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Geographical variation in reproductive traits and trade-offs between size and number of eggs in the king ratsnake, *Elaphe carinata*

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We collected gravid king ratsnakes (*Elaphe carinata*) from three geographically separated populations in Chenzhou (CZ), Lishui (LS) and Dinghai (DH) of China to study the geographical variation in female reproductive traits and trade-offs between the size and number of eggs. Not all reproductive traits varied among the three populations. Of the traits examined, five (egg-laying date, post-oviposition body mass, clutch size, egg mass and egg width) differed among the three populations. The egg-laying date, ranging from late June to early August, varied among populations in a geographically continuous trend, with females at the most northern latitude (DH) laying eggs latest, and females at the most southern latitude (CZ) laying eggs earliest. Such a trend was less evident or even absent in the other traits that differed among the three populations. CZ and DH females, although separated by a distance of approximately 1100 km as the crow flies, were similar to each other in most traits examined. LS females were distinguished from CZ and DH females by the fact that they laid a greater number of eggs, but these were smaller. The egg size–number trade-off was evident in each of the three populations and, at a given level of relative fecundity, egg mass was significantly greater in the DH population than in the LS population. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **104**, 701–709.

ADDITIONAL KEYWORDS: clutch size – Colubridae – egg-laying date – egg size – egg size–number trade-off – life-history variation – reproductive output.

INTRODUCTION

Reproductive traits, such as seasonal timing of reproduction, frequency of reproduction, fecundity, offspring (egg or neonate) size, and age or size at first reproduction, vary among species, among populations and among individuals of a population (Stearns, 1992; Roff, 2002). Reptiles are of particular interest because most aspects of their reproduction are influenced by environmental factors, such as temperature and food availability (Ballinger, 1983; Angilletta, Steury & Sears, 2004; Niewiarowski, Angilletta & Leache, 2004; Shine, 2005). Reptiles with extensive distributions often display geographical variation in reproductive traits (Iverson *et al*., 1993; Ji & Wang, 2005; Zuffi *et al*., 2009; Tanaka & Mori, 2011; Wang, Xia & Ji, 2011). Such variation is assumed to result from a combined effect of both genetic and environmental factors at the geographical levels, with temporal variation being most likely due to proximate environmental variation. The study of geographical variation in reproductive traits by comparison of two or more conspecific populations can provide a basis for understanding the causes for such variation and the relationships between reproductive traits and environmental variables. Nonetheless, studies on geographical variation in reproductive traits are relatively limited compared with those on within-population variation. In snakes, for example, of some 3000 extant species (Greene, 1997), data gathered from two or more populations have been reported for no more than six colubrid, three elapid and four

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Table 1. A list of snakes for which the data on female reproductive traits are available for two or more populations

Family/species	Reproductive mode	Reference
Colubridae		
Elaphe quadrivirgata	O	Tanaka & Mori (2011)
Imantodes cenchoa	O	Zug, Hedges & Sunkel (1979); Pizzatto *et al*. (2008)
Natrix maura	O	Rugiero *et al*. (2000); Santos & Llorente (2001)
Storeria dekayi	V	Kofron (1979); King (1993)
Thamnophis proximus	V	Tinkle (1957); Clark (1974); Lancaster & Ford (2003)
Thamnophis sirtalis	V	Burt (1928); Dunlap & Lang (1990)
Elapidae		
Cacophis squamulosus	O	Shine (1980)
Drysdalia coronata	V	Shine (1981)
Naja atra	O	Ji & Wang (2005)
Viperidae		
Crotalus viridis oreganos	V	Diller & Wallace (1984, 2002)
Sistrurus catenatus	V	Seigel (1986); Goldberg and Holycross (1999)
Vipera aspis	V	Zuffi *et al*. (2009)
Vipera berus	V	Andrén & Nilson (1983); Madsen & Shine (1994)

O, oviparous; V, viviparous.

viperid snakes (Table 1). Hence, a broader collection of data from different populations across multiple taxonomic groups is necessary to elucidate the general patterns and/or to determine the mechanisms that result in unique patterns (Angilletta *et al*., 2004; Niewiarowski *et al*., 2004; Shine, 2005).

Offspring size and offspring number have received more attention than other reproductive traits primarily because maternal fitness is strongly dependent on these two mutually constrained variables (Stearns, 1992; Bernardo, 1996; Einum & Fleming, 2000; Agrawal, Brodie & Brown, 2001; Roff, 2002). Larger offspring are believed to be better able to survive than smaller offspring because of their better performances (Ferguson & Fox, 1984; McGinley, Temme & Geber, 1987; Sargent, Taylor & Gross, 1987; Mousseau & Fox, 1998; Janzen, Tucker & Paukstis, 2000a, b; but see also Ji *et al*., 2009). However, as the resources available for reproduction are finite, females cannot increase the size of their offspring without a concomitant reduction in the number of offspring produced (Stearns, 1992; Bernardo, 1996; Einum & Fleming, 2000; Agrawal *et al*., 2001; Roff, 2002). Life-history theory predicts that maximization of reproductive success should be achieved in females by producing the greatest number of surviving (not largest) young. A recent study of *Naja atra* (Chinese cobra) provides evidence that the extent to which females enjoy reproductive benefits depends on how well offspring size and number are balanced (Ji *et al*., 2009). However, as in other taxonomic groups, the relationship between offspring size and number is determined by complex interactions between numerous factors in snakes (Rohr, 2001). Our experience with both oviparous and viviparous snakes is that the offspring size–number trade-off is not always evident in natural populations (Ji *et al*., 1997, 2000; Ji, Xu & Du, 2001).

In this study, we compared a number of reproductive traits, including egg-laying date, post-oviposition body condition, clutch size, clutch mass, egg size, egg shape, variability in egg size and variability in clutch size, among king ratsnakes (*Elaphe carinata*) from three geographically separated populations in China. We address four questions: (1) Do particular reproductive traits vary among populations? (2) If so, do the traits that differ among populations vary in a geographically continuous trend? (3) Can the offspring size–number trade-off be detected in natural populations of *E. carinata*? (4) If so, does the level of the offspring size–number trade-off line vary among populations?

MATERIAL AND METHODS

STUDY SPECIES AND POPULATIONS

The king ratsnake (*Elaphe carinata*) is a large-sized [up to 170 cm snout–vent length, SVL] oviparous colubrid snake that can be found in a variety of habitats in the hilly countryside in south-eastern China, including Taiwan, northwards to Henan, Shaanxi and Guansu; it also occurs in northern Vietnam and Japan (Ryukyu Island, including the Senkaku Group) (Huang, 1998). Despite its wide

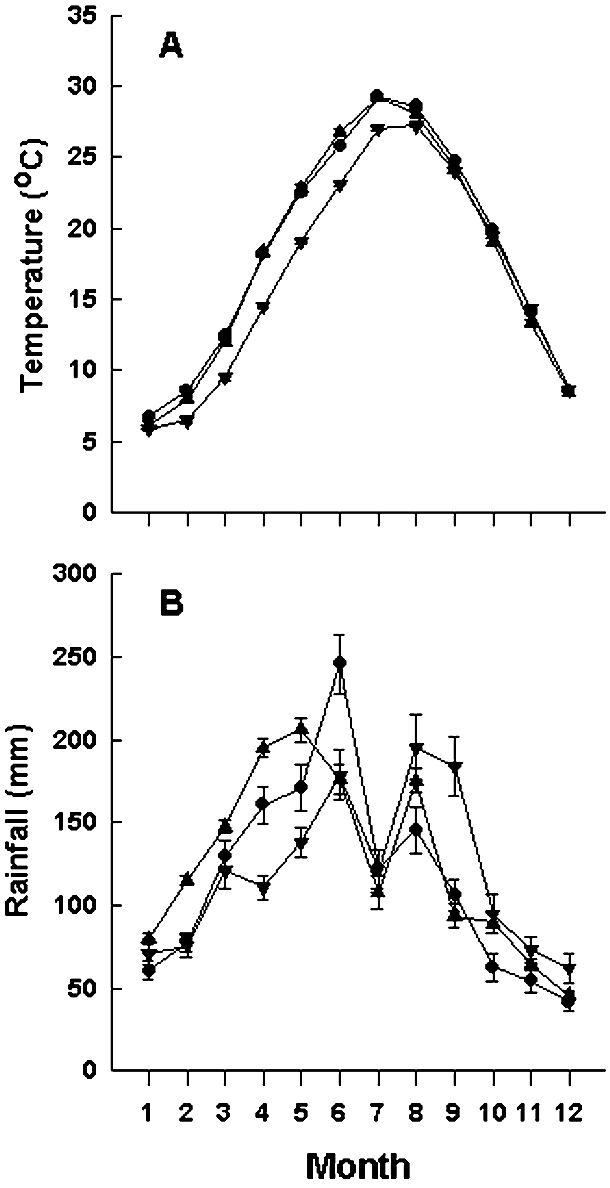

Figure 1. Means (± standard error) for monthly mean air temperature (A) and monthly mean rainfall (B) over the past 40 years (1970–2010) at the three localities (courtesy of the Provincial Bureaux of Meteorology of Zhejiang and Hunan), where females of *Elaphe carinata* were collected: ▲, Chengzhou (CZ); ●, Lishui (LS); ▼, Dinghai (DH).

geographical distribution, data on female reproduction have been collected only in one population in Zhoushan Island, east China (Ji *et al.*, 1997, 2000, 2006; Ji & Du, 2001). The three populations sampled here inhabit climatically distinct localities (Fig. 1) in two provinces (Zhejiang and Hunan) of China. One is in Dinghai (DH, 30°02′N, 122°10′E), Zhoushan Island, eastern Zhejiang. The other two are situated at different coordinates on the mainland: Lishui (LS, 28°46′N, 119°92′E) in central Zhejiang, and Chenzhou (CZ, 25°48′N, 113°02′E) in south-eastern Hunan. The annual mean temperature is highest in CZ (19.0 °C) and lowest in DH (16.6 °C), with LS (18.3 °C) in between (Fig. 1A); the annual rainfall is highest in CZ (~ 1490 mm) and lowest in LS (~ 1380 mm), with DH (~ 1420 mm) in between (Fig. 1B).

ANIMAL COLLECTION AND CARE

We employed local people to collect snakes in mid-June between 2005 and 2010, and transported females with yolking follicles or oviductal eggs to our laboratory at Hangzhou Normal University. We housed one or two females in each $50 \times 45 \times 35$ cm^3 (length × width × height) wire cage, and provided food (commercially sold eggs of *Coturnix coturnix* and *Gallus gallus domesticus*) and water enriched with multivitamins and minerals *ad libitum*. We placed cages in rooms in which the air temperature varied within the range 26–30 °C optimal for embryonic development (Ji & Du, 2001). Eggs were always collected, weighed and measured less than 3 h after laying, thereby avoiding any uncertainty about the initial mass caused by a loss of water (Ji & Du, 2001). Females that had laid eggs were palpated to confirm that all eggs had been laid. SVL, tail length and body mass were taken for each post-oviposition female. Eggs were incubated under multiple thermal regimes, and data will be reported elsewhere.

DATA ANALYSIS

Within-clutch variability in egg size (mass, length and width) was analysed using the coefficient of variation (equal to the standard deviation divided by the mean), as was the within-population variability in clutch and egg size. Relative clutch mass was calculated by dividing the clutch mass by the post-oviposition body mass. Data were tested for normality using the Kolmogorov–Smirnov test, and for homogeneity of variance using Bartlett's test. We used linear regression analysis, one-way analysis of variance (ANOVA), one-way analysis of covariance (ANCOVA), partial correlation analysis and Tukey's test to analyse the corresponding data. The homogeneity of the slopes was checked prior to testing for differences in adjusted means. All statistical analyses were performed with Statistica software (version 6.0 for PC; Tulsa, OK, USA). Throughout this article, values are presented as the mean ± standard error (SE), and the significance level is set at $\alpha = 0.05$.

RESULTS

Females from the three populations did not differ from each other in mean SVL; SVL-adjusted mean post-oviposition mass was greatest in the DH

Table 2. Descriptive statistics of female reproductive traits for three populations of *Elaphe carinata*. Values are expressed as mean ± standard error (range). F values of one-way analyses of variance (ANOVAs) [for snout–vent length (SVL), egg mass and coefficients of variation (CVs) of egg mass, egg length and egg width] and one-way analyses of covariance (ANCOVAs) (for post-oviposition mass, clutch size and clutch mass with SVL as the covariate, for egg length and egg width with egg mass as the covariate, and for relative clutch mass with post-oviposition mass as the covariate). Mean with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$, a > b)

	Population			
	Chenzhou	Lishui	Dinghai	F values and P levels
N	20	68	40	
SVL (cm)	126.6 ± 2.8	127.7 ± 1.2	130.5 ± 1.4	$F_{2,125} = 1.37$, $P = 0.258$
	95.0–149.5	106.3–150.5	111.8–149.0	
Post-oviposition mass (g)	498.0 ± 23.8	519.1 ± 16.8	595.2 ± 24.4	$F_{2,124} = 3.96$, $P = 0.021$
	304.0–697.0	277.6–894.0	283.6–940.7	CZ^{b}, LS^{ab}, DH^{a}
Clutch size	8.3 ± 0.4	10.0 ± 0.4	9.2 ± 0.5	$F_{2,124} = 4.67$, $P = 0.011$
	5–12	4–18	5–17	CZ^{b}, LS^{a}, DH^{b}
Clutch mass (g)	248.8 ± 15.8	285.3 ± 10.6	297.8 ± 15.0	$F_{2,124} = 1.60$, $P = 0.205$
	134.3–399.7	121.1–502.0	161.1–526.8	
Egg mass (g)	30.6 ± 1.6	29.2 ± 0.6	33.5 ± 1.1	$F_{2,125} = 6.04$, $P < 0.004$
	19.7–53.5	21.4–41.7	16.8–53.6	CZ^{ab}, LS^{b}, DH^{a}
Egg length (mm)	61.1 ± 2.0	58.7 ± 1.1	61.8 ± 1.5	$F_{2,124} = 2.09$, $P = 0.128$
	49.7–91.1	45.5–84.8	43.9–91.1	
Egg width (mm)	27.6 ± 0.5	28.7 ± 0.3	29.7 ± 0.4	$F_{2,124} = 4.29$, $P = 0.016$
	23.5–32.4	24.8–37.1	25.9–36.9	CZ^{b}, LS^{a}, DH^{a}
CV of egg mass	4.6 ± 0.5	6.0 ± 0.3	5.7 ± 0.6	$F_{2,125} = 1.54$, $P = 0.218$
	1.9–9.6	1.9–15.5	1.3–20.2	
CV of egg length	7.4 ± 0.6	7.0 ± 0.3	6.8 ± 0.4	$F_{2,125} = 0.30$, $P = 0.745$
	3.7–14.3	1.3–18.8	2.6–14.2	
CV of egg width	4.2 ± 0.4	3.7 ± 0.2	3.6 ± 0.2	$F_{2,125} = 1.21$, $P = 0.303$
	1.6–7.1	1.0–8.1	0.9–6.9	
Relative clutch mass	0.50 ± 0.02	0.56 ± 0.02	0.51 ± 0.02	$F_{2,125} = 1.71$, $P = 0.185$
	0.35–0.73	0.27–1.01	0.22–0.89	

population and smallest in the CZ population, with the LS population in between (Table 2). The egg-laying date, ranging from late June to early August (Fig. 2), differed among the three populations (one-way ANOVA; $F_{2,125} = 4.88$, $P < 0.01$), with CZ females laying eggs an average of 1.2 days earlier than LS females, and an average of 4.4 days earlier than DH females (Fig. 2).

Clutch size was dependent on female SVL in each of the three populations (linear regression analysis; $P < 0.02$ in all cases), with the proportion of variation in clutch size explained by female SVL ranging from 17.6% (DH) to 39.2% (LS). The mean clutch size varied among the three populations, with LS females laying more eggs than CZ and DH females of the same SVL (Table 2). The coefficient of variation in clutch size ranged from 23.9% (CZ) to 33.5% (DH), with the overall mean for the three population being 29.6%. Holding female SVL constant with a partial correlation analysis, we found that in none of the three populations was the clutch size correlated with the post-oviposition mass ($P > 0.770$ in all cases).

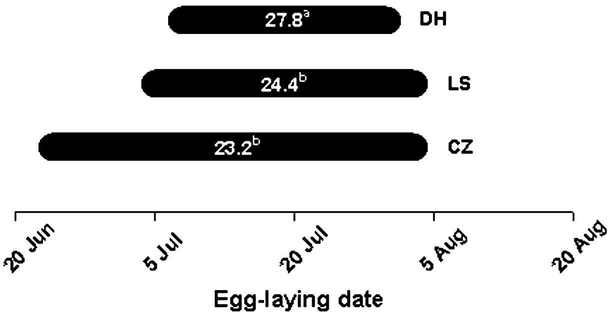

Figure 2. Egg-laying dates of females from three climatically different populations. Numbers on the horizontal bars indicate mean days since 20 June. Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$, a > b). CZ, Chengzhou; DH, Dinghai; LS, Lishui.

The clutch mass was dependent on female SVL in each of the three populations (linear regression analysis; $P < 0.019$ in all cases), with the proportion of variation in clutch mass explained by female SVL ranging from 26.9% (CZ) to 51.6% (LS). The mean clutch mass did not vary among the three populations when accounting for differences in female SVL (Table 2).

In none of the three populations was egg mass dependent on female SVL (linear regression analysis; $P > 0.265$ in all cases). The mean egg mass varied among the three populations, with DH females laying significantly larger eggs than LS females (Table 2). The coefficient of variation in population mean egg mass ranged from 17.7% (LS) to 23.1% (CZ), with the overall mean for the three population being 20.8%. Within-clutch variability in egg size (mass, length and width) did not differ among the three populations (Table 2). Holding female SVL constant with a partial correlation analysis, we found that egg mass was significantly negatively correlated with clutch size in each of the three populations ($P < 0.05$ in all cases). One-way ANCOVA, with relative fecundity as the covariate revealed homogeneous slopes ($F_{2,122} = 0.08$, $P = 0.921$), but different elevations ($F_{2,124} = 8.16$, $P < 0.0005$) of the egg size–number trade-off line, and therefore we adjusted regression lines for the three populations with a common slope (–0.394) to facilitate comparisons (Fig. 3). When setting the relative fecundity at the average level (value = 0), the mean clutch mean egg masses in the CZ, LS and DH populations were 29.9, 28.7 and 32.7 g, respectively.

Eggs laid by LS and DH females were more rounded than those laid by CZ females, primarily because of their comparatively greater width (Table 2). Egg width was (positively) correlated with female SVL in the LS and DH populations, but not in the CZ population; in none of the three populations was there a correlation between egg width and egg length, nor was there a correlation between egg length and female SVL (Table 3).

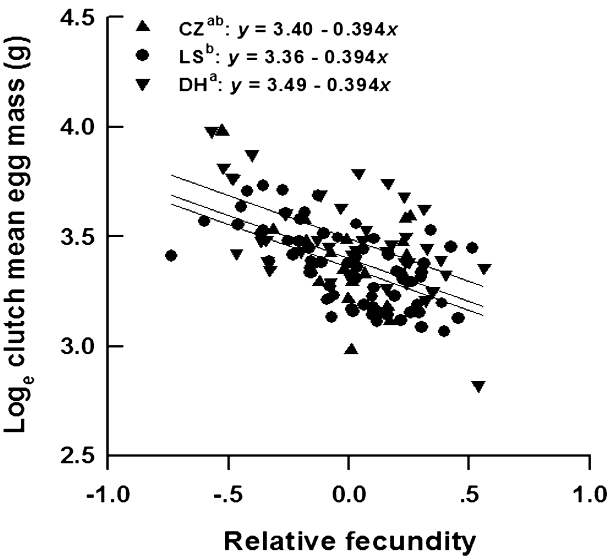

Figure 3. Among-population variation in the egg size–number trade-off. All data were log$_e$ transformed. Regression lines were adjusted for the three populations with a common slope (–0.394) to facilitate comparisons. Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$, a > b). CZ, Chengzhou; DH, Dinghai; LS, Lishui.

DISCUSSION

Not all reproductive traits varied among the three populations. Of the traits examined, the egg-laying date, post-oviposition body mass, clutch size, egg mass and egg width (and hence egg shape) differed among the three populations. The egg-laying date varied among populations in a geographically continuous trend, with females at the most northern latitude (DH) laying eggs latest, and females at the most southern latitude (CZ) laying eggs earliest (Fig. 2). Such a trend was less evident or even absent in the other traits that differed among the three populations. For example, CZ and DH females, although separated geographically by a distance of approximately 1100 km as the crow flies, were similar to each other in clutch size and egg size. LS females were distinguished from CZ and DH females by the fact that they laid a greater number of eggs, but they were smaller (Table 2).

The SVL-adjusted mean clutch size of the LS population outnumbered that of the other two populations by 1.3 eggs. However, whether this difference has any genetic correlation or just reflects the influence of proximate factors remains unknown. It is known that the previtellogenic body condition is crucial to the initiation of vitellogenesis of ovarian follicles, and that a female in a poor previtellogenic body condition

Table 3. Results of partial correlation analyses for the relationships between the selected pairs of female snout–vent length (SVL), egg length and egg width

	df	SVL vs. egg length	SVL vs. egg width	Egg length vs. egg width
Chenzhou	17	$r = -0.02$, $t = 0.09$, $P = 0.930$	$r = 0.05$, $t = 0.22$, $P = 0.830$	$r = 0.18$, $t = 0.78$, $P = 0.445$
Lishui	65	$r = -0.17$, $t = 1.40$, $P = 0.165$	$r = 0.59$, $t = 5.87$, $P < 0.0001$	$r = -0.08$, $t = 0.61$, $P = 0.542$
Dinghai	37	$r = -0.12$, $t = 0.71$, $P = 0.480$	$r = 0.62$, $t = 4.79$, $P < 0.0001$	$r = 0.06$, $t = 0.37$, $P = 0.719$

often tends to reduce the number of offspring produced or even not to reproduce (Ballinger, 1977; Ford & Seigel, 1989; Seigel & Ford, 1991, 1992; Ji & Wang, 2005; Ji *et al*., 2007). Female body condition is dependent on the opportunities for basking and feeding that may vary spatially and temporally, and therefore the pattern of geographical variation in clutch size observed in this study would not remain invariant if the previtellogenic body condition were the exclusive factor for such variation. CZ females differed from DH females in post-oviposition body mass, but not in clutch size, and CZ females differed from LS females in clutch size, but not in post-oviposition body mass (Table 2). These findings suggest that, as in *N. atra* (Ji & Wang, 2005), post-oviposition body condition is not a determinant of clutch size in *E. carinata*. The genetic correlation for geographical variation in particular reproductive traits was detected in a common garden experiment of *N. atra* (Ji & Wang, 2005). Females of *N. atra* collected from the DH and LS populations soon before oviposition differed in egg-laying date, clutch size and clutch mass (Ji & Wang, 2005). Maintaining females of *N. atra* from the two populations in a common garden for 1 year synchronized the egg-laying date that would be otherwise approximately 2 weeks later in the DH population, but still revealed nearly the same differences in clutch size and clutch mass as observed between field-caught females from the two populations (Ji & Wang, 2005).

Consistent with the prediction that clutch size should be more variable than egg size (Smith & Fretwell, 1974), our data showed that clutch size was more variable than egg size within and among populations. Larger females generally devoted more energy to the production of eggs, but in none of the three populations was egg size correlated with female SVL. These findings suggest that, as in other oviparous snakes, such as *Bungarus multicintus, Elaphe taeniura, Ptyas korros* and *Zaocys dhumnades* (Ji *et al*., 2000; Ji, Gao & Han, 2007), egg size is less likely to vary with total reproductive investment or female size in *E. carinata*.

The population mean egg mass did not differ between the most northern (DH) and the most southern (CZ) latitudes (Table 2), nor did the level of the egg size–number trade-off line (Fig. 3). These finding are inconsistent with the prediction from intraspecific comparisons of populations over a wide geographical range that larger offspring should be produced in colder localities (Parker & Begon, 1986; Forsman & Shine, 1995; Mathies & Andrews, 1995; Rohr, 1997; Wapstra & Swain, 2001; Ji *et al*., 2002). Why do females of *E. carinata* from colder localities not lay larger eggs? One plausible explanation is that the efforts of females to increase investment in individual offspring are constrained by fecundity selection, as revealed by the fact that females of *E. carinata* have to trade off egg size against number. Alternatively, it is possible that the size of eggs is likely to be constrained by female size, as revealed by the fact that egg width is positively correlated with female SVL in the two northern populations (Table 3). When egg width is limiting, an increase in egg mass may only be accomplished by means of an increase in egg length (Sinervo & Licht, 1991; Ji *et al*., 2006; Rollinson & Brooks, 2008). Interestingly, in none of the three populations was egg length correlated with female SVL (Table 3). Given the lack of differences in female size and egg length between the CZ and DH populations (Table 2), it is not surprising that the two populations do not differ in mean egg mass. Finally, as egg mass varied over a very wide range in each of the three populations (Table 2), the evolutionary significance of a shift in population mean egg mass, if any, might be less important.

Clutch mass was positively correlated with female SVL in each of the three populations. Thus, as in numerous other snakes, female size is an important determinant of reproductive investment in *E. cainata*. The upper limit of reproductive investment is ultimately determined by the abdominal space available to female snakes to hold eggs (Ji *et al*., 2006, 2009). In this study, females from the three populations did not differ from each other in clutch mass, presumably suggesting that their abdominal spaces were equally filled with clutches. Egg shape is indicative of the crowdedness of eggs in the uterus, and more rounded eggs are always associated with larger or heavier clutches (Castilla, Barbadillo & Bauwens, 1992; Ji & Braña, 2000; Ji & Wang, 2005; Ji *et al*., 2006). More rounded eggs in the LS and DH populations implied that the uteri of the females from these two populations were more tightly packed when they were gravid.

In summary, our data show that females of *E. carinata* from geographically separated populations differ in some reproductive traits, but not in others. Of the five traits that differed among the three populations studied, one (egg-laying date) had a geographically continuous trend. Clutch mass (a measure of total reproductive investment) remained remarkably constant among the three populations studied, but clutch size and egg size did not. The egg size–number trade-off was evident in each of the three populations, supporting the idea that females cannot increase the size of their offspring without a concomitant reduction in the number of offspring produced (Sinervo & Licht, 1991; Bernardo, 1996; Einum & Fleming, 2000; Agrawal *et al*., 2001; Roff, 2002). It is likely that there is selection for more, but smaller eggs in snakes from the LS population. As neither a common garden experiment nor a reciprocal transplant experiment was conducted, we are currently unaware of whether the observed differences have any genetic correlation or just reflect the influence of proximate factors. Further studies of life-history traits of *E. carinata* are necessary to identify the evolutionary and environmental factors that possibly drive the observed variations.

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