

Maternal Thermal Environment Induces Plastic Responses in the Reproductive Life History of Oviparous Lizards

Liang Ma^{1,2}
 Bao-Jun Sun¹
 Shu-Ran Li^{1,2}
 Wei Sha¹
 Wei-Guo Du^{1,*}

¹Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, People's Republic of China; ²University of Chinese Academy of Science, Beijing 100049, People's Republic of China

Accepted 6/23/2014; Electronically Published 8/21/2014

ABSTRACT

Adaptive plasticity may shift phenotypic traits close to a new optimum for directional selection and probably facilitates adaptive evolution in new environments. However, such plasticity has rarely been reported in life-history evolution, despite overwhelming evidence of life-history variation both among and within species. In this study, the temperatures experienced by gravid females of *Scincella modesta* were manipulated to identify maternally induced plasticity in reproductive traits and the significance of such changes in the evolution of life history. Consistent with the geographic pattern of life history, the study demonstrated that low temperatures delayed egg oviposition, resulting in a more advanced embryonic developmental stage at oviposition and shorter incubation periods compared with warm temperatures. In addition, females maintained at low temperatures produced larger eggs and hence heavier hatchlings than those at warm temperatures. This study demonstrated that environmental temperatures can induce plastic responses in egg retention and offspring size, and these maternally mediated changes in reproductive life history seem to be adaptive in the light of latitudinal clines of these traits in natural populations.

Introduction

Phenotypic plasticity provides organisms with the ability to alter their phenotypes in response to variations in environment. Tra-

ditionally, environmentally induced phenotypic variations were believed to constrain adaptive evolution by shielding genotypes from natural selection (Grant 1977). Recently, ecologists and evolutionary biologists have become increasingly concerned about the potential contribution of phenotypic plasticity in the process of evolution (Pigliucci et al. 2006), because increasing evidence suggests that a population can respond to a sudden environmental change via phenotypic plasticity and environmentally induced phenotypic variation could be integrated into genotypes by genetic assimilation (Pigliucci et al. 2006; Lande 2009). Given the diverse types of phenotypic plasticity (e.g., adaptive vs. nonadaptive) in response to environmental variation that have distinct consequences for evolution on ecological timescales, it is an important first step to distinguish between these types of plasticity before further exploring the ecological and evolutionary role of environmentally induced variation (Ghalambor et al. 2007).

Adaptive plasticity enables an organism to produce an average phenotype that is close to the optimum favored by selection and thus likely facilitate adaptive evolution in the new environment (Ghalambor et al. 2007). Maternally mediated changes in offspring phenotype (i.e., maternal effects) in response to environmental variation often increase offspring fitness in heterogeneous environments, exemplifying a typical case of adaptive plasticity (Bernardo 1996; Ghalambor et al. 2007; Sheriff and Love 2013). Such maternally mediated phenotypic plasticity may affect a range of reproductive life-history traits such as the timing of breeding, clutch size and egg (offspring) size (Pigliucci 2001). These life-history traits in ectothermic animals often vary substantially along the latitudinal cline, probably as a consequence of adaptation to geographic temperature variation (Denno and Dingle 1981; Stearns 1992; Niewiarowski 1994). Compared with low-latitude females, high-latitude mothers have longer egg retention, but later timing of breeding, which could increase embryonic development rate, and thus, reduce external incubation times, during which embryo survival success is negatively affected by the low temperature (Shine 1985, 2002b; Qualls and Andrews 1999). In addition, females from high-latitude environments tend to produce more and larger eggs, and hence, larger offspring than those from low-latitude environments (Laugen et al. 2003; Ji and Wang 2005; Morita et al. 2009), probably because larger offspring survive better in the thermally stressful environment at high latitude than smaller offspring (Yampolsky and Scheiner 1996; Fischer et al. 2003). Common garden experiments suggest that these geographic variations in life-history traits of ectothermic animals are because of the combined effects of genetic differences and phenotypic plasticity (Rodriguez-Diaz and Brana 2012; Sun et al. 2013).

* Corresponding author; e-mail: duweigu@ioz.ac.cn.

How would the reproductive life-history traits of a certain population respond if transferred to thermal conditions that differ from their natural habitat? If adaptive plasticity alters reproductive life history, it could be expected that females would retain their eggs and produce larger eggs and offspring when oviparous species shift to a cold region compared with those living in warm regions, in accordance with the latitudinal pattern of life-history variation found in lizards (Niewiarowski 1994; Angilletta and Dunham 2003; Sun et al. 2013). To test this hypothesis, a suitable system is required in which geographically separated populations have naturally developed and their life-history traits, including egg retention and egg size, show significant variation. The slender forest skink (*Scincella modesta*), a small-sized (to 55 mm snout-vent length [SVL]) oviparous scincid lizard inhabiting a relatively cold climate in eastern and central China (Lu et al. 2013), provides such an ideal model system to investigate the adaptive plasticity of life-history traits. Data on its reproductive life history are available for three geographically separated populations. Compared with their counterparts from low-latitude populations, females from high-latitude populations produce larger eggs with more developed embryos at oviposition (Luo et al. 2012; Lu et al. 2013). In this study, we manipulated the temperatures experienced by gravid females of *S. modesta* to test for the above-mentioned hypothesis of adaptive plasticity.

Material and Methods

Study Site and Animal Collection

The study site was located at a small gully among shaded forest in Beijing Songshan National Nature Reserve (1,000 m above sea level; 40°31'N, 115°47'E) in northern China. *Scincella modesta* is often active in the thick litter layer on the forest ground and basks in areas of sunlight penetrating the forest. The ambient temperatures were monitored at 1-h intervals during the reproductive season (from June 11 to June 30 in 2012) by randomly placing nine i-Buttons (Dallas Semiconductor, Dallas, TX; diameter, 15 mm; height, 6 mm) on the ground.

We captured adult females (>47 mm SVL) and adult males (>44 mm SVL) of *S. modesta* by hand from the Songshan population in May 2012. All captured lizards were transported to our laboratory in Beijing, where they were maintained together in communal cages (600 mm × 430 mm × 340 mm), containing a substrate of moist crushed coconut fiber. Each cage housed six or seven females and four males. For all individuals, SVL length was measured to 0.01 mm and body mass (BM) weighed to 0.001 g. Food (mealworms and crickets dusted with additional vitamins and minerals) and water were provided daily ad lib.

Thermal Treatment Applied to Gravid Females

We randomly assigned all gravid females to two thermal treatments: low temperature (18°C) and warm temperature (28°C). For both treatments, lizards were provided 8-h heating (from 0800 to 1600 hours) for behavioral thermoregulation by placing

a 40-W incandescent bulb above one side of each cage. We used two i-Buttons to record temperatures in each cage continuously for 20 d. The two thermal environments mimicked in the laboratory were either warmer or colder than the thermal environments from which the lizards were collected, while the extreme temperatures of both treatments were within the range of thermal environments in nature habitat (fig. 1). This experimental design enables us to look into how the reproductive life-history traits of a certain population would respond if transferred to thermal conditions that differ from their natural habitat. Although we did not measure the body temperature of lizards in this experiment, similar thermal treatments on the same species in our previous study have demonstrated that body temperatures of lizards during daytime differ among thermal regimes even when behavioral thermoregulation by lizards may partly compensate for differences in environmental temperature (Lu et al. 2013). The photoperiod was a natural light cycle (14L : 10D).

Egg Collection and Development Stage Identification

Females were palpated once every 3 d. We moved females with shelled oviductal eggs from communal cages to egg-laying cages (310 mm × 210 mm × 180 mm) with 2-cm moist crushed coconut fiber. We checked egg-laying cages four times per day for freshly laid eggs. Females laid the first clutch at 24 d after they were assigned to the thermal treatments. Fresh eggs were weighed (to 0.001 g) and marked with a unique number immediately after they were laid to minimize initial mass changes caused by water exchange. We measured and weighed post-oviposition females again before they were returned to the communal cages. One egg from each clutch was dissected to identify the embryonic stage according to the Dufaure and Hubert system (Dufaure and Hubert 1961).

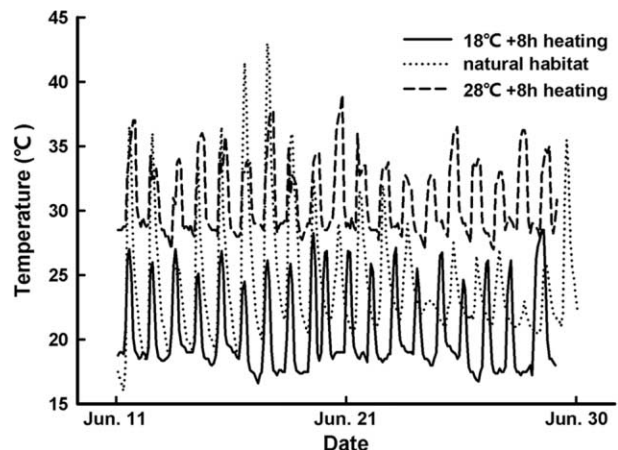


Figure 1. Thermal environment experienced by gravid females of *Scincella modesta* in natural habitats and in the laboratory.

Egg Incubation and Offspring Measurements

We half buried remaining eggs in plastic boxes (160 mm × 115 mm × 40 mm) filled with moist vermiculite (−220 kPa) and covered these boxes with perforated plastic membrane to retard water loss. These plastic boxes were then weighed once every week and if necessary were replenished with distilled water to compensate for water loss. Eggs from the same clutches were evenly distributed to two constant incubation temperatures (24° or 28°C) in two separate incubators (KB240, Binder, Stuttgart). These two temperatures represent low and high temperatures experienced by the eggs in their potential nests, respectively (fig. 1). We moved plastic boxes among shelves in incubators weekly to minimize effects of thermal gradients inside the incubators. Hatchling lizards were measured (SVL to 1 mm, BM to 0.01 g) once they emerged from eggs, and the time (days) between egg oviposition and hatching was calculated as the incubation period.

Statistical Analysis

The normality of distributions and homogeneity of all variances in the data were tested by the Kolmogorov-Smirnov test and Bartlett's test prior to analysis. To avoid pseudoreplication, analysis of incubation periods and hatchling traits (hatchling SVL and BM) were conducted on clutch means. The Mann-Whitney *U*-test was used to determine the effect of maternal thermal treatment on oviposition time (the number of days between the beginning of experimental treatment and oviposition) and the developmental stage of embryos at oviposition. We conducted Student's *t*-tests to compare between treatment differences in maternal SVL, BM, clutch mass, and mean egg mass. One-way ANCOVAs were used to test the effect of maternal thermal treatment on clutch size with maternal SVL as the covariate. We used χ^2 tests to detect the effect of temperature regimes on hatching success. Two-way ANOVAs or ANCOVAs were used to determine the effects of maternal thermal treatment and incubation temperature on incubation period and hatchling traits, with initial egg mass as the covariate. All experiments in this study were performed under the approval (IOZ14001) from the Animal Ethics Committee at the Institute of Zoology, Chinese Academy of Sciences.

Results

Gravid females maintained at low temperature laid a single clutch of pliable-shelled eggs significantly later (about 17 d) than those maintained at warm temperature ($Z = 4.14$, $n = 26$, $P < 0.001$; fig. 2a). The developmental stage of embryos obtained following cold treatment was one stage more advanced when compared to that of embryos from warm treatment ($Z = 2.24$, $n = 20$, $P < 0.05$; fig. 2b). Body size (SVL and BM) of postoviposition females did not differ significantly between the two treatments (table 1). Whereas clutch size and clutch mass did not differ between the two thermal treatments, mean egg mass was significantly greater following cold treatment than warm treatment (table 1).

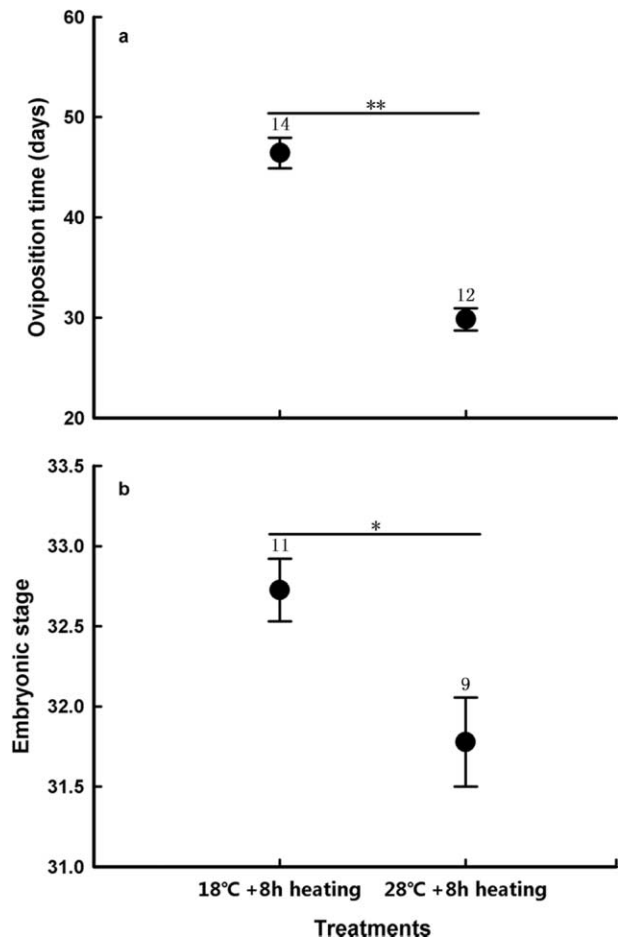


Figure 2. Oviposition time (a) and developmental stage of embryos at oviposition (b) in cold and warm treatments. Oviposition time was calculated as the number of days between the beginning of experimental treatment and oviposition. Statistical significance between groups was calculated by the Mann-Whitney *U*-test (one asterisk = $P < 0.05$; two asterisks = $P < 0.01$). Data are expressed as mean \pm SE. Numbers above error bars are sample sizes.

The egg incubation period not only was significantly affected by incubation temperature ($F_{1,35} = 344.7$, $P < 0.0001$), with a longer incubation period at 24° than 28°C, but also was affected by maternal thermal treatments, with eggs laid by females following cold treatment taking less time to hatch than those from females following warm treatment ($F_{1,35} = 4.24$, $P < 0.05$; fig. 3). Hatchling success was not affected by maternal thermal treatment ($X^2_1 = 2.7$, $P = 0.1$) or by incubation temperature ($X^2_1 = 0$, $P = 1$). Hatchlings from cold treatment were heavier than those from warm treatment both before ($F_{1,35} = 7.17$, $P = 0.01$) and after ($F_{1,34} = 5.62$, $P = 0.02$) the effect of initial egg mass had been statistically removed. Hatchling mass was also significantly affected by incubation temperature, with heavier hatchlings from 24° than from 28°C ($F_{1,34} = 8.95$, $P < 0.01$; fig. 4a). In contrast, the SVL of hatchlings did not differ between the two maternal thermal treatments ($F_{1,34} = 0.94$, $P = 0.33$) or the incubation thermal treatments ($F_{1,34} =$

Table 1: Body size and reproductive output of female slender forest skink *Scincella modesta* following cold and warm treatments

	Cold	Warm	<i>t</i>	<i>F</i>	df	<i>P</i>
<i>N</i>	14	12
SVL (mm)	53.63 ± .85	54.22 ± .92	.47	...	24	.64
Body mass (g)	2.12 ± .11	2.06 ± .12	.33	...	24	.75
Clutch size	5.6 ± .6	5.2 ± .624	1, 23	.63
Mean egg mass (g)	.144 ± .005	.124 ± .006	2.41	...	24	.02
Clutch mass (g)	.786 ± .094	.647 ± .086	1.08	...	24	.29

Note. Clutch size was positively related to maternal snout-vent length (SVL); an ANCOVA with SVL as the covariate was thus used to detect the between-treatment difference in clutch size.

0.16, $P = 0.69$; fig. 4b). Moreover, no significant interaction between maternal thermal treatment and incubation temperature was found on the incubation period ($F_{1,35} = 0.23$, $P = 0.64$), body mass ($F_{1,34} = 0.96$, $P = 0.33$), or SVL ($F_{1,34} = 0.79$, $P = 0.38$) of hatchlings.

Discussion

The reproductive life history of ectothermic animals such as breeding timing and offspring number and size often show adaptive evolution among geographic populations likely in response to environmental factors such as temperature (Angilletta and Dunham 2003; Sun et al. 2013). This study demonstrated that environmental temperature can induce adaptive plasticity in these life histories, which is consistent with the geographic pattern of life history among natural populations (fig. 2). We found that in *Scincella modesta*, cold temperature delayed egg oviposition and therefore resulted in a more advanced embryonic stage at oviposition, with a shorter incubation period compared to such events at warm temperature. In addition, females maintained in cold temperature produced larger eggs and hence heavier hatchlings than those in warm temperature.

It is well known that the females of ectothermic animals in cold regions tend to delay their egg oviposition and produce eggs with embryos at advanced developmental stages compared with their counterparts in warm regions (Fielding et al. 1999; Calderón-Espinosa et al. 2006; Rodríguez-Díaz and Brana 2012). Rarely, however, has this phenomenon of temperature effects on egg retention and embryonic development been reported to be associated with phenotypic plasticity (but see Telemeco et al. 2010). Consistent with a previous study that showed that low maternal body temperatures resulted in more advanced embryonic stage at oviposition in *Bassiana duperreyi* (Telemeco et al. 2010), this study indicated that experimental cold temperature postponed egg oviposition and extended the duration of egg retention, inducing females to produce a clutch of eggs with more developed embryos at oviposition. In contrast, our previous study indicated that experimental warming induced female *S. modesta* to lay eggs earlier but did not affect the developmental stage of embryos at oviposition (Lu et al. 2013).

Why do females produce eggs containing embryos at more advanced developmental stages in cold climates? First, embry-

onic development and offspring phenotypes are very sensitive to developmental conditions, particularly in the early post-oviposition stages; cold temperatures may reduce embryonic development and/or result in offspring of poorer quality (Qualls and Andrews 1999; Shine 2002a). A more advanced embryonic stage at oviposition may reduce the potential damage on embryos imposed by cold temperatures. Second, due to maternal thermoregulation, embryos in the maternal body cavity at a relatively high temperature may develop faster than those in the cold external environment. In consequence, the resultant offspring following prolonged egg retention should hatch sooner, having the advantage of increased time to acquire energy and seek shelter to survive the winter (Shine 1985; Rodríguez-Díaz et al. 2010). Third, long egg retention and advanced embryonic development at oviposition may shorten the incubation period (Calderón-Espinosa et al. 2006; Radder et al. 2008). A short incubation period reduces the time that embryos may be at risk of predation or exposure to potentially lethal extremes of temperature or moisture (Sun et al. 2013). Therefore, producing eggs at more advanced developmental stages

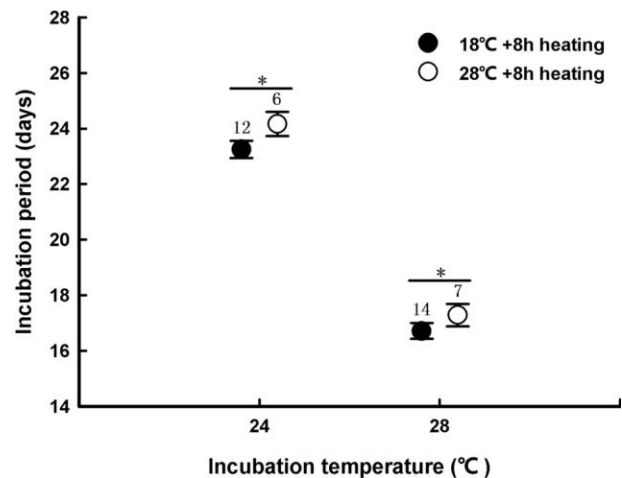


Figure 3. Incubation periods of eggs laid by females from cold and warm treatments when incubated at 24° or 28°C. Statistical significance between groups was calculated by ANOVA and the Tukey post hoc test (one asterisk = $P < 0.05$). Data are expressed as mean ± SE. Numbers above error bars are sample sizes.

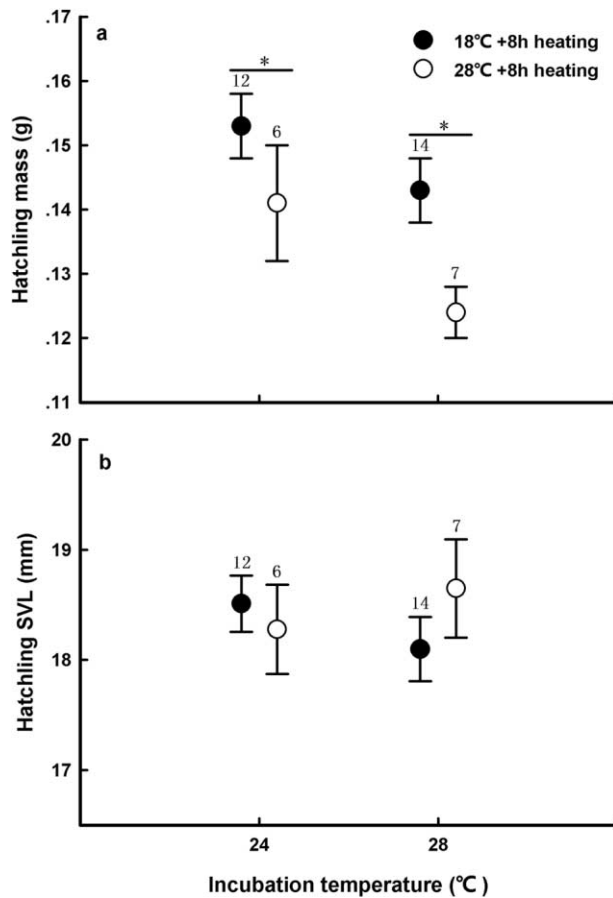


Figure 4. Body mass (a) and snout-vent length (SVL; b) of hatchlings from eggs laid by females following cold and warm treatments and incubated at 24° or 28°C. Statistical significance between groups was calculated by ANOVA and the Tukey post hoc test (one asterisk = $P < 0.05$). Data are expressed as mean \pm SE. Numbers above error bars are sample sizes.

in cold climates may decrease the potential disadvantage that cold temperature may impose on embryonic development and offspring, probably reflecting an adaptive life-history strategy to improve reproductive success and therefore the fitness of the species.

More interestingly, these results were consistent with the predictions of the cold climate hypothesis that females from cold climate habitats lay eggs with embryos at more advanced developmental stages (Shine 1985, 2002b; Qualls and Andrews 1999). The cold climate hypothesis posits that at high latitudes or altitudes, egg retention could increase embryonic development rate and thus reduce external incubation time during which embryos suffer negative effects on survival success (Shine 1985, 2002b; Qualls and Andrews 1999). In viviparous species, at the extreme of prolonged egg retention, embryos are retained within the female until they are ready for independent life (Shine 1985). The present geographical distribution of viviparous squamates is strongly associated with cold climates, suggesting the evolutionary advantages of prolonged egg retention

at lower temperatures (Shine 1985; Calderón-Espinosa et al. 2006). Our study provides evidence that oviparous species may be capable of responding to low temperature via egg retention, giving support to the cold climate hypothesis of viviparity evolution.

Offspring size has shown long-term adaptation to temperature in among-population comparisons along latitudes and altitudes. According to the theory of reproductive allocation that describes the trade-off between offspring number and size (Stearns 1992), females in environments that retard offspring growth (such as cold environments) would produce fewer and larger eggs in response to selective pressure of offspring performance (Yampolsky and Scheiner 1996; Fischer et al. 2003; Sun et al. 2013). Our results suggest that females may produce larger eggs and hence bigger hatchlings in response to cold temperature, but this would not necessarily result in a concomitant reduction in clutch size. The adaptive plasticity in egg (hatchling) size in response to low temperature has also been found in some other species (Atkinson et al. 2001). What is the proximate mechanism by which female lizards can enlarge their egg size? To increase egg size, females could either grow larger because of the positive relationship between egg size and maternal body size or produce enlarged eggs relative to certain maternal body sizes (Sinervo 1990; Du et al. 2010). Given that female body size did not differ between the two treatments at oviposition in our study, the females may enhance egg size through the second avenue mentioned above. Our results indicated that not only egg size but also hatching size from similar egg size was larger following cold treatment, suggesting that females may phenotypically enlarge offspring by increasing egg size or by investing more energy (yolk) into their eggs as found in natural populations (Du et al. 2010). In contrast, the differential effects of temperature on anabolism and catabolism may result in faster growth but smaller final sizes at higher temperatures (Angilletta and Dunham 2003).

Life-history traits such as egg retention and offspring size may exhibit plastic and evolutionary responses to temperature variation along latitudinal and altitudinal clines (Calderón-Espinosa et al. 2006; Tieleman 2009; Du et al. 2010; Rodríguez-Díaz and Brana 2012). Environmentally induced phenotypic plasticity does not preclude evolutionary change. Instead, the long-standing adaptive plastic variation could not only maintain the population but also allow enough time for a population to generate genetic adaptation by gene mutation and recombination in response to new selection pressures (Via et al. 1995; Pigliucci 2001; Schlichting and Smith 2002; Ghalambor et al. 2007). Our study demonstrated that reproductive life history, including egg retention and offspring size, may show adaptive plasticity in response to changes in maternal thermal environment; the plastic responses in egg retention and offspring size are in the same direction favored by selection in the cold environment (figs. 3, 4). Such temperature-dependent benefits of maternal effects on offspring fitness create norms of reaction that can be molded by natural selection in geographically separated populations exposed to distinct selective forces (Mousseau and Fox 1998; Einum and Fleming 1999) and will

be adaptive if the maternally induced phenotypic variation matches the offspring to future environments (Breuner 2008; Sheriff and Love 2013).

How the plastic response induced by changing temperature could be canalized in genotype and thus become integrated in the population is an intriguing area for future studies. Such studies may involve long-term studies that may identify the route and speed by which plasticity can lead to adaptive genetic differentiation (Rossiter 1996; Mousseau and Fox 1998; Ghalambor et al. 2007). For example, phenotypic plasticity in offspring size facilitates adaptive adaptation to low-predation environments in guppies, leading to significant genetic changes in offspring size after 11 yr via transgenerational plasticity and genetic assimilation (Reznick et al. 1997). In addition, an among-population comparison in the context of maternal phenotypic plasticity would also be crucial for our understanding of the role of phenotypic plasticity in evolutionary adaptation. Maternal phenotypic plasticity and its contribution (either acceleration or constraint) to evolutionary change may differ among populations; such studies would help us to completely understand the evolutionary role of both adaptive and non-adaptive phenotypic plasticity in the context of changing environments and yield more accurate predictions on species' responses to environmental change (Ghalambor et al. 2007; Räsänen and Kruuk 2007).

Acknowledgments

We thank Yu-Ze Zhao and Tian-Long Cai for their assistance in the field and laboratory. We are grateful to the anonymous reviewers for their suggestions and comments. This work was supported by grants from the One Hundred Talents Program of the Chinese Academy of Sciences and National Natural Sciences Foundation of China (31372203).

Literature Cited

- Angilletta M.J., Jr., and A.E. Dunham. 2003. The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. *Am Nat* 162:332–342.
- Atkinson D., S.A. Morley, D. Weetman, and R.N. Hughes. 2001. Offspring size responses to maternal temperature in ectotherms. Pp. 269–285 in D. Atkinson and M. Thorndyke, eds. *Environment and animal development: genes, life histories and plasticity*. BIOS Scientific, Oxford.
- Bernardo J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *Am Zool* 36:216–236.
- Breuner C. 2008. Maternal stress, glucocorticoids, and the maternal/fetal match hypothesis. *Horm Behav* 54:485–487.
- Calderón-Espinosa M., R. Andrews, and F. Méndez. 2006. Evolution of egg retention in the *Sceloporus spinosus* group: exploring the role of physiological, environmental, and phylogenetic factors. *Herpetol Monogr* 20:147–158.
- Denno R.F. and H. Dingle. 1981. *Insect life history patterns: habitat and geographic variation*. Springer, New York.
- Du W.G., X. Ji, Y.P. Zhang, Z.H. Lin, and X.F. Xu. 2010. Geographic variation in offspring size of a widespread lizard (*Takydromus septentrionalis*): importance of maternal investment. *Biol J Linn Soc* 101:59–67.
- Dufaure J. and J. Hubert. 1961. Table de développement du lézard vivipare: *Lacerta (Zootoca) vivipara* Jacquin. *Arch Anat Microsc Morphol Exp* 50:309–328.
- Einum S. and I.A. Fleming. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. *Proc R Soc B* 266:2095–2100.
- Fielding C.A., J.B. Whittaker, J.E.L. Butterfield, and J.C. Coulson. 1999. Predicting responses to climate change: the effect of altitude and latitude on the phenology of the spittlebug *Neophilaenus lineatus*. *Funct Ecol* 13:65–73.
- Fischer K., P.M. Brakefield, and B.J. Zwaan. 2003. Plasticity in butterfly egg size: why larger offspring at lower temperatures? *Ecology* 84:3138–3147.
- Ghalambor C.K., J.K. McKay, S.P. Carroll, and D.N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct Ecol* 21:394–407.
- Grant V. 1977. *Organismic evolution*. Freeman, San Francisco.
- Ji X. and Z.W. Wang. 2005. Geographic variation in reproductive traits and trade-offs between size and number of eggs of the Chinese cobra (*Naja atra*). *Biol J Linn Soc* 85:27–40.
- Lande R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *J Evol Biol* 22:1435–1446.
- Laugen A.T., A. Laurila, K. Rasanen, and J. Merila. 2003. Latitudinal countergradient variation in the common frog (*Rana temporaria*) development rates: evidence for local adaptation. *J Evol Biol* 16:996–1005.
- Lu H.L., Y. Wang, W.Q. Tang, and W.G. Du. 2013. Experimental evaluation of reproductive response to climate warming in an oviparous skink. *Integr Zool* 8:175–183.
- Luo L.G., Y.L. Wu, X.Y. Tian, and X.F. Xu. 2012. Sexual size dimorphism and female reproductive output in slender forest skink, *Scincella modesta*. *Chin J Zool* 47:23–30.
- Morita K., T. Tamate, Y. Sugimoto, Y. Tago, T. Watanabe, H. Konaka, M. Sato, Y. Miyauchi, K. Ohkuma, and T. Nagasawa. 2009. Latitudinal variation in egg size and number in anadromous masu salmon *Oncorhynchus masou*. *J Fish Biol* 74: 699–705.
- Mousseau T.A. and C.W. Fox. 1998. *Maternal effects as adaptations*. Oxford University Press, Oxford.
- Niewiarowski P.H. 1994. Understanding geographic life-history variation in lizards. Pp. 31–50 in L.J. Vitt and E.R. Pianka, eds. *Lizard ecology: historical and experimental perspectives*. Princeton University Press, Princeton, NJ.
- Pigliucci M. 2001. *Phenotypic plasticity: beyond nature and nurture*. Johns Hopkins University Press, Baltimore.
- Pigliucci M., C.J. Murren, and C.D. Schlichting. 2006. Phenotypic plasticity and evolution by genetic assimilation. *J Exp Biol* 209:2362–2367.

- Qualls C.P. and R.M. Andrews. 1999. Cold climates and the evolution of viviparity in reptiles: cold incubation temperatures produce poor-quality offspring in the lizard, *Sceloporus virgatus*. *Biol J Linn Soc* 67:353–376.
- Radder R., M. Elphick, D. Warner, D. Pike, and R. Shine. 2008. Reproductive modes in lizards: measuring fitness consequences of the duration of uterine retention of eggs. *Funct Ecol* 22:332–339.
- Räsänen K. and L.E.B. Kruuk. 2007. Maternal effects and evolution at ecological time-scales. *Funct Ecol* 21:408–421.
- Reznick D.N., F.H. Shaw, F.H. Rodd, and R.G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* 275:1934–1937.
- Rodriguez-Diaz T. and F. Brana. 2012. Altitudinal variation in egg retention and rates of embryonic development in oviparous *Zootoca vivipara* fits predictions from the cold-climate model on the evolution of viviparity. *J Evol Biol* 25:1877–1887.
- Rodriguez-Diaz T., F. Gonzalez, X. Ji, and F. Brana. 2010. Effects of incubation temperature on hatchling phenotypes in an oviparous lizard with prolonged egg retention: are the two main hypotheses on the evolution of viviparity compatible? *Zoology* 113:33–38.
- Rossiter M.C. 1996. Incidence and consequences of inherited environmental effects. *Annu Rev Ecol Evol* 27:451–476.
- Schlichting C.D. and H. Smith. 2002. Phenotypic plasticity: linking molecular mechanisms with evolutionary outcomes. *Evol Ecol* 16:189–211.
- Sheriff M.J. and O.P. Love. 2013. Determining the adaptive potential of maternal stress. *Ecol Lett* 16:271–280.
- Shine R. 1985. The evolution of viviparity in reptiles: an ecological analysis. Pp. 605–694 in C. Gans and F. Billett, eds. *Biology of the Reptilia*. Vol. 15. Wiley, New York.
- . 2002a. Eggs in autumn: responses to declining incubation temperatures by the eggs of montane lizards. *Biol J Linn Soc* 76:71–77.
- . 2002b. Reconstructing an adaptationist scenario: what selective forces favor the evolution of viviparity in montane reptiles? *Am Nat* 160:582–593.
- Sinervo B. 1990. The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* 44:279–294.
- Stearns S.C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.
- Sun B.J., S.R. Li, X.F. Xu, W.G. Zhao, L.G. Luo, X. Ji, and W.G. Du. 2013. Different mechanisms lead to convergence of reproductive strategies in two lacertid lizards (*Takydromus wolteri* and *Eremias argus*). *Oecologia* 172:645–652.
- Telemeco R.S., R.S. Radder, T.A. Baird, and R. Shine. 2010. Thermal effects on reptile reproduction: adaptation and phenotypic plasticity in a montane lizard. *Biol J Linn Soc* 100:642–655.
- Tieleman B.I. 2009. High and low, fast or slow: the complementary contributions of altitude and latitude to understand life-history variation. *J Anim Ecol* 78:293–295.
- Via S., R. Gomulkiewicz, G. Dejong, S.M. Scheiner, C.D. Schlichting, and P.H. Van Tienderen. 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol Evol* 10:212–217.
- Yampolsky L.Y. and S.M. Scheiner. 1996. Why larger offspring at lower temperatures? a demographic approach. *Am Nat* 147:86–100.