

## Sexual Dimorphism and Female Reproduction in *Lacerta vivipara* in Northeast China

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**Abstract.**- *Lacerta vivipara* is a small lacertid lizard that inhabits much of Europe and northern Asia. From the end of May to the beginning of October in 2003, these common lizards were collected from a population in Heilongjiang Province (northeast China) in order to study sexual dimorphism and female reproductive traits. Through the examination of external morphological traits, such as snout-vent length, head length, head width, head height, tail length, body weight, rows of ventral and mid-dorsals scales, ventral color, tail base and femoral pores, analyses revealed the presence of a distinct sexual dimorphism. Males possessed a bulging tail base, a salmon-pink venter and a thorn in the femoral pore. Females had significantly more rows of ventral scales and fewer mid-dorsal scales than males. Adult males were larger in head size and had a longer tail, whereas adult females were larger in body size and weight. Male juveniles and neonates were larger in head size than females of the same age and female neonates were larger in body size than male neonates. The rates at which head length, head width and head height increased with increasing SVL (snout-vent length) was allometric in females.

Females produced a single clutch every breeding season, with 3–12 young per clutch. While clutch size and neonate mass were not positively correlated with maternal SVL, clutch mass was, suggesting that sexual dimorphism in this species is due (in part) to differences in reproductive investment between the sexes. The larger head of males is likely an adaptation for male-male combat while the larger relative body length of females is a result of selection for higher fecundity.

**Keywords.**- Sexual dimorphism, female reproductive adaptations, allometry, Lacertidae, *Lacerta vivipara*.

### Introduction

Sexual dimorphism in body size, body shape, and coloration is widespread in many Chinese lizards, including *Takydromus septentrionalis*, *Sphenomorphus indicus*, *Eremias argus*, *Gekko japonicus*, *Plestiodon elegans*, *Plestiodon chinensis*, *Erendas brenchleyi*, *Phrynocephalus vlangalii* and *Eremias multiocellata* (Du and Ji, 2001; Ji and Du, 2000; Lin and Ji, 2000; Li et al., 2006; Xu and Ji, 2003; Zhang et al., 2005). Previous studies strongly suggest that sexual dimorphism results from a balance between numerous selective pressures differing in influence between the sexes (Shine, 1989; Schoener et al., 1982; Vitt and Cooper, 1985). Consequently, various hypotheses have been proposed to explain sexual dimorphism, including, female choice in mate selection, male aggressive behavior (Andersson, 1994; Cooper and Vitt, 1993), fecundity selection (a selection leading to larger body-cavity size in females) (Griffith, 1990), differential mortality due to differences in longevity (Shine et al., 2002), and food-niche divergence (Lin and Ji, 2000). Because reproductive output is associated with numerous morphological traits in lizards, data on female physiology and repro-

duction are crucial to understanding the origin of sexual dimorphism in the group (Du and Ji, 2001; Ji and Du, 2000; Lin and Ji, 2000; Li et al., 2006; Zhang et al., 2005).

The common lizard, *Lacerta vivipara* Jacquin, 1787, has the largest geographic range of any terrestrial squamate reptile, extending across Eurasia from western Europe to Japan. In China, it is found in Heilongjiang Province, Xijiang Province and Inner Mongolia. It is a small (approximately 4–5 g), diurnal, non-territorial lizard typically found in open spaces surrounded by pine-broadleaf mixed forest (Zhao et al., 2006).

Due to both its abundance in nature and unique dual oviparous and ovoviviparous reproductive modes, *Lacerta vivipara* has been the focus of numerous morphological studies (Guillaume, 2006; Šmajda and Majláth, 1999; Lecomte et al., 1992; Wermuth, 1955). Despite this abundance of detailed quantitative examination (Dong, et al. 2004; Fang and Tang, 1983; Zhao et al., 2006), however, details on Chinese populations of the species and the relationship between its reproductive ecology and morphometry remains poorly understood. To examine the relationships between sexually dimorphic, morphometric traits in males and females (from adults to neonates), and their relationships to offspring

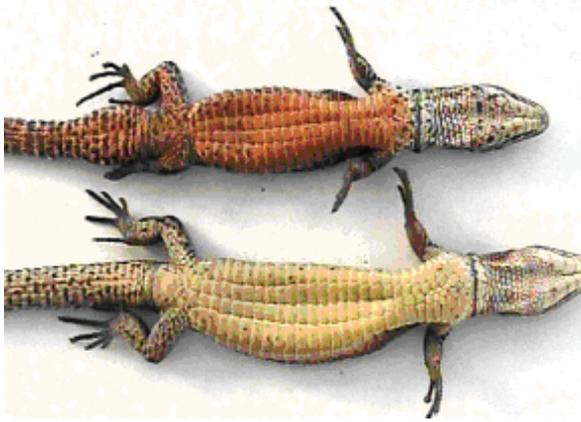


Figure 1. The tail base and ventral color of a male (top) and female (bottom) *Lacerta vivipara*.

number and mass, we studied a population of *L. vivipara* in Sunwu County, Heilongjiang Province, in northeast China (49° 39' 19.2" N, 127° 34' 10.1" E; elevation 304 m). Morphological measurements were taken from lizards collected in the field. Females gave birth to young under simulated field conditions. Particular attention was paid to examining (1) sexual dimorphism in ecologically important morphological traits and (2) the relationship between female size and offspring size and number. The results demonstrate that increased male head size is an adaptation for combat and increased female body length is an adaptation for higher fecundity.

## Materials and Methods

**Specimen collection and housing.**- From the end of May to the beginning of October in 2003, 183 lizards (121 females, 62 males) were collected and analyzed. It was assumed that the lizards were collected randomly, thereby making the sample representative of the population as a whole. Most of the males sampled were used only for the collection of morphological data and were released immediately following measurement; all females were retained for subsequent analysis. The retained lizards were transported to a nearby field station and housed in a 7.5 × 1.8 × 1.0 (length × width × height) m<sup>3</sup> enclosure on the ground. The bottom of the enclosure was covered with grass, branches and stones to simulate the lizards' natural habitat. Food (insects and spiders) and water in small dishes were provided ad libitum. A humid environment was maintained by spraying the substrate with water daily. The lizards were marked by toe clipping and back-painting.

**Morphometry.**- For each lizard collected, the following five variables were measured with digital calipers to the nearest 0.01 mm: snout-vent length (SVL; from the tip

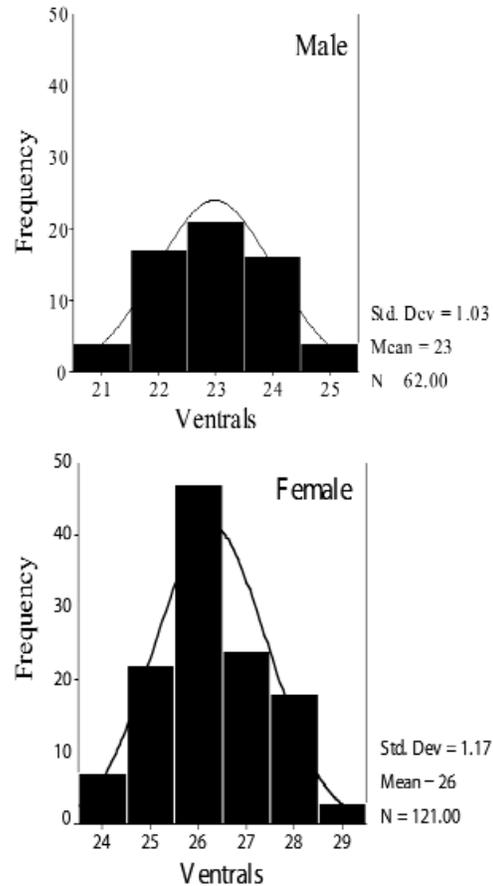


Figure 2. Frequency distribution of rows of ventral scales in males and females.

of the snout to the anterior margin of the cloacal lips); head length (HL; from the tip of the snout to the posterior margin of the skull); head width (HW; the largest width of the head); head height (HH; the largest height of the head); tail length (TL; from the anterior margin of the cloacal lips to the tip of the tail; specimens with regenerated tails were excluded); body weight (BW), number of ventral and mid-dorsals scale rows. Femoral pores, venter color and tail base width were used to sex individuals. Specimens with a SVL of 47 mm or more were considered to be sexually mature adults (139 specimens total); specimens with a SVL of 36-47 mm were considered juveniles (30 specimens); specimens with a SVL of less than 36 mm were considered neonates (14 specimens).

**Female reproduction.**- Gravid females were separated from each other in 30 × 25 × 25 (length × width × depth) cm<sup>3</sup> cages in order to accurately associate newborns with their mothers. Enclosures were checked at least once a day for neonates, which were immediately measured and weighed after birth. Postpartum females were individually weighed and measured for SVL. Clutches

Table 1. Descriptive statistics of morphological traits of *Lacerta vivipara* in China. Data are expressed as mean±SE and range (minimum-maximum) and compared using *t*-test (*t*) and ANCOVA (*F*) with SVL as the covariate. Length units are in mm, and mass in grams.

\**p* < 0.05, \*\**p* < 0.01, \*\*\**p* < 0.001

Trait	Neonates				Juveniles				Adults			
	Male (n = 5)	Female (n = 9)	<i>t</i>	<i>F</i>	Male (n = 15)	Female (n = 15)	<i>t</i>	<i>F</i>	Male (n = 42)	Female (n = 97)	<i>t</i>	<i>F</i>
SVL	31.80±1.30	34.56±1.74	-3.073**		42.39±2.27	43.11±2.55	-0.821		51.86±3.13	58.69±5.44	-9.304***	
	31.00–34.12	31.06–36.00			38.01–45.14	38.21–46.08			47.05–59.07	50.03–71.40		
	47.0±3.74	47.5±2.21			65.74±9.34	56.77±8.09			84.71±1.71	79.37±1.25		
TL	43.00–52.19	44.0–51.03	-0.244		43.25–80.14	41.84–66.25	1.59		57.07–96.21	43.76–93.86	2.519**	
	0.78±0.14	0.82±0.09			2.33±0.79	1.87±0.43			3.79±0.57	4.35±0.71		
BW	0.54–0.87	0.66–0.93	-0.601		1.17–3.97	1.00–2.52	1.954		2.65–5.00	2.26–7.36	-3.710***	
	7.80±0.27	7.11±0.22			9.07±1.43	7.90±1.10			10.94±0.65	10.47±0.69		
HL	7.53–8.03	7.11–7.52	5.155***	18.515**	6.03–11.00	6.03–9.50	2.490*	11.380**	10.10–11.69	9.00–11.03	3.791***	140.145***
	5.70±0.44	5.5±0.30			6.81±0.77	6.07±0.64			8.02±0.41	7.67±0.57		
HW	5.53–6.03	5.00–6.00	0.727	0.357	5.50–8.03	5.03–7.02	2.831**	12.134**	7.50–9.50	6.45–9.01	4.037***	48.800***
	4.40±0.42	4.61±0.42			4.81±0.51	4.52±0.39			5.90±0.64	5.66±0.65		
HH	4.14–5.04	4.13–5.03	-0.907	0.13	4.20–6.55	4.12–5.22	1.756	2.932	5.50–7.50	4.50–7.01	1.937	50.035***

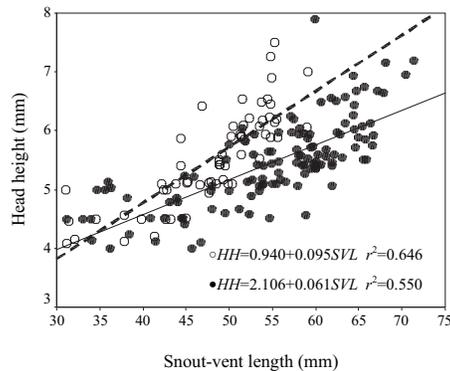
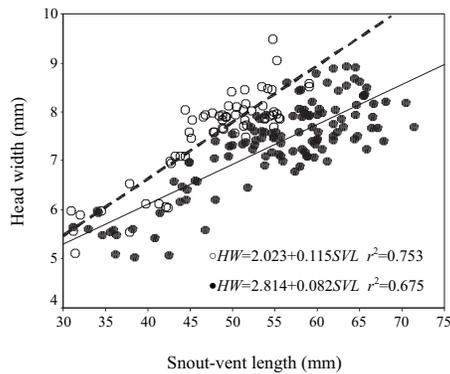
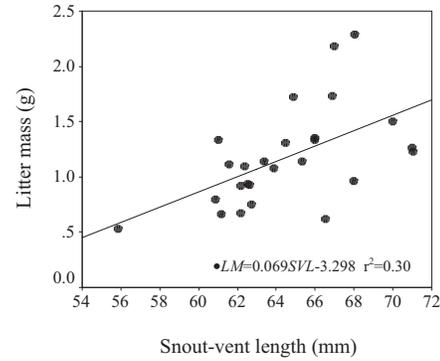
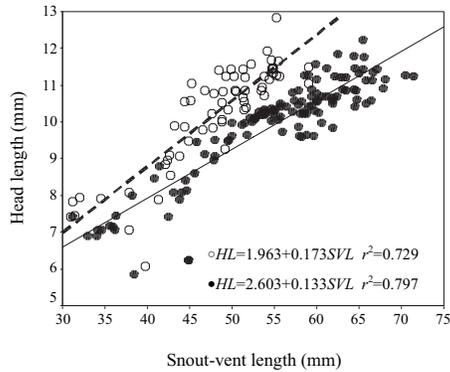


Figure 3. Linear regressions of head length, head width and head height with SVL in *Lacerta vivipara*. The regression equation is indicated in the figure. See text for statistical analyses. Solid dots and lines: females; open dots and dashed lines: males.

Figure 4. Linear regression of litter mass on female SVL in *Lacerta vivipara*. The regression equation is indicated in the figure. See text for statistical analyses.

including dead young, stillborns, or unfertilized eggs were excluded from statistical analyses. Clutch mass (RLM) was calculated by dividing litter mass by post-partum female mass (Shine, 1992). Relative fecundity was calculated by using the residuals derived from the regression of litter size on maternal SVL (Olsson and Shine, 1997).

**Statistical analysis.**- Whenever parametric statistics were applied, a normal distribution was verified using the Kolmogorov-Smirnov test. Homoscedasticity was verified using Levene's Test for Equality of Variances. For significant departures from normality or homoscedasticity, data were log<sub>e</sub>-transformed before analysis. To test for sexual dimorphism in the data, absolute values of morphometric measurements were compared between sexes using a linear regression analysis, one-way analysis of variance (ANOVA) and one-way analysis of covariance (ANCOVA) with SVL as the covariate.

All statistical analyses were performed using SPSS (Statistical Package for the Social Science) v11.5 for Windows. Homogeneity of slopes was checked prior to testing for differences between adjusted means. Values are presented as mean ± standard error and the significance level in set at  $p \leq 0.05$  for all statistical tests.

Table 2. Slope (b), intercept (a) and adjusted R square (r<sup>2</sup>) estimated from reduced major axis regressions for each trait against SVL in female neonates, juveniles, and adults.

Y	Neonates			Juveniles			Adults		
	a	b	r <sup>2</sup>	a	b	r <sup>2</sup>	a	b	r <sup>2</sup>
Head length	8.617	-0.044	0.118	4.316	0.083	0.037	4.939	0.094	0.555
Head width	7.378	-0.053	0.093	-0.968	0.163	0.42	4.653	0.051	0.241
Head height	1.837	0.08	0.112	3.939	0.014	0.008	1.117	0.077	0.407

Table 3. Descriptive statistics of female reproductive traits and snout-vent length of *Lacerta vivipara* (n = 26).

	Mean	Standard error	Range
Female snout-vent length (mm)	64.52	3.52	55.85–71.04
Postpartum body mass (g)	4.82	0.71	3.63–6.03
Litter size	7.11	2.47	3–12
Litter mass (g)	1.18	0.44	0.53–2.29
Neonate mass (g)	0.17	0.03	0.11–0.24
Relative litter mass	0.25	0.1	0.09–0.32

## Results

**Sexual dimorphism.-** In males, the base of the tail bulged because of the presence of the hemipenes and the venter of the tail was salmon pink. In females, the base of the tail was slender and the venter had a saffron-yellow to off-white tint (Fig. 1). Femoral pores (8–12) were small and black in females and neonates while it was accompanied by a thorn in adult male. There were more vertical scale rows in females (24–29) than in males (21–25) (Mann-Whitney Test,  $Z = -10.377$ ,  $p < 0.01$ ; Fig. 2), and males had more mid-dorsal scales ( $31.63 \pm 1.46$ ) than females ( $30.61 \pm 1.48$ ) (Mann-Whitney Test,  $Z = -3.514$ ,  $p < 0.01$ ).

The largest male and female were 59.07 and 71.40 mm SVL, respectively. The mean SVL was larger in adult females ( $58.69 \pm 5.44$  mm) than in adult males ( $51.86 \pm 3.13$  mm) ( $t = -9.304$ ,  $p < 0.001$ ). Body weight was greater in adult females ( $t = -3.710$ ,  $p < 0.001$ ) and tail length was larger in adult males ( $t = 2.519$ ,  $p < 0.01$ ). An ANCOVA test controlling for SVL found that adult males had a larger head size (head length, head width and head height) compared to adult females of the same SVL (ANCOVA; HL,  $F = 140.145$ ,  $p < 0.001$ ; HW,  $F = 48.800$ ,  $p < 0.001$ ; HH,  $F = 50.035$ ,  $p < 0.001$ ). Head length and head width were larger in juvenile males than in juvenile females (ANCOVA; HL,  $F = 11.380$ ,  $p < 0.01$ ; HW,  $F = 12.134$ ,  $p < 0.01$ ) and head length was larger in neonate males than in neonate females (ANCOVA; HL,  $F = 18.515$ ,  $p < 0.01$ ). Body length was larger in neonate females than in neonate males ( $t = -3.073$ ,  $p < 0.01$ ) (Table 1).

The rates at which head length, head width, and head height increased with increasing SVL were all greater in males than in females (Fig. 3). Although the rates of increase were the same in adult males as they were for juvenile and neonate males (ANCOVA; HL,  $F = 2.972$ ,  $p = 0.059 > 0.05$ ; HW,  $F = 0.476$ ,  $p = 0.624 > 0.05$ ; HH,  $F = 5.091$ ,  $p = 0.09 > 0.05$ ), this

was not the case for females (ANCOVA; HL,  $F = 8.175$ ,  $p < 0.001$ ; HW,  $F = 5.586$ ,  $p = 0.005 < 0.01$ ; HH,  $F = 6.143$ ,  $p = 0.03 < 0.05$ ). In female neonates, head length and width did not increase proportionally to SVL ( $b < 0$ ) and rate of head width was greater in female juveniles than in female adults ( $b = 0.163$  vs.  $b = 0.051$ ) (Table 2).

**Female reproductive traits.-** Female *Lacerta vivipara* produced a single clutch of 3–12 young every breeding season (Table 3). Clutch mass was positively correlated with maternal SVL ( $r = 0.55$ ,  $F = 5.43$ ,  $p < 0.01$ ; Fig. 4), whereas clutch size ( $r = 0.38$ ,  $F = 3.75$ ,  $p = 0.06$ ) and neonate mass ( $r = 0.37$ ,  $F = 3.38$ ,  $p = 0.06$ ) were not. Neonate mass was independent of relative fecundity ( $r = 0.15$ ,  $F = 0.56$ ,  $p = 0.46$ ).

## Discussion

Consistent with previous studies of European populations of *Lacerta vivipara* (Gvoždík and Damme, 2003; Kratochvil et al., 2003; Šmajda and Majláth, 1999; Wermuth, 1955), the present study found that sexual dimorphism in head size, abdomen length, and tail length was widespread in Chinese populations, suggesting that these sexually dimorphic traits evolved a very long time ago and has remained in the species as it dispersed across Asia. *Lacerta vivipara* is similar to other lizards (e.g., *Plestiodon laticeps*, *Plestiodon elegans*, *Phrynocephalus vlangalii*, *Takydromus septentrionalis*, *Tropidurus torquatus*) (Du and Ji, 2001; Vitt and Cooper, 1985; Zhang and Ji, 2000; Zhang et al., 2005) in that the males have a larger head and longer tail while females have a longer snout-vent length, increased body weight a longer abdomen, and more rows of ventral scales.

Sexual differences in head size are common within the Lacertidae (Huang, 1998; Molina-Borja et al., 1998). Since long periods of evolutionary time are often required to manifest these differences (Kratochvil et al., 2003), proximate environmental factors can be less important determinants of sexual dimorphism in head size than ultimate ones, such as phylogenetic history. Sexual dimorphism may simply be the result of phylogenetic history and is maintained through competition over mates (intra- and inter-sexual selection) (Kratochvil et al., 2003; Shine, 1989).

According to most speculation, variations in allometry in *Lacerta vivipara* are adaptive responses related to differences in both the ecology and reproductive behavior of the two sexes (Kratochvil et al., 2003). Although it has been reported that a larger head is a male adaptation to feeding on larger prey (Schoener et al., 1982), there is little intersexual dietary divergence in *L. vivipara*.

ra (Zhao et al., 2006). In contrast, the present study supports the conclusion that larger male heads are an adaptation for intersexual combat (Gvoždík and Damme, 2003). There is also evidence to support the possibility that a longer male tail provides armament in combat and improves the male's ability to escape (Barbadillo and Bauwens, 1997; Barbadillo et al., 1995; Braña, 1996; Herrel et al., 2001). Color dimorphism is hormonal in origin, becoming noticeable at the onset of sexual maturity; this dimorphism apparently aids in sexual identification and maintaining social hierarchy (Adriana, 2005).

Females have a considerably larger number of transverse rows of scales covering the venter of the abdomen and have a relatively large abdomen compared to males of the same size. The present data showed that maternal size is the main determinant of reproductive output in *Lacerta vivipara*, with larger females producing heavier clutches. This offers strong evidence to support the hypothesis that selection for higher fecundity results in the evolution of a longer trunk.

In other species of lizards such as *Takydromus septentrionalis*, *Podarcis muralis*, *Gekko japonicus*, *Plestiodon chinensis* and *Sphenomorphus indicus*, sexual dimorphism in head size occurs at earlier ontogenetic stages (Zhang et al., 2005). Our results reveal a similar pattern in *Lacerta vivipara*, in that changes in allometry vary at different ontogenetic stages between the sexes, resulting in a distinct dimorphism. The neonates have larger heads to obtain more foods to increase the trunk, so that the sex individuals have no significant difference in the size. With the growth of the body, the rate growth of the head slows in female and head length and head width is decreased, and quickly increased in juveniles till the adults. Adult females of *L. vivipara* sacrifice head and tail growth for increased abdomen (and body cavity) length in order to achieve a greater reproductive output. In conclusion, *Lacerta vivipara* exhibits a sexual dimorphism in size, color, and shape that can be linked to sexual selection. In females, characteristics allowing for higher reproductive output are selected for in females, resulting in larger bodies and energy allocation directed to early reproduction instead of growth. In males, characteristics selecting for increased numbers of copulations are selected for.

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