

Temperature acclimation affects thermal preference and tolerance in three *Eremias* lizards (Lacertidae)

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Abstract We acclimated adult males of three *Eremias* lizards from different latitudes to 28 °C, 33 °C or 38 °C to examine whether temperature acclimation affects their thermal preference and tolerance and whether thermal preference and tolerance of these lizards correspond with their latitudinal distributions. Overall , selected body temperature (Tsel) and viable temperature range (VTR) were both highest in *E. brenchleyi* and lowest in *E. multiozellata* , with *E. argus* in between; critical thermal minimum (CTMin) was highest in *E. multiozellata* and lowest in *E. brenchleyi* , with *E. argus* in between; critical thermal maximum (CTMax) was lower in *E. multiozellata* than in other two species. Lizards acclimated to 28 °C and 38 °C overall selected lower body temperatures than those acclimated to 33 °C ; lizards acclimated to high temperatures were less tolerant of low temperatures , and vice versa ; lizards acclimated to 28 °C were less tolerant of high temperatures but had a wider VTR range than those acclimated to 33 °C and 38 °C . Lizards of three species acclimated to the three temperatures always differed from each other in CTMin , but not in Tsel , CTMax and VTR. Our results show that : temperature acclimation plays an important role in influencing thermal preference and tolerance in the three *Eremias* lizards , although the degrees to which acclimation temperature affects thermal preference and tolerance differ among species ; thermal preference rather than tolerance of the three *Eremias* lizards corresponds with their latitudinal distributions [*Current Zoology* 55 (4) : 258 - 265 , 2009].

Key words Lizards , *Eremias* , Acclimation temperature , Thermal preference , Thermal tolerance , Viable temperature range , Food assimilation

As ectotherms , lizards can withstand a wide range of body temperatures. However , extremely low or high temperatures may certainly lead them to death. The upper (critical thermal maximum , CTMax) and lower (critical thermal minimum , CTMin) survival limits are often defined as the upper and lower extremes of thermal tolerance at which the animal cannot right itself when placed on its back , i. e. , the loss of righting response (Cowles and Bogert , 1944 ; Lowe and Vance , 1955 ; Brown and Feldmeth , 1971 ; Doughty , 1994 ; Lutterschmidt and Hutchison , 1997). Many lizards attempt to maintain relatively high and constant body temperatures when conditions allow them to do so , often because biochemical and physiological activities are maximized at moderate to relatively high temperatures (Huey and Stevenson , 1979 ; Huey , 1982 ; Huey and Kingsolver , 1989 ; Kaufmann and Bennett , 1989 ; Angilletta , 2001 ; Angilletta et al. , 2002). Lizards acquire and maintain appropriate body temperatures mainly through behavioral mechanisms , although physiological thermoregulation through cardiovascular adjustments , endogenous heat production and evaporative cooling may be also important (Avery , 1982 ;

Bartholomew , 1977 , 1982 ; Huey , 1982 , 1991). The body temperature preferred by a lizard often corresponds closely to the optimal temperature range for biochemical and physiological activities , and can be estimated by measuring its selected body temperature (Tsel) in a laboratory thermal gradient (Angilletta et al. , 2002 and references therein) .

Thermal preference (Tsel) and tolerance (CTMin and CTMax) have been studied in diverse animal taxa. Studies of lizards have shown that thermal preference and tolerance may vary among and within species as a response to changes in the thermal environment associated with habitat use , or geographic distribution (Huey and Kingsolver , 1993 ; Feder et al. , 2000 ; Angilletta et al. , 2002 ; Winne and Keck , 2005 ; Du , 2006) , and among individuals of the same population that differ in physiological , or developmental conditions (Hutchison , 1976 ; Daut and Andrews , 1993 ; Mathies and Andrews , 1997 ; Le Galliard et al. , 2003 ; Du et al. , 2008 ; Lin et al. , 2008). For example , lizards from cool habitats usually select lower body temperatures than do those from warm habitats (Xu and Ji , 2006 and references therein) , and females usually shift thermal preference when

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pregnant due to behavioral preferences or due to constraints on thermoregulation activities (Braña, 1993; Mathies and Andrews, 1997; Le Galliard et al., 2003; Ji et al., 2006; Lin et al., 2008).

Thermal preference and tolerance are subject to phenotypic alteration within limits that are genetically fixed. Phenotypic plasticity depends on a variety of factors the principal of which is thermal acclimation, a process by which organisms physiologically adjust to an altered thermal environment (Patterson and Davies, 1978; Cossins and Bowler, 1987; Lutterschmidt and Hutchison, 1997; Andrews, 1998; Rock et al., 2000; Brown and Griffin, 2005). Thus, determination of thermal preference and tolerance based on field observations may not always depict true preference and tolerance. Therefore, thermal preference and tolerance have usually been measured in the laboratory where animals are maintained under strictly controlled thermal conditions.

Here, we present data on thermal preference and tolerance of three species of lacertid lizards, *Eremias argus*, *E. brenchleyi* and *E. multiocellata*, acclimated to three temperatures (see below for details). We addressed the following questions: (1) Can temperature acclimation alter thermal preference and tolerance in the lizards studied? (2) Do these lizards show interspecific differences in thermal preference and tolerance when acclimated under identical thermal conditions? (3) If so, do any such differences correspond with their latitudinal distributions?

1 Materials and Methods

1.1 Study animals

The three congeneric species are all small-sized lizards with an exclusively temperate distribution.

Eremias argus (Mongolian racerunner) is an oviparous lizard that ranges from northern China (southward to Jiangsu and westward to Qinghai) to Russia (region of Lake Baikal), Mongolia and Korea (Zhao, 1999).

Eremias brenchleyi (Ordos racerunner) is an oviparous lizard that is endemic to China and lives in several eastern and northern provinces of the country (Chen, 1991).

Eremias multiocellata (multi-ocellated racerunner) is a viviparous lizard that ranges from northern China (southward to Gansu and eastward to Liaoning) to Mongolia, Kirgizstan, Kazakstan and Russia (Tuv District in Siberia) (Zhao, 1999).

We collected adults of *E. argus* from Linfen ($\sim 36^{\circ} 06' N$, $111^{\circ} 33' E$), Shanxi (northern China) in mid-April 2007, *E. brenchleyi* from Suzhou ($\sim 33^{\circ} 38' N$, $116^{\circ} 59' E$), Anhui (eastern China) in early April 2007, and *E. multiocellata* from Wulatehouqi ($\sim 41^{\circ} 27' N$, $106^{\circ} 59' E$), Inner Mongolia (northern China) in mid-May 2007. Fig. 1 shows monthly variation in air temperatures of the three localities. Lizards were transported to our laboratory at Hangzhou Normal University, where they were marked by a non-toxic waterproof label for future identification. Eight to 12 lizards of the same species were housed in a 750 mm \times 500 mm \times 450 mm (length \times width \times height) plastic cage that contained a substrate of sand, with rocks and pieces of clay tiles provided as cover. Cages were placed in a room kept at 22 - 28 $^{\circ}C$. A 100-W light bulb, suspended at one end of each cage, created a thermal gradient from the room temperature to 55 $^{\circ}C$ for 14 h daily. Lizards were exposed to a natural light cycle, and could thermoregulate during the photophase. Lizards were fed mealworms (larvae of *Tenebrio molitor*), house crickets *Achetus domesticus* and water enriched with vitamins and minerals *ad libitum*. Females laid eggs

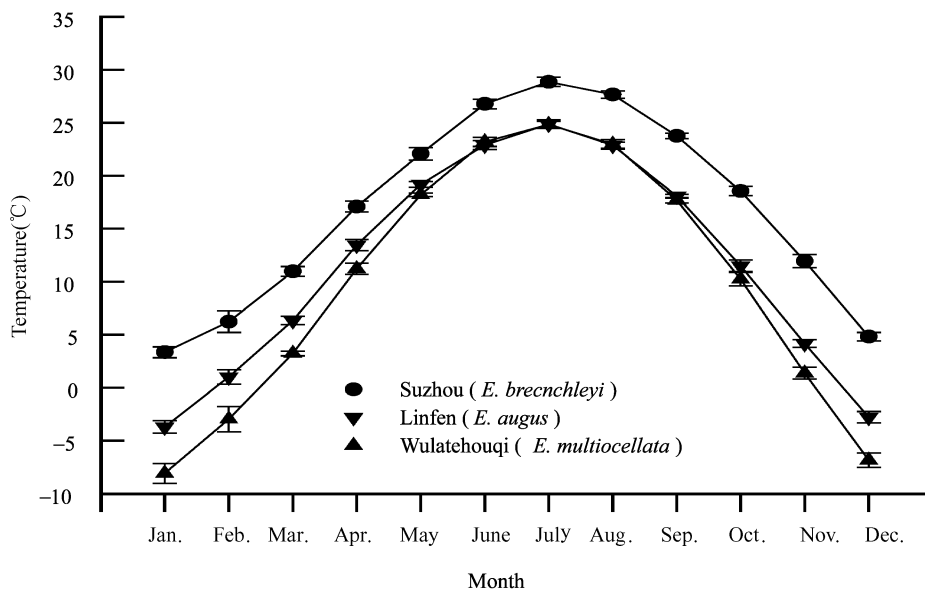


Fig. 1 Monthly mean (\pm SE) air temperatures for 1987 - 2007 at the three localities (courtesy of the Provincial Bureaus of Meteorology of Anhui, Shanxi and Inner Mongolia), where lizards were collected

(*E. argus* and *E. brenchleyi*), or gave birth to young *E. multiocellata* under the laboratory conditions described above.

1.2 Thermal acclimation of animals

In September when lizards had been kept under identical laboratory conditions for about 4 - 5 months, we selected 36 *E. argus* (2.8 - 4.7 g), 36 *E. brenchleyi* (3.3 - 5.8 g) and 36 *E. multiocellata* (3.6 - 6.4 g) males with an intact tail to conduct acclimation experiments. Lizards of each species were equally divided into three groups each of which was assigned to one of the three temperature treatments (28, 33 and 38 °C). These three temperatures were chosen because lizards of two (*E. argus* and *E. brenchleyi*) of the three species had been known to feed normally at temperatures within the range of 28 - 38 °C (Luo et al., 2006; Xu and Ji, 2006). Lizards individually housed in 300 mm × 250 mm × 300 mm glass cages were acclimated for three weeks at their designated temperatures, followed by Tsel, CTMin and CTMax measurements. During this period lizards did not have any heat source for basking and, based on the results reported for *E. argus* (Luo et al., 2006) and *E. brenchleyi* (Xu and Ji, 2006), the body temperatures of the test groups should be constant and very close to 28 °C, 33 °C, or 38 °C.

Feces, urates and subsamples of food (mealworms) corresponding to each lizard were dried to constant mass at 65 °C and weighed. Dried samples were burnt in a WGR-1 adiabatic calorimeter (Changsha Instrument, China), and data on energy density were automatically downloaded to a computer. The assimilation efficiency (AE) was calculated as $100 \times (I - F - U) / I$, where I = energy ingested, F = energy in feces and U = energy in urates. The apparent digestive coefficient (ADC) was calculated as $100 \times (I - F) / I$.

1.3 Determination of Tsel, CTMin and CTMax

We measured Tsel in 1000 mm × 800 mm × 500 mm plastic cages with 5 cm depth sand and pieces of clay tiles. A 100-W light bulb suspended above one end of the terrarium created a thermal gradient from the room temperature (22 °C) to 55 °C for 14 h daily. Lizards were individually introduced into the gradient at the cold end at 06:00 (Beijing time) when the lights were switched on. To minimize the potential influence of diel variation in Tsel, we began measurements every trial day at 15:00 and ended within two hours. Body (cloacal) temperatures (to the nearest 0.1 °C) were taken for each lizard that was basking on the surface with a UT325 digital thermometer (Shanghai Medical Instruments, China). The probe (~1 mm diameter) was inserted ~4 mm into the cloacae when used to measure a lizard's body temperature, and great care was taken to avoid heat transfer between the hand and the lizard. To address the repeatability of our measurements, we measured each lizard five times, once on each of five consecutive days. The five measures did

not differ significantly within each species × temperature combination (repeated measures ANOVA; all $P > 0.216$). We therefore considered the mean of the five measures as a lizard's Tsel. During the intervals of Tsel trials, lizards were put back to their house cages before CTMin and CTMax were measured.

We used FPQ incubators (Ningbo Life Instruments, China) to determine CTMin and CTMax. Trials were conducted between 10:00 - 15:00. We cooled or heated lizards from their designated acclimation temperatures at a rate of 0.25 min^{-1} , and at a slower rate of 0.1 min^{-1} when temperatures inside the incubator were lower than 12 °C or higher than 40 °C. During the trials, we observed the behavior of lizards through a window in the incubator door. Lizards were taken out of the incubator for the righting response test, and body temperatures associated with a transient loss of the righting response at the lower and the upper limits of thermal tolerance were considered to be the endpoints for CTMin and CTMax, respectively.

1.4 Statistical analyses

We used Statistica software package (version 5.0 for PC) to analyze the data. Body mass was not a significant predictor of all examined traits within each species × temperature combination (all $P > 0.229$). We therefore used two-way ANOVA to examine the effects of species, temperature acclimation and their interaction on the examined traits, combined with Tukey's *post hoc* test. Percentage data on ADC and AE were arcsine-transformed prior to parametric analyses. One-way ANOVA was used to examine whether lizards acclimated to any particular temperature showed interspecific differences in thermal preference and tolerance. All values are presented as mean ± SE, and the significance level is set at $\alpha = 0.05$.

2 Results

Data for the effects of body temperature on food intake, AE and ADC are given in Fig. 2. Food intake, AE and ADC differed among species, and among temperature treatments; food intake and ADC were affected by the species × temperature interaction, whereas AE was not (Table 1). Food intake was greatest in *E. brenchleyi* and smallest in *E. multiocellata*, with *E. argus* in between; lizards at 33 °C and 38 °C did not differ in food intake, but they both ingested more food than did those at 28 °C (Table 1). AE and ADE were both higher in *E. brenchleyi* than in other two species; AE and ADC were both highest at 38 °C and smallest at 28 °C, with the 33 °C treatment in between (Table 1).

Data for the effects of acclimation on thermal preference and tolerance are given in Fig. 3. Tsel, CTMin, CTMax and viable temperature range (the difference between CTMax and CTMin, VTR) differed among species and among temperature treatments; Tsel,

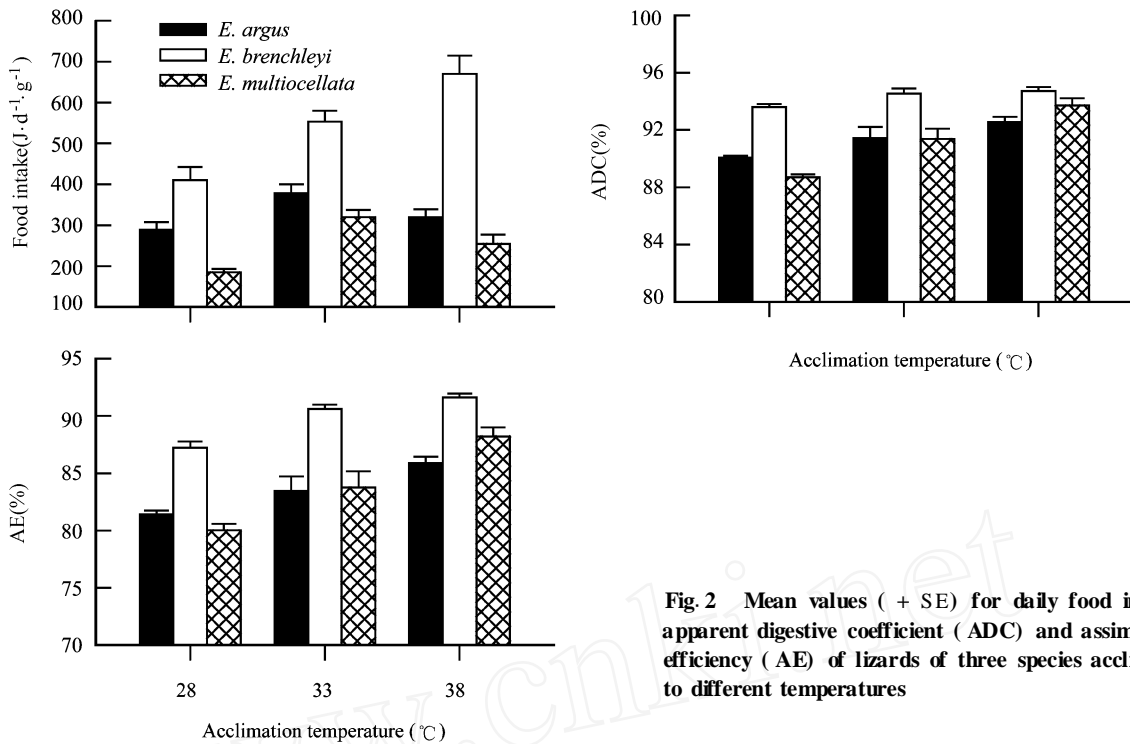


Fig. 2 Mean values (+ SE) for daily food intake, apparent digestive coefficient (ADC) and assimilation efficiency (AE) of lizards of three species acclimated to different temperatures

Table 1 Results of two-way ANOVA with temperature and species as the factors

	Effects		
	Species	Acclimation temperature	Interaction
Food intake	$F_{2, 99} = 103.72, P < 0.0001$ EA ^b , EB ^a , EM ^c	$F_{2, 99} = 22.16, P < 0.0001$ 28 ^b , 33 ^a , 38 ^a	$F_{4, 99} = 6.68, P < 0.0001$
Apparent digestive coefficient	$F_{2, 99} = 42.94, P < 0.0001$ EA ^b , EB ^a , EM ^b	$F_{2, 99} = 30.26, P < 0.0001$ 28 ^c , 33 ^b , 38 ^a	$F_{4, 99} = 4.73, P < 0.002$
Assimilation efficiency	$F_{2, 99} = 59.89, P < 0.0001$ EA ^b , EB ^a , EM ^b	$F_{2, 99} = 40.06, P < 0.0001$ 28 ^c , 33 ^b , 38 ^a	$F_{4, 99} = 2.28, P = 0.066$
Selected body temperature	$F_{2, 99} = 17.21, P < 0.0001$ EA ^b , EB ^a , EM ^c	$F_{2, 99} = 7.76, P < 0.001$ 28 ^b , 33 ^a , 38 ^b	$F_{4, 99} = 2.67, P = 0.037$
Critical thermal minimum	$F_{2, 99} = 167.48, P < 0.0001$ EA ^b , EB ^c , EM ^a	$F_{2, 99} = 152.44, P < 0.0001$ 28 ^c , 33 ^b , 38 ^a	$F_{4, 99} = 3.88, P < 0.006$
Critical thermal maximum	$F_{2, 99} = 24.64, P < 0.0001$ EA ^a , EB ^a , EM ^b	$F_{2, 99} = 29.54, P < 0.0001$ 28 ^b , 33 ^a , 38 ^a	$F_{4, 99} = 4.88, P < 0.002$
Viable temperature range	$F_{2, 99} = 116.82, P < 0.0001$ EA ^b , EB ^a , EM ^c	$F_{2, 99} = 12.84, P < 0.0001$ 28 ^a , 33 ^b , 38 ^b	$F_{4, 99} = 2.22, P = 0.072$

Percentage data on AE and ADC were arcsine-transformed prior to two-way ANOVA. Means corresponding to acclimation temperature or species with different superscripts differed significantly (Tukey's *post hoc* test, $\alpha = 0.05, a > b > c$).

CTMin and CTMax were all affected by the species × temperature interaction, whereas VTR was not (Table 1). Tsel was highest in *E. brenchleyi* and lowest in *E. multiocellata*, with *E. argus* in between; lizards acclimated to 28 and 38 overall selected lower body temperatures than did those acclimated to 33 (Table 1). CTMin was highest in *E. multiocellata* and lowest in *E. brenchleyi*, with *E. argus* in between; lizards acclimated to high temperatures were less tolerant of low temperatures, and vice versa (Table 1). *Eremias argus*

and *E. brenchleyi* were overall more tolerant of high temperatures than *E. multiocellata*; lizards acclimated to 28 were less tolerant of high temperatures than those acclimated to other two higher temperatures (Table 1). VTR was greatest in *E. brenchleyi* and smallest in *E. multiocellata*, with *E. argus* in between; VTR was greater in the 28 treatment than in other two treatments (Table 1).

Lizards of three species acclimated to the three temperatures always differed from each other in CTMin,

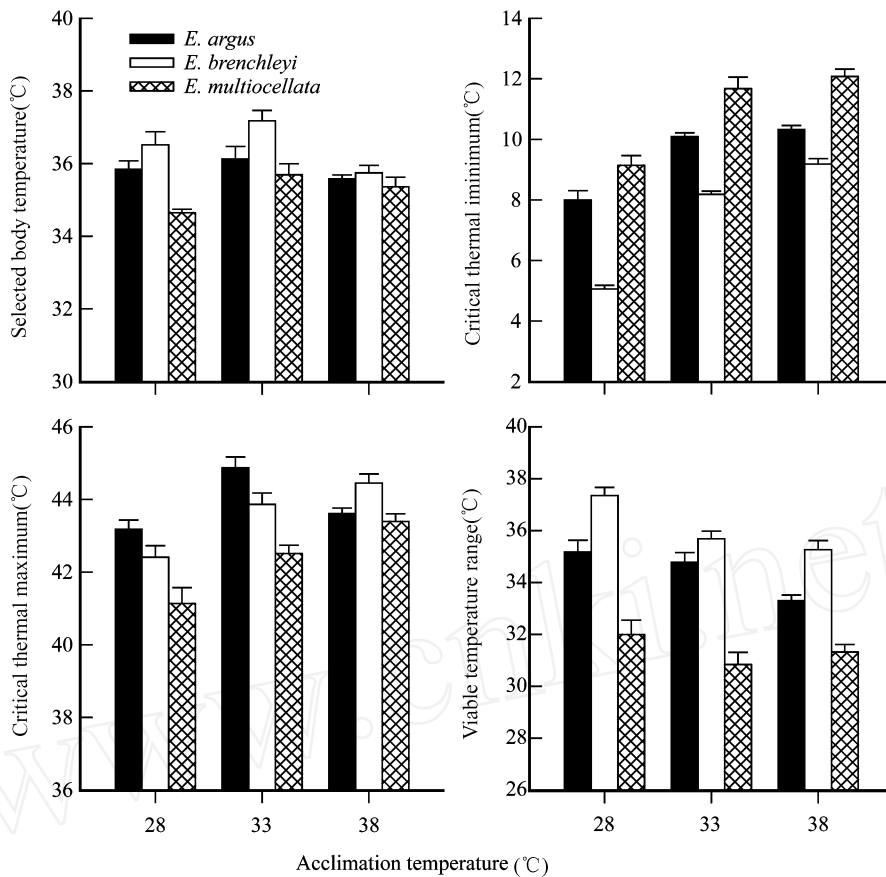


Fig. 3 Mean values (+ SE) for selected body temperature, critical thermal minimum, critical thermal maximum, and viable temperature range of lizards of three species acclimated to different temperatures

but not in Tsel, CTMax and VTR. Within each temperature treatment CTMin was highest in *E. multiocellata* and lowest in *E. brechleyi*, with *E. argus* in between (Tukey's test, all $P < 0.013$). The three *Eremias* lizards did not differ in Tsel in the 38 treatment (One-Way ANOVA; $F_{2,33} = 0.84$, $P = 0.442$), and in no temperature treatment did Tsel differ between *E. argus* and *E. brechleyi* (Tukey's test, all $P > 0.060$). CTMax did not differ between *E. argus* and *E. brechleyi* in the 28 treatment (Tukey's test, $P = 0.273$), nor between *E. argus* and *E. multiocellata* in the 38 treatment (Tukey's test, $P = 0.742$). VTR did not differ between *E. argus* and *E. brechleyi* in the 33 treatment (Tukey's test, $P = 0.238$). Thus, whereas two-way ANOVA overall revealed that thermal preference and tolerance differed among species, the three *Eremias* lizards did not always show interspecific differences in thermal preference and tolerance when acclimated under identical thermal conditions.

3 Discussion

Food intake, AE and ADC differed among the *Eremias* lizards studied, adding evidence in support of the conclusion that lizards of different species may differ in these variables even under identical laboratory

conditions (Xu and Ji, 2006 and references therein). Consistent with the many previous studies of lizards (e.g., Lowe and Vance, 1955; Brattstrom, 1971; Patterson, 1999; Huang et al., 2006; Yang et al., 2008), temperature acclimation had significant impacts on thermal preference and tolerance in the three *Eremias* lizards.

Thermal preference was more likely to be affected by acclimation temperature in *E. brechleyi* and *E. multiocellata* than in *E. argus*, suggesting that the degree to which thermal preference is affected by acclimation temperature differs among lizard species. The three *Eremias* lizards all had an ample opportunity to maintain their body temperatures at any level in the laboratory thermal gradient. Interestingly, however, in no species was Tsel maximized in individuals acclimated to the highest temperature (Fig. 3). The explanation for this result presumably lies in the trade-off between costs and benefits associated with thermoregulation. Thermoregulation may result in potential fitness benefits, but the benefits are offset by any costs associated with thermoregulation in any given set of environmental conditions (Shine and Madsen, 1996; Sartorius et al., 2002; Lin et al., 2008). Thus, lizards should shift their thermal preferences according to changes in thermal

environment towards the levels optimal for physiological or behavioral performances and, at the same time, minimize costs associated with thermoregulation to a large extent (Hertz et al., 1993; Christian and Weavers, 1996; Blouin-Demers et al., 2000; Angilletta et al., 2002; Lin et al., 2008). In many lizards including two *Eremias* lizards (*E. argus* and *E. brenchleyi*), body temperatures varying over a relatively wide range do not have statistically differential effects on several important performances such as food intake, food assimilation and locomotion, but energetic demands do increase with an increase in body temperature (Yang et al., 2008 and references therein). Thus, the result that lizards did not select higher-than-usual body temperatures when acclimated to the highest temperature could reflect a mechanism evolved in the three *Eremias* lizards to reduce energetic costs associated with the increased metabolic rates at high body temperatures.

Lizards acclimated to low temperatures were more tolerant of low temperatures than those acclimated to high temperatures, and vice versa (Fig. 3). Such a pattern is shared by the three *Eremias* lizards, and has been reported for other lizards such as the south China forest skink *Sphenomorphus incognitus* (Huang et al., 2006), the Taiwan forest skink *S. taiwanensis* (Huang et al., 2006) and the northern grass lizard *Takydromus septentrionalis* (Yang et al., 2008). The upper limit of thermal tolerance in general increased with an increase in acclimation temperature in *E. brenchleyi* and *E. multiocellata* (Fig. 3). This pattern also occurs in *S. incognitus*, *S. taiwanensis* and *T. septentrionalis* (Huang et al., 2006; Yang et al., 2008). In *E. argus*, however, individuals acclimated to a medium temperature (33 °C) were the most tolerant of high temperatures (Fig. 3). This difference is of interest, because it suggests that CT_{Max} may not always be maximized at the highest acclimation temperature in lizards.

Means of T_{sel}, CT_{Min} and CT_{Max} for adult *E. argus* from the same area measured in April (monthly mean air temperature is ~14 °C) are 36.0, 1.0 and 44.9 (°C, respectively (Luo et al., 2006); means of T_{sel}, CT_{Min} and CT_{Max} for adult *E. brenchleyi* from the same area measured in April (monthly mean air temperature is ~18 °C) are 33.5, 3.4 and 43.6 °C, respectively (Xu and Ji, 2006). In both species, means of T_{sel} and CT_{Max} for the field-caught individuals fall within the ranges of T_{sel} (33.6 - 36.7 °C in *E. argus*; 34.0 - 38.4 °C in *E. brenchleyi*) and CT_{Max} (41.6 - 44.7 °C in *E. argus*; 41.1 - 45.2 °C in *E. brenchleyi*) for individuals acclimated to 28 °C, the lowest acclimation temperature in this study. Nonetheless, means of CT_{Min} are much lower in the field-caught individuals than in those (6.5 - 9.5 °C in *E. argus*, with a mean of 8.0 °C; 4.3 - 5.8 °C in *E. brenchleyi*, with a mean of 4.3 °C)

acclimated to 28 °C. These results are consistent with an earlier study of *T. septentrionalis* that has found acclimation temperature to have a more significant impact on CT_{Min} than on CT_{Max} or T_{sel} (Yang et al., 2008).

Thermal environments change dramatically with latitude or altitude, with mean air temperature in general decreasing with an increase in latitude or altitude. In mainland China, northerly (high latitudinal) areas are characterized by a low mean but great amplitude of thermal fluctuations that may be an important factor restricting basking opportunities for ectotherms including lizards. Thus, intuitively, lizards with a northerly distribution should be more tolerant of extreme temperatures and select lower body temperatures than those with a southerly distribution. Interestingly, however, *E. multiocellata* had higher CT_{Min} but lower CT_{Max} than other two congeneric species (*E. argus* and *E. brenchleyi*) with more southerly distributions, and CT_{Min} was higher in *E. argus* than in *E. brenchleyi* with a more southerly distribution (Table 1). Thus, inconsistent with many previous studies of lizards that have found a clear relation between thermal tolerance and latitudinal or altitudinal distributions (Spellerberg, 1972; Hertz et al., 1979; Hertz, 1981; Wilson and Echternacht, 1987; Lemos-Espinal and Ballinger, 1995; Huang et al., 2006), the results of this study show that thermal tolerance of the three *Eremias* lizards does not correspond with their latitudinal distributions. Similar results (i. e., lacking correlations between thermal tolerance and geographic distributions) have been also reported for several lizard species such as the starred agama *Stellio stellio* (Hertz and Nevo, 1981), the eastern fence lizard *Sceloporus undulatus* (Crowley, 1985), the striped skink *Mabuya striata* (Patterson, 1999) and *T. septentrionalis* (Yang et al., 2008).

Correlations between thermal preference and latitudinal or altitudinal distributions could not be easily detected in many lizards, often because thermal preference is highly associated with their use of habitats rather than geographic distributions. For example, lizards such as the brown forest skink *Sphenomorphus indicus* (25.7 °C, Ji et al., 1997) using shaded (and thus, cold) habitats select lower body temperatures than do those such as the Chinese skink *Eumeces chinensis* (31.2 °C, Ji et al., 1995) living in the same area but using exposed (and thus, warm) habitats. The three *Eremias* lizards studied all use exposed habitats in nature but differ from each other in thermal preference, with T_{sel} being lower in higher latitudinal species than in lower latitudinal species (Table 1). This finding provides clear evidence showing that thermal preference of the three species corresponds with their latitudinal distributions.

Collectively, our results show that temperature acclimation plays an important role in influencing thermal preference and tolerance in three congeners of *Eremias*,

although the degrees to which thermal preference and tolerance are altered by acclimation temperature differ among species. Tsel, CTMin, CTMax and VTR overall differ among the three *Eremias* lizards, but these lizards always differ from each other in CTMin but not in other three variables when acclimated under identical thermal conditions. Our results also show that thermal preference rather than tolerance of the three *Eremias* lizards corresponds with their latitudinal distributions.

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