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Maternal warming influences reproductive frequency, but not hatchling phenotypes in a multiple-clutched oviparous lizard

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ABSTRACT

The understanding of life-history responses to increased temperature is helpful for evaluating the potential of species for tackling future climate change. Herein, adult southern grass lizards, *Takydromus sexlineatus*, were maintained under two thermal regimes simulating current thermal environment and a 4 °C warming scenario to determine the effects of experimental warming on female reproduction and offspring phenotypes. Experimental warming caused females to oviposit earlier and more frequently; however, it did not affect other reproductive traits, including clutch size, egg mass and clutch mass. Accelerated embryonic development and energy accumulation rate might have occurred in warmed females. Maternal warming appeared to increase early embryonic mortality, but did not shift hatchling size and locomotor performance. Embryos of oviparous lizards might be more vulnerable to climate change at early stages than at later stages. The impacts of climate change in oviparous lizards might be adverse in the longer term because of the shift in pre-ovipositional embryo viability, which possibly led to a decreased number of hatchlings.

1. Introduction

Temperature is an important environmental characteristic given its effects on nearly all biological and ecological processes (Angilleta, 2009). Global temperature has increased in the last century, and is predicted to continue to increase by 1.8–4.0 °C by the end of this century (IPCC, 2007). These temperature changes have already affected the distribution and survival of living organisms (Winkler et al., 2002; Thomas et al., 2004; Araújo et al., 2006), which has been observed in various species, from small insects (such as aphids) to large mammals (such as polar bears) (Bale, 1999; Stirling and Derocher, 2012). A few species can expand the distribution range and population size (Chamaille-Jammes et al., 2006; Ljungström et al., 2015), but others may reduce their distribution ranges or go extinct in response to climate warming (Dunbar, 1998; Stirling and Derocher, 2012). For those small-bodied ectotherms with limited dispersal capabilities, the ability to effectively respond to temperature changes directly affects their adaptability to future climate conditions, and determines their survival (Araújo et al., 2006; Paaijmans et al., 2013).

Phenotypic plasticity of life history, behavioural and physiological traits can facilitate and increase the resistance of animals to climate change (Urban et al., 2014; Seebacher et al., 2015; Gilbert and Miles, 2016). Consequently, plastic phenotypic responses to short-term temperature changes provide useful information for assessing the potential for adaptation to future climate change in small-bodied ectotherms (Chown et al., 2010; Merilä and Hendry, 2014). Many life-history traits (such as body size, oviposition timing, and reproductive frequency) of ectothermic animals can be modified in response to short-term temperature changes (Chamaille-Jammes et al., 2006; Marquis et al., 2008; Lepetz et al., 2009; LeGalliard et al., 2010). These responses are probably plastic and conducive to increasing their resistance to temperature change (Stearns, 1992; Niewiarowski, 1994). In lizards, behavioural modifications of gravid females can partially buffer environmental temperature variations. However, they may still be sensitive to climatic change because, as ectothermic animals, their body temperatures are primarily environmentally determined (Walther et al., 2002). Studies on life-history responses to temperature variations have been conducted in several viviparous species that reveal considerable variations in offspring morphology and performance (Sorci and Clobert, 1997; Shine and Downes, 1999; Zhang et al., 2010; Tang et al., 2012; Wang et al., 2014). However, the effects of the maternal thermal, especially warming, environment on the life history of oviparous species are seldom investigated (Du et al., 2005; Clarke and Zani, 2012; Lu et al., 2013; Schwanz, 2016).

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This study was aimed to investigate the effects of experimental warming on life history traits of a multiple-clutched, oviparous lizard species (the southern grass lizard, *Takydromus sexlineatus*) and to compare life history responses of this species to a warmed environment with those reported for other species. We maintained adult lizards under two thermal regimes (simulating current thermal environment and a 4 °C warming scenario, respectively). Then, eggs produced by females were incubated at two fluctuating temperatures to evaluate the effects of experimental warming on female reproductive output, embryonic development, and hatchling phenotypes. *T. sexlineatus* is small-sized (up to 60 mm snout-vent length, SVL) lizard, widely distributed in southern China, the Indochinese Peninsula and Indonesia (Zhao and Adler, 1993). It typically inhabits high grasslands and females lay eggs in shallow nests with pronounced temperature variations (Xu et al., 2007). Previous studies on a congeneric species, *T. septentrionalis*, showed that exposure of females to different constant temperatures causes changes in reproductive frequency and fecundity, but not in offspring phenotypes (Du et al., 2005; Luo et al., 2010). However, there is limited research on life-history responses of multiple-clutched species to fluctuating thermal environments. On the basis of previous results of maternal thermal effects on lizard reproductive output, embryonic development, and hatchling phenotypes, we predicted that: (1) while being exposed to experimental warming, female *T. sexlineatus* would oviposit earlier and more frequently, and thus alter their reproductive output; (2) egg-hatching success and hatchling locomotor performance would be reduced if experimental warming had exerted an adverse impact on pre-ovipositional (or post-ovipositional) development of embryos.

2. Materials and methods

2.1. Animal collection and husbandry

In early April 2011, we captured a total of 72 *T. sexlineatus* adults (52 females and 20 males) by hand or noose in Zhaoqing (23°03′N, 112°27′E) and transported them to the laboratory in Hangzhou Normal University. Immediately after arrival, the lizards were randomly assigned to one of three terraria (length × width × height: 120 × 50 × 40 cm, 20–24 females and 6–7 males in each terrarium) filled with moist sand and grass, and acclimated to the laboratory environment for three days. A supplementary heating source (a 70-W sunlamp specially designed for reptiles was suspended 20 cm above the ground on one side of each terrarium, and automatically switched on at 08:00 and off at 17:00) was provided to allow the lizards to bask. Two Thermocron iButton temperature loggers (DS1921, MAXIM Integrated Products/Dallas Semiconductor Ltd., Sunnyvale, USA) were placed on the sand surface in each terrarium (under the sunlamp and at the farthest place away from the sunlamp) to record the temperature every 10 min (Fig. 1A). Food, i.e., mealworms (*Tenebrio molitor*) and house crickets (*Achetus domesticus*), and water enriched with vitamins and minerals, were provided *ad libitum*.

Lizards in the Zhaoqing population become active from late March, and females produce multiple clutches with 1–4 eggs per clutch from late April to July (Xu et al., 2007). The air temperature in Zhaoqing shows a significant seasonal variation, with January being the coldest month and July being the warmest month of the year. The mean air temperature in April is approximately 22.6 ± 0.3 °C (data between 2003 and 2010, Meteorological Bureau of Guangdong Province). Therefore, we designed a thermal regime in an artificial atmospheric phenomena simulator (AAPS) room set at 22 °C, which was considered as the environmental temperatures potentially experienced by *T. sexlineatus* in the early period of active season (hereafter non-warmed treatment, 28 females and 11 males). The other thermal regime was designed in another AAPS room set at 26 °C, to mimic the thermal environment after warming of 4 °C from non-warmed treatment (hereafter warmed treatment, 24 females and 9 males). Two fluorescent lamps in

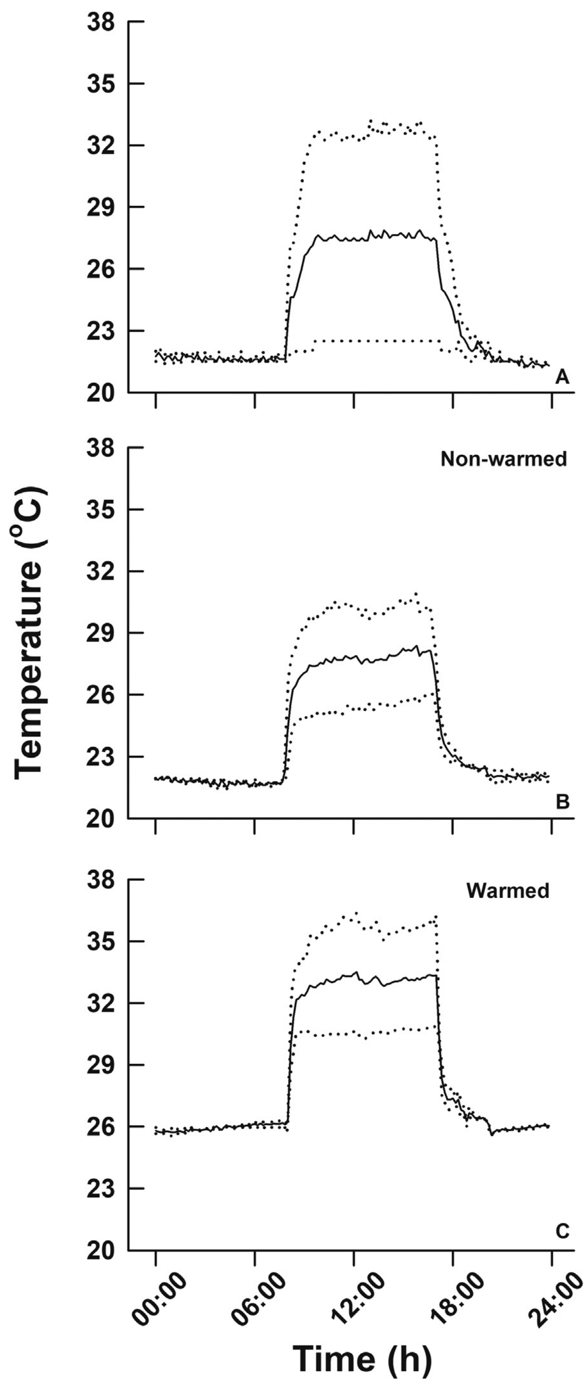

Fig. 1. Mean ambient temperatures in terraria, where adult *Takydromus sexlineatus* were maintained under different thermal environments. The upper and lower dotted lines represented the highest and lowest surface temperatures of substrate in terraria, respectively.

each AAPS room were switched on at 08:00 and off at 17:00. Lizards were maintained in seven terraria (60 × 45 × 40 cm, 7–8 females and 2–3 males in each terrarium), which were then placed in one of two AAPS rooms. A 40-W sunlamp that set to remain on between 08:00 and 17:00 was suspended 15 cm above the ground on one side of each terrarium. There were daily temperature variations in the two treatments at higher temperatures when the sunlamps were switched on. The mean surface temperatures were 24.2 and 28.7 °C (ranges of 21.5–30.8 and 25.5–35.9 °C) in non-warmed and warmed treatments, respectively (Fig. 1B, C). The mean surface temperature did not differ among different terraria in both treatments (non-warmed: $F_{3,\ 429}$ =