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Identifying sources of variation in reproductive and life-history traits among five populations of a Chinese lizard (*Takydromus septentrionalis*, Lacertidae)

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Research on life-history traits of squamate reptiles has focused on North American species, while Asian taxa have been virtually ignored. In order to understand general patterns in reptile life histories, we need a broader data base. Our study on the slender-bodied lacertid lizard *Takydromus septentrionalis* provides the first detailed information on factors responsible for intraspecific variation in reproductive output and life history in a Chinese reptile. Clutches of recently collected lizards from five widely separated localities in China revealed major divergences in female body size at maturation, mean adult female body size, body condition after oviposition, size-adjusted fecundity, relative clutch mass, and mass and shape of eggs. Most of these geographical differences persisted when the same groups of females were maintained in identical conditions in captivity. Additionally, reproductive frequency during maintenance under laboratory conditions differed according to the animals' place of origin. Thus, the extensive geographical variation in reproductive and life-history traits that occurs within *T. septentrionalis* is exhibited even in long-term captives, suggesting that proximate factors that vary among localities (local conditions of weather and food supply) are less important determinants of life-history variation than are intrinsic (presumably genetic) influences. The maternal abdominal volume available to hold the clutch may be one such factor, based on low levels of variation in Relative Clutch Mass among populations, and geographical variation in the position of trade-off lines linking offspring size to fecundity. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, **85**, 443–453.

ADDITIONAL KEYWORDS: allometry – body size – fecundity – geographical variation – offspring size – reproductive output – reptile – trade-off.

INTRODUCTION

Life-history variables such as body size at maturation, fecundity, offspring size and reproductive frequency, are central aspects of a species' ecology. For example, rates of reproductive output may play a large role in determining the viability of populations in the face of pressures such as habitat destruction, predation and interspecific competition (Caughley & Sinclair, 1994; Caughley, 1994; Roff, 2002). Accordingly, research to document patterns of variation in life-history traits, and to clarify the causes for such variation, has attracted increasing emphasis in recent years. One lineage of particular interest for such studies is the Squamata (lizards and snakes). As ectotherms, they are highly dependent upon ambient climatic conditions and, hence, display substantial environmentally induced variation in life-history features (e.g. Adolph & Porter, 1993). Thus, for example, attributes such as reproductive frequencies and output per clutch can be modified strongly by temporal or spatial variation in

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*Corresponding author. E-mail: duweiguo@mail.hz.zj.cn food availability (Ballinger, 1983; Madsen & Shine, 2000a; Bonnet *et al*., 2001). This flexibility raises substantial difficulties in interpreting the causal basis for observed variation in reproductive traits: even major divergences might have resulted from the proximate effects of local conditions rather than adaptive (genetically coded) responses to geographically variable selective regimes (Ballinger, 1979, 1983; Adolph & Porter, 1993).

Teasing apart proximate (e.g. food supply) vs. ultimate (genetic) sources of variation in reproductive parameters remains a major challenge for reptile biologists. The most robust evidence in this respect will come from experimental manipulations of factors such as thermal or nutritional conditions (e.g. Ford & Seigel, 1989; James & Whitford, 1994), but such studies have been conducted on only a small number of reptile species. Even for purely descriptive studies of variation in reproductive traits, very few taxa have been sampled adequately over their entire geographical range. Nonetheless, the magnitude of variation revealed by such intraspecific comparisons suggests that studies including widely separated populations of single species-level entities may provide a valuable opportunity to tease apart the causes of variation in reproductive biology. Thus, although earlier literature usually reported data on reproductive traits in terms of single ‘average’ values per species, more recent studies have looked increasingly at the population rather than the species as the unit of interest for such research (e.g. Adolph & Porter, 1993; Forsman & Shine, 1995; Downes & Adams, 2001).

Unfortunately, the scientific literature on squamate life histories is plagued by immense geographical and taxonomic bias. Reflecting historical factors, most researchers are based in North American and European countries, and unsurprisingly have focused their attention on the faunas of these countries. The magnitude of the resultant bias is evident from simple comparisons of published data vs. faunal diversity. For example, North America contains 257 squamate species (see http://www.cnah.org) and China 352 species (Zhao & Adler, 1993). If equal attention had been devoted to studies of each fauna, then we would expect published reviews to refer more often to Chinese than to North American species. In practice, there is a massive disparity in favour of North American taxa. For example, Dunham, Miles & Reznick’s (1988) extensive review of squamate life histories tabulated data for 258 populations for which the authors could locate published information on traits such as age and size at maturity, fecundity and offspring sizes. Of these 258 taxa, 119 (46%) were North American and only 27 were Asian; none were Chinese.

Although this geographical (and consequently, phylogenetic) bias has decreased in recent years, it remains true that there are relatively few detailed studies on geographical intraspecific variation in life-history traits for any non-American reptiles (but see Thierry, Xavier & Barbault *et al*., 1983; Castilla & Bauwens, 1989). This situation makes it difficult to ascertain the generality of patterns that have been detected in previous work. For example, studies in several areas and based on several different lineages of reptiles have noted a trend for tropical species to be oviparous rather than viviparous, and to produce smaller clutches of larger eggs more frequently than is the case for related taxa living in colder areas (e.g. Barbault, 1975; Rand, 1982; James & Shine, 1988; Shine & Keogh, 1996). However, counter examples are also seen (e.g. Fitch, 1985; Forsman & Shine, 1995). Associations between life-history traits and environmental factors such as climate or food supply, can tell us a great deal about the kinds of factors likely to have generated those patterns, and potentially can suggest hypotheses for further exploration using manipulative methods. However, the essential first step is to have detailed descriptions of such patterns from as broad a range as possible, both geographical and phylogenetic.

These considerations led us to investigate the life-history characteristics of a small, widely distributed Chinese lizard (the northern grass lizard, *Takydromus septentrionalis*). In order to determine whether or not local populations diverged from each other in such characteristics, we captured females and recorded attributes of them and the clutches they produced. To further explore the degree to which such divergences were the result of local proximate factors such as food supply or weather conditions, we conducted a ‘common garden’ experiment where we maintained the animals under identical conditions and continued to quantify the attributes of their successive clutches produced under these conditions.

MATERIAL AND METHODS

STUDY SPECIES

The northern grass lizard *Takydromus septentrionalis* is a small [adults 55–80 mm snout–vent length (SVL)] slender-bodied (mean adult mass 5.44 g), long-tailed (101–264 mm) lacertid that is distributed over a large area of eastern and northern China (Zhao & Adler, 1993). It is insectivorous, primarily diurnal and terrestrial. Females produce clutches of 1–5 elongate eggs in spring and summer (April to July: Ji, Zhou & Zhang, 1998).

COLLECTION LOCALITIES

In March and April from 1999 to 2001, we collected adult *Takydromus septentrionalis* from five widely separated localities along the eastern coast of China.

Four of these sites spanned a wide range in latitude but were similar in longitude: Chuzhou (32°18′N, 118°18′E), Hangzhou (29°50′N, 119°30′E), Lishui (28°26′N, 119°54′E) and Ningde (26°40′N, 119°33′E). The fifth locality, Guiyang (26°30′N, 106°40′E), is at the same latitude as Ningde but is much further inland, at a different longitude. Our collection localities spanned a wide range of air temperatures and precipitation levels, based on data from the local Bureau of Meteorology. Annual average air temperature increased with decreasing latitude, whereas annual total precipitation decreased with decreasing latitude. Monthly mean air temperature was higher than 11.4 °C year-round in Ningde, the southernmost locality, but reached a low of 2.8 °C in January in Chuzhou, the northernmost locality (Fig. 1). Annual average air temperature and annual total precipitation was lower in Guiyang, the locality furthest inland, than in Ningde, the coastal site at the same latitude (Table 1). Microhabitats for lizards were similar in all five localities, comprising open grassy areas among forests in mountainous regions. However, the surrounding forests were dominated by deciduous broad-leaved trees in Chuzhou, compared to subtropical evergreen vegetation at the other four sites.

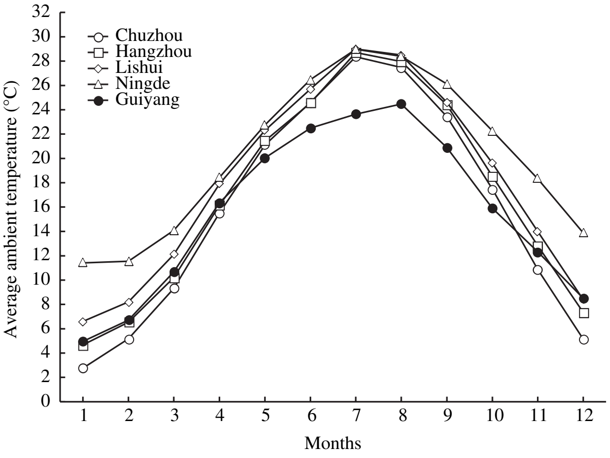

Figure 1. Monthly average ambient temperatures for different geographical localities where northern grass lizards *Takydromus septentrionalis* were collected.

DATA COLLECTION

All animals were caught by hand, transported to Hangzhou Normal College and kept in the laboratory until mid-July Immediately after arrival, the animals were weighed (± 0.001 g), measured (± 0.01 mm) and individually marked (toe-clipped). The measurements included SVL, tail length and abdominal length (from the collar scale to the cloacal scale). Then the lizards were allocated randomly to terraria (60 × 40 × 30 cm, each containing 10 females plus 5 males) with sand and grass to mimic natural habitats where these lizards are found. A 60 W light bulb suspended 15 cm above the floor provided opportunities for behavioural thermoregulation from 07.00 hours to 17.00 hours. Food (larvae of *Tenebrio molitor*) and water (containing mixed vitamins and minerals) were provided *ad libitum*. We palpated the abdomens of each female every five days, and any animal with oviductal eggs was transferred to a small glass terrarium (20 × 15 × 20 cm) filled with 2 cm-depth moist sand. Each small terrarium was checked at least three times a day for freshly laid eggs. All eggs were measured (length and width, ± 0.01 mm) and weighed (± 0.001 g) promptly in order to minimize postlaying changes in mass due to water exchange. Postpartum females were returned to their original terraria.

We calculated relative clutch mass (RCM) as the ratio of clutch mass to maternal postoviposition mass

Table 1. Climatic characteristics for five geographical localities where northern grass lizards (*Takydromus septentrionalis*) were collected

	Geographical location	Altitude (m)	Annual average temperature (°C)	Annual precipitation (mm)
Chuzhou	32°18′N 118°18′E	100	15.2	1031
Hangzhou	29°50′N 119°30′E	45	16.0	1475
Lishui	28°26′N 119°54′E	70	18.1	1427
Ningde	26°40′N 119°33′E	50	19.3	2070
Guiyang	26°30′N 106°40′E	270	16.0	1200

(Shine, 1980). All variables were tested for normality using the Kolmogorov–Smirnov test and for homogeneity of variance using Bartlett's test prior to further statistical analysis. Initial analyses revealed no significant differences in reproductive output of females from their second to fourth clutches ($P > 0.05$ for all reproductive traits in all populations), so we pooled the data from the second, third and fourth clutches for our analyses (and thus, could compare the reproductive output of recently collected lizards to the output of the same animals after they had been maintained in identical conditions). We quantified the level of divergence among the five populations and between first vs. later clutches by conducting analyses of variance for reproductive characters of females. For variables correlated with maternal SVL, we tested for differences among populations with analysis of covariance. A principal components analysis was used to explore multivariate divergence in reproductive output among populations, using size-independent scores for each trait calculated as residuals from the linear regression of each trait vs. maternal SVL.

RESULTS

DID CAPTIVITY AFFECT ATTRIBUTES OF THE FIRST CLUTCH AS WELL AS LATER CLUTCHES?

Several of the interpretations in this paper (below) rely upon the idea that reproductive output in a female's first clutch potentially reflected field conditions of food availability, weather, etc., whereas that of subsequent clutches was affected by captivity. The first clutch was produced an average of 28 days after female capture, with no significant geographical variation in this trait ($F_{4,222} = 1.66$, $P = 0.16$; range in mean values 26.6–29.9 days). Some of this 28-day delay would have been taken up with the period of uterine retention of developing eggs (i.e. after ovulation but before oviposition) but some females doubtless ovulated after capture; hence, their reproductive output may have been influenced by maintenance in captivity prior to ovulation. In order to look for such an effect, we regressed all reproductive variables (both as raw scores, and as residual scores from the regression of that trait vs. maternal body size) against the duration of retention in captivity prior to oviposition of the first clutch. All regressions for all populations were non-significant ($P > 0.05$), suggesting that females held longer in captivity prior to producing their first clutch did not modify attributes of those clutches. These results suggest that it is reasonable to treat first clutches as representative of field-caught females, for comparison with second and later clutches.

INTERVALS BETWEEN SUCCESSIVE CLUTCHES

Female lizards laid one to four clutches in the laboratory, with the mean number of clutches per female differing significantly among populations ($F_{4,243} = 6.54$, $P < 0.0001$). For example, females from Lishui population laid more clutches than did their counterparts from the Ningde population (Fig. 2C).

FEMALE BODY SIZE

Female body size at maturity differed significantly among populations, and was higher for the cooler-climate populations. The SVLs of the smallest reproduc-

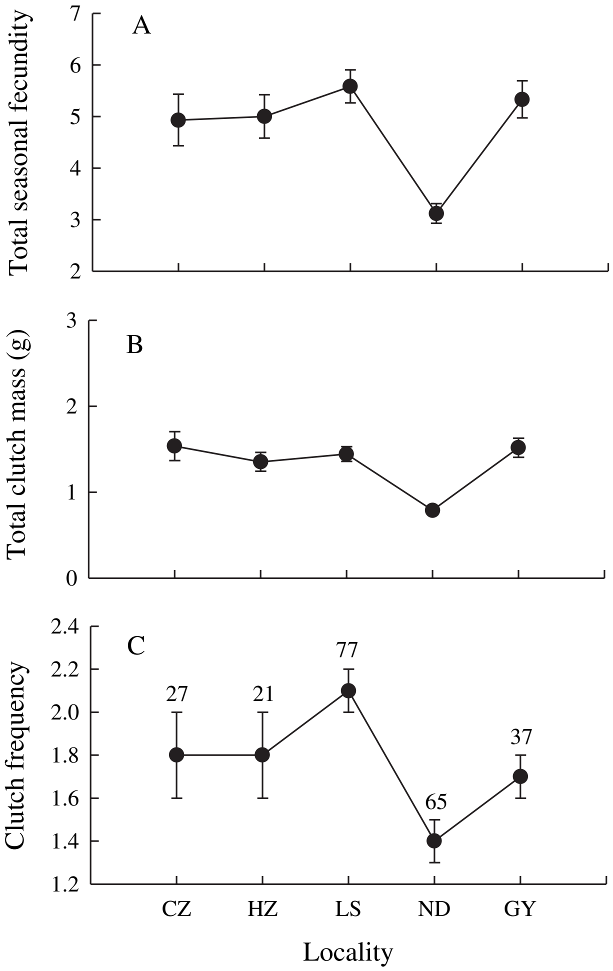

Figure 2. Total seasonal fecundity (total number of eggs, total clutch masses and number of clutches) of female northern grass lizards *Takydromus septentrionalis* from different geographical localities in China. Graphs show mean values and associated standard errors. Numbers above the error bars in the lower graph are sample sizes, and apply to all graphs within this figure. Locality abbreviations: CZ, Chungzhou; HZ, Hangzhou; LS, Lishui; ND, Ningde; GY, Guiyang.

tive females from Chuzhou, Hangzhou, Lishui, Ningde and Guiyang populations were 67.92, 64.35, 58.81, 55.55 and 58.18 mm, respectively. Similarly, mean SVLs of sexually mature females of northern populations were larger than those of southern (warmer-climate) populations (Table 2; Fig. 3A, B). Adult females from the inland population at Guiyang were larger than their similar-latitude counterparts from the coastal population at Ningde (Fig. 3A, B). Unsurprisingly, mean body sizes and body masses of females did not shift greatly during their period of captivity (Table 2; Fig. 3A, B).

Total seasonal fecundity

Larger females produced more eggs, and a greater total egg mass (SVL vs. total seasonal fecundity, $r^2 = 0.105$, $F_{1,245} = 28.73$, $P < 0.00001$; vs. total seasonal clutch mass, $r^2 = 0.154$, $F_{1,245} = 44.66$, $P < 0.00001$). When we included maternal SVL as a covariate in the analysis of geographical variation in fecundity, total seasonal fecundity at the mean SVL of 67.61 mm was significantly higher for lizards from Lishui (5.8) and Guiyang (5.3) than for those from Ningde (mean = 3.9; $F_{4,241} = 7.11$, $P < 0.0001$; see Fig. 2A). Similarly, total seasonal clutch mass was greater for lizards from Lishui (1.467 g) and Guiyang (1.451 g) than for animals from Ningde (0.972 g; $F_{4,241} = 5.58$, $P < 0.0001$; see Fig. 2B).

Clutch size and clutch mass

Both clutch size and clutch mass were positively correlated with female SVL (Clutch size, $r^2 = 0.295$, $F_{1,409} = 38.87$, $P < 0.00001$; Clutch mass, $r^2 = 0.421$, $F_{1,409} = 88.41$, $P < 0.00001$). Thus, we used two-way analysis of covariance with SVL as a covariate to detect variations in clutch size and clutch mass arising from (1) geographical origin and (2) conditions to which the females had been exposed prior to oviposition (field for the first clutch of each female; laboratory for all second and subsequent clutches). Clutch sizes varied significantly both among populations and between first and later clutches (Table 2). Clutch sizes of the inland population (Guiyang) were larger than those of the coastal population at similar latitude (Ningde), but no latitudinal trend in clutch size was evident (Fig. 4A). Females laid more eggs in their first clutch than in subsequent clutches, with no significant interaction between location and clutch number (Table 2; Fig. 4A). That is, lizards from all populations showed a similar degree of clutch-size reduction when maintained in captivity. The coefficient of variation of clutch size for all individuals and population mean clutch size were 31.5% and 13.2%, respectively. Clutch mass also differed significantly among populations and between first vs. later clutches (Table 2). Clutch mass was heavier for the first clutch than for subsequent clutches in all populations (Fig. 4E).

Table 2. Effects of geographical location and clutch number (first vs. later clutches) on maternal traits and reproductive output in northern grass lizards (*Takydromus septentrionalis*). Maternal traits were analysed by two-way ANOVA, and reproductive traits were analysed by two-way ANCOVA using maternal snout–vent length (SVL) as the covariate. Significant effects are shown in bold type

	Geographical variation	First vs. later clutches	Interaction
Maternal SVL (mm)	$F_{4,401} = 53.91$ **$P < 0.00001$**	$F_{1,401} = 3.52$ $P = 0.06$	$F_{4,401} = 1.51$ $P = 0.21$
Maternal body mass (g)	$F_{4,401} = 37.63$ **$P < 0.00001$**	$F_{1,401} = 4.46$ **$P < 0.05$**	$F_{4,401} = 0.39$ $P = 0.81$
Maternal body condition	$F_{4,401} = 8.21$ **$P < 0.00001$**	$F_{1,401} = 1.01$ $P = 0.32$	$F_{4,401} = 0.11$ $P = 0.98$
RCM	$F_{4,401} = 12.71$ **$P < 0.00001$**	$F_{1,401} = 11.07$ **$P < 0.001$**	$F_{4,401} = 0.32$ $P = 0.88$
Clutch size	$F_{4,400} = 8.37$ **$P < 0.00001$**	$F_{1,400} = 11.77$ **$P < 0.001$**	$F_{4,400} = 1.16$ $P = 0.33$
Egg length (mm)	$F_{4,378} = 14.56$ **$P < 0.00001$**	$F_{1,378} = 0.58$ $P = 0.44$	$F_{4,378} = 1.95$ $P = 0.10$
Egg width (mm)	$F_{4,378} = 10.16$ **$P < 0.00001$**	$F_{1,378} = 0.97$ $P = 0.32$	$F_{4,378} = 0.95$ $P = 0.44$
Egg mass (g)	$F_{4,400} = 20.13$ $P < 0.00001$	$F_{1,400} = 0.31$ $P = 0.57$	$F_{4,400} = 2.41$ **$P < 0.05$**
Clutch mass (g)	$F_{4,400} = 10.69$ **$P < 0.00001$**	$F_{1,400} = 10.17$ **$P < 0.01$**	$F_{4,400} = 0.29$ $P = 0.88$

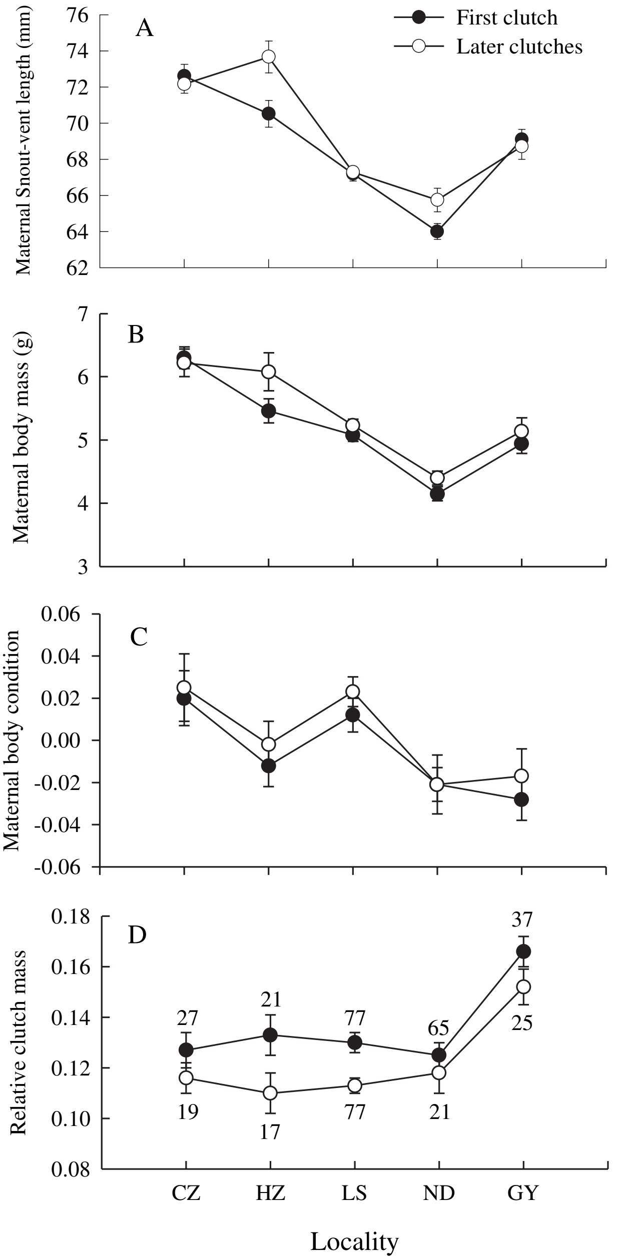

Figure 3. Variation in maternal body sizes, body condition and relative clutch mass (RCM) in the northern grass lizard *Takydromus septentrionalis* as a function of the locality from which females were collected, and whether their clutches were produced soon after capture (first clutch) or after maintenance in captivity for >6 weeks (later clutches). Graphs show mean values and associated standard errors. Maternal body condition = residual score from linear regression of SVL vs. ln mass. RCM = clutch mass divided by postpartum maternal mass. Numbers above the error bars in the lower graph are sample sizes, and apply to all graphs within this figure. Locality abbreviations as in Fig. 2. See Table 2 for statistical analysis of these data, and see the text for definition of RCM.

Body shape and relative clutch mass

We measured abdominal length of females in all populations except for Lishui, and found a significant interpopulation difference in abdominal length relative to maternal SVL (ANCOVA $F_{3,308} = 6.68$, $P < 0.001$). Posthoc Tukey's tests indicated that females from Hangzhou had significantly shorter abdomens than did those from other populations. Relative Clutch Mass (RCM) also varied significantly among populations and between clutches (Table 2; Fig. 3D). The mean RCM of Guiyang lizards was significantly higher than that of other populations, and the RCM of first clutches was higher than that for subsequent clutches (Fig. 3D). There was no significant interaction between these factors (Table 2), indicating that captivity reduced RCMs to a similar degree in lizards from all populations.

Egg size and shape

Mean egg mass was positively correlated with female body size ($r^2 = 0.371$, $F_{1,409} = 65.44$, $P < 0.00001$). Two-way analysis of covariance with SVL as the covariate revealed significant variation in mean egg mass among populations but not between first and later clutches, although there was a significant interaction between these two factors (Table 2). Inspection of the data reveals the reason for this interaction: egg mass increased for captive-produced clutches in the Chuzhou lizards, decreased for the Ningde and Guiyang lizards, and remained stable for the other two populations (Fig. 4B). Overall, population mean egg mass decreased with decreasing latitude in the coastal populations, but the inland (Guiyang) lizards did not fit this pattern (Fig. 4B). The coefficients of variation of egg mass for individual clutches, all individuals and population mean egg mass were 6.2, 15.7 and 8.8%, respectively, indicating that egg mass was less variable than clutch size both within and among populations. When the effects of differing egg sizes were removed by ANCOVA with egg mass as a covariate, mean egg lengths and widths differed significantly among populations but not between first vs. later clutches (Table 2, Fig. 4C, D). Eggs from Ningde were longer and thinner relative to their mass than was true for eggs from all other populations.

Geographical variation in reproductive output

Principal component analyses performed on the original variables of reproductive output yielded two new significant variables (Table 3). As for the component variables (above), we treated these two factors as dependent variables in a two-way ANOVA with geographical location and first vs. later clutches as the

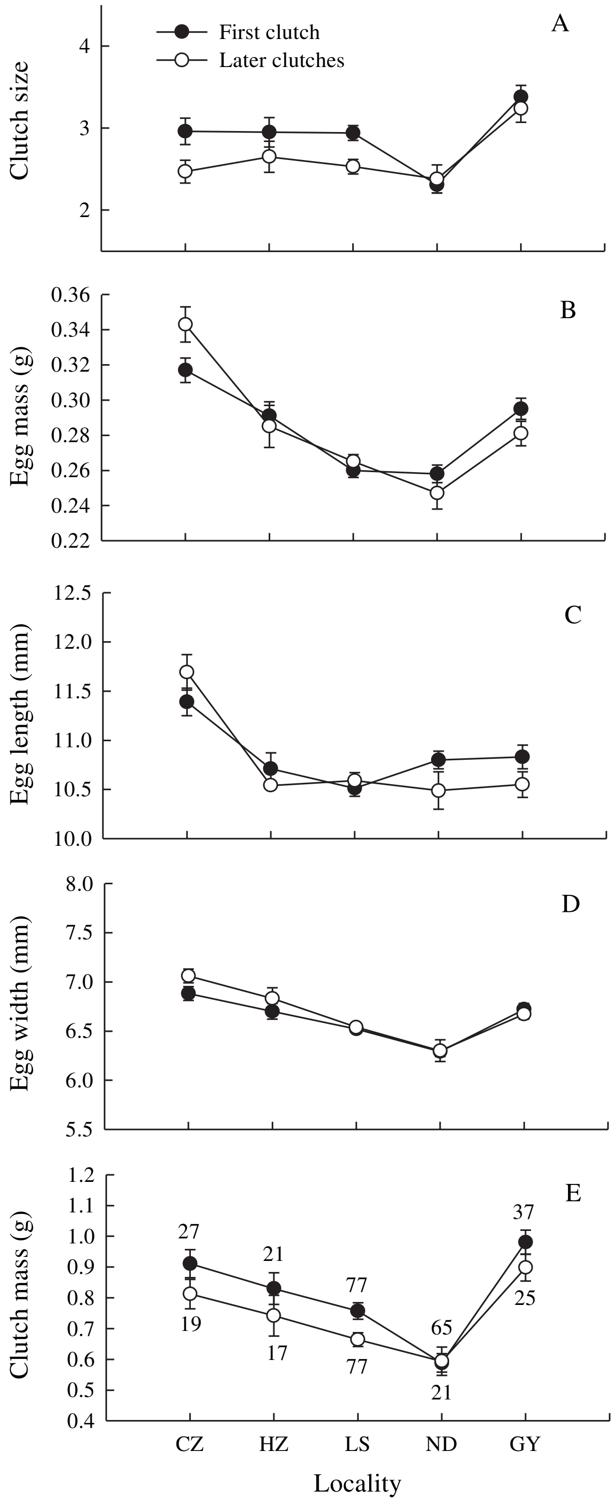

Figure 4. Variation in reproductive output of the northern grass lizard, *Takydromus septentrionalis* as a function of the locality from which females were collected, and whether their clutches were produced soon after capture (first clutch) or after maintenance in captivity for >6 weeks (later clutches). Graphs show mean values and associated standard errors. Numbers above the error bars in the lower graph are sample sizes, and apply to all graphs within this figure. Locality abbreviations as in Fig. 2. See Table 2 for statistical analysis of these data.

factors. Scores on factor 1 (indicative of total reproductive output) varied among locations ($F_{4,401} = 9.40$, $P < 0.00001$) and between first vs. later clutches ($F_{1,401} = 12.09$, $P < 0.001$), with no significant interaction between these factors ($F_{4,401} = 0.61$, $P = 0.65$).

Table 3. Principal component analyses on the reproductive traits of northern grass lizard populations from different geographical localities. Highly significant correlations between factor loadings and reproductive variables are indicated in bold type

	Factor 1	Factor 2
Eigenvalue	1.880	1.098
Variation explained	62.66	36.61
Clutch size	**0.962**	0.255
Egg mass	0.055	**–0.997**
Clutch mass	0.976	–0.195

Factor 2 (indicative of offspring size) also varied geographically ($F_{4,401} = 15.86, P < 0.00001$) but did not differ between first and later clutches ($F_{1,401} = 0.18$, $P = 0.67$). However, a significant interaction between these two factors was apparent for Factor 2: that is, the way in which captivity affected offspring sizes differed among populations ($F_{4,401} = 2.66$, $P = 0.03$)**.** This result mirrors that for egg mass (above), for the same reasons: egg mass was higher for captive-produced clutches than field clutches for one population, and lower for two others (Fig. 5).

TRADE-OFF BETWEEN CLUTCH SIZE AND EGG MASS

We statistically removed the effects of maternal SVL by calculating residual scores from the separate regressions of egg mass and clutch size on female SVL, respectively. Residual egg mass decreased with increasing residual clutch size when data were combined for all five populations ($r^2 = 0.039$, $F_{1,409} = 16.58$, $P < 0.0001$). However, there were significant differences in residual egg mass among populations when residual clutch size was kept constant ($F_{4,400} = 15.08$, $P < 0.00001$), suggesting geographical variation in the trade-off between clutch size and egg mass. Residual egg mass was higher in the Chuzhou and Guiyang lizards than in animals from other populations (Fig. 6).

DISCUSSION

Like other species of *Takydromus* (Telford, 1969; Takenaka, 1981; Huang, 1998; Xu & Ji, 2000), *T. septentrionalis* in our study produced small clutches of elongate eggs. The low mean clutch size, large relative size of the offspring (high egg mass: female mass ratio), and elongation of the egg are all characteristic of lizard and snake species with small adult body sizes (Tinkle, 1969; Tinkle, Wilbur & Tilley, 1970; Shine, 1977; Dunham *et al.*, 1988). These features have been interpreted as reflecting strong selection on minimum viable offspring size. If offspring must be above a minimum size to survive, small reptiles inevitably must produce a small number of eggs that are relatively large compared to the adult female. Also, maternal body-volume constraints mean that such eggs are likely to be very elongate (Shine, 1992; Qualls & Shine, 1995; Qualls & Andrews, 1999). As in almost all other reptile species that have been studied in detail, the northern grass lizard showed significant geographical variation in a wide range of life-history traits across our five sample localities in China. The magnitude of variation differed among traits, but in some cases was substantial. For example, mean egg masses in the first clutch varied from 0.26 to 0.32 g, and mean fecundity from 3.1 to 5.6 eggs per year (Figs 1, 3). These variations were correlated with body sizes of the adult female lizards, both among and within populations. Hence, geographical variation in reproductive output is linked to geographical variation in adult body size, as reported previously for other reptile species (reviewed by Fitch, 1985). Nonetheless, geographical differences in most reproductive traits

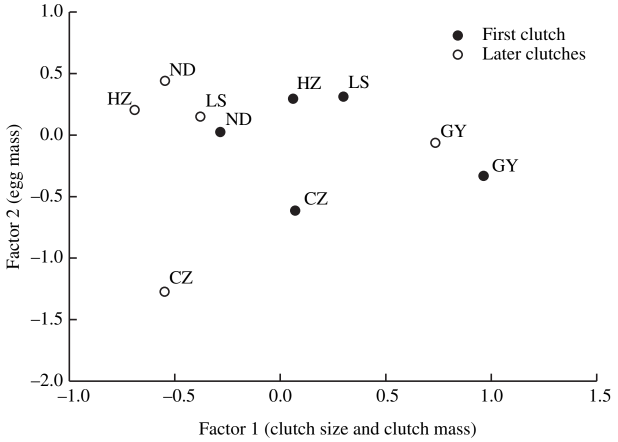

Figure 5. Results of principal components analysis of reproductive traits in five populations of northern grass lizards *Takydromus septentrionalis* from China. The graph shows the mean positions of lizards from each population in terms of the first two axes of variation generated by the PCA. Positions are shown separately for clutches produced soon after capture (first clutch) vs. after maintenance in captivity for >6 weeks (later clutches). Terms in parentheses show variables highly corrected with each PCA axis. Locality abbreviations as in Fig. 2.

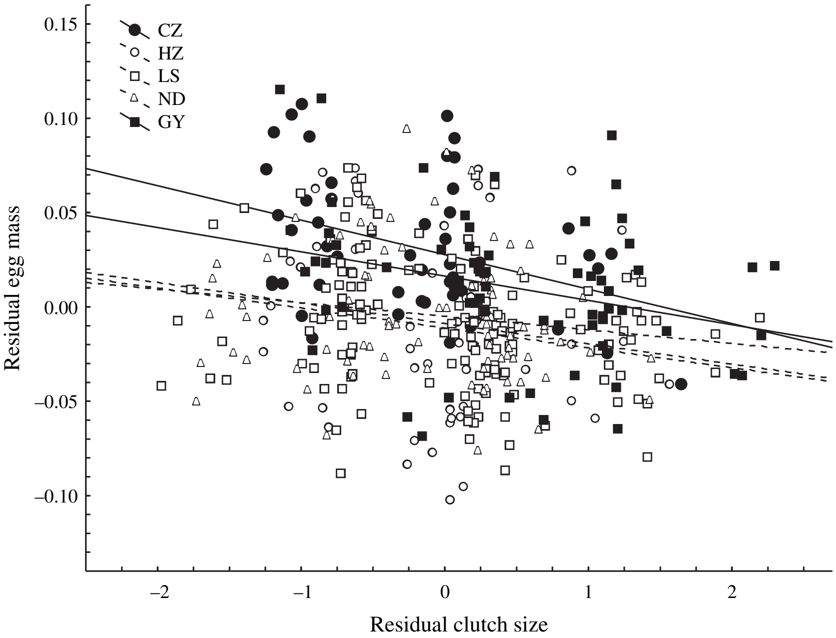

Figure 6. Interpopulation difference in the position of the trade-off between clutch size and egg mass in the northern grass lizard *Takydromus septentrionalis*. Locality abbreviations as in Fig. 2.

were not entirely attributable to maternal body-size variation; life-history traits varied significantly among locations even after the effect of differing maternal body sizes was removed from the analysis (ANCOVA results in Table 2).

The evolutionary mechanisms underlying life-history variation in reptiles are complex and still poorly understood. Geographical variation in life-history traits may stem from either (or both) genetic and environmental differences among populations. For example, even if individuals in two areas are genetically identical, the local environment may generate life-history divergence because of differing thermal regimes, food availability or predation pressures (Dunham *et al*., 1988; Hasegawa, 1994; Madsen & Shine, 2000b; Angilletta, 2001). Although many authors have attempted to identify proximate and ultimate causes for life-history variation in lizards (Tinkle & Ballinger, 1972; Dunham *et al*., 1988; Gill & Ballinger, 1992; Niewiarowski, 1994, 2001), no single hypothesis can account for all geographical variation in reptilian life histories. Frequently, critical data are lacking, and this is especially likely in study systems that have attracted little previous research (such as our own). For example, we know too little about environmental conditions at our five collection localities to evaluate the above-mentioned causes of geographical variation in detail. In general we found stronger differences between the inland locality (Guiyang) and the coastal ones, than we did between coastal localities separated by much greater distances (Table 2; Figs 2, 3, 4). Hence, latitude often induced relatively minor shifts in life-history traits compared to longitude, at least within the sample of populations that we studied. This conclusion stands in contrast to previous reports of strong latitudinal gradients in life-history traits of snakes and lizards, sometimes over smaller distances than those separating our own study populations (e.g. Fitch, 1985).

Because we maintained the lizards for long periods in a 'common garden' environment, any effects of proximate factors that differed among populations (climate, food supply) should have declined considerably by the end of the experiment. Thus, it is interesting to note that the magnitude of divergence among populations was as great for these later captive-produced clutches as it was for the first clutches, where we would expect to see more influence from proximate factors that differ among the local populations (Fig. 3). The greater constancy in traits such as egg mass and shape rather than in clutch size, accords well with optimality models (Smith & Fretwell, 1974). The decline in clutch sizes from first to later clutches (Fig. 3A) might be a reflection of captivity stress (and perhaps, food shortage), or alternatively might occur also in the wild (as has been reported for several other lizard species: e.g. James & Whitford, 1994). However, our current field study on *T. septentrionalis* from Beiji Island (Zheijang province) shows no evidence of any fecundity decline from first to later clutches in wild-caught females (Du & Ji, unpubl. data).

The persistence of among-population differences in mean clutch and egg sizes, even after the effects of maternal body size are removed from the analysis (Table 2) suggests that these differences either are coded genetically or that they are influenced by events (food supply, temperature, etc.) early in a female's life and are thereafter resistant to change. Long-term effects like this have been documented in a few reptile species; for example, growth rates in adult free-ranging snakes depend upon the animal's exposure to feeding opportunities early in life (Madsen & Shine, 2000a) and some lizards manipulate litter and offspring sizes depending upon their feeding experience in the preceding year (Doughty & Shine, 1998). Thus, we cannot simply conclude that differences persisting during a few months of captivity necessarily represent genetic (let alone adaptive) effects. In order to further clarify the causes for the significant geographical variation that we have documented among populations of *T. septentrionalis*, we would need to raise offspring from different populations under identical conditions from hatching (Ferguson & Talent, 1993); or even better, to translocate individuals among populations in the field (Niewiarowski & Roosenburg, 1993).

In the absence of experimental data of this kind, our study nonetheless suggests at least one plausible candidate for a genetically determined factor that varies among populations and may limit reproductive output. This is maternal body volume. In our samples of *T. septentrionalis* RCM displayed relatively little variation (Fig. 2D) because of compensating shifts in other traits (maternal body size and egg size). This low level of RCM variation suggests that RCM itself may be important, either as a target of selection or as a constraint on reproductive investment.

Previous studies on squamates have revealed similarly low levels of variation in RCMs across a wide range of body sizes both within and among populations (Shine & Schwarzkopf, 1992). This constancy may reflect a general tendency for female squamates, especially in small short-lived species like *T. septentrionalis*, to produce as large a clutch mass as can be physically accommodated within their body (Vitt & Congdon, 1978; Shine, 1992; Qualls & Andrews, 1999). If so, we might also expect selection to operate on body shapes of females to modify space availability at any given SVL. The significant differences among populations in fecundity relative to egg mass, despite an overall significant trade-off between these two parameters (Fig. 6), support the hypothesis that maternal body shape as well as size may be important. Alternatively, such differences may reflect different levels of maternal provisioning (Olsson & Shine, 1997). In the present study, however, most clutches were produced by females exposed to similar (and constant) levels of food availability in the laboratory. The most likely cause for a negative correlation between egg mass and clutch size under such circumstances is that there is a finite limit to the volume available for the clutch. Thus, the persistence of geographical differences in the position of the trade-off line suggests that females from different populations somehow differ in the amount of space they have available to hold the developing eggs. In keeping with this inference, Hangzhou females (the group with the shortest abdomens relative to SVL) also had the lowest egg mass at any given clutch size (Fig. 5). This result means that to truly understand geographical variation in life-history traits (such as clutch sizes and egg sizes) within *T. septentrionalis*, we need to consider why females from different populations differ in relative body proportions as well as in mean adult body sizes.

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