

## Original article

# Embryonic thermosensitivity and hatchling morphology differ between two coexisting lizards

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## ABSTRACT

We incubated eggs of two coexisting lizards, *Phrynocephalus frontalis* and *Phrynocephalus versicolor*, at three constant temperatures (24, 28 and 32 °C) to examine whether they differ in embryonic thermosensitivity and hatchling morphology. Eggs incubated at the three temperatures produced morphologically different hatchlings in *P. versicolor* but not in *P. frontalis*. Snout-vent length (SVL), body mass and head width were greater in *P. versicolor* hatchlings from the 24 °C treatment than those from the 32 °C treatment when accounting for differences in initial egg mass, and tail length was smaller in *P. versicolor* hatchlings from the 24 °C treatment than those from the 32 °C treatment when accounting for differences in initial or final egg mass. Body mass, head length, head width, tail length, fore-limb length and hind-limb length were greater in *P. frontalis* hatchlings than in *P. versicolor* hatchling when accounting for differences in initial or final egg mass. Moreover, *P. frontalis* females produce larger hatchlings than do *P. versicolor* females of the same SVL not only by laying larger eggs, but also by investing more dry materials (and thus, more energy) into the egg. Given a link between interspecific competition (and niche restriction) and morphology, it seems likely that morphological differences at hatching may facilitate the coexistence of the two lizards. The two lizards differed in embryonic thermosensitivity and water uptake by eggs during incubation, suggesting that they use different microhabitats in the area of sympatry.

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## 1. Introduction

The mechanisms promoting the coexistence of sympatric species have been studied for many decades (MacArthur and Levins, 1967; Schoener, 1974, 1982; Weins, 1977; Gordon, 2000). Species cannot coexist without a quantitative partitioning of resources along the axes of diet, space and time (Schoener, 1974; Partridge, 1978; Tokeshi, 1999; Gordon, 2000). Competition, resulting in character displacement which in turn reduces competition for similar resources, is the main factor proposed to explain differences in body size or other morphological traits directly associated with the niche exploitation among coexisting species (Hutchinson, 1959; Abbott et al., 1977; Grant and Grant, 1980; Juliano and Lawton, 1990a,b; Šimková et al., 2003). Temperature is a most important abiotic factor affecting many biological processes in organisms and has consequences on their habitat requirements and hence spatial distribution (Tinkle and Gibbons,

1977; Angilletta et al., 2002; Edwards and Richardson, 2004; Helland et al., 2007). It has been suggested that temperature is a part of an animal's multidimensional niche and should be treated as an ecological resource (Magnuson et al., 1979; Cerda et al., 1998).

Sympatric reptiles may respond differently to variation in temperature at the spatial scale of the local community by using microhabitats with different thermal regimes (Du et al., 2006; Daly et al., 2008). As in other vertebrates (Johnston et al., 1996; Lindström, 1999), the effects of temperature on developing embryos are much more pronounced than those observed in later ontogenetic stages in reptiles (Birchard, 2004). Thus, the embryonic stage provides an ideal time phase to study the coexistence of sympatric reptiles. The optimum range of temperatures for the development of reptilian embryos is relatively narrow and may vary not only among but also within species, being broadly correlated with a species' or a population's natural incubation environment (Overall, 1994; Deeming, 2004; Booth, 2006). Co-existing reptiles that use microhabitats with different thermal regimes often differ in embryonic temperature sensitivity, and this is especially true for species depositing eggs in shallow nests (Lu et al., 2009).

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Toad-headed lizards of the genus *Phrynocephalus* (Agamidae) are widely distributed in arid or semiarid regions in Central and West Asia, westwards to South Jordan and eastwards to Hebei Province of China (Zhao, 1999). Their taxonomies are nomenclatural headaches to systematists. Recent work has shed considerable light on the systematics of this group, but resulted in considerable changes in nomenclature in members of the genus (Barabanov and Ananjeva, 2007). Of some 40 currently recognized species, nineteen can be found in China, with *Phrynocephalus frontalis* having the most easterly distribution (Zhao, 1999). Widespread sympatry between different species pairs occurs in several areas of China, such as *P. frontalis* and *Phrynocephalus versicolor* in central Inner Mongolia, *Phrynocephalus przewalskii* and *P. versicolor* in western Inner Mongolia, and *Phrynocephalus axillaris* and *Phrynocephalus forsythii* in southern Xinjiang (Zhao, 1999). Regional distribution of co-occurring pairs of *Phrynocephalus* lizards over a wide geographic range is indeed interesting, but nothing is known about why and how these co-occurring species exist in their sympatric areas. Co-existence of species pairs could have arisen via divergence in niche in sympatric areas if differences in morphological characters are naturally selected traits by this thermally challenging environment and/or by interspecific competition.

Here, we describe a study incubating eggs of two small sized toad-headed lizards (*P. frontalis* and *P. versicolor*) at three constant temperatures (24, 28 and 32 °C) to examine whether they differ in embryonic thermosensitivity and hatchling morphology. *P. frontalis* is endemic to China, occurring in Gansu, Hebei, Inner Mongolia, Ningxia, Qinghai, Shaanxi and Shanxi; *P. versicolor* ranges from North-Northwest China (Inner Mongolia, Ningxia and Xinjiang) to Mongolia, Kazakstan and Kyrgyzstan (Zhao, 1999). Lizards in this study were collected in the central part of Inner Mongolia, where the two species coexist (Fig. 1). We address four questions: (1) Do the two species differ in embryonic thermosensitivity? (2) If so, are differences in embryonic thermosensitivity indicative of variations in selection of thermally different microhabitats for oviposition in the sympatric area? (3) Do the two species differ in morphology at hatching? (4) If so, do differences in morphological traits support the prediction of species coexistence through niche divergence?

## 2. Materials and methods

### 2.1. Animal collection and care

We collected lizards by noose or hand in May 2005 in an area between Ordos (40°02'N, 107°01'E) and Wulatehouqi (41°27'N, 106°59'E), Inner Mongolia (Fig. 1). Females with yolking follicles or oviductal eggs were transported to our laboratory in Nanjing, where between 10–15 individuals were housed together in each

100 cm × 60 cm × 40 cm (length × width × height) communal cage, in an indoor animal holding facility. The cages contained a substrate of sand (~15 cm depth), with rocks and pieces of clay tiles provided as shelter and basking sites. Thermoregulatory opportunities were provided during daylight hours (05:00–19:00 h) by a 100-W incandescent lamp suspended over one end of the cage; overnight temperatures followed indoor ambient temperatures (23–28 °C). Mealworms (*Tenebrio molitor*) and house crickets (*Achetus domesticus*) dusted with multivitamins and minerals and water were provided daily, so that excess food was always available in the communal cages. Females with shelled oviductal eggs were removed from the communal cages, and housed individually in 20 cm × 15 cm × 20 cm egg-laying cages with 4 cm depth moist soil and a 20-W spotlight mounted in each cage to allow thermoregulation.

### 2.2. Egg collection and incubation

Females of both species laid a single clutch of 2–6 pliable-shelled eggs per season between late May and early July. Eggs were collected, measured (to the nearest 0.01 mm) for length and width using Mitutoyo digital calipers and weighed (to the nearest 1 mg) on a Mettler balance often within 3 h after oviposition, thereby minimizing the uncertainty about the egg mass at oviposition (hereafter initial egg mass) due to loss or gain of water. Post-oviposition females were measured for snout-vent length (SVL) and weighed before they were returned to the communal cages, where they remained until release to the field in August. Detailed data on female reproduction will be reported elsewhere.

Ninety-nine eggs laid by 31 *P. frontalis* females (44–59 mm SVL) and 100 eggs laid by 26 *P. versicolor* females (48–59 mm SVL) were used in this study. Sixteen *P. frontalis* eggs and 15 *P. versicolor* eggs, each from one of the 31 clutches with more than three eggs, were dissected for identification of embryonic stage at oviposition, according to the criteria proposed by Dufaure and Hubert (1961). Egg contents (yolk plus embryo) were weighed; eggshells were rinsed in water, dried by blotting with a paper towel, and weighed. Egg contents and eggshells were oven dried to a constant mass at 60 °C for determination of water content. The remaining eggs were systematically incubated at 24, 28 and 32 (±0.2) °C using Shellab incubators (Sheldon MFG Inc., USA), such that eggs from single clutches could be distributed as equally as possible among the three temperature treatments. One 200 mm × 150 mm × 80 mm plastic container was used to hold all eggs of the same species in a given treatment. The containers contained known amounts of vermiculite and distilled water (2 g water: 1 g dried vermiculite) to produce approximately –12 kPa water potential (Lin and Ji, 1998), and were covered with a perforated plastic membrane to retard water loss.

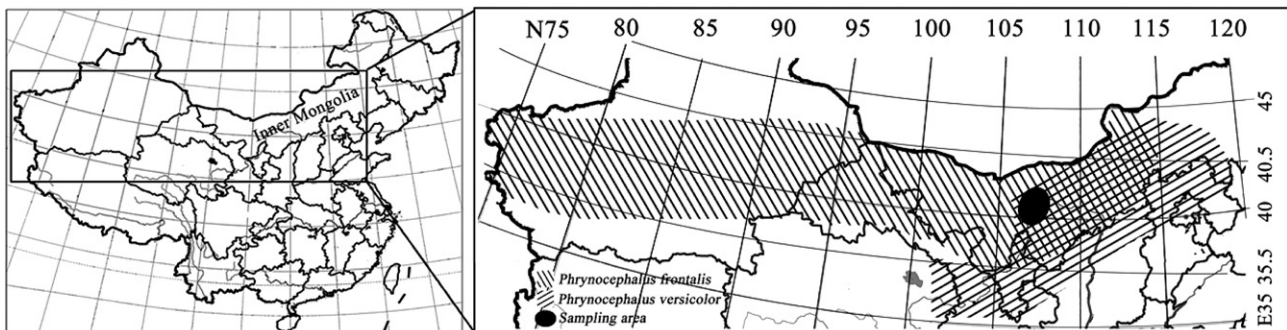


Fig. 1. Map of mainland China (left) and the distributional ranges of *P. frontalis* and *P. versicolor* in the area of sympatry (right). The area where the two species coexist and the sampling area of lizards in this study are indicated in the figure.

Eggs were half-buried lengthwise in the substrate, with the surface near the embryo exposed to air inside the container. Eggs were isolated from each other using dividers that created 25 mm × 25 mm × 70 mm chambers inside the container. We weighed containers and eggs at 5-day intervals, and added water into the substrate to compensate for evaporative losses and water taken up by eggs. To minimize any possible effects of a moisture gradient in the substrate on the incubating eggs, we temporarily dismantled dividers when adjusting water potential. Our treatments were not replicated for logistic reasons. This shortcoming might lead our results to the putative incubator effects (Hurlbert, 1984), but the problems with our experimental design, if any, were considered less important for two reasons: (1) the incubators were the same model and were precalibrated with a standard thermometer; and (2) the same incubators were used in our previous studies on other species of reptiles, and data generated were repeatable (e.g., Hao et al., 2006; Ji et al., 2007; Lu et al., 2009; Lin et al., 2007, 2008, 2010).

2.3. Size and morphology of hatchlings

Incubation length was defined as the time between oviposition and pipping. Newly emerged hatchlings were weighed and cooled to about 5 °C in a woody box for the collection of morphological data. Measurements taken for each hatchling included: SVL, tail length, head length (from the snout to the posterior end of the skull), head width (taken at the posterior end of the mandible), fore-limb length (humerus plus ulna), and hind-limb length (femur plus tibia).

2.4. Statistical analyses

Statistical analyses were performed with STATISTICA software (version 6.0 for PC). We used G-test, linear regression analysis, one-way analysis of variance (ANOVA), two-way ANOVA, repeated measures ANOVA, multivariate analysis of covariance (MANCOVA), Tukey's *post hoc* test and principal component analysis to analyze the corresponding data. Prior to parametric analyses, data were tested for normality using Kolmogorov–Smirnov test, and for homogeneity of variances using Bartlett's test (at univariate level) or Box's M test (at multivariate level). Values are presented as mean ± standard error (SE), and the significance level is set at  $\alpha = 0.05$ .

3. Results

Freshly laid *P. frontalis* eggs contained 54.5–61.2% water, whereas freshly laid *P. versicolor* eggs contained 55.8–64.8% water. The mean water content was lower in *P. frontalis* (57.4%) than in *P. versicolor* (60.8%) (one-way ANOVA on arcsine transformed data;  $F_{1,29} = 16.23, P < 0.0004$ ). Embryonic stages at oviposition, ranging from Stage 30 to Stage 32 in both species, did not differ between *P. frontalis* (mean = 31.3) and *P. versicolor* (mean = 31.0) (one-way ANOVA;  $F_{1,29} = 0.43, P = 0.518$ ).

Mean values for initial egg mass (0.41–0.87 g in *P. frontalis* and 0.37–0.63 g in *P. versicolor*) did not differ between the two species (two-way ANOVA;  $F_{1,119} = 3.03, P = 0.084$ ), nor among the three treatments ( $F_{2,119} = 2.30, P = 0.105$ ); the species × temperature interaction was not a significant source of variation in initial egg mass ( $F_{2,119} = 0.39, P = 0.678$ ). All eggs gained mass during incubation because of absorption of water (Fig. 2). Mean values for final egg mass (weighed at the time step closest to hatching) differed between the two species (repeated measures ANOVA;  $F_{1,119} = 17.87, P < 0.0001$ ), and among the three treatments ( $F_{2,119} = 21.98, P < 0.0001$ ); the species × temperature interaction had no role in influencing final egg mass ( $F_{2,119} = 1.46, P = 0.237$ ). Overall,

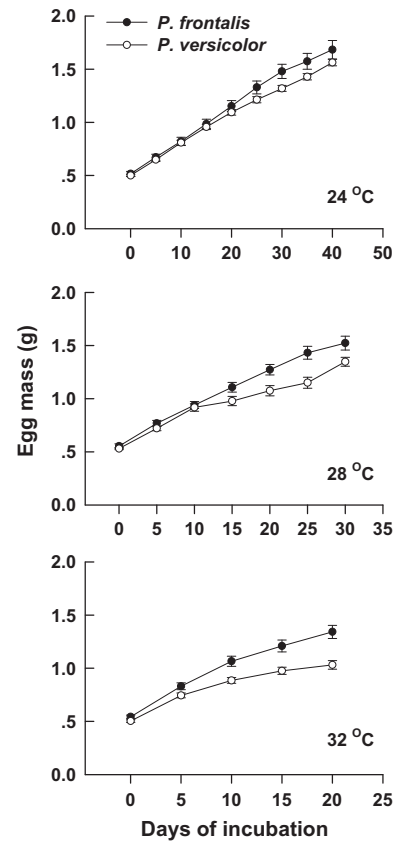


Fig. 2. Temporal changes in mass of eggs incubated at three constant temperatures. Data are expressed as mean ± SE. Solid dots represent *P. frontalis* eggs, and open dots represent *P. versicolor* eggs.

*P. frontalis* eggs gained more mass during incubation than did *P. versicolor* eggs ( $P < 0.0002$ ), eggs incubated at 24 °C did not differ from those incubated at 28 °C in mass gain (Tukey's *post hoc* test;  $P = 0.063$ ), and eggs incubated at 24 °C and 28 °C gained more mass than did those incubated at 32 °C (Tukey's *post hoc* test; both  $P < 0.0004$ ).

Neither in *P. frontalis* nor in *P. versicolor* did hatching successes differ among the three treatments (G-test; both  $P > 0.50$ ) (Table 1). Incubation length was not correlated with initial egg mass within each species × temperature combination (linear regression analysis; all  $P > 0.118$ ). Mean values for incubation length differed

Table 1 Effects of incubation temperature on incubation length and hatching success in two *Phrynocephalus* lizards, *P. frontalis* and *P. versicolor*, coexisting in Inner Mongolia, China. Data on incubation length are expressed as mean ± SE and range.

Species	Thermal treatment (°C)	Eggs incubated	Incubation length (d)	Hatching success (%)
<i>P. frontalis</i>	24	27	44.8 ± 0.7 42–50	59.3 (16/27)
	28	28	32.5 ± 0.4 30–36	75.0 (21/28)
	32	28	24.2 ± 0.2 22–26	89.3 (25/28)
<i>P. versicolor</i>	24	29	45.5 ± 0.7 40–51	82.8 (24/29)
	28	27	32.1 ± 0.6 30–38	63.0 (17/27)
	32	29	23.7 ± 0.3 22–27	75.9 (22/29)

**Table 2**  
Descriptive statistics for size and morphology of *P. frontalis* and *P. versicolor* hatchlings incubated at three constant temperatures. Data on initial and final masses of the eggs that hatched are expressed as mean  $\pm$  SE and range. Data on size and morphology of hatchlings are expressed as adjusted mean  $\pm$  SE and range, with initial egg mass set at 0.51 g.

	<i>P. frontalis</i>			<i>P. versicolor</i>		
	24 °C	28 °C	32 °C	24 °C	28 °C	32 °C
N	16	21	25	24	17	22
Initial egg mass (g)	0.52 $\pm$ 0.02 0.41–0.74	0.55 $\pm$ 0.02 0.41–0.87	0.54 $\pm$ 0.02 0.41–0.74	0.50 $\pm$ 0.01 0.37–0.56	0.53 $\pm$ 0.01 0.45–0.63	0.50 $\pm$ 0.01 0.42–0.63
Final egg mass (g)	1.68 $\pm$ 0.09 1.19–2.19	1.52 $\pm$ 0.07 1.05–2.04	1.34 $\pm$ 0.06 0.87–2.02	1.56 $\pm$ 0.03 1.23–1.88	1.35 $\pm$ 0.04 1.12–1.86	1.03 $\pm$ 0.04 0.84–1.48
Wet mass (g)	0.64 $\pm$ 0.02 0.53–0.73	0.65 $\pm$ 0.01 0.54–0.81	0.61 $\pm$ 0.01 0.43–0.71	0.60 $\pm$ 0.01 0.48–0.80	0.60 $\pm$ 0.01 0.51–0.71	0.55 $\pm$ 0.02 0.33–0.66
Snout-vent length (mm)	24.4 $\pm$ 0.2 22.8–25.7	24.6 $\pm$ 0.2 23.3–26.9	24.6 $\pm$ 0.2 21.5–27.0	24.3 $\pm$ 0.3 22.1–27.2	24.0 $\pm$ 0.3 21.2–26.9	23.2 $\pm$ 0.3 19.2–25.5
Head length (mm)	7.2 $\pm$ 0.07 6.8–7.8	7.1 $\pm$ 0.05 6.7–7.5	7.1 $\pm$ 0.06 6.6–7.8	6.9 $\pm$ 0.07 6.3–7.6	7.1 $\pm$ 0.08 6.4–7.7	6.9 $\pm$ 0.08 6.2–7.5
Head width (mm)	5.4 $\pm$ 0.05 5.2–5.8	5.5 $\pm$ 0.04 5.0–5.8	5.4 $\pm$ 0.05 4.9–5.9	5.4 $\pm$ 0.06 4.8–6.1	5.3 $\pm$ 0.08 4.6–5.9	5.0 $\pm$ 0.05 4.4–5.3
Tail length (mm)	29.7 $\pm$ 0.5 25.0–32.9	30.8 $\pm$ 0.5 22.8–33.6	29.6 $\pm$ 0.5 23.9–33.9	26.3 $\pm$ 0.4 22.1–29.3	26.7 $\pm$ 0.6 21.0–30.4	27.1 $\pm$ 0.6 22.5–31.8
Forelimb length (mm)	8.5 $\pm$ 0.1 7.8–9.1	8.6 $\pm$ 0.1 8.0–9.6	8.6 $\pm$ 0.1 7.4–9.5	8.1 $\pm$ 0.1 7.2–9.2	8.0 $\pm$ 0.1 7.0–8.6	8.0 $\pm$ 0.1 6.6–9.5
Hindlimb length (mm)	14.4 $\pm$ 0.2 13.4–15.7	14.6 $\pm$ 0.1 13.9–16.0	14.3 $\pm$ 0.1 12.5–15.6	13.2 $\pm$ 0.2 11.0–14.8	13.3 $\pm$ 0.2 11.8–14.9	13.2 $\pm$ 0.2 11.5–15.2

among the three treatments (two-way ANOVA;  $F_{2, 119} = 895.20$ ,  $P < 0.0001$ ), but not between the two species ( $F_{1,119} = 0.03$ ,  $P = 0.873$ ); the species  $\times$  temperature interaction was not a significant source of variation in incubation length ( $F_{2, 119} = 1.03$ ,  $P = 0.359$ ). Incubation length was nonlinearly sensitive to temperature in both species: from 24 °C to 28 °C, the mean incubation length was shortened by 12.3 days in *P. frontalis*, and 13.4 days in *P. versicolor*; from 28 °C to 32 °C, the mean incubation length was shortened by 8.3 days in *P. frontalis*, and 8.4 days in *P. versicolor* (Table 1).

Descriptive statistics for size and morphology of hatchlings incubated at the three temperatures are given in Table 2. MANCOVAs with initial egg mass as the covariate revealed that incubation of eggs at the three temperatures produced morphologically different hatchlings in *P. versicolor* (Wilks'  $\lambda = 0.44$ ,  $df = 14, 106$ ,  $P < 0.0001$ ) but not in *P. frontalis* (Wilks'  $\lambda = 0.74$ ,  $df = 14, 104$ ,  $P = 0.299$ ); MANCOVAs with final egg mass as the covariate also revealed that the three incubation temperatures produced morphologically different hatchlings in *P. versicolor* (Wilks'  $\lambda = 0.65$ ,  $df = 14, 106$ ,  $P = 0.040$ ) but not in *P. frontalis* (Wilks'  $\lambda = 0.75$ ,  $df = 14, 104$ ,  $P = 0.310$ ). Specifically, SVL, body mass and head width were greater in *P. versicolor* hatchlings from eggs incubated at 24 °C than their counterparts from eggs incubated at 32 °C when accounting for differences in initial egg mass (Tukey's *post hoc* test; all  $P < 0.023$ ), and tail length was smaller in *P. versicolor* hatchlings from eggs incubated at 24 °C than their counterparts from eggs incubated at 32 °C when accounting for differences in final egg mass (Tukey's *post hoc* test;  $P < 0.002$ ). Hatchlings of *P. versicolor* from eggs incubated at 24 °C and 28 °C did not differ significantly in any examined trait when accounting for differences in initial or final egg mass (Tukey's *post hoc* test; all  $P > 0.077$ ).

Data pooled for hatchlings from eggs incubated at 24 °C and 28 °C, the two temperatures having no differential effects on the traits (including mass gain during incubation) examined in both species, showed that *P. frontalis* hatchlings differed from *P. versicolor* hatchlings [MANCOVA with initial (Wilks'  $\lambda = 0.37$ ) or final (Wilks'  $\lambda = 0.38$ ) egg mass as the covariate;  $df = 7, 69$  and  $P < 0.0001$  in both cases] in that egg size-free mean values for body mass, head length, head width, tail length, fore-limb length and hind-limb length were significantly greater in *P. frontalis* (all  $P < 0.03$ ). A principal component analysis resolved two components (eigenvalues  $\geq 1$ ) from the seven morphological variables,

accounting for 68.4% of variation in the original data (Table 3). The first component (57.4% variance explained) had significant positive loadings for egg size-free values of body mass, SVL, head width, fore-limb length and hind-limb length (Table 3). Hatchlings of the two species differed in their scores on the first ( $F_{1,76} = 30.33$ ,  $P < 0.0001$ ) and the second principal component axes ( $F_{1,76} = 11.09$ ,  $P < 0.002$ ) (Fig. 3).

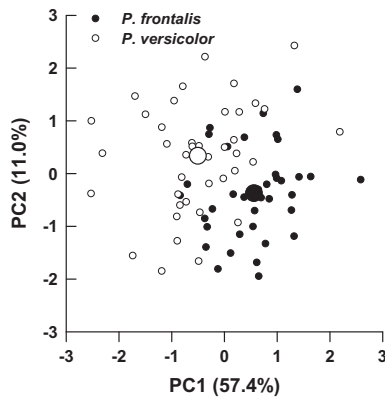
#### 4. Discussion

High temperatures influence embryonic development differently than low temperature in reptiles. For example, exposure of eggs to extremely high temperatures not only reduces hatching success but also increases embryonic abnormality, whereas low temperatures, though slowing or arresting embryonic development, often have no important effects on hatching success and embryonic abnormality (Lin et al., 2010 and references therein). Environmental temperatures in Inner Mongolia are characterized by the low mean temperatures and wide amplitude of thermal fluctuations. In face of these thermal environments, the extent to which the coexisting lizards are able to maximize their reproductive fitness in these thermally challenging sympatric environments is dependent on how well their embryos are able to tolerate extreme temperatures. Compared with the results reported for other lizards inhabiting warmer and thermally more stable regions

**Table 3**  
Loading of the first two axes of a principal component analysis on 7 variables of hatchling morphological traits. Size effects are removed in all cases by using residuals from the regressions on initial egg mass. Variables with the main contribution to each factor in bold face font.

	Factor loading	
	PC 1	PC 2
Hatchling wet mass	<b>0.801</b>	0.132
Snout-vent length	<b>0.772</b>	0.341
Head length	0.689	0.533
Head width	<b>0.700</b>	-0.242
Tail length	0.677	-0.503
Forelimb length	<b>0.827</b>	-0.118
Hindlimb length	<b>0.819</b>	-0.158
Variance explained (%)	57.4	11.0





**Fig. 3.** Positions of *P. frontalis* and *P. versicolor* hatchlings incubated at 24 °C and 28 °C, the two temperatures having no differential effects on the traits examined in the two species, in the space defined by the first two axes of a principal component analysis based on 7 hatchling morphological variables. Effects of egg size were removed using residuals from the regressions of corresponding variables on initial egg mass. Larger symbols show the mean values for scores on the two axes.

(Lin and Ji, 1998; Ji and Zhang, 2001; Pan and Ji, 2001; Ji et al., 2002), hatching successes at 24 °C and 32 °C were high in both species studied herein, thus adding evidence for the existence of a widened range of viable incubation temperatures in lizards inhabiting cooler and thermally more variable regions (Hao et al., 2006).

The incubation temperatures of 24 °C and 28 °C did not have any differential effects on the hatchling traits examined in *P. versicolor*, whereas body sizes (both SVL and body mass) were larger in hatchlings from incubation temperatures of 24 °C and 28 °C compared with 32 °C. Thus, the temperature 32 °C is suboptimal for incubation of *P. versicolor* eggs. On the contrary, *P. frontalis* hatchlings from eggs incubated at 32 °C did not differ from hatchlings derived from eggs incubated at 24 °C and 28 °C in any examined trait. What can be inferred from this difference is that embryonic thermosensitivity differs between *P. frontalis* and *P. versicolor*. The upper threshold over which incubation temperatures are suboptimal differs among reptilian species, being broadly correlated with a species' natural incubation environments (Deeming, 2004; Booth, 2006; Lu et al., 2006, 2009). In the five lizards coexisting in several areas of China, for example, eggs can be incubated at 30 °C without any adverse effects on hatchling phenotypes in *Takydromus septentrionalis* (Lin and Ji, 1998), *T. wolteri* (Pan and Ji, 2001), *Eumeces chinensis* (Ji and Zhang, 2001; Chen et al., 2003) and *E. elegans* (Du et al., 2003) using open and relatively warm microhabitats, whereas the upper threshold (28 °C) is lower in *Scincella modesta* using shaded and relatively cool microhabitats where temperatures are rarely higher than 30 °C even in the hottest months (Lu et al., 2006). Given that the ability of embryos to tolerate high temperatures is greater in *P. frontalis*, we hypothesize that nest microenvironments are on average warmer in *P. frontalis* than in *P. versicolor*. Niche divergence in the spatial dimension resulting from depositing eggs in thermally different environments has been found to facilitate the coexistence of sympatric lizards in North-Northwest China (Qu, 2006; Li, 2009).

The mean SVL of adults is slightly but significantly smaller in *P. frontalis* (~51 mm in both sexes) than in *P. versicolor* (~52 mm in both sexes), and *P. frontalis* females produce fewer but larger eggs (and thus, larger hatchlings) than do *P. versicolor* females of the same SVL (Qu, 2006). Data of this study further show that the two species are morphologically different at hatching, as indicated by all the morphological traits examined, except SVL, were greater in *P. frontalis* than in *P. versicolor* when accounting for differences in initial egg mass. However, the lack of comparable data on the niche

exploitation for the two lizards makes it difficult for us to clarify the ecological correlates of these morphological differences. Related species use more similar resources than do unrelated species (Hutchinson, 1959; Abbott et al., 1977; Grant and Grant, 1980; Abrams, 1998; Šimková et al., 2003), so do the two lizards studied herein with extremely high interspecific dietary overlap (Zhao, 1999). Thus, any niche divergence resulting from morphological differences could be of importance in facilitating species coexistence by reducing interspecific competition for similar resources. Given that a larger predator consumes larger prey to maximize net energy gain (Schoener et al., 1982; Barden and Shine, 1994; Lin and Ji, 2000; Zhang and Ji, 2004), it seems likely that the species producing larger hatchlings will on average consume larger prey during their early days of life. The head-size divergence might amplify this niche divergence, as it does in at least some other lizard species (Lin and Ji, 2000; Zhang and Ji, 2000, 2004; Ma and Ji, 2001; Qiu et al., 2001).

Water accounted for a smaller proportion of the total egg mass in *P. frontalis* than in *P. versicolor*, suggesting that *P. frontalis* females produce larger hatchlings than do *P. versicolor* females of the same SVL not only by laying larger eggs (Qu, 2006), but also by investing more dry materials and thus more energy into the egg. That females are able to further increase the size of their offspring by investing more energy into the egg is also found in *T. septentrionalis* (Du et al., 2010). Largely because *P. frontalis* eggs contained more dry materials at oviposition, they absorbed more water and thus gained more mass during incubation than did *P. versicolor* eggs. Presumably, the elevated water requirement during incubation may prevent *P. frontalis* females from depositing their eggs in the environments suitable for incubation of *P. versicolor* eggs.

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