

The vulnerability of developing embryos to simulated climate warming differs between sympatric desert lizards

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Abstract

The vulnerability of species to climate warming varies along latitudinal and elevational clines, but how sympatric species vary in vulnerability to climate warming remains largely unknown. We experimentally simulated nest temperatures of two sympatric lizards with divergent microhabitat preferences (*Phrynocephalus przewalskii* and *Eremias argus*), under climate warming scenarios, to determine the response of embryos to increased mean temperatures and heat waves. Our study demonstrated that simulated climate warming reduced hatching success and hatchling size and growth in *E. argus* (that prefers closed microhabitats), but had less effect in *P. przewalskii* (that occupies open microhabitats). The reduced growth rate of *E. argus* hatchlings was associated with a decrease in metabolic rate, which was more evident in hatchling *E. argus* than in *P. przewalskii*. Our results suggest lizards that prefer closed microhabitats may be more vulnerable to climate warming than those that prefer open microhabitats; further studies are needed to test this hypothesis. More generally, the divergent responses of sympatric species to climate warming highlights the importance of distinguishing the thermal sensitivity of behavior and physiology for each species of a community, in order to make predictions about the impacts of climate warming at regional scales.

KEYWORDS

climate warming, embryonic development, microhabitat, nest temperature, physiological divergence, sympatric species

1 | INTRODUCTION

The ongoing process of climate warming has pervasive impacts on organisms and their ecosystems (Gonzalez, Neilson, Lenihan, & Drapek, 2010; Laloe, Cozens, Renom, Taxonera, & Hays, 2017; Pacifici et al., 2015). Ectotherms are extremely vulnerable to climate warming because they are highly dependent on environmental temperatures (Deutsch et al., 2008; Huey et al., 2012). The vulnerability of ectotherms to climate warming is thus critical for predicting the future survival prospects of these organisms (Huey et al., 2009; Kearney et al. 2009), and has important management implications for biodiversity conservation (Buckley & Jetz, 2007; Walters, Blanckenhorn, & Berger, 2012). Despite increased research efforts in this field (e.g., Esperk, Kjaersgaard, Walters, Berger, & Blanckenhorn, 2016; Kingsolver & Buckley, 2015; Walters et al., 2012), the responses of ectotherms to climate warming remain poorly understood.

First, recent studies have demonstrated that the vulnerability of species to climate warming may differ along latitude and altitude

gradients (Deutsch et al., 2008; Sunday et al., 2014). However, whether sympatric species respond differently to climate warming remains largely unknown (but see Logan, Huynh, Precious, & Calsbeek, 2013), even though this directly relates to regional conservation decisions. Sympatric species may diverge in thermal physiological traits as an adaptation to the thermal conditions available in their respective microhabitats (Du, Shou, & Shen, 2006; Scheers & Van Damme, 2002). For example, species inhabiting open microhabitats often show higher selected body temperatures, while those inhabiting closed microhabitats select lower body temperatures (Hertz et al., 2013; Li et al., 2017; Scheers & Van Damme, 2002). The divergent thermal preferences and thermal sensitivity of ectotherms may directly determine species' vulnerability to climate warming (Buckley & Huey, 2016; Oyen et al. 2016; Pincebourde & Casas, 2015). Consequently, despite facing similar climate-induced heat stress, sympatric species may respond to such challenges in different ways.

Second, examining the biological response of species to climate warming has relied primarily on mean temperatures, with much

less attention on temperature variability (Garcia, Cabeza, Rahbek, & Araujo, 2014). However, recent climate projections suggest that besides an increase in mean temperature, climate warming will involve an increase in thermal variability and more extreme temperatures (IPCC, 2014). As temperatures become more variable, species are more likely to be exposed to temperatures beyond their thermal tolerance limits (Deutsch et al., 2008; Vasseur et al., 2014), causing stress, a decrease in reproductive effort (Moreno & Moller, 2011), a bias in sex ratio (temperature-dependent sex determination, e.g., Refsnider, Bodensteiner, Reneker, & Janzen, 2013) or even death (Ma, Rudolf, & Ma, 2015). In addition, increased temperature variability and extreme temperatures are likely to have serious impacts on many organisms, and may play a more direct role in driving biogeographic shifts and community dynamics than increased mean temperatures alone (Harley, 2011; Thornton, Ericksen, Herrero, & Challinor, 2014; Zander, Bersier, & Gray, 2017).

Third, thermal stress can impact organisms at different life-history stages, from embryos to adults. However, many previous studies have focused on the effect of thermal stress on postembryonic life-history stages rather than on embryos (e.g., Esperk et al., 2016; Sentis, Hemptinne, & Brodeur, 2017; Wang et al. 2016), despite of the fact that embryos are often more sensitive and vulnerable to temperature variation than later life-history stages. Most reptile embryos are restricted to small spaces and have limited thermoregulatory opportunities (Deeming, 2004; but see Du, Zhao, Chen, & Shine, 2011). For example, the range of viable temperatures for embryonic development is much narrower than those required by later life stages (Deeming & Ferguson, 1991; Du & Shine, 2015). In oviparous species, eggs are laid in nests, and are directly exposed to the prevailing environmental conditions during development (Muth, 1980; Packard, Tracy, & Roth, 1977). Temperature variation during embryonic development may alter developmental time, hatching success, hatchling morphology, behavior, and physiology (Deeming, 2004; Du & Ji, 2006). Thermal stress induced by extreme temperatures in nests can have serious impacts on hatchling phenotypes, or even cause death (Angilletta, Zelic, Adrian, Hurliman, & Smith, 2013; Sentis et al., 2017). Therefore, it is essential to incorporate embryonic responses to thermal stress when estimating the vulnerability of organisms due to climate warming.

To address the abovementioned issues, we experimentally manipulated nest temperatures of two sympatric lizards from the arid region of northern China (*Phrynocephalus przewalskii* and *Eremias argus*) to simulate climate warming scenarios. Lizards in arid regions are not only especially vulnerable to climate warming (Clusella-Trullas, Blackburn, & Chown, 2011), but also are largely neglected in worldwide conservation planning and practice (Roll et al., 2017). The desert agama (*P. przewalskii*) is a small oviparous agamid lizard found in open habitat of arid and semi-arid regions, whereas the racerunner (*E. argus*) is a small oviparous lacertid lizard occupying closed habitats of grassy sand dunes and thickets (Zeng et al., 2016; Zhao, Zhao, & Zhou, 1999). Our aim was to investigate how embryos of these two sympatric species, with different microhabitat preferences, would respond to increased mean temperatures and heat waves during development. Species that prefer closed microhabitats may be less resilient to high temperatures compared to other species which prefer more open habitat (Hertz

et al., 2013; Li et al., 2017; Scheers & Van Damme, 2002). Thus, we predicted that embryos of *E. argus* will be more affected by increased mean temperatures and heat waves than *P. przewalskii*, resulting in more negative consequences for *E. argus* due to climate warming.

2 | MATERIALS AND METHODS

2.1 | Study species and nest temperature

P. przewalskii and *E. argus* have a sympatric distribution in the desert steppe of northern China, and at our study site at Jungar Banner, Inner Mongolia (40° 12' N, 111° 07' E, elevation 1036 m). The desert agamas (*P. przewalskii*) occupy open sand microhabitats, whereas the lacertids (*E. argus*) prefer habitats with dense vegetation (Zeng et al., 2014). During the reproductive season (May–August), gravid *P. przewalskii* dig burrow nests in open sandy areas (Li et al., 2018), and often, female *E. argus* use the burrows built by *P. przewalskii* as nests. Female *P. przewalskii* lay 1–4 eggs per clutch, while female *E. argus* lay 2–5 eggs per clutch (Zhao et al., 1999).

In the summer of 2014, we found 13 *P. przewalskii* nests containing fresh eggs (found within 1 day of oviposition) at our study site in Inner Mongolia (Li et al., 2018). We inserted iButtons (Dallas Semiconductor, Dallas, Texas, USA; diameter 15 mm; height 6 mm) in these nests (without destroying burrow structures) to record temperatures experienced by the embryos for 45 days. We deployed iButtons in the first nest on 23 May 2014 and retrieved iButtons from the last nest on 28 August 2014. This period covered most of the reproductive season when embryonic development occurs at our study site. The nest temperatures oscillate both daily and seasonally, ranging from 18°C to 32°C (Figure 1a). We averaged these nest temperatures to get a 24-hr temperature regime for egg incubation of the control group in both species (Figure 1b). This diel cycle ranged from 22.7°C to 29.0°C, with a mean temperature of 25.8°C. In the summer of 2015, we found two *E. argus* nests containing fresh eggs at the same study site, with a similar mean temperature (25.6°C) and daily temperature fluctuation (Figure 1b) to those of *P. przewalskii*. Accordingly, we used the fluctuating temperatures of $26 \pm 3^\circ\text{C}$ on a daily basis to simulate the thermal environment of nests in these two species of lizards.

2.2 | Egg collection and incubation

In June 2015, we collected gravid female *P. przewalskii* ($n = 54$) and *E. argus* ($n = 46$), with shelled eggs, from our field site and transported them to our lab in Beijing within 5 days of collection. We kept each gravid female in an egg-laying plastic container (310 × 210 × 180 mm) with a 2-cm thick substrate of moist sand. We checked egg-laying containers at least four times per day for freshly-laid eggs. Fresh eggs were then marked with unique numbers and weighed immediately after they were laid to minimize initial mass changes caused by water exchange. We half-buried each egg in a plastic cup (66 × 49 × 75 mm) filled with moist vermiculite (−220 kPa) and covered these cups with perforated plastic membrane to allow gaseous exchange, but to avoid water loss.

We divided eggs from the same clutches into three treatments with different mean temperatures and a daily fluctuation of 3°C: control

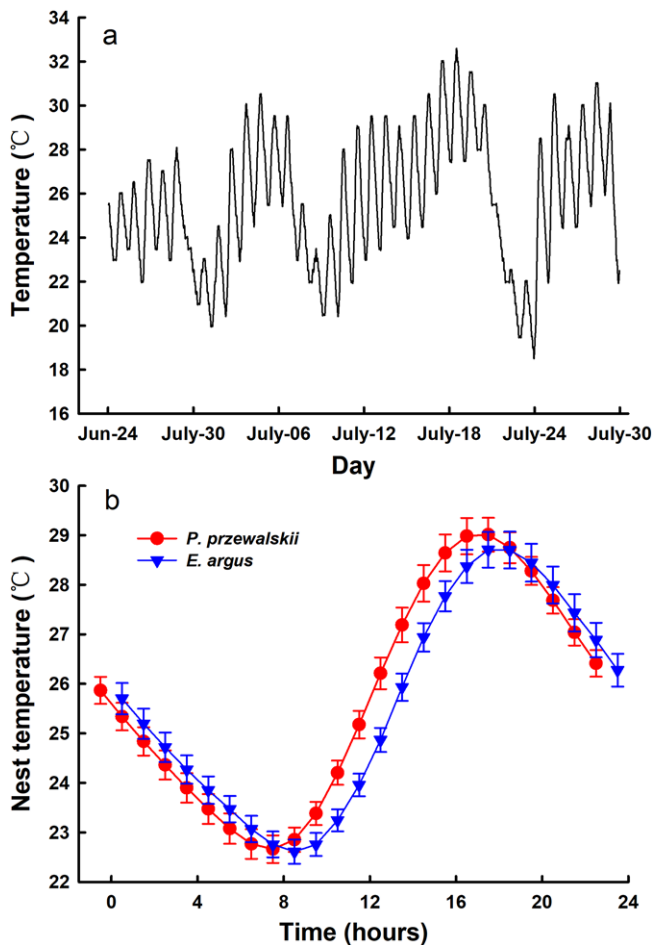


FIGURE 1 (a) Temperatures over the incubation period (June 24th–July 30th, 2014) for a typical nest of *P. przewalskii* (*E. argus* experience similar nest temperatures with those of *P. przewalskii*); (b) Averaged daily nest temperatures of *P. przewalskii* in the desert steppe of Inner Mongolia, China. The 24-hr average temperature regime was calculated from temperatures recorded in 13 field nests found in 2014. Data are expressed as mean \pm SE [Color figure can be viewed at wileyonlinelibrary.com]

($26 \pm 3^\circ\text{C}$), warming ($28 \pm 3^\circ\text{C}$), or heat wave ($26 \pm 3^\circ\text{C}$ for 15 days, $31 \pm 3^\circ\text{C}$ for 10 days, and then $28 \pm 3^\circ\text{C}$ until hatching; see Figure 2 for temperature regimes and Table 1 for sample sizes). The control group mimicked nest temperatures in the current condition. The warming group increased mean nest temperatures by 2°C , which mimicked warming conditions at the end of this century (with an increase of $1\text{--}4^\circ\text{C}$ at different scenarios according to IPCC, 2014). The heat wave group increased mean nest temperatures by 5°C for 10 days during the incubation to simulate a heat wave event defined by the World Meteorological Organization (also see Fischer, Klockmann, & Reim, 2014). Despite different variabilities, mean temperatures in the warming and heat wave treatments were the same (28°C). Incubators (KB240, Binder, Germany) were used to provide the thermal regimes for our incubation treatments. We moved plastic cups among shelves in incubators weekly to minimize effects of thermal gradients inside the incubators.

2.3 | Hatchling morphology and growth

After the first hatchling appeared we checked for hatchlings four times per day. We measured hatchling snout-vent length (SVL) to ± 0.01 mm and body mass (BM) to ± 0.001 g immediately after hatching. Incubation periods were calculated as the number of days between oviposition date and hatching date. We marked hatchlings with non-toxic marker pens and kept them individually in containers ($310 \times 210 \times 180$ mm). Hatchlings from all treatments were housed in a temperature-controlled room at 28°C , with a photoperiod of 14:10 (L:D). We used full-spectrum bulbs (50W) to provide a heat source for lizard thermoregulation from 0900–1700 h. Food (mealworms and crickets dusted with vitamins and minerals) were provided daily ad libitum. We measured the body sizes of offspring again at 14 days after hatching and calculated their change in SVL and BM per day as growth rates.

2.4 | Locomotor performance and metabolic rate of hatchlings

When offspring were 14 days old, we measured locomotor performance (at 30°C) and resting metabolic rate of one offspring (randomly chosen) from each clutch in each treatment. For the locomotor performance trials, we acclimated lizards in an incubator at 30°C for 2 hr prior to each trial. Individuals were then placed at the beginning of the racetrack ($100 \times 10 \times 15$ cm) and encouraged to run the length of the track with a paintbrush. Each lizard was run two times, with a 30-min rest between trials, and to standardize the stimulus, the same person conducted all locomotor trials. We filmed each lizard from above with a video camera (Sony DCR-SR220E). A distance scale printed on the racetrack (0–80 cm, four 20-cm intervals) allowed us to determine lizard running speeds. Sprint speed was calculated as the fastest speed in a 20-cm interval, and average speed was measured over the entire length of the track (80 cm).

We used flow-through respirometry (Model TR3, Sable Systems, Henderson, NV) to measure resting metabolic rate (RMR) of hatchlings at four temperatures (22°C , 26°C , 30°C , and 34°C). The volume of the respirometry system was 38 ml. We fasted individuals for at least 12 hr prior to the respirometry trials and then acclimated them to the respective test temperatures for 2 hr. Initially we used a flow-through cycle with airflow rate of 240 ml/min. Then, once the baseline readings stabilized, we switched to a closed system and recorded the carbon dioxide (CO_2) production continuously for at least 10 min. To control for differences in offspring size, we divided the rate of CO_2 production by body mass raised to the power 0.75 as an estimate of RMR for each individual lizard ($\text{ml} \times (\text{g}^{0.75})^{-1} \times \text{h}^{-1}$). We did not expose the lizards to light, and all measurements were conducted from 0900 h to 1700 h to minimize the effect of circadian rhythms.

2.5 | Statistical analysis

We used R software (version 3.3.1; R Core Team, 2016) to perform all the statistical analyses. Chi-square analysis was used to detect

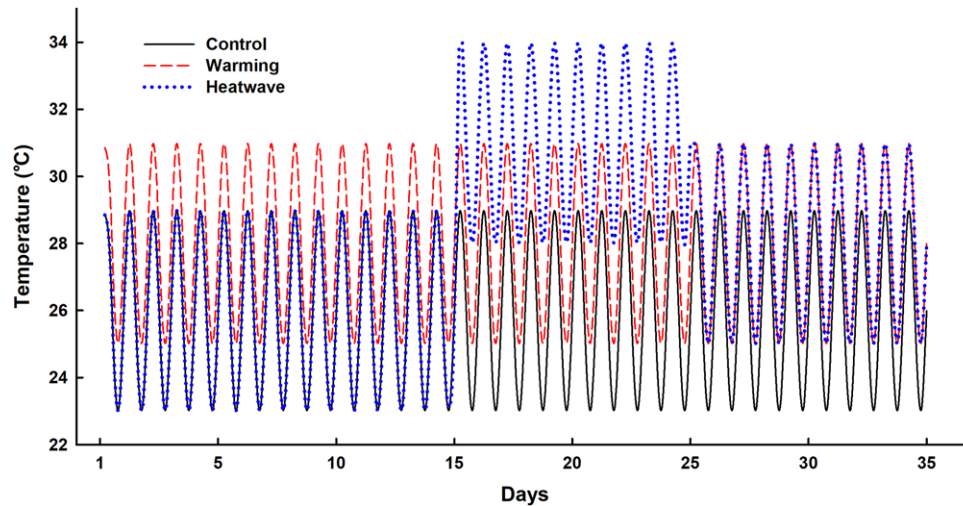


FIGURE 2 Thermal regimes of control, warming, and heat wave treatments (daily thermal regimes are the same as those from day 26 to 35 if eggs do not hatch before day 35) [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Hatching success and incubation periods of two sympatric lizard species (*P. przewalskii* and *E. argus*) after incubation at three different thermal treatments: control ($26 \pm 3^\circ\text{C}$), warming ($28 \pm 3^\circ\text{C}$), or heat wave ($26 \pm 3^\circ\text{C}$ for 15 days, $31 \pm 3^\circ\text{C}$ for 10 days, and then $28 \pm 3^\circ\text{C}$ until hatching). Incubation periods are expressed as mean \pm SE

Species	Treatments	Incubated (n)	Hatched (n)	Hatching success	Incubation period (days)
<i>P. przewalskii</i>					
	Control	27	22	81.48%	37.9 ± 0.3
	Warming	22	14	63.64%	32.4 ± 0.2
	Heat wave	24	20	83.33%	31.9 ± 0.2
<i>E. argus</i>					
	Control	31	27	87.10%	46.3 ± 0.3
	Warming	29	18	62.07%	38.1 ± 0.2
	Heat wave	29	16	55.17%	38.5 ± 0.3

the effect of temperature regimes on hatching success ('chisq.test'). We ran linear mixed effects models ('lmer' and 'lmerTest:anova' in library 'lmerTest'; Kuznetsova, Brockhoff, & Christensen, 2017) to test whether there are significant between-treatment and between-species differences in incubation period, hatchling size, and hatchling growth rate (treatment, species as fixed effects, clutch as random effect). We ran linear models ('lm') to test effects of treatment and species on hatchling metabolic rate (with treatment, species, and testing temperature as fixed effects; also ran the test at each testing temperature for each species respectively), and to test effects of treatment and species on hatchling locomotor performance (sprint speed and average speed). Because we found differences between species in most hatchling traits, we also ran the analysis for each species respectively (with only treatment as the fixed effect).

2.6 | Ethical statement

The methods in our study were approved by the Animal Ethics Committee at the Institute of Zoology, Chinese Academy of Sciences (IOZ14001).

3 | RESULTS

3.1 | Hatching success and incubation period

Simulated climate warming did not affect the hatching success of eggs in *P. przewalskii* ($X^2 = 3.038$, $df = 2$, $P = 0.219$; Table 1). In *E. argus*, however, hatching success was much lower in the warming and heat wave treatments compared to the control treatment ($X^2 = 7.917$, $df = 2$, $P = 0.019$; Table 1). Incubation period differed significantly among thermal treatments and between species as well (treatment: $F_{2,62,602} = 1078.53$, $P < 0.001$; species: $F_{1,51,477} = 551.81$, $P < 0.001$; treatment \times species: $F_{2,62,618} = 33.83$, $P < 0.001$). Both warming and heat wave treatments shortened incubation period by about 6 days in *P. przewalskii*, and 8 days in *E. argus*, when compared to the control treatment (Tables 1 and 2).

3.2 | Hatchling morphology and growth rate

Hatchlings of *P. przewalskii* were significantly shorter but heavier than those of *E. argus*. Thermal treatments significantly influenced hatchling SVL, with the warming treatment reducing hatchling SVL in *E.*

TABLE 2 Statistical results of between-treatment differences in incubation period and hatchling traits of two sympatric lizard species (*P. przewalskii* and *E. argus*) incubated at three different thermal treatments: control ($26 \pm 3^\circ\text{C}$), warming ($28 \pm 3^\circ\text{C}$), or heat wave ($26 \pm 3^\circ\text{C}$ for 15 days, $31 \pm 3^\circ\text{C}$ for 10 days, and then $28 \pm 3^\circ\text{C}$ until hatching). We use bold font when $P < 0.05$

Hatchling traits	Species	F	P
Incubation period (days)	<i>P. przewalskii</i>	$F_{2,26.352} = 377.38$	<0.001
	<i>E. argus</i>	$F_{2,34.545} = 727.88$	<0.001
SVL (mm)	<i>P. przewalskii</i>	$F_{2,36.074} = 0.230$	0.796
	<i>E. argus</i>	$F_{2,37.631} = 5.400$	0.009
Body mass (g)	<i>P. przewalskii</i>	$F_{2,30.737} = 0.931$	0.405
	<i>E. argus</i>	$F_{2,33.576} = 0.654$	0.526
SVL growth rate (mm/day)	<i>P. przewalskii</i>	$F_{2,38.000} = 0.726$	0.49
	<i>E. argus</i>	$F_{2,36.146} = 1.058$	0.358
Body mass growth rate (g/day)	<i>P. przewalskii</i>	$F_{2,38.010} = 1.271$	0.292
	<i>E. argus</i>	$F_{2,34.594} = 4.577$	0.017
Sprint speed (m/s)	<i>P. przewalskii</i>	$F_{2,37.000} = 0.641$	0.532
	<i>E. argus</i>	$F_{2,29.000} = 0.105$	0.900
Average speed (m/s)	<i>P. przewalskii</i>	$F_{2,37.000} = 5.094$	0.011
	<i>E. argus</i>	$F_{2,29.000} = 0.194$	0.825

argus, but not in *P. przewalskii* (Table 2). However, thermal treatments did not affect hatchling body mass (Treatment: $F_{2,66.212} = 2.102$, $P = 0.130$; Species: $F_{1,21.592} = 185.367$, $P < 0.001$; treatment \times species: $F_{2,66.182} = 0.213$, $P = 0.809$; Figure 3).

Two weeks after hatching, hatchlings of *P. przewalskii* grew less than those of *E. argus* in term of both SVL and body mass, however, thermal treatments had no effects on hatchling growth rates in terms of SVL (treatment: $F_{2,73.956} = 1.147$, $P = 0.323$; species: $F_{1,49.408} = 15.958$, $P < 0.001$; treatment \times species: $F_{2,73.956} = 0.466$, $P = 0.630$) or body mass (treatment: $F_{2,82.509} = 0.070$, $P = 0.933$; species: $F_{1,48.423} = 24.402$, $P < 0.001$; treatment \times species: $F_{2,82.509} = 4.423$, $P = 0.015$) (Figure 4). However, the heat wave treatment slightly reduced the growth rate of hatchling body mass in *E. argus*, but not in *P. przewalskii*, when we ran the statistic model for two species respectively (Table 2).

3.3 | Locomotor performance and metabolic rate of hatchlings

Hatchlings of *P. przewalskii* had higher sprint speed but similar average speed than those of *E. argus*, however, thermal treatments did not affect sprint speed (treatment: $F_{2,66} = 0.549$, $P = 0.580$; species: $F_{1,66} = 5.870$, $P = 0.018$; treatment \times species: $F_{2,66} = 0.565$, $P = 0.571$) or average speed of hatchlings (treatment: $F_{2,66} = 2.755$,

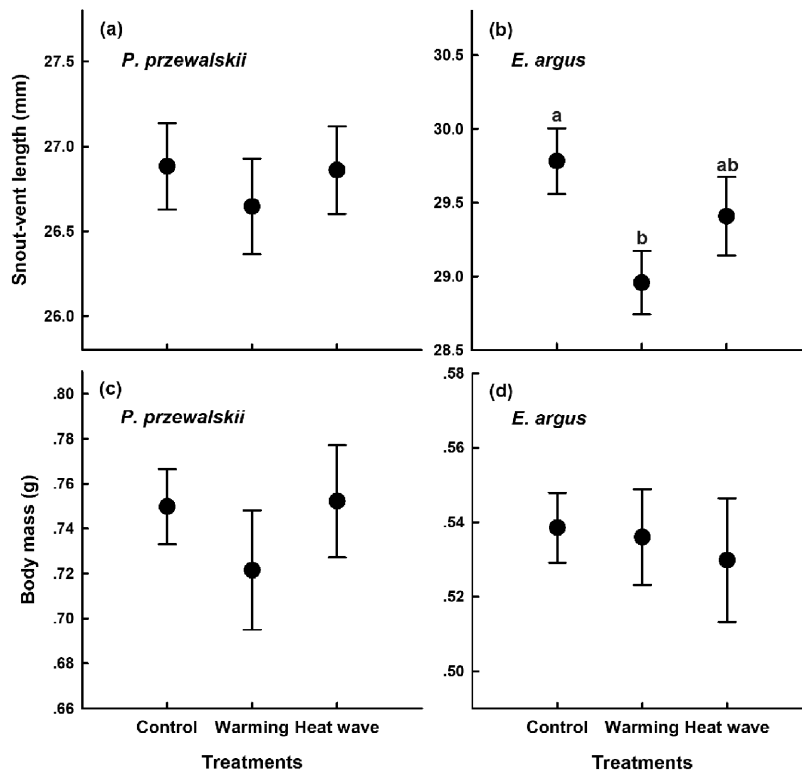


FIGURE 3 The snout-vent length (SVL) and body mass of hatchlings from three incubation thermal treatments in two sympatric lizard species (*P. przewalskii* and *E. argus*) from the desert steppe of Inner Mongolia, China. The sample sizes for control, warming, and heat wave treatments were $n = 22, 14$, and 20 in *P. przewalskii*, and $n = 27, 18$, and 16 in *E. argus*, respectively. Significant differences between treatments are indicated by letters above the error bars ($P < 0.05$). Data are expressed as mean \pm SE

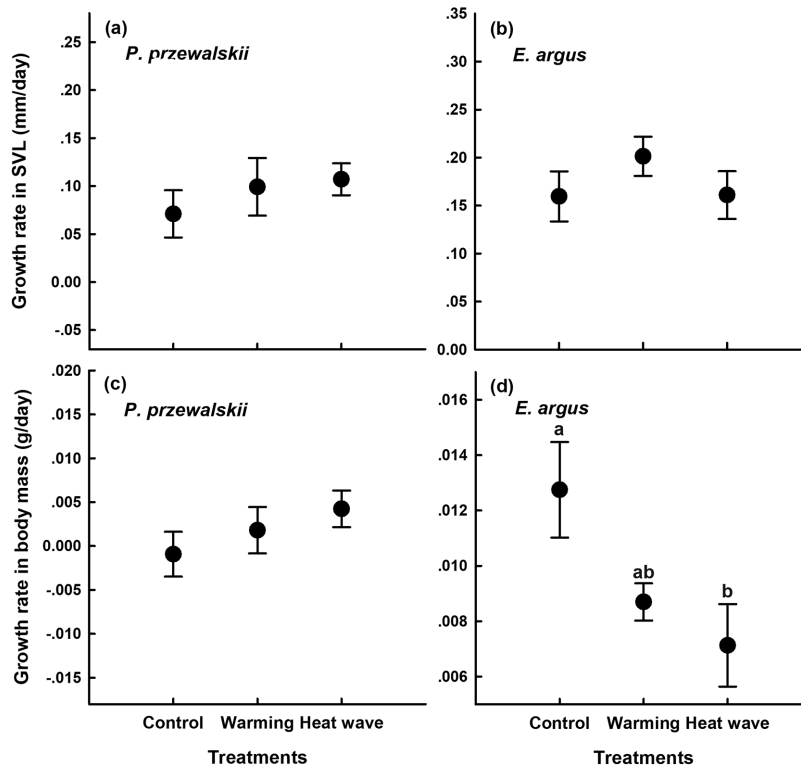


FIGURE 4 The effect of incubation thermal treatments on hatchling growth rates (snout-vent length [SVL] and body mass) of two sympatric lizard species (*P. przewalskii* and *E. argus*) from the desert steppe of Inner Mongolia, China. Sample sizes for control, warming, and heat wave treatments were $n = 16, 10,$ and 15 in *P. przewalskii*, and $n = 17, 17,$ and 16 in *E. argus*, respectively. Significant differences between treatments are indicated by letters above the error bars ($P < 0.05$). Data are expressed as mean \pm SE

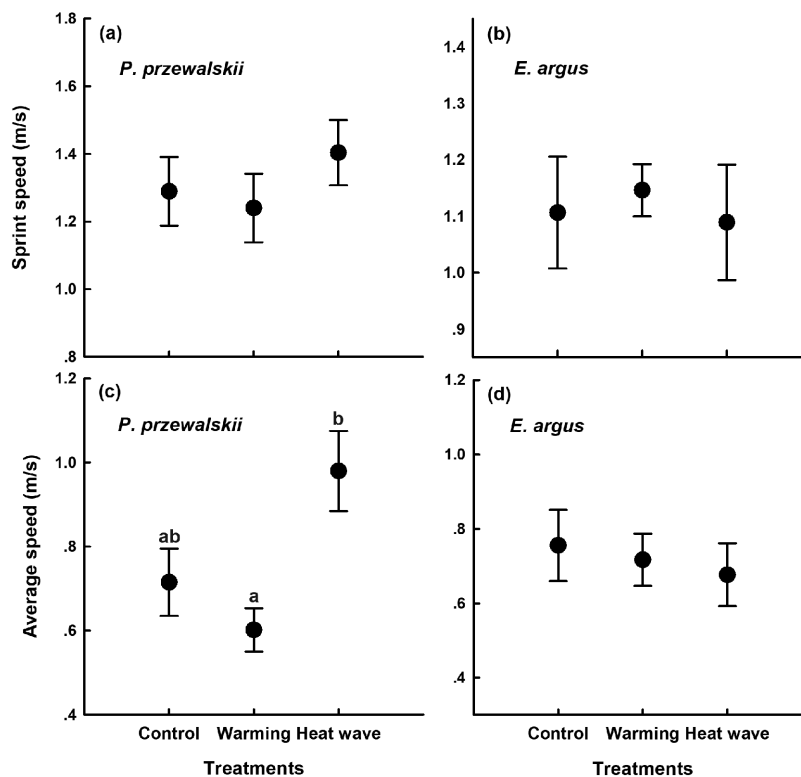


FIGURE 5 The effect of incubation thermal treatments on hatchling locomotor performance of two sympatric lizard species (*P. przewalskii* and *E. argus*) from the desert steppe of Inner Mongolia, China. Sample sizes for control, warming, and heat wave groups were $n = 16, 10,$ and 14 in *P. przewalskii*, and $13, 11,$ and 8 in *E. argus*, respectively. Significant differences between treatments are indicated by letters above the error bars ($P < 0.05$). Data are expressed as mean \pm SE

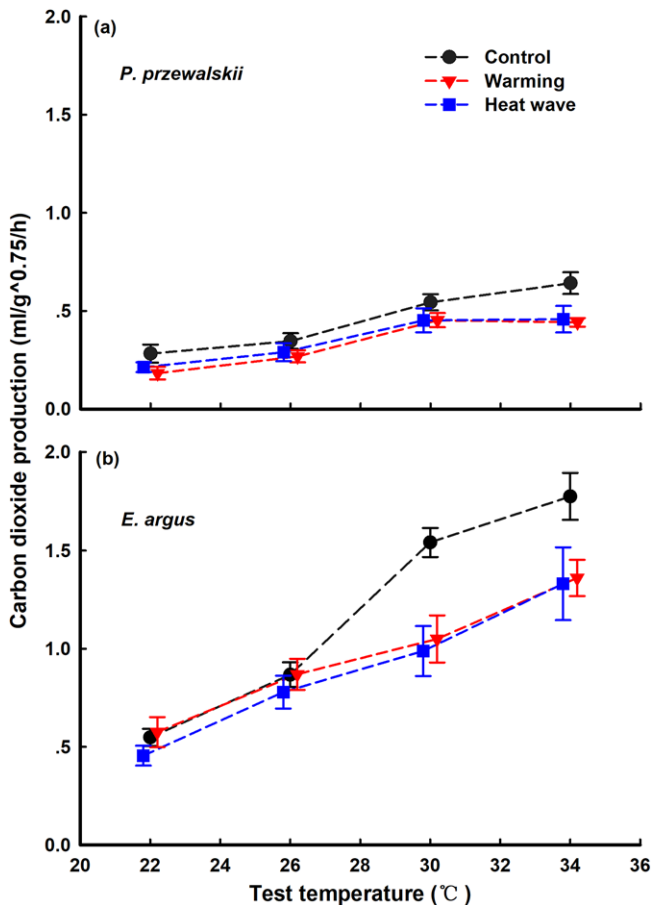


FIGURE 6 The resting metabolic rate (carbon dioxide production determined at a series of temperatures) of hatchlings from three incubation thermal treatments in two sympatric lizard species (*P. przewalskii* and *E. argus*) from the desert steppe of Inner Mongolia, China. Data are expressed as mean \pm SE [Color figure can be viewed at wileyonlinelibrary.com]

$P = 0.071$; species: $F_{1,66} = 0.274$ $P = 0.603$; treatment \times species: $F_{2,66} = 2.995$, $P = 0.057$). However, we found incubation in the heat wave treatment slightly increased the average speed of *P. przewalskii* hatchlings when we analyzed the two species respectively (Table 2; Figure 5).

Hatchlings of *P. przewalskii* had lower metabolic rate than those of *E. argus* ($F_{1,256} = 467.792$, $P < 0.001$). Compared to the control treatment, incubation at the warming and heat wave treatments reduced hatchling metabolic rate ($F_{2,256} = 24.687$, $P < 0.001$). Further analysis of this effect within each test temperature showed that between-treatment differences were only significant at 30°C in *P. przewalskii* ($F_{2,64} = 3.862$, $P = 0.026$), but were significant at both 30°C ($F_{2,28} = 8.652$, $P = 0.001$) and 34°C ($F_{2,28} = 3.976$, $P = 0.030$) in *E. argus* (Figure 6).

4 | DISCUSSION

We found that simulated climate warming (increased mean temperature or heat waves) reduced hatching success and hatchling growth

in *E. argus*, but not in *P. przewalskii*. These results are consistent with our prediction that embryos of lizard species preferring closed microhabitats would be more affected by increased mean temperatures and heat waves than those of lizard species occupying open microhabitats. Previous constant-temperature incubation experiments indicated that incubation temperatures from 24°C to 32°C did not affect hatching success or hatchling morphology (Wang, Ma, Shao, & Ji, 2013), but a high temperature of 34°C reduced hatching success, hatchling size, and locomotor performance in *P. przewalskii* (Tang et al., 2012). In contrast, *E. argus* hatchlings incubated at 30°C and 33°C had worse locomotor performance than those at 24°C and 27°C, although hatching success was not affected by these incubation temperatures (Hao, Liu, & Ji, 2006). Therefore, results from constant-temperature incubation imply that *E. argus* seems to be more sensitive to high temperatures than *P. przewalskii*, which is in line with our conclusion. Below we explain the potential reasons for this between-species difference in the vulnerability of embryos to climate warming, and its implication for conservation management.

This between-species difference in embryonic thermal tolerance is likely a result of phylogenetic differences, or physiological adaptation to their respective microhabitats (Curtis, Gollan, Murray, & Leigh, 2016; Scheers & Van Damme, 2002). Although our data do not allow us to tease apart these two causes, phylogenetic differences and physiological adaptation may not be mutually exclusive because phylogenetic differences may be a result of physiological adaptation during the evolutionary history of these species (Garland, Bennett, & Rezende, 2005; Khaliq et al., 2015). It is tempting to infer that embryos of *P. przewalskii*, which prefer open microhabitats, have a correspondingly higher thermal tolerance than those of their sympatric neighbors (*E. argus*), which prefer closed microhabitats. In proximate terms, the difference in embryonic thermal tolerance between these sympatric lizards may be attributed to maternal effects and/or thermal acclimation of developing embryos (Du, Ye, Zhao, Warner, & Shine, 2010; Ma, Sun, Li, Sha, & Du, 2014). Warmer environments experienced by adult female *P. przewalskii* may induce higher thermal tolerance of their embryos compared with those of *E. argus*. In contrast, thermal acclimation may contribute little, if any, to the difference in embryonic vulnerability to heat stress, because gravid females of both species lay their eggs in relatively open areas, and embryos of these two species experience similar developmental temperatures, despite the adults having different microhabitat preferences (Li et al., 2017).

The between-species difference in vulnerability to simulated climate warming was not only apparent as a divergence in embryonic survival, but can also be inferred from the phenotypic traits of the resultant hatchlings. In our study, increased mean temperature reduced hatchling SVL in *E. argus*, but not in *P. przewalskii*. Similarly, hatchlings from warm incubation temperatures are smaller or lighter than those from cold incubation temperatures in some lizards including the study species (Dayananda, Gray, Pike, & Webb, 2016; Hao et al., 2006; Ma et al., 2014; Tang et al., 2012), but not in other lizards (Lu, Wang, Tang, & Du, 2013). High temperatures speed up the developmental rate of embryos (e.g. Du, Radder, Sun, & Shine, 2009; DuRant, Hopkins, Hawley, & Hepp, 2012; Eme et al., 2015), by enhancing mitochondrial function, and thus, energetic metabolism (Sun, Li, Gao, Ma, & Du, 2015). As

a result, embryos develop into smaller hatchlings due to higher energy consumption during development at high temperatures. In addition, the heat wave treatment reduced hatchling growth rates in body mass in *E. argus*, but not in *P. przewalskii*. This could be due to the reduction of hatchling metabolic rate (which was more evident in hatchling *E. argus* than in *P. przewalskii*; Figure 6), because low metabolic rates may reduce food intake and depress energy assimilation (Du, Yan, & Ji, 2000; Xu & Ji, 2006). As a result, the reduced growth rates could result in smaller body size of lizards before hibernation, which could be closely related to overwinter survival and fitness (e.g., Dayananda et al., 2016; Zani, 2008; but see Clark & Zani, 2012; Warner & Shine, 2007). Given that larger hatchling size is positively related to offspring traits that affect survival (e.g., foraging ability, antipredator behavior, and growth) and therefore fitness (Andrews, Mathies, & Warner, 2000; Dayananda et al., 2016; Noble, Stenhouse, & Schwanz, 2018), we suggest that *E. argus* may be influenced by strong selective forces when mean developmental temperatures increase, or heat wave conditions occur.

A comparison of adult thermal physiology indicated that lizards occupying open microhabitats (*P. przewalskii*) had higher body temperatures, selected body temperature (36.6°C vs. 35.3°C) and critical thermal maximum (47.1°C vs. 45.8°C), and a wider thermal safety margin (5.2°C vs. 3.9°C) than lizards occupying closed microhabitats (*E. argus*) (Li et al., 2017). Results from the current study further suggest that embryos of *E. argus* are more sensitive to increasing mean temperatures and heat waves than are those of *P. przewalskii*. Taken together, these results suggest that *E. argus* may be more vulnerable to climate warming than *P. przewalskii*, implying that lizards preferring closed microhabitats could be more vulnerable to climate warming than those preferring open microhabitats. Although females might choose shadier and cooler nest sites when temperatures increase (e.g., Doody et al., 2006, but see Telemeco et al., 2017), the reduction of vegetation cover resulting from climate warming may limit this buffering effect (Wang, Price, & Arora, 2006). Nonetheless, our study only compared one pair of closely related species. Future research into the effects of climate warming on reptiles may benefit from more comparative studies, using a broad range of species, and taking phylogenetic relationships into account, to further test this hypothesis.

More generally, the phenomenon of divergent responses between sympatric species to climate warming may be widespread in different regions (Logan et al., 2013). This highlights the importance of distinguishing the thermal sensitivity of behavior and physiology in each species of a community, and of considering the response of each species as a unit of interest rather than simply the response of the community as a whole. Such an approach provides a more detailed picture of the impact of climate warming on organisms and allows us to predict outcomes and develop more effective conservation strategies. Physiological and behavioral studies at the species level are important, because such studies yield essential parameters that can be incorporated in mechanistic models to predict impacts of climate warming at regional scales (Kearney & Porter, 2009). Unfortunately, such empirical knowledge is often unavailable for many systems, and thus, warrants further research efforts.

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