动物学报 51(6):1006 - 1012, 2005
Acta Zoologica Sinica

Sexual dimorphism and female reproduction in the Qinghai toad-headed lizard *Phrynocephalus vlangalii* *

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Abstract The Qinghai toad-headed lizard *Phrynocephalus vlangalii* is a viviparous agamid lizard. We collected lizards in early May 2005 from a population in Qinghai (northwestern China) to study sexual dimorphism in morphological traits and female reproductive traits. The examined morphological traits included coloration, body size, abdomen length, tail length, head length and head width. Newly ovulated females were maintained on the laboratory thermal gradients until parturition. Sexual dimorphism was evident in adults but not in sexually immature individuals. The largest male was 70.2 mm SVL (snout-vent length) and the largest female was 82.8 mm SVL. Adult males were larger in head size and tail length, whereas females were larger in body size and abdomen length. A principal component analysis on adults resolved two components (eigenvalues ≥0.5) from four SVL-free morphological variables, accounting for 83.9 % of variation in the original data. The first component (57.8 % of variance explained) had higher positive loading for SVL-free values of tail length, head length and head width. The second component had higher negative loading for SVL-free values of abdomen length (26.1 % of variance explained). Females on the laboratory thermal gradients produced a single litter per breeding season stretching from late June to mid-July, with a litter size of 2 - 6 young. Litter size and litter mass were both positively correlated with maternal SVL, and neonate size (mass) was not. We did not find the trade-off between size and number of offspring in *P. vlangalii* [*Acta Zoologica Sinica* 51 (6): 1006 - 1012, 2005].

Key words Reptilia, Agamidae, Toad-headed lizard, *Phrynocephalus vlangalii*, Sexual dimorphism, Female reproduction, Litter size, Litter mass

青海沙蜥的两性异型和雌性繁殖 *

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摘 要 作者研究了青海沙蜥(*Phrynocephalus vlangalii*)形态特征的两性异形和雌体繁殖特征。蜥蜴于2005年5月初捕自西宁以西约150 km的倒淌河, 被检形态特征包括体色、体长、腹长、尾长、头长和头宽, 新排卵雌体维持在实验室梯度热环境中直至产仔。成体两性异形显著, 而性未成熟个体缺乏两性异形。最大的成年雄体和雌体分别为70.2 mm SVL (snout-vent length) 和 82.8 mm SVL。雄性成体具有相对较大的头长、头宽和尾长, 雌性成体 SVL 大于雄体且具有相对较大的腹长。对4个形态特征进行主成分分析(特征值 ≥0.5)区分出2个主成分, 共解释83.9 %的两性相关形态特征的变异。去除 SVL 差异的影响后, 尾长、头长和头宽在第一主成分有较高的正负载系数(解释57.8 %的变异), 腹长在第二主成分有较高的负负载系数(解释26.1 %的变异)。实验室梯度热环境下的雌体于6月下旬至7月中旬产单窝、2 - 6个后代。窝仔数和窝仔重与母体 SVL 呈正相关, 幼仔重与母体 SVL 无关。未在青海沙蜥中检测到后代数量与大小之间的权衡 [动物学报 51 (6): 1006 - 1012, 2005]。

关键词 爬行纲 鬣蜥科 青海沙蜥 两性异形 雌性繁殖 窝仔数 窝仔重

Received Aug. 28, 2005; accepted Sep. 09, 2005

* This research was funded by the grants from Nanjing Normal University and the local government of Zhejiang Province for the Key Discipline of Zoology.

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c 2005 动物学报 *Acta Zoologica Sinica*

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Sexual dimorphism in body size, body shape as well as coloration is widespread in animals (Darwin, 1871; Cooper and Vitt, 1989; Andersson, 1994). Whereas sexual selection acting via female choice or male-male contests for mating opportunities is the most frequently cited explanation for the evolution of sexual dimorphism, other factors such as natural selection acting to reduce intersexual resource competition, fecundity selection (a selection leading to larger body size or body cavity in females) and differential mortality between the sexes due to differences in longevity are increasingly reported to be the alternative causes of sexual dimorphism (Slatkin, 1984; Cooper and Vitt, 1989; Shine, 1989; Andersson, 1994; Shine et al., 2002). These explanations are often not mutually exclusive, because a sexually dimorphic trait initially induced by sexual selection may result in a shift in resource use between the sexes (Shine, 1991; Vincent et al., 2004). For example, males are the larger sex in *Eumeces chinensis* (Chinese skink; Lin and Ji, 2000; Ma and Ji, 2001) and *E. elegans* (blue-tailed skink; Du and Ji, 2001; Zhang and Ji, 2004) owing to pronounced male-male contests and larger individuals of the two species can eat larger prey. Previous studies strongly suggest that sexual dimorphism is the net outcome resulting from a balance of many selective pressures differing between the sexes in strength and/or in direction. Because reproductive output is associated with morphological traits in lizards (Cooper and Vitt, 1989; Shine et al., 1998), data on female reproduction are crucial to understanding the origins of the phenomenon in this taxon of animals.

The Qinghai toad-headed lizard *Phrynocephalus vlangalii* is a relatively thickset bodied, terrestrial, viviparous agamid lizard that is endemic to China. Its distributional range covers Qinghai, Gansu, Xinjiang and northwestern Sichuan (Zhao and Adler, 1993), and lizards are typically found in open spaces in arid or semi-arid regions covered by sparse vegetation at elevations ranging from 2 000 to 4 500 m. The region occupied by *P. vlangalii* is climatically severe, where daily and seasonal fluctuations in ambient temperature are very pronounced and the active season often stretches from May to October. Previous studies of *P. vlangalii* focused mainly on spatial distribution, active pattern, food habits, microhabitat use, home range and population age structure (Bao et al., 1998; Ma et al., 1999; Wu et al., 2002, 2004; Wang et al., 2004). Female reproduction and sex dimorphism have been noted, but only descriptive data have been available (Wu et al., 2002; Huang and Liu, 2002). Consequently, the degree and origin of sexual dimorphism and life-history traits such as the relationships among neonate size, litter size and female size still remain obscure in this species.

Here, we present data on sexual dimorphism and female reproductive characteristics gathered from a population of *P. vlangalii* in Daotanghe, approximately 150 km west to Xi'ning (36°34′N, 101°49′E), Qinghai. We pay particular attention to examining (1) sexual dimorphism in ecologically important morphological traits such as body size, head size, abdomen length and tail length; and (2) the relationships among offspring size, offspring number and female size.

1 Materials and methods

Lizards were collected by hand or noose in early May 2005. Most of these were used only for collection of morphological data and, after measurements were taken, the individuals were released to the site originally collected. Measurements were taken for each lizard, including body mass, snout-vent length (SVL), abdomen length (AL, from the posterior base of the fore-limb to the anterior base of the hind-limb), tail length (TL, from the vent to the tail tip), head length (HL, from the snout to the posterior end of the skull) and head width (HW, taken at the posterior end of the mandible). Individuals larger than 48 mm SVL were considered as adults, because females larger than this size have the potential to reproduce.

The remaining lizards were transported to our laboratory in Hangzhou, where adult females were individually palpated to assess their reproductive conditions and were marked by toe-clipping in a unique combination for future identification. Ten adult males and 10 females with yolking follicles were housed in each 50 ×40 ×30 (length ×width ×height) cm^3 plastic communal cage filled with 20 cm depth fine sand and pieces of clay tiles. Mealworms (larvae of *Tenebrio molitor*) and water enriched with vitamins and minerals were provided *ad libitum*. The communal cages were placed in a room where ambient temperatures were never higher than 28 ℃. A 100-W light bulb, suspended at one end of each cage, created a thermal gradient from the room temperature to 55 ℃ for 12 h daily. Lizards were exposed to a natural daylight cycle and some direct sunlight, and could regulate body temperature behaviorally during the photophase. Newly ovulated females were removed from the communal cages, and housed 15 - 18 in each 100 cm ×60 cm ×40 cm glass cages with 20 cm depth fine sand. These cages were placed in a 8 cm^2 constant-temperature room inside which the temperature was controlled at 18 ℃, and a 250-W spotlight mounted in each cage to allow thermoregulation.

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We checked the glass cages at least twice daily for newborns since the first female gave birth, so that all neonates could be collected, measured and weighed immediately after being produced. Females giving birth during the same period were insolated from each other using 100 cm ×20 cm ×40 cm lanes so that offspring could be allocated accurately to the mother. Postpartum females were measured and weighed before they were returned to the communal cages. We calculated relative litter mass (RLM) by dividing litter mass by the postpartum female mass (Shine, 1992), and relative fecundity by using the residuals derived from the regression of $\log_e$ (litter size) on $\log_e$ (maternal SVL) (Olsson and Shine, 1997; Ji and Wang, 2005).

Abnormal litters with various numbers of dead young, stillborns, or unfertilized eggs were excluded from statistical analyses. All data were tested for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Bartlett test), and $\log_e$-transformation was performed when necessary to satisfy conditions for parametric tests. We used linear regression analysis, one-way analysis of variance (ANOVA) and one-way analysis of covariance (ANCOVA) and principal component analysis (PCA) to analyze the corresponding data. Homogeneity of slopes was checked prior to testing for difference between adjusted means. Throughout this paper, values are presented as mean ±standard error, and the significance level is set at $\alpha = 0.05$.

2 Results

2.1 Sexual dimorphism

Sexual dimorphism in coloration pattern was evident in adults but not in neonates and juveniles. The whole tail tip was black-brown in adult males and the ventral part of the tail tip is slight saffron yellow in adult females.

In our sample, the largest male and female were 70.2 and 82.8 mm SVL, respectively (Table 1). The mean SVL was greater in adult females (67.4 mm) than in adult males (61.0 mm) (ANOVA: $F_{1,98} = 18.58$, $P < 0.0001$); thus, *P. vlangalii* is among SSD (sexual size dimorphism) species of lizards, with females being the larger sex (Table 1). The rates at which abdomen length, tail length, head length and head width increased with increasing SVL did not differ between both sexes in neonates and juveniles (ANCOVA: all $P > 0.05$), and all these examined morphological traits did not differ between both sexes in neonates and juveniles when controlled for difference in SVL (ANCOVA: all $P > 0.095$). These results indicate that sexually immature individuals of *P. vlangalii* do not show sexual dimorphism in morphological traits.

Table 1 Descriptive statistics of morphological traits of *P. vlangalii* **collected from Daotanghe, Qinghai, northwestern China**

	Neonates		Juveniles		Adults	
	Female	Male	Female	Male	Female	Male
n	21	16	52	52	58	42
Snout-vent length	29.1 ±0.3 25.5 - 31.9	29.2 ±0.4 23.7 - 31.1	43.7 ±0.4 34.0 - 47.9	43.8 ±0.4 35.1 - 47.8	67.4 ±1.0 48.2 - 82.8	61.0 ±1.1 48.1 - 70.2
Abdomen length	13.6 ±0.3 10.3 - 15.2	13.6 ±0.3 10.7 - 15.1	23.2 ±0.3 16.3 - 27.5	23.3 ±0.2 17.7 - 25.9	38.0 ±0.7 24.9 - 51.0	33.0 ±0.6 24.2 - 38.7
Head length	8.6 ±0.1 6.8 - 9.4	8.8 ±0.1 7.9 - 9.4	11.2 ±0.1 9.4 - 12.3	11.1 ±0.1 9.4 - 12.0	14.6 ±0.1 11.7 - 16.7	14.2 ±0.2 11.8 - 15.8
Head width	7.0 ±0.1 6.2 - 7.5	6.9 ±0.1 5.5 - 7.5	9.9 ±0.1 8.1 - 10.9	9.9 ±0.1 8.3 - 10.7	13.2 ±0.1 10.5 - 14.9	12.9 ±0.2 10.4 - 14.5
Tail length	26.9 ±0.4 23.0 - 30.5	27.3 ±0.4 23.0 - 29.7	41.5 ±0.6 28.0 - 50.0	41.8 ±0.5 33.0 - 49.0	60.5 ±0.8 44.0 - 73.0	62.3 ±1.4 44.0 - 74.0
Body mass	1.15 ±0.03 0.66 - 1.40	1.20 ±0.03 0.97 - 1.45	3.39 ±0.12 1.63 - 4.69	3.34 ±0.10 1.75 - 4.50	11.6 ±0.35 4.23 - 17.1	9.32 ±0.4 4.66 - 12.4
HL/SVL (%)	29.6 ±0.3 26.9 - 31.6	30.1 ±0.2 28.5 - 31.8	25.6 ±0.1 24.0 - 29.2	25.4 ±0.1 23.9 - 27.3	21.7 ±0.2 19.5 - 25.5	23.4 ±0.1 21.7 - 25.4
HW/SVL (%)	23.8 ±0.3 21.6 - 26.1	23.8 ±0.3 22.6 - 27.1	22.8 ±0.1 21.4 - 24.9	22.5 ±0.1 21.1 - 24.3	19.7 ±0.1 17.7 - 22.3	21.2 ±0.1 19.9 - 22.9
TL/SVL (%)	92.7 ±0.8 86.9 - 100.5	93.7 ±0.9 87.0 - 99.1	94.8 ±0.7 82.3 - 108.0	95.4 ±0.5 86.6 - 102.5	90.0 ±0.6 82.1 - 103.9	101.8 ±0.7 91.2 - 110.6

Date are expressed as mean ±standard error and range. Length units are in mm, and mass unites in gram.

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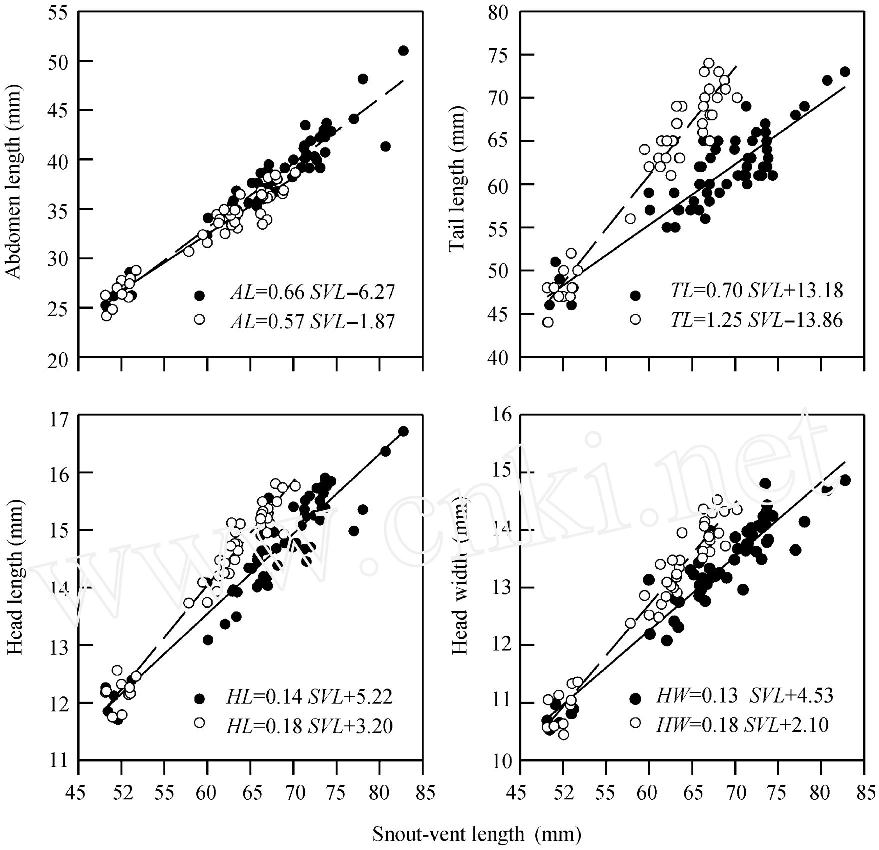

Fig. 1 Linear regressions of abdomen length, tail length, head length and head width on SVL in adult *P. vlangalii*
Solid dots and lines: females; open dots and dash line: males.

Our data show that sexual dimorphism in morphological traits is evident in adults but not in sexually immature individuals. The rate at which abdomen length increased with increasing SVL did not differ significantly between male and female adults (ANCOVA, $F_{1,96} = 3.71$, $P = 0.057$), but the intercepts were greater in females than in males ($F_{1,97} = 10.08$, $P < 0.002$) (Fig. 1). This result suggests that the abdomen cavity relative to SVL is larger in adult females than in adult males in *P. vlangalii*.

The rates at which tail length, head length and head width increased with increasing SVL were all greater in adult males than in adult females (ANCOVA; TL, $F_{1,96} = 46.64$, $P < 0.0001$; HL, $F_{1,96} = 13.79$, $P < 0.001$; HW, $F_{1,96} = 21.25$, $P < 0.0001$) $F_{1,310} = 8.89$, $P < 0.003$) (Fig. 1). The mean values of residuals derived from the regressions of $\log_e$ (TL), $\log_e$ (HL) and $\log_e$ (HW) on $\log_e$ (SVL) were all significantly greater in adult males (TL, $F_{1,98} = 150.15$, $P < 0.0001$; HL, $F_{1,98} = 60.80$, $P < 0.0001$; HW, $F_{1,98} = 88.10$, $P < 0.0001$). Thus, adult males have larger heads and longer tails than do adult females of the same size (Fig. 1).

Table 2 Loading of the first two axes of a principal component analysis on four morphological variables in adult *P. vlangalii*

	Factor loading	
	PC1	PC2
Abdomen length	- 0.133	**- 0.986**
Tail length	**0.814**	0.250
Head length	**0.905**	0.069
Head width	**0.902**	0.077
Variance explained (%)	57.8	26.1

The influence of the size (SVL) effect on abdomen length, tail length, head length and head width is removed by using residuals from the regressions of the involved variables on SVL. Variables with the main contribution to each factor are in bold face.

A principal component analysis on adults resolved two components (eigenvalues ≥0.5) from four SVL-free morphological variables, accounting for 83.9% of variation in the original data (Table 2). The first component (57.8% of variance explained) had high positive loading for SVL-free values of tail length, head length and head width. The second component had high negative loading for SVL-free values of abdomen length (26.1% of variance explained). The mean scores on the first (ANOVA, $F_{1,98} = 80.34$, $P < 0.0001$) and the second axes ($F_{1,98} = 4.73$, P

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$= 0.032$) differed significantly between both sexes, with males having greater mean values on both axes (Fig. 2).

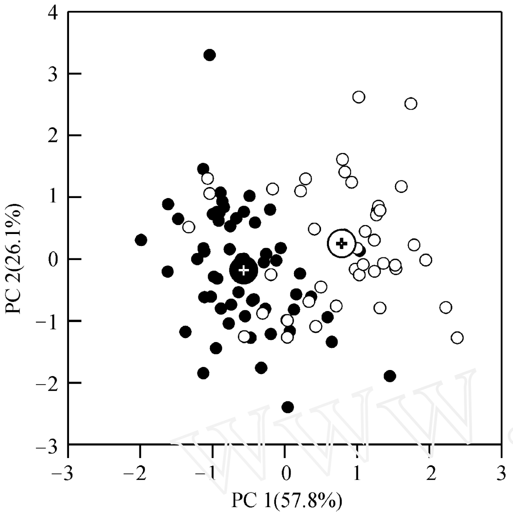

Fig. 2 Positions of adult P. vlangalii **in the space defined by the first two axes of a principal component analysis (eigenvalues ≥0.5) based on four SVL-adjusted morphological variables, on which size effects were removed by using residuals from the regressions on snout-vent length**

Solid dots: females; open dots: males; enlarged symbols show the mean values of scores on the first two axes.

Table 3 Descriptive statistics of female reproductive traits of P. vlangalii **(n = 34)**

	Mean	Standard error	Range
Female snout-vent length (mm)	68.5	0.7	61.2 - 74.6
Postpartum body mass (g)	9.6	0.3	7.1 - 12.7
Litter size	3.6	0.2	2 - 6
Litter mass (g)	3.7	0.2	2.1 - 7.3
Neonate mass (g)	1.05	0.02	0.77 - 1.24
Relative litter mass	0.40	0.02	0.17 - 0.68

2.2 Female reproductive traits

Female *P. vlangalii* produced a single litter per breeding season, with a litter size of 2 - 6 young (Table 3). Under the laboratory conditions, parturition occurred between late June and mid-July, approximately one month earlier than the birth date recorded in the filed (Ji et al., unpubl. data). This difference resulted mainly from that ambient temperatures were overall higher in the laboratory than in the field. Litter size ($r = 0.44$, $F_{1,32} = 7.56$, $P < 0.01$) and litter mass ($r = 0.49$, $F_{1,32} = 10.13$, $P < 0.004$) were both positively correlated with maternal SVL (Fig. 3), and neonate mass was not ($r = 0.17$, $F_{1,32} = 0.93$, $P = 0.343$). Neonate mass was independent of relative fecundity ($r = 0.10$, $F_{1,32} = 0.25$, $P = 0.623$), suggesting that the trade-off between size and number of offspring is absent in *P. vlangalii*.

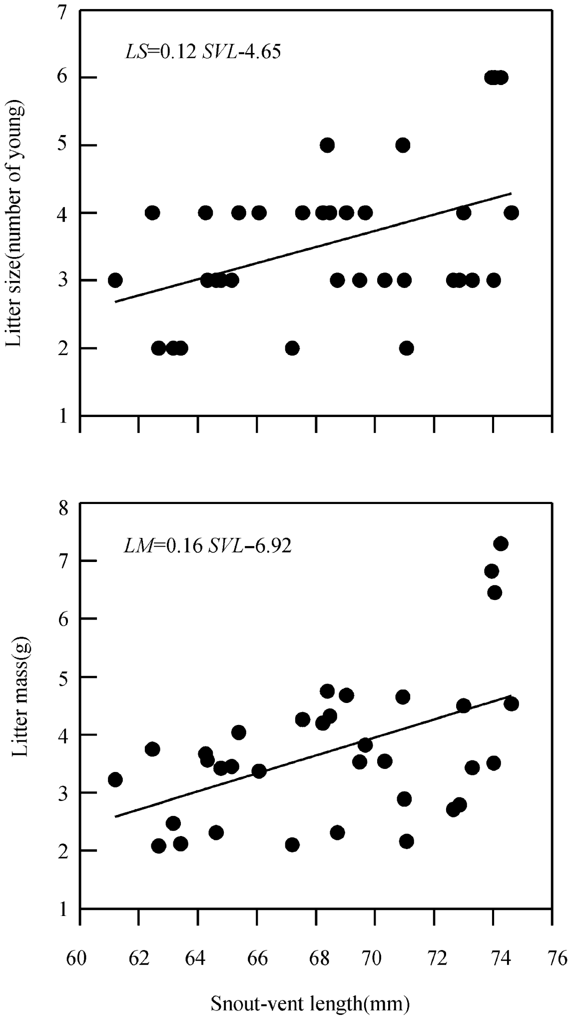

Fig. 3 Linear regressions of litter size and litter mass on female SVL in P. vlangalii

3 Discussion

As in *Gekko japonicus* (Japanese gecko; Ji et al., 1991) and *Sphenomorphus indicus* (brown forest skink; Ji and Du, 2000), adult females are the larger sex in *P. vlangalii*. Sexual size dimorphism (SSD) is predicted to evolve in lizards because of between-sex differences in reproductive success relating to adult body size (Cooper and Vitt, 1989; Hews, 1990; Mouton and Van Wyk, 1993). Under this prediction, males should be the larger sex in species where reproductive success is more tightly linked to body size in adult males, whereas females should be the larger sex in species where reproductive success is more tightly linked to body size in adult females. For example, selection via male-male contests has been proved to be the ultimate factor resulting in

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increased male size in *E. chinensis* (Lin and Ji, 2000) and *E. elegans* (Du and Ji, 2001), whereas selection acting to increase fecundity and litter volume is the main cause for increased female size in S. indicus (Ji and Du, 2000). Less obvious male-male contests as well as less obvious physical constraints from maternal body volume on reproductive output explain why adults are monomorphic in *Calotes versicolor* (oriental garden lizard; Ji et al., 2002), *Eremias brenchleyi* (upland lizard; Xu and Ji, 2003), and *Takydromus septentrionalis* (northern grass lizard; Zhang and Ji, 2000).

Both *P. vlangalii* and *S. indicus* are viviparous species of lizards producing a single litter per breeding season, and have the same the direction of SSD. As in *S. indicus* (Ji and Du, 2000), offspring size was independent of maternal size in *P. vlangalii*. However, the rate at which litter mass increases with increasing SVL is greater in *P. vlangalii* (0.16; Fig. 3) than in *S. indicus* (0.12; Ji and Du, 2000), although the mean litter size is greater in *S. indicus* (7.2; Ji and Du, 2000). The greater increasing rate of litter mass with increasing maternal SVL suggests that the selection leading to increased female size could be greater in *P. vlangalii* than in *S. indicus*. Thus, the evolution of SSD in *P. vlangalii* is most probably promoted mainly by the selection acting on females to increase reproductive output in single reproductive episodes.

Sexual dimorphism in head size, tail length and abdomen length is widespread among lizards, with males having larger heads and longer tails than do females and females having longer abdomen length than do males in nearly all saurian species studied to date. *P. vlangalii* also share these features. As in *E. elegans* (Du and Ji, 2001), only adults show sexual dimorphism in head size in *P. vlangalii*. However, in other species of lizards such as *T. septentrionalisn*, *Podarcis muralis* (common wall lizard), *C. versicolor*, *E. chinensis* and *S. indicus*, sexual dimorphism in head size occurs at earlier ontogenetic stages (Braña and Ji, 2000; Ji and Du, 2000; Lin and Ji, 2000; Zhang and Ji, 2000; Ji et al., 2002). Based on our original data, the rates at which head length (mean = 0.16), head width (mean = 0.16), tail length (mean = 1.18) and abdomen length (mean = 0.57) increase with increasing SVL did not differ between both sexes in juveniles but, in adult, these rates were all greater in males (Fig. 1). Adult females of *P. vlangalii* increasingly sacrifice head growth (HL: adult vs juvenile = 0.14 vs 0.16; HW: 0.13 vs 0.16; Fig. 1) and tail growth (0.70 vs 1.18; Fig. 1) for rapid growth in abdomen length (0.66 vs 0.57; Fig. 1) to realize the greater potential reproductive output from a larger body cavity, whereas adult males exhibit increasingly rapid growth rates of head size and tail length (HL: 0.18 vs 0.16; HW: 0.18 vs 0.16; TL: 1.25 vs 1.18; Fig. 1). Broadly speaking, between-sex differences in head size, tail length and abdomen length in *P. vlangalii* are at least attributed partly to fecundity selection acting on females to increase reproductive output, because litter mass, a measure of reproductive output, is positively correlated with maternal SVL in the species. As a larger head means an increased ability of a lizard to eat larger prey (Schoener et al., 1982; Barden and Shine, 1994) and, according to optimal foraging models, a predator tends to increase the rate of net energy intake by consuming larger prey items so as to maximize net energy gain, any relative decrease in head size potentially decreases an individual's fitness. We therefore suggest that the head size of *P. vlangalii* should be shaped by a conflict between the costs and benefits for both sexes.

Our data showed that maternal size is the main determinant of reproductive output in *P. vlangalii*, with larger females producing more offspring and thus, heavier litters (Fig. 3). The predicted trade-off (an inverse relationship) between size and number of offspring and variation in offspring size as a function of maternal SVL were not found in this study. Because the offspring size should vary with maternal size and/or clutch (litter) size in species where offspring are not optimized for size (Ford and Seigel, 1989; Doughty and Shine, 1997; Olsson and Shine, 1997; Ji et al., 1997; Lin and Ji, 2000), our results, although not completely conclusive because other untested potential causes might contribute to variation in offspring size, show that female *P. vlangalii* tend to produce optimally sized offspring.

Acknowledgements We are grateful to Bian Jiang-Hui, Chen Bo, Han Jun, Li Hong, Lin Long-Hui, Liu Hong-Xia, Liu Ya-Qing, Lu Hong-Liang and Qu Yan-Fu for their help during the research.

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