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Differences in Thermal Preference and Tolerance among Three *Phrynocephalus* Lizards (Agamidae) with Different Body Sizes and Habitat Use

Zheng WANG[1, 2], Hongliang LU[3], Li MA[3] and Xiang JI[2*]

[1] *College of Forest Resources and Environment*, *Nanjing Forestry University*, *Nanjing* 210037, *Jiangsu*, *China*
[2] *Jiangsu Key Laboratory for Biodiversity and Biotechnology*, *College of Life Sciences*, *Nanjing Normal University*, *Nanjing* 210046, *Jiangsu*, *China*
[3] *Hangzhou Key Laboratory for Animal Adaptation and Evolution*, *School of Life Sciences*, *Hangzhou Normal University*, *Hangzhou* 310036, *Zhejiang*, *China*

Abstract We acclimated adults of two viviparous (*Phrynocephalus guinanensis* and *P. vlangalii*) and one oviparous (*P. versicolor*) species of toad-headed lizards (Agamidae) to 28 °C, 33 °C and 38 °C to examine whether thermal preference (preferred body temperature, Tp) and thermal tolerance (critical thermal minimum, CTMin; critical thermal maximum, CTMax) were affected by acclimation temperature, and correlate with body size and habitat use. Both Tp and CTMax were highest in *P. versicolor* and lowest in *P. vlangalii*, with *P. guinanensis* in between. The two viviparous species did not differ in CTMin and thermal tolerance range, and they both were more resistant to low temperatures and had a wider range of thermal tolerance than the oviparous species. Both CTMin and CTMax shifted upward as acclimation temperature increased in all the three species. Tp was higher in the lizards acclimated to 33 °C than in those to 28 °C or 38 °C. The range of thermal tolerance was wider in the lizards acclimated to 28 °C than in those to 33 °C or 38 °C. The data showed that: 1) thermal preference and tolerance were affected by acclimation temperature, and differed among the three species of *Phrynocephalus* lizards with different body sizes and habitat uses; 2) both Tp and CTMax were higher in the species exchanging heat more rapidly with the environment, and CTMin was higher in the species using warmer habitats during the active season; and 3) thermal preference and tolerance might correlat with body size and habitat use in *Phrynocephalus* lizards.

Keywords Agamidae, *Phrynocephalus* lizards, thermal preference, thermal tolerance, body size, habitat use

1. Introduction

Temperature is one of the most important abiotic factors influencing organisms (Hochachka and Somero, 2002; Angilletta, 2009). As terrestrial ectotherms small lizards are especially affected by this factor. Though having the ability to withstand a wide range of body temperatures, lizards attempt to maintain relatively high and constant temperatures while active often because these temperatures maximize biochemical and physiological activities (Huey, 1982). Lizards acquire and maintain appropriate body temperatures primarily via behavioral mechanisms that allow them to selectively use environmental thermal flux (Huey, 1982). A lizard's thermal preference can be estimated in the laboratory by measuring its preferred body temperature (Tp) in a thermal gradient, and its thermal tolerance can also be determined in the laboratory by measuring the lower (critical thermal minimum, CTMin) and higher (critical thermal maximum, CTMax) survival limits (Lowe and Vance, 1955; Hutchison, 1961; Lutterschmidt and Hutchison, 1997). Exposure of lizards to temperatures outside the thermal tolerance range (TTR, the range between CTMin and CTMax) for prolonged periods of time may lead to death (Yang *et al*., 2008;

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[*] Corresponding author: Prof. Xiang JI, from College of Life Sciences, Nanjing Normal University, Jiangsu, China, with his research focusing on physiological and evolutionary ecology of reptiles.
E-mail: xji@mail.hz.zj.cn

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Qu *et al*., 2011b).

Thermal preference and/or tolerance have been examined worldwide in some 280 lizard species. Of these species, 194 were measured in the laboratory for Tp, 111 for CTMin, 166 for CTMax, and 106 for TTR (Qu *et al.*, unpublished data). Previous studies show that Tp ranges from 16.6 °C in *Goniurosaurus kuroiwae* (Werner *et al*., 2005) to 37.9 °C in *Sauromalus ater* (Brattstrom, 1965), CTMin from 0.7 °C in *Eremias multiocellata* (Li *et al*., 2009b) to 15.4 °C in *Liolaemus abaucan* (Cruz *et al*., 2005), CTMax from 28.9 °C in *G. kuroiwae* (Werner *et al*., 2005) to 49.3 °C in *Eremias prezwalskii* (Li *et al*., 2009a), and TTR from 19.7 °C in *Eublepharis macularius* (Werner *et al*., 2005) to 48.3 °C in *E. prezwalskii* (Li *et al*., 2009a). Previously published data show that thermal preference and tolerance differ among lizard species that differ in distribution, habitat use and activity pattern, and are affected by a lizard's physiological conditions (Lutterschmidt and Hutchison, 1997; Lin *et al*., 2008; Qu *et al*., 2011b; Sagonas *et al*., 2013) and its experience of thermal acclimation (Kour and Hutchison, 1970; Patterson, 1991; Huang *et al*., 2006; Yang *et al*., 2008; Li *et al*., 2009b).

Here, we present data on thermal preference and tolerance of three toad-headed lizards of the genus *Phrynocephalus* (Agamidae): *P. guinanensis*, *P. vlangalii* and *P. versicolor*, acclimated to three constant temperatures (see below for details). The three lizards all have an exclusively cold-climate distribution, and occur in climatically severe areas with great daily fluctuations in air temperature during the active season lasting from May to October. Both *P. guinanensis* and *P. vlangalii* are viviparous and endemic to China, with the former found only in sand dunes in Qinghai at elevations ranging from 2700 to 3500 m, and the latter in arid and semiarid areas in Qinghai, Gansu, Xinjiang and Sichuan at elevations ranging from 2000 to 4500 m (Zhao, 1999; Ji *et al*., 2009; Wang, 2011). *P. versicolor* is an oviparous lizard that ranges from Inner Mongolia, Ningxia and Xinjiang of China to Mongolia, Kazakstan and Kyrgyzstan, and is found in arid and semiarid areas at elevations ranging from 200−1800 m (Zhao, 1999). The mean adult size (snout-vent length, SVL) is largest in *P. guinanensis* (73 mm in both sexes) and smallest in *P. versicolor* (52 mm in both sexes), with *P. vlangalii* (70 mm in females, and 67 mm in males) being intermediate in size (Qu *et al*., 2011a; Wang, 2011). We hypothesized that thermal preference and tolerance would differ among the three lizards. More specifically, we predicted that: 1) lizards would shift their thermal preference and tolerance according to changes in the thermal environment; 2) Tp and CTMax, two variables more tightly related to the highest temperature lizards encounter in the field (Qu *et al*., 2011b), would be higher in the species more likely to get overheated when exposed to high temperatures; and 3) CTMin, a variable more tightly related to the lowest temperature lizards encounter in the field (Qu *et al*., 2011b), would be higher in the species using warmer habitats during the active season. Our study could provide insight into the thermal plasticity and adaptability of these three lizard species.

2. Materials and Methods

2.1 Animal collection and maintenance All lizards used in this study were collected in early May 2011. Adult *P. guinanensis* were collected from Senduo (35°34' N, 101°05' E, 3350 m a.s.l.) in Qinghai, adult *P. vlangalii* from Daotanghe (36°34' N, 101°49' E, 3200 m a.s.l.) in Qinghai, and adult *P. versicolor* from Wulatehouqi (41°27' N, 106°59' E, 1230 m a.s.l.) in Inner Mongolia. The mean air temperature of the warmest quarter (June−August) is lowest in Senduo (10.4 °C) and highest in Wulatehouqi (19.1 °C), with Daotanghe (−12.7 °C) in between; the mean air temperature of the coldest quarter (December–February) is lowest in Wulatehouqi (11.5 °C) and highest in Daotanghe (−6.0 °C), with Senduo (−10.1 °C) in between (Meteorological Departments of Qinghai and Inner Mongolia).

The captured lizards were transported to our laboratory in Hangzhou, where 7−10 individuals of the same species were housed in one 900 mm × 650 mm × 600 mm (length × width × height) cage with a substrate of moist sand (100 mm depth) and pieces of clay tiles. Thermoregulatory opportunities were provided between 07:00–19:00 h using a 100 w full-spectrum lamp (EuroZoo, Germany); overnight temperatures varied between 20–28 °C. Mealworms (*Tenebrio molitor*) and house crickets (*Acheta domestica*) dusted with multivitamins and minerals were provided in excess, and drinking water was refreshed daily.

2.2 Experimental design A total of 132 lizards (*P. guinanensis*: 22♀/15♂, 69−78 mm SVL; *P. vlangalii*: 24♀/20♂, 57−75 mm SVL; *P. versicolor*: 31♀/20♂, 47−59 mm SVL) were measured for Tp, CTMin, CTMax and TTR in October, when they had been maintained under the identical laboratory conditions mentioned above for about five months. Lizards were randomly divided into three groups, of which each was assigned to one of the three temperature treatments: 28 °C (*P. guinanensis*: 7♀/5♂; *P. vlangalii*: 7♀/6♂; *P.*

versicolor: 7♀/6♂), 33 °C (*P. guinanensis*: 8♀/5♂; *P. vlangalii*: 8♀/6♂; *P. versicolor*: 11♀/7♂), and 38 °C (*P. guinanensis*: 7♀/5♂; *P. vlangalii*: 9♀/8♂; *P. versicolor*: 13♀/7♂). These three temperatures were chosen because lizards from Qinghai and Inner Mongolia had been known to feed normally at temperatures within the range of 28–38 °C (Li *et al*., 2009a, b; Shu *et al*., 2010; Qu *et al*., 2011b). Lizards were acclimated at their designated temperatures for three weeks, and then were measured. During the course of thermal acclimation, lizards had free access to food. Our experimental design allows us to examine the extent to which thermal preference and thermal tolerance vary not as a proximate response to changes in the thermal environment.

2.3 Measurements of Tp, CTMin and CTMax We measured Tp in 1000 mm × 800 mm × 500 mm cages with moist sand (100 mm depth) and pieces of clay tiles. A 100 w light bulb suspended above one end of the cage created a thermal gradient ranging between 20–60 °C on which lizards could regulate body temperature within their voluntary range. Lizards were individually introduced from the cold side (opposite to the heating bulb) into the cage at 07:00 h. To minimize the possible effect of diel variation in Tp, we began measurements on each trial day at 15:00 h and ended within 2 h. Cloacal temperature was taken for each lizard with a UT-325 thermometer (Shanghai Medical Instruments, China). We measured each lizard six times, once on each of six consecutive days. The six measures did not differ significantly (repeated measures ANOVA; all $P > 0.189$), so the mean was considered as a lizard's Tp.

Following Tp measurements, we used FPQ-1 incubators (Ningbo Life Instruments, China) to determine CTMin and CTMax. Trials were conducted during 10:00–15:00 h. We followed the procedures by Qu *et al*. (2011b) to cool or heat lizards from their acclimation temperatures at a rate of 0.25 °C min^{-1}, and more slowly (0.1 °C min^{-1}) when temperatures were lower than 5 °C or higher than 40 °C. Body temperatures associated with a transient loss of the righting response at the lower and the upper limits of thermal tolerance were considered as the endpoints for CTMin and CTMax, respectively. All lizards recovered after testing, with none dying in the following month.

2.4 Statistical analyses We used Statistica 6.0 (StatSoft, Tulsa, USA) to analyze data. Data were tested for normality using Kolmogorov-Smirnov tests, and for homogeneity of variances using Bartlett's test. Sex was ignored as a factor in all analyses, because preliminary analyses revealed that none of the examined variables differed between the sexes within each species × temperature combination (all $P > 0.391$). We used two-way ANOVA to test the effects of species, acclimation temperature and their interaction on Tp, CTMin, CTMax and TTR. Multiple comparisons were performed using Tukey's test. Throughout this paper, values were presented as mean + SE, and the significance level was set at $\alpha = 0.05$.

3. Results

Figure 1 shows mean values (+SE) for Tp, CTMin, CTMax and TTR of the lizards acclimated to the three temperatures. Tp, CTMin, CTMax and TTR differed among the three species and among the three temperature treatments; the species × temperature interaction was a significant source of variation in two (CTMin and TTR) of the four variables (Table 1). Both Tp and CTMax were highest in *P. versicolor* and lowest in *P. vlangalii*, with *P. guinanensis* in between (Table 1). The two viviparous species did not differ from each other in CTMin and TTR, and both species were more resistant to low temperatures and had a wider TTR than *P. versicolor* (Table 1). CTMin and CTMax both shifted upward as acclimation temperature increased (Table 1) and, at the change-over of acclimation temperature from 28 °C to 38 °C, the overall mean CTMin shifted from 2.7 °C to 5.4 °C and the overall mean CTMax from 45.9 °C to 46.8 °C. The lizards acclimated to 28 °C did not differ from those to 38 °C in Tp, and the lizards acclimated to 33 °C did not differ from those to 38 °C in TTR (Table 1). Overall, Tp was elevated by a mean of 1.3 °C in the lizards acclimated to 33 °C as compared with those to 28 °C or 38 °C, and TTR was widened by a mean of 1.7 °C in the lizards acclimated to 28 °C as compared with those to 33 °C or 38 °C (Table 1).

Table 1 Results of two-way ANOVAs with species and acclimation temperature as the factors. Means with different superscripts differ significantly (Tukey's *post hoc* test; a > b > c). Gui: *P. guinanensis*; Vla: *P. vlangalii*; Ver: *P. versicolor*.

Effects	Preferred body temperature	Critical thermal minimum	Critical thermal maximum	Thermal tolerance range
Species (S)	$F_{2, 123} = 167.30, P < 0.0001$ Gui^{b}, Vla^{c}, Ver^{a}	$F_{2, 123} = 312.54, P < 0.0001$ Gui^{b}, Vla^{b}, Ver^{a}	$F_{2, 123} = 28.23, P < 0.0001$ Gui^{b}, Vla^{c}, Ver^{a}	$F_{2, 123} = 212.27, P < 0.0001$ Gui^{a}, Vla^{a}, Ver^{b}
Acclimation temperature (AT)	$F_{2, 123} = 76.74, P < 0.0001$ 28^{b}, 33^{a}, 38^{b}	$F_{2, 123} = 133.51, P < 0.0001$ 28^{c}, 33^{b}, 38^{a}	$F_{2, 123} = 25.75, P < 0.0001$ 28^{c}, 33^{b}, 38^{a}	$F_{2, 123} = 42.19, P < 0.0001$ 28^{a}, 33^{b}, 38^{b}
S × AT interaction	$F_{4, 123} = 1.68, P = 0.158$	$F_{4, 123} = 2.13, P = 0.081$	$F_{4, 123} = 2.56, P = 0.042$	$F_{4, 123} = 11.35, P < 0.0001$

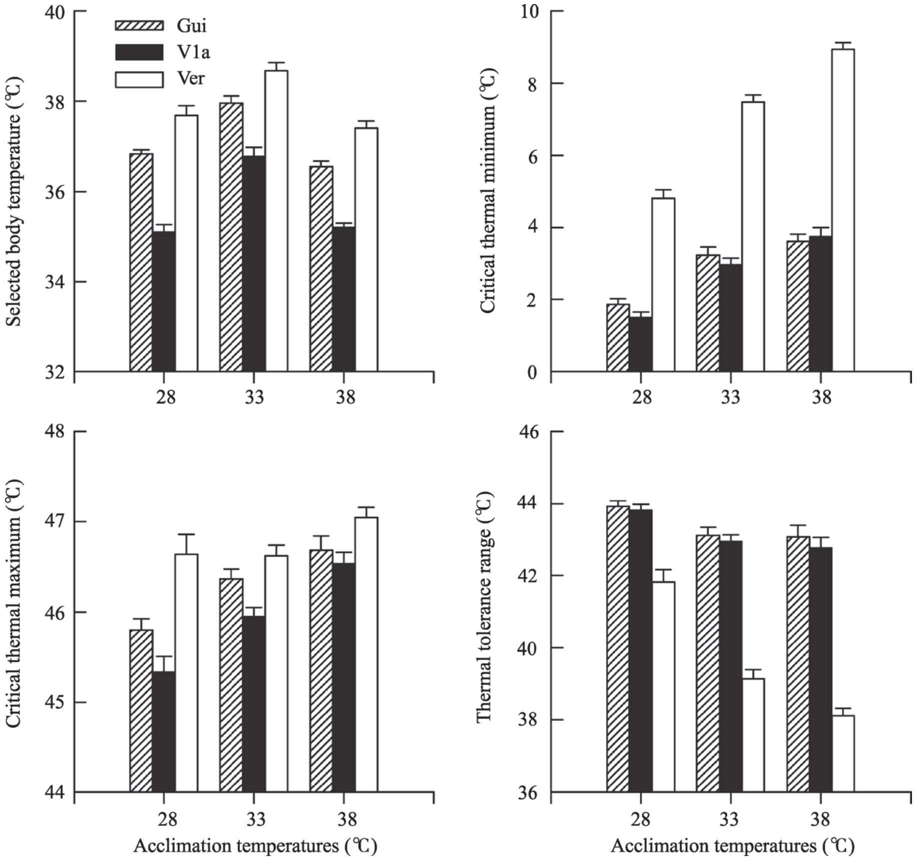

Figure 1 Mean values (+SE) for preferred body temperature, critical thermal minimum, critical thermal maximum and thermal tolerance range of lizards acclimated at three temperatures. Gui: *P. guinanensis*; Vla: *P. vlangalii*; Ver: *P. versicolor*.

4. Discussion

Data of this study show that thermal acclimation affects Tp, CTMin, CTMax and TTR in the three *Phrynocephalus* lizards (Table 1), thus validating the prediction that lizards would shift thermal preference and tolerance according to changes in thermal environment. This finding is consistent with the studies of other lizard taxa, including lacertids (Yang *et al.*, 2008; Li *et al.*, 2009b), phrynosomatids (Lowe and Vance, 1955; Kour and Hutchison, 1970), dactyloids (Kour and Hutchison, 1970; Corn, 1971), and scincids (Brattstrom, 1971; Patterson, 1991; Huang *et al.*, 2006) that have found acclimation temperature affects thermal preference and/or tolerance. In this study the species × temperature interaction significantly affected CTMax and TTR but not Tp and CTMin (Table 1), whereas in an earlier study of three *Eremias* lizards (Lacertidae) using the same experimental design, such an interaction affects Tp, CTMin and CTMax but not TTR (Li *et al.*, 2009b). This inconsistency suggests that the response of a particular variable relating to thermal preference or tolerance to acclimation temperature may differ among lizard species.

Preferred body temperatures on average are highest in cold-climate lizards and lowest in warm-climate lizards, with temperate lizards in between (Qu *et al.*, 2011b; but see also Meiri *et al.*, 2013). What can be inferred from this conclusion is that a lizard's thermal preference correlates with its distribution. All three species studied are cold-climate lizards, and the lizards in this study had an ample opportunity to maintain their body temperatures at the same level while thermoregulating in the thermal gradient. So, why did the three species differ from each other in Tp (Table 1)? The answer presumably lies in that a lizard species' thermal preference might correlate with its body size and habitat use. Both *P. vlangalii* and *P. versicolor* use habitats covered by very sparse vegetation, whereas *P. guinanensis* uses habitats almost not covered by any vegetation (Zhang *et al.*, 2005; Qu *et al.*, 2011a, b; Wang, 2011). While active in the field, all three lizards may encounter high surface temperatures (up to 65 °C on the hottest day) potentially lethal to them. Lizards using thermally challenging habitats have to retreat into nests or shaded sites to avoid getting overheated when the operative temperature, a measure of an animal's operative heat load, is higher than Tp (Sinervo *et al.*, 2010). As a general rule, a smaller animal has a greater relative surface area, thus exchanging heat with its surrounding environment more rapidly than does a larger one (Schmidt-Nielsen, 1984). In this study, *P. versicolor* is the smallest species that can be therefore expected to get overheated more easily than the other two larger species when exposed to high temperatures. Thus, the result that Tp was higher in *P. versicolor* could reflect a mechanism evolved in this smaller lizard to enhance its adaptability to high environmental temperatures. By shifting thermal preference upward, lizards can prolong the time period for foraging and other activities before they have to retreat into nests or shaded sites. This benefit could also explain why Tp was higher in *P. guinanensis* than in *P. vlangalii*, because the former species uses desert habitats with higher thermal conductivity substrates on which lizards can more quickly get overheated when exposed to high temperatures.

By summarizing the data reported previously for some 45 lizard species belonging to seven families, Qu *et al*. (2011b) conclude that: 1) CTMin is not correlated with Tp; and 2) CTMax is positively correlated with Tp. Similar conclusions have been drawn in a study of 21 Australian scincid lizards (Bennett and John-Alder, 1986). Our data generally support these conclusions because: 1) Tp was higher in *P. guinanensis* than in *P. vlangalii*, but the two species did not differ from each other in CTMin; and 2) Tp was highest in *P. versicolor* with highest CTMax and lowest in *P. vlangalii* with lowest CTMax (Table 1). Excluding nocturnal lizards and diurnal lizards using shaded habitats, Qu *et al*. (2011b) found that lizards from thermally different regions or with different distributions differ in CTMin, CTMax and TTR but not in Tp. In this study, two (CTMax and Tp) of the four variables differed among the three *Phrynocephalus* lizards, whereas the other two (TMin and TTR) differed between oviparous and viviparous species (Table 1). These results are consistent with a study of three *Eremias* species that shows that lizards from thermally different regions differ from each other in Tp (Li *et al*., 2009b). Qu *et al*. (2011b) draw their conclusions without taking phylogenetic context, body size and habitat use into account. Our study using three congeneric species provides an inference that a lizard's thermal preference and tolerance might correlate with its body size and habitat use.

Data on thermal tolerance (CTMin and/or CTMax) at known acclimation temperatures have been available for more than 20 lizard species (lacertids: Yang *et al*., 2008; Li *et al*., 2009b; phrynosomatids: Lowe and Vance, 1955; Wilhoft and Anderson, 1960; Alexander, 1966; Kour and Hutchison, 1970; polychrotids: Licht, 1968; Kour and Hutchison, 1970; Corn, 1971; scincids: Brattstrom, 1971; Patterson, 1991; Huang *et al*., 2006; xantusiids; Kour and Hutchison, 1970). Our study is the first to examine the effects of acclimation temperature on thermal tolerance in agamid lizards, and shows that CTMin and CTMax both shift upward as acclimation temperature increases in the three *Phrynocephalus* lizards (Figure 1, Table 1). Similar effects of acclimation temperature on thermal tolerance have been observed in all lizards so far studied, with one exception of a lacertid lizard (*Eremias argus*) where individuals acclimated to a medium acclimation temperature (33 °C) were most tolerant of high temperatures (Li *et al*., 2009b). This exception is of interest because it suggests that CTMax is not always maximized in lizards acclimated to the highest temperature.

Data on thermal preference at known acclimation temperatures have been reported only for seven lizard species (lacertids: Yang *et al*., 2008; Li *et al*., 2009b; phrynosomatids: Wilhoft and Anderson, 1960; polychrotids: Licht, 1968; Scincidae: Patterson, 1991). Of these species, two (*Mabuya striata* and *Takydromus septentrionalis*) shift Tp upward as acclimation temperature increases (Patterson, 1991; Yang *et al*., 2008), three (*E. argus*, *E. brenchleyi* and *E. multiocellata*) prefer higher temperatures at a moderate acclimation temperature (Li *et al*., 2009b), one (*Anolis carolinensis*) does not shift Tp with a shift in acclimation temperature (Licht, 1968), and one (*Sceloporus occidentalis*) shifts Tp downward as acclimation temperature increases (Wilhoft and Anderson, 1960). Consistent with the study of three *Eremias* lizards (Li *et al*., 2009b), our data showed that lizards acclimated to a medium temperature (33 °C) preferred higher body temperatures than those to a lower (28 °C) or higher (38 °C) temperature (Figure 1, Table 1). The result that Tp is not maximized at the highest acclimation temperature might result from a trade-off between costs and benefits associated with thermoregulation. Thermoregulation results in potential fitness benefits, but entails costs associated with the increased energy demands and predation risks (Huey and Slatkin, 1976; Shine and Madsen, 1996; Sartorius *et al*., 2002; Lin *et al*., 2008; Li *et al*., 2009b). In a given set of environmental conditions, lizards should shift their thermal preference towards the level optimal for biological and physiological activities and, meanwhile, try every possibility to reduce costs associated with thermoregulation (Hertz *et al*., 1993; Christian and Weavers, 1996; Lin *et al*., 2008;

Angilletta, 2009; Li *et al*., 2009b). It has been reported for many lizards including two *Phrynocephalus* lizards (*P. vlangalii* and *P. versicolor*) studied herein that 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 (Ji *et al*., 1996; Li *et al*., 2009b; Lin *et al*., 2008; Shu *et al*., 2010; Qu *et al*., 2011b). Thus, not selecting the highest body temperature when acclimated to the highest temperature might reflect a mechanism evolved in lizards to reduce energetic costs associated with the increased metabolic rates at high body temperatures.

In summary, our results show that acclimation temperature affects Tp, CTMin, CTMax and TTR in the three *Phrynocephalus* lizards, although the response of a particular variable to acclimation temperature may differ among species. CTMin and CTMax both shift upward as acclimation temperature increases, whereas Tp is higher in the lizards acclimated to an intermediate temperature. Tp, CTMin, CTMax and TTR all differ among the three *Phrynocephalus* lizards. Tp and CTMax are higher in the species that are more likely to get overheated when exposed to high temperatures, and CTMin is higher in the species using warmer habitats during the active season. Our study is the first to examine the effects of acclimation temperature on thermal preference and tolerance in agamid lizards, and provide an inference that a lizard's thermal preference and tolerance might correlate with its body size and habitat use.

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