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Selection for increased maternal body volume does not differ between two *Scincella* lizards with different reproductive modes

Jing Yang[a], Yan-Yan Sun[a], Tian-Boa Fu[a], Da-De Xu[b], Xiang Ji[a,*]

[a] *Jiangsu Key Laboratory for Biodiversity and Biotechnology, College of Life Sciences, Nanjing Normal University, Nanjing 210046, Jiangsu, China*
[b] *Department of Biology, Zhaoqing University, Zhaoqing 526062, Guangdong, China*

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ABSTRACT

Body size and shape are among the most important determinants of reproductive output in diverse animal taxa. We compared morphology and reproductive output between two *Scincella* lizards (Scincidae), *Scincella modesta* (oviparous) and *Scincella reevesii* (viviparous), to examine whether viviparous females compensate for their lower reproductive output by modifying maternal body size and/or shape. As predicted, reproductive output was lower in *S. reevesii* than in *S. modesta* when corrected for body size. The two lizards differed morphologically, but were similar in three aspects: females were the larger sex, the relative head size was greater in adult males, and the relative abdomen size was greater in adult females. Sexual dimorphism in abdomen length (AL) was more evident in *S. reevesii* than in *S. modesta*, but this difference was attributable to a smaller sexual difference in AL in *S. modesta*, rather than to the greater relative maternal AL in *S. reevesii*. Female *S. reevesii* on average were larger than female *S. modesta* in snout–vent length (SVL), but this increase in overall body size cannot be viewed as a way of allowing female *S. reevesii* to compensate for lower reproductive output, as the linear slope of reproductive output against maternal SVL did not differ between the two species. Our data show that selection for increased maternal body volume does not differ between the two *Scincella* lizards with different reproductive modes.

1. Introduction

An organism's life history is characterized by a whole suit of traits adapted to the environment and adapted to each other, with its survival and reproductive success affected by co-adapted traits (Stearns, 1992; Roff, 2002; Pigliucci, 2003). Reproductive output, measured as the product of offspring size and number, which are both tightly linked to fitness, is a fundamental life-history trait and is subject to trade-offs and constraints (Stearns, 1992; Mousseau et al., 2000; Roff, 2002). For example, if a female allocates energy to the production of offspring rather than body growth in a given period of reproduction, then more or larger offspring might be produced at that time. However, if fecundity is dependent on body size, then the female might achieve higher lifetime reproductive success by reducing current reproductive investment in favor of body growth. Body size and shape constrain reproductive output in diverse animal taxa where selection on these two morphological variables yields a correlated response in reproductive output (Kaplan and Salthe, 1979; Wickman and Karlsson, 1989; Isaac, 2005; Lourdais et al., 2006; Goodman et al., 2009).

Lizards are ideal subjects for tests of life-history theory, due to the broad range of life-history variation and strategies they display (Ballinger, 1983). Like many other organisms (Fairbairn et al., 2007), lizards can be sexually dimorphic in body size and shape, and in particular, two aspects that differ between the sexes are the greater relative size of the head in males and the greater relative length of the abdomen in females (Braña, 1996; Olsson et al., 2002; Cox et al., 2003; Pincheira-Donoso and Tregenza, 2011). The relatively larger head benefits males in bouts of intrasexual combat (Huyghe et al., 2005; Lappin and Husak, 2005; Shine, 2005) and potentially amplifies food niche divergence between the sexes in species with a positive correlation between head size and prey size (Braña, 1996; Lin and Ji, 2000; Qiu et al., 2001; Zhang and Ji, 2004). In females, selection for increased reproductive output is correlated with an increase in abdomen size, causing an increase in the amount of abdominal volume available to hold the clutch (Shine, 1992; Olsson et al., 2002; Du et al., 2005; Du and Lü, 2010).

There are several studies addressing differences in reproductive output between lizards that differ in body shape, foraging mode or habitat use (Vitt and Congdon, 1978; Vitt, 1981; Shine, 1992; Goodman et al., 2009; Griffith, 2009). These studies show that (i) lizard species with robust or stout bodies, which are ambush foragers, have greater relative clutch masses (RCMs) than do more streamlined or elongated, active foraging species (Vitt and

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* Corresponding author. Tel.: +86 25 85891597; fax: +86 25 85891526.
E-mail address: xji@mail.hz.zj.cn (X. Ji).

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Congdon, 1978; Vitt, 1981; Griffith, 2009); (ii) RCMs are significantly correlated with body shape (Shine, 1992); and (iii) lizards can compensate for reduced abdominal volume and thus reduced reproductive output by being more "full" of eggs (Goodman et al., 2009).

Lizards are either oviparous or viviparous, and the transition from oviparity to viviparity is a major evolutionary event propelled by natural selection promoting fitness and successful reproduction of the species involved (Shine, 2005). So far, however, the causal link between morphological design and reproductive output is poorly studied in lizards that differ in reproductive mode, with data reported only for a reproductively bimodal scincid lizard, *Lerista bougainvillii* (Qualls and Shine, 1995).

Most oviparous lizards lay flexible-shelled eggs that take up substantial amounts of water, and expand accordingly, during incubation (Vleck, 1991). Eggs retained in the oviducts also gain mass and volume (Qualls and Shine, 1995; Qualls and Andrews, 1999; Yang, 2009). Rapid water uptake takes place after Dufaure and Hubert's (1961) stage 30 in both oviparous and viviparous lizards (Shadrix et al., 1994; Ji and Zhang, 2001; Ji et al., 2002; Yang, 2009; Qu et al., 2011). However, eggs of viviparous species absorb less water than eggs of oviparous species throughout development because the ability of eggs to absorb water is physically constrained in the oviducts (Yang, 2009). Despite this difference, viviparous females will have to leave sufficient space for their eggs that reach their maximum mass and volume in the oviducts and, as such, they will have to produce lighter clutches than would oviparous females with the same body size and shape. The decreased reproductive output constitutes one selective disadvantage for the evolution of viviparity (Tinkle and Gibbons, 1977), so the question is whether viviparous female lizards compensate for this disadvantage by modifying maternal body size and/or shape, thus allowing them to increase the amount of space available to hold eggs. If so, we predict that body plans may differ even between phylogenetically related (e.g., congeneric) species that differ in reproductive mode, and in particular, selection should favor the evolution of larger maternal body volume at a given body size in species with viviparous reproduction.

Here, we used two *Scincella* lizards (Scincidae), the slender forest skink *Scincella modesta* (oviparous) and Reeves' smooth skink *Scincella reevesii* (viviparous), both of which are income breeders using currently acquired energy to fuel reproduction, as model systems for testing the above prediction. The former species is endemic to China, occurring in the eastern and central parts of the country, northwards to Liaoning and southwards to Hong Kong (Huang, 1998). Female *S. modesta* lay eggs at embryonic stages varying from Dufaure and Hubert's (1961) stage 31–32 (Lu et al., 2006; Li, 2009). The latter species' range is from South China to Southeast Asia (Huang, 1998). These two congeneric lizards are similar in terms of habitat preferences, food habits and general behavior (Huang, 1998), thus allowing a comparison of morphology and reproductive output between oviparous and viviparous lizards with limited confounding effects from phylogenetic and ecological differences.

2. Materials and methods

2.1. Animal collection and care

We collected adult *S. modesta* from Hangzhou (30°02′N, 122°10′E) in Zhejiang, and adult *S. reevesii* from Zhaoqing (23°02′N, 112°27′E) in Guangdong, in April and May of 2007–2010. Males were released at their point of capture following the collection of morphological data, and females with yolking follicles or oviductal eggs and copulation marks were transported to our laboratory in Nanjing, where 6–8 lizards were housed in 800 mm × 500 mm × 400 mm (length × width × height) communal cages in an indoor animal holding facility. The cages contained a substrate of moist soil (~50 mm depth), with litter layers and small pieces of clay tiles provided as shelter and basking sites. Thermoregulatory opportunities were provided during daylight hours (06:00–18:00 h) by a 60 W full spectrum lamp suspended over one end of the cage; overnight temperatures followed indoor ambient temperatures (18–24 °C). Mealworm larvae (*Tenebrio molitor*) and house crickets (*Achetus domestica*) dusted with multivitamins and minerals, and water were provided daily, so that excess food was always available in the communal cages.

Females were isolated from each other using dividers that created 200 mm × 150 mm × 200 mm chambers if they laid eggs (*S. modesta*) or gave birth (*S. reevesii*) during the same period in the same cage, such that eggs or neonates could be accurately allocated to the mother. None of these females was isolated for more than 36 h, and a 20 W spotlight was mounted in each divider to allow thermoregulation. Eggs of *S. modesta* were collected and weighed less than 3 h post-laying, and were then incubated at temperatures ranging from 22 to 26 °C, which is optimal for embryonic development (Li, 2009). Hatchlings were collected, weighed and measured less than 3 h post-hatching (*S. modesta*), or post-parturition (*S. reevesii*). Postpartum females were measured and weighed before they were returned to the communal cages, where they remained until release to the field in August. Relative clutch mass was calculated by dividing clutch (*S. modesta*) or litter (*S. reevesii*) mass by the postpartum body mass (Shine, 1992).

2.2. Measurement of morphological traits

Based on the smallest snout–vent length (SVL) of reproductive females, 38.8 mm in *S. modesta* and 40.2 mm in *S. reevesii*, we considered 103 individuals (63 ♀♀ and 40 ♂♂) of *S. modesta* (>38 mm SVL) and 150 individuals (87 ♀♀ and 63 ♂♂) of *S. reevesii* (>40 mm SVL) as adults. Measurements were taken for each adult using Mitutoyo digital calipers (Mitutoyo Corp., Kawasaki, Japan) and included SVL, abdomen length (AL, from the posterior base of the fore-limb to the anterior base of the hind-limb), head length (HL, from the snout to the anterior edge of the tympanum), and head width (HW, taken at the posterior end of the mandible). Adults were not measured for tail length (TL), as the majority of them (~70% in *S. modesta* and ~60% in *S. reevesii*) autotomize some portion of the tail at least once during their lifetime in nature. Hatchlings were measured for SVL, AL, TL, HL and HW using the same calipers, and data from the same clutch or litter were pooled prior to further statistical analyses.

2.3. Statistical analyses

All statistical analyses were performed with Statistica version 6.0 for PC (StatSoft Inc., Tulsa, OK, USA). We used linear regression analysis, partial correlation analysis, one-way analysis of variance (ANOVA), two-way ANOVA, one-way analysis of covariance (ANCOVA) and multivariate analysis of variance (MANOVA) to analyze the corresponding data. Regression residuals were calculated and analyzed when all slopes differed from zero but were unequal. Prior to parametric analyses, we tested the data for normality using the Kolmogorov–Smirnov test, and for homogeneity of variances using Bartlett's test (univariate level) or Box's *M* test (multivariate level). Log_e transformations were performed when necessary to satisfy the assumptions for parametric tests. The homogeneity of slopes was checked prior to examining differences in the adjusted means. Throughout the present paper, values are presented as mean ± standard error (SE), and the significance level was set at $\alpha = 0.05$.

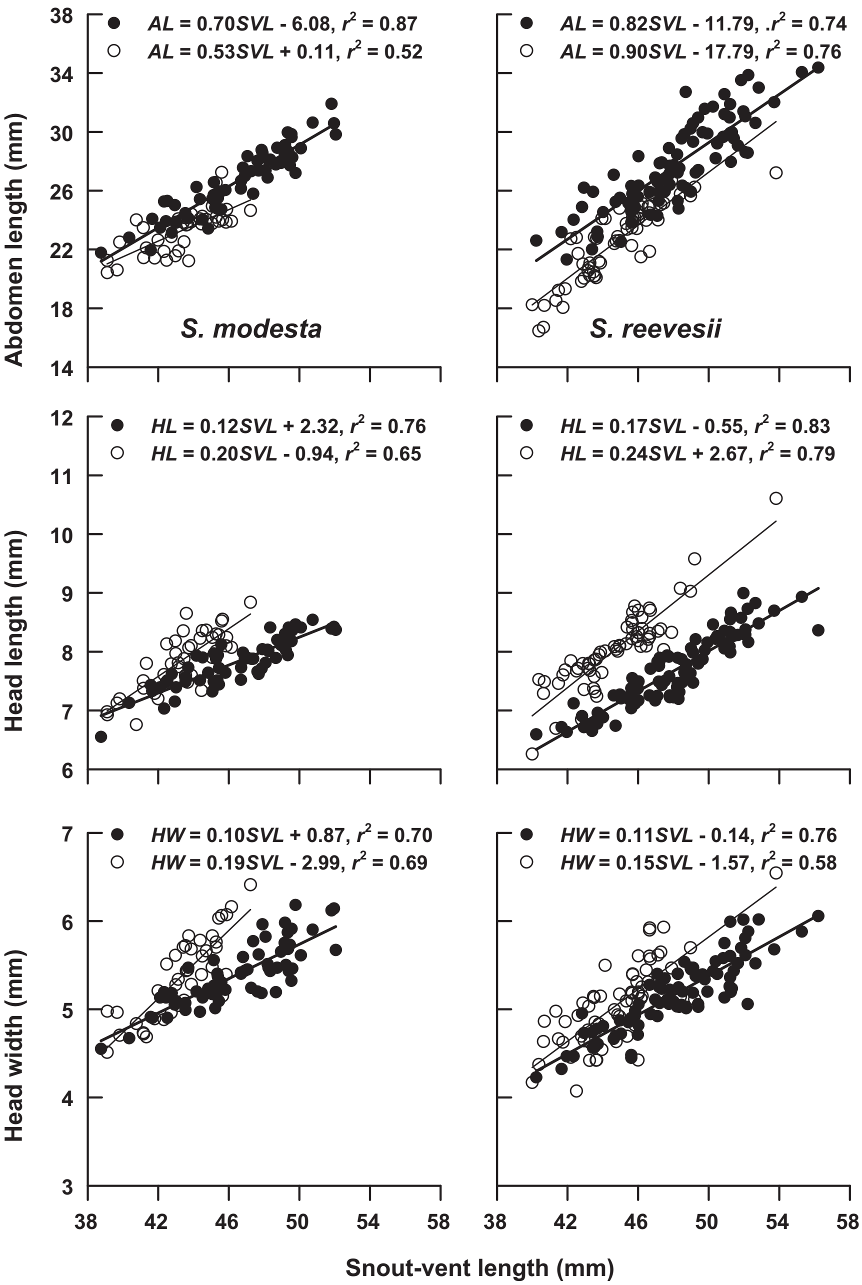

Fig. 1. Linear regressions of abdomen length (AL), head length (HL) and head width (HW) against snout–vent length (SVL) for adults of *S. modesta* and *S. reevesii*. Solid dots and thick lines: females; open dots and thin lines: males; plots on the left side: *S. modesta*; plots on the right side: *S. reevesii*. The regression equations and coefficients are given in the figure.

Table 1
Morphometric data, expressed as means ± SE and ranges, for adults of *Scincella modesta* and *Scincella reevesii*.

	S. modesta		*S. reevesii*	
	Females	Males	Females	Males
N	63	40	87	63
Snout–vent length (mm)	46.5 ± 0.4 38.8 – 52.1	43.3 ± 0.3 39.1 – 47.2	48.1 ± 0.3 40.2 – 56.2	44.8 ± 0.3 40.0 – 53.8
Abdomen length (mm)	26.6 ± 0.3 21.8 – 31.9	23.3 ± 0.2 20.4 – 27.2	27.7 ± 0.3 21.3 – 34.4	22.6 ± 0.3 16.5 – 27.2
Head length (mm)	7.8 ± 0.05 6.6 – 8.5	7.9 ± 0.08 6.8 – 8.8	7.7 ± 0.06 6.6 – 9.0	8.1 ± 0.08 6.3 – 10.6
Head width (mm)	5.4 ± 0.04 4.6 – 6.2	5.4 ± 0.07 4.5 – 6.4	5.2 ± 0.04 4.2 – 6.1	5.0 ± 0.06 4.1 – 6.5

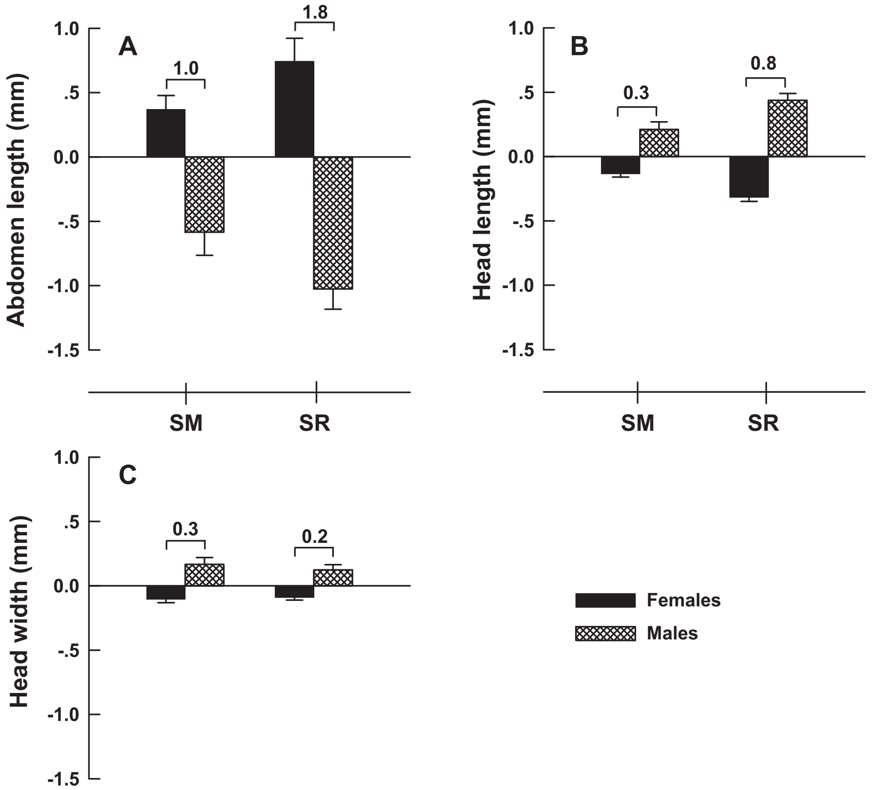

Fig. 2. Mean values (±SE) for regression residuals of abdomen length, head length and head width against snout–vent length of two species of *Scincella* lizards, *S. modesta* (SM) and *S. reevesii* (SR). Numbers in each plot are differences in mean regression residual between the sexes.

3. Results

Table 1 shows the morphometric data collected from adults. The mean adult SVL was greater in *S. reevesii* than in *S. modesta* (two-way ANOVA; $F_{1,249} = 17.78$, $P < 0.0001$), and was greater in females than in males ($F_{1,249} = 77.46$, $P < 0.0001$); the sex × species interaction was not a significant source of variation in SVL ($F_{1,249} = 0.05$, $P = 0.815$). AL, HL and HW positively covaried with SVL within each species × sex combination (Fig. 1; $P < 0.0001$ in all cases). Using a series of partial correlations, we found that AL, HL and HW were positively correlated with SVL, but not with each other, within each species × sex combination (Table 2).

A MANOVA on regression residuals of AL, HL and HW against SVL revealed that these three variables differed between the sexes (Wilks' $\lambda = 0.56$, $df = 3, 247$, $P < 0.0001$) and between the two species (Wilks' $\lambda = 0.55$, $df = 3, 247$, $P < 0.0001$); the sex × species interaction was a significant source of variation in these three variables (Wilks' $\lambda = 0.84$, $df = 3, 247$, $P < 0.0001$). When analyzing the data for each sex separately, we found again that AL, HL and HW differed between the two species in both male (MANOVA on regression residuals of the three variables against SVL; Wilks' $\lambda = 0.42$, $df = 3, 99$, $P < 0.0001$) and female (Wilks' $\lambda = 0.44$, $df = 3, 146$, $P < 0.0001$) adults. Adult males of *S. modesta* were larger in AL and HW ($P < 0.0002$ in both cases), but did not differ from adult males of *S. reevesii* in HL ($P = 0.062$) after accounting for SVL. Adult females of *S. modesta* were larger in HL and HW ($P < 0.0001$ in both cases), but did not differ from adult females of *S. reevesii* in AL ($P = 0.430$) after accounting for SVL.

Females were larger in AL but smaller in HL and HW than males in both species after accounting for SVL (Figs. 1 and 2). The sexual difference was greater in AL (Fig. 2 A) than in HL (Fig. 2B) and HW (Fig. 2C) in both species, and the sexual difference in AL was greater in *S. reevesii* than in *S. modesta* (Fig. 2A).

Hatchling mass was highly dependent on egg mass at oviposition in *S. modesta* ($F_{1,61} = 236.32$, $P < 0.0001$; Fig. 3), and hatchling mass outweighed egg mass at oviposition by an average of 13 mg (Table 4). Hatchlings of *S. modesta* were larger than neonates of *S. reevesii* in mean SVL (ANOVA; $F_{1,148} = 50.30$, $P < 0.0001$; Table 3). The other four hatchling morphometric variables (AL, TL, HL and HW) also differed between the two species (Wilks' $\lambda = 0.45$, $df = 4, 144$,

Table 2
Results of partial correlation analyses for the relationships between the selected pairs of snout–vent length (SVL), head length (HL), head width (HW) and abdomen length (AL) measured in adults. Significant values are rendered in bold.

	Scincella modesta		*Scincella reevesii*	
	Females	Males	Females	Males
Df	59	36	83	59
SVL vs. HL	$r = \mathbf{0.52}$, $t = \mathbf{4.71}$, $P < \mathbf{0.0001}$	$r = \mathbf{0.49}$, $t = \mathbf{3.35}$, $P < \mathbf{0.002}$	$r = \mathbf{0.67}$, $t = \mathbf{8.24}$, $P < \mathbf{0.0001}$	$r = \mathbf{0.61}$, $t = \mathbf{5.96}$, $P < \mathbf{0.0001}$
SVL vs. HW	$r = \mathbf{0.35}$, $t = \mathbf{2.83}$, $P < \mathbf{0.007}$	$r = \mathbf{0.52}$, $t = \mathbf{3.68}$, $P < \mathbf{0.001}$	$r = \mathbf{0.56}$, $t = \mathbf{6.11}$, $P < \mathbf{0.0001}$	$r = \mathbf{0.52}$, $t = \mathbf{4.71}$, $P < \mathbf{0.0001}$
SVL vs. AL	$r = \mathbf{0.76}$, $t = \mathbf{9.16}$, $P < \mathbf{0.0001}$	$r = \mathbf{0.47}$, $t = \mathbf{3.23}$, $P < \mathbf{0.003}$	$r = \mathbf{0.40}$, $t = \mathbf{4.03}$, $P < \mathbf{0.0002}$	$r = \mathbf{0.63}$, $t = \mathbf{6.27}$, $P < \mathbf{0.0001}$
HL vs. AL	$r = -0.14$, $t = 1.07$, $P = 0.291$	$r = -0.08$, $t = 0.47$, $P = 0.643$	$r = 0.06$, $t = 0.53$, $P = 0.594$	$r = 0.005$, $t = 0.04$, $P = 0.967$
HL vs. HW	$r = 0.16$, $t = 1.24$, $P = 0.219$	$r = 0.20$, $t = 1.21$, $P = 0.234$	$r = 0.11$, $t = 1.08$, $P = 0.281$	$r = -0.07$, $t = 0.51$, $P = 0.611$
HW vs. AL	$r = -0.02$, $t = 0.16$, $P = 0.834$	$r = 0.01$, $t = 0.06$, $P = 0.950$	$r = 0.08$, $t = 0.77$, $P = 0.444$	$r = -0.21$, $t = 1.64$, $P = 0.105$

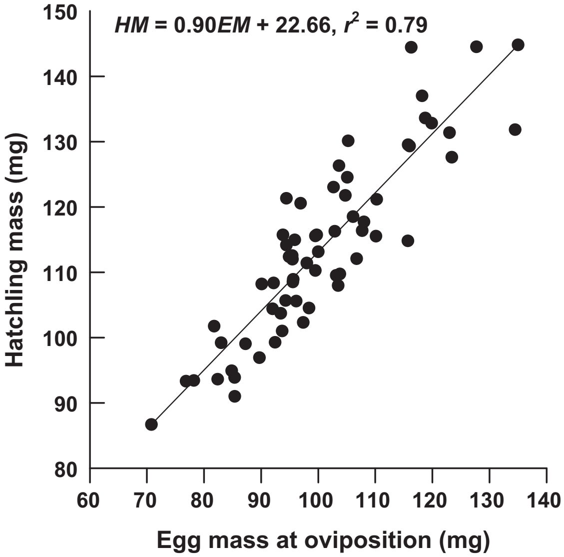

Fig. 3. Linear regression of hatchling mass (HM) against egg mass (EM) at oviposition in *S. modesta*. The regression equation and coefficient are given in the figure.

$P < 0.0001$). Specifically, hatchlings of *S. reevesii* were larger in HW but smaller in TL and HL than neonates of *S. reevesii* ($P < 0.0001$ in all cases), but hatchlings/neonates of the two species did not differ in AL ($P = 0.360$) after accounting for SVL.

Female *S. modesta* ($N = 63$) produced a single clutch of 4–16 pliable-shelled eggs between mid-May and mid-June, and female *S. reevesii* ($N = 87$) a single litter of 2–10 young between mid-May and late June (Table 4). Fecundity (clutch or litter size) positively covaried with maternal SVL and AL in both species ($P < 0.0001$ in both cases; Fig. 4A and B), so did reproductive output (clutch or litter mass; $P < 0.0001$ in both cases; Fig. 4C and D). Female *S. modesta* produced more offspring than did female *S. reevesii* of the same SVL (ANCOVA with SVL as the covariate; $F_{1,147} = 259.25$, $P < 0.0001$), but did not differ from female *S. reevesii* of the same SVL in postpartum mass (ANCOVA with SVL as the covariate; $F_{1,147} = 1.26$, $P = 0.263$). Female *S. modesta* produced heavier clutches (ANCOVA with SVL as the covariate; $F_{1,147} = 310.27$, $P < 0.0001$) and had greater RCMs (ANCOVA with postpartum mass as the covariate; $F_{1,147} = 278.10$, $P < 0.0001$) than did female *S. reevesii* after accounting for SVL (for clutch mass) or postpartum mass (for RCM). When setting maternal SVL at 47.5 mm (the overall mean SVL of the reproductive females), the mean clutch (*S. modesta*) and litter (*S. reevesii*) masses were 951 mg and 395 mg, respectively. The linear slope of maternal AL on reproductive output did not differ between *S. modesta* and *S. reevesii* (ANCOVA with reproductive output as the covariate; $F_{1,146} = 0.73$, $P = 0.393$; Fig. 5).

Table 3
Morphometric data, expressed as means ± SE and ranges, for hatchlings of *Scincella modesta* and *Scincella reevesii*.

	S. modesta	*S. reevesii*
N	63	87
Snout–vent length (mm)	18.1 ± 0.1 16.6 – 20.0	17.3 ± 0.07 15.3 – 18.6
Abdomen length (mm)	8.4 ± 0.06 7.3 – 9.6	7.9 ± 0.06 6.1 – 9.1
Tail length (mm)	21.8 ± 0.1 19.3 – 25.1	22.4 ± 0.2 18.1 – 26.3
Head length (mm)	4.3 ± 0.02 4.0 – 4.6	4.3 ± 0.02 3.6 – 4.8
Head width (mm)	3.2 ± 0.02 3.0 – 3.5	2.7 ± 0.02 2.2 – 3.1

Table 4
Descriptive statistics, expressed as means ± SE and ranges, for female reproductive traits of *Scincella modesta* and *Scincella reevesii*.

	S. modesta	*S. reevesii*
N	63	87
Snout–vent length (mm)	46.5 ± 0.4 38.8 – 52.1	48.2 ± 0.3 40.2 – 56.2
Postpartum body mass (g)	1.27 ± 0.03 0.80 – 1.91	1.40 ± 0.03 0.84 – 2.17
Clutch or litter size	9.1 ± 0.3 4 – 16	4.8 ± 0.2 2 – 10
Clutch or litter mass (mg)	912.8 ± 32.5 421.0 – 1509.0	411.0 ± 19.1 126.0 – 913.0
Egg mass (mg)	100.7 ± 1.7 70.8 – 135.0	–
Hatchling mass (mg)	113.7 ± 1.7 86.7 – 144.8	84.6 ± 1.4 49.0 – 111.3
Relative clutch mass	0.72 ± 0.02 0.38 – 1.20	0.29 ± 0.01 0.09 – 0.55

Egg mass (*S. modesta*) was independent of maternal SVL and AL ($P > 0.419$ in both cases; Fig. 4E and F), whereas neonate mass (*S. reevesii*) positively covaried with maternal SVL and AL ($P < 0.0007$ in both cases; Fig. 4E and F). Female *S. modesta* produced heavier offspring than did female *S. reevesii* in both absolute (ANOVA; $F_{1,148} = 49.56$, $P < 0.0001$) and relative (ANOVA on regression residuals of hatchling mass against maternal SVL; $F_{1,148} = 146.31$, $P < 0.0001$) terms. Holding maternal SVL constant with a partial correlation analysis, we found that hatchling mass was not correlated with fecundity (clutch or litter size) in both species ($P > 0.470$ in both cases).

4. Discussion

The two *Scincella* lizards differed morphologically at birth and during adulthood, but were similar in three aspects: females were the larger sex, the relative head size (both length and width) was greater in adult males, and the relative abdomen length was greater in adult females. Between-sex differences in body volume primarily resulted from differences in AL, as neither in *S. modesta* nor in *S. reevesii* did the width and height of the abdomen differ between the sexes after accounting for SVL (Li, 2009). The two lizards differed in all female reproductive traits examined, with the exception of postpartum body mass. Our finding that in the two lizards clutch or litter size is dependent on maternal SVL is consistent with the prediction of the fecundity selection hypothesis that increasing fecundity results from larger body size in females (Williams, 1966; Fitch, 1981; Cox et al., 2007). Clutch mass positively covaried with maternal AL in *S. modesta*, so did litter mass in *S. reevesii* (Fig. 4D). These results indicate that maternal body volume is an important determinant of reproductive output in both species.

Female *S. reevesii* produced fewer and smaller offspring than did female *S. modesta* in both absolute and relative terms. This finding is inconsistent with that in *L. bougainvillii* where the evolution of viviparity is accompanied by an increase in reproductive output because viviparous females are more “full” of eggs than oviparous females (Qualls and Shine, 1995). This inconsistency at least partly resulted from differences in the method used to calculate reproductive output between the two species. For *L. bougainvillii*, litter mass was calculated by subtracting the mass of a female after parturition from her mass before parturition (Qualls and Shine, 1995), but for *S. reevesii* it was calculated by adding up the mass of neonates

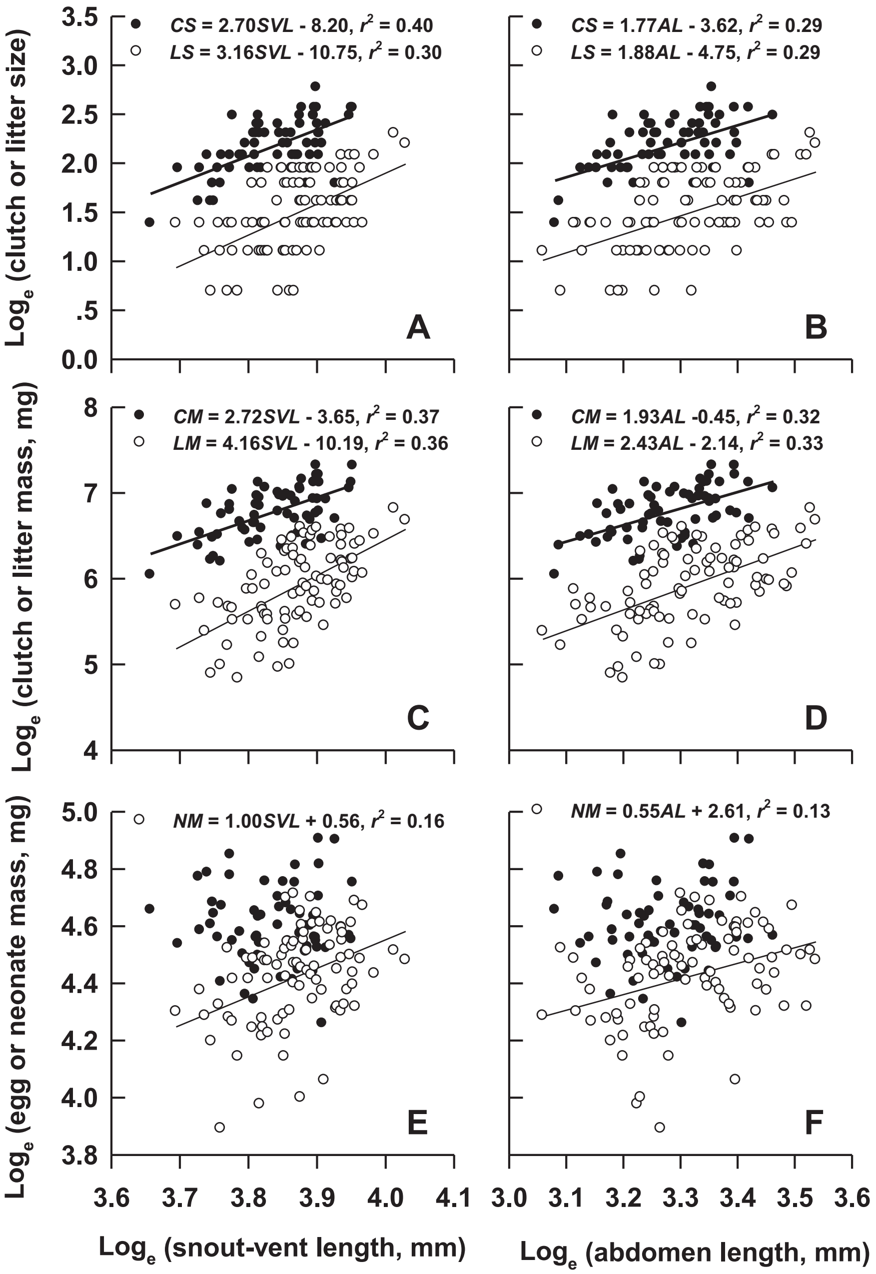

Fig. 4. Linear regressions of fecundity (clutch or litter size), reproductive output (clutch or litter mass) and offspring size (egg or neonate mass) against maternal snout–vent length (plots on the left side) or abdomen length (plots on the right size). Solid dots and thick lines: *S. modesta*; open dots and thin lines: *S. reevesii*. All data were log$_e$ transformed. For the relationships that are significant, the regression equations and coefficients are given in the figure.

produced by a female. Reproductive output could have been overestimated in *L. bougainvillii*, as it also included the mass of fluids lost in the course of parturition and was thus equal to the total burden to females before parturition (Qualls and Shine, 1995).

The linear slope of maternal AL on reproductive output provides a measure of the extent to which selection for large maternal AL is likely to increase reproductive output, thus offering a reliable index of the intensity of selection for increased maternal AL. The linear slope of maternal AL on reproductive output (clutch or litter mass) did not differ between *S. modesta* and *S. reevesii* (Fig. 5), suggesting that the two species do not differ in the intensity of selection toward increased maternal AL. Not surprisingly, the linear elevation (intercept) of maternal AL on reproductive output was higher in *S. reevesii* than in *S. modesta* (Fig. 5). This difference primarily reflects the different space requirements for eggs in the two lizards. Unlike female *S. modesta* that lay eggs at those embryonic stages (31–32; Li, 2009) when rapid water uptake has not yet taken place, female *S. reevesii* have to leave space for eggs that reach their maximum mass and volume in the oviducts and have to experience the full mass of the clutch. The increased space requirement of individual eggs reduces the maximum level of reproductive output at which females are physically full of eggs.

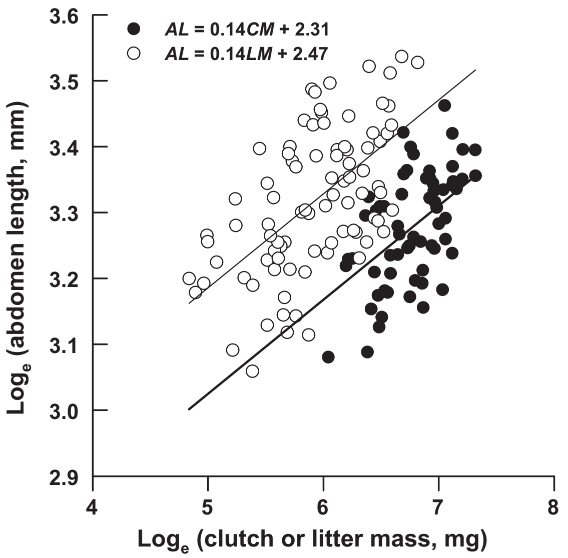

Fig. 5. Linear regressions of maternal abdomen length (AL) against clutch (CM, *S. modesta*) or litter (LM, *S. reevesii*) mass. All data were log$_e$ transformed. Regression lines were adjusted for the two species with a common slope to facilitate comparison. Solid dots and thick line: *S. modesta*; open dots and thin line: *S. reevesii*. The corrected regression equations are given in the figure.

Our finding that larger females produce heavier clutches than smaller ones in both oviparous and viviparous species validates the prediction of the body volume constraint hypothesis that females are unlikely to increase reproductive output without increasing overall body size (Vitt and Congdon, 1978; Du et al., 2005; Goodman et al., 2009; Griffith, 2009; Pincheira-Donoso and Tregenza, 2011). However, contrary to what was expected we did not find that viviparous females increased reproductive output by increasing the relative size of the abdomen.

To our knowledge, no previous comparative study has examined differences in the relationship between morphological design and reproductive output between lizards that differ in reproductive mode, with the exception of *L. bougainvillii* (Qualls and Shine, 1995). In *L. bougainvillii*, the evolution of viviparity was accompanied by an increase in maternal SVL (Qualls and Shine, 1995). Indeed, female *S. reevesii* were larger than female *S. modesta* in mean adult SVL. Nonetheless, this increase in overall body size cannot be viewed as a way of allowing female *S. reevesii* to compensate for their lower reproductive output, as the linear slope (and thus, the intensity of selection for increased body size) of reproductive output on maternal SVL did not differ between *S. reevesii* and *S. modesta* (Fig. 4C). In the present study, the viviparous species did display more pronounced sexual dimorphism in AL than the oviparous species (Fig. 2). However, this difference was primarily attributable to a smaller difference in AL between the sexes in *S. modesta*, rather than to the greater relative maternal AL in *S. reevesii*. If fact, the SVL-specific AL did not differ between the two species in adult females, and in adult males it was greater in *S. modesta* than in *S. reevesii*. These findings, together with a homogeneity of slopes test (with reproductive output as the independent variable and maternal AL as the independent variable; Fig. 4C and D), provide strong evidence that female *S. reevesii* do not compensate for lower reproductive output by increasing the relative size of the abdomen.

In summary, our data show that the two *Scincella* lizards differ in most traits examined, but not in general patterns of sexual dimorphism and rates at which fecundity and reproductive output increase with maternal SVL or AL. Reproductive output is lower in *S. reevesii* than in *S. modesta*, but selection for increased maternal body volume does not differ between the two lizards with different reproductive modes. The reasons why female *S. reevesii* do not compensate for their lower reproductive output by increasing overall body size, or by increasing relative abdomen size, are currently unknown, but gestation costs such as increased metabolism (Angilletta and Sears, 2000), decreased locomotor capacity (Miles et al., 2000), impaired immune function (Ilmonen et al., 2003), reduced growth (Cox et al., 2010) and decreased postpartum body condition (Bleu et al., 2011) cannot be precluded as an important factor. Future work should investigate whether an adaptive reduction of reproductive output will enhance fitness in viviparous females.

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References

Angilletta, M.J., Sears, M.W., 2000. The metabolic cost of reproduction in an oviparous lizard. Funct. Ecol. 14, 39–45.

Ballinger, R.E., 1983. Life-history variations. In: Huey, R.B., Pianka, E.R., Schoener, T.W. (Eds.), Lizard Ecology: Studies of a Model Organism. Harvard University Press, Cambridge, pp. 241–260.

Bleu, J., Massot, M., Haussy, C., Meylan, S., 2011. Experimental litter size reduction reveals costs of gestation and delayed effects on offspring in a viviparous lizard. Proc. R. Soc. Lond. B 279, 489–498.

Braña, F., 1996. Sexual dimorphism in lacertid lizards: male head increase vs. female abdomen increase? Oikos 75, 511–523.

Cox, R.M., Skelly, S.L., John-Alder, H.B., 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. Evolution 57, 1653–1669.

Cox, R.M., Butler, M., John-Alder, H.B., 2007. The evolution of sexual size dimorphism in reptiles. In: Fairbairn, D.J., Blanckenhorn, W.U., Székely, T. (Eds.), Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, Oxford, pp. 38–49.

Cox, R.M., Parker, E.U., Cheney, D.M., Liebl, A.L., Martin, L.B., Calsbeek, R., 2010. Experimental evidence for physiological costs underlying the trade-off between reproduction and survival. Funct. Ecol. 24, 1262–1269.

Du, W.-G., Lü, D., 2010. An experimental test of body volume constraint on female reproductive output. J. Exp. Zool. A 313, 123–128.

Du, W.-G., Ji, X., Shine, R., 2005. Does body volume constrain reproductive output in lizards? Biol. Lett. 1, 98–100.

Dufaure, J.P., Hubert, J., 1961. Table de développement du lézard vivipare: *Lacerta* (*Zootoca*) *vivipara* Jacquin. Arch. Anat. Microsc. Morphol. Exp. 50, 309–328.

Fairbairn, D.J., Blanckenhorn, W.U., Székely, T., 2007. Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, Oxford.

Fitch, H.S., 1981. Sexual size differences in reptiles. Misc. Publ. Mus. Nat. Hist. Univ. Kans. 70, 1–72.

Goodman, B.A., Hudson, S.C., Isaac, J.L., Schwarzkopf, L., 2009. The evolution of body shape in response to habitat: is reproductive output reduced in flat lizards? Evolution 63, 1279–1291.

Griffith, H., 2009. Body elongation and decreased reproductive output within a restricted clade of lizards (Reptilia: Scincidae). J. Zool. 233, 541–550.

Huang, Q.-Y., 1998. Scincella. In: Zhao, E.-M., Zhao, K.-T., Zhou, K.-Y. (Eds.), Fauna Sinica, vol. 2 (Squamata, Lacertilia). Science Press, Beijing, pp. 312–336.

Huyghe, K., Vanhooydonck, B., Scheers, H., Molina-Borja, M., Van Damme, R., 2005. Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. Funct. Ecol. 19, 800–807.

Ilmonen, P., Hasselquist, D., Langefors, Å., Wiehn, J., 2003. Stress, immunocompetence and leukocyte profiles of pied flycatchers in relation to brood size manipulation. Oecologia 136, 148–154.

Isaac, J.L., 2005. Potential causes and life history consequences of sexual size dimorphism in mammals. Mammal Rev. 35, 101–115.

Ji, X., Zhang, C.-H., 2001. Effects of thermal and hydric environments on incubating eggs, hatching success, and hatchling traits in the Chinese skink (*Eumeces chinensis*). Acta Zool. Sin. 47, 250–259.

Ji, X., Qiu, Q.-B., Diong, C.-H., 2002. Influence of incubation temperature on hatching success, embryonic use of energy, and size and morphology of hatchlings in the oriental garden lizard, *Calotes versicolor* (Agamidae). J. Exp. Zool. 292, 649–659.

Kaplan, R.H., Salthe, S.N., 1979. The allometry of reproduction: an empirical view in salamanders. Am. Nat. 113, 671–689.

Lappin, A.K., Husak, J.F., 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collard lizard (*Crotaphytus collaris*). Am. Nat. 166, 426–436.

Li, H., 2009. The evolution of reptilian viviparity and its adaptive significance using lizards as the model systems. Ph.D. Thesis, Nanjing Normal University, Nanjing, China.

Lin, Z.-H., Ji, X., 2000. Food habits, sexual dimorphism and female reproduction of the skink (*Eumeces chinensis*) from a Lishui population in Zhejiang. Acta Ecol. Sin. 20, 304–310.

Lourdais, O., Shine, R., Bonnet, X., Brichoux, F., 2006. Sex differences in body composition, performance and behaviour in the Columbian rainbow boa (*Epicrates cenchria maurus*, Boidae). J. Zool. 269, 175–182.

Lu, H.-L., Ji, X., Lin, L.-H., Zhang, L., 2006. Relatively low upper threshold temperature in lizards using cool habitats. J. Therm. Biol. 31, 256–261.

Miles, D.B., Sinervo, B., Frankino, W.A., 2000. Reproductive burden, locomotor performance, and the cost of reproduction in free ranging lizards. Evolution 54, 1386–1395.

Mousseau, T.A., Sinervo, B., Endler, J.A., 2000. Adaptive Genetic Variation in the Wild. Oxford University Press, New York.

Olsson, M., Shine, R., Wapstra, E., Ujvari, B., Madsen, T., 2002. Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. Evolution 56, 1538–1542.

Pigliucci, M., 2003. Phenotypic integration: studying the ecology and evolution of complex phenotypes. Ecol. Lett. 6, 265–272.

Pincheira-Donoso, D., Tregenza, T., 2011. Fecundity selection and the evolution of reproductive output and sex-specific body size in the *Liolaemus* lizard adaptive radiation. Evol. Biol. 38, 197–207.

Qiu, Q.-B., Ma, X.-M., Ji, X., 2001. Ontogenetic shifts of morphology and food habits in the oriental garden lizard, *Calotes versicolor* (Agamidae). Zool. Res. 22, 367–374.

Qu, Y.-F., Li, H., Gao, J.-F., Ji, X., 2011. Embryonic thermosensitivity and hatchling morphology differ between two coexisting lizards. Acta Oecol. 37, 375–380.

Qualls, C.P., Andrews, R.M., 1999. Maternal body volume constrains water uptake by lizard eggs *in utero*. Funct. Ecol. 13, 845–851.

Qualls, C.P., Shine, R., 1995. Maternal body volume as a constraint on reproductive output in lizards: evidence from the evolution of viviparity. Oecologia 103, 73–78.

Roff, D.A., 2002. Life History Evolution. Sinauer Associates, Sunderland.

Shadrix, C.A., Crotzer, D.R., McKinney, S.L., Stewart, J.R., 1994. Embryonic growth and calcium mobilization in oviposited eggs of the scincid lizard, *Eumeces fasciatus*. Copeia 1994, 493–498.

Shine, R., 1992. Relative clutch mass and body shape in lizards and snakes: is reproductive investment constrained or optimized? Evolution 46, 828–833.

Shine, R., 2005. Life-history evolution in reptiles. Annu. Rev. Ecol. Evol. Syst. 36, 23–46.

Stearns, S.C., 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Tinkle, D.W., Gibbons, J.W., 1977. The distribution and evolution of viviparity in reptiles. Misc. Publ. Univ. Mich. Mus. Zool. 154, 1–55.

Vitt, L.J., 1981. Lizard reproduction: habitat specificity and constraints on relative clutch mass. Am. Nat. 117, 506–514.

Vitt, L.J., Congdon, J.D., 1978. Body shape, reproductive effort and relative clutch mass in lizards: resolution of a paradox. Am. Nat. 112, 595–608.

Vleck, D., 1991. Water economy and solute regulation of reptilian and avian embryos. In: Deeming, D.C., Ferguson, M.W.J. (Eds.), Egg Incubation: Its Effects on Embryonic Development in Reptiles and Birds. Cambridge University Press, Cambridge, pp. 245–259.

Wickman, P.O., Karlsson, B., 1989. Abdomen size, body size and the reproductive effort of insects. Oikos 56, 209–214.

Williams, G.C., 1966. Adaptation and Natural Selection. Princeton University Press, Princeton, NJ.

Yang, J., 2009. Life-history traits and the influence of thermal environment on embryogenesis and offspring phenotype in two skink species, *Sphenomorphus indicus* and *Eumeces chinensis*. Master Thesis, Hangzhou Normal University, Hangzhou, China.

Zhang, Y.-P., Ji, X., 2004. Sexual dimorphism in head size and food habits in the blue-tailed skink *Eumeces elegans*. Acta Zool. Sin. 50, 745–752.