

Reproductive traits of the gray ratsnake *Ptyas korros* from three geographically distinct populations

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Abstract We collected gravid gray rat snakes *Ptyas korros* from three geographically distinct populations in China, Chenzhou (CZ), Jiangshan (JS) and Dinghai (DH), to study geographical variation in female reproductive traits. Egg-laying dates differed among the three populations such that at the most northern latitude egg-laying was latest, and earliest at the most southern latitude. Clutch size, clutch mass, egg mass, egg shape, within clutch variability in egg sizes and relative clutch mass differed among the three populations, whereas post-oviposition body mass did not. Except for egg-laying date, none of the traits examined varied in a geographically continuous trend. CZ and DH females, although separated by a distance of approximately 1100 km as the crow flies, were similar in nearly all traits examined. JS females were distinguished from CZ and DH females by their higher fecundity (clutch size), greater reproductive output (clutch mass) and more rounded eggs. Our data do not validate the prediction that larger offspring should be produced in colder localities. The absence of an egg size-number trade-off in each of the three populations presumably suggests that *P. korros* is among species where eggs are well optimized for size within a population [Current Zoology 58 (6): 820–827, 2012].

Keywords Colubridae, Life-history, Reproductive output, Egg size, Clutch size, Geographical variation, Egg-laying date

Life-history traits such as body size and age at first reproduction, fecundity, offspring (egg or neonate) size and reproductive frequency vary within and among species (Ballinger, 1983; Stearns, 1992; Roff, 2002; Shine, 2005). As ectotherms, reptiles are highly dependent on environmental conditions, making them very attractive subjects for studying environmentally induced variation in life-history traits (Angilletta et al., 2004; Niewiarowski et al., 2004; Shine, 2005). Reptiles with wide distributional ranges often display geographical variation in life-history traits (Iverson et al., 1993; Shine, 2000; Zuffi et al., 2009; Tanaka and Mori, 2011; Wang et al., 2011). Such variation reflects partly genetic divergence caused by natural selection as the consequence of adaptive responses to local environments, and partly the proximate effects of environmental factors such as temperature and food availability (Shine, 2005). Studying geographical variation in life-history traits among conspecific populations can provide a basis for understanding the causes for such variation and the relationships between life-history traits and environmental variables. The typical approach for examining geo-

graphical variation in life-history traits is to compare two or more populations and understand the differences between them with reference to their environments.

Studies on geographical variation in the reproductive life-histories of reptiles are relatively limited compared to 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 only a handful of taxa, including several colubrid, e.g., *Elaphe carinata* (Qu et al., 2011), *E. quadrivirgata* (Tanaka and Mori, 2011), *E. taeniura* (Ji et al., 2000; Du and Ji, 2008), *Storeria dekayi* (Kofron, 1979; King, 1993), *Thamnophis proximus* (Tinkle, 1957; Clark, 1974; Lancaster and Ford, 2003) and *T. sirtalis* (Burt, 1928; Dunlap and Lang, 1990), elapid, e.g., *Cacophis squamułosus* (Shine, 1980) and *Naja atra* (Ji and Wang, 2005), and viperid, e.g., *Crotalus viridis oreganus* (Diller and Wallace, 1984, 2002), *Vipera aspis* (Zuffi et al., 2009) and *V. berus* (Andrén and Nilson, 1983; Madsen and Shine, 1994). Datasets describing geographic variation in life-histories from more species across multiple taxonomic groups are needed to eluci-

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date the general patterns and/or to determine the mechanisms that result in unique patterns (Angilletta et al., 2004; Niewiarowski et al., 2004; Shine, 2005).

Here, we compared a number of female reproductive traits among gray ratsnakes *Ptyas korros* from three geographically distinct populations in China (Fig. 1), including egg-laying date, post-oviposition body condition, clutch size, clutch mass, egg size, egg shape, and variability in egg and clutch sizes. We address three

main questions: (1) Do the three populations differ in some female reproductive traits, but not in others? (2) Do the traits that differ among populations vary in a geographically continuous trend? (3) Does egg size vary in response to variation in total reproductive investment or maternal size and therefore provide evidence contrary to theoretical predictions that there should be a single optimum offspring size within any population (Smith and Fretwell, 1974)?

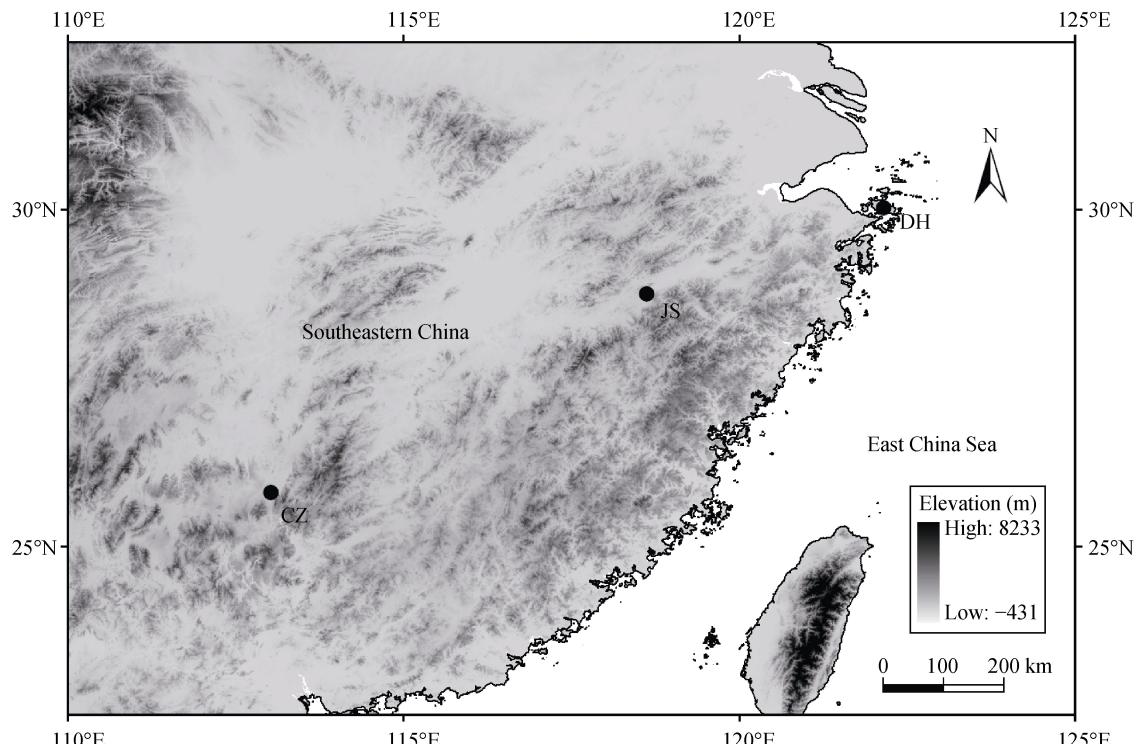


Fig. 1 Map of southeastern China, showing localities where snakes were collected
CZ: Chenzhou; JS: Jiangshan; DH: Dinghai

1 Materials and Methods

1.1 Study species and populations

Ptyas korros is an oviparous colubrid snake that has a distribution covering the southeastern part of China (including Taiwan, Hainan and Hongkong), Indo-China Peninsula, India and Indonesia, and is found in a variety of habitats in the hilly countryside (Zong, 1998). Despite its wide geographic distribution, data on female reproduction and egg incubation have been limited to a population in Zhoushan Island, eastern China (Ji and Sun, 2000; Ji et al., 2000; Du and Ji, 2002). The three populations we sampled 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; ~100 m altitude), Zhoushan Island, eastern Zhejiang, which is approximately 25 km away from the nearest

mainland coastline. The other two are located at different coordinates on the mainland: Jiangshan (JS, 28°45'N, 118°38'E; ~150 m altitude) in western Zhejiang, and Chenzhou (CZ, 25°48'N, 113°02'E; ~200 m altitude) in southeastern Hunan. The annual mean temperature (Fig. 2A) and annual rainfall (Fig. 2B) are highest in CZ (18.0 °C, and ~1750 mm) and lowest in DH (16.6 °C, and ~1420 mm), with JS (17.2 °C, and ~1480 mm) in between.

1.2 Animal collection and care

We employed local people to collect snakes in early June between 2001 and 2011 and transported females with yolked follicles or oviductal eggs to our laboratory in Hangzhou (30°19'N, 120°23'E). We housed one or two females in 450 × 400 × 300 (length × width × height) mm wire cages, and provided food [cricket frogs *Rana (Fejervarya) limnocharis*] and water enriched

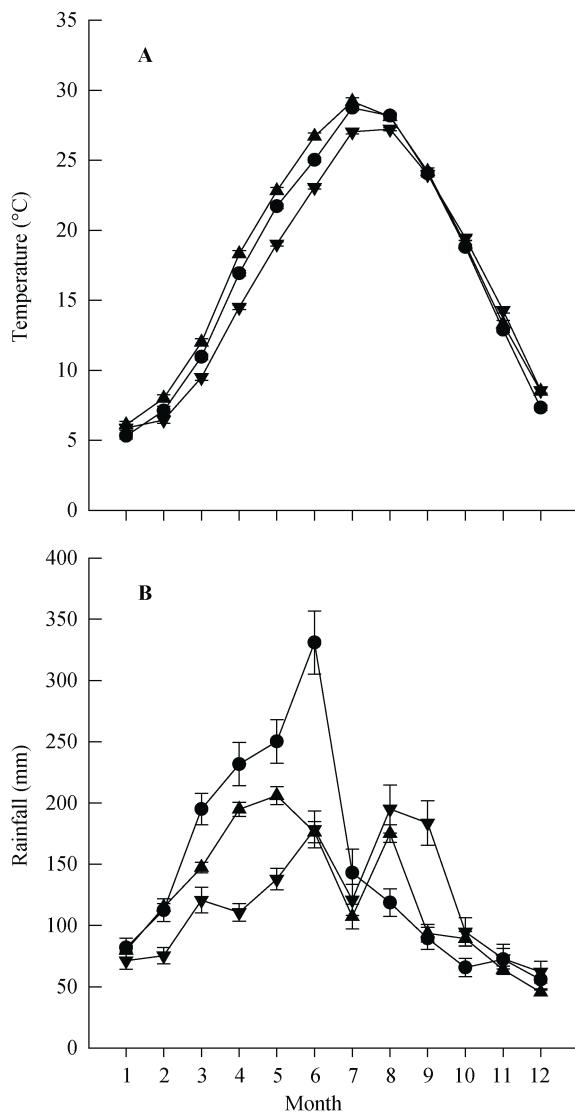


Fig. 2 Means (\pm SE) for monthly mean air temperature (A) and monthly mean rainfall (B) from 1970–2010 at the three localities (courtesy of the Provincial Bureaux of Meteorology of Zhejiang and Hunan), where females of *Ptyas korros* were collected

▲: Chenzhou; ●: Jiangshan; ▼: Dinghai

with multivitamins and minerals *ad libitum*. We placed cages in rooms where air temperature varied from 26–30 °C. After the first female laid eggs, we checked cages three times daily for eggs and more frequently when there was a sign of oviposition, so that eggs were always collected, weighed and measured less than 3 h post-laying. Females that had laid eggs were palpated to confirm that all eggs had been laid. Snout-vent length (SVL) and post-oviposition body mass were taken for each female. Eggs were incubated under multiple thermal regimes, and data will be reported elsewhere.

1.3 Data analysis

Within clutch variability in egg sizes (mass, length

and width) were analysed using the coefficient of variation calculated by dividing the standard deviation by the mean, so was within population variability in clutch and egg sizes. Relative clutch mass was calculated by dividing clutch mass by the post-oviposition body mass. Data were tested for normality using the Kolmogorov-Smirnov test, and for homogeneity of variances using the Bartlett's test. Percentage data were arcsine-transformed prior to parametric analyses. We used linear regression analysis, One-Way ANOVA, one-way ANCOVA, partial correlation analysis and Tukey's *post hoc* test to analyse data. The homogeneity of slopes was checked prior to testing for differences in adjusted means. All statistical analyses were performed with Statistica (version 6.0 for PC, Tulsa, OK, USA). Throughout this paper, values are presented as mean \pm standard error (SE), and the significance level is set at $\alpha = 0.05$.

2 Results

Females from the three populations did not differ from each other in mean SVL, nor in post-oviposition mass after accounting for SVL (Table 1). Females from the CZ population laid eggs between mid-June and early July, and females from the JS and DH populations laid eggs between late June and mid-July. Egg-laying dates differed among females from the three populations (One-Way ANOVA; $F_{2,74} = 47.20, P < 0.0001$), with CZ females laying eggs an average of 11 days earlier than JS females, and an average of 15 days earlier than DH females.

Clutch size was positively correlated with female SVL in each of the three populations ($P < 0.007$ in all cases; Fig. 3A). The proportion of variation in clutch size explained by female SVL was approximately 35% in the CZ population, 33% in the JS population and 49% in the DH population (Fig. 3A). JS females laid more eggs than did CZ and DH females of the same SVL, and CZ females did not differ from DH females in clutch size after accounting for SVL (Table 1). Within population variability in clutch size was 26.5% in the CZ population, 24.5% in the JS population and 25.0% in the DH population. Holding female SVL constant with a partial correlation analysis, we found that clutch size was positively correlated with post-oviposition mass in JS ($r = 0.56, t = 2.88, df = 18, P < 0.01$) and DH ($r = 0.42, t = 2.43, df = 28, P = 0.022$) females, but not in CZ females ($r = 0.11, t = 0.50, df = 22, P = 0.619$).

Clutch mass was positively correlated with female SVL in each of the populations (all $P < 0.005$; Fig. 3B). The proportion of variation in clutch mass explained by

Table 1 Descriptive statistics of female reproductive traits for three populations of *Ptyas korros*. F values of One-Way ANOVAs (for SVL, egg mass and CVs of egg mass, egg length and egg width) and One-Way ANCOVAs (for post-oviposition body 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) and significance levels are given in the table. Means with different superscripts differ significantly (Tukey's *post hoc* test, $\alpha = 0.05$, a > b)

	Populations			Statistical results
	Chenzhou	Jiangshan	Dinghai	
n	25	21	31	
Snout-vent length (mm)	863.8 ± 12.0 747–961	858.9 ± 23.6 719–1135	841.8 ± 16.6 660–1001	$F_{2,74} = 0.48, P = 0.620$
Post-oviposition mass (g)	176.0 ± 8.3 97.0–264.0	180.8 ± 14.6 107.0–337.0	173.1 ± 10.4 81.8–280.9	$F_{2,73} = 0.18, P = 0.834$
Clutch size	9.6 ± 0.5 6–15	11.1 ± 0.6 7–17	9.4 ± 0.4 4–14	$F_{2,73} = 4.68, P = 0.012$ CZ ^b , JS ^a , DH ^b
Clutch mass (g)	78.0 ± 5.0 44.9–126.8	102.1 ± 6.4 53.3–161.4	80.7 ± 4.9 22.8–149.6	$F_{2,73} = 8.50, P < 0.0005$ CZ ^b , JS ^a , DH ^b
Egg mass (g)	8.1 ± 0.3 5.8–10.1	9.1 ± 0.3 7.1–12.0	8.4 ± 0.3 5.2–10.9	$F_{2,74} = 3.15, P = 0.048$ CZ ^b , JS ^a , DH ^{ab}
Egg length (mm)	37.0 ± 0.8 31.7–48.2	36.6 ± 0.6 32.1–43.9	38.1 ± 0.5 33.3–43.5	$F_{2,73} = 6.10, P < 0.004$ CZ ^a , JS ^b , DH ^a
Egg width (mm)	18.5 ± 0.2 16.3–20.5	19.7 ± 0.2 18.3–21.9	18.4 ± 0.3 13.2–21.2	$F_{2,73} = 3.80, P = 0.027$ CZ ^{ab} , JS ^a , DH ^b
CV of egg mass	3.1 ± 0.3 0.5–5.9	3.5 ± 0.3 1.8–6.0	6.0 ± 0.8 1.9–16.9	$F_{2,74} = 8.55, P < 0.0005$ CZ ^b , JS ^b , DH ^a
CV of egg length	5.8 ± 0.7 1.3–18.7	6.0 ± 1.2 3.4–29.7	5.6 ± 0.4 2.0–12.0	$F_{2,74} = 0.06, P = 0.925$
CV of egg width	2.2 ± 0.3 0.3–7.0	2.1 ± 0.2 1.1–4.0	3.9 ± 0.5 0.9–14.1	$F_{2,74} = 7.89, P < 0.001$ CZ ^b , JS ^b , DH ^a
Relative clutch mass	0.45 ± 0.02 0.21–0.66	0.58 ± 0.02 0.39–0.84	0.48 ± 0.02 0.24–0.78	$F_{2,73} = 11.05, P < 0.0001$ CZ ^b , JS ^a , DH ^b

female SVL was approximately 30% in the CZ population, 43% in the JS population and 47% in the DH population (Fig. 3B). JS females produced heavier clutches than did CZ and DH females, and CZ females did not differ from DH females in clutch mass, after accounting for SVL or post-oviposition mass (Table 1).

Egg mass was independent of female SVL in the CS and JS populations ($P > 0.162$ in both cases), but was marginally dependent on female SVL in the DH population ($F_{1,29} = 4.30, P = 0.047$) (Fig. 3C). The mean egg mass was greatest in the JS population and smallest in the CZ population, with the DH population in between (Table 1). Holding female SVL constant with a partial correlation analysis, we found that in none of the three populations was egg mass correlated with clutch size ($P > 0.252$ in all cases). Within clutch variability in egg mass differed among the three populations, so did within clutch variability in egg width (Table 1). Egg mass and width size were more variable in the DH

population than in the other two populations (Table 1). Within population variability in egg mass was 16.6% in the CZ population, 13.0% in the JS population, 18.1% in the DH population.

Eggs laid by JS females were more rounded than those laid by CZ and DH females because of their shorter length but greater width (Table 1). Egg width was positively correlated with female SVL in each of the three populations (Table 2). Egg width was positively correlated with egg length in the CZ population, but not in the JS and DH populations (Table 2). Egg length was negatively correlated with female SVL in the CZ, but not in the JS and DH populations (Table 2).

3 Discussion

Egg-laying date differed among the three populations such that at the most northern latitude (DH) egg-laying was latest and at the most southern latitude (CZ) earliest. These differences in egg-laying date could be related to

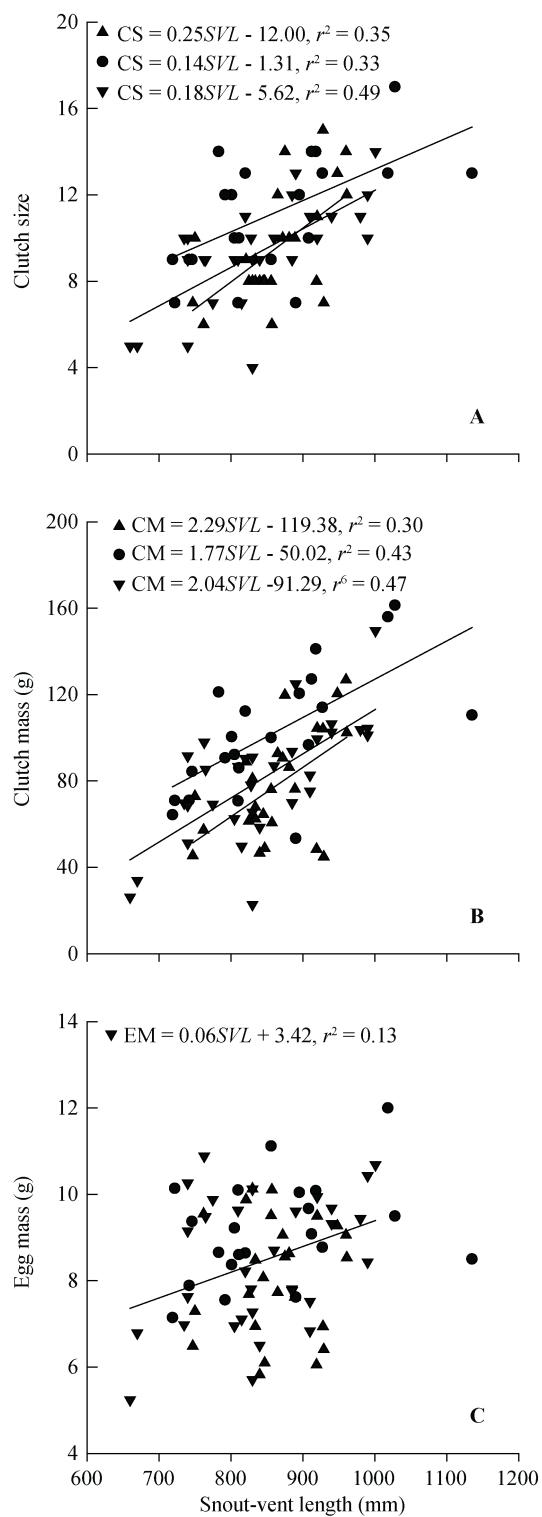


Fig. 3 Linear regressions of clutch size (A), clutch mass (B) and egg mass (C) against maternal SVL

Regression lines, equations and coefficients are given in the figure for the variables that are dependent on maternal SVL in each population. ▲: Chenzhou; ●: Jiangshan; ▼: Dinghai

temperature differences among the three localities (Fig. 2). It has been reported for snakes that the date of emergence from hibernation is earlier in warmer locali-

Table 2 Results of partial correlation analyses for the relationships between female SVL, egg length and egg width

	df	SVL vs Egg length	SVL vs Egg width	Egg length vs Egg width
Chenzhou	22	$r = -0.49$, $t = 3.15$, $P < 0.005$	$r = 0.54$, $t = 3.47$, $P < 0.003$	$r = 0.43$, $t = 2.16$, $P = 0.042$
		$r = 0.28$, $t = 1.24$, $P = 0.231$	$r = 0.46$, $t = 2.19$, $P = 0.041$	$r = -0.12$, $t = 0.49$, $P = 0.629$
Dinghai	28	$r = 0.08$, $t = 0.44$, $P = 0.666$	$r = 0.36$, $t = 2.07$, $P = 0.048$	$r = 0.05$, $t = 0.26$, $P = 0.796$

ties, and that the time elapsed from emergence to ovulation as well as food intake rates play a key role in determining some reproductive traits including egg-laying (for oviparous species) or parturition (for viviparous species) dates (Seigel and Ford, 2001; Ji and Wang, 2005). Most of the other traits examined differed among the populations, but no trait (clutch size, clutch mass, egg shape, variability in egg sizes and relative clutch mass) that differed among populations varied in a geographical trend as did egg-laying date. For example, CZ and DH females, although separated by a distance of 1100 km as the crow flies, were similar to each other in nearly all traits examined. JS females were distinguished from CZ and DH females by their higher fecundity (clutch size), greater reproductive output (clutch mass) and more rounded eggs (Table 1). The greater relative clutch mass in JS females could be largely attributable to their greater reproductive output, as females from the three populations did not differ from each other in post-oviposition body mass (Table 1).

The SVL-adjusted mean clutch size of the JS population outnumbered that of the other populations by 1.8 eggs. However, whether this difference has any genetic correlation or just reflects the consequence of differences in proximate factors such as food availability and previtellogenesis body condition among populations remains unknown. It has been found in several species of reptiles that previtellogenesis body condition is crucial to initiating vitellogenesis of ovarian follicle, and that a female in a poor previtellogenesis body condition often tends to reduce the number of offspring produced or even not reproduce (Ballinger, 1977; Ford and Seigel, 1989; Seigel and Ford, 1991, 1992; Ji and Wang, 2005; Ji et al., 2007). Female body condition is highly dependent on the opportunities for basking and feeding that may vary spatially and temporally, so the pattern of geographic variation in clutch size observed in this

study would not remain invariant if previtellogenetic body condition were the exclusive factor for such variation. The genetic correlation for geographic variation in particular reproductive traits was detected in a common garden experiment of *Naja atra* where environmental factors such as temperature, humidity, light and food availability are standardized (Ji and Wang, 2005). Females of *N. atra* collected from DH and Lishui (a locality approximately 100 km from JS in central Zhejiang) soon before oviposition differed in egg-laying date and SVL-adjusted mean values for clutch size and clutch mass (Ji and Wang, 2005). The common garden experiment where females from the two localities were maintained under identical laboratory enclosures for one year synchronized egg-laying date that would be otherwise about two weeks later in the DH population, but still showed between-population differences in clutch size and clutch mass (Ji and Wang, 2005).

Clutch size was more variable than egg mass within and among populations. This is in accordance with the prediction that offspring number should be more variable than offspring size (Smith and Fretwell, 1974). Evidence from diverse animal taxa shows that females can adjust the size of their offspring by assessing the environment that their offspring will face based on their own experience (Boersma, 1997; Johnston and Leggett, 2002; Jordan and Snell, 2002; Bashey, 2008), or offspring size can vary in response to variation in total reproductive investment or maternal size (Sargent et al., 1987; Winkler and Wallin, 1987; Reznick et al., 1990; Caley et al., 2001; Ji et al., 2006, 2009; Wang et al., 2011). In the present study, larger females generally devoted more energy to the production of eggs, as revealed by the fact that clutch mass was positively correlated with female SVL in each of the three populations. Interestingly, however, in none of the three populations was egg mass correlated with clutch size when female SVL was controlled for with a partial correlation analysis. This finding suggests that females of *P. korros* with different amounts of energy to invest are more likely to vary the number but not the size of eggs. Moreover, egg mass was marginally positively correlated with female SVL only in one population, suggesting that egg mass is less likely to vary in response to variation in maternal size in *P. korros*.

As in *E. carinata* (Qu et al., 2011), the population mean egg mass did not differ between the most southern (CZ) and northern (DH) latitudes in *P. korros* (Table 1). This finding is not in accordance with the prediction from intraspecific comparisons of species with wide

geographic ranges that larger offspring should be produced in colder localities (Parker and Begon, 1986; Forsman and Shine, 1995; Mathies and Andrews, 1995; Rohr, 1997; Wapstra and Swain, 2001; Ji et al., 2002). Why do females of *P. korros* from the CZ and DH populations not differ in population egg mass? One explanation is that the efforts of females to increase investment in individual offspring are constrained by fecundity selection (leading to increased clutch size). Alternatively, it is possible that the lack of differences in egg mass between these two populations reflects the fact that the egg mass is constrained by female size. Egg dimensions (and hence egg mass) are determined by both egg length and egg width. Egg width rather than egg length was positively correlated with female SVL in each of the three populations (Table 2), suggesting that egg width is the measure of egg dimensions that is more likely to be constrained by female size. When egg width is limited, an increase in egg mass may only be accomplished by means of an increase in egg length (Sinervo and Licht, 1991; Ji et al., 2006; Rollinson and Brooks, 2008). Given the lack of significant differences in female size (and hence constraint on egg width) and egg width between the CZ and DH populations (Table 1), it is not surprising that the population mean egg mass would remain almost unchanged between these two populations. Finally, as egg mass varied within almost the same range in the two populations (Table 1), we cannot see any important evolutionary significance of a shift in egg mass.

As in numerous other snakes, female size is a key determinant of reproductive investment in *P. korros* (Ji et al., 2000). The upper limit of reproductive investment is ultimately determined by the abdominal space available to hold eggs (Ji et al., 2006, 2009). In the present study, clutches produced by JS females more completely filled the available abdominal space than did those produced by CZ and DH females. This conclusion is 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 always associated with larger or heavier clutches (Castilla et al., 1992; Ji and Braña, 2000; Ji and Wang, 2005; Ji et al., 2006, 2009). More rounded eggs in the JS population implied that the oviducts of females in the population were more tightly packed when they were gravid.

In summary, our data show that females of *P. korros* from three geographically distinct populations differ in most reproductive traits examined. Of the traits examined, only egg-laying date has a clear-cut geographical

trend. Our data do not validate the prediction that larger offspring should be produced in colder localities. The absence of the egg size-number trade-off in each of the three populations presumably suggests that *P. korros* is among species where eggs are well optimized for size within a population. It seems likely that there is selection for more and larger eggs in snakes from the JS population. However, as neither a common garden experiment nor 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.

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