



# Life-history variation among three populations of the toad-headed lizard *Phrynocephalus vlangalii* along an elevation gradient on the northeastern Tibetan Plateau

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Elevation and related environmental factors is a main factor for life-history variation in ectothermic species. To test if altitude can explain variation in life-history traits in the toad-headed lizard *Phrynocephalus vlangalii*, we sampled gravid females from three localities (Delingha: elevation 2910m, Daotanghe: 3367m; Maduo: 4257m) and measured parturition time, snout-vent length (SVL) at sexual maturity, female body size and postpartum body condition, litter size, litter mass, relative litter mass (RLM), size and mass of newborn offspring. Females gave birth between 25 July and 28 August, and females from lower elevations were earlier than those from higher elevations. Female SVL at sexual maturity and mean SVL, litter size, litter mass, relative litter mass and offspring size varied among populations, whereas female post-parturition body mass and offspring mass remained invariant. Females from the highest elevation had a greater SVL at sexual maturity, mean SVL and abdominal length. Both litter size and litter mass were positively correlated with female SVL. Females from the higher elevation localities (Maduo and Daotanghe) had a lower RLM than those from the lowest elevation (Delingha). Furthermore, females from the highest elevation produced fewer and larger (SVL but not mass) offspring than those from the other localities. Trade-offs between offspring size and number were detected in Delingha and Daotanghe, respectively, but not in Maduo. At a given level of litter size, offspring size was similar between Delingha and Daotanghe.

*Key words:* Agamidae, life-history traits, litter size, maturity, offspring size, *Phrynocephalus vlangalii*, trade-off

## INTRODUCTION

Life-history traits such as body size at sexual maturity, reproductive investment, litter size and offspring size can be regarded as investments into future growth, reproduction and survival, which are central aspects of animal ecology. For example, rates of reproductive investment are expected to trade-off with future survival and reproduction, thus having a large contribution to the viability of populations in the face of pressures such as predation and interspecific competition (Roff, 2002). Additionally, offspring size is assumed to be a fitness-related trait, because maternal investment per offspring not only affects offspring size per se, but also other size-related traits such as embryonic development, juvenile physiology and performance (Ferguson & Fox, 1984; Sinervo, 1990; Roff, 1993; Enum & Fleming, 2000).

A main aim of life-history studies is to document patterns of variation in life-history traits and to explain the forces behind them (Zamora-Abrego et al., 2007). Early life-history studies mainly focused on interspecific variation (Dunham et al., 1988; Bauwens & Diaz-Uriarte, 1997; Zamora-Abrego et al., 2007), before intraspecific

variation of life-history traits within one species garnered more attention (Adolph & Porter, 1993; Tinkle et al., 1993; Du et al., 2005; Ji & Wang, 2005; Qualla et al., 2009; Zuffi et al., 2009; Wang et al., 2011). Variation in life-history traits may arise from inherent restrictions (such as allometric, design and phylogenetic effects) and phenotypic plasticity induced by environmental factors (Stearns, 1992; Jordan & Snell, 2002). Both genetic and environmental sources were identified as important determinants of intraspecific life-history variation (Bernardo, 1994; Niewiarowski, 1995), with altitude (Rohr, 1997), latitude (Wilson & Cooke, 2004; Du et al., 2005), food availability (Dunham, 1978; Bonnet et al., 2003) and thermal regimes (Beaupre, 1995; Zuffi et al., 2009) being most important for the latter. However, our knowledge about causal mechanisms of life-history variation is still limited (Forsman & Shine, 1995; Wapstra & Swain, 2001).

Being ectothermic species, lizard life-history traits are highly dependent on habitat conditions, and elevation and related environmental factors contribute largely to intraspecific geographical variation (Adolph & Porter, 1993; Rohr, 1997; Jin & Liu, 2007). Although data on

**Table 1.** Female life-history traits of *Phrynocephalus vlangalii* from the three populations. Data are expressed as mean±SE, number and range. Comparisons among populations are performed by using one-way ANOVA (for SVL and RLM) or one-way ANCOVA (for other variables, with maternal SVL as the covariate). Means corresponding to population abbreviations with different superscripts differ significantly (Tukey's test,  $\alpha=0.05$ , a>b>c show a size gradient).

Variable	Populations			Statistical analyses	Multiple comparisons
	DLH	DTH	MD		
Maternal SVL (mm)	55.74±0.49,67 43.70–63.71	57.01±0.43,52 50.30–66.42	58.41±0.39,66 50.1–65.45	$F_{2,182}=9.69$ , $p<0.001$	DLH <sup>b</sup> , DTH <sup>a</sup> , MD <sup>a</sup>
Maternal TL (mm)	52.43±0.41,67 43.2–62.3	45.96±0.33,52 38.6–54.32	52.55±0.41,66 43.00–63.65	$F_{2,181}=136.46$ , $p<0.001$	DLH <sup>a</sup> , DTH <sup>c</sup> , MD <sup>b</sup>
Abdominal length (mm)	29.68±0.45,57 21.71–35.86	29.74±0.34,52 24.10–33.50	32.21±0.32,66 25.60–37.50	$F_{2,171}=9.37$ , $p<0.001$	DLH <sup>b</sup> , DTH <sup>b</sup> , MD <sup>a</sup>
Maternal ante-partum mass (g)	9.53±0.25,67 5.17–13.91	8.90±0.22,50 6.34–13.61	9.52±0.24,65 5.21–15.85	$F_{2,178}=17.76$ , $p<0.001$	DLH <sup>a</sup> , DTH <sup>b</sup> , MD <sup>b</sup>
Maternal Post-partum mass (g)	6.13±0.16,67 2.94–8.48	6.19±0.16,50 4.60–9.53	6.58±0.17,65 3.75–11.29	$F_{2,178}=0.94$ , $p=0.39$	DLH <sup>a</sup> , DTH <sup>a</sup> , MD <sup>a</sup>
Litter size	3.97±0.13,67 2–6	2.74±0.10,51 2–5	3.15±0.11,66 1–5	$F_{2,180}=71.05$ , $p<0.001$	DLH <sup>a</sup> , DTH <sup>b</sup> , MD <sup>b</sup>
Litter mass(g)	2.81±0.10,67 1.18–4.79	2.05±0.76,50 1.33–3.58	2.40±0.09,65 0.59–4.05	$F_{2,178}=58.9$ , $p<0.001$	DLH <sup>a</sup> , DTH <sup>b</sup> , MD <sup>b</sup>
Offspring SVL (mm)	24.48±0.07,67 20.70–27.30	24.83±0.11,50 19.80–27.65	25.87±0.08,65 22.23–29.00	$F_{2,178}=20.49$ , $p<0.01$	DLH <sup>b</sup> , DTH <sup>b</sup> , MD <sup>a</sup>
Offspring Mass (g)	0.71±0.01,67 0.40–0.93	0.75±0.01,50 0.37–1.04	0.76±0.01,65 0.45–1.0	$F_{2,178}=2.17$ , $p=0.12$	DLH <sup>a</sup> , DTH <sup>a</sup> , MD <sup>a</sup>
RLM (g)	0.46±0.013,67 0.27–0.73	0.33±0.009,50 0.18–0.48	0.36±0.013,65 0.10–0.69	$F_{2,179}=30.16$ , $p<0.001$	DLH <sup>a</sup> , DTH <sup>b</sup> , MD <sup>b</sup>

intraspecific geographical variation in life-history traits are available elsewhere, there are few detailed studies on reptiles on the Tibetan plateau (Zhang et al., 2005; Jin & Liu, 2007). *Phrynocephalus vlangalii* is a small Chinese toad-headed viviparous sand lizard which shows a broad altitudinal distribution range (2700 to 4600m, Jin & Liu, 2007). Females from higher elevations were previously shown to produce fewer and larger offspring with lower amounts of reproductive investment than those from low elevations (Jin & Liu, 2007). To strengthen our understanding on variation in life-history traits, we compare an extended set of life-history traits from three different elevations.

## MATERIALS AND METHODS

### Sampling sites

We collected adult *P. vlangalii* from three localities (Delingha, DLH: 2910 m, 37°07'43"N and 97°24'54"E; Daotanghe, DTH: 3367 m, 36°18'41"N and 101°02'05"E; Madoo, MD: 4257 m, 34°44'54"N and 98°07'27"E) in Qinghai Province, northeast Qinghai-Tibetan Plateau of China, during their breeding season (June–August) in three consecutive years (2010–2012). Microhabitats for *P. vlangalii* were similar across the three localities, comprising scrub and desert terrain. Temperature data from China's meteorological data sharing service show decreasing temperature with increasing elevation.

### Lizards sampling and housing

We obtained a maximum of 25 gravid *P. vlangalii* females from each locality every year (DLH:  $n=22/25/20$  for 2010/2011/2012; DTH:  $n=18/19/15$ ; MD:  $n=19/23/24$ ). Gravid females from each locality were obtained approximately one week before the onset of reproduction. All lizards were caught by hand, and then brought to Lanzhou University, Gansu (northwestern China). Females and males from each locality were housed in 70cm × 50cm × 40cm indoor terraria (maximally eight females/terrarium). Each terrarium contained a water dish, a food dish, rocks and 10 cm sand. Supplementary heating was provided by a 60W light bulb suspended 100 mm above the sand, between 0800 and 1800 hours. Lizards were fed with *Tenebrio molitor* larvae, and water containing vitamins and minerals. The terraria were checked at least three times per day to record offspring born. Newborn specimens were fed with small mealworms.

### Data collection

Lizards were weighed ( $\pm 0.01$ g), measured ( $\pm 0.01$ mm) and marked individually by toe-clipping. Females were weighed every day at noon to record the antepartum body mass. We also recorded snout-vent length (SVL), tail length (TL), and body mass of both postpartum females and their offspring, as well as litter size. Reproductive investment (relative litter mass, RLM) was calculated as litter mass divided by the female postpartum mass

(Shine, 1980). We also recorded mean offspring SVL (MOSVL) and mean offspring mass (MOM) for each litter. Female body condition was estimated as the residual of the female post-partum mass regressed against SVL (following Van Damme et al., 1992). Offspring body condition was estimated as the residual of the mean offspring mass regressed against mean offspring SVL. Relative fecundity was calculated by using the residuals derived from the regression of litter size on female SVL (Olsson & Shine, 1997; Ji & Wang, 2005; Zhang et al., 2005).

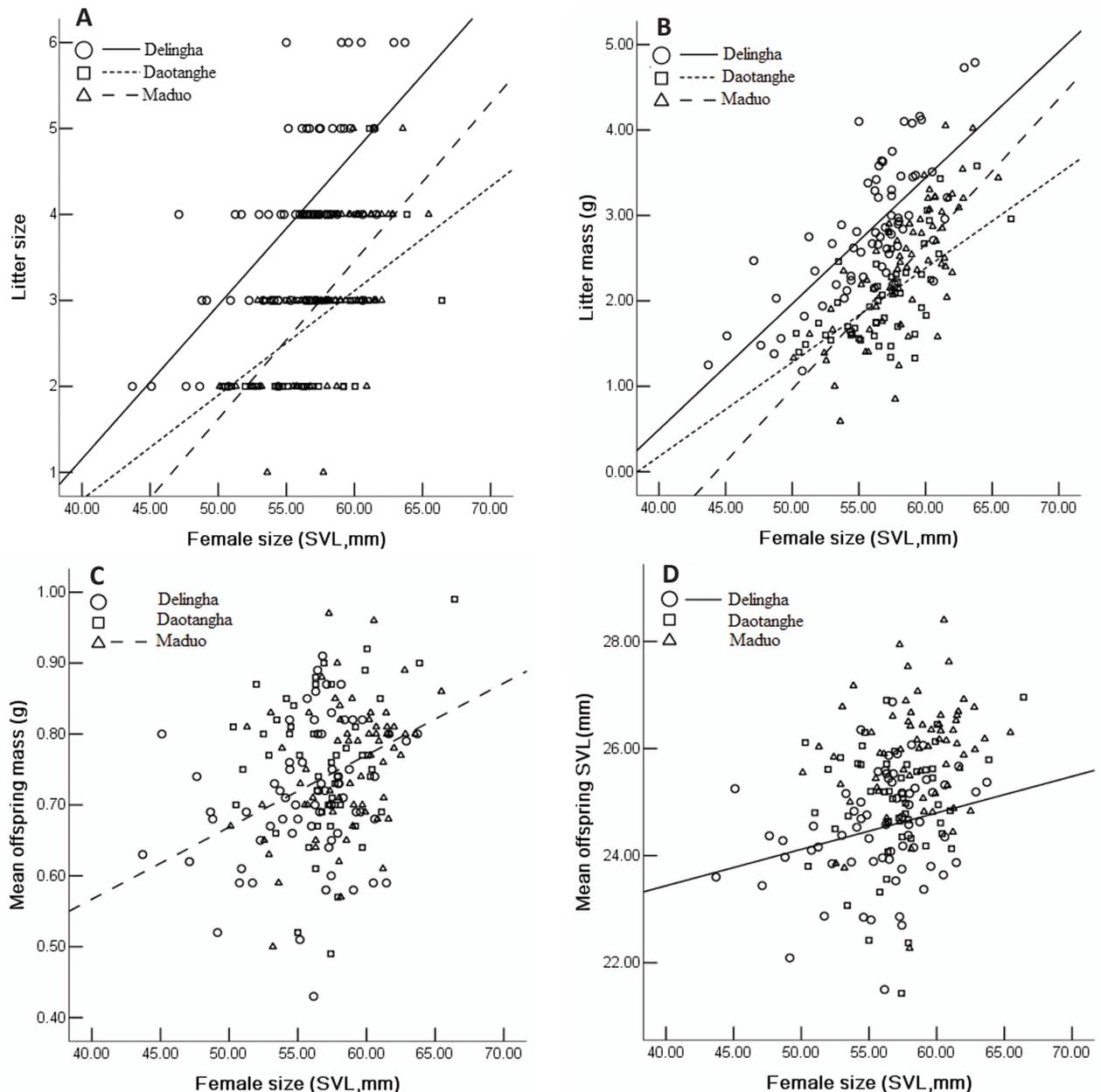
All data were tested for normality (Shapiro-Wilk  $W$ -test) and homogeneity of variances (Bartlett's  $F$ -test) using SPSS v.13.0. Some data were transformed to achieve parametric test conditions. Life-history traits did not significantly vary between years (detailed data not shown), and data between years were pooled. We employed linear regressions to quantify the correlation between each trait, elevation and female SVL. We

quantified the divergence among the populations via the reproductive characters of females by conducting analyses of variance (ANOVA). We used analysis of covariance (ANCOVA) to correct for female SVL in comparisons among populations when variables were correlated with female SVL. We used partial correlation analysis and Tukey's tests (multiple comparisons) to analyse the corresponding data.

## RESULTS

### Elevational variation of parturition time and female body size

Females gave birth between 25 July and 28 August. Females from Delingha (25 July to 17 August) were approximately one week earlier than those from Daotanghe (1 August to 22 August), and two weeks earlier than those from Maduo (10 August to 28 August).



**Fig. 1.** Relationships between female size and litter size (A), litter mass (B), mean offspring mass (C) and mean offspring SVL (D) in three populations of *Phrynocephalus vlangalii*.

There was a significant difference in pregnant female SVL among populations (ANOVA,  $F_{2,182}=9.69, p<0.001$ ), with females from Delingha being smaller than those from Daotanghe and Maduo (Tukey's test,  $p<0.001$  in both cases) which did not differ from each other (Tukey's test,  $p>0.05$ ). The SVL of the smallest reproductive females from Delingha, Daotanghe and Maduo populations were 43.70, 50.30 and 50.10 mm, respectively (Table 1).

Female abdominal length was positively correlated with SVL ( $r^2=0.44, F_{1,173}=137.27, p<0.0001$ ). There was a significant difference in relative female abdominal length among populations (ANCOVA, female SVL as covariate,  $F_{2,171}=9.37, p<0.001$ ). The slope of female abdominal length-SVL relationship was consistent among populations ( $F_{2,169}=1.80, p=0.17$ ). Females from Maduo had a relatively larger abdominal length compared to females from Delingha and Daotanghe (Tukey's test, both  $p<0.001$ ), while females from Delingha and Daotanghe did not differ from each other (Tukey's test,  $p>0.05$ , Table 1). Female post-parturition mass was positively correlated with female SVL ( $r^2=0.44, F_{1,180}=142.47, p<0.001$ ). The difference in female post-parturition mass among populations was not significant when female SVL was corrected for (ANCOVA:  $F_{2,178}=0.94, p=0.39$ , Table 1). The slope of the female post-parturition mass versus female SVL did not differ significantly among populations ( $F_{2,176}=1.51, p=0.18$ ).

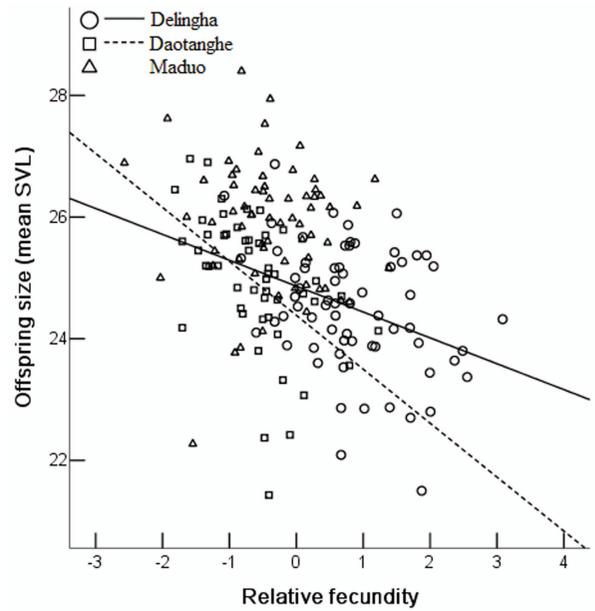
**Elevational variation of litter size and litter mass**

Both litter size and litter mass were positively correlated with female SVL (litter size,  $r^2=0.188, F_{1,182}=42.10, p<0.001$ ; litter mass  $r^2=0.309, F_{1,180}=80.51, p<0.001$ ) (Fig. 1A, B). We used ANCOVA with female SVL as a covariate to study the difference in litter size and litter mass among the three populations. There were significant differences in litter size/SVL and litter mass/SVL relationships among populations (ANCOVA for all, litter size,  $F_{2,180}=71.05, p<0.001$ ; litter mass,  $F_{2,178}=58.9, p<0.001$ ), and the slope of these relationships was consistent (litter size  $F_{2,178}=1.368, p=0.257$ ; litter mass,  $F_{2,176}=2.01, p=0.14$ ). Size-adjusted mean litter size and litter mass was larger for lizards from Delingha than for Daotanghe and Maduo, whereas they were almost the same in the latter two populations (Table 1). Litter size was not correlated to the female postpartum mass when the SVL was controlled using a partial correlation analysis (DLH,  $r=0.016, n=64$ ; DTH,  $r=0.006, n=47$ ; DLH,  $r=0.11, n=62$ ; all,  $p>0.05$ ).

RLM was not significantly correlated with female SVL ( $r^2=0.019, F_{1,180}=3.58, p=0.06$ ). RLM varied significantly among populations of *P. vlangalii* (ANOVA,  $F_{2,178}=30.16, p<0.001$ ). RLM was greater for lizards from Delingha than for those from Daotanghe and Maduo (Tukey's test, both  $p<0.001$ ), whereas RLM in the latter two populations were almost identical (Tukey's test,  $p>0.05$ , Table 1).

**Elevational variation of offspring size and mass**

Mean offspring SVL was positively correlated with female SVL in Delingha ( $r^2=0.07, F_{1,65}=4.90, p=0.03$ ); however, similar significant relationships were not found in the Daotanghe and Maduo (Daotanghe,  $r^2=0.02, F_{1,48}=0.97,$



**Fig. 2.** Trade-off between size-corrected litter size and offspring size (SVL) in populations of *P. vlangalii*.

$p=0.33$ ; Maduo,  $r^2=0.05, F_{1,63}=3.19, p=0.08$ ) (Fig. 1D). Mean offspring mass was positively correlated with the female SVL in Maduo ( $r^2=0.13, F_{1,63}=9.30, p=0.003$ ), but no significant correlation was found in Delingha ( $r^2=0.06, F_{1,65}=3.92, p=0.052$ ) and Daotanghe ( $r^2=0.03, F_{1,48}=1.34, p=0.25$ , Fig. 1C). When pooling the data of all populations, both offspring size and offspring mass are positively associated with female body size (offspring SVL,  $r^2=0.328, F_{1,180}=21.70, p<0.001$ ; offspring mass  $r^2=0.291, F_{1,180}=16.65, p<0.001$ ). Offspring mass was positive correlated with female body condition in each population (DLH,  $r^2=0.147, F_{1,165}=11.24, p=0.001$ ; DTH,  $r^2=0.147, F_{1,48}=8.50, p=0.005$ ; DLH,  $r^2=0.132, F_{1,63}=9.54, p=0.003$ ).

Mean offspring SVL and mean offspring mass varied significantly among populations (ANOVA, MOSVL  $F_{2,179}=28.16, p<0.001$ ; MOM,  $F_{2,179}=4.17, p=0.017$ ). When taking female SVL into account, differences in offspring SVL remained significant (ANCOVA,  $F_{2,178}=20.49, p<0.001$ ), but offspring mass differences disappeared (ANCOVA,  $F_{2,178}=2.17, p=0.12$ , Table 1). The slope of these relationships did not vary among populations (MOSVL,  $F_{2,176}=0.94, p=0.47$ ; MOM,  $F_{2,176}=0.57, p=0.57$ ). Mean offspring SVL was larger for Maduo than for Delingha and Daotanghe (Tukey's test, both  $p<0.001$ ), while mean offspring SVL of the latter two populations did not differ (Tukey's test,  $p>0.05$ ).

Mean offspring mass increased with offspring SVL ( $r^2=0.60, F_{1,180}=274.90, p<0.001$ ). Offspring body condition differed significantly among populations ( $F_{2,178}=19.26, p<0.0001$ , Table 1). Offspring from Maduo had a larger SVL and a lower relative mass than those from Delingha and Daotanghe (Tukey's test, both  $p<0.001$ ).

Offspring SVL decreased with increasing relative fecundity when the data was combined for the three populations ( $r^2=0.134, F_{1,180}=27.85, p<0.001$ ), suggesting a trade-off between egg size and fecundity in *P. vlangalii*. Such a significant relationship was not found when only

considering the Maduo population ( $r^2=0.007$ ,  $F_{1,63}=0.45$ ,  $p=0.51$ , Fig. 2). There were no significant differences in offspring SVL between Delingha and Daotanghe when relative fecundity was kept as constant (ANCOVA,  $F_{1,114}=2.39$ ,  $p=0.125$ ), suggesting no differences in the trade-off between litter size and offspring size for these two populations.

## DISCUSSION

A main result of our study is that female parturition dates are delayed with increasing elevation. The date of emergence from hibernation is earlier at lower elevation, and the time between emergence and ovulation can determine egg-laying or parturition dates (Seigel & Ford, 2001; Ji & Wang, 2005; Lin et al., 2012). A critical temperature is further needed for embryonic development (Medina et al., 2009). At low elevations, lizards may reach the critical temperature earlier than at high elevation, developing faster. In this study, parturition in the Daotanghe population occurred approximately one month after the date reported by Zhang et al., (2005) for the same location. This is likely due to an earlier capture date (early May) followed by a longer maintenance in the laboratory with ample food supply and at temperatures which were higher than in the field.

Mean and minimum female SVL differed among the three populations of *P. vlangalii* and increased with elevation. This is likely due to delayed maturity and thus a larger size at maturity at higher elevation (see also Shine & Charnov, 1992; Adolph & Porter, 1996; Rohr, 1997; Wapstra & Swain, 2001; Ji & Wang, 2005), which is seen as an adaption for cold environments because litter size increases with body size (Shine & Schwarzkopf, 1992; Rohr, 1997; Roff, 2002). We also found a positive relationship between female body size and reproductive investment. In reptiles, physiological factors inhibit reproduction of animals below a certain size and energy is predominantly allocated to growth at small body size (Shine, 1977; Rohr, 1997). Size at maturity is generally a consequence of natural selection (Tinkle, 1969; Tinkle & Ballinger, 1972) or resource allocation towards local environments (Damme et al., 1989; Van Damme et al., 1991; Tinkle et al., 1993).

Variation in the reproductive traits examined across our three localities was in line with Jin & Liu (2007). Low-elevation females produced larger litters with smaller offspring and had a significantly higher relative litter mass (RLM) than females from higher elevations. Litter and offspring size and mass were correlated with female body size both among and within populations. The geographic variation in reproductive output could therefore be caused by the observed geographic variation in maternal body size, as reported in other reptile species (Fitch, 1985; Vitt & Colli, 1994; Du et al., 2005). We however still found significant population differences in most reproductive traits when accounting for maternal size, which might be due to genetic and/or environmental differences (food availability, thermal regimes or predation pressures; Tinkle & Ballinger, 1972; Niewiarowski, 2001; Du et al., 2005; Ji & Wang, 2005).

In intraspecific comparisons of squamate reptiles, differences in reproductive investment are accompanied by significant changes in RLM (Sinervo, 1990; Du et al., 2005; Jin & Liu, 2007). Differences in RLM among the three populations of *P. vlangalii* indicated that reproductive investment might be more constrained at high elevation, as has previously been observed by Jin & Liu (2007). Previous studies on squamate reptiles showed that food availability can result in changes of litter size and RLM (Shine & Schwarzkopf, 1992; Rohr, 1997; Seigel & Ford, 2001). Therefore, small litter size and low RLM for *P. vlangalii* from high elevations might be caused by local resource limitations, in addition to a less favourable thermal environment which constraints intraspecific variation in life-history traits through the relationships between metabolic rate and temperature (Grant & Dunham, 1990; Adolph & Porter, 1993; Rohr, 1997). Lizards from high elevation experience a longer inactive period over winter and presumably have shorter daily and seasonal activity periods than those from low elevations. Since high elevation females tend to have a decreased foraging and digestion time, and may have a limited amount of energy available for reproduction, they would have less total offspring mass and litter size than low altitude females.

Previous studies on reptiles showed that pre-vitellogenic body condition is crucial to initiate vitellogenesis of ovarian follicles, and poor pre-vitellogenic body condition often leads to reduced investment in reproduction (Seigel & Ford, 1991; Ji & Wang, 2005; Ji et al., 2007). Post-partum body condition may be influenced by condition prior to vitellogenesis, maternal reproductive investment, and food availability during vitellogenesis. Hence, post-partum body condition was not a determinant of litter size. In each population, offspring mass was positively correlated with female body condition, but litter size was uncorrelated to female body condition. In other words, females in a better post-partum body condition produced heavier offspring, but did not produce a larger number of offspring relative to their own body size.

We found that offspring from the three populations had almost the same mass but differed in SVL which was larger for the Maduo population. This contradicts the prediction that larger offspring should be produced at higher elevation where offspring growth and/or survival are low (Ferguson et al., 1980; Begon & Parker, 1986; Forsman & Shine, 1995; Rohr, 1997; Wapstra et al., 2001), although similar patterns were already revealed for other species (Ji & Wang, 2005; Lin et al., 2012). Fecundity selection might constrain the efforts of females to increase investment into individual offspring, and a larger SVL might increase survival rates at high elevation. Our data somewhat contradict Jin and Liu's (2007) conclusion that offspring mass increases with altitude. This may be due to their use of scaled embryos that were removed from females for analysis, which might have been at different stages of development.

The trade-off between offspring size and number is assumed to be due to energy and volume constraints (Olsson & Shine, 1997; Doughty & Shine, 1998; Ji & Brana,

2000; Du et al., 2005; Ji & Wang, 2005). We indeed found negative correlations between offspring size and relative fecundity for the Delingha and Daotanghe populations when SVL was held constant, although Zhang et al. (2005) failed to find such a relationship for individuals from the same location which were held in captivity for long periods. However, we failed to find such a relationship for the Maduo population. Individual densities of *P. vlangalii* in Maduo are lower (personal observation), which might result in more resources being available. A relatively large SVL at small RLM might also reduce volume constraints.

To conclude, our study suggests that the observed differences in life-history parameters among populations are due to elevation, although habitat-related correlates cannot be excluded to be responsible for our observations. Future studies should increase the sample size to multiple populations in combination with 'common garden experiments' with standardised environmental conditions.

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