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Geographic variation in offspring size of a widespread lizard (*Takydromus septentrionalis*): importance of maternal investment

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Geographic variation in offspring size is widespread, but the proximate causes of this variation have not yet been explicitly determined. We compared egg size and egg contents among five populations of a lizard (*Takydromus septentrionalis*, Günther, 1864) along a latitudinal gradient, and incubated eggs at two temperatures to determine the influence of maternal investment and incubation temperature on offspring size. The mean values for female size and egg size were both greater in the two northern populations (Chuzhou and Anji) than in the three southern populations (Lishui, Dongtou, and Ningde). The larger eggs were entirely attributable to the body size of females in the Anji population, but their increased size also stemmed from further enlargement of egg size relative to female body size in Chuzhou, the northernmost population sampled in this study. Eggs of the Chuzhou population contained more yolk and less water than those of southern populations. Despite the lower lipid content in the yolk, eggs from the Chuzhou population had higher energy contents than those from the two southern populations, owing to the larger egg size and increased volume of yolk. Hatchling size was not affected by incubation temperature, but differed significantly among populations, with hatchlings being larger in the Chuzhou population than in the other populations. Our data provide an inference that oviparous reptiles from cold climates may produce larger offspring, not only by increasing egg size but also by investing more energy into their eggs. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, **101**, 59–67.

ADDITIONAL KEYWORDS: developmental plasticity – egg size – egg yolk – Reptilia.

INTRODUCTION

Offspring size is an important life-history trait that often determines growth and survival at the juvenile stage, and, in turn, body size and reproductive success at the adult stage (Stearns, 1992; Sinervo, 1993; Shine, 2005). Variation in offspring size is widespread among and within species, and understanding the proximate and ultimate causes of this variation is one of the central topics in life-history evolution (Stearns, 1992). Such variation may stem from both a genetic component, derived from the parents, and maternal investment and developmental plasticity (Reznick, 1982; Olsson *et al*., 1996; Shine, 2004). For example, female reptiles may invest different quantities of energy and nutrient into eggs to produce various sized offspring (Booth, 2003; Oufiero, Smith & Angilletta, 2007), or the reproducing females may modify offspring size via the selection of physical conditions that the embryos experience during development (e.g. by using thermally suitable nest sites) (Shine, 2004). Therefore, maternal investment and developmental plasticity are two important causes that can proximately determine offspring size in reptiles.

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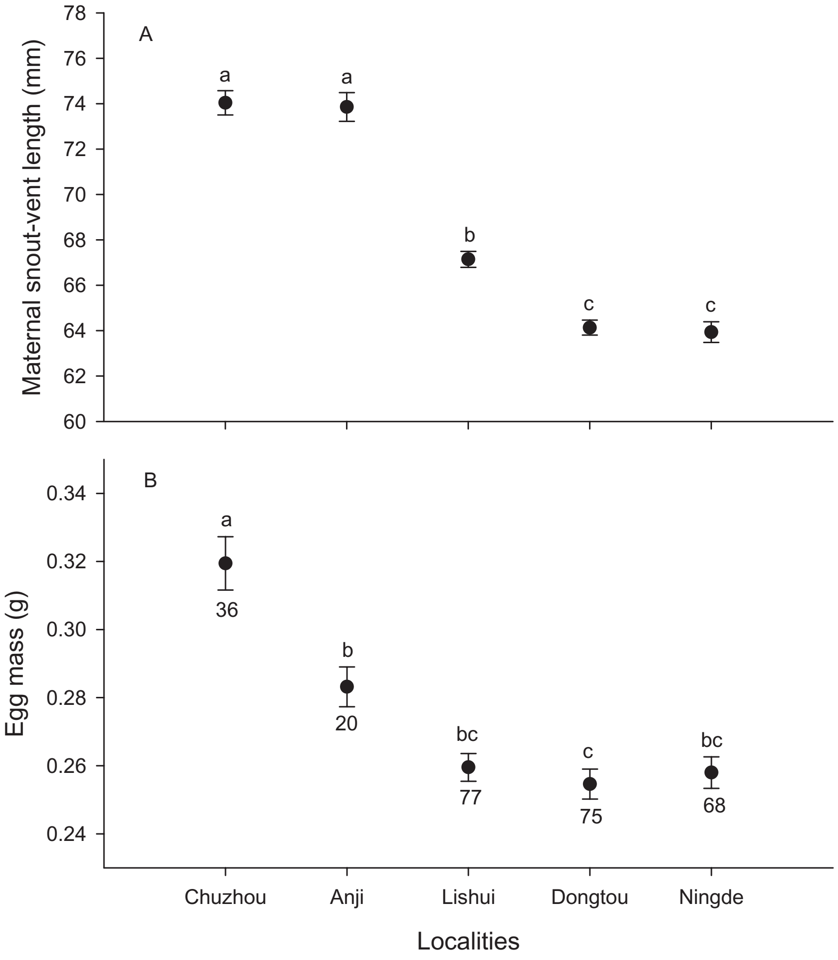

Figure 1. Geographic variation in maternal snout–vent length (SVL) and egg mass in the northern grass lizard *Takydromus septentrionalis*. The egg mass panel shows mean egg mass adjusted for maternal SVL. Sample sizes are indicated under the error bars in the lower graph, but also apply to the upper graph. Means indicated by different letters above their error bars differ significantly (Tukey's test).

Among geographically separated populations occupying different climate zones, offspring are expected to be larger in colder environments, which retard the growth of offspring, because larger offspring perform better and have higher growth than those that are smaller in size (Taylor & Williams, 1984; Yampolsky & Scheiner, 1996). In oviparous reptiles, previous studies have revealed that eggs are larger in high-latitude populations compared with those in low-latitude populations (e.g. Du *et al*., 2005; Ji & Wang, 2005), probably reflecting the different optimal sizes of offspring along the latitudinal gradient predicted by the optimality theory of life-history evolution (Smith & Fretwell, 1974; Angilletta, Oufiero & Leache, 2006). However, the underlying mechanism for females to produce larger offspring in high-latitude populations is not explicitly understood. Given the importance of maternal investment and developmental plasticity in offspring size, we may expect that a female could produce larger offspring by: (1) increasing egg size – a female may grow larger to produce bigger eggs, because egg size is positively related to maternal body size (Sinervo, 1990; Du *et al*., 2005), or may produce enlarged eggs relative to her body size; (2) investing more energy in eggs – a female may invest more yolk or a higher percentage of lipids (and thus more energy) in her eggs to produce larger hatchlings without enlarging the egg size (Nagle, Burke & Congdon, 1998; Oufiero *et al*., 2007); and (3) selecting suitable nests – hatchling size can be significantly affected by incubation conditions such as temperature and moisture (Deeming, 2004).

Takydromus septentrionalis (Günther, 1864) is a lizard that is widespread across eastern China (Zhao, Zhao & Zhou, 1999). Females differ significantly in maternal investment both among and within

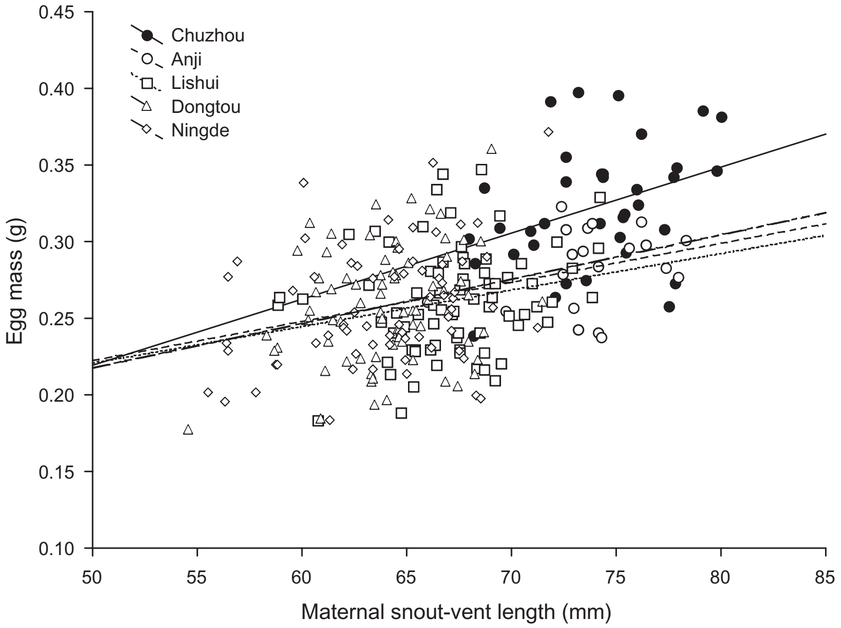

Figure 2. Relationships between maternal snout–vent length (SVL) and egg size in the five geographically separated populations of the northern grass lizard *Takydromus septentrionalis*. Relative to body size, females from the Chuzhou population produced larger eggs than those from the other four populations.

populations (Du *et al.*, 2005; Ji *et al.*, 2007). Incubation conditions may significantly affect hatchling traits in this species (Lin & Ji, 1998; Du & Ji, 2006; Du & Feng, 2008). The lizard thus provides an ideal opportunity to test for the effects of maternal investment and developmental plasticity on offspring size. Female *T. septentrionalis* from northern populations are larger and produce bigger eggs than those from southern populations (Du *et al.*, 2005). However, the proximate mechanisms underlying this geographic variation have not been explicitly studied. In this study, we collected gravid females from five geographically separated populations along a latitudinal gradient. These lizards and their eggs were maintained under standardized conditions to test the relative importance of mother and egg characteristics, as well as incubation temperature, on offspring size, and thereby to verify the aforementioned mechanisms for females to produce larger offspring in high-latitude populations.

MATERIAL AND METHODS

EGG COLLECTION

We collected 276 adult females of *T. septentrionalis* from five geographically separated localities along a latitudinal gradient in eastern China: Chuzhou (32°18′N, 118°18′E), Anji (30°38′N, 119°41′ E), Lishui (28°26′N, 119°54′E), Dongtou (27°50′N, 121°28′E), and Ningde (26°40′N, 119°33′E). The annual average temperature at these localities was 15.2, 16.0, 18.1, 17.3, and 19.3°C, respectively. Of the 276 females, 36 were collected from Chuzhou, 20 from Anji, 77 from Lishui, 75 from Dongtou, and 68 from Ningde. The lizards were captured from two or three sites separated by several kilometres in each locality, and were transported to our laboratory at Hangzhou Normal University, where they were housed indoors following the measurement of snout–vent length (SVL) (see detail in Du *et al.*, 2005). Gravid females were kept individually in terraria (200 × 150 × 200 mm) with a layer of 10 mm of moist sand where they laid their eggs. The terraria were checked several times a day, and freshly laid eggs were moved and weighed (±0.001 g) promptly. Females laid their first clutch soon after they were collected in the field (Du *et al.*, 2005): the eggs from the first clutch were used in this study.

EGG CONTENT

One egg was randomly selected from 16–53 clutches, depending on populations, to determine the egg components. We opened the egg, transferred the fresh egg yolk into a pre-weighed small foil dish and weighed it. Yolk and eggshells were then dried for 48 h in an oven at 65°C and weighed again. The lipid and energy contents of the yolk were determined for the Chuzhou, Lishui, and Dongtou populations. Non-polar lipids were extracted from dried samples using the Soxhlet apparatus for a minimum of

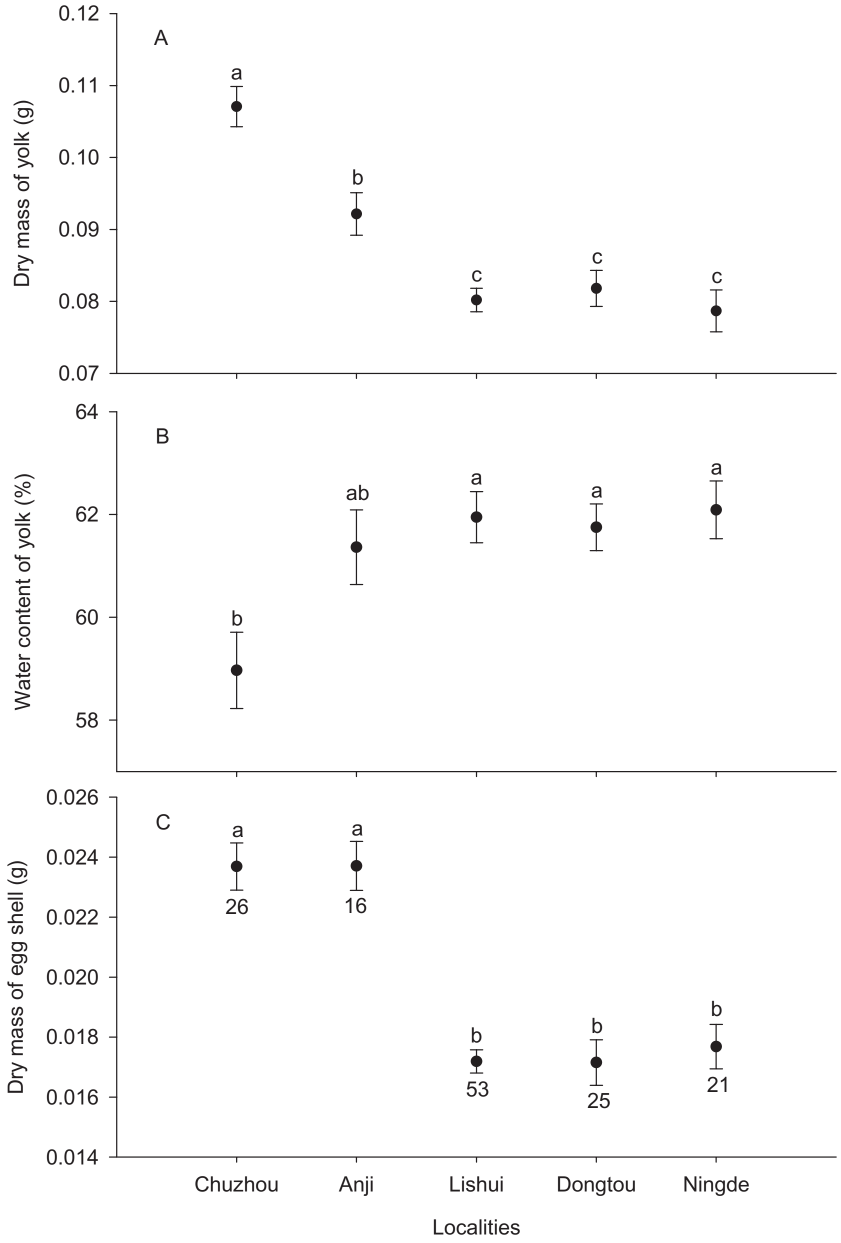

Figure 3. Interpopulation variations in yolk mass, water content and eggshell mass of eggs in the northern grass lizard *Takydromus septentrionalis*. Yolk mass and eggshell mass are shown as mean values adjusted for egg size. Sample sizes are indicated under the error bars in the lower graph, but also apply to the upper panels. Means indicated by different letters above their error bars differ significantly (Tukey's test).

5.5 h, with absolute ether as the solvent. The energy densities of yolks were determined by burning them in a WGR-1 adiabatic calorimeter (Changsha Instruments, China).

EGG INCUBATION AND HATCHLING SIZE

Eggs were incubated in small containers filled with vermiculite (water potential, –12 kPa), and assigned to two temperature treatments of 24 and 27°C using a split-clutch design. Each container had about 15 eggs from different clutches. All containers were weighed daily, and, if necessary, water was added to compensate for evaporative losses and water absorbed by the eggs. The containers were moved daily among shelves to minimise the potential effects of the thermal gradient inside the incubator. Towards the end of the incubation period, we checked the

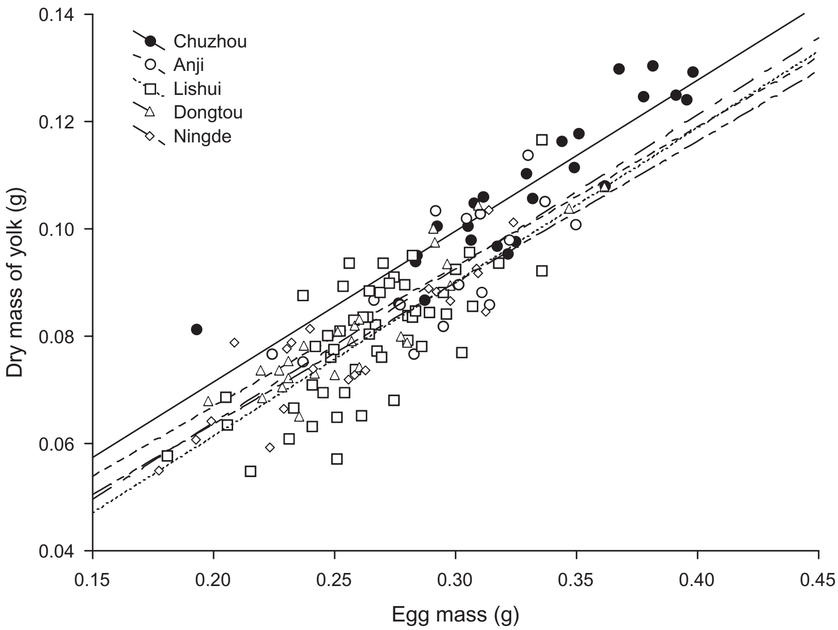

Figure 4. Relationships between egg size and dry mass of the yolk in the five geographically separated populations of the northern grass lizard *Takydromus septentrionalis*. If controlled for size, eggs from the Chuzhou population contained more yolk than those from other populations.

containers several times a day to collect hatchlings. Once hatchlings emerged, they were weighed (±0.001 g) and measured SVL (±0.01 mm) promptly.

STATISTICAL ANALYSIS

One-way ANOVAs were used to test interpopulation differences in maternal SVLs, and water and lipid contents of yolks. One-way ANOVAs and ANCOVAs with maternal SVL or egg mass as a covariate were used to determine the differences among populations in mean egg mass, shell mass, yolk mass and egg energy. Mixed-model ANOVAs and ANCOVAs with egg mass as a covariate were employed to determine the interpopulation and among-temperature differences in hatchling SVL and body mass. The incubation container was included as a random factor in the mixed-model ANOVAs and ANCOVAs. Tukey's post hoc multiple comparisons tests were used to distinguish among the means of traits for each population.

RESULTS

GEOGRAPHIC VARIATION IN MATERNAL BODY SIZE AND EGG SIZE

Maternal SVL decreased from north to south along the latitudinal gradient ($F_{4,271} = 93.43$, $P < 0.00001$; Fig. 1A). Egg size showed a geographic pattern similar to that of maternal body size, with larger eggs in the two northern populations, Chuzhou and Anji, compared with the three southern populations, Lishui, Dongtou, and Ningde ($F_{4,271} = 24.55$, $P < 0.00001$; Fig. 1B). This geographic variation in egg size (ES) was related to maternal SVL (ES = 0.004SVL – 0.008, $r^2 = 0.244$, $F_{1,274} = 88.28$, $P < 0.00001$), but was also caused by sources other than maternal size. At a given body size, Chuzhou females produced larger eggs than those from other populations ($F_{4,270} = 7.26$, $P < 0.0001$; Fig. 2).

GEOGRAPHIC VARIATION IN EGG CONTENT

Egg content varied significantly among populations, with more yolk ($F_{4,136} = 24.10$, $P < 0.00001$) and less water ($F_{4,136} = 4.34$, $P = 0.002$) in the Chuzhou and Anji populations than in other populations (Fig. 3A, B). The dry mass of the eggshell was heavier in Chuzhou and Anji populations than in the other three populations ($F_{4,136} = 26.63$, $P < 0.00001$; Fig. 3C). The difference in egg yolk was still significant among populations, even after the effect of egg size was removed ($F_{4,135} = 6.59$, $P < 0.0001$), with more yolk in Chuzhou eggs than in those of other populations (Fig. 4). Although egg yolks had a lower percentage of lipid in the Chuzhou population than the Lishui and Dongtou populations ($F_{2,94} = 5.34$, $P = 0.006$; Fig. 5A), eggs of the Chuzhou population contained more energy than those of the other populations, both before ($F_{2,94} = 32.64$, $P < 0.00001$) and after ($F_{2,93} = 4.63$, $P = 0.01$) the effect of egg size was removed (Fig. 5B). The energy content

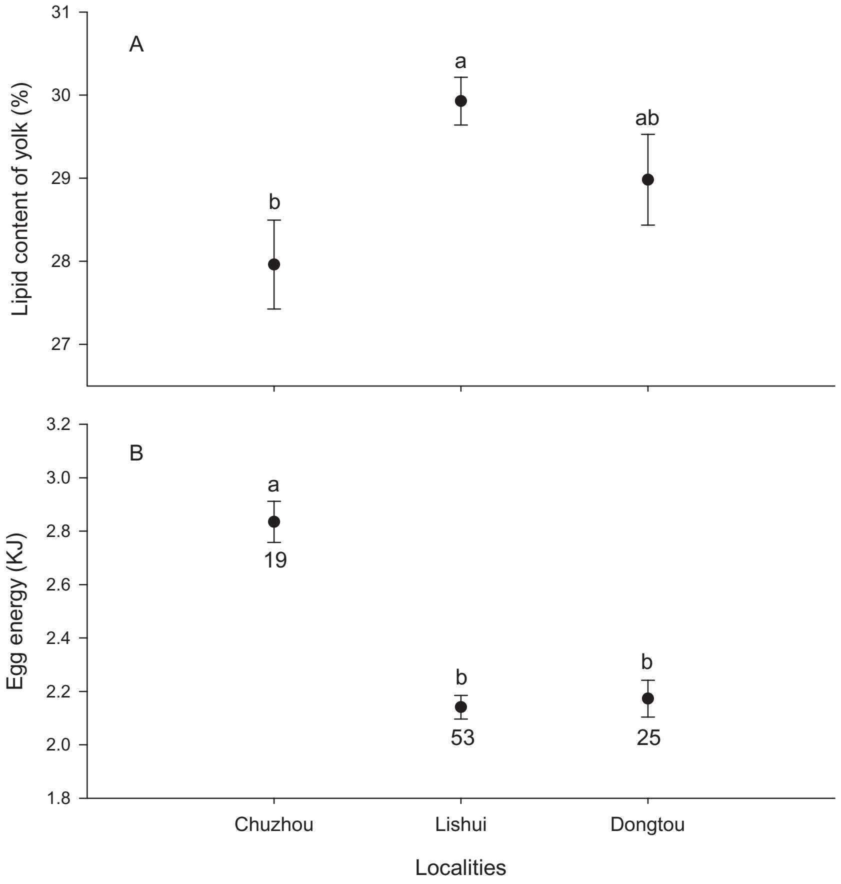

Figure 5. Interpopulation variations in lipid and energy contents of egg yolk in the northern grass lizard *Takydromus septentrionalis*. Data are shown as means ± SEs. Sample sizes are indicated underneath the error bars in the lowest panel, and apply to all panels in the figure. Means indicated by different letters above their error bars differ significantly (Tukey's test).

of eggs from Chuzhou population was still higher than the other two populations after adjustment for lipid content ($F_{2,93} = 27.32$, $P < 0.00001$).

THE EFFECTS OF POPULATION ORIGIN AND INCUBATION TEMPERATURE ON HATCHLING MASS

The hatchling body mass (HBM) and hatchling snout–vent length (HSVL) of hatchlings differed significantly among populations (HBM, $F_{4,89} = 11.26$, $P < 0.001$; HSVL, $F_{4,89} = 6.10$, $P < 0.01$), but were not affected by incubation temperature (all $P > 0.2$), or by an interaction between population and incubation temperature (all $P > 0.7$). Hatchling size was significantly larger in the Chuzhou population than in the other populations (Fig. 6). Egg size variation partly accounted for this geographical variation in hatchling size, given the positive relationship between hatchling size (HBM and HSVL) and egg mass (EM) in all populations ($HBM = 1.255EM - 0.016$, $F_{1,137} = 469.76$, $P < 0.00001$; $HSVL = 32.48EM + 17.30$, $F_{1,137} = 190.31$, $P < 0.00001$), as well as in individual populations (all $P < 0.01$). Even after the effect of egg size was statistically removed, the pattern of geographic variation in hatchling mass did not change, with heavier hatchlings from similar sized eggs in the Chuzhou population compared with those in other populations ($F_{4,88} = 3.03$, $P = 0.04$).

DISCUSSION

Females produced larger eggs and thus larger offspring in northern populations compared with the females of southern populations of *T. septentrionalis*. Such geographic patterns in egg size and offspring size are common in reptiles (Dunham, Miles & Reznick, 1988; Ji *et al.*, 2002; Ji & Wang, 2005; Oufiero *et al.*, 2007). Two different theoretical models both predict larger eggs and offspring in northern populations. Models of energetic constraints predict that females should produce relatively large offspring when environmental conditions (e.g. cold environment in

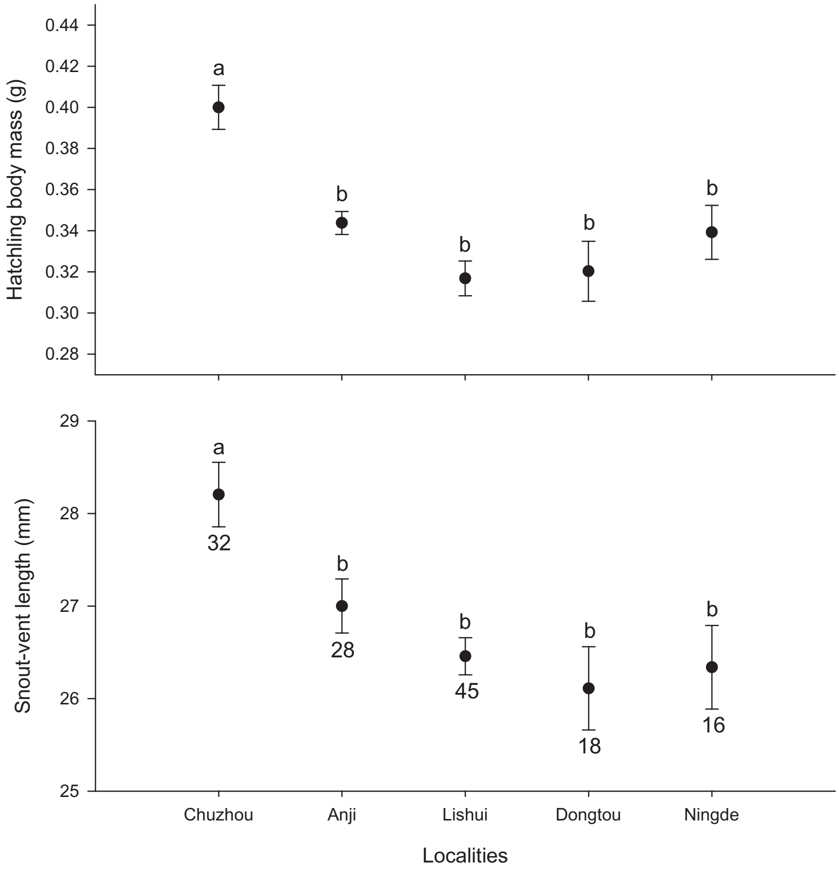

Figure 6. Geographic variations in hatchling size (body mass and snout–vent length) in the northern grass lizard *Takydromus septentrionalis*. Data are shown as means ± SEs. Sample sizes are indicated underneath the error bars in the lowest panel, and apply to both panels in this figure. Means indicated by different letters above their error bars differ significantly (Tukey's test).

northern populations) retard the growth of offspring (McGinley, Temme & Geber, 1987; Perrin, 1988; Yampolsky & Scheiner, 1996). Optimality models predict that selection would favour an offspring size that optimizes parental fitness (Smith & Fretwell, 1974; Parker & Begon, 1986; Einum & Fleming, 2000). Lizards in northern populations are exposed to a short activity season and therefore experience low food availability, and so large individuals would be more likely to survive to maturity, and thus may be favoured by natural selection (Adolph & Porter, 1993; Angilletta *et al*., 2004). In addition, large egg (offspring) might be a consequence of the evolution of larger females that can be achieved by delayed maturation in northern populations (Angilletta *et al*., 2004; Angilletta *et al*., 2006). Our study demonstrates that egg size increases hierarchically in northern populations. In the Anji population, females produced large eggs simply through an increase in their body size. In the Chuzhou population, egg size not only increased as a result of larger females, but also increased through the production of larger eggs relative to the female's body size. This implies that the proximate mechanisms underlying the superficially similar phenotypic trait of larger egg size may differ among populations.

Females may produce large hatchlings not only by increasing egg size, but also by investing more energy into eggs. Female *T. septentrionalis* from Chuzhou, the northernmost population, invested more yolk, and thus energy, into eggs than did those from the southern populations (Fig. 4). Why do females from the northern populations invest more energy into eggs in addition to increasing egg size? Despite that females can increase egg size and hatchling size to maximize their fitness in northern populations, the enlargement of egg size may be constrained either by a trade-off between egg size and clutch size, or by physical limits such as the female pelvic girdle (Congdon & Gibbons, 1987). Given these limits, increasing yolk investment allows females in the northern populations to further increase hatchling size in addition to enlarging egg size. Interestingly, females from the northern population of Chuzhou laid eggs with more yolk, but with a lower proportion of lipids, than those from southern populations. The lower lipid level could be attributable to the limited availability of lipids that a female can accumulate before producing a clutch of eggs or an increasing proportion of protein investment in yolk. Disentangling these causes requires further studies to quantify the lipids stored by females and the component of the lipoproteins that are invested in eggs. A similar pattern of lipid concentration was found in eggs from different geographic populations of the North American lizard *Sceloporus undulatus* (Bosc & Daudin in Sonnini & Latreille, 1801), but again the reason for this trend was not identified (Oufiero *et al*., 2007).

Although incubation temperature may affect the energy conversion coefficient during embryonic development (Angilletta, Winters & Dunham, 2000; Booth, Thompson & Herring, 2000), and in turn, hatchling size, in oviparous reptiles (Deeming, 2004), the hatchling size of *T. septentrionalis* remained remarkably constant at the incubation temperatures of 24 and 27°C that span the main range of mean nest temperatures (Du & Ji, 2006; Du & Feng, 2008). Therefore, we can reasonably conclude that differences in nest temperatures would explain little of the geographic variation in hatchling size.

In oviparous species, egg size is traditionally regarded as a proxy of offspring size. Our study indicates that both egg size and energy investment in eggs may determine offspring size. Given the substantial variations in energy and nutrients of eggs among and within species (Nagle *et al*., 1998; Booth, 2003; Oufiero *et al*., 2007; this study), quantifying the difference in maternal investment in eggs is critical to understanding how females affect offspring size. More generally, apart from energy and nutrients, other maternal resources such as hormones, antioxidants, and antibodies allocated by females to eggs may play important roles in determining offspring fitness in oviparous species (Mousseau & Fox, 1998; Lovern & Wade, 2003; Boulinier & Staszewski, 2008). Given the diversity of eggs both among and within species in reptiles, there are ample opportunities to explore maternal effects on offspring fitness.

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