Asian Herpetological Research 2019, 10(3): 190–196
DOI: 10.16373/j.cnki.ahr.190007

ORIGINAL ARTICLE

Thermal-physiological Strategies Underlying the Sympatric Occurrence of Three Desert Lizard Species

Xueqing WANG[1,2], Shuran LI[3], Li LI[1], Fushun ZHANG[4], Xingzhi HAN[5], Junhuai BI[1*#] and Baojun SUN[2*#]

[1] *College of Life Science*, *Inner Mongolia Normal University*, *Hohhot* 010022, *Inner Mongolia*, *China*
[2] *Key Laboratory of Animal Ecology and Conservation Biology*, *Institute of Zoology*, *Chinese Academy of Sciences*, *Beijing* 100101, *China*
[3] *College of Life and Environmental Science*, *Wenzhou University*, *Wenzhou* 325035, *Zhejiang*, *China*
[4] *Grassland research institute*, *Chinese Academy of Agricultural Sciences*, *Hohhot* 010010, *Inner Mongolia*, *China*
[5] *College of wildlife Resources*, *Northeast Forestry University*, *Harbin* 150040, *Heilongjiang*, *China*

Abstract Sympatric reptiles are the ideal system for investigating temperature-driven coexistence. Understanding thermally physiological responses of sympatric lizards is necessary to reveal the physiological mechanisms that underpin the sympatric occurrence of reptiles. In this study, we used three lizard species, *Eremias argus*, *E. multiocellata*, and *Phrynocephalus przewalskii*, which are sympatric in the Inner Mongolia desert steppe, as a study system. By comparing their resting metabolic rates (RMR) and locomotion at different body temperatures, we aimed to better understand their physiological responses to thermal environments, which may explain the sympatric occurrence of these lizards. Our results showed that *E. argus* had significantly higher RMR and sprint speed than *E. multiocellata*, and higher RMR than *P. przewalskii*. In addition, the optimal temperature that maximized metabolic rates and locomotion for *E. argus* and *E. multiocellata* was 36°C, whereas for *P. przewalskii* it was 39°C. Our study revealed the physiological responses to temperatures that justify the sympatric occurrence of these lizards with different thermal and microhabitat preferences and active body temperatures. *Eremias argus* and *E. multiocellata*, which have lower body temperatures than *P. przewalskii*, depend on higher RMR and locomotion to compensate for their lower body temperatures in field conditions. Our study also highlights the importance of using an integrative approach, combining behavior and physiology, to explore the basis of sympatric occurrence in ectothermic species.

Keywords Sympatric lizards, resting metabolic rate, locomotion, *Eremias argus*, *E. multiocellata*, *Phrynocephalus przewalskii*

1. Introduction

Understanding the mechanisms that allow species coexistence is one of the core issues in community ecology. Niche differentiation is considered to be the basis of coexistence among sympatric species. Niche differentiation is a process by which competing species utilize environmental resources differently, and it can include aspects such as activity period, use of space, and food preferences (Hardin, 1960; Shurin *et al.*, 2004). Pacala and Roughgarden (1985), for example, reported the existence of several anole lizards that shared food resources (i.e., insects) on the Caribbean islands but occupied different microhabitats such as leaf litter floor and branches to avoid any possible competition for microhabitats or food resources. *Lophophorus sclateri* and *Ithaginis cruentus*, two pheasant species, were observed to share high-altitude habitats in Gaoligong Mountain but to feed on different plants or different parts of the same plants (Luo *et al.*, 2016).

In ectotherms, performances of specific activities such as locomotion, immunity, growth, and even reproduction are greatly affected by body temperatures (Angilletta, 2009; Angilletta *et al.*, 2002). Within thermal tolerance

---

[#] Both authors contributed equally to this work.

[*] Corresponding authors: Dr. Baojun SUN, from Institute of Zoology, Chinese Academy of Sciences, with his research focusing on ecological evolution and conservation physiology; Prof. Junhuai BI, from College of Life Science, Inner Mongolia Normal University, with his research focusing on animal ecology and conservation.

E-mail: sunbaojun@ioz.ac.cn (SUN B.); bijunhuai@imnu.edu.cn (BI J.)

Received: 24 January 2019 Accepted: 25 March 2019

range, the physiological performance of ectotherms is known to enhance as body temperature increases until the optimal temperature is reached; after that, performance rapidly decreases if body temperature continues to increase (Huey and Kingsolver, 1989). Because of its effect on body temperature and thus on function and performance, environmental temperature is one of the most important ecological factors for ectotherm animals (Angilletta, 2009) and, therefore, is also considered an important resource (e.g., Li *et al.*, 2017). Among sympatric ectotherms, different temperature preferences may result in different body temperatures, which in turn may result in segregation of microhabitat utilization and allow sympatric occurrence (Adolph, 1990; Hertz, 1992; Martinvallejo *et al.*, 1995; Wilkinson and Grover, 1996). Understanding how variation in thermal environment affects sympatric species has become a hot topic in animal ecology (e.g., Li *et al.*, 2017; Osojnik *et al.*, 2013; Rusch *et al.*, 2018; Žagar *et al.*, 2015).

As ectotherms, sympatric lizards constitute ideal systems for investigating temperature-driven niche differentiation and coexistence (Pianka, 1986). Lizards can regulate their body temperatures in a narrow range mainly through behaviors to facilitate physiological functions (Adolph, 1990; Angilletta, 2009). On the Mongolian plateau, three ground-dwelling sympatric lizard species coexist in arid, semi-arid, or grass lands area: *Eremias argus*, *E. multiocellata*, and *Phrynocephalus przewalskii* (Zhao *et al.*, 1999). These sympatric species have been demonstrated to occupy different microhabitats (e.g., vegetation coverage) and to have significantly different thermal preferences and active body temperatures. *Phrynocephalus przewalskii* mainly selects open and warm microhabitats and has a higher preferred body temperature range (T_{sel}: 33.9–39.2℃) than *E. argus* (T_{sel}: 32.8–37.5°C) and *E. multiocellata* (T_{sel}: 33.4–36.8°C), which occupy shaded and cool habitats (Table S1) (Li *et al*., 2017). Accordingly, the active body temperatures are significantly higher in *P. przewalskii* than in *E. argus* and *E. multiocellata* (Table S1) (Li *et al*., 2017). These species' demands for thermal environmental resources were speculated to be met because of microhabitat differentiation, which may be an important basis for their sympatric occurrence (Li *et al.*, 2017). Nevertheless, as ectotherms, their body temperatures should be effective on fitness-related physiological functions before they affect their sympatric occurrences (Angilletta, 2009; Angilletta *et al.*, 2002; Hochachka and Somero, 2002). Our current knowledge on these species' differences regarding thermal preference or active body temperatures is insufficient to explain the effect of their thermal niche-partitioning on promoting their sympatric occurrence. Therefore, in order to reveal the physiological basis that underpins their temperature-driven sympatric occurrence, it is critical to investigate the effects of body temperature on important physiological traits of *E. argus*, *E. multiocellata*, and *P. przewalskii*.

Metabolism is one of the most important physiological processes because it determines an organism's demands from the environment and energy allocation among functions (Brown *et al.*, 2004; McNab, 2002). Lizards' metabolic rates have been demonstrated to be significantly sensitive to body temperatures; these, in turn, require the animals' fast response to any environment thermal variation (e.g., Ma *et al.*, 2018a; Ma *et al.*, 2018b; Sun *et al.*, 2018). For example, the metabolic rates were enhanced as body temperature increasing, and could respond to thermal variation by acclimation in lizard (e.g., Sun *et al.,* 2018). Furthermore, the segregation of metabolic rates at the same temperatures may help niche differentiation (Žagar *et al.*, 2018; Žagar *et al.*, 2015). In addition, locomotion is thermal dependent and critical to escape danger, forage, and choose mating partners, and thus affects survival and reproduction in ectotherms (Robson and Miles, 2010; Shine, 2003; Shu *et al.*, 2010; Wilson, 2001).

Here, with sympatric *E. argus*, *E. multiocellata* and *P. przewalskii* from Shierliancheng of Inner Mongolia area as a study system, we measured the metabolic rates and locomotion of each species at a range of body temperatures from 15–42°C in order to determine inter-specific differences in physiology and fitness-related performances. We predicted that: 1) *E. argus* and *E. multiocellata*, which occupied shaded microhabitats and have lower active body temperatures, would have higher metabolic rates and sprint speeds but lower optimal temperatures for sprint speed than *P. przewalskii* at a same temperature within a moderate range before the optimal temperature is reached; 2) combined with temperature-related curves of metabolic rates and sprint speed, the three sympatric species would perform better when at their own active body temperatures under preferred microhabitat conditions.

2. Materials and Methods

2.1. Lizard collection and husbandry The ground-dwelling lizards *E. argus, E. multiocellata*, and *P. przewalskii* were collected from late June to early July at the Shierliancheng field station, Institute of Grassland

Research of the Chinese Academy of Agricultural Sciences (111°09′ E, 40°21′ N, elevation 1010–1021 m), where the ground-dwelling lizards (i.e., *E. argus, E. multiocellata*, and *P. przewalskii*) sympatry (Li *et al.*, 2017). During collection, gravid female lizards were determined by palpate and released. Male and nongravid female adults of each species were transferred to our laboratory in Beijing, where they were weighed (to the nearest 0.001 g) and measured (to the nearest 1 mm). Every five or six lizards of each species were kept in a terrarium ($550 \times 400 \times 350$ mm^3, length × width × height). The terraria were placed in a temperature-controlled room at 20°C with photoperiod cycles of 10 h dark: 14 h light (6:00–20:00). A heating bulb (50 w) was placed above one end of each terrarium to provide a temperature gradient inside the terrarium from 20–50°C within each photoperiod. Food (crickets dusted with vitamins) and water were provided *ad libitum*.

2.2. Resting metabolic rate After seven days of husbandry, the resting metabolic rates (RMR) of 14 *E. argus* (7 ♂ and 7 ♀), 13 *E. multiocellata* (5 ♂ and 8 ♀), and 14 *P. przewalskii* (7 ♂ and 7 ♀) (total $n = 41$) were measured at ten test temperatures (15, 18, 21, 24, 27, 30, 33, 36, 39, and 42°C), with one temperature every other day in a random sequence. Lizards were fasted for at least 12 hours before each measurement. Initially, each lizard was placed in an incubator (Sanyo, Japan) at the selected test temperature for 90 min; then, the lizard was placed in a respirometry chamber within the incubator and the measurement was performed. RMR was measured using a closed-flow respirometry system with a volume of 281.4 ml (Stable Systems International Inc. Las Vegas, NV, USA) and estimated via CO_2 production rate following a previously established method (Sun *et al.*, 2018). In brief, the system contained the following modules: Universal interface II (UI2), Subsampler TR-S (SS3), Mass flow control unit (MFC-2), Oxygen analyzer (FC-10a), and Carbon dioxide analyzer (Ca-10a). At the beginning of each measurement, the system was opened for two to three minutes so that air came through an entrance tube with a flow rate of 300 ml/min to make the baseline stable. Afterward, the measurement system was transferred to a closed-circuit respirometry, and then carbon dioxide production rates (V_{CO2}) in closed-circuit were continuously recorded for 10 min. The entire environment was dark (no light exposure) during measurements, and all measurements were conducted from 10:00–18:00 to minimize the effects of circadian rhythms. The metabolic rates were calculated as the CO_2 production per gram$^{0.75}$ of body mass per hour (ml/g$^{0.75}$/hr) following the 'metabolic theory of ecology' (Brown *et al.*, 2004), with the equation of metabolic rates = V_{CO2} × volume/body mass, where V_{CO2} is the CO_2 production rate in percentage (%/hr) in the closed circuit with the volume of 281.4 ml (Sun *et al.*, 2018). After each measurement, lizards were transferred back to the terraria until the next measurement initiated. After around 20 days of RMR tests, the locomotion tests were performed.

2.3. Locomotion The locomotion of 37 lizards was determined using a 1 000 mm custom-made race track at ten test temperatures randomly (15, 18, 21, 24, 27, 30, 33, 36, 39 and 42°C) after the RMR measurements. Locomotion measurements were not performed in four *E. argus* as they were out of conditions (i.e., inactive or unwilling to move under stimulation) one day after the RMR experiments. Before the locomotion measurement, lizards were placed in an incubator at each test temperature for 90 min. The sprint speed was then determined in a 1 000 mm race track with photoelectric timers every 200 mm. For measurements, the lizard was placed in one end of the track and then stimulated on the tail with a paintbrush to run along the race track. The time spent by the lizard to run over every 200 mm interval was recorded using the photoelectric timer. Tests were conducted from 10:00–14:00. Each individual was tested twice with an interval of one hour between tests; the fastest speed of the two tests (i.e., 10 speed records) was recorded as the sprint speed for each lizard. Tests were conducted every other day.

2.4. Statistical analysis Before statistical analysis, Kolmogorov-Smirnov test and *Levene's* test were conducted to detect data normality and variance homogeneity. Repeated-measures ANOVAs were conducted to determine species differences in RMR and locomotion, with species as a main factor and test temperatures as a repeated factor. When interaction between species and test temperatures was detected, a further comparison was conducted to analyze the differences among species at relevant test temperature ranges.

3. Results

3.1 Resting metabolic rates The RMRs were significantly different among the three species. *Eremias argus* had a higher RMR than *E. multiocellata* and *P. przewalskii* (*E. argus*^{a} > *E. multiocellata*^{b} > *P. przewalskii*^{b}; $F_{2,38} = 3.65$, $P = 0.036$) (Figure 1). RMR increased with test temperature until the optimal temperature was reached; then, RMR decreased as temperature continued to increase (repeated factor 'test temperature': $F_{9,342} = 97.956$, $P < 0.0001$). The optimal temperature of RMR for *E. argus* and *E. multiocellata* was 36°C, whereas for *P. przewalskii* it was 39°C. The effect of the test temperatures on RMR was species-dependent. At low temperatures (from 15–36°C), *E. argus* had a significantly higher RMR than *P. przewalskii*, with *E. multiocellata* in between (*E. argus*^{a} > *E. multiocellata*^{ab} > *P. przewalskii*^{b}; $F_{2,38} = 8.251$, $P = 0.001$). At high temperatures (39–42°C), the RMR of *P. przewalskii* was significantly higher than those of *E. argus* and *E. multiocellata* (*P. przewalskii*^{a} >*E. argus*^{b} > *E. multiocellata*^{b}; $F_{2,38} = 18.023$, $P < 0.0001$) (Figure 1).

3.2. Locomotion Sprint speed of *E. argus* was significantly higher than that of *E. multiocellata*, whereas sprint speed of *P. przewalskii* was not significantly different from those of either species (*E. argus*^{a} > *P. przewalskii*^{ab} > *E. multiocellata*^{b}; $F_{2,34} = 5.376$, $P = 0.009$) (Figure 2). Test temperature had a significant effect on sprint speed ($F_{9,306} = 61.687$, $P < 0.0001$). Sprint speed increased with temperature until the optimal temperature, after which it decreased as temperature continued to increase. The optimal temperature of sprint speed for *E. argus* and *E. multiocellata* was 36°C, whereas for *P. przewalskii* it was 39°C. At low temperatures (15–36°C), the sprint speed of *E. argus* was significantly higher than that of *E. multiocellata*; the sprint speed of *P. przewalskii* was not significantly different from those of either species (*E. argus*^{a} > *P. przewalskii*^{ab} > *E. multiocellata*^{b}; $F_{2,34} = 4.439$, $P = 0.019$). At high temperatures (39–42°C), the sprint speeds of *P. przewalskii* and *E. argus* were similar and both higher than that of *E. multiocellata* (*P. przewalskii*^{a} > *E. argus*^{a} > *E. multiocellata*^{b}; $F_{2,34} = 6.792$, $P = 0.003$) (Figure 2).

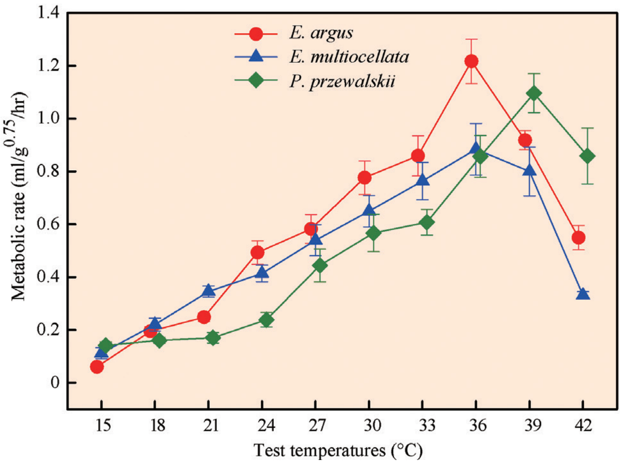

Figure 1 Resting metabolic rate (RMR) of *Eremias argus*, *E. multiocellata*, and *Phrynocephalus przewalskii* at 15, 18, 21, 24, 27, 30, 33, 36, 39, and 42°C. RMR was expressed as CO_2 production per $g^{0.75}$ body mass per hour ($ml/g^{0.75}/hr$). Red circles, blue triangles, and green rectangles indicate the RMR of *E. argus*, *E. multiocellata*, and *P. przewalskii*, respectively. The optimal temperatures for *E. argus*, *E. multiocellata*, and *P. przewalskii* were 36°C, 36°C, and 39°C, respectively. Data are shown as mean ± SE. The RMRs (expressed as ml/g/hr) are also provided in Table S2, for the convenience of interspecific comparison in 'Meta-Analysis'.

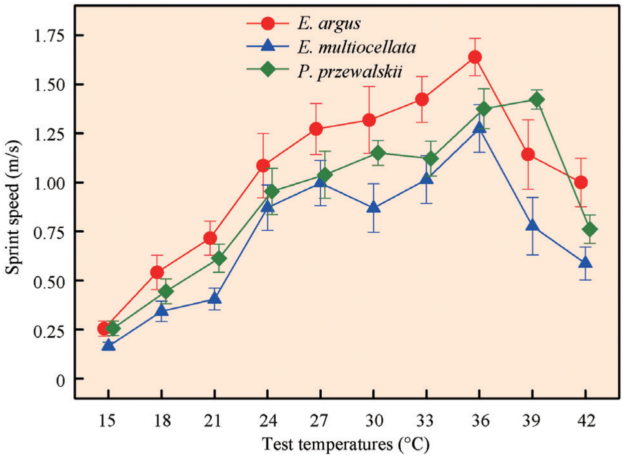

Figure 2 Locomotion of *Eremias argus*, *E. multiocellata*, and *Phrynocephalus przewalskii* at 15, 18, 21, 24, 27, 30, 33, 36, 39, and 42℃ . Locomotion was expressed as sprint speed (m/s). Red circles, blue triangles, and green rectangles indicate the sprint speed of *E. argus*, *E. multiocellata*, and *P. przewalskii*, respectively. The optimal temperatures for *E. argus*, *E. multiocellata*, and *P. przewalskii* were 36℃ , 36℃ , and 39℃ , respectively. Data are shown as mean ± SE.

4. Discussion

On the basis of previously known thermal biology traits such as active body temperatures, and thermal preference of the sympatric lizards *E. argus*, *E. multiocellata*, and *P. przewalskii* (Tables S1) (Li *et al.*, 2017), in the present study we determined the interspecific differences in RMR and locomotion at different body temperatures from 15 to 42°C. We found that *E. argus* have significantly higher RMR and locomotor performance, and *E. multiocellata* has significant higher RMR, when compared to *P. przewalskii*, especially at low body temperatures from 15 to 36°C, but lower optimal temperatures for RMR and locomotion, which indicates the existence of a physiological adaptation to the decrease in body temperature that also influences their performances. Therefore, we found that physiology and performance are both fine-tuned to the thermal preferences of the studied lizard species.

The interspecific differences in metabolic rates among *E. argus*, *E. multiocellata*, and *P. przewalskii* are consistent with the differences that were observed in hatchlings incubated under fluctuant temperatures (Ma *et al.*, 2018a, 2018b). The metabolic rates of hatchlings of *E. argus* and *E. multiocellata* were higher than in those of *P. przewalskii* and enhanced with the increase in the test temperatures; this may indicate that the interspecific differences are fixed at the different life cycle stages of these species. As the fundamental physiological process, metabolic rates may reflect the organism's physiological response to the environment (Brown *et al.*, 2004; McNab, 2002). However, unlike endotherms—which have thermal neutral zones within which organismal metabolic rates are thermally insensitive—, ectothermic metabolic rates are significantly thermally dependent, with a slow increasing rate at low temperatures and a rapid increase at high temperatures, followed by a steep drop after optimal temperature is reached (Gillooly *et al.*, 2001; White, 2011). As the fundamental 'pacemaker' of biological rate, metabolic rate is related to lizard species' body temperature, which is in turn affected by thermal environments (Brown *et al.*, 2004; Glazier, 2015). *Eremias argus* and *E. multiocellata* select shaded microhabitats and thus have lower body temperatures than *P. przewalskii* (Table S1) (Li *et al.,* 2017). Having high metabolic rates at low temperatures (15–36°C, Figure 1) may create advantages for *E. argus* and *E. multiocellata* at low temperatures by allowing the allocation of more metabolic energy for the performance of activities such as escaping or foraging (e.g., Sun *et al.*, 2018; White *et al.*, 2012; White and Kearney, 2013). In contrast, as a higher RMR may enable a higher metabolic energetic production, a higher RMR at high temperatures in *P. przewalskii* may be responsible for improving this species' performance, accompanied by higher thermal preferences and active body temperatures. Alternatively, a higher RMR at high temperatures may induce more energetic allocation for maintenance, which might be a cost (Sokolova *et al.*, 2012).

The existence of interspecific differences in locomotion across body temperatures has been demonstrated in numerous species of lizards (Chen *et al.*, 2003; Du *et al.*, 2000; Ji, 1995; Ji *et al.*, 1996; Sun *et al.*, 2014; Xu, 2001; Zhang and Ji, 2004). Locomotion could reflect the species' ability to escape, forage, and even reproduce (Husak and Fox, 2006; Shu *et al.*, 2010). The higher sprint speed in *E. argus* than in *P. przewalskii* and *E. multiocellata* may result in selective advantages in escaping, foraging, and even reproduction, especially at low temperatures (Bergmann and Irschick, 2010; Xu, 2001; Zamora-Camacho *et al.*, 2014).

As they are desert species, the optimal temperatures for sprint speed in *E. argus* (36°C), *E. multiocellata* (36°C), and *P. przewalskii* (39°C) are higher than those reported for skinks (32–34°C) (Du *et al.*, 2000; Ji, 1995; Xu, 2001) and grass lizards (28–34°C) (Chen *et al.*, 2003; Ji *et al.*, 1996; Zhang and Ji, 2004). In addition, the high optimal temperature for *P. przewalskii* found in this study is consistent with this species' higher active body temperatures, thermal preference, and thermal tolerance (Li *et al.*, 2017) if compared to the sympatric *E. argus* and *E. multiocellata*. The differences in optimal temperatures may be an evolutionary consequence of adaptation to different climatic environments (Zhang and Ji, 2004). Lizards in open and warm environments (e.g., deserts) tend to have high body temperatures, and their optimal temperatures for functions are normally positively correlated with body temperatures (e.g., Ji, 1995; Zhang and Ji, 2004). Potentially, active body temperatures and optimal temperatures for function may be both affected by habitat thermal environments through natural selection or acclimation (Gilbert and Miles, 2017; Sinclair *et al.*, 2016). Within a species' distribution area, other climatic factors (i.e., humidity) may also directly or indirectly induce variation in thermal traits in lizards, including optimal temperatures of thermal performance curve or critical temperatures (Sinclair *et al.*, 2016; Sunday *et al.*, 2012). Nonetheless, in the present study, these three sympatric species lived in adjacent microhabitats with very similar precipitation and evaporation indices (Wang *et al.*, 2016); thus, we propose that the divergences in optimal temperatures of metabolic rates and locomotion among species were driven by thermal environments. However, future studies on the effect of multiple factors on thermal traits in sympatric ectotherms systems would be very important and necessary.

In general, the sympatric species *E. argus*, *E. multiocellata*, and *P. przewalskii* have different preferred microhabitats, resulting in interspecies variation of thermal preferences and active body temperatures (Table S1) (Li *et al.*, 2017). *Eremias argus* and *E. multiocellata* resort to high physiological processes within a low temperatures range (i.e., 15–36°C) to compensate for their lower body temperatures in field conditions. Alternatively, *P. przewalskii* occupies open and warm microhabitats, and it has higher body temperatures. Lower metabolic rates and sprint speed at low body temperatures may be an adaptive strategy for *P. przewalskii*; its low energetic production at low body temperatures results in a lower energetic cost—indicated by low sprint speed—, which in turn reduces energy expenditure (Brown *et al.*, 2004; Young *et al.*, 2011). Similarly, within a certain geographical scale, populations or species that occupy warm habitats (e.g., tropical region) also have higher body temperatures, and therefore tend to have lower performance (e.g., swimming speed) and metabolism rates when compared to species from cold environments at even temperatures, as 'Metabolic Cold Adaptation' predicts (e.g., White *et al.*, 2012). Given that, the combination of different active body temperatures and physiological trait responses is an effective solution that allows the sympatric occurrence of the three desert lizards, by enabling their functions within an active body temperature range. Our study highlights the importance of integrative investigations on temperature-driven sympatric occurrence at a physiological level, based on thermal biological traits and active body temperatures. Future studies should focus on the dynamic of the effects of body temperatures on physiological responses in field to reveal the modification of physiological and body temperatures to thermal variation. Especially in the context of climate warming, studies integrating body temperatures alterations and thermal performance curves may provide insight into the responses and the evaluation of the vulnerabilities of sympatric species (Sinclair *et al.*, 2016).

Acknowledgements We thank WANG C. X. and MA L. for their assistance. Animal Ethics Committees at the Institute of Zoology, Chinese Academy of Sciences approved the ethics and protocol (IOZ14001) for the collection, handling, and husbandry of the study animals. BI J. H. (No.31660615) and SUN B. J. (No. 31870391 and 31500324) are supported by grants from the National Natural Science Foundation of China.

References

Adolph S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by two sceloporus lizards. Ecology, 71(1): 315–327

Angilletta M. J. 2009. Thermal adaptation: A theoretical and empirical synthesis. Oxford: Oxford University Press

Angilletta M. J., Niewiarowski P. H., Navas C. A. 2002. The evolution of thermal physiology in ectotherms. J Therm Biol, 27(4): 249–268

Bergmann P. J., Irschick D. J. 2010. Effects of temperature on maximum clinging ability in a diurnal gecko: evidence for a passive clinging mechanism? J Exp Zool A, 303A(9): 785–791

Brown J. H., Gillooly J. F., Allen A. P., Savage V. M., West G. B. 2004. Toward a metabolic theory of ecology. Ecology, 85(7): 1771–1789

Chen X. J., Xu X. F., Ji X. 2003. Influence of body temperature on food assimilation and locomotor performance in white-striped grass lizards, *Takydromus wolteri* (Lacertidae). J Therm Biol, 28(5): 385–391

Du W. G., Yan S. J., Ji X. 2000. Selected body temperature, thermal tolerance and thermal dependence of food assimilation and locomotor performance in adult blue-tailed skinks, *Eumeces elegans*. J Therm Biol, 25(3): 197–202

Gilbert A. L., Miles D. B. 2017. Natural selection on thermal preference, critical thermal maxima and locomotor performance. Proc Biol Sci, 284(1860): 20170536

Gillooly J. F., Brown J. H., West G. B., Savage V. M., Charnov E. L. 2001. Effects of size and temperature on metabolic rate. Science, 293: 2248–2250

Glazier D. S. 2015. Is metabolic rate a universal 'pacemaker'for biological processes? Biol Rev, 90(2): 377–407

Hardin G. 1960. The competitive exclusion principle. Science, 131(3409): 1292–1297

Hertz P. E. 1992. Evaluating thermal resource partitioning by sympatric lizards *Anolis cooki* and *A. cristatellus*: a field test using null hypotheses. Oecologia: 90: 127–136

Hochachka P. W., Somero G. N. 2002. Biochemical adaptation. Oxford: Oxford University Press

Huey R. B., Kingsolver J. G. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends Ecol Evol, 4: 131–135

Husak J. F., Fox S. F. 2006. Field use of maximal sprint speed by collared lizards (*Crotaphytus collaris*): Compensation and sexual selection. Evolution, 60(9): 1888–1895

Ji X. 1995. Some aspects of thermal biology of the skink (*Eumeces chinensis*). Acta Zool Sin, 41: 268–274

Ji X., Du W. G., Sun P. Y. 1996. Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards, *Takydromus septentrionalis*. J Therm Biol, 21(3): 155–161

Li S. R., Wang Y., Ma L., Zeng Z. G., Bi J. H., Du W. G. 2017. Thermal ecology of three coexistent desert lizards: Implications for habitat divergence and thermal vulnerability. J Comp Physiol B, 187(7): 1009–1018

Luo X., Wu T. P., Huang A. Q. 2016. Diet analysis and foraging strategy of two sympatric pheasants at Mt. Gaoligong in winter. Chinese J Ecol, 35(4): 1003–1008

Ma L., Sun B. J., Cao P., Li X. H., Du W. G. 2018a. Phenotypic plasticity may help lizards cope with increasingly variable temperatures. Oecologia, 187: 37–45

Ma L., Sun B. J., Li S. R., Hao X., Bi J. H., Du W. G. 2018b. The vulnerability of developing embryos to simulated climate warming differs between sympatric desert lizards. J Exp Zool A, 329(4-5): 252–261

Martinvallejo J., Garciafernandez J., Perezmellado V., Vicentevillardon J. L. 1995. Habitat selection and thermal ecology of the sympatric lizards *Podarcis muralis* and *Podarcis hispanica* in a mountain region of central spain. Herpetol J, 5(1): 181–188

McNab B. K. 2002. The physiological ecology of vertebrates: a view from energetics. New York: Cornell University Press

McNab B. K. 2003. Standard energetics of phyllostomid bats: the inadequacies of phylogenetic-contrast analyses. Com Biochem and Phys A, 135(3): 357–368

Osojnik N., Zagar A., Carretero M. A., Garcia-Munoz E., Vrezec A. 2013. Ecophysiological dissimilarities of two sympatric lizards. Herpetologica, 69(4): 445–454

Pacala S. W., Roughgarden J. 1985. Population experiments with the anolis lizards of St. Maarten and St. Eustatius. Ecology, 66(1): 129–141

Pianka B. E. R. 1986. Ecology and natural history of desert lizards. Princeton University Press

Robson M. A., Miles D. B. 2010. Locomotor performance and dominance in male tree lizards, *Urosaurus ornatus*. Funct Ecol, 14(3): 338–344

Rusch T. W., Sears M. W., Angilletta M. J. 2018. Lizards perceived abiotic and biotic stressors independently when competing for shade in terrestrial mesocosms. Horm and Behav, 106: 44–51

Shine R. 2003. Locomotor speeds of gravid lizards: placing 'costs of reproduction' within an ecological context. Funct Ecol, 17(4): 526–533

Sinclair B. J., Marshall K. E., Sewell M. A., Levesque D. L., Willett C. S., Slotsbo S., Dong Y. W., Harley C. D. G., Marshall D. J., Helmuth B. S., Huey R. B. 2016. Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? Ecol Lett, 19(11): 1372–1385

Shu L., Sun B. J., Du W. G. 2010. Effects of temperature and food availability on selected body temperature and locomotor performance of *Plestiodon* (*Eumeces*) *chinensis* (Scincidae). Anim Biol, 60(3): 337–347

Shurin J. B., Amarasekare P., Chase J. M., Holt R. D., Hoopes M. F., Leibold M. A. 2004. Alternative stable states and regional community structure. J Theor Biol, 227(3): 359–368

Sokolova I. M., Frederich M., Bagwe R., Lannig G., Sukhotin A. A. 2012. Energy homeostasis as an integrative tool for assessing limits of environmental stress tolerance in aquatic invertebrates. Mar Environ Res, 79(4): 1–15

Sun B. J., Ma L., Li S. R., Williams C. M., Wang Y., Hao X., Du W. G. 2018. Phenology and the physiological niche are co-adapted in a desert dwelling lizard. Funct Ecol, 32: 2520–2530

Sun B. J., Tang W. Q., Zeng Z. G., Du W. G. 2014. The seasonal acclimatisation of locomotion in a terrestrial reptile, *Plestiodon chinensis* (Scincidae). Asian Herpetol Res, 5(3): 197–203

Sunday J. M., Bates A. E., Dulvy N. K. 2012. Thermal tolerance and the global redistribution of animals. Nat Clim Change, 2(9): 686–690

Wang Y., Zeng Z. G., Li S. R., Bi J. H., Du W. G. 2016. Low precipitation aggravates the impact of extreme high temperatures on lizard reproduction. Oecologia, 182(4): 961–971

White C. R. 2011. Allometric estimation of metabolic rates in animals. Comp Biochem Phys A, 158(3): 346–357

White C. R., Alton L. A., Frappell P. B. 2012. Metabolic cold adaptation in fishes occurs at the level of whole animal, mitochondria and enzyme. Proc Biol Sci, 279(1734): 1740–1747

White C. R., Kearney M. R. 2013. Determinants of inter-specific variation in basal metabolic rate. J Comp Physiol B, 183(1): 1–26

Wilkinson M., Grover M. J. 1996. Climate change and the threat from infection. Trends Microbiol, 4(9): 340–341

Wilson R. S. 2001. Geographic variation in thermal sensitivity of jumping performance in the frog *Limnodynastes peronii*. J Exp Biol, 204: 4227–4236

Xu X. F. 2001. Selected Body temperature, thermal tolerance and influence of temperature on food assimilation and locomotor performance in lacertid lizards,*Eremias brenchleyi*. Zool Res, 22(6): 443–448

Young K. M., Cramp R. L., White C. R., Franklin C. E. 2011. Influence of elevated temperature on metabolism during aestivation: implications for muscle disuse atrophy. J Exp Biol, 214(22): 3782–3789

Žagar A., Carretero M. A., Marguč D., Simčič T., Vrezec A. 2018. A metabolic syndrome in terrestrial ectotherms with different elevational and distribution patterns. Ecography, 41(10): 1728–1739

Žagar A., Carretero M. A., Osojnik N., Sillero N., Vrezec A. 2015. A place in the sun: interspecific interference affects thermoregulation in coexisting lizards. Behav Ecol Sociobi, 69(7): 1127–1137

Zamora-Camacho F. J., Reguera S., Rubiño-Hispán M. V., Moreno-Rueda G. 2014. Effects of limb length, body Mass, gender, gravidity, and elevation on escape speed in the lizard *Psammodromus algirus*. Evol Biol, 41(4): 509–517

Zhang Y. P., Ji X. 2004. The thermal dependence of food assimilation and locomotor performance in southern grass lizards, *Takydromus sexlineatus* (Lacertidae) J Therm Biol, 29: 45–53

Zhao E. M., Zhao K. T., Zhou K. Y. 1999. Fauna Sinica Reptilia Vol. 2 Squamata. Beijing: Chinese Science Press

Appendix

Table S1 Average active body temperatures (T_a), active body temperatures at open microhabitat (T_a open), active body temperatures at shaded microhabitat (T_a shade), and thermal preference (T_{sel}) of *Phrynocephalus przewalskii*, *Eremias argus*, and *E. multiocellata*. Lizards were collected at the Shierliancheng field station, Institute of Grassland Research of the Chinese Academy of Agricultural Sciences (111°09′ E, 40°21′ N, elevation 1 010–1 021 m). Data are expressed as mean ± SE and follow Li *et al.* (2017).

	N	*P. przewalskii*	*N*	*E. argus*	*N*	*E. multiocellata*
T_a (°C)	129	38.1 ± 0.2	84	37.5 ± 0.2	116	36.6 ± 0.2
T_a open (°C)	43	40.19 ± 0.88	29	39.07 ± 0.67	39	38.33 ± 0.14
T_a shade (°C)	40	35.83 ± 1.78	27	35.70 ± 1.69	32	34.81 ± 0.19
T_{sel} (°C)	17	36.6 ± 0.2 33.9–39.2	21	35.3 ± 0.2 32.8–37.5	21	35.2 ± 0.2 33.4–36.8

References

Li S. R., Wang Y., Ma L., Zeng Z. G., Bi J. H., Du W. G. 2017. Thermal ecology of three coexistent desert lizards: Implications for habitat divergence and thermal vulnerability. J Comp Physiol B, 187(7): 1009–1018

Table S2 Results of resting metabolic rate (RMR) of each species at different temperatures. RMR was calculated as the CO_2 production per gram of body mass per hour (ml/g/hr)[*]. Data are shown as mean ± SE.

	N	RMR at 15℃	RMR at 18℃	RMR at 21℃	RMR at 24℃	RMR at 27℃	RMR at 30℃	RMR at 33℃	RMR at 36℃	RMR at 39℃	RMR at 42℃
Eremias argus	14	0.045 ± 0.003	0.145 ± 0.013	0.185 ± 0.012	0.368 ± 0.033	0.436 ± 0.042	0.579 ± 0.048	0.642 ± 0.057	0.909 ± 0.066	0.687 ± 0.031	0.407 ± 0.031
Eremias multiocellata	13	0.077 ± 0.015	0.150 ± 0.017	0.235 ± 0.016	0.282 ± 0.024	0.371 ± 0.044	0.445 ± 0.044	0.521 ± 0.052	0.605 ± 0.071	0.545 ± 0.067	0.224 ± 0.011
Phrynocephalus przewalskii	14	0.109 ± 0.011	0.121 ± 0.007	0.130 ± 0.016	0.182 ± 0.021	0.335 ± 0.046	0.428 ± 0.053	0.466 ± 0.043	0.650 ± 0.060	0.835 ± 0.060	0.647 ± 0.073

[*] The RMR values are the same as those shown in the main text, but they are herein differently expressed.