The influence of maternal thermal environments on reproductive traits and hatchling traits in a Lacertid lizard, *Takydromus septentrionalis*

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Abstract

The thermal environment can induce substantial variation in important life-history traits. Experimental manipulation of the thermal environment can help researchers determine the contribution of this factor to phenotypic variation in life-history traits. During the reproductive season, we kept female northern grass lizards, *Takydromus septentrionalis* (Lacertidae), in three temperature-controlled rooms (25, 28 and 32 °C) to measure the effect of the maternal thermal environment on reproductive traits. Maternal thermal environment remarkably affected reproductive frequency and thereby seasonal reproductive output, but had little effect on reproductive traits per clutch or hatchling traits. Females kept at 32 °C produced more clutches and thus had shorter clutch intervals than females from 28 to 25 °C. Clutch size, clutch mass, relative clutch mass, egg size and hatchling traits did not vary among the three treatments. The eggs produced by the females were incubated at 27 °C and the traits of hatchlings were measured. The result that egg (offspring) size was independent of maternal thermal environments is consistent with the prediction of the optimal egg size (offspring) theory. The eggs produced by low temperature females (28 and 25 °C) took longer time to complete their post-oviposition development than did eggs produced by high temperature females (32 °C). This suggests that the eggs from low temperatures might have been laid when the embryos were at relatively early stages. Therefore, maternal thermal environment prior to oviposition could affect post-oviposition development in *T. septentrionalis*.

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1. Introduction

Understanding phenotypic plasticity of life-history traits and its proximate and ultimate causes are of the central importance in life-history theory (Roff, 2002). Squamate reptiles make excellent model for studies on this topic (Tinkle, 1969; Dunham et al., 1988; Niewiar-owski, 1994; Forsman and Shine, 1995) because their life-history traits are strongly influenced by environmental factors (Adolph and Porter, 1993). Such studies indicate that life-history variation is due to both genetic differences and proximate effects. For example, a large proportion of inter-population differences in reproductive output of reptiles may be simply caused by local conditions such as thermal environment and/or food availability rather than genetically coded responses to geographically variable selective regimes (Ballinger, 1983; Ford and Seigel, 1989; James and Whitford,

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1994; Madsen and Shine, 2000b). To interpret the causal basis for observed variation in life histories, some authors sought adaptive explanations for life-history patterns on the basis of predictions form life-history theory, while others emphasize proximate causes of life-history variation (Dunham et al., 1988; Niewiarowski, 1994; Madsen and Shine, 2000c). Nonetheless, teasing apart proximate (e.g. temperature, food availability) versus ultimate (genetic) sources of variation in reproductive parameters remains a major challenge for biologists. The most robust evidence comes from experimental manipulations of environmental factors such as thermal conditions and food availability, but such studies have only been conducted on a few reptilian species (Ford and Seigel, 1989; Shine and Harlow, 1993; James and Whitford, 1994).

Thermal environment can change reptilian life-history traits via its effect on embryogensis, postnatal development, or reproduction (Sinervo and Adolph, 1989; Deeming and Ferguson, 1991; Adolph and Porter, 1993; Shine and Downes, 1999). In viviparous reptiles, several studies indicate that thermal environment experienced by gravid reptiles can affect their offspring phenotypes (Shine and Harlow, 1993; Qualls and Shine, 1996; Sorci and Clobert, 1997; Shine and Downes, 1999). Similarly, in oviparous reptiles, the effects of incubation temperature on embryonic development and hatchling traits are well known (Deeming and Ferguson, 1991; Shine, 2003). However, little information is available on such effects of thermal environments experienced by oviparous species during pregnancy prior to oviposition. The most interesting questions in this respect would be: (1) Do maternal thermal environments affect embryonic development and survival? and (2) Do maternal thermal environments influence phenotypic traits of hatchlings?

We carried out an experiment on a Chinese Lacertid lizard, *Takydromus septentrionalis*, to examine the above-mentioned topics. Female *T. septentrionalis* were kept in temperature-controlled rooms during the reproductive season. To test the effect of the maternal thermal environment on female reproductive strategies, we measured female reproductive output during the period that the lizards were kept in captivity. To determine the influence of the maternal thermal environment on offspring traits, we incubated all eggs produced by these females at a constant temperature, and measured morphology and locomotor performance of the resultant hatchings.

2. Materials and methods

2.1. Study species

The northern grass lizard, *T. septentrionalis*, is a small (up to 80 mm snout-vent length [SVL]), diurnal, oviparous lizard widely distributed in central and southern China (Zhao and Adler, 1993). Female *T. septentrionalis* produce 1–5 clutches with 1–5 eggs per clutch from early April to later July (Ji et al., 1998). In this species, field body temperatures average 28.3 °C in May and 32.4 in July for populations from Zhoushan islands, Zhejiang (Ji et al., 1996); reproductive traits such as seasonal fecundity and egg size significantly differ among geographically separated populations that experience different thermal environments (Du, 2003).

2.2. Methods

In early April 2003, a total of 104 adult *T. septentrionalis* (75 females and 30 males) was captured from Dongyang (29°27′N 120°23′E) in Zhejiang province of eastern China. The wild lizards may maintain active body temperature ranging from 19.5 to 36.3 °C during the reproductive season (Ji et al., 1996). We thus test the effects of temperature on reproductive traits at 25, 28, and 32 °C, which represent the low, mediate and high thermal environments experienced by the animals in the field. After being transported to Hangzhou Normal College, the animals were individually marked (toe-clipped) and randomly separated into three groups with 25 females and 10 males in each group. Each group of animals was evenly housed in three enclosures ($120 \times 60 \times 30 \, cm^3$) with sand substrate before they were transported to three temperature-controlled rooms set at the experimental temperatures, respectively (25, 28, 32 ± 1 °C). The lights in the rooms were switched on at 0730 h and off at 1830 h. Food (larvae of *Tenebrio molitor*) and water (containing mixed vitamins and minerals) were provided ad libitum.

We palpated the abdomen of females every 5 days, and any lizard with oviductal eggs was transferred to a small glass terrarium ($20 \times 15 \times 20 \, cm^3$) filled with 2 cm-depth of moist sand. Each small terrarium was checked at least six times a day for freshly laid eggs. By the end of July, we found no evidence of oviductal eggs or large yolked follicles in the females, and all animals were released in the field where they were captured.

All eggs produced by the females were weighed (± 0.001 g) promptly so as to minimize initial mass change due to water exchange. Immediately after being weighed, one egg from each clutch was dissected. Yolks from dissected eggs were placed in preweighed small aluminum foil dishes and weighed. Shells were rinsed in distilled water, dried by blotting with a paper towel, and weighed. Egg yolks and shells were then oven dried to a constant mass at 65 °C and weighed again. The remaining eggs ($n = 138$) were individually numbered and placed in containers filled with moist vermiculate (Du et al., 2003b) and then incubated at 27 °C. The water content of the substrate was kept constant by

adding water on daily basis to compensate for evaporative loss and water absorbed by eggs. To minimize any effects of thermal gradients inside the incubator, we moved containers among shelves daily according to a predetermined schedule.

Towards the end of incubation, containers were checked at least five times a day. After being weighed, each hatchling was assessed for its locomotor performance immediately by chasing the lizards with an artist's paintbrush along a 1.5-m racetrack. Prior to each trial, the hatchling was placed in an incubator at 30 °C for 30 min. The locomotor performance of each lizard was recorded with a Panasonic video camera. Videotapes were then examined for sprint speed over the fastest 150-mm interval and maximum distance in a dash. After the locomotor tests, we measured SVL, tail length, and head size (length and width) of the lizards.

We calculated relative clutch mass (RCM) as the ratio of clutch mass to maternal postoviposition mass (Shine, 1980). One-way ANOVA and ANCOVA were used to compare the between-temperature differences in seasonal reproductive output. Two-way ANCOVA was used to detect the effect of temperature and clutch number (first vs later clutches) on the reproductive traits, and the effect of temperature and sex on hatchling traits. Tukey's multiple comparisons were used as post hoc tests to determine the differences among the reproductive traits of females from different thermal environments.

3. Results

3.1. Reproductive output

The maternal thermal environment significantly affected the proportion of females that were reproductive during the experiment ($\chi^2 = 8.03$, df $= 2$, $P < 0.05$). Ninety-six percent (24/25) of 28 °C females produced at least one clutch in the reproductive season, whereas only 72% (18/25) of females laid eggs both in 25 and in 32 °C. Maternal thermal environment also significantly affected total seasonal reproductive output of the females that laid eggs. An analyses of ANOVA indicated that clutch frequency significantly affected by the thermal environments ($F_{2,57} = 9.91$, $P = 0.0002$). Total seasonal fecundity (total number of eggs) and total clutch mass were positively correlated with snout-vent length of females (all $P < 0.05$). So, ANCOVAs with maternal snout-vent length as the covariate were used in data analyses, and showed that total seasonal fecundity and total clutch mass differed among the females from different thermal environments (total seasonal fecundity: ANCOVA-$F_{2,56} = 6.56$, $P = 0.003$; total clutch mass: ANCOVA-$F_{2,56} = 4.61$, $P = 0.01$). Post hoc tests

indicated that the females from 32 °C produced more clutches and had greater total seasonal fecundity and total clutch mass than did those from 28 and 25 °C (Fig. 1a–c). Clutch intervals were shorter for 32 °C females than for 28 and 25 °C females in all clutches (temperature: $F_{2,145} = 12.68$, $P = 0.00001$; clutch: $F_{1,145} = 1.36$, $P = 0.24$; interaction: $F_{2,145} = 0.29$, $P = 0.75$; Fig. 2).

Because there were no significant differences in reproductive outputs for the second, third and fourth clutches (all $P > 0.05$), we pooled the data from these clutches together (henceforth termed later clutches). All reproductive traits, including clutch size, clutch mass, egg mass and relative clutch mass, were independent of environmental temperatures experienced by the gravid females, but differed between the first and later clutches (Table 1, Fig. 3).
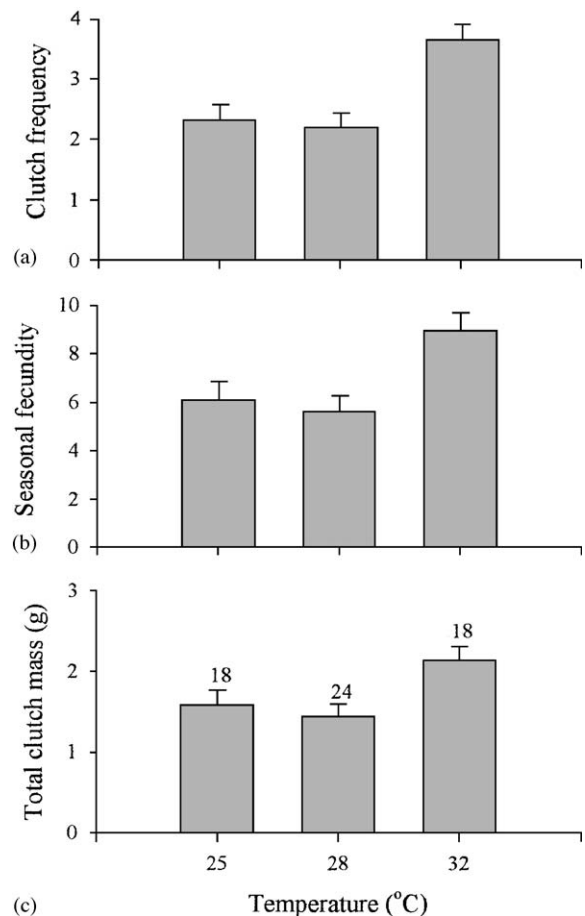

Fig. 1. The effect of the maternal thermal environment on seasonal reproductive output in the northern grass lizard, *T. septentrionalis*. The graphs show mean values and associated standard errors. Numbers above the error bars in the lower graph are sample sizes, and apply to all graphs within this figure.
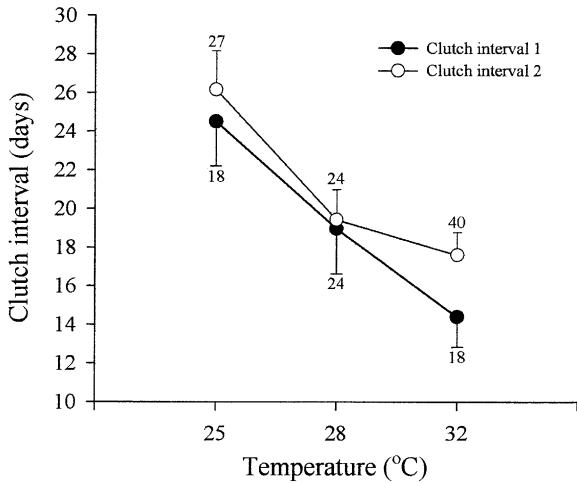
Fig. 2. Clutch intervals in female northern grass lizards, *T. septentrionalis*, kept in different thermal environments. The graphs show mean values and associated standard errors. Numbers above or under the error bars are sample sizes. Clutch interval 1 = delayed days of the first clutch after the female were captured from field; Clutch interval 2 = clutch intervals between successive clutches.

Table 1
The results of two-way ANCOVA analyses between temperature and among clutch differences on reproductive traits in northern grass lizards (*T. septentrionalis*)

	Temperature	First vs later clutches	Interaction
Clutch size	$F_{2,144} = 0.04$ $P = 0.96$	$F_{1,144} = 22.72$ $\boldsymbol{P < 0.00001}$	$F_{2,144} = 1.82$ $P = 0.17$
Egg mass	$F_{2,144} = 2.14$ $P = 0.12$	$F_{1,144} = 12.20$ $\boldsymbol{P < 0.001}$	$F_{2,144} = 0.74$ $P = 0.48$
Clutch mass	$F_{2,144} = 0.39$ $P = 0.68$	$F_{1,144} = 40.77$ $\boldsymbol{P < 0.00001}$	$F_{2,144} = 1.13$ $P = 0.32$
Relative clutch mass	$F_{2,144} = 0.98$ $P = 0.38$	$F_{1,144} = 23.30$ $\boldsymbol{P < 0.00001}$	$F_{2,144} = 1.98$ $P = 0.14$

For relative clutch mass, clutch mass was included as a dependent variable and postpartum body mass was used as a covariate. For other variables, maternal snout-vent length was used as the covariate. Significant effects are shown in bold type.

3.2. Female body condition

A two-way ANCOVA with SVL as the covariate indicated that female body mass significantly differed
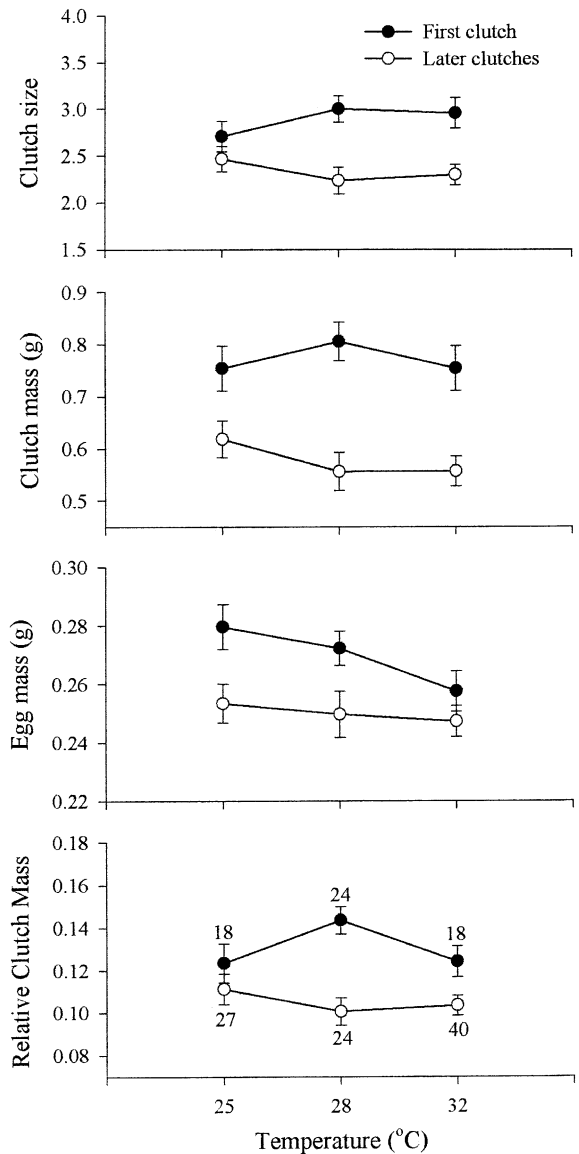

Fig. 3. Clutch size, egg size and clutch mass of female northern grass lizards, *T. septentrionalis*, kept in different thermal environments. The graphs show mean values and associated standard errors. Numbers above the error bars in the lower graph are sample sizes, and apply to all graphs within this figure.

between clutches, but not among temperatures (temperature: $F_{2,144} = 2.22$, $P = 0.11$; clutch: $F_{1,144} = 13.73$, $P < 0.001$; interaction: $F_{2,144} = 2.22$, $P = 0.11$). We quantified maternal body condition using residual scores from the linear regression of log-transformed body mass to log-transformed SVL. Females had higher body condition after the first clutch than after later clutches. An analysis of partial correlation among maternal SVL, body mass and total clutch mass revealed negative
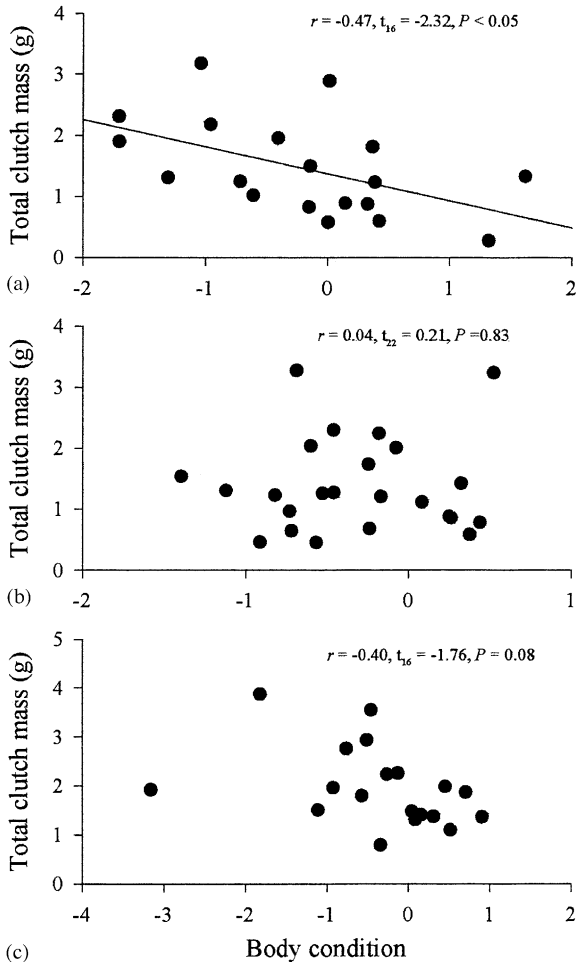
Fig. 4. The relationships between postpartum body conditions and total clutch mass of females from different thermal environments. "Body condition" was calculated as residual scores from the linear regression of the log-transformed body mass to the log-transformed SVL. (a) 25 °C; (b) 28 °C; (c) 32 °C.

correlations between female postpartum body condition and the amount of reproductive output in 25 °C females, but not in 28 and 32 °C (Fig. 4).

3.3. Egg contents

No significant differences in dry mass of egg yolk were found among temperatures or clutches (temperature: $F_{2,79} = 0.98$, $P = 0.38$; clutch: $F_{1,79} = 0.15$, $P = 0.69$; interaction: $F_{2,79} = 0.10$, $P = 0.91$). Similarly, there were no significant differences in water contents of the eggs from different thermal environments and clutches

(temperature: $F_{2,79} = 0.21$, $P = 0.81$; clutch: $F_{1,79} = 2.55$, $P = 0.11$; interaction: $F_{2,79} = 0.64$, $P = 0.53$).

3.4. Egg incubation and hatchling traits

Maternal thermal environment did not affect hatching success (G-test, $G = 1.82$, df = 2, $P > 0.05$; Fig. 5a) or hatchling sex (G-test, $G = 0.08$, df = 2, $P > 0.05$). Incubation duration was independent of egg mass ($r = 0.01$, $F_{1,59} = 0.01$, $P = 0.92$), but was significantly influenced by the environmental temperatures that females had experienced prior to oviposition ($F_{1,58} = 5.42$, $P < 0.01$). Hatchlings from 25 °C piped their eggshells later than did their counterparts from 28 and 32 °C (Fig. 5b).

All hatchling traits measured in this study, including morphology (body size and head size) and locomotor performance (sprint speed and maximum distance in a dash), did not differ among the three thermal treatments or between sexes (Tables 2 and 3).
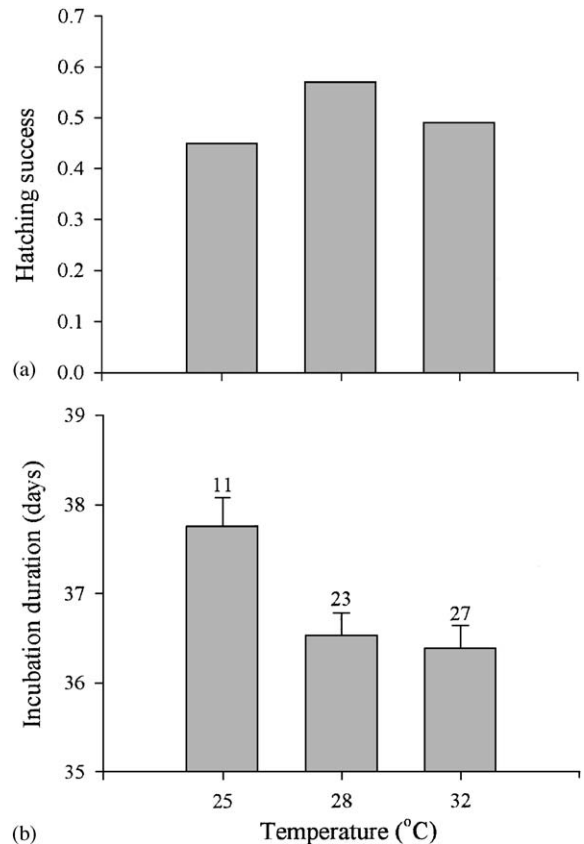

Fig. 5. Hatching success and incubation duration of eggs produced by females kept in different thermal environments. Incubation durations are shown mean values and associated standard errors. Numbers above the error bars are sample sizes.

Table 2
Morphology and locomotor performance of hatchling northern grass lizard, *T. septentrionalis*, produced by females from different thermal environments

Maternal thermal environment		25 °C	28 °C	32 °C
Snot-vent length	M	25.40±0.22 (8)	25.86±0.25 (14)	24.87±0.42 (12)
	F	23.31±1.40 (2)	25.34±0.47 (7)	25.27±0.37 (12)
Wet body mass	M	0.346±0.013 (8)	0.374±0.009 (14)	0.341±0.010 (12)
	F	0.303±0.005 (2)	0.355±0.014 (7)	0.336±0.009 (12)
Dry body mass	M	0.060±0.003 (8)	0.070±0.002 (14)	0.063±0.002 (12)
	F	0.055±0.001 (2)	0.066±0.002 (7)	0.062±0.003 (12)
Tail length	M	51.48±1.40 (8)	54.79±1.03 (14)	50.25±1.54 (12)
	F	42.51±0.99 (2)	53.14±1.38 (7)	52.57±1.16 (12)
Head length	M	6.57±0.08 (8)	6.80±0.05 (14)	6.49±0.10 (12)
	F	6.26±0.18 (2)	6.54±0.05 (7)	6.55±0.05 (12)
Head width	M	4.06±0.03 (8)	4.13±0.04 (14)	4.04±0.03 (12)
	F	3.97±0.09 (2)	4.06±0.08 (7)	3.99±0.03 (12)
Sprint speed	M	108.7±32.7 (8)	94.1±9.2 (13)	75.5±6.7 (10)
	F	80.0±62.9 (2)	81.7±9.4 (7)	82.3±9.4 (12)
Maximum distance	M	91.9±13.4(8)	75.8±4.9 (13)	79.5±10.9 (10)
	F	85.0±30.0 (2)	87.1±19.4 (7)	67.5±5.5 (12)

Data are expressed as mean ± SE. Sample sizes were indicated in parentheses.

4. Discussion

The maternal thermal environments significantly affect clutch frequency in *T. septentrionalis*. As found in other reptiles (Naulleau, 1986; Shine and Harlow, 1993; Shine and Downes, 1999), the delayed parturition of females from low temperatures is expected. Low temperatures can retard embryonic development (Deeming and Ferguson, 1991), or significantly decrease food intake and assimilation efficiency, and thereby affect net energy intake of *T. septentrionalis* (Ji et al., 1996). Accordingly, compared with the high-temperature females, the low-temperature females take longer time to accumulate the same amount of energy for formation of a clutch and thus have longer clutch intervals. Such effects of the maternal thermal environment are of ecological importance. Female *T. septentrionalis* produce their first clutch depending on both energy stored in body reserves and current food intake, whereas later clutches exclusively depending on current food intake (Du et al., 2003a). The number of eggs produced by a female per season would largely depend on how much energy the mother can get. Therefore, we believe that, in addition to its importance to life-history traits such as growth and survival rates (Sinervo and Adolph, 1989;

Adolph and Porter, 1993), the thermal environment can directly affect the reproductive output of the wild females, and is an important cause that can induce geographic variation in life-history traits in this species.

Unlike clutch frequency, clutch size, clutch mass and egg size were not affected by the maternal thermal environment. Although longer gestation means lower clutch frequency and thus lower seasonal fecundity, the low-temperature females did not compensate by decreasing clutch size or egg size to achieve high fecundity. Instead, female *T. septentrionalis* discontinued reproduction in the current reproductive season or postponed oviposition until they had access to enough energy to produce a clutch of eggs. Therefore, if the females have access to enough energy to form a clutch of eggs, they try to produce a relatively unchanged number of eggs with "fixed" egg size regardless of environmental temperatures. To achieve this aim, those low-temperature females facing energy assimilation constrains even sacrifice their body reserves to maintain the reproductive output per clutch (Fig. 4). This strategy fits well with predictions from the "fecundity-independent costs" hypothesis, which suggests that reproduction will occur only when the available energy exceeds some threshold level in animals with fecundity-independent costs (Bull

Table 3
Effects of temperature and sex on hatchling traits in the northern grass lizard, *T. septentrionalis*

	Temperature	Sex	Interaction
Snot-vent length	$F_{2,48} = 0.82$ $P = 0.44$	$F_{1,48} = 2.27$ $P = 0.14$	$F_{2,48} = 2.31$ $P = 0.11$
Wet body mass	$F_{2,48} = 0.77$ $P = 0.47$	$F_{1,48} = 2.41$ $P = 0.13$	$F_{2,48} = 0.29$ $P = 0.75$
Dry body mass	$F_{2,48} = 1.51$ $P = 0.23$	$F_{1,48} = 0.77$ $P = 0.39$	$F_{2,48} = 0.002$ $P = 0.99$
Tail length	$F_{2,48} = 1.28$ $P = 0.29$	$F_{1,48} = 0.04$ $P = 0.83$	$F_{2,48} = 0.21$ $P = 0.82$
Head length	$F_{2,48} = 1.45$ $P = 0.24$	$F_{1,48} = 1.98$ $P = 0.17$	$F_{2,48} = 1.48$ $P = 0.24$
Head width	$F_{2,48} = 1.29$ $P = 0.28$	$F_{1,48} = 0.82$ $P = 0.37$	$F_{2,48} = 0.24$ $P = 0.79$
Sprint speed	$F_{2,45} = 0.46$ $P = 0.63$	$F_{1,45} = 0.17$ $P = 0.68$	$F_{2,45} = 0.15$ $P = 0.85$
Maximum distance	$F_{2,45} = 0.76$ $P = 0.47$	$F_{1,45} = 0.0001$ $P = 0.99$	$F_{2,45} = 0.82$ $P = 0.45$

Neither temperature nor sex significantly affected the body size, morphology and locomotor performance of the hatchlings. Analyses of covariance were used to test the between treatment difference for body size and body mass using egg mass as a covariate and for morphology and locomotor performance using hatchling snout-vent length as a covariate.

and Shine, 1979; Madsen and Shine, 2000a). Such costs (in energy, risk, time, etc.) are those that are paid by any reproducing females, and do not increase with increasing clutch size (Bull and Shine, 1979). Unlike *T. septentrionalis*, some other squamates may change their clutch size to accumulate the variations in environmental factors (Demarco, 1989; Ford and Seigel, 1989; Seigel and Ford, 1991; James and Whitford, 1994; Madsen and Shine, 2000b; Bonnet et al., 2001).

Female *T. septentrionalis* did not change egg size and hatchling size in response to the thermal environment. In addition, there were no direct impacts of the maternal thermal environment on hatchling morphology and performance. Due to the lack of comparable data from other species, we cannot conclude whether the pattern that maternal thermal environment does not affect hatchling traits is widespread or not at all in oviparous reptiles. Instead of being affected by maternal thermal environment during gestation, offspring phenotypes of oviparous species may influence by post-oviposition thermal environment selected by the females via

maternal behavior, namely nest-site selection (Bull et al., 1988; Burger, 1990; Shine and Harlow, 1996; Shine et al., 1997). In viviparous lizards, however, the thermal environments during the gestation can significantly affect offspring traits (Shine and Harlow, 1993; Shine and Downes, 1999).

One interesting result of our study is that the maternal thermal environment significantly affects incubation duration of eggs, with longer incubation duration in the eggs produced by low-temperature females (Fig. 5b). In oviparous reptiles, incubation temperature significantly affects development rate of embryos, with low incubation temperature retarding embryonic development (Deeming and Ferguson, 1991). So it is reasonable to speculate that such effects equally occur to the embryos inside mother's body; the low female body temperature retards embryogensis during the developmental process of eggs. Therefore, our result suggests that maternal thermal environment may affect embryonic development and the eggs from low-temperature females might have been laid when the embryos were at relative early stages, although identifying the developmental stage of embryos from different environmental temperatures are needed to confirm this suggestion. In contrast, due to egg retention, the embryos of some lizard species are more developed at low temperatures than high temperature when hatching (Huey, 1977). Apart from the development of embryos, viability of embryos was also affected by maternal thermal environment. Previous studies on egg incubation in this species indicate that constant temperatures of 30 °C and upward damage embryos of *T. septentrionalis* and lead to low hatching success (Lin and Ji, 1998; Du, 2003). If such an effect is also true when early embryos develop in utero, the eggs from females kept at 32 °C are thus expected to have relatively low hatching success. However, our results showed that not only the hatching success of eggs from 32 °C but also that of eggs from the other two thermal regimes was low in this study (Fig. 5a). This suggests that constant temperatures (regardless of what temperature it is) experienced by females during gestation may be harmful to embryos in their early stage and hence, reduce the viability of the eggs, although the underlying mechanism of this phenomenon is unraveled.

In conclusion, the clear results from this study are that thermal environments experienced by female *T. septentrionalis* significantly affect embryonic development, clutch frequency and seasonal fecundity, but not egg size, clutch size, clutch mass or hatchling traits. This suggests that maternal thermal environments during the gestation may alter reproductive frequency rather than reproductive output per clutch in *T. septentrionalis*. Nonetheless, for teasing apart the causes of geographic variation in life history traits of this species, our experiment is preliminary, and long-term common garden and reciprocal transplant protocols are more

powerful approaches. These types of experiments may produce more detailed information on the proximate and ultimate causes of variation in life-history traits.

Acknowledgements

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