



Original article

Life history variation among geographically close populations of the toad-headed lizard (*Phrynocephalus przewalskii*): Exploring environmental and physiological associations



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ABSTRACT

Geographic variation in life history traits has been extensively studied along latitudinal and altitudinal clines, but life history variation among geographically close populations has received much less attention. We collected gravid female toad-headed lizards (*Phrynocephalus przewalskii*) and environmental data from three localities (Alxa Zuoqi, Alxa Youqi, and Shandan) across the Gobi desert in China, to examine among-population differences in reproductive strategies. The precipitation was significantly lower in Alxa Youqi than Alxa Zuoqi and Shandan. Food availability was highest in Shandan, lowest in Alxa Zuoqi, with Alxa Youqi in between. Females from Shandan population were larger and produced more and larger eggs than their counterparts from the other two populations. Incubation period also differed among the populations, with the lowest incubation period in Alxa Youqi population, and the longest incubation period in Alxa Zuoqi population. Our data on the physiological mechanisms of incubation period indicated that the shortened incubation period in Alxa Youqi population was due to advanced embryogenesis completed prior to oviposition rather than higher embryonic heart rates during incubation. Therefore, our data support the hypothesis that geographically close populations can show different reproductive strategies if environmental factors vary among these populations.

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1. Introduction

Comparative studies both among and within species have demonstrated that life history traits may vary geographically in a diversity of species from insects to mammals (Denno and Dingle, 1981; Dunham et al. 1988; Stearns, 1992; Du et al. 2005). This geographic variation in life history is thought to be associated with the change in environmental factors such as temperature, precipitation and food availability along geographic clines. In the light of the findings from life history comparisons, investigators carry out manipulative experiments (e.g. environmental-factor manipulation and reciprocal transplant experiments) to further confirm that, in addition to genetic effects, these environmental factors do affect life history traits (Niewiarowski and Roosenburg, 1993; James and Whitford, 1994; Seigel and Ford, 2001; Du, 2006). Therefore, comparative studies on life history provide cues to identify the causes of life history variation, and are thus the first step in understanding life history evolution.

The majority of studies on geographic variation in life history focus on the variation in large scales such as latitudinal or altitudinal clines, because the drastic change in environmental factors (e.g. temperature) along these clines may induce significant life history variation (e.g. Niewiarowski, 1994; Sears and Angilletta, 2004; Du et al. 2005). However, life history variation among geographically close populations has received much less attention, probably because investigators are apt to assume that the difference in environmental factors is too small to induce measurable life history variation among geographically close populations of vertebrates. In contrast to this assumption, environmental factors may differ significantly in geographically close localities even within a single climatic zone due to the change of temperature, topography and vegetation, and such environmental differences may induce life history variation (Rohr, 1997; Skelly, 2004; Ruttenberg et al. 2005; Robbins, 2010; Kim et al. 2012; Shine et al. 2012). Life history comparisons among geographically close conspecific populations may shed light on our knowledge of life history evolution. Furthermore, such studies may demonstrate ecological divergence among populations driven by environmental selective pressures, and therefore improve our understanding of local speciation.

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Reproductive output may differ among geographically separate populations of the same species. For example, individuals living at cold regions tend to produce larger clutches with bigger eggs than do those at warm regions (e.g. Forsman and Shine, 1995; Ji et al. 2002; Du et al. 2005). This among-population difference in reproductive output is a result of combined effects of genetic determination and phenotypic variation in response to environmental changes. Previous studies have shown that a number of intrinsic and extrinsic factors (e.g. adult body size, temperature, food availability, photoperiod) play an important role in determining reproductive traits in most organisms (Stearns, 1992; Liu et al., 1996; Zhao et al., 2011). For example, large females tend to produce more and/or larger eggs, leading to greater reproductive output (e.g. Bonnet et al. 2000; King, 2000; Du et al. 2005). Females provided with abundant food may produce more eggs than those with less food (e.g. James and Whitford, 1994; Du, 2006). These findings imply that reproductive strategies could even vary among geographically close populations if the females of these populations experience distinct environments.

Incubation period is a critical reproductive trait in oviparous reptiles, because it determines the embryo's duration of exposure to disadvantageous conditions in nests (e.g. predation and extreme temperature or moisture), and the time of hatching (a determinant of hatchling fitness in many reptile species: Moreira and Barata, 2005; Olsson and Shine, 1997; Warner and Shine, 2007). Incubation period may differ among geographic populations within a species, with, for instance, shorter incubation period for eggs from cold environments than from warm environments when the eggs are incubated at identical temperatures (Ewert, 1985; Oufiero and Angilletta, 2006; Liewting et al. 2009). The shortened incubation period for eggs from cold environments is due to advanced embryogenesis prior to oviposition in some species but fast embryonic development during incubation in other species (Oufiero and Angilletta, 2006; Du et al. 2010; Sun et al. 2012). However, we do not know whether incubation period differs among geographically close populations or not, let alone physiological mechanisms underlying any among-population variation in incubation period.

We captured gravid toad-headed lizards (*Phrynocephalus przewalskii*) from three geographically close populations and brought them to the laboratory for oviposition to understand among-population variation in reproductive investment (e.g. clutch size, egg mass, and relative clutch mass). In addition, we compared incubation period of eggs from different populations to identify the potential ecological causes (environment) and physiological mechanisms (heart rate and developmental stage at oviposition) underlying any among-population difference in incubation period. With our reproductive and environmental data, we aim to test the hypothesis that geographically close populations can show different reproductive strategies if environmental factors vary among populations. We discuss our finding with regard to existing theory based on large scale environmental influences.

2. Materials and methods

2.1. Study species

Toad-headed lizards (*P. przewalskii*) are small oviparous lizards (up to 60 mm snout-vent length) that are widely distributed in Gobi desert of northern China and adjacent Mongolia (Urquhart et al., 2009). Reproductive cycles of males and females of this species have been found to be associated with environmental factors like photoperiod (Liu et al., 1996; Zhao et al., 2011).

2.2. Animal collection and environmental factors

We collected adult lizards in May, 2011 from three populations in the area of Gobi desert, Western China: Alax Zuoqi (38°50' N, 105°37' E) (40♀ and 25 ♂), Alax Youqi (39°13' N, 101°59' E) (22♀ and 15♂), and Shandan (38°35' N, 101°21' E) (31♀ and 20♂). All captured lizards were transferred to Institute of Zoology (Beijing). The animals were palpated around the abdomen to determine reproductive status (about 30% of females conceived eggs), and were then housed in plastic terraria (600 × 300 × 400, L × W × D mm) filled with 50 mm of moist sand. These terraria were kept in a room with a temperature of 24 ± 1 °C and a light cycle of 12L:12D (0700 h on and 1900 h off). Each terrarium housed 6–8 gravid females and five adult males. A 100 W light bulb was suspended 50 mm above each terrarium to provide opportunities for behavioural thermoregulation from 0800 to 1600 h. Food (mealworm, *Tenebrio molitor* and crickets, *Acheta domesticus*, dusted with mixed vitamins and minerals) and water were provided *ad libitum* for adult lizards. The experiment was carried out between May 15th and July 15th.

We collected monthly average ambient temperatures and average precipitation for the three localities from the website of weather.news.sina.com.cn. Insect abundance was surveyed with pitfall traps (20 traps; 200 × 100 × 100 mm) placed in the habitat where the lizards were collected. The traps were set for a 24-h period and the mass of all the insects in each trap was weighed to 0.01 g. We searched lizards in walking-velocity of 0.5 m/s between 1000 h and 1500 h to estimate the relative population density of lizards, which was calculated as the number of individuals encountered per hour during the field search. Relative food availability was estimated by dividing insect mass by lizard population density.

2.3. Maternal body size and reproductive life history

All lizards were measured for snout-vent length (SVL) to 0.5 mm, mass to 0.01 g, and toe-clipped for individual identification. Relative clutch mass (RCM) was calculated as the ratio of clutch mass to maternal post-oviposition mass. In the laboratory, we palpated the abdomens of each female every five days, and any animal with oviductal eggs was transferred to a small glass terrarium (200 × 150 × 200 mm) filled with 20 mm-depth moist sand. Each small terrarium was checked at least three times a day for freshly laid eggs. When laid clutches were found, eggs were counted and weighed (±0.001 g) promptly so as to minimize potential changes in mass due to water exchange. Postpartum females were returned to their original terraria.

2.4. Embryonic development

We determined the embryonic stage at oviposition according to the classification scheme of Dufaure and Hubert (1961) by dissecting one egg that was randomly selected from 6 to 9 clutches in each population. The remaining eggs were placed in plastic boxes (160 × 115 × 40 mm) filled with moist vermiculite (–220 KPa, 1 g water/1 g vermiculite) and incubated at 28 °C. Incubation period was calculated as the number of days between oviposition and hatching.

We measured heart rates of embryos (beats per minute, bpm) at approximately halfway (day 15) through the total incubation period using an infrared heart rate monitor (Buddy Digital Egg Monitor: Avian Biotech, Cornwall, UK; see detailed procedures in Du et al., 2009). The eggs were acclimated in an incubator set at 28 °C for 2 h prior to being placed individually on the Buddy egg monitor (inside the incubator) to record heart rates.

2.5. Statistical analysis

We only used the data on the first clutch to test for among-population differences in reproductive traits, because the majority of females only laid one clutch in the laboratory (95% for Alxa Zuoqi population, 81% for Alxa Youqi population, and 94% for Shandan population). Friedman ANOVA was used to test for differences in monthly mean temperature and precipitation among the three localities. We used one-way ANOVAs to determine among-population differences in food availability, female body size, clutch size, egg size, clutch mass, RCM, heart rates and incubation period. Correlation was used to analyse the relationship between heart rate and incubation period. ANCOVAs were conducted to determine among-population differences in clutch size, egg size and clutch mass with female body size as a covariate, and to assess differences in incubation period between populations with heart rate as a covariate. To avoid pseudoreplication, all analyses were conducted on clutch means for heart rate and incubation period. A median test was used to compare differences in embryonic stages at oviposition between populations. All values are reported as the mean \pm SE.

3. Results

3.1. Environmental factors

Temperature, precipitation and food availability differed among the three geographically close populations. Annual average temperature was higher in Alxa Zuoqi and Alxa Youqi than Shandan ($\chi^2 = 22.55$, $df = 2$, $P < 0.00001$, Fig. 1a). Annual precipitation was greater in Alxa Zuoqi and Shandan than in Alxa Youqi ($\chi^2 = 20.36$, $df = 2$, $P < 0.0001$, Fig. 1b). Relative food availability was highest in Shandan, lowest in Alxa Zuoqi, with Alxa Youqi in between ($F_{2,30} = 18.94$ $P < 0.00001$, Fig. 1c).

3.2. Body size and reproductive traits

Body size was greater in Alxa Youqi and Shandan populations than in Alxa Zuoqi population (SVL: $F_{2,90} = 7.66$, $P < 0.001$; Body mass: $F_{2,90} = 7.96$, $P < 0.001$) (Fig. 2). Clutch size, clutch mass and egg size all differed among the populations (Clutch size: $F_{2,90} = 9.55$, $P < 0.001$; Clutch mass: $F_{2,90} = 15.89$, $P < 0.00001$; Mean egg mass: $F_{2,90} = 3.49$, $P = 0.03$). The clutch size and mass were greater in Shandan population than in Alxa Zuoqi and Alxa Youqi populations (Fig. 3a, b). Females from Shandan and Alxa Zuoqi populations laid larger eggs than those from Alxa Youqi population (Fig. 3c). These among-population differences were still significant even after the effect of maternal size was statistically removed (Clutch size: $F_{2,89} = 4.19$, $P = 0.02$; Clutch mass: $F_{2,89} = 8.59$, $P < 0.001$; Mean egg mass: $F_{2,89} = 3.17$, $P = 0.04$). As a result, the reproductive effort (measured as relative clutch mass, RCM) also differed significantly among the populations ($F_{2,89} = 16.99$, $P < 0.00001$), with higher RCM in Shandan population than in Alxa Zuoqi and Alxa Youqi populations (Fig. 3d).

3.3. Embryonic development

Incubation period was longest for eggs from the Alxa Zuoqi population, shortest for eggs from the Alxa Youqi population, with eggs from Shandan population in between ($F_{2,34} = 5.92$, $P < 0.01$; Fig. 4a). The embryonic stage at oviposition was earliest in the Alxa Zuoqi population and latest in the Shandan population, with the Alxa Youqi population in between ($\chi^2 = 7.43$, $df = 2$, $P = 0.02$; Fig. 4b). Heart rate was negatively related to incubation period ($r = -0.39$, $F_{1,26} = 4.67$, $P < 0.05$), but did not differ statistically among the three populations ($F_{2,25} = 1.46$ $P = 0.25$) (Fig. 4c). The

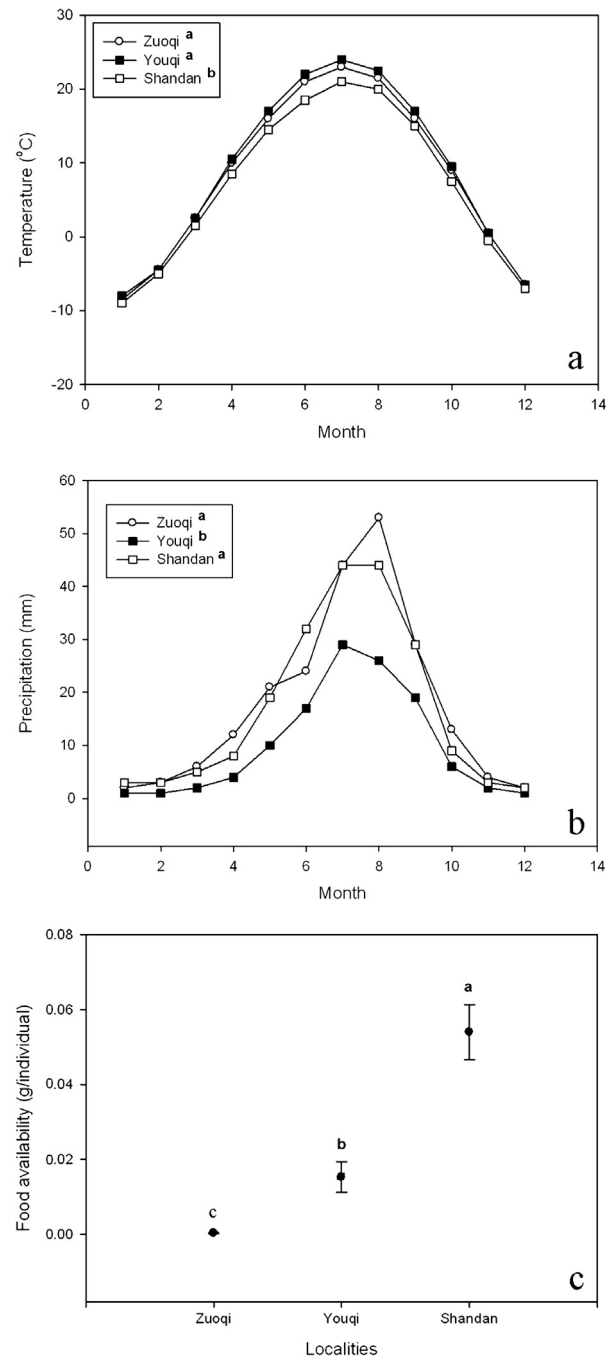


Fig. 1. Differences in environmental factors among the three localities where the toad-headed lizards, *Phrynocephalus przewalskii*, were collected. (a) monthly average ambient temperatures (b) monthly average precipitation, (c) food availability. Means with different letters above the error bars or after the names of the sites in the legends are statistically different (Tukey's test). Data on temperature and precipitation were obtained from weather.news.sina.com.cn. Food availability was calculated as the ratio of insect mass to lizard population density.

among-population difference in incubation period was still significant ($F_{2,24} = 5.78$, $P < 0.01$) after the effect of heart rate on incubation period had been removed by an ANCOVA including heart rate as a covariate.

4. Discussion

Previous studies have demonstrated life history variation over a large geographic scale, such as latitudinal and altitudinal clines in

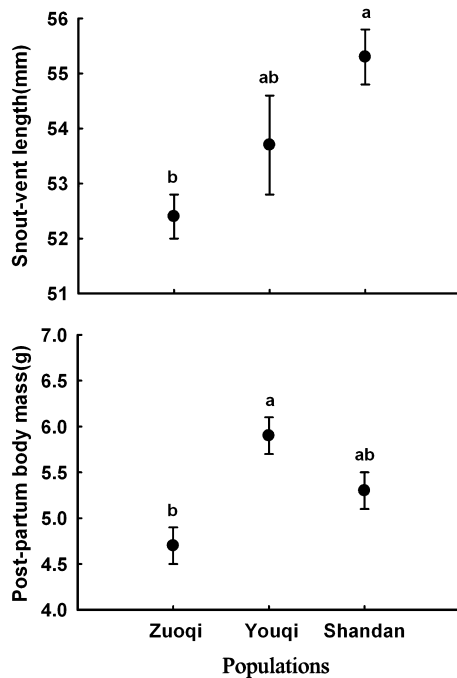


Fig. 2. Snout-vent length and post-partum body mass of toad-headed lizards, *Phrynocephalus przewalskii*, from three geographically close populations in Gobi, China. Data are expressed as means ± 1 SE. Means with different letters above the error bars are statistically different (Tukey's test). Sample sizes for the Alxa Zuoqi, Alxa Youqi, and Shandan populations were 40, 22 and 31, respectively.

reptiles (Dunham et al. 1988; Niewiarowski, 1994) as well as in other animals from insects to mammals (Denno and Dingle, 1981; Stearns, 1992). Our study indicates that life history traits can vary significantly even among geographically close populations (only 110–370 km apart in our samples). The among-population

variation not only exists in maternal body size and reproductive output, but also in incubation period and developmental stages of embryos at oviposition.

In maternal body size there exists a considerable among-population variation in a number of animal species ranging from insects to mammals (Patton and Brylski, 1987; Stillwell et al. 2007; Louzao et al. 2008). Along a latitudinal cline, for instance, body size is larger in high-latitude populations than low-latitude populations in many species, a trend known as Bergmann's rule (e.g. Ashton and Feldman, 2003; Angilletta et al. 2004; Sears and Angilletta, 2004). We found that maternal body size varied among geographically close populations in *P. przewalskii*. However, the ultimate and proximate mechanisms underlying the variation in body size can not be identified until we have gathered more data related to such mechanisms. These data include, but are not limited to, the growth rate and age at maturity of post-hatching individuals, and the selective forces driving body size evolution among the populations in this species (Angilletta et al. 2004; Du et al. 2012).

As reported in many other lizard species (Du et al. 2005; Ji et al. 2002; Pincheira-Donoso and Tregenza, 2011), large females laid more and larger eggs than small females in *P. przewalskii*. Nonetheless, the among-population difference in reproductive output was not entirely attributable to body size variation. This result suggests that other factors in addition to body size also contribute to the variation in female reproductive output. Therefore, the optimal reproductive energy allocated by females could differ among populations. Female *P. przewalskii* from Shandan population produced more and larger eggs than other populations, and thus had higher reproductive efforts (RCM) (Fig. 3). In the other two populations, reproductive efforts were similar, but the trade-off between egg size and number seems different. Females tended to produce more eggs in Alxa Youqi, but larger eggs in Alxa Zuoqi (Fig. 3).

Incubation period is not only determined by developmental stage of embryos at oviposition, but is also a function of heart rate, because there is likely a fixed number of heart beats during

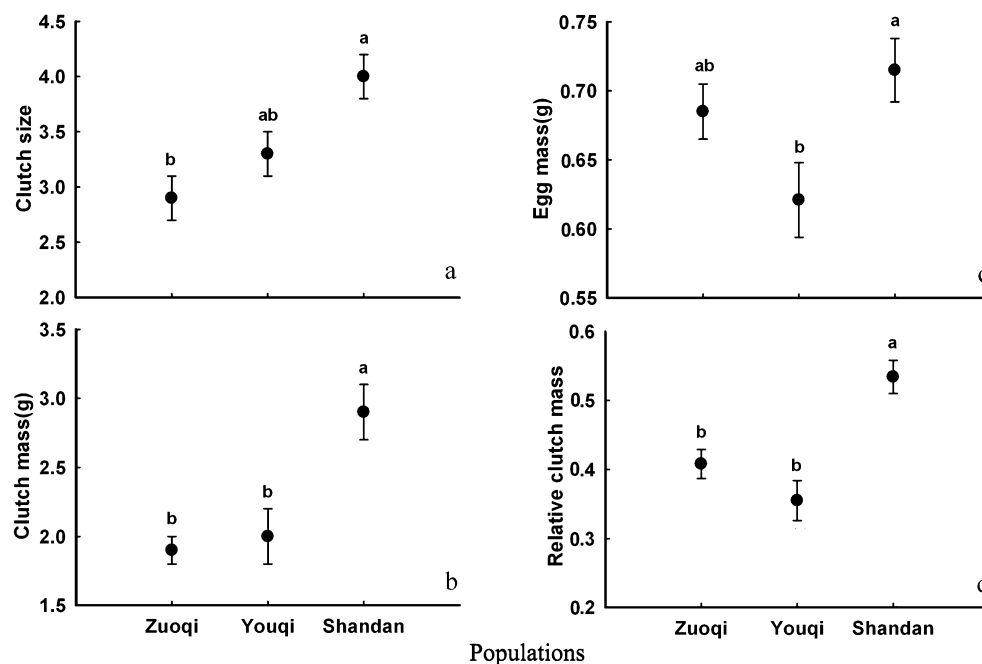


Fig. 3. Geographic variation in clutch size (a), clutch mass (b), egg mass (c), and relative clutch mass (RCM) (d) of the toad-headed lizards, *Phrynocephalus przewalskii*. Graphs show least square mean ± 1 SE (SVL as the covariate). Means with different letters above the error bars are statistically different (Tukey's test). Sample sizes for the Alxa Zuoqi, Alxa Youqi, and Shandan populations were 40, 22 and 31, respectively.

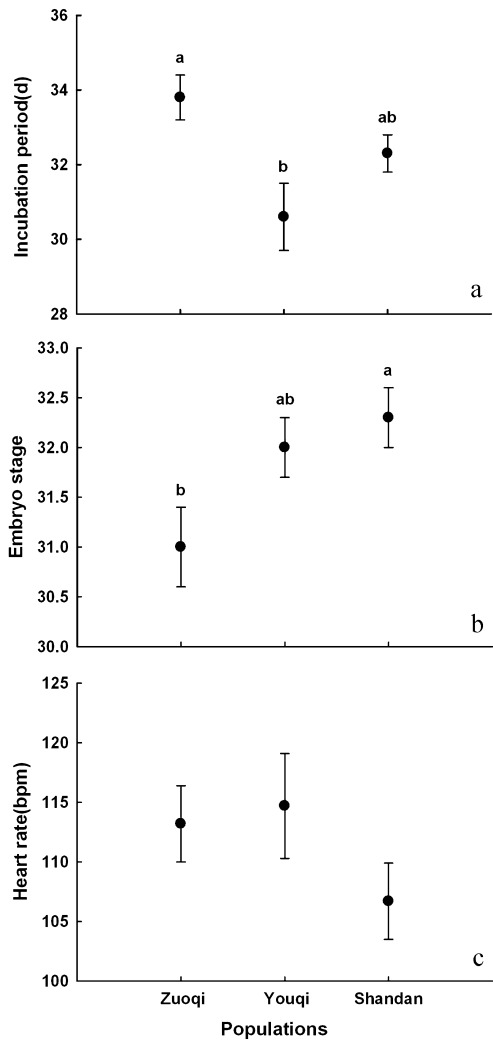


Fig. 4. The incubation period (a), embryonic stage at oviposition (b) and heart rate (c) of the toad-headed lizards, *Phrynocephalus przewalskii*. Eggs were incubated at 28 °C, and heart rates were measured at 28 °C approximately halfway through the incubation period. Graphs show mean values \pm 1 SE (SVL as the covariate). Means with different letters above the error bars are statistically different (Tukey's test). Sample sizes for the Alxa Zuoqi, Alxa Youqi, and Shandan populations were 13, 7 and 17 for incubation period, 11, 6 and 11 for heart rate, and 8, 9 and 6 for embryonic stage at oviposition, respectively.

incubation (Du et al. 2009). Our data indicated that the shortened incubation period in Alxa Youqi population was due to advanced embryogenesis completed prior to oviposition rather than higher embryonic heart rates during incubation. Embryos from Alxa Youqi population hatched 3 days earlier than those from Alxa Zuoqi population, because the embryos were 1 stage later in development at oviposition in Alxa Youqi population than Alxa Zuoqi population. In contrast, compared with Alxa Youqi population, embryos from Shandan population hatched 2 days later, but had similar developmental stages at oviposition. The relatively low heart rate in the Shandan population, although not statistically significant, was likely enough to cause the two day delay in hatching. Heart rate was negatively related to incubation period in this lizard, although other physiological traits that may affect metabolic rate. For example, as reported in an American lizard, *Sceloporus undulatus* (Du et al. 2010), heart size could be smaller in Shandan population than Alxa Youqi population, leading to low metabolic (developmental) rates.

Do environmental differences account for life history variation among geographically close populations? On the basis of the rank of environmental and life history variables among the three populations (Table 1), we identify the most probable environmental factors determining the among-population patterns of life history. First, body size and reproductive traits are more closely associated with food availability than temperature and precipitation in our geographically close populations. Females were larger and produced more and larger eggs in localities with high food availability than those with low food availability (Table 1). Comparative and manipulative experiments on food availability have confirmed that female lizards can lay more eggs by increasing clutch size or clutch frequency when food is sufficient (James and Whitford, 1994; Shou et al. 2005; Du, 2006). By contrast, reproductive output is likely associated with temperature in widespread species along latitudinal clines. Females from high-latitude populations tend to produce more and larger eggs than those from low-latitude populations (Stearns, 1992; Angilletta et al. 2006), probably because larger offspring survive better in cold environments than do smaller offspring (Yampolsky and Scheiner, 1996; Fischer et al. 2003). The role that food availability plays along latitudinal gradients in reproductive traits should not be ruled out, however, as it is not well understood. Second, the among-population variation in incubation period is most closely associated with precipitation rather than temperature and food availability in our study. Environmental moisture might be able to shape the evolution of incubation period, possibly through its relation with embryonic stage at oviposition or embryonic heart rate, with lizards from dry environments having shorter incubation periods than those from wet environments (Table 1).

Our comparative study found that reproductive life history traits differed among geographically close populations of desert lizards. This among-population difference could be caused by (1) genetic effects, as a result of adaptation to local environment; (2) maternal effects, attributable to maternal nutrition and energy accumulation in the previous season or just prior to our collection (James and Whitford, 1994; Bonnet et al. 2001); or (3) plasticity, simply due to phenotypic variation in response to environmental differences among populations. Future studies using common garden and reciprocal transplant experiments would be able to identify these mechanisms underlying the among-population difference in life history traits. Investigations on life histories of the lizards in Gobi are thus encouraged to facilitate inter-continent comparisons of adaptive strategies of lizards in response to desert environments.

Table 1
Summary by rank of environmental factors and reproductive traits of toad-headed lizards, *Phrynocephalus przewalskii*, among three geographically close populations in Gobi, China. Ranks were determined by statistical results. Different categories denote significantly different values unless otherwise noted (i.e. medium (NS) denotes a middle value that was not significantly different than the higher and lower values).

Trait	Alxa Zuoqi	Alxa Youqi	Shandan
Environmental factors			
Ambient temperatures	High	High	Low
Average precipitation	High	Low	High
Food availability	Low	Medium	High
Reproductive traits			
Body size	Small	Medium (NS)	Large
Clutch size	Small	Medium (NS)	Large
RCM	Small	Small	Large
Egg size	Medium (NS)	Small	Large
Incubation period	Long	Short	Medium (NS)
Embryonic stage	Early	Medium (NS)	Late

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