Oecologia
DOI 10.1007/s00442-012-2524-4

PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Different mechanisms lead to convergence of reproductive strategies in two lacertid lizards (*Takydromus wolteri* and *Eremias argus*)

Bao-Jun Sun · Shu-Ran Li · Xue-Feng Xu · Wen-Ge Zhao · Lai-Gao Luo · Xiang Ji · Wei-Guo Du

Received: 27 April 2012 / Accepted: 25 October 2012

Abstract Life history traits may vary within and among species. Rarely, however, are both variations examined concurrently to identify the life history adaptation. We found that female body size, offspring number and size, and incubation period showed convergent evolution in two lacertid lizards (*Takydromus wolteri* and *Eremias argus*) that occur sympatrically in high-latitude and low-latitude localities. Females from the high-latitude population were larger and produced larger clutches than those from the low-latitude population. In both species, the incubation period was shorter for the high-latitude population than for the low-latitude population. However, the physiological mechanism underlying the shorter incubation period differed between the species. These results suggest that: (1) sympatric lizards may adopt similar reproductive strategies in response to their common environments, and (2) embryonic development of the two species follows different pathways for adaptation to low temperatures. This study highlights the importance of understanding the adaptive evolution of life history in response to environmental changes at the embryonic life stages.

Keywords Embryonic development · Geographic variation · Incubation period · Life history

Introduction

Life history traits vary within and among species (Stearns 1992). One major challenge in evolutionary biology is to identify the pattern and adaptive significance of these variations. A diversity of species from insects to mammals coexist along geographic gradients such as latitude and altitude. Life history traits of these species may show significant geographic variation at both embryonic and post-embryonic stages (Denno and Dingle 1981; Stearns 1992; Niewiarowski 1994). At the same time, sympatric species may show ecological segregation (e.g., divergences in habitat use and phenotypes) to facilitate the coexistence of these species (Losos 2000; Ohlberger et al. 2008), or exhibit convergence in morphology, behavior and physiology in response to their common environment (Matos et al. 2004; Losos 2011). Rarely, however, are both the between-species difference and geographic variation in life history traits examined concurrently to identify the adaptation to local environments in sympatric species (Losos 2011).

Offspring number and size often vary substantially among geographically separated populations (Stearns 1992; Niewiarowski 1994). Environmental factors like temperature may affect these two reproductive traits by directly affecting the optimal size of the offspring, or indirectly influencing maternal body size. The latter is a

---

Communicated by Jean-François Le Galliard.

B.-J. Sun · S.-R. Li · W.-G. Du (✉)
Key Laboratory of Animal Ecology and Conservation Biology,
Institute of Zoology, Chinese Academy of Sciences,
Beijing 100101, People's Republic of China
e-mail: duweiguo@ioz.ac.cn

X.-F. Xu · L.-G. Luo
Department of Biology, Chuzhou University, Chuzhou 239012,
Anhui, People's Republic of China

W.-G. Zhao
College of Biological Sciences, Harbin Normal University,
Harbin 150080, Heilongjiang, People's Republic of China

X. Ji
College of Life Sciences, Nanjing Normal University,
Nanjing 210046, Jiangsu, People's Republic of China

critical variable that determines reproductive characteristics in most organisms (Stearns 1992; Angilletta et al. 2006). Life history theory predicts that the animal body size would be larger in high-latitude than low-latitude populations (Angilletta et al. 2004). These larger females would produce larger clutches than their smaller counterparts at low latitudes (Angilletta et al. 2006). Alternatively, high-latitude (colder) environments that retard the growth of offspring favor the production of fewer and larger eggs, perhaps because larger offspring survive better in such environments than do smaller offspring (Yampolsky and Scheiner 1996; Fischer et al. 2003). Nonetheless, there is not yet a universal theory to explain the geographic pattern of body size and reproductive traits as well as its underlying causes. For instance, as in other reptiles, some lizards follow Bergmann's rules, but others the opposite (Ashton and Feldman 2003). Delayed maturation is thought to be the underlying mechanism by which ectotherms achieve larger body size in colder environments, but this may not apply in all species (Sears and Angilletta 2004). Therefore, more comparative studies on different species both at low-latitude and high-latitude localities are needed to understand these species-specific responses of reproductive life history to environmental changes. Such studies would shed light on the proximate and ultimate causes of geographic pattern of life history adaptation.

Countergradient variation in embryonic development along latitudinal clines has been shown in many organisms, from flies to reptiles, with shorter incubation periods for high-latitude populations than for low-latitude conspecifics at controlled temperatures (Ewert 1985; Oufiero and Angilletta 2006; Liefting et al. 2009). This countergradient variation can compensate for the effect of low environmental temperatures on embryonic development in high-latitude populations, allowing developmental similarity between high- and low-latitude populations, despite exposure to different environmental conditions (Du et al. 2010a). A shortened incubation period in high-latitude populations may be due to advanced embryogenesis completed prior to oviposition, and thus the later developmental stage of embryos at oviposition. Alternatively, the shortened incubation period may be due to higher rates of embryonic development during incubation (Du et al. 2010a). For example, the countergradient variation in the incubation period found in fence lizards (*Sceloporus undulatus*) is related to the developmental (growth) rate during incubation rather than the degree of embryonic development prior to oviposition (Oufiero and Angilletta 2006; Du et al. 2010a). Nonetheless, studies on other species are needed to see if different species would show divergent pathways of embryonic development in response to the thermal gradient along latitudinal clines.

In this study, we measured female body size, reproductive output and incubation period of two lacertid lizards (*Takydromus wolteri* and *Eremias argus*) in the high-latitude and low-latitude localities where the two species coexist. The developmental stage of the embryos at oviposition and the embryonic heart rate during incubation were also determined to identify the physiological mechanism underlying the geographic variation in incubation period. In both species, embryonic development and hatchling traits (size and locomotion) can be significantly affected by incubation temperature (Pan and Ji 2001; Hao et al. 2006). However, little information is available with regard to how reproductive output and embryonic development differ among populations. Similar patterns of between-population variations in female size, reproductive output or incubation period would be expected in these two species if convergent evolution has occurred for reproductive strategies. More importantly, identifying the mechanisms underlying between-population variation in these life history traits would enable us to understand the life history adaptation of the sympatric lizards in response to environmental changes between high and low latitudes.

According to the aforementioned hypotheses on geographic variation of life history traits, for both species we predicted that: (1) adult females from the high-latitude population would be larger, and produce more or larger eggs than females from the low-latitude population; and (2) incubation periods would be shorter for lizards from the high-latitude population than for the low-latitude population under identical incubation temperature regimes. As for the underlying mechanism of geographic variation in incubation period (Du et al. 2010a), we predicted that higher-latitude females would produce eggs with embryos at later stages if the geographic divergence in incubation period is driven by the variation in the degree of uterine retention of developing eggs. Alternatively, embryos from the higher-latitude population could have faster heart rates [and thus metabolic rate (Du et al. 2010b)] if the geographic divergences in incubation period were driven by differences in developmental rates.

Materials and methods

Study species

Takydromus wolteri [up to 60 mm snout-vent length (SVL)] and *Eremias argus* (up to 70 mm SVL) are two small oviparous lacertid lizards. Phylogenetic analysis indicated that the two species belong to different clades: *Takydromus* is in the Eurasia group, whereas *Eremias* is in the African group (Fu 2000). These two species coexist in a number of localities along the east coast of China (Zhao et al. 1999). From May to July, female *T. wolteri* lay multiple clutches with from one to nine parchment-shelled eggs in each; female *E. argus* lay multiple clutches with from two to five parchment-shelled eggs in each (Zhao et al. 1999).

Study sites and thermal profiles of potential nests

The study was conducted in a low-latitude locality, Chuzhou of Anhui (34°16′N, 90°02′W), and a high-latitude locality, Harbin of Heilongjiang (39°17′N, 86°50′W), where the two species coexist. These two sites are located at the opposite latitudinal edges of the distribution range of these two species in China, and show distinct mean annual temperatures (15.1 °C in Chuzhou versus 4 °C in Harbin; http://www.weatherbase.com). From June to August of 2010, we monitored soil temperatures in the natural habitat of the lizards at 1-h intervals by placing thermal data loggers (Tinytag; Gemini data loggers) at a depth of 5 cm, such that we could quantify thermal profiles of potential nest sites in both high- and low-latitudinal localities in spite of the difficulty in locating nests of the two lacertid lizards in nature (Fig. 1).

Animal collection and husbandry

Gravid female *T. wolteri* and *E. argus* from the two localities were captured in May 2011, either by hand or noose. All captured lizards were transferred to our laboratory in Beijing, where they were individually measured (to 0.5 mm) for SVL, weighed (to 0.01 g) and toe-clipped for identification. The lizards were maintained in terraria (600 × 430 × 340 mm), in which the bottom was filled with 10 mm of moist sand, and kept at 24 ± 1 °C on a natural light cycle (14 h light:10 h dark). Each terrarium housed from eight to ten gravid females and three adult males. A 100-W light bulb suspended 50 mm above the terrarium provided supplementary heating from 0800 to 1600 hours. Food (mealworms and crickets dusted with additional vitamins and minerals) and water were provided ad libitum.

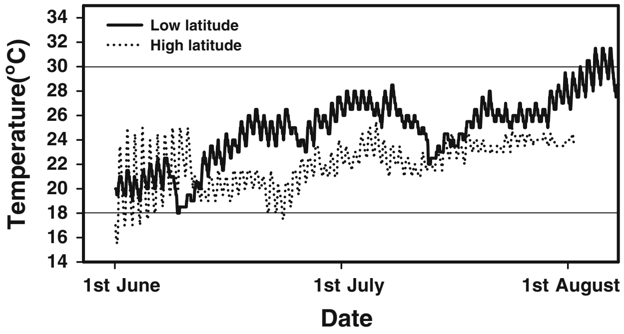

Fig. 1 Thermal profiles of potential nests in natural habitat used by the two lacertid lizards (*Takydromus wolteri* and *Eremias argus*) in low-latitude and high-latitude localities. Soil temperatures at depth of 5 cm under vegetation in the high and low latitudes from June to early August, spanning the majority of incubation duration in nature for these two species. *Reference lines* indicate the fluctuating magnitudes of temperatures (24 ± 6 °C) mimicked in the laboratory

Reproductive output

We examined egg mass, clutch size, and clutch mass associated with individuals from each population. We palpated females every other day, and moved individually those with oviductal eggs to egg-laying terraria (310 × 210 × 180 mm) with 20 mm of moist sand. We checked terraria 4 times daily for freshly laid eggs, which were weighed (±0.001 g) immediately to minimize initial mass changes due to water exchange. To minimize the confounding effects resulting from laboratory conditions, only eggs of the first clutch were compared in this study. The females' first clutches were produced soon (average 7 days) after they had arrived in the laboratory.

Embryonic stage at oviposition and egg incubation

One egg from each clutch was dissected to determine the embryonic stage at oviposition according to the classification scheme of Dufaure and Hubert (1961). The remaining eggs were placed in plastic boxes (160 × 115 × 40 mm) filled with moist vermiculite (−220 kPa) and incubated at fluctuating temperatures of 24 ± 6 °C, which mimicked the thermal environments of potential nests in the field (Fig. 1). All eggs experienced a similar incubation environment so we could distinguish intrinsic differences in incubation period between populations (i.e., common garden experiment).

Embryonic heart rate

We measured heart rates (beats per minute) of embryos using an infrared heart rate monitor [Buddy digital egg monitor; Avian Biotech, Cornwall, UK; see detailed procedures in Du et al. (2009)]. Heart rates were measured at approximately halfway through the total incubation period (days 17–21 for *T. wolteri* and days 25–28 for *E. argus*). Incubation time (the day of heart rate measurement) did not affect heart rates ($P > 0.05$), and was thus not included in the subsequent statistics testing the difference in heart rates. The eggs were transferred to an incubator set at 24 or 28 °C for 2 h prior to being placed individually on the heart rate monitor placed inside the incubator to record heart rates. These two test temperatures represent the low and high temperatures experienced by the eggs during the incubation, respectively.

Hatchling size

Toward the end of incubation, we checked the boxes every morning for newly emerging hatchlings. The hatchlings' SVL and body mass were immediately determined using a ruler (±1 mm) or a balance (±0.01 g), respectively.

Statistical analysis

Prior to analysis the normality of distributions and homogeneity of variances in the data were tested using the Kolmogorov–Smirnov test and Bartlett's test, respectively. Linear regression was used to analyze the relationship between maternal body size (SVL) and reproductive traits (clutch size, clutch mass and egg size). One-way ANOVAs and analysis of covariance (ANCOVAs) were used to determine between-population differences in female body size, reproductive traits and hatchling sizes. To avoid pseudoreplication, all analyses were conducted on clutch means for heart rate and incubation period. Repeated-measures ANOVA were used to test for between-population differences in heart rates, because the heart rate of each embryo was determined at two different temperatures. We used the least square method in the repeated-measures ANOVA, and put a random effect for the repeated measures. One-way ANOVA was conducted to assess differences in incubation period between populations. A Mann–Whitney *U*-test was used to compare differences in embryonic stages at oviposition between populations, because the data were not normally distributed. All values are reported as the mean ± SE.

Results

Female body size and reproductive output

In both species females from the high-latitude population on average were larger (SVL and postpartum mass) than those from the low-latitude population (Table 1). Clutch size and mass were greater in the high-latitude population than in the low-latitude population, whereas egg mass did not differ between the two populations in either species (Table 1).

Clutch size and mass were positively related to maternal SVL (*T. wolteri*—clutch size, $r^2 = 0.60$, $F_{1,44} = 65.2$, $P < 0.0001$; clutch mass, $r^2 = 0.57$, $F_{1,44} = 57.3$, $P < 0.0001$; *E. argus*—clutch size, $r^2 = 0.41$, $F_{1,43} = 29.4$, $P < 0.0001$; clutch mass, $r^2 = 0.49$, $F_{1,43} = 41.3$, $P < 0.0001$), but mean egg mass was not (*T. wolteri*—$r^2 = 0.02$, $F_{1,44} = 0.68$, $P = 0.41$; *E. argus*—$r^2 = 0.01$, $F_{1,44} = 0.30$, $P = 0.59$). After we had moved the effect of body size statistically, the between-population difference in clutch size and mass was still significant in *T. wolteri* (clutch size, $F_{1,43} = 36.6$, $P < 0.0001$; clutch mass, $F_{1,43} = 25.6$, $P < 0.0001$), but not in *E. argus* (clutch size, $F_{1,42} = 2.3$, $P = 0.13$; clutch mass, $F_{1,42} = 0.50$, $P = 0.48$). Partial correlation (controlling for maternal SVL) indicated that egg mass was negatively correlated with clutch size in both species (*T. wolteri*—$r = -0.35$, $P < 0.05$; *E. argus*—$r = -0.46$, $P < 0.05$).

Incubation period, embryonic stage at oviposition and heart rates during incubation

Some clutches of eggs did not hatch successfully or were used in other experiments, leading to smaller sample sizes for incubation period and embryonic heart rate than for reproductive output. Incubation period differed between populations in both species (*T. wolteri*—$F_{1,33} = 116.7$, $P < 0.0001$; *E. argus*—$F_{1,15} = 144.6$, $P < 0.0001$), with eggs from the high-latitude population taking a shorter time to hatch than those from the low-latitude population (Fig. 2). The embryonic stage at oviposition was later in the high-latitude population than in the low-latitude population in *T. wolteri* ($Z = 4.80$, $P < 0.0001$), but did not differ between the high-latitude and low-latitude populations in *E. argus* ($Z = 0.87$, $P = 0.38$) (Fig. 3). Heart rate did not differ between the two populations in *T. wolteri* ($F_{1,22} = 1.10$, $P = 0.31$), but was higher in the high-latitude population than in the low-latitude population in *E. argus* ($F_{1,12} = 13.3, P = 0.003$) (Fig. 3). Given a significant interaction between population and test temperature in *E. argus* ($F_{1,12} = 17.5, P = 0.001$), we conducted separate ANOVAs to test geographic differences at each test temperature, and found that heart rate was higher in the high-latitude population than in the low-latitude population at 28 °C ($F_{1,12} = 20.7$, $P < 0.001$), but not at 24 °C ($F_{1,12} = 2.7$, $P = 0.13$) (Fig. 3).

Hatchling size

Hatchling SVL and body mass did not differ between the two populations either in *T. wolteri* or in *E. argus* (Table 1). After the effect of egg size had been removed by ANCOVA with initial egg mass as the covariate, the between-population difference in hatchling sizes was still not significant except for the SVL of *T. wolteri* (*T. wolteri*—SVL, $F_{1,32} = 5.40$, $P = 0.03$; body mass, $F_{1,32} = 1.52$, $P = 0.23$; *E. argus*—SVL, $F_{1,14} = 3.87$, $P = 0.07$; body mass, $F_{1,14} = 0.03$, $P = 0.89$). The least square mean of hatchling SVL, adjusted for initial egg mass by ANCOVA, was greater in the high-latitude population (22.58 ± 0.30 mm, $n = 16$) than in the low-latitude population (21.62 ± 0.28 mm, $n = 19$) in *T. wolteri*.

Table 1 Female body size, reproductive output and hatchling size of two sympatric lacertid lizards (*Takydromus wolteri* and *Eremias argus*) from low-latitude and high-latitude populations

	Species	Low-latitude population	High-latitude population	ANOVA
Maternal snout-vent length (mm)	*T. wolteri*	51.90 ± 0.49	55.35 ± 0.82	$F_{1,44} = 11.89$, $P < 0.01$
	E. argus	56.30 ± 0.69	60.51 ± 0.58	$F_{1,43} = 20.94$, $P < 0.001$
Post-partum body mass (g)	*T. wolteri*	2.59 ± 0.09	2.96 ± 0.11	$F_{1,44} = 6.11$, $P < 0.05$
	E. argus	3.63 ± 0.14	4.17 ± 0.13	$F_{1,43} = 7.56$, $P < 0.01$
Clutch size	*T. wolteri*	2.7 ± 0.2	5.0 ± 0.3	$F_{1,44} = 52.75$, $P < 0.0001$
	E. argus	3.5 ± 0.2	4.8 ± 0.2	$F_{1,43} = 15.08$, $P < 0.001$
Clutch mass (g)	*T. wolteri*	0.53 ± 0.03	0.94 ± 0.05	$F_{1,44} = 43.20$, $P < 0.0001$
	E. argus	1.29 ± 0.08	1.71 ± 0.08	$F_{1,43} = 11.82$, $P < 0.01$
Egg mass (g)	*T. wolteri*	0.19 ± 0.01	0.20 ± 0.01	$F_{1,44} = 2.64$, $P = 0.11$
	E. argus	0.37 ± 0.01	0.36 ± 0.01	$F_{1,43} = 0.25$, $P = 0.62$
Hatchling snout-vent length (mm)	*T. wolteri*	21.8 ± 0.3	22.4 ± 0.3	$F_{1,33} = 2.13$, $P = 0.15$
	E. argus	25.5 ± 0.6	26.8 ± 0.4	$F_{1,15} = 3.01$, $P = 0.10$
Hatchling body mass (g)	*T. wolteri*	0.271 ± 0.008	0.245 ± 0.009	$F_{1,33} = 4.01$, $P = 0.053$
	E. argus	0.498 ± 0.031	0.505 ± 0.022	$F_{1,15} = 0.03$, $P = 0.87$

Data are expressed as the mean ± SE. The sample sizes of female body size and reproductive traits for the low-latitude and high-latitude populations were 21 and 25 for *T. wolteri* and 17 and 28 for *E. argus*, respectively. The sample sizes of hatchling size for the low-latitude and high-latitude populations were 19 and 16 for *T. wolteri* and six and 11 for *E. argus*, respectively

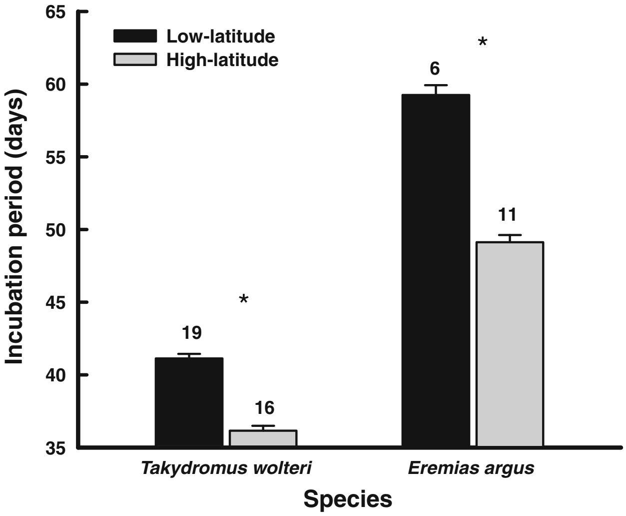

Fig. 2 Incubation periods of eggs at 24 ± 6 °C in the two lacertid lizards (*T. wolteri* and *E. argus*) from low-latitude and high-latitude populations. Data are expressed as the mean ± SE. *Numbers above error bars* represent the number of clutches used for each population

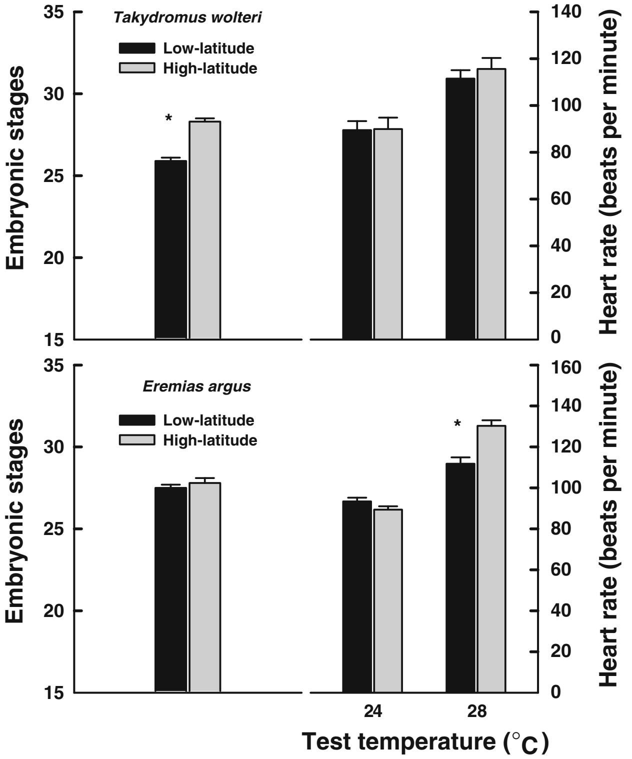

Fig. 3 The embryonic stage at oviposition and heart rate of the embryos of two lacertid lizards (*T. wolteri* and *E. argus*) from low-latitude and high-latitude populations. Eggs were incubated at 24 ± 6 °C, and heart rates were measured at 24 °C and 28 °C approximately halfway through the incubation period. Sample sizes for the low-latitude and high-latitude populations were 15 and nine in *T. wolteri*, and six and eight in *E. argus*, respectively. Data are expressed as the mean ± SE

Discussion

Sympatric species may generate similar adaptive phenotypes via analogous evolutionary responses (Losos et al. 1998). Our study demonstrated analogous adaptation in life history traits, including female body size, offspring number and size, and incubation period of two lacertid lizards that occur sympatrically in low-latitude and high-latitude populations spanning a 5° latitudinal distance. This phenotypical analogy between species may arise from convergent or parallel evolution. Developmental mechanisms underlying analogous phenotypes are often used to distinguish parallelism from convergence that can arise through different developmental mechanisms (Losos 2011). We found that the physiological mechanism underlying the shorter incubation period differed between the two species (egg retention in *T. wolteri* vs. developmental rate acceleration in *E. argus*). This suggests that reproductive traits such as incubation period have convergently evolved among populations in these two species. Similarly, convergent evolution may occur in a number of other phenotypes such as morphology, behavior and growth in other organisms (Blackledge and Gillespie 2004; Oufiero and Angilletta 2006, 2011), but the underlying mechanisms are rarely understood.

Consistent with our initial prediction, the two lacertid lizards exhibit a similar geographic pattern (convergent evolution) in body size and clutch size, with larger body size and clutch sizes in high-latitude populations. A larger adult size may result from a larger hatchling, a longer duration of growth (delayed maturation) or a faster growth rate (Angilletta et al. 2004; Du et al. 2012). Basically, hatchlings size was similar for the two populations of both lizards, although the between-population difference was marginally significant in the body mass of hatchling *T. wolteri*. Accordingly, larger adult size in the high-latitude populations is not likely attributable to larger hatchlings. Further studies on hatchling growth and maturation would thus be of great interest to identify the proximate mechanism underlying the large body size. Such studies would provide support for the convergent evolution of body size between the two species if they adopt different proximate mechanisms. More interestingly, the between-population difference in clutch size was exclusively attributed to maternal body size in *T. wolteri*, but only in part in *E. argus*. This suggests that the two species may have different pathways [e.g., body cavity vs. energy storage (Parker and Begon 1986)] to achieve greater reproductive output in high-latitudinal populations, giving support to the convergent evolution in life history traits in these two species.

In contrast to the theoretical prediction that larger females in high-latitudinal populations would produce larger eggs, egg size (hence hatchling size) was similar between high- and low-latitudinal populations. Why is the between-population difference in egg size not consistent with the prediction? First, the larger clutches of the high-latitude females lead to the decrease in egg size as a result of a trade-off between clutch and egg sizes in these two species as well as in many other animals (Stearns 1992; Ji et al. 2009). Second, this theoretical prediction is based on an assumption of “bigger is better” especially in harsher and colder environments, which may not stand well in all species. In lizards, for example, bigger offspring are not necessarily associated with higher survival or growth rates. Our field investigations indicate that the survival of hatchling *T. wolteri* is not dependent on body size (L.-G. Luo et al., unpublished data). Similarly, the fitness of juveniles depends on seasonal timing of hatching, but not on offspring body size in a agamid lizard, *Amphibolurus muricatus* (Warner and Shine 2007).

The life history adaptation may be driven by both abiotic and biotic factors, including temperature, food availability and predation (Oro et al. 1999; Zanette et al. 2006; Angilletta 2009). Although the two sympatric species of lizards experience similar thermal environments in the two localities, they occupy different microhabitats (grassland for *T. wolteri* and sandy land for *E. argus*) that may differ in food availabilities as well as predation pressures (Zhao et al. 1999). Therefore, the convergence of these life history traits between these two species is more likely driven by abiotic factors (e.g., temperature and precipitation) than by biotic factors (e.g., food availability and predation pressure).

As we expected, countergradient variation in the incubation period was found in the two lacertid lizards. A similar pattern of countergradient variation has been found in two clades of the North American fence lizard, *S. undulatus*. In both clades embryonic development rates accounted for the latitudinal variation in incubation period (Oufiero and Angilletta 2006; Niewiarowski and Angilletta 2008). The two species of lizards in our study, however, followed different physiological pathways to achieve the convergence of incubation period. In *E. argus*, the latitudinal variation in variation in incubation period was associated with the between-population difference in developmental rates. Our study detected a 7 % increase in heart rate, but a 21 % decrease in incubation period in the high-latitude population as compared to the low-latitude population in *E. argus*. There are two plausible reasons underlying this phenomenon. First, other mechanisms accelerating the developmental rate in the high-latitude population [e.g., differences in heart size or stroke volume (Du et al. 2010a)] may lead to the mismatch between heart rate increase and incubation period decrease. Second, this mismatch could occur if embryonic growth depends exponentially on metabolic rates. In addition, the increase in heart rate only occurred at high temperature (28 °C), but not at low temperature (24 °C). This between-population difference in thermal dependence of heart rate may be due to the nonlinear relationship between heart rate and temperature, with heart rate increasing slowly at low temperatures, but dramatically at high temperatures (Du et al. 2011). In *T. wolteri*, however, geographic variation in incubation period was due to the between-population difference in developmental stages of embryos at oviposition.

The high-latitude population had an incubation period that was 5.1 days shorter (at 24 ± 6 °C), because embryos were 2.4 stages later in development at oviposition in the high-latitude population than the low-latitude population. Given that lizard embryos at stages 25–30 advance by one stage every 1–2 days when developing at 28 °C (Andrews 2004), thus the 2.4-stage difference in development at oviposition accounting for a 2–5 day difference in incubation period (or even longer at the lower incubation temperature of 24 ± 6 °C in this study). Therefore, the between-population difference in incubation period is largely attributable to the degree of embryonic development before oviposition in *T. wolteri*.

The response of life history traits of sympatric species to their common environments is an important but poorly understood aspect of life history evolution. Our study demonstrated that sympatric species may show convergent evolution in a number of life history traits in response to environmental changes between high and low latitudes, both at embryonic and post-embryonic stages. Sympatric species provide opportunities for future studies to identify the patterns of life history adaptation and the underlying selective forces, using both comparative studies and manipulative experiments. In addition, our results demonstrate that incubation periods can adapt to environments via complex physiological mechanisms. This highlights the importance of identifying life history adaptation at early life stages, such as the embryonic stage. For example, different proximate mechanisms (embryonic development prior to oviposition vs. developmental rate after oviposition) may underlie a similar trait of incubation period that shows countergradient variation along latitudinal clines.

Acknowledgments We thank P. Liu, Y. Wang, Z. Y. Zhang and W. B. Yan for their assistance in the field or laboratory. We are grateful to T. R. Robinns, J.-F. Le Galliard and one anonymous reviewer for their comments on the manuscript. This work was supported by grants from the Natural Science Foundation of China (project no. 30770274), the One Hundred Talents Program of the Chinese Academy of Sciences to W.-G. Du and the local government of Anhui Province to X.-F. Xu (KJ2010A249).

References

Andrews R (2004) Patterns of embryonic development. In: Deeming DC (ed) Reptilian incubation: environment, evolution and behaviour. Nottingham University Press, Nottingham, pp 75–102

Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford

Angilletta MJ, Niewiarowski PH, Dunham AE, Leache AD, Porter WP (2004) Bergmann's clines in ectotherms: illustrating a life-history perspective with sceloporine lizards. Am Nat 164:E168–E183

Angilletta MJ, Oufiero CE, Leache AD (2006) Direct and indirect effects of environmental temperature on the evolution of reproductive strategies: an information-theoretic approach. Am Nat 168:E123–E135

Ashton KG, Feldman CR (2003) Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. Evolution 57:1151–1163

Blackledge TA, Gillespie RG (2004) Convergent evolution of behavior in an adaptive radiation of Hawaiian web-building spiders. PNAS 101:16228–16233

Denno RF, Dingle H (1981) Insect life history patterns: habitat and geographic variation. Springer, New York

Du WG, Radder RS, Sun B, Shine R (2009) Determinants of incubation period: do reptilian embryos hatch after a fixed total number of heart beats? J Exp Biol 212:1302–1306

Du WG, Warner DA, Langkilde T, Robbins T, Shine R (2010a) The physiological basis of geographic variation in rates of embryonic development within a widespread lizard species. Am Nat 176:522–528

Du WG, Ye H, Zhao B, Warner DA, Shine R (2010b) Thermal acclimation of heart rates in reptilian embryos. PLoS ONE 5(12):e15308

Du WG, Ye H, Zhao B, Pizzatto L, Ji X, Shine R (2011) Patterns of interspecific variation in the heart rates of embryonic reptiles. PLoS ONE 6:e29027

Du WG, Warner DA, Langkilde T, Robbins T, Shine R (2012) The roles of pre- and post-hatching growth rates in generating a latitudinal cline of body size in the eastern fence lizard (*Sceloporus undulatus*). Biol J Linn Soci 106:202–209

Dufaure JP, Hubert J (1961) Table de développement du lézard vivipare: *Lacerta* (*Zootoca*) *vivipara* Jacquin. Arch Anat Microsc Morphol Exp 50:309–328

Ewert MA (1985) Embryology of turtles. In: Gans C, Billett F, Maderson PFA (eds) Biology of the reptilia, vol 14. Wiley, New York, pp 75–268

Fischer K, Brakefield PM, Zwaan BJ (2003) Plasticity in butterfly egg size: why larger offspring at lower temperatures? Ecology 84:3138–3147

Fu JZ (2000) Toward the phylogeny of the family Lacertidae—why 4708 base pairs of mtDNA sequences cannot draw the picture. Biol J Linn Soci 71:203–217

Gleiss AC et al (2011) Convergent evolution in locomotory patterns of flying and swimming animals. Nat Commun 2. doi: 10.1038/ncomms1350

Hao QL, Liu HX, Ji X (2006) Phenotypic variation in hatchling Mongrolian racerunners *Eremias argus* from eggs incubated at constant versus fluctuating temperatures. Acta Zool Sin 52: 1049–1057

Ji X, Du WG, Qu YF, Lin LH (2009) Nonlinear continuum of egg size-number trade-offs in a snake: is egg-size variation fitness related? Oecologia 159:689–696

Liefting M, Hoffmann AA, Ellers J (2009) Plasticity versus environmental canalization: population differences in thermal responses along a latitudinal gradient in *Drosophila serrata*. Evolution 63:1954–1963

Losos JB (2000) Ecological character displacement and the study of adaptation. PNAS 97:5693–5695

Losos JB (2011) Convergence, adaptation, and constraint. Evolution 65:1827–1840

Losos JB, Jackman TR, Larson A, de Queiroz K, Rodriguez-Schettino L (1998) Contingency and determinism in replicated adaptive radiations of island lizards. Science 279:2115–2118

Matos M, Simoes P, Duarte A, Rego C, Avelar T, Rose MR (2004) Convergence to a novel environment: comparative method versus experimental evolution. Evolution 58:1503–1510

Niewiarowski PH (1994) Understanding geographic life-history variation in lizards. In: Vitt LJ, Pianka ER (eds) Lizard ecology:

historical and experimental perspectives. Princeton University Press, Princeton, pp 31–50

Niewiarowski PH, Angilletta MJ (2008) Countergradient variation in embryonic growth and development: do embryonic and juvenile performances trade off? Funct Ecol 22:895–901

Ohlberger J, Mehner T, Staaks G, Hölker F (2008) Temperature-related physiological adaptations promote ecological divergence in a sympatric species pair of temperate freshwater fish, *Coregonus* spp. Funct Ecol 22:501–508

Oro D, Pradel R, Lebreton J-D (1999) Food availability and nest predation influence life history traits in Audouin's gull, *Larus audouinii*. Oecologia 118:438–445

Oufiero CE, Angilletta MJ (2006) Convergent evolution of embryonic growth and development in the eastern fence lizard (*Sceloporus undulatus*). Evolution 60:1066–1075

Pan Z-C, Ji X (2001) The influence of incubation temperature on size, morphology and locomotor performance of hatchling grass lizards (*Takydromus wolteri*). Acta Ecol Sin 21:2031–2038

Parker GA, Begon M (1986) Optimal egg size and clutch size: effects of environment and maternal phenotype. Am Nat 128:573–592

Sears MW, Angilletta MJ (2004) Body size clines in *Sceloporus* lizards: proximate mechanisms and demographic constraints. Int Comp Biol 44:433–442

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Warner DA, Shine R (2007) Fitness of juvenile lizards depends on seasonal timing of hatching, not offspring body size. Oecologia 154:65–73

Yampolsky LY, Scheiner SM (1996) Why larger offspring at lower temperatures? A demographic approach. Am Nat 147:86–100

Zanette L, Clinchy M, Smith JNM (2006) Food and predators affect egg production in song sparrows. Ecology 87:2459–2467

Zhao EM, Zhao KT, Zhou KY (1999) Fauna sinica reptilia, vol 2 Squamata. Chinese Science Press, Beijing