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Ontogenetic and sexual differences of thermal biology and locomotor performance in a lacertid lizard, *Eremias multiocellata*

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ABSTRACT

A viviparous lizard, *Eremias multiocellata*, was used to investigate the possible sexual and ontogenetic effects on selected body temperature, thermal tolerance range and the thermal dependence of locomotor performance. We show that adults are sexually dimorphic and males have larger bodies and heads than females. Adults selected higher body temperatures (34.5 vs. 32.4 °C) and could tolerate a broader range of body temperatures (8.1–46.8 vs. 9.1–43.1 °C) than juveniles. The sprint speed and maximum sprint distance increased with temperature from 21 °C to 33 °C, but decreased at 36 °C and 39 °C in both juveniles and adults. Adults ran faster and longer than juveniles at each tested temperature. Adult locomotor performance was not correlated with snout–vent length (SVL) or sex, and sprint speed was positively correlated with hindlimb length. Juvenile locomotor performance was positively correlated with both SVL and hindlimb length. The ontogenetic variation in selected body temperature, thermal tolerance and locomotor performance in *E. multiocellata* suggests that the effects of morphology on temperature selection and locomotor performance vary at different ontogenetic stages.

1. Introduction

In reptiles, individuals may experience large fluctuations in body temperature because they mainly depend on external heat sources for thermoregulation (Sepúlveda et al., 2008; Besson and Cree, 2010). However, many reptiles have the potential ability to maintain or to select their body temperature within a fairly narrow range by means of physiological and behavioral regulation, which usually coincides with the ideal or optimal temperature for functions in variable thermal environments (Cabanac, 2006). Meanwhile, animals' locomotor performance becomes disorganized under critical thermal maximum (CT_{max}) or critical thermal minimum (CT_{min}) conditions. Thus, selected body temperature, CT_{max} and CT_{min} are considered important indicators of species' thermal regulation ability. As an effect of different habitat conditions and genetic factors, the selected temperature and thermal tolerance of individuals may vary inter- and intra-specifically, as well as within different ontogenetic stages or sexes (Brown, 1996; Du et al., 2000; Xu et al., 2001; Besson and Cree, 2010). Data gathered from laboratory and field studies have demonstrated that adults and juveniles may differ not only in morphological traits but also in habitat choice, behavior regulation and functional capacities (Paulissen, 1988; Irschick et al., 2000; Xu and Ji, 2006; Huey, 2008). Therefore, some easily measured behavior traits such as locomotor performance are usually used to examine the possible variations in thermosensitivity of behavior and physiological functions. Locomotor performance (including sprint speed, stop time, maximum distance) is considered to be ecologically relevant and closely associated with individual fitness due to its importance in predator avoidance and foraging success (Vervust et al., 2008). Some previous studies suggested that differences in locomotor performance between adults and juveniles may contribute to differential habitat use and behavior (Irschick et al., 2000). However, the relationship among morphology, thermoregulation and locomotion is still blurry and needs more investigation.

Here, we present data on the selected temperature, CT_{max}, CT_{min} and the thermal dependence of locomotor performance in *Eremias multiocellata.* This species has been studied extensively over the past decades, and recently our group paid particular attention on temperature-dependent sex determination (Zhang et al., 2010; Tang et al., 2012a; Xin et al., 2012), neonate phenotypes (Yan et al., 2011), operational sex ratio (Tang et al., 2012b) and energy consumption during reproduction (Yue et al., 2012) in this species. *E. multiocellata* is a diurnal viviparous lizard with small body size (mean adult snout–vent length ≈65 mm). It exhibits a non-random selection of thermal microhabitats in adults and juveniles, and this

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could impact feeding rate and food diversity (Liu and Geng, 1995). The purpose of the present study was therefore to investigate (i) possible ontogenetic and sex specific shifts in selected body temperature, thermal tolerance, and thermal dependence of locomotor performance; (ii) the relationship between morphology and locomotor performance in *E. multiocellata.*

2. Materials and methods

2.1. Study species

E. multiocellata is commonly found in Xinjiang, Qinghai, Inner Mongolia and western Liaoning in northern China, as well as Mongolia, eastern Kyrgyzstan and Russia (Zhao and Adler, 1993; Zhao et al., 1999). For the present study, adult males, females and juveniles of *E. multiocellata* were collected in Minqin (38°38′ N, 103°05′ E), Gansu province, China, in May 2011. This semi-desert area is situated at the southwest edge of the Tenggeli Desert (mean annual rainfall of 113.6 mm and mean temperature of 18.29 °C over the last five decades; Zhang et al., 2010). According to previous studies, lizards smaller than 35 mm snout–vent length (SVL) were classified as juveniles (Li et al., 2011; Yan et al., 2011). The lizards were transported to our laboratory and the sex of adults was identified by hemipene eversion. Body mass was measured using an electronic balance (accuracy: 0.01 g; Sartorius, Goettingen, Germany) and length-related morphological traits were measured with a vernier caliper (accuracy: 0.01 cm). 15–18 lizards were maintained in a 150 cm × 40 cm × 50 cm terrarium with 5 cm depth of silver sand; sufficient water and mealworms were provided every day. Supplementary heating was provided by a 200 W light bulb (suspended 15 cm above the terrarium floor), on an 8 h on:16 h off cycle (0900–1700 h). Broad spectrum fluorescent tube light was programmed to simulate natural conditions (12 h light:12 h dark cycle, 0700–1900 h).

2.2. Selected body temperatures

Selected body temperatures of 11 juveniles and 21 adults (10 females and 11 males) were determined for one continuous week. A light bulb (200 W) was suspended above one end of the terrarium (200 cm × 50 cm × 50 cm), creating a thermal gradient ranging from 55 °C to 18 °C for 8 h daily (0900–1700 h). Broad spectrum fluorescent tube lights were programmed on a 12 h light:12 h dark cycle (0700–1900 h). In order to limit the effect of diel variation on selected body temperature, all measurements were taken at 1200–1500 h. The body temperature was measured through the cloaca using a K-type thermocouple (1.5 mm diameter, accuracy: 0.1 °C) connected to a digital thermometer.

2.3. Measurement of critical temperatures (CT_{max} and CT_{min})

The critical temperatures were determined using a BI-160A incubator (STIK, Shanghai, China). We cooled (for CT_{min} determination) or heated (for CT_{max} determination) lizards starting from 25 °C at a rate of 1 °C min^{-1}. When temperatures inside the incubator were lower than 10 °C or higher than 35 °C, the lizards were checked for a righting response every 30 s. Body temperatures associated with a transient loss of the righting response (individual lizards were not able to reverse when they were turned over) at the upper or lower limits of thermal tolerance were considered to be CT_{max} or CT_{min} (Xu and Ji, 2006). All measurements of CT_{max} and CT_{min} were recorded through the cloaca using the same protocol as for selected body temperature measurement.

2.4. Locomotor performance

Locomotor performance of 19 adults (10 males and 9 females) and 9 juveniles was measured at seven body temperatures ranging from 21 to 39 °C. The trial sequence was randomized across temperatures (30, 21, 27, 33, 36, 24 and 39 °C). Lizards were placed in an incubator which was set at the test temperature for approximately 2 h before each trial. Locomotor performance was assessed by chasing lizards (with a soft brush) along a 1.8 m racetrack. Each lizard was sprinted twice at each test temperature with a 1 h rest between trials. All lizards were given a 24 h rest between different temperature trials.

The entire locomotor performance test was recorded with a digital video camera (Canon, Tokyo, Japan). The videos were examined using Ulead Video Studio 11 (Ulead Systems Inc., Taipei, Taiwan) for (i) sprint speed in the fastest 25-cm interval, and (ii) maximum distance traveled between stops.

2.5. Statistical analyses

All 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 ANOVA was used to analyze the differences of morphological characteristics, selected body temperatures, CT_{min} and CT_{max} among adult females, adult males and juveniles. Repeated measures ANOVA with SVL as the covariance (with ontogenetic stage as the between-subject factor and body temperature as the within-subject factor) were utilized to analyze locomotor performance difference. All statistical analyses were tested using SPSS (Release 16.0.0; SPSS Inc., Chicago, IL, USA). Descriptive statistics were presented as mean ± standard error, and the significance level was set at $\alpha = 0.05$.

3. Results

3.1. Morphology of adult male, female and juvenile lizards

E. multiocellata is sexually dimorphic, with males being longer and broader than females. Compared with adult females, adult males have larger mean SVL and higher body mass (Table 1). Also, all recorded morphological traits were significantly different between adults and juvenile lizards (Table 1).

3.2. Selected body temperature and critical temperatures

The selected body temperatures ranged from 31.4 to 37.3 °C (averaged: 34.6 °C) for adult males and from 31.2 to 36.9 °C (averaged: 34.5 °C) for adult female lizards. No significant difference was found in selected body temperatures between adult females and males ($F_{1,78} = 0.067$, $P = 0.796$). The selected body temperatures of juveniles were significantly lower than those of adults, ranging from 30.2 to 36.1 °C (averaged: 32.4 °C; $F_{1,134} = 6.345$, $P = 0.013$) (Fig. 1). Selected body temperatures were not related with body mass or SVL in both adults and juveniles (all $P > 0.05$).

Adults can tolerate a wider range of body temperature than juveniles. CT_{min} was 8.1 ± 0.5 °C (range 5.5–10.3 °C) and 9.1 ± 0.4 °C (range 6.9–11.2 °C) for adults and juveniles, respectively. CT_{max} was lower in juveniles than in adults (43.1 ± 0.7 °C vs. 46.8 ± 0.5 °C; $F_{1,20} = 7.271$, $P < 0.001$).

3.3. Locomotor performances

In both adults and juveniles, sprint speed and maximum sprint distance increased with body temperature within the range of 21–33 °C, but decreased at 36 and 39 °C. Repeated measures ANOVA

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Table 1
Morphological variables (mean ± SD) for juveniles and adults of *Eremias multiocellata*.

Morphological traits	*N*	Mean ± SD	*F*-value
Body mass (g)			
Female	31	6.59 ± 0.21	42.303***
Male	42	7.56 ± 0.21	
Juvenile	28	1.67 ± 0.10	66.432***
Adult	73	6.99 ± 0.25	
SVL (cm)			
Female	31	6.08 ± 0.08	14.722**
Male	42	6.54 ± 0.09	
Juvenile	28	3.17 ± 0.07	44.956***
Adult	73	6.34 ± 0.08	
Tail length (cm)			
Female	31	8.47 ± 0.22	18.677***
Male	42	9.86 ± 0.23	
Juvenile	28	4.61 ± 0.21	6.145**
Adult	73	9.38 ± 0.21	
Forelimb length (cm)			
Female	31	1.67 ± 0.04	18.547***
Male	42	1.84 ± 0.02	
Juvenile	28	0.67 ± 0.16	14.629***
Adult	73	1.77 ± 0.03	
Hindlimb length (cm)			
Female	31	2.61 ± 0.04	33.022***
Male	42	2.91 ± 0.04	
Juvenile	28	0.94 ± 0.24	17.025***
Adult	73	2.77 ± 0.04	
Head length (cm)			
Female	31	1.51 ± 0.02	10.359**
Male	42	1.67 ± 0.04	
Juvenile	28	0.84 ± 0.06	19.5***
Adult	73	1.60 ± 0.03	
Head width (cm)			
Female	31	0.93 ± 0.02	32.197***
Male	42	1.10 ± 0.02	
Juvenile	28	0.59 ± 0.10	31.741***
Adult	73	1.02 ± 0.02	

N, number of individuals sampled.
** $P < 0.01$.
*** $P < 0.001$.

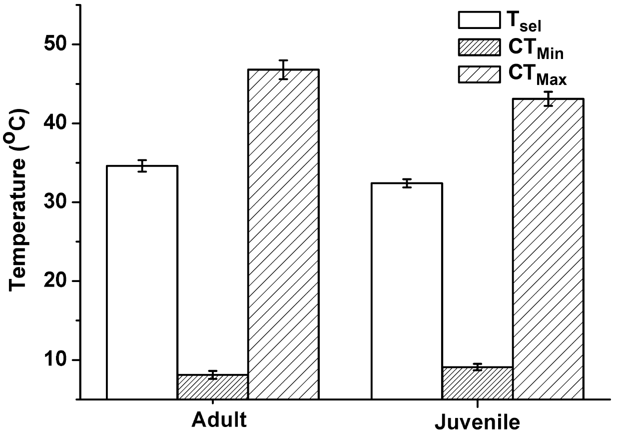

Fig. 1. Selected body temperature (T_{sel}) and critical temperatures (CT_{min}, CT_{max}) of adults and juveniles in *Eremias multiocellata*. Data are expressed as mean ± SE.

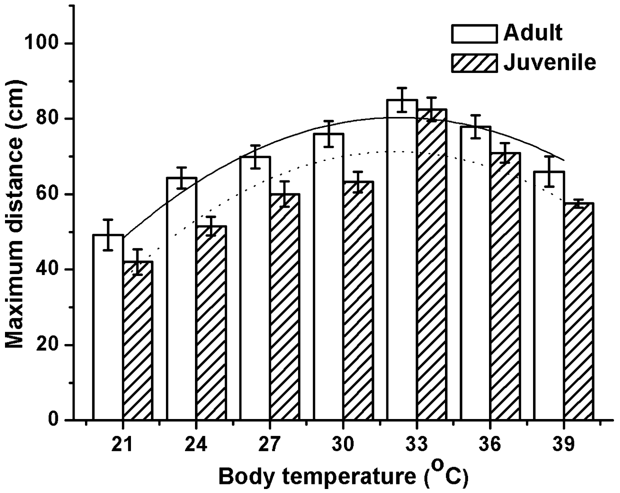

Fig. 2. Maximum sprint distance of adults and juveniles at different body temperatures in *Eremias multiocellata*. The curves were generated from a negative exponential fit on the original data.

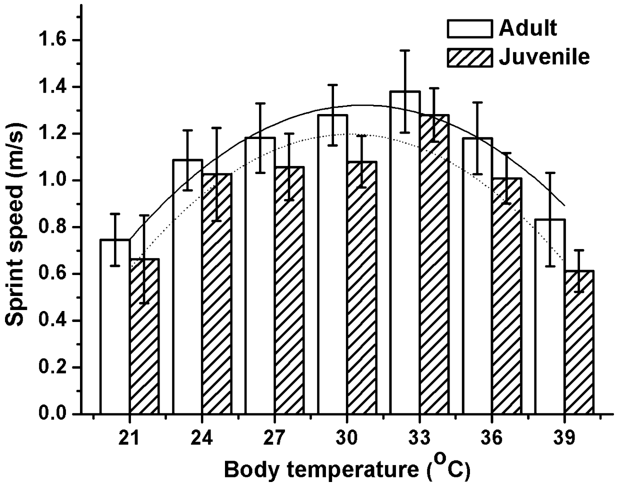

Fig. 3. Sprint speed of adults and juveniles at different body temperatures in *Eremias multiocellata*. The curves were generated from a negative exponential fit on the original data.

showed that the effects of ontogenetic stage ($F_{1,27} = 38.58$, $P < 0.001$) and body temperature ($F_{6,179} = 14.91$, $P < 0.001$) on maximum distance (Fig. 2) and sprint speed (Fig. 3) were significant, but the effect of their interaction was not ($F_{6,179} = 14.91$, $P = 0.176$). At each test temperature, there was no significant difference between adult females and males in sprint speed and maximum distance ($F_{1,18} = 1.583$, $P = 0.482$). The locomotor performances (sprint speed and maximum distance) were not correlated with SVL in adult female and male lizards, but sprint speed was positively correlated with hindlimb length (♀: $R^2 = 0.342$, $P = 0.015$; ♂: $R^2 = 0.249$, $P = 0.030$). Locomotor performance was positively correlated with both SVL and hindlimb in juveniles (all $P < 0.001$).

4. Discussion

Ectotherm phenotypes including thermoregulation and locomotion may vary notably at different ontogenetic stages or sexes and may also be influenced significantly by habitat conditions (Angilletta et al., 2002; Seebacher, 2005). In the present study, we found that the contribution of morphology to selected body temperature, tolerance range and locomotor performance varied at the different ontogenetic stages in *E. multiocellata*. Selected body temperature and critical temperatures, which have been extensively studied in reptiles, are considered important indicators of the fitness to the local environmental conditions (Huey and Slatkin, 1976; Angilletta et al., 2002). The selected body temperature may vary among and within species, and previous studies suggest that lizards with large body size may exhibit higher body temperatures than small ones in equilibrium with the same thermal conditions (Du et al., 2000; Harlow et al., 2010).

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Table 2
Comparison of selected temperature (T_{sel}) and critical temperatures (CT_{min}, CT_{max}) among different species.

Species		T_{sel} (°C)	CT_{min} (°C)	CT_{max} (°C)	Source
Eumeces chinensis	Adult	31.2	6.3	42.3	Ji (1995)
Takydromus septentrionalis	Adult	30.0	4.9	42.3	Ji et al. (1996)
Takydromus sexlineatus	Adult	31.5	6.4	42.2	Zhang and Ji (2004)
Phrynocephalus vlangalii	Adult	33.3	0.9	46.9	Shu et al. (2010)
Eremias multiocellata	Adult	34.6	8.1	46.8	Present study
	Juvenile	32.4	9.1	43.1	
Eremias brenchleyi	Adult	33.5	3.4	43.6	Xu and Ji (2006)
	Juvenile	31.7	5.1	40.8	
Eremias argus	Adult	36.0	1.0	44.9	Luo et al. (2006)

Our results indicate that selected body temperature and tolerance range of *E. multiocellata* are significantly different between adults and juveniles. Another study on *Eremias brenchleyi*, which has a close phylogenetic relationship with *E. multiocellata*, also indicated that juvenile *E. brenchleyi* selected a lower body temperature; they achieved a faster growth rate and benefited more from a relatively lower body temperature (Xu and Ji, 2006). The lower selected body temperature in juveniles of *E. multiocellata* in the present study suggests that they may exhibit a non-random selection of microhabitats to mitigate juvenile–adult intraspecific competition and that they will spend more time in the shade to avoid hazardous basking and predators (Du et al., 2000; Herczeg et al., 2008). However, whether juveniles benefit more from lower body temperature in natural conditions is still uncertain and merits further attention in the future.

The differences in selected body temperature and critical temperatures between adults and juveniles cannot be explained by the variations in body size or shape. Other factors, especially altered habitat use, feeding activities and predator avoidance must be considered as the causes of different selected body temperatures and tolerance ranges during ontogeny (Hertz et al., 1993; Christian and Bedford, 1995), as shown for other lizare species. For instance, the selected body temperatures of both adult and juvenile *E. brenchleyi* (33.5 ± 0.3 and 31.7 ± 0.2 °C, respectively) were lower than those of *E. multiocellata*. We assume that this may be associated with their habitat conditions, for *E. brenchleyi* lives in mountainous and relatively cooler environmental conditions and utilizes more shade habitat (Xu and Ji, 2006). Another species, *Phrynocephalus przewalskii* that inhabits the same area as *E. multiocellata* selected higher body temperature (37.5 °C for adults) than *E. multiocellata*. This is possibly due to the fact that *P. przewalskii* uses more open habitats and has longer active time (Li and Liu, 1992).

Our results show that CT_{max} and CT_{min} of *E. multiocellata* are higher than those of other species living in comparable habitats (Table 2). These results coincide with our previous prediction that lizards with a wider tolerance range occupy warmer habitats (Du et al., 2000; Zhang and Ji, 2004; Xu and Ji, 2006). *E. multiocellata* lives in arid and semi-arid regions and the mean temperature in its habitat is relatively higher than that of other lizards' habitats.

Locomotor performance has widely been viewed as a link between environmental conditions and individual phenotype (Lailvaux et al., 2003). A considerable volume of literature predicts that lizards exhibit pronounced variations of locomotor performance across test temperatures (Damme et al., 1990; Du et al., 2000). Corresponding results were also found in *E. multiocellata*. Body temperature was found to significantly affect sprint speed and maximum sprint distance, which is consistent with previous studies on lizard locomotor capacities (Damme et al., 1990; Du et al., 2000; Angilletta et al., 2002). At each test temperature, mean sprint speed and maximum distance of adults were greater than those of juveniles. The optimal temperature for maximum distance and sprint speed consistently ranged between 30 and 33 °C, coinciding with the mean value of selected body temperature. These results provide additional evidence that thermoregulatory behavior and thermal physiological capacities may have co-adapted in this species. Furthermore, the ranges of body temperatures at which lizards maintained 80% of maximum sprint speed (B80) were 24.1–37.2 °C and 24.2–36.0 °C for adults and juveniles, respectively, and these ranges cover almost completely the selected body temperature ranges (31.2–37.3 °C for adults and 30.2–36.1 °C for juveniles) measured under laboratory conditions. This indicates that the activity range of *E. multiocellata* is relatively wide, but favors cool conditions.

Another interesting result of the present study is the relationship between morphological traits and locomotor performance. Our data demonstrate that adults with bigger body size had better locomotor performance than juveniles. SVL and hindlimb length were positively related with sprint speed and maximum distance in juveniles, but only relatively longer hindlimb length could enhance sprinting ability in adults. These results suggest that the contribution of morphology to locomotor performance varies at different ontogenetic stages and may be greater in juveniles than in adults.

The morphological analyses of *E. multiocellata* adults indicate substantial sexual dimorphism in body size. Adult males have larger SVL than females, and tend to have bigger body mass, longer limbs and larger head sizes (cf. Li et al., 2006). Adult males may benefit from these morphological traits, for instance, by achieving better performance during mating and in avoiding predators. Furthermore, male lizards with bigger head size may be able to consume larger and harder prey items than females and juveniles (Verwaijen et al., 2002; Brecko et al., 2008). However, surprisingly for such a sexually dimorphic species, we did not find any significant differences in selected body temperature, tolerance range and locomotor performance between adult males and females, and all these traits were not correlated to body size. Only sprint speed was found to be positively correlated with hindlimb length. This study was conducted in early May, when the lizards had just emerged from hibernation, so we could exclude effects of nutrition, mating or reproduction on selected body temperature. Furthermore, previous research and field observation (Li et al., 2006, 2011) did not find any obvious ecological or behavioral differences between adult males and females of *E. multiocellata*; they use similar microhabitats and exhibit similar activity times. These similar habits could be the major reason why there were no significant differences in selected body temperature and locomotion between adult females and males. However, it is difficult to precisely determine these traits in the field, especially for species with small body size. To ascertain whether the sexual and ontogenetic differences in selected body temperature and locomotor performance determined in the laboratory truly reflect the adaptability in the wild, further research will be necessary.

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