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# Life-history Variation with Respect to Experienced Thermal Environments in the Lizard, *Eremias multiocellata* (Lacertidae)

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We compared adult size, female reproductive traits, and offspring phenotypes between multiocellated racerunners (*Eremias multiocellata*) from two thermally different sites (populations) in Inner Mongolia (North China): the colder one in Wulatehouqi (WQ) and the warmer one in Dalateqi (DQ). Both adults and neonates were smaller in the colder site. Females from the two sites both produced a single litter of 2–5 young per season, and did not differ in allocation of energy to reproduction after accounting for differences in body size. Female neonates had more ventral scales than did males, and the WQ neonates had fewer ventral scales than did the DQ neonates. The WQ neonates were slower than the DQ neonates. When body length was normalized across populations, we found that (1) hindlimb length correlated positively with sprint speed in both WQ and DQ neonates, (2) forelimb length correlated positively with sprint speed only in the DQ neonates, and (3) tail length correlated positively with sprint speed only in the WQ neonates. Hindlimb length played a more important role in locomotion than did tail length or forelimb length. Though differing in size and morphology, neonates from the two sites did not differ in early growth and survival under identical laboratory conditions. Our data are consistent with many studies that have shown counter-gradient variation in physiological traits (growth rate and reproductive output) and cogradient variation in morphological traits.

**Key words:** Lacertidae, *Eremias multiocellata*, female reproduction, morphology, growth, locomotor performance, geographic variation

## INTRODUCTION

There are many well-documented examples of geographic variation in life-history traits of ectotherms, particularly with respect to size, growth, and reproduction (Arnett and Gotelli, 1999; Billerbeck et al., 2000; Trussell, 2000; Ashton, 2001; Vila-Gispert and Moreno-Amich, 2002; Morrison and Hero, 2003). Life-history variation may stem from genetic and/or environmental differences among populations, and has at least two possible adaptive explanations: (1) each habitat has its own special selective regime and therefore selects for individuals with appropriate phenotypic traits, which may differ from those in other habitats, and (2) organisms that have plastic phenotypic traits may use environmental cues to adapt to such conditions by adopting those phenotypes. Similar to other ectotherms, lizards are highly dependent upon environmental conditions, and may therefore display substantial environmentally induced life-history variation (Adolph and Porter, 1993; Forsman and Shine, 1995; Ji et al., 2002; Angilletta et al., 2004). There is convincing evidence for both genetic and environmental mechanisms in lizards (Ballinger, 1977; Sinervo and Adolph,

1989; Grant and Dunham, 1990; Rawson and Hilbish, 1991; Sorci et al., 1996).

Life-history studies of geographic variation in lizards are relatively limited compared to studies of within-population variation, and the studies that have been conducted moreover span few taxonomic groups (Hasegawa, 1994; Forsman and Shine, 1995; Wapstra and Swain, 2001; Ji et al., 2002; Du et al., 2005; Zhu et al., 2009). Therefore, a broader collection of datasets describing geographic variation in life-histories across multiple taxonomic groups is needed to elucidate general patterns and/or determine mechanisms that result in unique patterns (Angilletta et al., 2004; Niewiarowski et al., 2004). Here, we compared adult size, female reproductive traits, and offspring phenotypes between multiocellated racerunners (*Eremias multiocellata*) from two thermally different sites (populations) in Inner Mongolia (North China) to examine whether the observed patterns of variation are consistent with cogradient or countergradient variation (Marcil et al., 2006; Covover and Schultz, 1995; Conover et al., 2009) with respect to the experienced thermal environments.

## MATERIALS AND METHODS

### Study species and populations

*Eremias multiocellata* is a viviparous lacertid lizard that has a distribution covering North-northwest China, Mongolia, Kyrgyzstan, and southern Tuvin District in Siberian Russia (Zhao, 1999). The

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lizard is often found in open spaces in arid or semiarid regions covered by sparse vegetation (Zhao, 1999). Adults are not sexually dimorphic with respect to body size (Li et al., 2006). The two populations we compared inhabit thermally different sites in Inner Mongolia, one is in Wulatehouqi (WQ; 41°27'N, 106°59'E; ~1620 m elevation) and the other in Dalateqi (DQ; 40°16'N, 109°58'E; ~1080 m elevation), which is approximately 2–11°C warmer than WQ depending on the season (Inner Mongolia Bureau of Meteorology).

#### Animal collection and care

We collected a total of 460 male and female lizards by hand or noose from the two populations in May 2007. After confirming adult status by palpating all females for eggs, we rated 399 as adults, of which 252 (171 females and 81 males; > 52 mm snout-vent length, SVL) were from the WQ population, and 147 (93 females and 54 males; > 57 mm SVL) were from the DQ population. Most of these lizards were released at their site of capture after determining sex, measuring SVL and tail length, and checking for signs of tail loss. Seventy females (45 from WQ, and 25 from DQ) with yolking follicles or newly ovulated eggs as well as copulation marks were transported to our laboratory in Nanjing, where they were marked using a non-toxic waterproof ink for identification.

Between 8–10 females were housed together in 900 mm × 650 mm × 600 mm (length × width × height) plastic cages, in an indoor animal holding facility. The cages contained a substrate of sand (~50 mm depth), with rocks and pieces of clay tiles provided as shelter and basking sites. Thermoregulatory opportunities were provided during daytime hours by a 100-W incandescent lamp; overnight temperatures followed indoor temperatures (18.0 ± 1.0°C). Mealworms (larvae of *Tenebrio molitor*), house crickets (*Achetus domesticus*) and field-captured grasshoppers (*Catantops* spp.) dusted with multivitamins and minerals were provided daily, so that excess food was always available in the cages. Fresh water was also provided daily. Lizards from the two populations were never housed together in the same cage.

We checked the cages twice daily for neonates after the first female gave birth, and immediately collected and weighed them after birth. Females giving birth during the same period were isolated from each other using dividers that created 200 mm × 200 mm × 200 mm chambers so that neonates could be accurately allocated to the mother. None of these females was isolated for more than 36 h, and a 20-W spotlight was mounted in each divider to allow thermoregulation during daytime hours. Body mass and SVL were taken for each postpartum female. Of the 70 females, 66 gave birth to well-developed young, and the remaining four produced abnormal litters with dead young, or stillborns. Abnormal litters, two from each population, were excluded from analyses. We calculated relative fecundity by using the residuals derived from the regression of  $\log_e$  litter size on  $\log_e$  maternal SVL (Olsson and Shine, 1997).

#### Offspring phenotypes

Fifty-four neonates from single litters were measured at birth for locomotor performance and morphological traits; the remaining neonates only were weighed and measured for SVL and tail length. We conducted all locomotor trials at the body temperature of 30°C, which was achieved by placing the neonates in an incubator (Sheldon MFG inc., USA) at 30°C for 30 min prior to testing. Locomotor performance was assessed by chasing the neonates along a 2-m racetrack with one side transparent, which allowed videotaping with a Panasonic NV-DS77 digital video camera. The racetrack was kept in a room set at 30°C. Each neonate was run twice, with a 30 min rest between the two successive trials and, during the resting interval, it was placed back in the incubator. The tapes were later examined with a computer using MGI VideoWave III software for PC (MGI Software Co., Toronto, Canada) for sprint speed in the fastest 25 cm interval, and the maximal sprinting distance traveled without stopping.

Immediately following the locomotor trials, we cooled the neonates to about 5°C by placing them on a wooden cooling box, and then measured them with Mitutoyo digital calipers. The box contained a substrate of ice (~50 mm depth), with a metal bracket where the temperature could be controlled by adjusting its distance from the ice substrate. Morphological measurements taken for each neonate included: SVL, tail length, abdomen length (from the posterior base of the fore-limb to the anterior base of the hind-limb), head length (from the snout to the anterior edge of the tympanum), head width (taken at the posterior end of the mandible), fore-limb length (humerus plus ulna), hind-limb length (femur plus tibia), and the number of ventral scales. We determined neonate sex by gently pressing on both sides of tail base using forceps to check for the presence or absence of hemipenes.

Following morphological measurements, neonates were housed in the laboratory to measure growth rates. We individually numbered neonates, often at 10-day intervals, using a non-toxic waterproof marker for future identification, and then randomly moved them into one of five 500 mm × 400 mm × 400 mm plastic cages placed in a room set at a constant 20°C. Neonates from the two populations were never housed together in the same cage. A 60-W spotlight was mounted in each cage to allow thermoregulation for 14 h daily. Small mealworms, grasshoppers and house crickets were provided in excess and spread throughout the cage, such that newborns had free access to the food. We evaluated early growth (the first 90-day period) by weighing offspring at 15-day intervals.

#### Statistical analyses

We used the STATISTICA software package (version 6.0 for PC) to analyze data. We tested data for normality using the Kolmogorov-Smirnov test, and for homogeneity of variances using the Bartlett's test (univariate level) and/or the Box's M test (multivariate level). We used the G-test, linear regression analysis, partial correlation analysis, one- and two-way analysis of variance (ANOVA), repeated measures ANOVA, one-way analysis of covariance (ANCOVA), and multivariate analysis of covariance (MANCOVA) to analyze the corresponding data. Descriptive statistics are presented as mean ± SE, and the significance level is set at  $\alpha = 0.05$ .

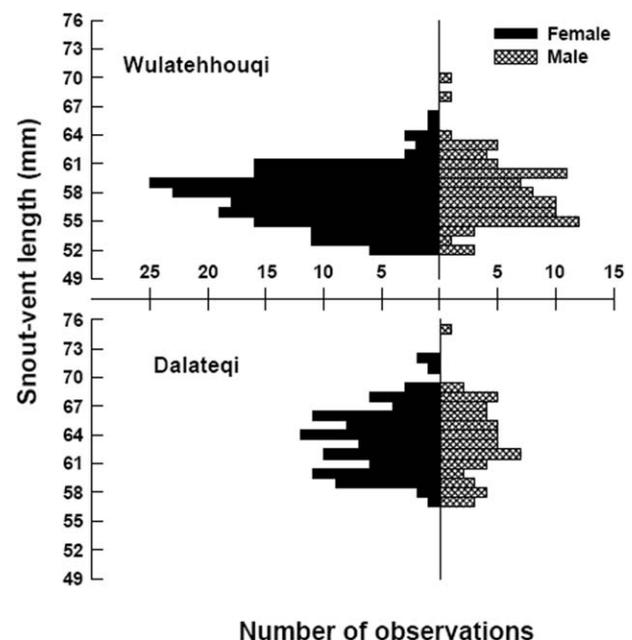


Fig. 1. Frequency distributions of adult SVL of two populations of *E. multiocellata*.

**Table 1.** Descriptive statistics for female reproductive traits of *Eremias multiocellata*. Values are expressed as mean  $\pm$  SE (range). F values of one-way ANOVA (for SVL and neonate mass) and one-way ANCOVA (for postpartum mass, litter size and litter mass with SVL as the covariate).

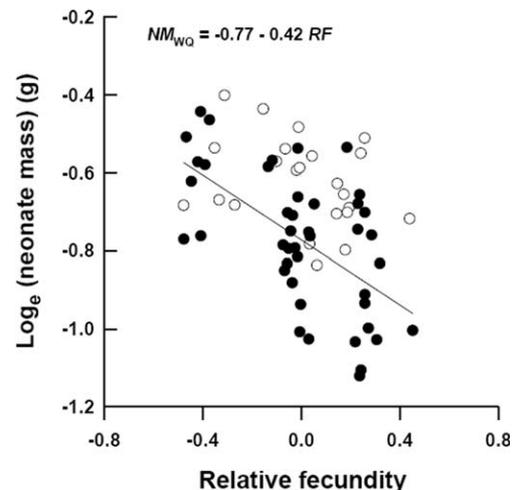
Variable	Populations		F values and P levels
	Wulatehouqi	Dalateqi	
N	43	23	
Snout-vent length (mm)	59.3 $\pm$ 0.4 (54.1–66.4)	63.9 $\pm$ 0.6 (59.1–68.8)	$F_{1,64} = 40.11, P < 0.0001$
Postpartum mass (g)	4.3 $\pm$ 0.1 (2.8–6.1)	4.8 $\pm$ 0.1 (3.9–6.0)	$F_{1,63} = 3.64, P = 0.061$
Litter size	3.2 $\pm$ 0.1 (2–5)	3.0 $\pm$ 0.2 (2–5)	$F_{1,63} = 3.63, P = 0.061$
Litter mass (g)	1.46 $\pm$ 0.05 (0.93–2.34)	1.64 $\pm$ 0.09 (1.01–2.44)	$F_{1,63} = 0.37, P = 0.544$
Neonate mass (g)	0.47 $\pm$ 0.01 (0.33–0.64)	0.54 $\pm$ 0.01 (0.43–0.67)	$F_{1,64} = 13.19, P < 0.0006$
Birth date (days since 20 May)	67.6 $\pm$ 2.4 (52–87)	47.1 $\pm$ 1.4 (38–63)	$F_{1,64} = 64.19, P < 0.0001$

## RESULTS

### Adult size, tail loss and female reproduction

Mean values for adult SVL differed between the two populations (two-way ANOVA;  $F_{1,395} = 267.45, P < 0.0001$ ), but not between the sexes ( $F_{1,395} = 0.34, P = 0.559$ ); the sex  $\times$  population interaction was not a significant source of variation in adult SVL ( $F_{1,395} = 0.76, P = 0.382$ ). The WQ adults were smaller than the DQ adults in SVL (Fig. 1). Of the 252 WQ adults, 86 (~34%; 55 females and 31 males) autotomized some portion of the tail at least once. Ninety-three (~63%; 59 females and 24 males) of the 147 QD adults showed signs of tail loss. The proportion of individuals with signs of tail loss was much lower in the WQ (colder) population ( $G = 32.09, df = 1, P < 0.001$ ).

Females from the two populations both produced a single litter of 2–5 young per breeding season. Birth date, expressed as the number of days since 20 May, differed between the two populations, with the WQ females giving birth about three weeks later than did the DQ females (Table 1). In neither the WQ population (linear regression analysis;  $F_{1,41} = 0.40, P = 0.531$ ) nor the DQ population ( $F_{1,21} = 3.12, P = 0.092$ ) was neonate mass dependent on maternal SVL. A significant negative correlation between neonate mass and relative fecundity could be detected in the WQ population ( $r = -0.59, F_{1,41} = 21.67, P < 0.0001$ ; Fig. 2), but not in the DQ population ( $r = -0.29, F_{1,21} = 1.98, P = 0.174$ ). The WQ females on average produced smaller young than did the DQ females, but did not differ from the DQ females of the same SVL in postpartum mass, litter size and litter mass (Table 1).



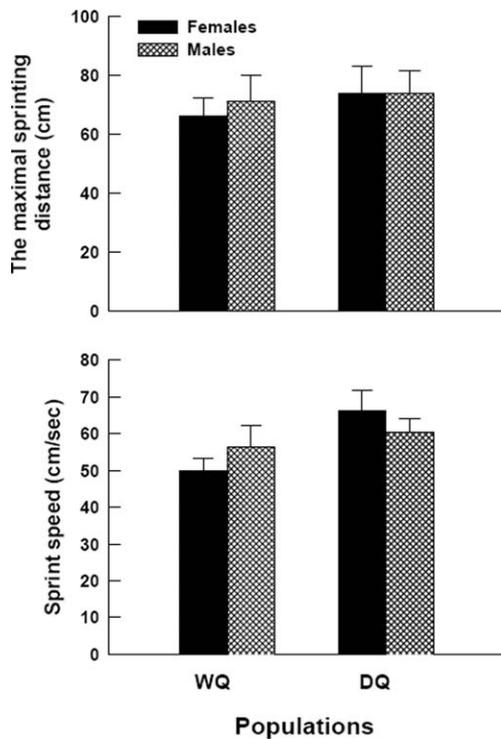
**Fig. 2.** The relationship between offspring size and relative fecundity (see text for definition). All data are  $\log_e$  transformed, and the regression equation for the WQ population is indicated in the figure. Solid dots represent the WQ neonates, and open dots represent the DQ neonates.

### Offspring phenotypes

Mean values for neonate SVL differed between the two populations (two-way ANOVA;  $F_{1,50} = 31.48, P < 0.0001$ ), but not between the sexes ( $F_{1,50} = 1.92, P = 0.172$ ); the sex  $\times$  population interaction was not a significant source of variation in SVL ( $F_{1,50} = 2.15, P = 0.149$ ) (Table 2). The WQ

**Table 2.** Size, mass and morphology of neonates produced by females of *Eremias multiocellata* from two populations inhabiting thermally different habitats. Values are expressed as mean  $\pm$  SE (range).

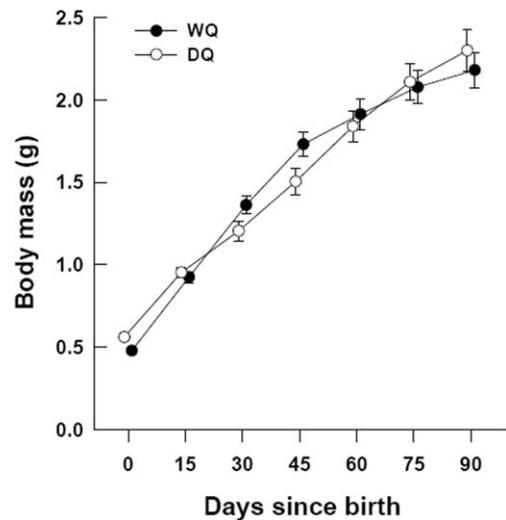
Variables	Wulatehouqi		Dalateqi	
	Females	Males	Females	Males
N	15	9	13	17
Snout-vent length (mm)	26.2 $\pm$ 0.4 (23.2–28.8)	25.2 $\pm$ 0.3 (23.6–27.0)	27.5 $\pm$ 0.3 (25.2–29.1)	27.5 $\pm$ 0.2 (26.4–29.2)
Tail length (mm)	32.0 $\pm$ 0.7 (27.8–37.8)	31.9 $\pm$ 0.7 (29.2–36.2)	40.0 $\pm$ 1.0 (33.5–46.6)	39.0 $\pm$ 0.7 (33.4–45.3)
Body mass (g)	0.44 $\pm$ 0.02 (0.31–0.60)	0.41 $\pm$ 0.02 (0.33–0.50)	0.52 $\pm$ 0.02 (0.34–0.66)	0.51 $\pm$ 0.02 (0.38–0.64)
Abdomen length (mm)	11.5 $\pm$ 0.3 (9.6–14.1)	10.8 $\pm$ 0.2 (9.5–12.0)	12.1 $\pm$ 0.2 (10.6–13.1)	11.9 $\pm$ 0.2 (10.6–13.0)
Head length (mm)	6.5 $\pm$ 0.05 (6.1–6.8)	6.4 $\pm$ 0.1 (6.0–6.9)	6.6 $\pm$ 0.05 (6.3–6.9)	6.6 $\pm$ 0.1 (6.3–7.0)
Head width (mm)	4.7 $\pm$ 0.04 (4.4–5.0)	4.5 $\pm$ 0.04 (4.3–4.7)	4.7 $\pm$ 0.03 (4.6–5.0)	4.8 $\pm$ 0.1 (4.3–5.1)
Fore-limb length (mm)	5.5 $\pm$ 0.1 (4.7–5.9)	5.2 $\pm$ 0.1 (4.7–5.6)	6.0 $\pm$ 0.1 (5.4–6.4)	6.0 $\pm$ 0.1 (5.4–6.3)
Hind-limb length (mm)	7.8 $\pm$ 0.1 (6.7–8.6)	7.6 $\pm$ 0.2 (6.8–8.6)	8.4 $\pm$ 0.1 (7.7–8.9)	8.5 $\pm$ 0.1 (7.7–9.3)
Ventral scales	31.5 $\pm$ 0.2 (31–33)	29.9 $\pm$ 0.4 (28–32)	33.4 $\pm$ 0.3 (32–35)	31.3 $\pm$ 0.2 (30–33)



**Fig. 3.** Mean values ( $\pm$  SE) for locomotor performance (the maximal sprinting distance and sprint speed) of neonates from the WQ and DQ populations.

neonates on average were smaller than the DQ neonates in SVL. Females had more ventral scales than did males (two-way ANOVA;  $F_{1, 50} = 53.05$ ,  $P < 0.0001$ ), and the DQ neonates had more ventral scales than did the WQ neonates ( $F_{1, 50} = 42.31$ ,  $P < 0.0001$ ); the sex  $\times$  population interaction was not a significant source of variation in ventral scale counts ( $F_{1, 50} = 1.08$ ,  $P = 0.304$ ). Other morphological variables overall were affected by population (MANCOVA; Wilks' Lambda = 0.44,  $df = 7, 43$ ,  $P < 0.0001$ ), but not by sex (Wilks' Lambda = 0.89,  $df = 7, 43$ ,  $P = 0.650$ ), nor by sex  $\times$  population interaction (Wilks' Lambda = 0.85,  $df = 7, 43$ ,  $P = 0.396$ ). Specifically, the WQ neonates exhibited shorter tail length, forelimb length, and hindlimb length, but longer abdomen length than did DQ neonates of the same SVL (all  $P < 0.021$ ).

Sprint speed was affected by population (two-way ANOVA;  $F_{1, 50} = 5.77$ ,  $P = 0.020$ ), but not by sex ( $F_{1, 50} < 0.01$ ,  $P = 0.989$ ) nor the sex  $\times$  population interaction ( $F_{1, 50} = 2.05$ ,  $P = 0.158$ ), with the WQ neonates being slower than the DQ neonates (Fig. 3). The maximal sprinting distance was not affected by population (two-way ANOVA;  $F_{1, 50} = 0.43$ ,  $P = 0.516$ ), sex ( $F_{1, 50} = 0.08$ ,  $P = 0.775$ ) and the sex  $\times$  population interaction ( $F_{1, 50} = 0.11$ ,  $P = 0.737$ ). Hindlimb length, forelimb length, and tail length correlated positively with sprint speed in at least one population when body size (SVL) was partialled out by partial correlation analysis. Specifically, hindlimb length correlated positively with sprint speed in both populations (both  $r > 0.46$ , and both  $P < 0.03$ ), forelimb length correlated positively with sprint speed in the DQ population ( $r = 0.40$ ,  $t = 2.29$ ,  $df = 27$ ,  $P = 0.030$ ), but not in the WQ population ( $r = 0.31$ ,  $t = 1.50$ ,  $df = 21$ ,  $P =$



**Fig. 4.** Mean values ( $\pm$  SE) for early growth (to 90 days) of neonates from the WQ and DQ populations.

0.149), and tail length correlated positively with sprint speed in the WQ population ( $r = 0.46$ ,  $t = 2.35$ ,  $df = 21$ ,  $P = 0.028$ ), but not in the DQ population ( $r = 0.32$ ,  $t = 1.73$ ,  $df = 27$ ,  $P = 0.096$ ). In none of the above partial correlation analyses did we find that SVL correlated positively with sprint speed (all  $P > 0.149$ ).

Three WQ and five DQ neonates died during the experiment. The number of dead neonates did not differ between the two populations ( $G = 0.19$ ,  $df = 1$ ,  $P > 0.50$ ). Early growth was very evident (repeated measures ANOVA;  $F_{6, 264} = 332.05$ ,  $P < 0.0001$ ; Fig. 4), but did not differ between the two populations ( $F_{1, 44} = 0.09$ ,  $P = 0.763$ ). For the WQ neonates, mass gain in the first 45-day period was positively related to body mass at birth (all  $P < 0.05$ ), but such a relation was absent thereafter (all  $P > 0.143$ ). For the DQ neonates, mass gain was unrelated to body mass at birth in the first 45-day period and thereafter (all  $P > 0.129$ ).

## DISCUSSION

Adults from the colder site (WQ) were smaller than those from the warmer site (DQ), suggesting that *E. multiocellata* is among those ectothermic vertebrates that do not exhibit a negative correlation between body size and environmental temperature (Ashton, 2001; Angilletta et al., 2004; Olalla-Tárraga et al., 2006; Pincheira-Donoso et al., 2007). One factor likely affecting adult body size is the time allowed for growth, which is often constrained by survival. Survival is often negatively correlated with caudal autotomy, a defensive tactic used by many lizards, including lacertids, to evade fatal predatory encounters. This negative relationship between survival and caudal autotomy occurs either through an index of predation pressure, or through the physiological, ecological and behavioral effects of tail loss after the fact (Bellairs and Bryant, 1985; Arnold, 1988). We found a lower frequency of tail loss associated with lizards from the colder site. Although we do not know if survival is negatively correlated with caudal autotomy among our populations, the lower frequency of tail loss associated with lizards from the colder site implies greater survival, and therefore

more time to grow, which is at least inconsistent with the smaller body sizes associated with lizards from the colder site. In the present study, the smaller adult size in the colder site may be better explained by two factors: (1) reaching of sexual maturity at a smaller body size; and (2) the shorter length of the growing season.

Energy acquired throughout the life of an animal should be allocated towards two main competing demands, maintenance and production. Maintenance costs include the energy costs for the activities essential for the continuity of life, whereas energy allocated towards production supports growth and reproduction (Congdon et al., 1982; Luo et al., 2010). Allocating energy to reproduction generally retards growth in lizards (Ji and Braña, 2000; Ji et al., 2007). It is therefore not surprising that the adult size is smaller in a population where energy allocation to reproduction begins at a smaller body size. Interestingly, maternal energy allocation to reproduction did not differ between the two populations after accounting for the difference in adult SVL, as revealed by the fact that the WQ females did not differ from the DQ females of the same SVL in postpartum mass and litter mass. So, lizards in the colder site may acquire less energy and therefore have smaller body sizes because the season suitable for growth is shorter, but they still realize the same reproductive potential as their conspecifics in the warmer site, at the expense of somatic growth.

Neonates born under identical laboratory conditions of both populations differed in most traits examined. Although there were differences in size and mass at birth between neonates from the two populations, the larger DQ neonates gained no more mass than did the smaller WQ neonates in the first 90-day period, and the difference in neonate body size found at hatching (one-way ANOVA;  $F_{1,44} = 12.67$ ,  $P < 0.001$ ) did not persist after the 90 days of growth ( $F_{1,44} = 0.06$ ,  $P = 0.814$ ). Moreover, early survival did not differ between neonates from the two populations. These observations suggest that, in the laboratory, population of origin has no significant effect on offspring survival and growth in *E. multiocellata*. In nature, however, larger offspring may be more fit than their smaller conspecifics. Larger individuals are better prepared to face periods of starvation, to avoid predators, to forage on a wider set of prey, or to invest in immune responses against parasites (Fox and Czesak, 2000; Einum, 2003; Zhang and Ji, 2004; Marshall and Keough, 2006; Webb et al., 2006). Our study, however, cannot differentiate between the effects of population of origin and offspring-size variation.

Compared with the WQ neonates of the same SVL, the DQ neonates were longer in tail length, forelimb length, and hindlimb length, but shorter in abdomen length (Table 2). These findings may have implications for differential embryonic allocation of resources to disparate morphological variables between the two populations and, more importantly, they provide evidence for correlated evolution of morphological traits that affect locomotor abilities in lizards. For example, hindlimb length correlates positively with sprint speed in both populations. Overall, hindlimb length accounted for approximately 49% of the variation in sprint speed in neonates. This finding validates the prediction that hindlimb length is an important determinant of running speed in lizards (Losos, 1990; Garland and Losos, 1994;

Bauwens et al., 1995). Tail and forelimb may be less important than hindlimb with respect to their functional roles in locomotion, as tail length (~26%) and forelimb length (~29%) both accounted for a much smaller proportion of variation in sprint speed than did hindlimb length. Body length correlates positively with sprint speed in a clade of *Anolis* lizards (Losos, 1990), however, such a correlation was not found in this study. Shorter protruding parts, such as fore- and hindlimbs and tail, reduce heat loss, and may be advantageous in cooler environments. However, shorter protruding parts entail locomotor costs, as revealed by the fact that running speed was positively correlated to both hindlimb length and tail length in the colder population. Possible trade-offs due to antagonistic selection between heat loss and locomotion would be an interesting focus for further study.

It is common among lacertid lizards for females to have more ventral scales than do males (Gosá et al., 1986; Pan and Ji, 2001; Du and Ji, 2006; Hao et al., 2006; Li et al., 2009). As a lacertid lizard, *E. multiocellata* shares this feature. The number of ventral scales is a thermally plastic trait in some, but not all, lacertid lizards studied. For example, embryonic temperature can affect the trait in *Takydromus septentrionalis* (northern grass lizard; Du and Ji, 2006), *Eremias argus* (Mongolian racerunner; Hao et al., 2006) and *E. przewalskii* (Gobi racerunner; Li et al., 2009) but not in *T. wolteri* (white-striped grass lizard; Pan and Ji, 2001). Data of this study show that neonates from the colder site have fewer ventral scales than do those from the warmer site. This discrepancy is unlikely to result from the proximate effect of temperature during embryogenesis because neonates of the two populations completed the whole or nearly the whole part of embryonic development under identical laboratory conditions in the present study.

Countergradient variation is expected when stabilizing selection favors similar phenotypes in different environments, or intrinsic influences on phenotypes oppose environmental influence; cogradient variation is expected when changes in phenotypes are environmentally induced, or when selection favors phenotypes in a pattern consistent with environmental influence (Marcil et al., 2006; Covover and Schultz, 1995; Conover et al., 2009). For the traits examined in the present study with respect to the experienced thermal environments, variation in neonate growth and reproductive output is largely countergradient, and variation in morphological traits is largely cogradient. These data are consistent with many studies that have shown countergradient variation in physiological traits, such as growth rate and reproductive output, and cogradient variation in morphological traits (Marcil et al., 2006; Covover and Schultz, 1995; Conover et al., 2009 and references therein).

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