

Geographic variation in reproductive traits and trade-offs between size and number of eggs of the Chinese cobra (*Naja atra*)

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We collected gravid Chinese cobras (*Naja atra*) from one island (Dinghai) and three mainland (Yiwu, Lishui and Quanzhou) populations in south-eastern China to study geographical variation in female reproductive traits and the trade-off between the size and number of eggs. We then conducted a common experiment on cobras from two of the four populations to further identify factors contributing to the observed trade-offs. The mean size (snout–vent length) of the smallest five reproductive females increased with increasing latitude. Oviposition occurred between late June and early August, with females from the warmer localities laying eggs earlier than those from the colder localities. Maternal size was a major determinant of the reproductive investment in all populations, with larger females producing not only more but also larger eggs. Clutch size was more variable than egg size within and among populations. The observed geographical variation in clutch size, egg size, clutch mass and post-oviposition body condition was not a simple consequence of variation in maternal size among populations, because interpopulation differences in these traits were still evident when the influence of maternal size was removed. The upper limit to reproductive investment was more likely to be set by the space availability in the island population, but by the resource availability in the three mainland populations. Trade-offs between size and number of eggs were detected in all populations, with females that had larger clutches for their size having smaller eggs. Egg size at any given level of relative fecundity differed among populations, primarily because of interpopulation differences in the resource availability rather than the space availability. Except for the timing date of oviposition and the mean size of the smallest five reproductive females, all other examined traits did not vary in a geographically continuous trend. The common garden experiment, which standardized environmental factors, synchronized the timing date of oviposition, but it did not modify the conclusion drawn from the gravid females collected from the field. The observed geographical variation in the female reproductive traits could be attributed to the consequence of the effects of either proximate or ultimate factors. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, 85, 27–40.

ADDITIONAL KEYWORDS: clutch size – egg size – reproductive investment – size–number trade-off.

INTRODUCTION

The trade-off between size and number of offspring is one of the central themes of life-history research (e.g. Smith & Fretwell, 1974; Roff, 1992; Stearns, 1992; Charnov & Downhower, 1995; Downhower & Charnov,

1998; Sakai & Harada, 2004). Offspring sizes are assumed to be fitness related for many organisms, because larger offspring are believed to have better performance and hence a greater chance of survival than do smaller offspring (Ferguson & Fox, 1984; McGinley, Temme & Geber, 1987; Sargent, Taylor & Gross, 1987; Sinervo & Adolph, 1989; Sinervo, 1990; Reznick, 1991; Roff, 1992; Einum & Fleming, 2000). This assumption implies that a female should, whenever possible, produce large offspring, thereby poten-

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tially increasing their survival probability which, in turn, enhances her reproductive success. However, as total reproductive resources available to any female are finite, she cannot increase the size of individual offspring without a concomitant reduction in the number of offspring produced (Sinervo & Licht, 1991; Bernardo, 1996; Downhower & Charnov, 1998; Einum & Fleming, 1999, 2000; Agrawal, Brodie & Brown, 2001). Thus, a female's choice to produce fewer but larger, or more but smaller, offspring largely reflects a strategy adopted by her to maximize the number of surviving young. It has been suggested that offspring size should be determined through natural selection at an optimal size to forage and avoid predation effectively and that offspring number reflects a result of the division of total reproductive resources into optimally sized offspring (Smith & Fretwell, 1974; Lloyd, 1987). However, increasing evidence indicates that offspring size can be highly variable within a population (e.g. Roff, 1992; Stearns, 1992; Ji *et al.*, 2000; Jordan & Snell, 2002). In reptiles, the balance between size and number of offspring may also shift seasonally (e.g. Ferguson & Snell, 1986; Sinervo & Doughty, 1996; Olsson & Shine, 1997; Ji & Braña, 2000). However, whether or not reproductive investment and, particularly, the size–number trade-off vary among populations remains an unanswered question, although several researchers have addressed this topic (e.g. Forsman & Shine, 1995; Wapstra & Swain, 2001; Ji *et al.*, 2002b).

Reptiles that occupy wide latitudinal or altitudinal ranges often display among-population variation in life-history traits such as body size, body shape, fecundity and offspring size (e.g. Fitch, 1985; Forsman & Shine, 1995; Wapstra & Swain, 2001; Ji *et al.*, 2002b). Such variation reflects partly genetic divergence caused ultimately by natural selection as a consequence of adaptation to different environmental conditions at the evolutionary level, and partly phenotypic plasticity induced proximately by environmental factors such as temperature and prey availability (Ballinger, 1977, 1983; Fitch, 1985; Seigel & Fitch, 1985, 1991; Dunham, Miles & Reznick, 1988; Ford & Seigel, 1989; Stearns, 1989). However, even in species for which a substantial amount of data has been reported, an understanding of the causes for intraspecific phenotypic variation in life-history traits among populations frequently remains elusive. Therefore, independent datasets from different populations and reptilian taxa are necessary to understand both the general patterns of covariation among life-history traits, and the relationships between life-history traits and environmental variables (Forsman & Shine, 1995; Wapstra & Swain, 2001).

In this study, we investigate geographical variation in reproductive traits and trade-offs between size and number of eggs of the Chinese cobra (*Naja atra*). This

large-sized and highly venomous snake is widely distributed in south-eastern China, including Taiwan, Hongkong and Hainan, southward to Vietnam (Wüster, Golay & Warrell, 1997). The cobra is found in a variety of habitats in the hilly countryside, and is locally abundant. In Zhejiang (eastern China), the northern limit of the species' distributional range, the cobra can be very abundant in the southern region (including islands) but absent in the northern parts of the province (Ji & Du, 2001). Given the relatively large range in the climates and degree of seasonality within the cobra's distribution, we hypothesize that geographical variation in life-history traits should exist in this species. To test our hypothesis, we collected gravid cobras from four geographically separated populations in south-eastern China, of which three are in Zhejiang and one in Guangxi (southern China). To test for the effects of proximate factors on reproductive traits, we conducted a common garden experiment by maintaining females from two of the four populations under the same conditions. Specifically, we examine (1) geographical variation in egg size (and hence offspring size, Ji & Du, 2001) and egg number, (2) geographical variation in the trade-off between size and number of eggs, and (3) geographical pattern in female reproductive traits.

MATERIAL AND METHODS

Four localities (populations) were chosen in which to conduct this study. One locality is in Dinghai (DH, 30°02'N, 122°10'E), Zhoushan Islands, eastern Zhejiang, which is approximately 25 km away from the nearest mainland coastline. The other three localities are situated at different latitudes on the mainland: Yiwu (YW, 29°31'N, 120°07'E), central Zhejiang; Lishui (LS, 28°46'N, 119°92'E), southern Zhejiang; Quanzhou (QZ, 25°96'N, 111°05'E), northern Guangxi. Data on monthly mean air temperature and monthly mean rainfall show differences in climate among the four localities (Fig. 1). The annual mean temperatures in Dinghai, Yiwu, Lishui and Quanzhou are approximately 16.5, 16.1, 18.1 and 19.0 °C, respectively. Activity is rare for *N. atra* at air temperatures lower than 15 °C (Ji *et al.*, 2002a), so the period when the species is active should be shorter in the two colder localities (Dinghai and Yiwu) than in the two warmer localities (Lishui and Quanzhou) (Fig. 1).

We employed local people to collect cobras from the field, palpated all collected females to assess their reproductive conditions, and paid particular attention to the smallest single reproductive females of each population. Cobras from the three mainland populations were collected in mid-June 1998, and those from the island population in mid-June 1998 and 1999. Some cobras (including all juveniles) were released to

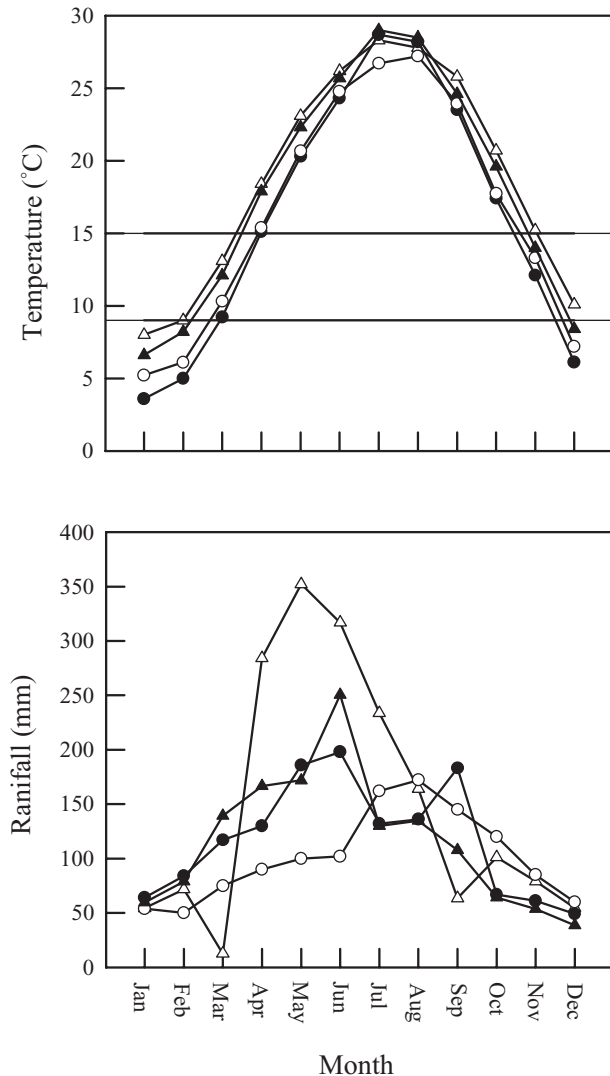


Figure 1. Monthly mean air temperatures and monthly mean rainfall for 1982–2001 at the four localities (courtesy of the Provincial Bureaux of Meteorology of Zhejiang and Guangxi), from which *Naja atra* were collected. Activities are rare for the cobra at air temperatures lower than 15 °C (the upper horizontal line); exposure of the cobra to air temperatures lower than 9 °C (the lower horizontal line) for a prolonged period has a lethal effect (Ji *et al.*, 2002a). Dinghai (●, DH); Yiwu (○, YW); Lishui (▲, LS); Quanzhou (△, QZ).

the sites where they were captured after being measured for snout–vent length (SVL) and tail length; the remaining ones were transported to our laboratory in Hangzhou, where they were individually marked by clipping between one and three ventral scales in a unique combination for future identification, and one or two were then housed in each 500 × 450 × 350 (length × width × height) mm wire cage inside which

there were a water dish and two or three common toads (*Bufo gargarizans*). All females transported to Hangzhou in 1998 and 1999 had already ovulated, and most of them laid eggs 1–4 weeks after being captured. Females occasionally ate when they were gravid, but food taken by gravid females had no direct influence on developing eggs during uterine retention. Moreover, although there is evidence to suggest that the period in captivity will affect egg development during uterine retention, the influence of captivity during the interval after capture but before oviposition on egg size, if any, could be negligible because of the lack of a correlation between days to laying and egg size in each of the four populations (partial correlation analysis holding maternal size constant).

Egg-laying cages were placed in rooms inside which the surrounding temperature varied from 26 to 30 °C. The cages were checked twice daily for eggs and more frequently when there was a sign of oviposition, so that eggs were often collected within a few hours of being laid, thereby minimizing changes in egg mass at oviposition due to loss or gain of water (Ji & Du, 2001). Females that had laid eggs were removed from their cages and palpated to confirm that all eggs had been laid. Snout–vent length, tail length and post-oviposition body mass measurements were taken for each female. Females were later released to the sites where they were collected in accordance with the internationally accepted principles concerning the care and use of laboratory animals (National Research Council, 1985). Eggs were numbered individually with a pencil, measured for length and width to the nearest 0.1 mm with a Mitutoyo digital calliper and weighed to the nearest 1 mg on a Mettler balance. We calculated egg volume (V) using the equation of an ellipsoid:

$$V = (4/3) \pi ab^2$$

where $a = 1/2$ largest diameter and $b = 1/2$ shortest diameter of the egg. All viable eggs were either incubated under multiple thermal and hydric conditions until hatching or dissected for determination of egg composition, and detailed data on the dissected eggs, incubating eggs and hatchlings were reported elsewhere (e.g. Ji & Du, 2001). We analysed within population variances in clutch size and egg size using the coefficient of variation (equal to the standard deviation divided by the mean, Shine & Seigel, 1996). Relative clutch mass (RCM) was calculated by dividing clutch mass by the female post-oviposition mass.

A common experiment, in which females from the Lishui and Zhoushan populations were maintained in the same laboratory enclosure (12 × 7 × 2.5 m; Ji *et al.*, 2002a), was conducted from August 2002 to August 2003. Females used in this experiment were new ones caught specifically from the field. Food [common toads (*Bufo gargarizans*) and Chinese skinks (*Eumeces chin-*

ensis)] and water were provided ad libitum. Of the 66 reproductive females, 15 died during the course of the experiment, and 42 laid eggs in July 2003. Clutches produced by the females in this experiment and the aforementioned females laying eggs in 1998 or 1999 were named as 'laboratory clutches' and 'natural clutches', respectively.

A preliminary analysis showed that females collected from the Dinghai population in 1998 and 1999 did not differ in any reproductive trait, including individual females' choices regarding trade-offs, so we pooled data for both years. All data were tested for normality using the Kolmogorov–Smirnov test, and for homogeneity of variances using Bartlett's test. Log_e and arc-sine transformations were performed for percentage data when necessary to achieve the conditions for using parametric tests. We used linear regression, one- and two-way ANOVA, one- and two-way ANCOVA, partial correlation analysis and Tukey's

test (multiple comparisons) to analyse the corresponding data. Prior to testing for differences in adjusted means, the homogeneity of slopes was checked. A principal component analysis (varimax rotation) was used to investigate the possible existence of reproductive space characteristic of females from different populations. Throughout this paper, values are presented as mean \pm 1 SE, and the significance level is set at $\alpha = 0.05$.

RESULTS

BODY SIZE AND POST-OVIPOSITION BODY CONDITION

We measured a total of 327 reproductive females from the four populations (Fig. 2), and found that mean values of SVL differed among populations (ANOVA, $F_{3,323} = 30.64$, $P < 0.0001$). Females from the three mainland populations did not differ from each other in

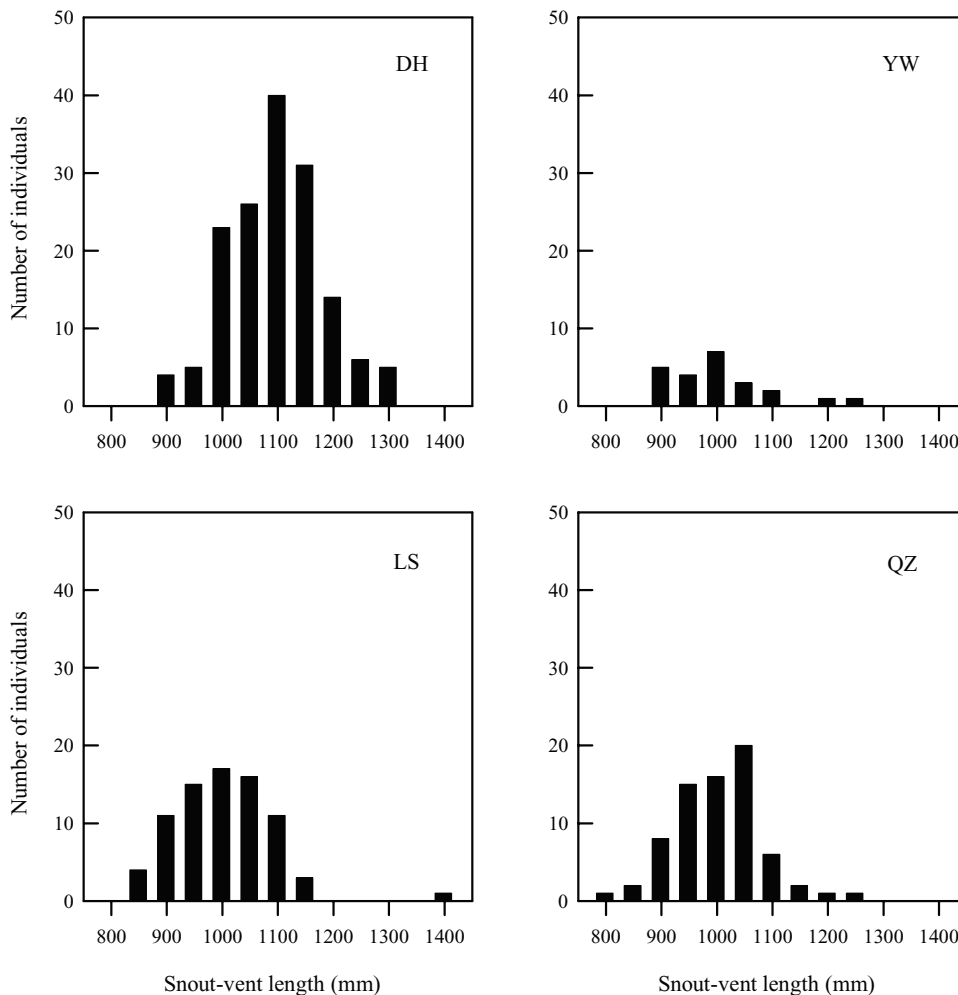


Figure 2. SVL distributions of reproductive females collected in 1998 and 1999 from the four populations (Dinghai, 154; Yiwu, 23; Lishui, 78; Quanzhou, 72).

mean SVL (Tukey's test, $P > 0.98$ in all cases), but they were on average smaller than females from the Dinghai population (Tukey's test, $P < 0.001$ in all cases). The mean SVL of the smallest five cobras from each population differed significantly among populations (ANOVA, $F_{3,16} = 20.48$, $P < 0.0001$), with the smallest females being larger in the Dinghai (coldest) population than in the three mainland populations (Tukey's test, $P < 0.05$ in all cases). The smallest reproductive female (798.0 mm SVL) in our sample was from the Quanzhou population (Table 1). Females from the Lishui population had shorter SVL-adjusted tails than did those from the other three populations (Table 1).

Oviposition occurred between 25 June and 5 August, with females from the Quanzhou population laying eggs approximately one week earlier than did those from the Lishui population, and three weeks earlier than did those from the Yiwu and Dinghai populations. Females from the Dinghai, Lishui and Quanzhou populations did not differ from each other in size-adjusted post-oviposition body mass (indicative of post-oviposition body condition), and on average they had better post-oviposition body conditions than females from the Yiwu population (Table 1).

CLUTCH SIZE AND CLUTCH MASS

The mean clutch size ranged from 10.4 (Yiwu) to 15.5 (Dinghai) eggs, and varied significantly among the four populations (Table 1). Clutch size was positively correlated with maternal SVL in all populations ($P < 0.001$ in all cases), and variances in clutch size explained by the maternal SVL ranged from 33.7% (Dinghai) to 42.5% (Lishui). The overall coefficient of variation of population mean clutch size was 28.4% [ranging from 27.2% (Dinghai) to 30.0% (Lishui)]. The rate (slope) at which clutch size increased with increasing maternal SVL did not differ among the four populations (ANCOVA on \log_e transformed data, $F_{3,144} = 0.51$, $P = 0.676$) (Fig. 3A). Size-adjusted mean clutch size was greater in the Dinghai population than in the three mainland populations, and the latter three populations did not differ from each other in the trait (Table 1). When maternal SVL was set at 1000 mm, the adjusted mean clutch sizes of the Dinghai, Yiwu, Lishui and Quanzhou populations were 13.7, 11.0, 11.4 and 11.3, respectively; clutch size of the Dinghai population overall outnumbered that of the three mainland populations by 2.4 eggs. When maternal SVL was held constant with a partial correlation analysis, clutch size was positively correlated with post-oviposition body condition in the Quanzhou population ($r = 0.23$, $t = 2.15$, d.f. = 51, $P = 0.036$), but such a correlation was not found in the other three populations ($P > 0.177$ in all cases).

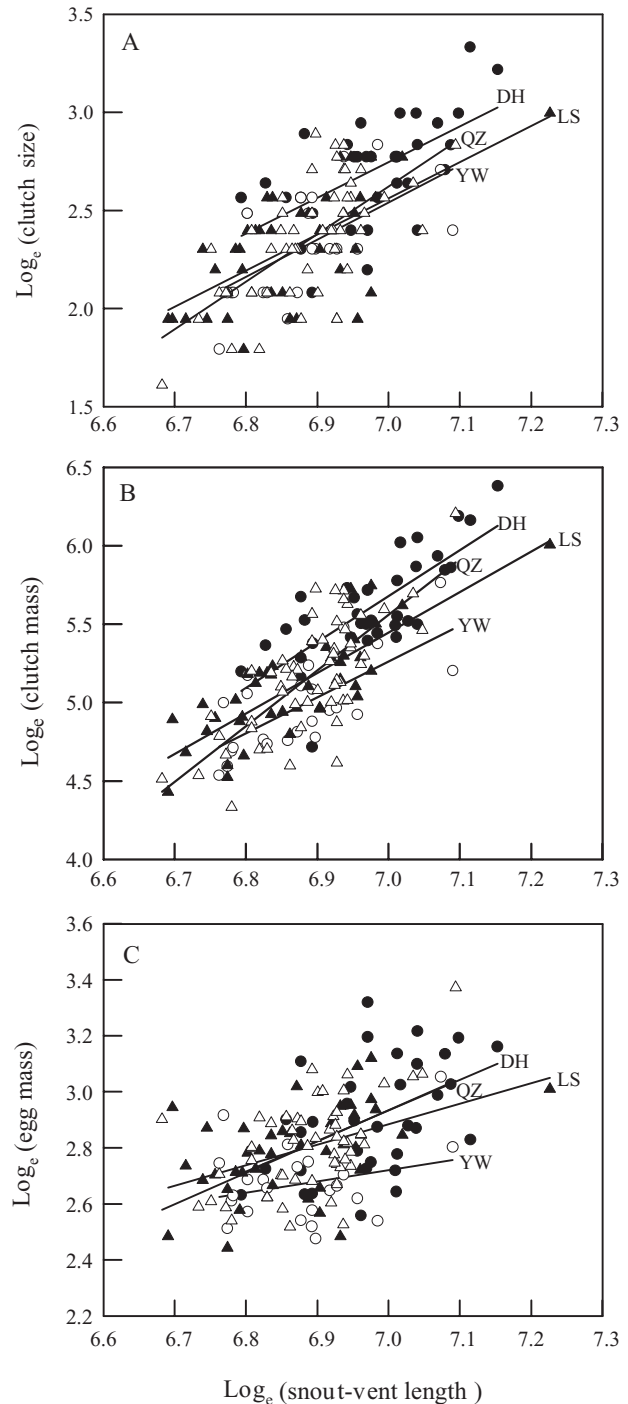


Figure 3. The relationships between clutch size (A), clutch mass (B) and egg mass (C) and maternal SVL of *Naja atra* from the four different populations. See Fig. 1 for key to symbols.

The mean clutch mass ranged from 152.3 (Yiwu) to 288.2 (Dinghai), and varied significantly among the four populations (Table 1). Clutch mass was positively correlated with maternal SVL in all populations

Table 1. Female reproductive traits of *Naja atra* from the four populations. All females had already ovulated when they were collected. Data are expressed as mean \pm 1 SE and range. Comparisons among populations are performed by using one-way ANOVA (for SVL and RCM) 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, $\alpha = 0.05$, $a > b > c$)

Variable	Populations				Statistical analyses			Multiple comparisons
	Dinghai	Yiwu	Lishui	Quanzhou	F-values	P levels		
Snout-vent length (mm)	$N = 34$ 1075.5 \pm 15.8 892.0–1278.0	$N = 23$ 974.5 \pm 19.1 865.0–1200.0	$N = 41$ 965.8 \pm 16.4 805.0–1375.0	$N = 54$ 986.9 \pm 10.4 798.0–1205.0	$F_{3,148} = 10.84$	<0.0001		DH ^a , YW ^b , LS ^b , GQ ^b
	Tail length (mm)	174.6 \pm 3.2 137.0–209.0	165.5 \pm 4.6 122.0–205.0	154.5 \pm 3.0 122.0–205.0				
Post-oviposition body mass (g)	415.4 \pm 24.5 192.0–751.4	236.3 \pm 19.1 126.5–549.8	282.7 \pm 18.6 138.8–810.0	309.9 \pm 11.7 143.8–592.0	$F_{3,147} = 14.15$	<0.0001		DH ^a , YW ^b , LS ^a , GQ ^a
	Clutch size	15.5 \pm 0.7 8–28	10.4 \pm 0.6 6–17	10.6 \pm 0.5 6–20				
Clutch mass (g)	288.2 \pm 17.1 111.7–589.7	152.3 \pm 10.8 93.3–318.0	174.1 \pm 9.9 83.9–405.7	189.1 \pm 10.1 76.1–495.5	$F_{3,147} = 9.74$	<0.0001		DH ^a , YW ^c , LS ^{bc} , GQ ^b
	Egg mass (g)	18.9 \pm 0.7 12.9–27.6	14.6 \pm 0.4 11.9–21.2	16.4 \pm 0.4 11.5–22.7				
Relative clutch mass	0.71 \pm 0.02 0.43–0.94	0.67 \pm 0.03 0.46–1.00	0.63 \pm 0.02 0.40–0.95	0.61 \pm 0.02 0.26–0.96	$F_{3,148} = 3.77$	= 0.012		DH ^a , YW ^{ab} , LS ^{ab} , GQ ^b

($P < 0.0002$ in all cases), and variances in clutch mass explained by the maternal SVL ranged from 49.1% (Yiwu) to 65.9% (Lishui). The rate at which clutch mass increased with increasing maternal SVL did not differ among populations (ANCOVA on \log_e transformed data, $F_{3,144} = 1.60$, $P = 0.193$) (Fig. 3B). When maternal SVL was set at 1000 mm, the adjusted mean clutch masses of the Dinghai, Yiwu, Lishui and Quanzhou populations were 228.8, 162.3, 188.4 and 190.9 g, respectively. Thus, the size-adjusted clutch mass was greatest in the Dinghai population, intermediate in the Lishui and Quanzhou populations, and smallest in the Yiwu population (Table 1).

Because the value of RCM is highly dependent on maternal body mass, ANOVA may have a risk of wrongly estimating the differences in RCM among populations. Thus, the differences in RCM among populations were tested using ANCOVA with clutch mass as the variable and post-oviposition body mass as the covariate. The analysis showed that slopes of the regressions were homogeneous (\log_e transformed data, $F_{3,144} = 0.91$, $P = 0.437$) but elevations varied significantly among populations ($F_{3,147} = 6.14$, $P < 0.001$). Again, RCM was greater in the Dinghai population than in the three mainland populations (Tukey's test, $P < 0.01$ in all cases), whereas the latter three populations did not differ from each other in the trait (Tukey's test, $P > 0.932$ in all cases).

EGG SIZE AND EGG SHAPE

Egg size (mass), presented as the clutch mean of egg mass, was positively correlated with maternal SVL within all populations ($P < 0.05$ in all cases), and maternal SVL explained 12.7% (Yiwu) to 27.7% (Quanzhou) of the variance in egg mass. The overall coefficient of variation of the mean of the population egg mass was 17.2% [ranging from 14.7% (Yiwu) to 20.5% (Dinghai)]. The rate at which egg mass increased with increasing maternal SVL did not differ significantly among the four populations (ANCOVA on \log_e transformed data, $F_{3,144} = 1.16$, $P = 0.327$) (Fig. 3C). When keeping maternal SVL constant at 1000 mm, we found that the adjusted means of egg mass of the Dinghai, Yiwu, Lishui and Quanzhou populations were 17.5, 15.0, 17.0 and 17.1 g, respectively; egg mass of the Yiwu population was overall 2.2 g smaller than that of other three populations.

Egg shape varied significantly among the four populations. Eggs laid by females from the Dinghai population were more rounded than those from the three mainland populations, because of their relatively shorter length but wider width (Table 2). Based on the volume equation for an ellipsoid, egg width contributes more to egg volume than egg length, so mass-specific egg volume was also greater in the Dinghai

Table 2. Length, width, shape (length/width) and volume of *Naja atra* eggs from the four populations. Data are expressed as mean \pm 1 SE and range. Comparisons among populations are performed by using one-way ANCOVA (for egg length, width and volume, with egg mass as the covariate) or one-way ANOVA (for egg shape). Means corresponding to population abbreviations with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$, $a > b$)

Variable	Populations				Statistical analyses		
	Dinghai	Yiwu	Lishui	Quanzhou	F-values	P levels	Multiple comparisons
Egg length (mm)	N = 18 48.4 \pm 1.1 41.7–59.6	N = 21 47.5 \pm 0.9 41.1–60.1	N = 33 49.1 \pm 0.7 41.4–58.8	N = 30 50.0 \pm 0.8 40.6–61.8	$F_{3,97} = 4.95$	<0.003	DH ^b , YW ^a , LS ^a , GQ ^a
Egg width (mm)	26.2 \pm 0.5 22.5–29.6	22.2 \pm 0.4 20.0–27.2	23.2 \pm 0.3 19.7–26.6	24.2 \pm 0.3 20.5–28.3	$F_{3,97} = 7.49$	<0.0001	DH ^a , YW ^b , LS ^b , GQ ^b
Egg width/egg length	0.55 \pm 0.01 0.43–0.63	0.47 \pm 0.01 0.33–0.56	0.48 \pm 0.01 0.36–0.56	0.49 \pm 0.01 0.39–0.65	$F_{3,98} = 7.53$	<0.0001	DH ^a , YW ^b , LS ^b , GQ ^b
Egg volume (mm ³)	17565.7 \pm 835.1 12333.5–23098.0	12322.6 \pm 444.8 9715.3–19190.8	13891.6 \pm 363.4 10412.5–18762.9	15434.9 \pm 541.5 10673.8–14564.0	$F_{3,97} = 4.65$	<0.005	DH ^a , YW ^b , LS ^b , GQ ^b

population (Table 2). Eggs from the three mainland populations did not differ in either length or width when the influence of variation in egg size was removed, and hence these eggs had almost the same shape and mass-specific volume (Table 2).

TRADE-OFF BETWEEN EGG SIZE AND FECUNDITY

To remove the influence of variation in maternal SVL on fecundity, we followed Olsson & Shine (1997) to calculate relative fecundity by using the residuals derived from the regression of $\log_e(\text{clutch size})$ on $\log_e(\text{female SVL})$. Overall, relative fecundity showed a significant negative correlation with egg mass ($r = -0.26$, $F_{1,150} = 10.88$, $P < 0.001$), which indicates that the trade-off between egg size and fecundity is evident in *N. atra*. When data for each population were analysed separately, the trade-off between egg mass and relative fecundity was still evident in each population, but the position of the trade-off line varied significantly among populations (Fig. 4). One-way ANCOVA (with the relative fecundity as the covariate) revealed homogeneous slopes ($F_{3,144} = 1.44$, $P = 0.233$) but different elevations ($F_{3,147} = 9.91$, $P < 0.0001$), so we adjusted regression lines for the four populations with a common slope (-0.267) to facilitate comparisons (Fig. 4). When setting relative fecundity at the average level (value = 0), mean clutch mean egg masses in

the Dinghai, Yiwu, Lishui and Quanzhou were 18.3, 14.6, 16.3 and 16.7 g, respectively.

GEOGRAPHIC PATTERN IN FEMALE REPRODUCTIVE TRAITS

The principal component analysis resolved two components (with eigenvalues > 1) from six size-adjusted female reproductive characteristics, which cumulatively explained 72.9% of variation in the original data (Table 3). The first component (which explained 38.8% of the variance) had high positive loading for size-adjusted egg size (mass and volume), and the second component (which explained 34.1% of the variance) had high positive loading for size-adjusted fecundity and total egg mass. Females from different populations differed in their scores on both the first ($F_{3,96} = 9.34$, $P < 0.0001$; DH^a, YW^b, LS^a, QZ^a, Tukey's test, $a > b$) and the second axes ($F_{3,96} = 4.24$, $P < 0.008$; DH^a, YW^b, LS^{ab}, QZ^{ab}, Tukey's test, $a > b$). A cluster analysis on the first two principal components showed a clear geographical pattern in the female reproductive traits examined. Females from the Lishui and Quanzhou populations were very similar in nearly all traits examined; females from the Dinghai and Yiwu populations differed considerably from each other and from females from the Lishui and Quanzhou populations (Fig. 5).

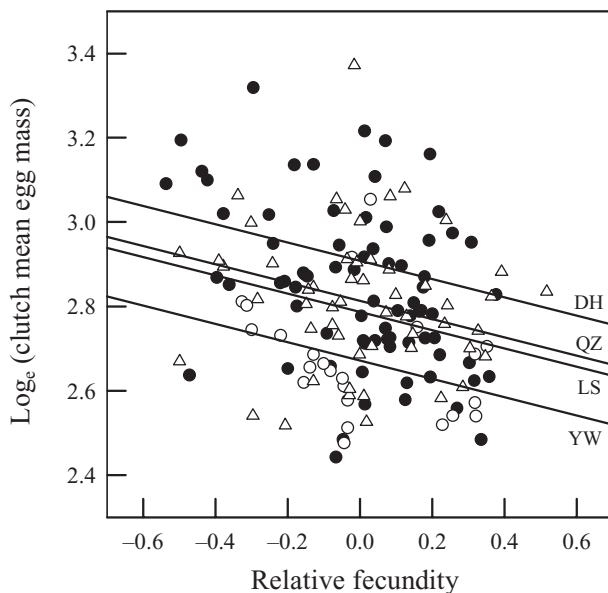


Figure 4. Among-population variation in the trade-off between egg mass (g) and relative fecundity. All data were \log_e transformed. Regression lines were adjusted for the four populations with a common slope (-0.267) to facilitate comparisons. See Fig. 1 for key to symbols.

RESULTS FROM THE COMMON GARDEN EXPERIMENT

Females from both populations (Dinghai and Lishui) laid eggs almost synchronically between 12 and 23 July 2003. Thus, the observed difference in the timing date of oviposition between the Dinghai and Lishui populations could be due to the proximate effect of

Table 3. Loading of the first two axes of a principal component analysis on six female reproductive variables in *Naja atra*. Size effects are removed in all cases by using residuals from the regressions on snout-vent length. All data were \log_e transformed, and variables with the main contribution to each factor are in bold

Variable	Factor loading	
	PC1	PC2
Post-oviposition body mass	0.421	0.591
Tail length	-0.170	0.188
Clutch size	-0.281	0.935
Clutch mass	0.390	0.882
Egg mass	0.975	-0.029
Egg volume	0.969	0.102
Variance explained	38.8%	34.1%

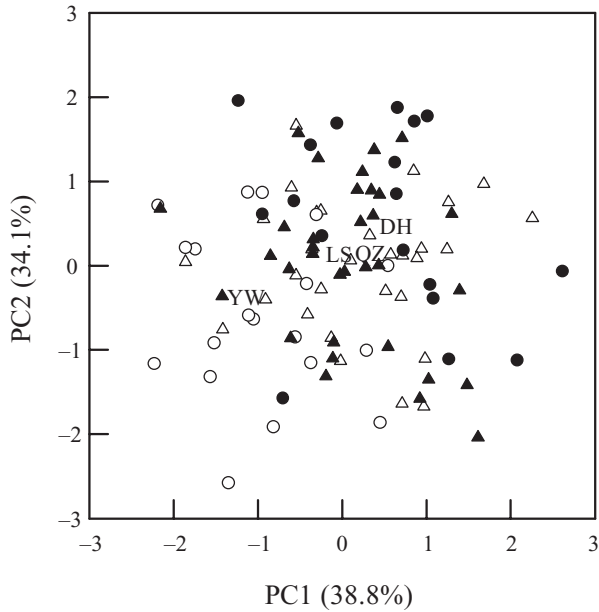


Figure 5. Position of female *Naja atra* from different populations in the space defined by the first two axes of a principal component analysis based on six size-adjusted reproductive variables, on which size effects were removed by using residuals from the regressions on snout-vent length. See Fig. 1 for key to symbols.

ambient temperatures. Our common garden experiment confirmed that clutch size, clutch mass and relative clutch mass were greater in the Dinghai population than in the Lishui population, when effects of variation in maternal SVL or post-oviposition body mass (for RCM) were statistically removed (Table 4). The experiment also confirmed that, at the same maternal SVL, egg size did not differ between females from the Dinghai and Lishui populations (Table 4). The population (Dinghai vs. Lishui populations) × clutch (field vs. laboratory clutches) interaction was not a source of variation for any examined reproductive trait (Table 4). Thus, clutches formed in the laboratory did not differ from clutches formed in the field, although post-oviposition body conditions were on average better in females from the Dinghai population than in females from the Lishui population (Table 4).

The trade-off between egg mass and relative fecundity was evident within both populations ($P < 0.05$ in both cases), but the position of the trade-off line (common slope = -0.305) was still higher in the Dinghai population than in the Lishui population ($F_{1,39} = 11.57$, $P < 0.002$; Fig. 6). At any given level of relative fecundity, clutch size of the Dinghai population outnumbered that of the Lishui population by 2.4 eggs. These results showed that maintenance of females from two different populations under the same conditions for

Table 4. Female reproductive traits of *Naja atra* in the common garden experiment conducted from August 2002 to August 2003. Data are expressed as mean ± 1 SE and range, and compared with the corresponding data on the gravid females collected from the field in 1998 (Table 1). Size and post-oviposition body condition [estimated by using residuals from the regression of \log_e (post-oviposition body mass) on \log_e (maternal SVL)] were analysed by two-way ANOVA. Post-oviposition body mass, clutch size, clutch mass and egg mass were analysed by two-way ANCOVA with maternal SVL as the covariate, and RCM was analysed by two-way ANCOVA with post-oviposition body mass as the covariate

	Populations		Statistical analyses		
	Dinghai N = 20	Lishui N = 22	Population (Dinghai vs. Lishui)	Clutch (Field vs. laboratory)	Population × clutch interaction
Snout-vent length (mm)	1089.7 ± 17.9 963.0–1245.0	983.6 ± 13.1 895.0–1118.0	$F_{1,112} = 40.29$ $P < 0.0001$	$F_{1,112} = 1.29$ $P = 0.259$	$F_{1,112} = 0.09$ $P = 0.768$
Post-oviposition body mass (g)	452.4 ± 26.2 284.5–746.5	281.6 ± 14.4 183.2–420.1	$F_{1,111} = 7.56$ $P < 0.007$	$F_{1,111} = 0.27$ $P = 0.606$	$F_{1,111} = 2.81$ $P = 0.960$
Post-oviposition body condition	0.069 ± 0.026 -0.097–0.261	-0.052 ± 0.025 -0.268–0.166	$F_{1,112} = 6.05$ $P < 0.02$	$F_{1,112} = 0.14$ $P = 0.704$	$F_{1,112} = 2.92$ $P = 0.902$
Clutch size	16.6 ± 1.1 9–27	11.4 ± 0.6 6–16	$F_{1,111} = 9.54$ $P < 0.003$	$F_{1,111} = 0.40$ $P = 0.526$	$F_{1,111} = 0.03$ $P = 0.870$
Clutch mass (g)	310.0 ± 23.0 164.2–587.5	183.3 ± 10.1 105.7–306.4	$F_{1,111} = 20.81$ $P < 0.0001$	$F_{1,111} = 0.33$ $P = 0.564$	$F_{1,111} = 0.17$ $P = 0.682$
Egg mass (g)	18.7 ± 0.6 13.2–24.0	16.3 ± 0.4 12.0–20.5	$F_{1,111} = 2.37$ $P = 0.126$	$F_{1,111} = 0.04$ $P = 0.834$	$F_{1,111} = 0.06$ $P = 0.809$
Relative clutch mass	0.68 ± 0.03 0.53–0.96	0.66 ± 0.02 0.49–0.95	$F_{1,111} = 12.30$ $P < 0.001$	$F_{1,111} = 0.14$ $P = 0.710$	$F_{1,111} = 0.55$ $P = 0.472$

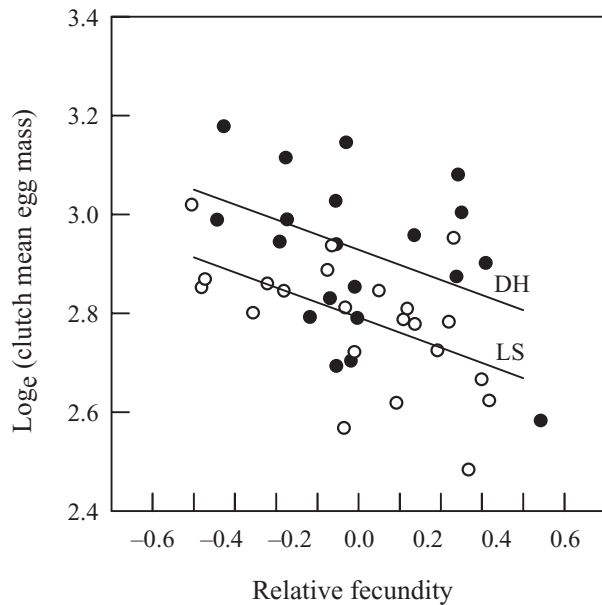


Figure 6. The trade-offs between clutch mean egg mass (g) and relative fecundity recorded in the females maintained in the laboratory for one year. All data were log_e transformed. Regression lines were adjusted for the two populations with a common slope (−0.305) to facilitate comparisons. ●: Dinghai (DH); ○: Lishui (LS).

one year did not remove their differences in fecundity, total reproductive output or the size–number trade-off line.

DISCUSSION

The four populations of *N. atra* sampled in this study are separated by at least 150 km without any continuous distribution, not even between the two closest populations (Yiwu and Lishui). The separation between the island population and the three mainland populations is long-standing rather than being a recent phenomenon due to the influence of human activities. Thus, of the four populations, at least the island population can be considered to be isolated genetically from the mainland populations. Over the range considered, female *N. atra* displayed significant geographical variation in all reproductive traits examined, which could be attributed partly to the consequence of proximate effects of environmental factors and partly to the evolved differences resulting from different local selective pressures (see below). Variation in clutch size, clutch mass, relative clutch mass, egg size, egg shape and post-oviposition body mass (condition) was not a simple consequence of variation in maternal size among populations, because inter-population differences for these traits were still evi-

dent when the influence of maternal size was removed. However, except for the timing date of oviposition and the mean size of the five smallest reproductive females, the traits examined did not vary in a geographically continuous trend (Fig. 5). For example, females from the Lishui and Quanzhou populations, although separated approximately by a distance of 1600 km, were similar to each other in nearly all traits examined. Overall, females from the Yiwu population were distinguished from those from other populations by their smaller egg size and lower reproductive investment, and females from the Dinghai population by their higher fecundity and greater total reproductive investment.

The differences in the mean SVL of the smallest five reproductive females among the four populations were unlikely to be a consequence of sampling bias, because the number of females collected from each population was much greater than that measured in this paper and none of the small gravid females were excluded arbitrarily. But why does the minimal size of reproductive females increase with increasing latitude? One explanation is that the delayed maturity in females from the higher latitudinal (or colder) localities results in larger size at maturity (e.g. Tinkle, Wilbur & Tilley, 1970; Andrews, 1982; Shine & Charnov, 1992; Forsman & Shine, 1995; Adolph & Porter, 1996; Rohr, 1997; Wapstra & Swain, 2001). This explanation can be extended to our study, because delaying maturity can be anticipated for *N. atra* living in Dinghai and Yiwu, where the annual active periods (and hence the growth periods) are shorter (Fig. 1). Delaying maturity is assumed to be costly to individual fitness, but females reap the benefits in future reproduction if they have a high probability of realising their residual reproductive potentials (Stearns & Crandall, 1981; Shine & Schwarzkopf, 1992; Ford & Seigel, 1994; Niewiarowski & Dunham, 1994). Another plausible explanation is that selection favours an increased minimal offspring size simply as a response to slower growth and/or stronger selection on offspring survival in the colder localities. Given that egg size is positively correlated with maternal size in *N. atra*, an increased mature size might potentially prevent females from producing offspring that will be too small to survive in a harsher environment where winter temperatures are low and the first activity season is short (Fig. 1).

In our experience with the cobra, previtellogenic body condition (indicative of resource storage) is crucial to initiating vitellogenesis of ovarian follicles, and a female in a poor previtellogenic body condition usually choose to reduce reproductive investment or even not to reproduce. Post-oviposition body condition was not a determinant of clutch size. For example, females from the three mainland populations differed considerably in post-oviposition body condition but had

nearly the same size-adjusted clutch size, and females from the Dinghai population had almost the same post-oviposition body condition as did females from the Lishui and Quanzhou populations, but had a greater size-adjusted clutch size (Table 1). Variation in clutch size can be explained by multiple factors, so the relationship between female condition and clutch size may be more complex than expected. A female in a poor condition prior to vitellogenesis can be expected to have low reproductive investment and also a poor post-oviposition status. However, a female in a very good condition prior to vitellogenesis may also have a poor post-oviposition condition because of a relatively larger maternal investment in reproduction and/or low food availability during the period of vitellogenesis. Body condition can be much improved through feeding (Ji, Xu & Zheng, 1994). In less stressful environments where thermal conditions are benign and food is abundant, a female may have ample opportunities of producing offspring and, meanwhile, keeping body condition at a level that allows her to compromise current reproduction and future reproduction to a large extent (Schwarzkopf, 1994). However, in stressful environments, a female may have to produce offspring by mobilizing more stored resources and, consequently, has a poor post-oviposition condition. In this study, poor post-oviposition body conditions of females from the Yiwu population largely resulted from an over-exploitation of stored resources, and the smaller egg sizes recorded in the population were unlikely to be determined genetically but could be attributed to the increased resource limitation.

Previous studies on squamate reptiles showed that low food availability resulted in a reduction in clutch size (e.g. Ballinger, 1977; Seigel & Fitch, 1985; Ford & Seigel, 1989; Seigel & Ford, 1991, 1992). Our data showed that SVL-adjusted clutch sizes of the Dinghai population overall outnumbered that of the three mainland populations by 2.4 eggs. Did this difference reflect variation in food availability among populations? Unfortunately, we did not have information on food availability for the four localities. However, food availability was unlikely to be a direct factor influencing the clutch size of *N. atra*, because it could be expected to vary significantly among the three mainland populations in which SVL-adjusted clutch sizes were almost the same. In normal years, clutch size of *N. atra* is determined approximately one month after winter dormancy when vitellogenesis has initiated. Food availability during this month cannot be an important factor for cobras in the field, because they do not forage actively in early spring due to lower ambient temperatures (Hu *et al.*, 1966; Huang & Jin, 1990). In fact, in the first half of the year, cobras feed more heavily in May and June, when the female's choice on clutch size has been made. Thus, although

the potential genetic correlations for geographic variation in clutch size remain unknown, variation in post-hibernation body condition cannot be excluded from an important source of variation in clutch size. Cobras from the Zhoushan Islands have been shown to have better post-hibernation body conditions than those from other parts of Zhejiang and the nearby provinces (Huang & Jin, 1990). Presumably, this difference could be the main reason for the higher fecundity in the Dinghai population.

Clutch size was more variable than egg size within and among populations. This pattern is in accordance with the prediction from models on the evolution of offspring size and number that clutch size should be more variable than egg size (Smith & Fretwell, 1974; Winkler & Wallin, 1987). Apart from females in the Yiwu population that unusually laid small eggs for the aforementioned reason, females from the other three populations were found to lay almost the same sized eggs when the influence of variation in maternal size was statistically removed. This result suggests that *N. atra* eggs could be well optimized for size according to maternal size rather than geographical locality when the resource availability is not a constraining factor. This result, however, is not in accordance with the previous prediction from intraspecific comparisons of species with wide geographical ranges that larger offspring should be produced in colder localities where offspring's growth and/or survival are presumably low (e.g. Ferguson, Bohlen & Wooley, 1980; Berven & Gill, 1983; Parker & Begon, 1986; Forsman & Shine, 1995; Mathies & Andrews, 1995; Rohr, 1997; Wapstra & Swain, 2001; Ji *et al.*, 2002b; but also see Sinervo, 1990). Why did female *N. atra* in colder localities not differ from those in warmer localities in size-adjusted egg mass? One possible explanation is that the efforts of females to increase investment in individual offspring are constrained by fecundity selection (Fig. 4). Moreover, as egg mass varied over a very wide range in each population (Table 1), we cannot see any important evolutionary significance of a shift in size-adjusted egg mass. In fact, as mentioned above, an increased size at first reproduction in colder localities potentially prevents females from producing offspring that are too small to survive in the climatically more severe localities.

Our data showed that maternal size was a major determinant of reproductive investment in each of the four populations: larger females had greater reproductive investment per clutch, so that they laid a greater number of larger eggs. However, reproductive investment varied significantly among populations, with females in the Dinghai population investing more than did females from the other populations. The upper limit to reproductive investment was more likely to be constrained by the space availability

(abdominal space) in the Dinghai population. Such a conclusion can be indirectly supported by the geographic variation in egg shape, as egg shape is indicative of crowdedness of eggs in the uterus and more rounded eggs are usually associated with larger clutch size and/or egg size (Ji & Braña, 2000; Ji *et al.*, 2002b). Thus, more rounded eggs in the Dinghai population implied that the uteri of females were more tightly packed when they were gravid.

The trade-off between size and number of eggs was found in each population, as in all of the four populations egg size was negatively correlated with clutch size when maternal SVL was held constant (Fig. 4). This finding indicated that females with larger clutches produce smaller eggs. However, the mean egg size at any level of relative fecundity differed among the four populations (Fig. 4). These differences resulted clearly from differences in the resource availability rather than the space availability.

Our common garden experiment only synchronized the timing date of oviposition, which was otherwise approximately two weeks later in the Dinghai population than in the Lishui population. The mean egg mass of the two populations was the same, but differences between populations in other important reproductive traits such as clutch size, clutch mass, relative clutch mass and the level of the size–number trade-off line were still evident (Table 4). Thus, the common experiment, which standardizes environmental factors such as temperature, humidity, light and food availability, suggests quite strongly that these traits are somewhat fixed (i.e. genetic).

Taken together, our study demonstrates the importance of proximate and ultimate factors as a source of phenotypic variation in female reproductive traits of *N. atra*, although direct evidence for genetic correlations for the traits examined was not provided in this study. Phenotypic variation induced by either proximate or ultimate factors could be important for cobras living in the wild, but the extent to which phenotypic variation has an effect on individual fitness in nature remains unknown, and offers considerable potential for future work.

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