Journal of Thermal Biology 36 (2011) 187–192

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Influence of ambient temperature on maternal thermoregulation and neonate phenotypes in a viviparous lizard, *Eremias multiocellata*, during the gestation period

Xue-Feng Yan, Xiao-Long Tang, Feng Yue, De-Jiu Zhang, Ying Xin, Cui Wang, Qiang Chen *

Institute of Biochemistry and Molecular Biology, School of Life Science, Lanzhou University, 222 Tian Shui South Road, Lanzhou 730000, China

ARTICLE INFO

Article history:
Received 29 September 2010
Accepted 22 February 2011

Keywords:
Viviparous lizard
Eremias multiocellata
Gestation temperature
Morphology
Locomotor performance
Early growth rate

ABSTRACT

To assess the potential gestational effects on post-hatching morphology, locomotor performance, and early growth rate, we maintained gravid *Eremias multiocellata* under four constant treatment temperatures (25, 29, 31, and 35 °C). Ambient temperature had significant effects on some morphometric traits of offspring, including tail length, head size, forelimb length and hindlimb length, but not on body mass or snout-vent length. The data of females' body temperature indirectly support the maternal manipulation hypothesis. Juvenile *E. multiocellata* had better locomotor performance and faster early growth rate at 29 °C than at the other three treatment temperatures (25, 31, and 35 °C). Our results suggest that gestation temperature may be optimized at 29 °C for *E. multiocellata* from Tianzhu, Gansu Province, China.

1. Introduction

Phenotypic variation is a fundamental component of reptile evolution, and investigating the factors that influence this variation is critical to understanding this process (Shine and Harlow, 1996; Rhen and Lang, 1999; Paitz et al., 2009). During embryonic development, the thermal environment can profoundly affect post-hatching phenotype and, potentially, the thermal fitness of ectotherms (Braña, 1993; Goodman and Walguarnery, 2007; Calsbeek and Hasselquist, 2010). Many reptile species can develop their embryos successfully over a relatively wide range of incubation temperatures, and different temperatures may affect hatchling sex ratio (Valenzuela and Lance, 2004; Zhang et al., 2010), hatchling size (Shine et al., 1997; Ji et al., 2006), locomotor performance (Vanhooydonck et al., 2001; Blouin-Demers et al., 2004), thermoregulation (Downes and Shine, 1999; Flatt et al., 2001), and growth rate (Van Damme et al., 1992; Deeming, 2004) under both natural conditions and in controlled laboratory settings. However, it is difficult to explain how temperature induces these changes because post-hatching phenotypic traits are largely variable and undocumented in many species. In order to better understand these relationships in reptiles, researchers have focused on two particular areas (Booth, 2006): (1) the relationship between gestation temperature and offspring sex ratio and (2) the potential influence of gestation (or incubation) temperature on offspring phenotype and fitness. Now there is evidence that gestation temperature may influence the offspring sex ratio in the viviparous lizard, *Eremias multiocellata* (Zhang et al., 2010), which is considered as a possible model species for investigating the effects of embryonic thermal environment on post-hatchling phenotype among viviparous reptiles. However, the effect of gestation temperature on offspring growth and locomotor performance is still unknown in this species.

Morphological variation among offspring is important for individual fitness and survival, and there is an increasing amount of evidence that varied environmental conditions during embryogenesis can induce morphological variation in reptiles (Braña and Ji, 2000; Goodman and Walguarnery, 2007; Vervust et al., 2010). However, the association between morphometric traits and environmental factors is complex and poorly understood in many species (Deeming, 2004). For example, there is a general increase in body size with elevated incubation temperature in *Cyclura nubila* (Alberts et al., 1997) but the reverse situation was found in *Sphenomorphus indicus* (Ji et al., 2006). In addition to morphology, incubation temperature also influences locomotor performance and early growth rate of some reptile hatchlings (Booth et al., 2004; Nelson et al., 2004); both factors are considered to have great effect on hatchling fitness (Booth, 2006). Many studies investigating the effects of gestation temperature on post-hatchling phenotype have been conducted on oviparous reptile species (Shine and Harlow, 1996; Qualls and Shine, 1998), whereas parallel studies focusing on viviparous species are relatively limited (Beuchat, 1988; Swain and Jones, 2000; Wapstra et al., 2004). Unlike oviparous females that cannot

---

* Corresponding author. Tel./fax: +86 931 8915316.
E-mail address: chenq@lzu.edu.cn (Q. Chen).

0306-4565/$ - see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jtherbio.2011.02.005

effectively adjust their eggs' incubation temperature after oviposition (Wang, 1966; Shine et al., 1997), gravid viviparous females have the ability to select optimal temperature for their developing embryos by behavioral thermoregulation. However, if gravid females are exposed to a relatively constant environmental temperature, they may have limited opportunities to regulate their body temperature (Lourdais et al., 2004).

The idea that maternal behavior can influence offspring phenotypes in lizard species is by no means a novel one (Lancaster et al., 2010). Shine (1995) first proposed the maternal manipulation hypothesis, which noted that mothers can enhance fitness-relevant phenotypic traits of their offspring by manipulating thermal conditions during embryogenesis (Shine, 1995; Webb et al., 2006). However, empirical data supporting this hypothesis are still very limited (Ji et al., 2007). The hypothesis generates two main predictions: (1) females should adjust thermoregulation during pregnancy to provide optimal thermal conditions for developing embryos and (2) phenotypic variation by maternal thermoregulation should enhance offspring fitness (Ji et al., 2007). We chose a TSD viviparous lizard species, *E. multiocellata*, to investigate the effects of ambient temperature on maternal thermoregulation and offspring phenotype during the gestation period. The present study has two main objectives: (1) to analyze the effects of gestation temperature on offspring morphology, locomotor performance and growth rate and (2) to discuss the potential relationship between neonatal phenotypic variation and neonate fitness in *E. multiocellata*.

2. Materials and Methods

2.1. Study species and area

E. multiocellata is a small viviparous (mean adult snout-vent length is about 65 mm) diurnal lizard. It is widely distributed and ranges from Qilian Mountains to the Northeast China Plain and extends to Mongolia, Kazakhstan, and Kyrgyzstan. Habitat elevation ranges from 200 to 3000 m. Females produce a single clutch per year with a litter size of 2–5 neonates (Zhao, 1999). Our study analyzed a population from Tianzhu (37°6′N, 103°9′E), Gansu province, China. The area is located to the east of the Qilian Mountains, approximately 2800–2900 m in altitude, and annual rainfall is 700–800 mm. Ninety-six adult lizards (48 males and 48 females) were collected in early June 2009 and brought to the laboratory in Lanzhou University.

2.2. Constant temperature treatments and animal care

Both male and female lizards were collected in order to exclude the influence of operational sex ratio (OSR), which occurs in another viviparous lizard (Warner and Shine, 2007). Gravid female (with obvious copulation marks) and male lizards were equally divided into four groups using a random sampling method and in each group every two males and two females were maintained in a $60\times30\times40\ \mathrm{cm}^3$ (length × width × height) glass cage, which contained a substrate depth of approximately 5 mm of sand. Four treatment groups were maintained in four thermally controlled rooms under constant temperature controlled at 25 ± 0.5, 29 ± 0.5, 31 ± 0.5, and 35 ± 0.5 °C for 0900–1700 h (according to the activity pattern of the natural population). The temperatures during intervening hours were controlled at 18 ± 0.5 °C in order to simulate natural conditions (Zhang et al., 2010; Zhao, 1999). Lizards were placed under broad-spectrum fluorescent lights that simulated natural light on a cycle of 12 h light: 12 h dark (0700–1900 h). Experiments lasted from early June to late August. Body temperatures of female lizards and chamber temperatures were monitored daily (at 1000–1030 h) and continuously from the beginning of the experiment to parturition, and using a DM6801A (accuracy: 0.1 °C) electronic thermometer (Shenzhen Medical Instrument) through the cloaca. The probe (1.5 mm diameter) was inserted about 4 mm into the cloaca when measurements were made, and great care was taken to avoid heat transfer between the human hand and the lizard. All lizards were fed with mealworms (larvae of *Tenebrio molitor*) and water enriched with vitamins and minerals.

2.3. Care of neonates and phenotype measurements

The cages were checked daily for neonates as soon as the first female gave birth. Each neonate was then toe clipped in a pattern that facilitated individual identification. All neonates were raised under the same environmental conditions (about 30 °C during 0900–1700 h), fed with small mealworms and vitamin-enriched water. Morphology measurements were taken for each neonate using a vernier caliper (accuracy: 0.02 mm) and electronic balance (accuracy: 10 mg), including body mass, snout-vent length (SVL), tail length (TL), head length (HL), head width (HW), and forelimb and hindlimb lengths. Locomotor performance was determined six days after birth. As locomotory ability is highly sensitive to the body temperature in lizards, all trials were taken at 30 °C, which is close to the optimal body temperature for the *E. multiocellata* (Zhang et al., 2010). Locomotor performance was assessed by chasing the neonates (with an appropriate brush) along a 1 m racetrack. The entire process was recorded by a digital video camera (Canon, Japan). Each individual ran three times with an approximately 30-min rest between successive trials. The videos were examined later with a computer using MGI VideoWave III software (MGI Software Co.). Locomotor performance was analyzed, including (1) burst speed in the fastest 25-cm interval, (2) number of stops during the entire trial, and (3) maximum distance traveled between stops. Growth rate was assessed through analysis of the variance of body mass within initial 30 days.

2.4. Statistical analyses

The data were tested for normality and homogeneity of variances to meet the assumptions of parametric testing prior to analysis, and no significant deviations from these assumptions were evident in the data. One-way repeated measures ANOVA was used to evaluate the effect of maternal body temperature and chamber temperature, and two-way mixed model ANOVA was used to evaluate the interactive effect of sex and gestation temperature on neonate SVL and head length. Two-way ANOVA analyses of covariance with snout-vent length (SVL) as the covariate were used to determine whether gestation temperature and sex have influence on other morphological traits except for SVL and head length, burst speed, maximum distance traveled between stops, number of stops during the entire trial and early growth rate. In addition, hindlimb length and gestation temperature in two-factor ANCOVAs (with SVL as covariate) were analyzed for their effects and possible interactions in explaining variation in locomotor performance. Tukey's test was used in all multiple comparisons. All statistical analyses were tested using SPSS (Release 16.0.0, SPSS, Inc., Chicago, IL) with a critical α of 0.05.

3. Results

3.1. Effect of ambient temperature on female body temperature

The body temperature of female lizards was elevated with increased ambient temperature: the recorded chambers' temperatures were 25.0 ± 0.8, 28.5 ± 0.9, 30.6 ± 0.4, and 35.7 ± 0.7 °C (mean ± SD) in the four rooms ($F_{3,348}=260.558$, $p<0.001$). The females' body temperatures were 25.6 ± 0.1, 29.1 ± 0.1, 31.2 ± 0.1, and 34.0 ± 0.1 °C (mean ± SD), and the four treatments were significantly different ($F_{3,658}=260.558$, $p<0.001$). Under the two extreme temperatures (25 and 35 °C), there was a notable difference between chambers' temperature and body temperature. Female body temperature was significantly higher than ambient temperature in the 25 °C group and was significantly lower than that observed in the 35 °C group. These results indicate that gravid females may have the ability to regulate their body temperature under constant ambient temperature.

3.2. *Effect of gestation temperature on morphometric traits*

Among all four gestation temperatures no significant size differences were detected between sexes in all morphometric traits of neonates (Table 1). Gestation temperature significantly influenced the neonate's TL, head size (both HL and HW), forelimb length and hindlimb length, but it did not affect body mass or SVL (Table 1). The morphometric traits of the offspring produced under low temperatures (25 and 29 °C) were larger than those produced under high temperatures (31 and 35 °C).

3.3. *Effect of gestation temperature on locomotor performance*

We incorporated hindlimb length in addition to gestation temperature in two-way ANOVAs (with SVL as covariate) to analyze their effect and possible interaction in explaining variation of locomotor performance. Hindlimb length did not influence locomotor performance (all $p>0.05$). The neonates from the 29 °C group exhibited better locomotor performance than those from the other three groups. The data showed that the burst speed ($F_{3,129}=3.637$, $p=0.015$) (Fig. 1) and the number of stops during the entire trial ($F_{3,129}=4.424$, $p=0.038$) were significantly different among four treatments but the maximal distance traveled without stops ($F_{3,129}=2.012$, $p=0.115$) was not different. Furthermore, no significant differences in locomotor performance were detected between female and male among four gestation temperatures (all $p>0.05$).

3.4. *Effect of gestation temperature on early growth rate*

Gestation temperature affected the early growth rate of juveniles in the laboratory (Fig. 2). Our results showed that gestation temperature and sex had significant effects on the growth of body mass (Table 1), and offspring from 29 °C group grew faster than those from the 25, 31, and 35 °C groups.

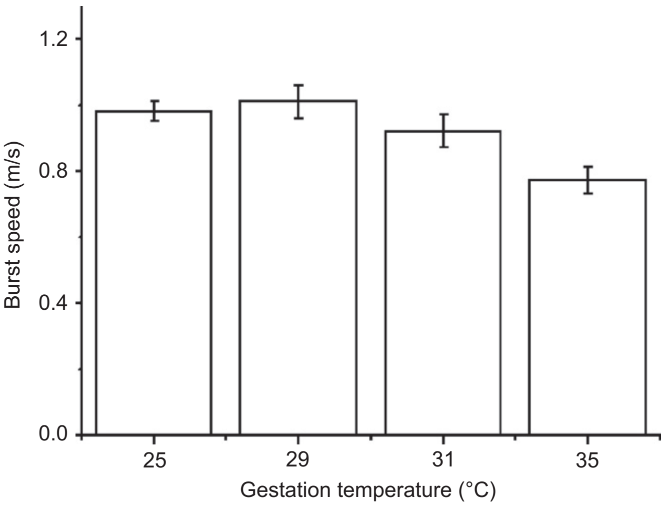

Fig. 1. Effect of gestation temperature on the burst speed of offspring in the viviparous lizard, *E. multiocellata.*

Table 1

Phenotypes and early growth rates of hatchling lizards (*Eremias multiocellata*) according to sex and gestation temperature (mean ± sd)[a].

Hatchling traits		Gestation temperature				Effects		
		25 °C ($N=33$)	29 °C ($N=41$)	31 °C ($N=37$)	35 °C ($N=22$)	Sex, $F_{1,131}$	Gestation temperature, $F_{3,129}$	Interaction, $F_{3,129}$
Body mass (g)	F	0.51 ± 0.04	0.50 ± 0.05	0.49 ± 0.08	0.49 ± 0.06	0.640 ns	1.289 ns	1.016 ns
	M	0.51 ± 0.04	0.51 ± 0.05	0.49 ± 0.06	0.50 ± 0.08			
Snout-vent length (mm)	F	27.3 ± 0.66	27.3 ± 1.11	26.8 ± 1.52	26.4 ± 1.19	0.006 ns	0.762 ns	1.095 ns
	M	26.7 ± 1.17	27.1 ± 1.73	27.1 ± 1.45	27.0 ± 1.01			
Tail length (mm)	F	39.5 ± 3.01	38.8 ± 2.12	36.7 ± 5.01	35.7 ± 2.76	2.751 ns	3.966**	0.306 ns
	M	39.3 ± 2.18	39.1 ± 2.81	37.6 ± 4.53	38.3 ± 3.33			
Head length (mm)	F	7.33 ± 0.29	7.37 ± 0.51	6.90 ± 0.41	7.07 ± 0.29	0.296 ns	4.839**	0.016*
	M	7.10 ± 0.36	7.25 ± 0.33	7.12 ± 0.38	7.35 ± 0.16			
Head width (mm)	F	4.22 ± 0.29	4.06 ± 0.29	3.96 ± 0.29	3.96 ± 0.24	3.097 ns	5.622**	0.775 ns
	M	4.35 ± 0.36	4.05 ± 0.30	4.00 ± 0.37	4.20 ± 0.34			
Forelimb length (mm)	F	6.75 ± 0.55	6.08 ± 0.34	6.11 ± 0.54	6.42 ± 0.25	0.640 ns	21.347***	2.892*
	M	6.74 ± 0.35	6.30 ± 0.39	5.90 ± 0.34	6.20 ± 0.31			
Hindlimb length (mm)	F	9.20 ± 0.50	8.45 ± 0.76	8.33 ± 0.66	8.43 ± 0.33	0.494 ns	16.834***	0.311 ns
	M	9.20 ± 0.35	8.48 ± 0.49	8.20 ± 0.76	8.24 ± 0.44			
Early growth rates of body mass (g)	F	0.147 ± 0.07	0.23 ± 0.06	0.15 ± 0.05	0.09 ± 0.01	4.640*	1.813***	0.058*
	M	0.083 ± 0.09	0.15 ± 0.08	0.07 ± 0.01	0.04 ± 0.01			

[a] *F* ratios correspond to single effects and factor interactions in two-factor ANOVA (temperature and sex as fixed factors) or ANCOVAs (with SVL as covariate, for all other traits). Tukey's test was used in all multiple comparisons.

* $p<0.05$.

** $p<0.01$.

*** $p<0.001$.

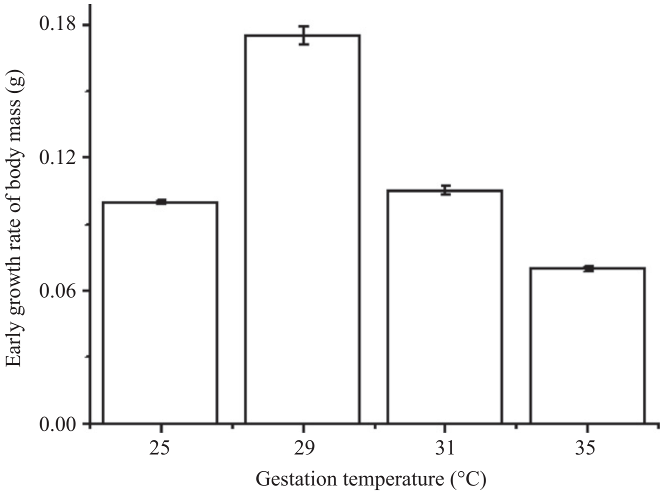

Fig. 2. Effect of gestation temperature on the early growth rate of offspring in the viviparous lizard, *E. multiocellata.*

4. Discussion

Our study examined the impact of gestation temperature on post-hatching phenotypes that are likely to affect the fitness level of offspring. In the present study, gestation temperature significantly affected several fitness-related phenotypic traits in *E. multiocellata*, including several morphometric traits, locomotor performance, and early growth rate.

4.1. Ability of gravid females to modify their body temperature

Our study analyzed the effects of four constant temperature conditions to test the influence of different gestation temperatures on offspring phenotype. In order to investigate the relationship between ambient temperature and body temperature of gravid female lizards, we measured body temperature during the gestation period. The results showed that ambient temperature and female body temperature were linearly correlated. Body temperature of gravid female was slightly higher than the ambient temperature in 25 °C treatment, but lower in 35 °C treatment. This indicates that gravid females may have the ability to regulate their body temperature and to maintain body temperatures near optimal for embryonic development. In fact, the change in preferred body temperature or thermoregulatory behavior during gestation is typical among squamate reptiles (Beuchat, 1988), and it seems more likely to occur in live-bearing species (Braña, 1993). Our results provide indirect evidence for a maternal manipulation hypothesis and we suggest that viviparity may provide a mechanism for some reptile species to buffer changing environmental and deleterious temperature regimes during embryonic development.

4.2. Lower gestation temperature produces advantaged neonates

Our results indicate that gestation temperature could significantly affect the morphology, locomotor performance, and early growth rate of neonates in *E. multiocellata*, reinforcing the results of previous studies on the same species (Zhang et al., 2010). In our study, each group was maintained under the same conditions except for the gestation temperature. The mother's body temperature was very close to the ambient temperature. This suggests that the different neonate phenotypes among groups are the result of different gestation temperatures. Among different treatments, the neonates that developed at lower temperatures (25 and 29 °C) were larger in body size than those at higher temperatures (31 and 35 °C). This is consistent with studies on many other reptile species, which display a tendency for larger (in terms of body dimensions) but not always heavier hatchlings to be produced at lower temperatures (Deeming, 2004; Booth, 2006). Cooler temperatures produce larger hatchlings in most species of reptiles that exhibit temperature-induced plasticity, and it is usually accompanied by an increase in the length of incubation period (Birchard, 2004). Compared to neonates incubated at higher temperature with short incubation periods, neonates incubated at lower temperature could absorb more nutrients from yolk and mother (in viviparous species); thus they eventually reach bigger body size at hatching or birth (Deeming, 2004). This may enhance fitness through many ecological interactions, including competitive dominance (Stamps, 1984), ability to eat larger and more diverse prey (Vitt, 2000), decreased predation vulnerability (Ferguson and Fox, 1984; Vitt, 2000), increased thermal inertia in thermoregulation (Porter and Gates, 1969; Stevenson, 1985), and starvation resistance in low resource periods (Schultz and Conover, 1999).

Besides morphological features, gestation temperature influenced other hatchling traits such as locomotor performance and early growth rate in *E. multiocellata,* and the neonates from lower temperature groups had better locomotor performance and faster early growth rate. Our results indicated that the neonates with bigger body size also had advantages in locomotor performance and early growth, which provided evidence for the "bigger is better" hypothesis (Booth, 2006). However, it should be noted that our results are not consistent with those previous studies, which determined that locomotor ability and growth rate were augmented with the increase of gestation temperature in other species of lizards (Downes and Shine, 1999; Andrews et al., 2000; Braña and Ji, 2000). The population of *E. multiocellata* we studied is located in a mountainous region with an altitude of about 2800 m and has relatively lower mean temperature during the breeding season. Because lower gestation temperatures produce optimal neonates, this may be an adaptive feature for viviparous lizards to acclimate cool environments. It may also represent a trade-off effect for pregnant females that experience low gestation temperature. In addition, our results showed that hindlimb length did not significantly influence the neonate locomotor performance, which is similar to some other lizards (Garland and Losos, 1994; Martín and López, 2001). However, it is not consistent with some studies in which hindlimb length was associated with locomotor performance in lizards (Miles, 1994; Bauwens et al., 1995; Bonine and Garland, 1999; Parker and Andrews, 2007). One possible explanation is that plenty of factors could be associated with locomotor performance. For example, Zani (1996) found that sprint speed correlated positively with the length of the caudifemoralis longus muscle, and some studies suggest that speed may be related to muscle fiber type composition (Bonine et al., 1997). However, further research is needed to investigate the mechanism that neonates developed under different gestation temperature had varied locomotor performance in *E. multiocellata*. In the present study, early growth rate tends to be positively correlated to locomotor performance. The lizards may benefit a lot from better locomotor performance. They can capture more prey under intraspecies competition and facilitate early growth rates (Huey and Pianka., 1981; Magnusson et al., 1985; Booth, 2006).

4.3. 29 °C may be the optimal gestation temperature for E. multiocellata

Relatively low gestation temperatures may be advantageous for neonate phenotype in some reptilian species (Braña and Ji, 2000). In the present study neonates from 29 °C group displayed the best values in some traits such as morphometrics and locomotor performance, including burst speed and the number of stops during the entire trial, and early growth rate of weight. In addition, our previous study that focused on the effect of gestation temperature on neonate sex ratio also showed that 29 °C may be the optimal temperature for *E. multiocellata* as determined by female reproductive success and offspring sex ratio (Zhang et al., 2010). These two studies analyzed individuals from different populations of the same species. These different locations are typified by different environmental conditions, and differ in geographic and climatic features. Our studies on these two populations proved that they may have the same optimal temperature of 29 °C. Previous studies reported that some species exhibit similar thermal physiology across a wide range of climates (Van Berkum, 1988; Van Damme et al., 1990; Andrews, 1998). The results of these two studies may indicate that *E. multiocellata* have the same optimal incubation temperature, although the two populations inhabit in distinct climatic conditions. It could give support to the static view of thermal physiology, which claims that thermal physiology is evolutionarily stationary and resistant to directional selection (Van Damme et al., 1990).

5. Conclusion

In summary, different gestation temperatures have notable effects on the morphmetrics, locomotor performance, and early growth rates of neonates in *E. multiocellata*, and the results suggested that gestation temperature may be optimized at 29 °C. Our data provide evidence that support several previous studies demonstrating the pervasive effects of gestation temperature on the post-hatchling phenotypes of reptilian offspring (Zhang et al., 2010). It should be useful for examining the relative importance of environmental effects as sources of variation in lizard morphology, locomotor performance, and early growth rates. Additional work is also required to address the functional consequences of incubation-induced shifts in thermoregulation at the physiological and organism levels, which may in turn impact thermal fitness (Goodman and Walguarnery, 2007).

Acknowledgments

We thank A.M. Yang, S.Y. Lv, Y.J. Yang, Y.K. Ji, Q.Z. Yang, W.W. Ge, T. He, Z.Y. Mi, and M.H. Xiu for helping in various ways. Research funds were provided by the National Natural Science Foundation of China (no. 30670263).

References

Alberts, A.C., Perry, A.M., Lemm, J.M., Phillips, J.A., 1997. Effects of incubation temperature and water potential on growth and thermoregulatory behavior of hatchling Cuban rock iguanas (*Cyclura nubila*). Copeia 1997 (4), 766–776.

Andrews, R.M., 1998. Geographic variation in field body temperature of *Sceloporus* lizards. J. Therm. Biol. 23 (6), 329–334.

Andrews, R.M., Mathies, T., Warner, D.A., 2000. Effect of incubation temperature on morphology, growth and survival of juvenile *Sceloporus undulatus*. Herpetol. Monogr. 14, 420–431.

Bauwens, D., Garland, T.J., Castilla, A.M., Van Damme, R., 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioural covariation. Evolution 49 (5), 848–863.

Beuchat, C.A., 1988. Temperature effects during gestation in a viviparous lizard. J. Therm. Biol. 13 (3), 135–142.

Birchard, G.F., 2004. Effects of incubation temperature. In: Deeming, D.C. (Ed.), Reptilian Incubation: Environment, Evolution and Behaviour. Nottingham University Press, UK.

Blouin-Demers, G., Weatherhead, P.J., Row, J.R., 2004. Phenotypic consequences of nest-site selection in black rat snakes (*Elaphe obsoleta*). Can. J. Zool. 82 (3), 449–456.

Bonine, K.E., Garland, T.J., Gleeson, T.T., 1997. Muscle fiber-type variation and locomotion in phrynosomatid lizards. Am. Zool. 37, 104A.

Bonine, K.E., Garland, T.J., 1999. Sprint performance of phrynosomatid lizards measured on a high-speed treadmill, correlates with hind limb length. J. Zool. (Lond.). 248, 255–265.

Booth, D.T., Burgess, E., McCosker, J., Lanyon, J.M., 2004. The influence of incubation temperature on post-hatching fitness characteristics of turtles. Int. Congr. Ser. 1275, 226–233.

Booth, D.T., 2006. Influence of incubation temperature on hatchling phenotype in reptiles. Physiol. Biochem. Zool. 79 (2), 274–281.

Braña, F., 1993. Shift in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. Oikos 66, 216–222.

Braña, F., Ji, X., 2000. Influence of incubation temperature on morphology, locomotor performance, and early growth of hatchling wall lizards (*Podarcis muralis*). J. Exp. Zool. 286 (4), 422–433.

Calsbeek, B., Hasselquist, D., 2010. Multivariate phenotypes and the potential for alternative phenotypic optima in wall lizard (*Podarcis muralis*) ventral colour morphs. J. Evol. Biol. 23 (6), 1138–1147.

Deeming, D.C., 2004. Post-hatching phenotypic effects of incubation in reptiles In: Deeming, D.C. (Ed.), Reptilian Incubation Environment, Evolution and Behaviour. Nottingham University Press, UK, pp. 229–251.

Downes, S.J., Shine, R., 1999. Do incubation-induced changes in a lizard's phenotype influence its vulnerabuility to predators? Oecologia 120 (1), 9–18.

Ferguson, G.W., Fox, S.F., 1984. Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. Evolution 38 (2), 342–349.

Flatt, T., Shine, R., Borges-Landaez, P.A., Downes, S.J., 2001. Phenotypic variation in an oviparous montane lizard (*Bassiana duperreyi*): the effects of thermal and hydric incubation environments. Biol. J. Linn. Soc. 74 (3), 339–350.

Garland Jr, T., Losos, J.B., 1994. Ecological morphology of locomotor performance in squamate reptiles. In: Wainwright, P.C., Reilly, S.M. (Eds.), Ecological Morphology: Integrative Organismal Biology. University of Chicago Press, Chicago, pp. 240–302.

Goodman, R.M., Walguarnery, J.W., 2007. Incubation temperature modifies neonatal thermoregulation in the lizard *Anolis carolinensis*. J. Exp. Zool. 307 (8), 439–448.

Huey, R.B., Pianka, E.R., 1981. Ecological consequences of foraging mode. Ecology 62 (4), 991–999.

Ji, X., Lin, L.H., Luo, L.G., Lu, H.L., Gao, J.F., Han, J., 2006. Gestation temperature affects sexual phenotype, morphology, locomotor performance, and growth of neonatal brown forest skinks, *Sphenomorphus indicus*. Biol. J. Linn. Soc. 88 (3), 453–463.

Ji, X., Lin, C.X., Lin, L.H., Qiu, Q.B., Du, Y., 2007. Evolution of viviparity in warm-climate lizards: an experimental test of the maternal manipulation hypothesis. J. Evol. Biol. 20 (3), 1037–1045.

Lancaster, L.T., McAdam, A.G., Sinervo, B., 2010. Maternal adjustment of egg size organizes alternative escape behaviours, promoting adaptive phenotypic integration. Evolution 64 (6), 1607–1621.

Lourdais, O., Shine, R., Bonnet, X., Guillon, M., Naulleau, G., 2004. Climate affects embryonic development in a viviparous snake, *Vipera aspis*. Oikos 104, 551–560.

Magnusson, W.E., Depaiva, L.J., Darocha, R.M., Franke, C.R., Kasper, L.A., Lima, A.P., 1985. The correlates of foraging mode in a community of Brazilian lizards. Herpetologica 41 (3), 324–332.

Martín, J., López, P., 2001. Hind limb asymmetry reduces escape performance in the lizard *Psammodromus algirus*. Physiol. Biochem. Zool. 74 (5), 619–624.

Miles, D.B., 1994. Covariation between morphology and locomotory performance in sceloporine lizards. In: Vittt, L.J., Pianka, E.R. (Eds.), Lizard Ecology: Historical and Experimental Perspectives. Princeton University Press, Princeton, pp. 207–235.

Nelson, N., Thompson, M.B., Pledger, S., Keall, S.N., Daugherty, C.H., 2004. Do TSD, sex ratios and nest characteristics influence the vulnerability of tuatura to global warming? Int. Congr. Ser. 1275, 250–257.

Paitz, R.T., Gould, A.C., Holgersson, M.C.N., Bowden, R.M., 2009. Temperature, phenotype, and the evolution of temperature-dependent sex determination: how do natural incubations compare to laboratory incubations? J. Exp. Zool. 314 (1), 86–93.

Parker, S.L., Andrews, R.M., 2007. Incubation temperature and phenotypic traits of *Sceloporus undulatus*: implications for the northern limits of distribution. Oecologia 151 (2), 218–231.

Porter, W.P., Gates, D.M., 1969. Thermodynamic equilibria of animals with environment. Ecol. Monogr. 39 (3), 227–244.

Qualls, F.J., Shine, R., 1998. Geographic variation in lizard phenotypes: importance of the incubation environment. Biol. J. Linn. Soc. 64, 477–491.

Rhen, T., Lang, J.W., 1999. Temperature during embryonic and juvenile development influences growth in hatchling snapping turles, *Chelydra serpentina*. J. Therm. Biol. 24 (1), 33–41.

Schultz, E.T., Conover, D.O., 1999. The allometry of energy reserve depletion: test of a mechanism for size-dependent winter mortality. Oecologia 119 (4), 474–483.

Shine, R., 1995. A new hypothesis for the evolution of viviparity in reptiles. Am. Nat. 145 (5), 809–823.

Shine, R., Harlow, P.S., 1996. Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. Ecology 77 (6), 1808–1817.

Shine, R., Elphick, M.J., Harlow, P.S., 1997. The influence of natural incubation environments on the phenotypic traits of hatchling lizards. Ecology 78 (8), 2559–2568.

Shine, R., Madsen, T., Elphick, M.J., Harlow, P.S., 1997. The influence of nest temperature and maternal brooding on hatchling phenotypes of water pythons. Ecology 78 (6), 1713–1721.

Stamps, J.A., 1984. Rank-dependent compromises between growth and predator protection in lizard dominance hierachies. Anim. Behav. 32 (4), 1101–1107.

Stevenson, R.D., 1985. Body size and limits to the daily range of body temperature in terrestrial ectotherms. Am. Nat. 125 (1), 102–117.

Swain, R., Jones, S.M., 2000. Maternal effects associated with gestation conditions in a viviparous lizard, *Niveoscincus metallicus*. Herpetol. Monogr. 14, 432–440.

Valenzuela, N., Lance, V., 2004. Temperature Dependent Sex Determination in Vertebrates. Smithsonian Institute Press, Washington, DC.

Van Berkum, F.H., 1988. Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. Am. Nat. 132 (3), 327–343.

Van Damme, R., Bauwens, D., Verheyen, R.F., 1990. Evolutionary rigidity of thermal physiology: the case of the cool temperature lizard *Lacerta vivipara*. Oikos 57, 61–67.

Van Damme, R., Bauwens, D., Braña, F., Verheyen, R.F., 1992. Incubation temperature differentially affects hatching time, egg survival, and hatchling performance in the lizard *Padarcis muralis*. Herpetologica 48 (2), 220–228.

Vanhooydonck, B., Van Damme, R., Van Dooren, T.J., Bauwens, D., 2001. Proximate causes of intraspecific variation in locomotor performance in the lizard *Gallotia galloti*. Physiol. Biochem. Zool. 74 (6), 937–945.

Vervust, B., Pafilis, P., Valakos, E.D., Van Damme, R., 2010. Anatomical and physiological changes associated with a recent dietary shift in the lizard *Podacis sicula*. Physiol. Biochem. Zool. 83 (4), 632–642.

Vitt, L.J., 2000. Ecological consequences of body size in neonatal and small-bodied lizards in the Neotropics. Herpetol. Monogr. 14, 388–400.

Wang, P.C., 1966. Studies on the ecology of four species of lizards in Hangzhou. Acta Zool. Sin. 18, 170–185.

Wapstra, E., Olsson, M., Shine, R., Edwards, A., Swain, R., JMP, Joss, 2004. Maternal basking behaviour determines offspring sex in a viviparous reptile. Proc. R. Soc. Lond. B—Biol. Sci 271 (4), 230–232.

Warner, D.A., Shine, R., 2007. Reproducing lizards modify sex allocation in response to operational sex ratios. Biol. Lett. 3 (1), 47–50.

Webb, J.K., Shine, R., Christian, K.A., 2006. The adaptive significance of reptilian viviparity in the tropics: testing the maternal manipulation hypothesis. Evolution 60 (1), 115–122.

Zani, P.A., 1996. Patterns of caudal-autotomy evolution in lizards. J. Zool. 240 (2), 201–220.

Zhang, D.J., Tang, X.L., Yue, F., Chen, Z., Li, R.D., Chen, Q., 2010. Effect of gestation temperature on sexual and morphological phenotypes of offspring in a viviparous lizard, *Eremias multiocellata*. J. Therm. Biol. 35, 129–133.

Zhao, K.T., 1999. Lacertidae. In: Zhao, E.M., Zhao, K.T., Zhou, K.Y. (Eds.), Fauna Sinica, Reptilia, vol. 2 (Squamata: Lacertilia). Science Press, Beijing, pp. 219–242.