The roles of pre- and post-hatching growth rates in generating a latitudinal cline of body size in the eastern fence lizard (*Sceloporus undulatus*)

WEI-GUO DU[1,2*], DANIEL A. WARNER[3], TRACY LANGKILDE,[4] TRAVIS R. ROBBINS[4,5] and RICHARD SHINE[1]

[1]*School of Biological Sciences A08, University of Sydney, NSW 2006, Australia*
[2]*Key Lab of Animal Ecology and Conservational Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China*
[3]*Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA 50011, USA*
[4]*Department of Biology, Pennsylvania State University, PA 16802, USA*
[5]*Department of Integrative Biology, University of South Florida, Tampa, FL 33620, USA*

Countergradient variation in norms of reaction can dampen the direct effects of environmental influences on phenotypic traits, allowing phenotypic similarity among populations despite exposure to different environmental conditions. Such norms of reaction may occur at any phase of the life-history (e.g. growth rates during both embryonic and postembryonic stages may influence geographical variation in adult body size). We collected gravid female lizards (*Sceloporus undulatus*) from northern (Indiana), central (Mississippi), and southern (Florida) populations, spanning almost the full latitudinal range of the species. Adult females from the southern population were smaller. Intrinsic growth rates of hatchlings were higher for the central population than for the other two populations. This pattern does not parallel the countergradient variation previously found in embryonic developmental rates among these populations. Earlier hatching enhanced survival rates of juveniles to a similar degree among populations, although juvenile survival rates in the field generally increase with latitude in this species. Our data reveal geographical variation in the ways in which intrinsic developmental/growth rates and survival shift during ontogeny, and suggest that latitudinal patterns in adult body size (such as Bergmann's rule) can result from both faster growth, and longer periods of growth. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **106**, 202–209.

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INTRODUCTION

Body size can influence many aspects of an organism's behaviour and physiology, including fitness-related traits such as locomotor performance, metabolic rate, and reproductive output (Peters, 1986; Speakman, 2005). Understanding body size variation among and within species is a central question in ecology and evolution (Peters, 1986; Schlichting & Pigliucci, 1998). Bergmann's rule (i.e. an increase in body size with increasing latitude or decreasing temperature) is the best-known pattern of geographical variation in body size. This rule was originally developed to explain geographical variation in the body sizes of endothermic animals (Freckleton, Harvey & Pagel, 2003) but has also been applied to some groups of ectotherms (Huey *et al*., 2000; Ashton, 2002; Ashton & Feldman, 2003). Recently, the mechanisms underlying Bergmann's rule have attracted considerable research interest because investigators have

*Corresponding author. E-mail: duweiguo@ioz.ac.cn

tried to identify the ultimate and proximate causes of this variation in the framework of evolutionary ecology and life-history theory (Ashton & Feldman, 2003; Angilletta *et al*., 2004a).

The mechanisms underlying Bergmann's cline in body size are complex (Ashton & Feldman, 2003; Angilletta *et al*., 2004a; Sears & Angilletta, 2004), although growth rate during early life-history stages may be critical (Rowe, 1997; Angilletta, Steury & Sears, 2004b). A larger body size may result from a faster growth rate and/or a longer duration of growth (Angilletta *et al*., 2004a); all else being equal, faster growth rate would lead to larger body size at maturity. Importantly, growth rate is influenced not only by genotype, but also by environmental factors such as temperature and food availability, particularly in ectotherms (Sinervo & Adolph, 1989; Niewiarowski, 1995; Andrews, Mathies & Warner, 2000). To better understand the role of growth rate in generating geographical variation in body size, we need to identify the relative roles of extrinsic versus intrinsic factors generating geographical variation in these traits (Ferguson & Talent, 1993). We also need to tease apart the relative role of intrinsic factors during different ontogenetic stages. Combining observations of field-caught individuals with 'common garden' experiments, whereby individuals from different geographical populations are raised under identical conditions, can provide valuable insight into the relative importance of these mechanisms (Niewiarowski, 1994; Du *et al*., 2005).

Populations of geographically wide-ranging species may exhibit countergradient variation in physiological and life-history traits such as growth rates, reproduction, and morphology, whereby environmental influences on the phenotype are opposed by intrinsic (genetic) factors (Schultz, Reynolds & Conover, 1996; Grether, Cummings & Hudon, 2005; Conover, Duffy & Hice, 2009). Countergradient variation has been demonstrated along latitudinal gradients in temperature or length of activity season in a diversity of ectothermic species from fruit flies to lizards (Conover & Schultz, 1995; Conover *et al*., 2009). Rates of extrinsic embryonic development (that which may be affected by extrinsic factors, such as temperature) and post-embryonic growth are reduced by low ambient temperatures. However, the effects of this reaction norm across a latitudinal gradient are minimized by countergradient variation in intrinsic rates of development and growth (which are often faster for high-latitude populations than for low-latitude conspecifics) (Oufiero & Angilletta, 2006; Liefting, Hoffmann & Ellers, 2009). During embryonic development, such countergradient variation can compensate for effects of cooler environments (where thermal conditions otherwise would delay hatching) and facili-

tate earlier hatching of offspring. Countergradient variation in intrinsic rates of both development and growth could help explain the larger body sizes found in cooler climates. If intrinsic developmental rates do not translate directly to intrinsic growth rates (e.g. as a result of trade-offs between embryonic development and hatchling growth; Niewiarowski & Angilletta, 2008), this would suggest different selection pressures associated with each life stage (i.e. different ontogenetic selection regimes) among populations.

The Eastern Fence Lizard (*Sceloporus undulatus*) is widely distributed across the eastern two-thirds of the USA and occupies diverse habitats, including eastern woodlands, prairie or grasslands, and western canyonlands (Tinkle & Ballinger, 1972; Angilletta *et al*., 2004a). There are two clades separated by the Appalachian Mountains in the eastern woodlands (Leache & Reeder, 2002; Leache, 2009). In the present study, we selected three populations from Indiana, Mississippi, and Florida, all within the western clade, to minimize potential phylogenetic effects. Nonetheless, life-history variation among populations of this species is not strongly associated with phylogenetic relationships among populations (Niewiarowski, Angilletta & Leache, 2004).

The body size of *S. undulatus* typically follows Bergmann's cline across latitudes (Angilletta *et al*., 2004a). The proximate mechanism for larger body sizes in colder environments is delayed maturation; lizards in northern populations (at latitudes of some 39°) take approximately 20 months to mature, whereas the lizards in a central population (at a latitude of 34°) only take 12 months to mature at a similar body size [approximately 70 mm snout–vent length (SVL); Angilletta *et al*., 2004a]. That disparity suggests that other proximate causes (e.g. differences in growth rate), in addition to differences in time to maturation, contribute to geographical variation in the body size of this species. Previous studies have demonstrated countergradient variation with respect to developmental rate of embryos; northern populations have shorter incubation duration than southern populations when the eggs are incubated in identical thermal environments (Oufiero & Angilletta, 2006; Du *et al*., 2010). Rapid embryonic development in northern populations may reduce hatchling growth rates as a result of a trade-off between embryonic developmental rate and hatchling growth rate (Niewiarowski & Angilletta, 2008). However, this trade-off is seen only among populations, and not within populations (Niewiarowski & Angilletta, 2008), suggesting that the putative trade-off between embryonic development rate and hatchling growth rate warrants further study. In the present study, we conducted a common garden experiment to assess intrinsic differences in embryonic developmental

rates, juvenile growth rates, and survival in three geographically- and climatically-distinct populations from temperate Indiana to subtropical Florida. We integrate data on pre- and post-hatching growth rates to understand the proximate basis for the observed clinal variation in body size in this species.

MATERIAL AND METHODS

ANIMAL COLLECTION AND MATERNAL BODY SIZE

We collected a total of 79 adult lizards in May 2009 from three populations in the eastern United States; a northern site (Monroe county, Indiana; 39°17' N, 86°50' W; 18♀ and 8♂), a central site (Teasdale county, Mississippi; 34°16' N, 90°02' W; 18♀ and 7♂), and a southern site (Hillsborough County, peninsular Florida; 27°45′ N, 82°15′ W; 20♀ and 8♂). All captured lizards were placed in individual bags and transferred to Iowa State University, where they were measured (SVL to 0.5 mm), weighed (to 0.01 g), and individually toe-clipped for identification.

EGG COLLECTION AND INCUBATION

The animals were housed in glass terraria ($600 \times 300 \times 400$, L × W × D mm) filled with 10 mm of moist sand. Each terrarium contained three females plus one male and was kept in a room under a 12 :12 h light/dark cycle (lights on 07.00 h) at 22 ± 1 °C. A 100-W conventional light bulb was suspended 5 cm above each terrarium to provide supplementary heat from 08.00 to 16.00 h. Food (crickets, *Acheta domesticus*, dusted with mixed vitamins and minerals) and water were provided *ad libitum* for adult lizards. A nesting box placed at one end of each terrarium was checked at least three times daily for freshly laid eggs. Once found, eggs were weighed ($\pm$ 0.001 g). A total of 119 first-clutch eggs were individually incubated at 28 °C in 64-mL glass jars filled with moist vermiculite (-150 kPa) and covered with plastic wrap (sealed with a rubber band).

DEVELOPMENTAL AND GROWTH RATES OF EMBRYOS

We calculated relative developmental rate of embryos at 28 °C by dividing the observed incubation duration by the shortest incubation duration recorded in this experiment (44 days), and taking the inverse of this value (Shine & Harlow, 1996). The incubation duration of each egg was recorded as the days between egg oviposition and hatchling emergence. To determine the growth rate of embryos, we randomly dissected one egg from each clutch at approximately 40% through incubation (at day 20), and separated the embryo from the egg contents. Embryos were then weighed, and the remaining eggs were left in the incubators to hatch. After hatching, we used clutch mean values of hatchling mass as the final measure of 'embryo' mass at full term. With these data, embryonic growth rates were quantified as the daily rate of increase in embryonic mass, which was calculated as (final body mass – embryonic body mass at 40% through incubation)/(days from the date of egg dissection to hatching). This measurement reflects the majority of growth of reptilian embryos, which takes place during the last two-thirds of incubation (Andrews, 2004).

BODY SIZE, INTRINSIC GROWTH RATES, AND SURVIVAL OF HATCHLINGS

As soon as hatchlings emerged, they were measured (SVL to 0.5 mm), weighed (to 0.001 g) and their sex identified by the presence (male) or absence (female) of enlarged scales below the cloaca. The hatchlings were individually toe-clipped for identification and raised in glass terraria ($600 \times 300 \times 400$ mm, length × width × depth), with the same heating and light schedule as used for adults. Each cage housed eight to ten hatchlings, which were allocated among cages to ensure that cage-mates were similar in age (hence size). To ensure that treatment effects were not confounded by rearing environment (available food or temperatures), each population was equally represented within each terrarium as best as possible. Paper towels lined the bottom of each terrarium, and plastic shelters and sticks for perching were provided. Hatchling lizards were fed live crickets (*Acheta domesticus*; dusted with minerals and vitamins) twice a week. Water was provided *ad libitum*, and cages were misted once daily with water. On three occasions (23 September, 7 October, and 5 November 2009), the lizards were weighed and measured to calculate growth rate. Growth rates were quantified as the daily rate of increase in SVL and body mass.

Because of variation in the timing of hatching as a result of variation in oviposition date, the ages over which hatchling growth was quantified varied among individuals, in the range 26–119 days. We therefore tested for an age effect on growth rates. Growth rates were linear with respect to hatchling age in these animals (x = age, y = SVL; Indiana: $y = 0.1099x + 25.567$, $R^2 = 0.7723$; Mississippi: $y = 0.1032x + 28.177$, $R^2 = 0.5694$; Florida: $y = 0.098x + 24.041$, $R^2 = 0.6792$), as is also the case for other populations from similar latitudes measured weekly for 16 weeks (Langkilde & Freidenfelds, 2010). As a result, the daily growth rates that we measured were independent of age in all three populations (regression analyses, all $P > 0.1$), despite the range of ages at which hatchlings were measured.

Also, age was used as a covariate when analyzing hatchling growth.

Geographical variation in intrinsic hatchling survival rate was also examined. During the common garden experiment, we checked cages daily for the presence of any dead hatchlings. We measured survival for 4 weeks after hatching.

STATISTICAL ANALYSIS

A preliminary analysis indicated that hatchling morphology and post-hatching growth did not differ between the sexes (all $P > 0.2$) and thus sexes were pooled for subsequent analyses of hatchling traits. Only hatchlings from the first clutches produced by a female were included in our analyses because not all females laid second clutches. Clutch mean values of hatchling traits were used as our unit of analysis to avoid pseudoreplication.

We used one-way analysis of variance to detect population differences in maternal SVL and body mass, developmental and growth rates of embryos and hatchling morphology. To determine population differences in growth rate, we used a mixed-model analysis of covariance with hatchling age (days since hatching) as a covariate (because hatchling size was measured on three specific dates not related to age), and cage as a random factor. Tukey's post-hoc multiple-comparisons tests were used to distinguish among means of significantly-affected traits for all analyses. Logistic regression was used to analyze the influence of population and hatching date on hatchling survival.

We used correlation analysis to evaluate the relationships among embryo developmental rates, embryo growth rates, and post-embryonic growth both among and within populations to quantify potential countergradient patterns across the latitudinal range of *S. undulatus* and the trade-off between embryonic developmental rate and hatchling growth.

RESULTS

MATERNAL AND OFFSPRING BODY SIZE

Adult females from the northern and central populations were significantly larger than those from the southern population (in both SVL and body mass; Table 1). Hatchling size varied considerably among populations (Table 1). Hatchlings from the northern and central populations were longer or heavier at hatching than were those from the southern population (Table 1).

DEVELOPMENTAL AND GROWTH RATES OF EMBRYOS

Developmental rates of embryos decreased from the northern population to southern population ($F_{2,39} = 44.14$, $P < 0.0001$) (Fig. 1A). Similarly, growth rates of embryos were higher in the northern population than the southern population ($F_{2,17} = 8.14$, $P < 0.01$) (Fig. 1B).

INTRINSIC GROWTH RATES OF HATCHLINGS

Post-hatching growth differed among populations, with higher rates of growth in SVL ($F_{2,5.6} = 9.29$, $P = 0.017$) and body mass ($F_{2,7.8} = 8.16$, $P = 0.012$) in the central population than in the northern and southern populations (Fig. 2A, B). The growth rates of hatchlings did not correlate with developmental rates or growth rates of embryos both among these populations (developmental rate: $R = 0.03$ $t = 0.28$, d.f. = 64, $P = 0.78$, Fig. 3; growth rate: $R = 0.21$ $t = 0.87$, d.f. = 19, $P = 0.39$) and within each population (all $P > 0.2$).

SURVIVAL OF HATCHLINGS

In the first month after hatching, 74%, 78%, and 79% of hatchlings survived from the northern, central, and southern populations, respectively. Intrinsic hatchling survival was higher for lizards that hatched earlier

Table 1. Maternal body size and hatchling size (snout–vent length and body mass) of *Sceloporus undulatus* from the northern (Indiana), central (Mississippi), and southern (Florida) populations

	Maternal snout–vent length (mm)	Maternal body mass (g)	Hatchling snout–vent length (mm)	Hatchling body mass (g)
Northern population	78.3 ± 0.9^a	18.02 ± 0.65^a	25.31 ± 0.30^a	0.528 ± 0.016
Central population	75.5 ± 1.2^a	16.81 ± 0.80^a	25.01 ± 0.21^a	0.496 ± 0.013
Southern population	66.1 ± 0.8^b	9.47 ± 0.42^b	23.95 ± 0.24^b	0.480 ± 0.013
Analysis of variance	$F_{2,53} = 44.67$	$F_{2,53} = 55.89$	$F_{2,39} = 6.92$	$F_{2,39} = 2.72$
	$P < 0.0001$	$P < 0.0001$	$P < 0.01$	$P = 0.07$

Hatchlings were from eggs incubated at 28 °C. Sample sizes for the northern, central and southern populations were 18, 18, and 20 for adult females, and 14, 17, and 11 clutches for hatchlings, respectively. Data are expressed as the mean ± SE. Means with different superscripts are statistically different (Tukey's test).
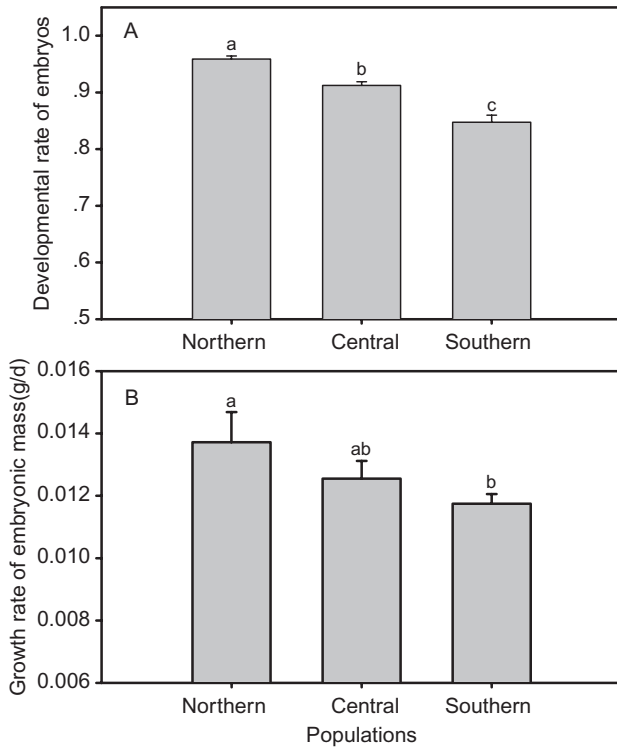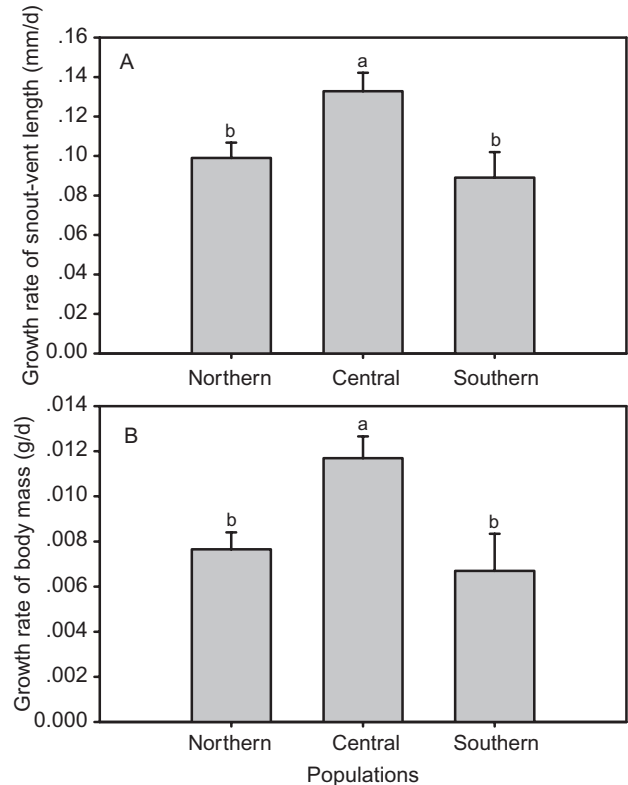
Figure 1. Developmental and growth rates of *Sceloporus undulatus* embryos from the northern (Indiana), central (Mississippi), and southern (Florida) populations. Sample sizes for the northern, central and southern populations were 14, 17, and 11 for the developmental rate, and 9, 6, and 5 for the growth rate, respectively. Developmental rate (A) and growth rates (B) in body mass of embryos are expressed as the mean ± SE. Means with different letters above the error bars are statistically different (Tukey's test).

$(\chi^2 = 8.11$, d.f. $= 1$, $P < 0.01)$ but did not differ among populations $(\chi^2 = 0.08$, d.f. $= 2$, $P = 0.78)$.

DISCUSSION

Consistent with Oufiero & Angilletta (2006), our common garden experiment revealed countergradient variation in rates of embryonic development. However, geographical variation in intrinsic hatchling growth rates did not exhibit a latitudinal trend. The geographical variation in hatchling growth rates, therefore, does not parallel the countergradient variation that occurs in rates of embryonic development (Figs 1, 2). The different trends in pre- and post-embryonic growth suggest geographical variation in the ways in which selection pressures shift during ontogeny.

Our common garden experiment detected population differences in intrinsic post-hatching growth rates. These findings are partially consistent with

Figure 2. Post-hatching growth of *Sceloporus undulatus* hatchlings from the northern (Indiana), central (Mississippi), and southern (Florida) populations. Sample sizes for the northern, central, and southern populations were 19, 34, and 10. Growth rates in snout–vent length (A) and body mass (B) of hatchlings are expressed as the mean ± SE. Means with different letters above the error bars are statistically different among populations (Tukey's test).

past studies that show relatively slow intrinsic growth rates in juveniles of northern populations (Angilletta *et al*., 2004b; Sears & Angilletta, 2004). However, individuals from our southern population also showed relatively slow growth, similar to that of the northern population. The geographical difference in intrinsic growth rate indicates different proximate causes of body size at maturity in these populations. In the northern population, the slow intrinsic growth rates support the hypothesis that the proximate mechanism for larger body sizes in colder environments is delayed maturation (old ages at maturity, approximately 20 months) rather than faster growth (Angilletta *et al*., 2004a). In the central population, high intrinsic growth rates suggest that faster growth could be the proximate mechanism for relatively large body size given the young ages at maturity likely (approximately 12 months), based on populations at similar latitudes (McKinney, 1982). By contrast,
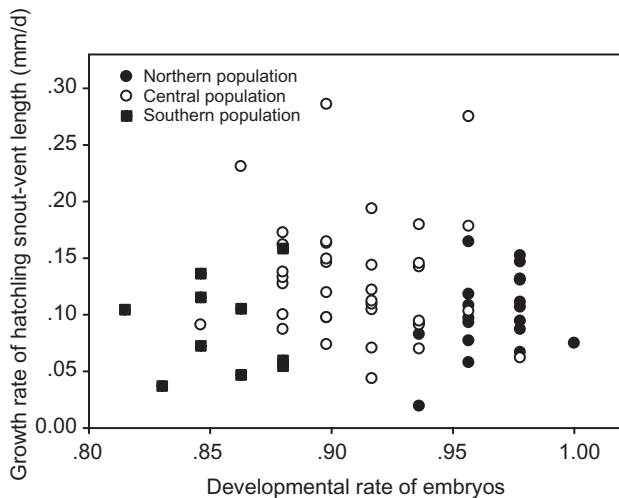
Figure 3. Growth rates of hatchlings were not correlated with developmental rates of embryos in *Sceloporus undulatus* from northern, central, and southern populations. Growth rate was quantified as the daily rate of increase in snout–vent length over the first 4 weeks. Developmental rate of embryos were calculated by dividing the incubation duration at the temperatures by the shortest incubation duration recorded in this experiment (44 days at 28 °C), and taking the inverse of this value.

lizards from the southern population exhibit low intrinsic growth rate and mature at a small body size (Table 1). Analogous to different physiological mechanisms underlying countergradient variation in rates of embryonic development in these populations (Du *et al*., 2010), different proximate mechanisms appear to underpin the Bergmann's size cline along the latitude in this species.

Niewiarowski & Angilletta (2008) found a negative relationship between rates of embryonic development and rates of hatchling growth among *S. undulatus* populations across a latitudinal gradient, describing a trade-off between these ontogenetic stages associated with countergradient variation (although the trade-off was not found within populations). This between-population trade-off can apply to the northern and central populations of this study, which span a latitudinal range similar to the populations sampled previously by Niewiarowski & Angilletta (2008). However, in contrast to the expectation of a trade-off between embryonic developmental rate and hatchling growth rate, individuals from the southern population in Florida with lower embryonic developmental rates showed a lower (instead of higher) intrinsic growth rate at post-embryonic stages. Our data suggest that geographical variation in the ontogenetic selection regime does not necessarily follow the same latitudinal gradient from embryonic to post-hatching stages.

The mechanistic bases for rapid embryonic development (heart size versus heart rate; Du *et al*., 2010) may not persist long after hatching, leading to a breakdown in this pattern of hatchling growth rate. The slow growth rates of hatchlings from the northern and southern populations may therefore be caused by different mechanisms controlling hatchling growth. Further studies could usefully elucidate the mechanistic basis (i.e. competitive ability, consumption rates or metabolic rates) for population-specific hatchling growth rates.

The lack of difference in intrinsic juvenile survival rates of each population in the laboratory contrasts with the general latitudinal trend in extrinsic juvenile survival rates across the range of *S. undulatus*. Extrinsic juvenile survival rates in the field generally increase with increasing latitude (Angilletta *et al*., 2004b). Therefore, our data do not support the prediction that intrinsic and extrinsic survival will be positively correlated (Stearns, 2000; Stearns *et al*., 2000); however, the extrinsic survival rate associated specifically with each of these populations is not known. A putative latitudinal trend in extrinsic juvenile survival suggested the hypothesis that larger adult body sizes in cooler, northern environments occur as a result of longer growth periods (Angilletta *et al*., 2004b; Sears & Angilletta, 2004). It is likely that differences in adult body sizes of lizards from these populations are partly driven by longer growth periods in more northern populations (permitted by greater extrinsic survival rates at these higher latitudes), rather than intrinsic hatchling survival or growth rates (neither of which covary with adult body size).

CONCLUSIONS

The findings of the present study reveal that faster intrinsic rates of embryonic development do not necessarily translate to faster (or slower) intrinsic rates of juvenile growth. Thus, geographical variation in ontogenetic selective pressures may involve relationships more complex than simple trade-offs. Faster growth rates and greater juvenile survival are not mutually exclusive pathways to larger adult body size and, indeed, both contribute (possibly to different extents at different latitudes) to the Bergmann's cline observed in adult body sizes of *S. undulatus*.

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REFERENCES

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

Andrews RM, Mathies T, Warner DA. 2000. Effect of incubation temperature on morphology, growth, and survival juvenile *Sceloporus undulatus*. *Herpetological Monographs* **14:** 420–431.

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

Angilletta MJ, Steury TD, Sears MW. 2004b. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology* **44:** 498–509.

Ashton KG. 2002. Do amphibians follow Bergmann's rule? *Canadian Journal of Zoology* **80:** 708–716.

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

Conover DO, Duffy TA, Hice LA. 2009. The covariance between genetic and environmental influences across ecological gradients: reassessing the evolutionary significance of countergradient and cogradient selection. *Annals of the New York Academy of Sciences* **1168:** 100–129.

Conover DO, Schultz ET. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology & Evolution* **10:** 248–252.

Du WG, Ji X, Zhang YP, Xu XF, Shine R. 2005. Identifying sources of variation in reproductive and life-history traits among five populations of a Chinese lizard (*Takydromus septentrionalis*, Lacertiade). *Biological Journal of the Linnean Society* **85:** 443–453.

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

Ferguson GW, Talent LG. 1993. Life-history traits of the lizard *Sceloporus undulatus* from two populations raised in a common laboratory environment. *Oecologia* **93:** 88–94.

Freckleton RP, Harvey PH, Pagel M. 2003. Bergmann's rule and body size in mammals. *American Naturalist* **161:** 821–825.

Grether GF, Cummings ME, Hudon J. 2005. Countergradient variation in the sexual coloration of guppies (*Poecilia reticulata*): drosopterin synthesis balances carotenoid availability. *Evolution* **59:** 175–188.

Huey RB, Gilchrist GW, Carlson ML, Berrigan D, Serra L. 2000. Rapid evolution of a geographic cline in size in an introduced fly. *Science* **287:** 308–309.

Langkilde T, Freidenfelds NA. 2010. Consequences of envenomation: red imported fire ants have delayed effects on survival but not growth of native fence lizards. *Wildlife Research* **37:** 566–573.

Leache AD. 2009. Species tree discordance traces to phylogeographic clade boundaries in North American fence lizards (*Sceloporus*). *Systematic Biology* **58:** 547–559.

Leache AD, Reeder TW. 2002. Molecular systematics of the eastern fence lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood, and Bayesian approaches. *Systematic Biology* **51:** 44–68.

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.

McKinney RB. 1982. The reproductive cycle of *Sceloporus undulatus* from Alabama, with corresponding plasma steroid levels and comments on reproductive variation. MS Thesis, University of Alabama.

Niewiarowski PH. 1994. Understanding geographic life-history variation in lizards. In: Vitt LJ, Pianka ER, eds. *Lizard ecology: historical and experimental perspectives*. Princeton, NJ: Princeton University Press, 31–50.

Niewiarowski PH. 1995. Effects of supplemental feeding and thermal environment on growth rates of eastern fence lizards, *Sceloporus undulatus*. *Herpetologica* **51:** 487–496.

Niewiarowski PH, Angilletta MJ. 2008. Countergradient variation in embryonic growth and development: do embryonic and juvenile performances trade off? *Functional Ecology* **22:** 895–901.

Niewiarowski PH, Angilletta MJ, Leache AD. 2004. Phylogenetic comparative analysis of life-history variation among populations of the lizard *Sceloporus undulatus*: an example and prognosis. *Evolution* **58:** 619–633.

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

Peters RH. 1986. *The ecological implications of body size*. Cambridge: Cambridge University Press.

Rowe JW. 1997. Growth rate, body size, sexual dimorphism and morphometric variation in four populations of painted turtles (*Chrysemys picta bellii*) from Nebraska. *American Midland Naturalist* **138:** 174–188.

Schlichting CD, Pigliucci M, **eds**. **1998.** *Phenotypic evolution: a reaction norm perspective*. Sunderland, MA: Sinauer Sunderland.

Schultz ET, Reynolds KE, Conover DO. 1996. Countergradient variation in growth among newly hatched *Fundulus heteroclitus*: geographic differences revealed by common-environment experiments. *Functional Ecology* **10:** 366–374.

Sears MW, Angilletta MJ. 2004. Body size clines in *Sceloporus* lizards: proximate mechanisms and demographic constraints. *Integrative and Comparative Biology* **44:** 433–442.

Shine R, Harlow P. 1996. Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. *Ecology* **77:** 1808–1817.

Sinervo B, Adolph SC. 1989. Thermal sensitivity of growth rate in hatchling *Sceloporus* lizards: environmental, behavioral and genetic aspects. *Oecologia* **78:** 411–419.

Speakman JR. 2005. Body size, energy metabolism and lifespan. *Journal of Experimental Biology* **208:** 1717–1730.

Stearns SC. 2000. Life history evolution: successes, limitations, and prospects. *Die Naturwissenschaften* **87:** 476–486.

Stearns SC, Kaiser M, Ackermann M, Doebeli M. 2000. The evolution of intrinsic mortality, growth, and reproduction in fruit flies. *Proceedings of the National Academy of Sciences of the United States of America* **97:** 3309–3313.

Tinkle DW, Ballinger RE. 1972. *Sceloporus undulatus*: a study of the intraspecific comparative demography of a lizard. *Ecology* **53:** 570–584.