active in relatively stable home ranges, of which the mean size is greater in males than in females of the same SVL and greater in larger individuals than in smaller ones of the same sex, and that males increase mating opportunities primarily by increasing their home range (and thus the number of females encountered) rather than male–male competition (Ji et al. 1994). Size-assortative mating was found in this study, but such a trend of mate preference was weak as revealed by the fact that the correlation coefficient (0.23) was small (Figure 1). Taken together, despite the importance of male size for mate-acquiring, selection driving males to achieve larger body sizes than females is not strong in *T. septentrionalis*. Male mating success may also depend on its physiological conditions (Sinervo and Lively 1996; Sinervo and Zamudio 2001; Richard et al. 2005; Shine et al. 2005). Body size is positively correlated with age in many ectothermic vertebrates and reproductive senescence has been documented in most studied species including reptiles where mating frequency is maximized in middle-aged (intermediate-sized) males (Richard et al. 2005). Mating frequency decreased sharply in males larger than 67.4 mm SVL (Figure 2). This finding is of interest because it suggests that aging may lead to reduced male mating frequency in *T. septentrionalis*.

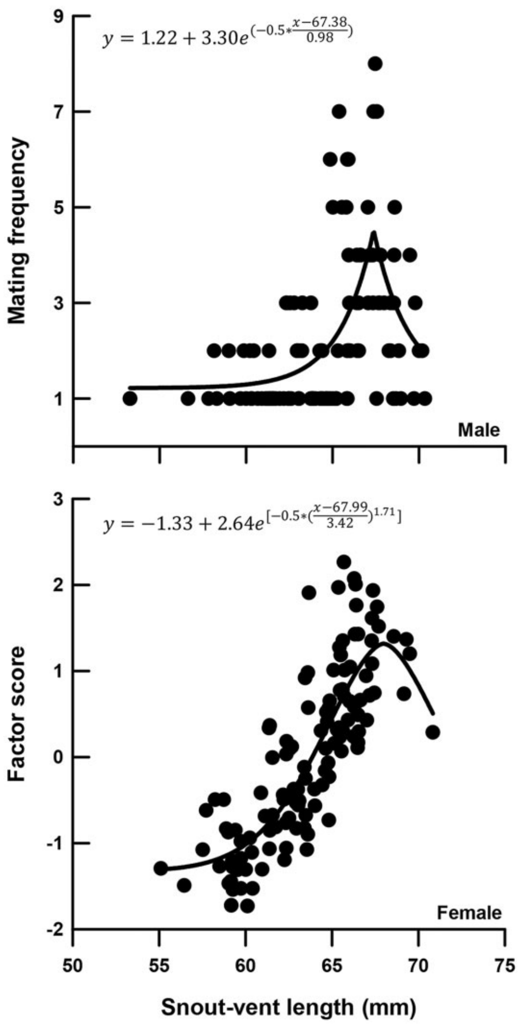

Figure 2. The curvilinear relationships between reproductive performance and body size (SVL) in both sexes of *T. septentrionalis*. A modified Gaussian model was used to fit the original data to generate the curved lines.

The upper limit to female reproductive investment (or reproductive output) per reproductive episode is set by maternal body volume that is tightly related to maternal body size in lizards including *T. septentrionalis*, and larger females potentially have more energy available for reproduction (Shine 1988; Bonnet et al. 2000; Ji et al. 2007; Luo et al. 2010; Sun et al. 2012). *Takydromus septentrionalis* is among species reproducing frequently where fecundity selection acts to maximize clutch frequency. Species reproducing frequently are predicted to exhibit a positive relationship between reproductive frequency and female size and a small female-biased SSD relative to species reproducing infrequently (Cox et al. 2003). Data from *T. septentrionalis* clearly support this prediction. Here, we found that female reproductive performance (jointly determined by clutch frequency, annual fecundity, and annual reproductive output) was also maximized in the intermediate-sized individuals rather than the largest ones (Figure 2). Reproductive performance decreased dramatically in females larger than 68.0 mm SVL, a body size similar to that (67.4 mm SVL) maximizing male mating frequency (Figure 2). The size-related reproductive performance in females smaller than 68.0 mm SVL can be better explained by the maturation hypothesis, which predicts that reproductive investment increases with age in

Table 2. Descriptive statistics for body size, annual fecundity, clutch mean egg mass, and annual reproductive output of female *T. septentrionalis*

	Clutch frequency						
	Single-clutched	2-clutched	3-clutched	4-clutched	5-clutched	6-clutched	7-clutched
N	8	21	24	30	25	11	5
SVL (mm)	59.0 ± 0.4	60.4 ± 0.4	62.1 ± 0.4	64.9 ± 0.4	65.7 ± 0.5	66.0 ± 0.4	66.1 ± 0.6
	56.4–60.1	55.1–63.6	57.7–64.8	58.7–70.8	60.9–69.5	63.6–67.7	63.7–67.6
Tail length (mm)	147.8 ± 13.4	160.0 ± 6.5	164.4 ± 6.6	144.7 ± 7.1	157.1 ± 7.7	158.7 ± 12.7	153.8 ± 18.0
	101.5–198.2	105.5–203.0	103.8–193.4	91.7–216.5	86.2–217.3	92.0–220.2	110.4–215.9
Body mass (g)	4.1 ± 0.2	4.2 ± 0.1	4.5 ± 0.1	5.0 ± 0.1	5.2 ± 0.1	5.1 ± 0.2	5.1 ± 0.1
	3.3–5.2	3.2–5.4	3.5–5.8	4.0–6.0	4.1–6.0	4.5–6.7	4.8–5.5
Annual fecundity (eggs)	2.7 ± 0.2	4.2 ± 0.2	6.3 ± 0.2	10.2 ± 0.4	12.0 ± 0.6	15.9 ± 0.9	17.6 ± 0.7
	2–4	3–6	5–9	6–14	4–17	11–21	16–20
Clutch mean egg mass (g)	0.25 ± 0.01	0.24 ± 0.01	0.24 ± 0.01	0.25 ± 0.01	0.25 ± 0.01	0.26 ± 0.01	0.25 ± 0.01
	0.22–0.29	0.15–0.36	0.19–0.30	0.21–0.30	0.17–0.32	0.23–0.29	0.23–0.26
Annual reproductive output (g)	0.65 ± 0.07	1.00 ± 0.05	1.48 ± 0.05	2.57 ± 0.10	3.01 ± 0.17	4.05 ± 0.22	4.34 ± 0.10
	0.43–1.04	0.60–1.53	1.13–2.00	1.37–3.99	1.04–4.32	3.14–5.39	4.10–4.55

early adulthood due to improvements in physiology, morphology, and/or experience or due to high expectations of future reproduction (Clutton-Brock 1988; Pärt 1995; Robertson and Rendell 2001; Reid et al. 2003). On the other hand, the size-related reproductive performance in females larger than 68.0 mm SVL can be better explained by the senescence hypothesis, which predicts that reproductive investment decreases in old individuals because their declined physiological capacities lead to lower reproduction (Williams 1957; Partridge 2001). That the reproductive maturation hypothesis better explains size-related reproduction in young or prime aged females and the senescence hypothesis better explains size-related reproduction in old females has been reported for the Mongolian racerunner *Eremias argus*, a lacertid species where females can lay up to 5 clutches per breeding season (Ma et al. 2019).

In summary, there are 2 interesting findings in this study. First, reproductive performance is maximized in the intermediate-sized individuals rather than the largest ones in both sexes. Second, the body size maximizing reproductive performance is similar for both sexes. The latter one is consistent with the hypothesis that sexual size monomorphism may evolve in lizards where reproductive performance is maximized at a similar body size for both sexes. Future work could usefully investigate other lineages of lizards with sexually monomorphic species in a phylogenetic context to corroborate the hypothesis of this study.

Authors' Contributions

H.-L.L. and X.J. conceived the ideas. X.J. supervised the study. H.-L.L., J.-F.G., K.G., and X.J. collected and analyzed the data. H.-L.L. and X.J. wrote the paper. All authors reviewed and contributed to editing of the manuscript and approved of its final publication.

Conflict of interest

The authors declared that they had no conflicts of interest to this work.

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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