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The effects of incubation thermal environments on size, locomotor performance and early growth of hatchling soft-shelled turtles, *Pelodiscus sinensis*

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Abstract

We incubated eggs of the soft-shell turtle (*Pelodiscus sinensis*) at constant (ranging from 23°C to 34°C) and fluctuating temperatures (varying from 22.3°C to 32.8°C) to assess influence of incubation thermal environments on duration of incubation, hatching success and hatchling traits likely affecting fitness. Duration of incubation decreased as temperature increased, from 97.2 days at 23°C to 39.4 days at 34°C. Hatching success differed considerably among temperature treatments, with eggs incubated at lowest (23°C) and highest (34°C) temperatures exhibiting much lower hatching success (23°C: 44.0%; 34°C: 73.7%) than did those incubated at intermediate temperatures (81.7–96.9%). Eggs incubated at different temperatures produced hatchlings that differed in both carapace width and body mass, with those incubated at 23°C producing the smallest hatchlings. Hatchlings from different incubation thermal environments did not differ each other in carapace width, but eggs incubated at fluctuating temperatures produced the heaviest hatchlings, which were significantly heavier than those derived from eggs incubated at 24°C, 33°C and 34°C. Within the range from 24°C to 33°C (including fluctuating temperatures), hatchlings from 24°C performed more poorly in the racetrack than did those from higher incubation temperatures. Within the range from 26.5°C to 34°C, hatchlings from 26.5°C grew significantly faster than did those from 34°C. The most noticeable advantage of incubating eggs at the fluctuating temperature regime designed in this study is to widen the range of incubation temperatures yielding larger and well-performed hatchlings.

Keywords: Reptilia; Trionychidae; *Pelodiscus sinensis*; Egg incubation; Hatchling; Locomotor performance; Early growth

1. Introduction

Numerous studies have shown that incubation thermal environments may affect many aspects of egg incubation of reptiles, which include duration of incubation, hatching success, and sex (for species with temperature-dependent sex determination), size, morphology and physiological and behavioral performances of hatchlings (e.g., Bull, 1980; Deeming and Ferguson, 1988, 1991; Booth and Thompson, 1991; Burger, 1991, 1998; Overall, 1994; Shine et al., 1997a, b; Lin and Ji, 1998; Ji et al., 1999, 2002a, b; Braña and Ji, 2000; Ji and Du, 2001a, b; Ji and Zhang, 2001; Pan and Ji, 2001; Zhang and Ji, 2002). Obviously, reptilian eggs cannot be incubated at extremely high or low temperatures, although a brief period of daily exposure of incubating eggs to extreme temperatures may not necessarily result in an increase in embryonic mortality (Sexton and Marion, 1974; Overall, 1994; Shine and Harlow, 1996; Andrews et al., 1997). For any species of oviparous reptiles, there is a range of viable incubation temperatures yielding living hatchlings. However, within this

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range, temperatures may differentially affect hatchling traits of which some are likely to have long-term effects on an individual's performance and would therefore influence its life-time fitness (Webb and Cooper-Preston, 1989; Burger, 1991, 1998; Van Damme et al., 1992; Shine, 1995; Shine and Harlow, 1996; Alberts et al., 1997; Lin and Ji, 1998; Braña and Ji, 2000; Ji and Zhang, 2001; Ji et al., 2002b).

Reptilian eggs incubated at moderate temperatures generally produce larger and well-performed hatchlings, whereas eggs incubated at high temperatures usually produce smaller, less developed and poorly performed hatchlings with a higher proportion of deformed individuals (Gutzke and Packard, 1987; Packard and Packard, 1988; Phillips et al., 1990; Van Damme et al., 1992; Phillips and Packard, 1994; Ji and Braña, 1999; Braña and Ji, 2000; Ji and Du, 2001a; Ji et al., 2002b). Eggs incubated at low temperatures usually do not induce deformed hatchlings, but increase embryonic mortality largely because of the increased exposure time of eggs to the effects of adverse biotic or abiotic factors (Ji and Du, 2001a, b; Ji et al., 2002b). Moreover, eggs incubated at low temperatures have been proved to have higher metabolic expenditure by embryos primarily because of the longer incubation length and, consequently, produce hatchlings that are smaller in size and/or have lower energy reserves (Booth et al., 2000; Ji and Du, 2001b; Ji and Zhang, 2001; Ji et al., 2002b). Because larger hatchlings are believed to be more successful than smaller ones, they may therefore enhance reproductive success of females (Fox, 1978; Christian and Tracy, 1981; Avery et al., 1982; Ferguson et al., 1982; Ferguson and Fox, 1984; Webb, 1986; Sinervo and Adolph, 1989; Garland et al., 1990; Ji and Zhang, 2001).

In this study, we investigate the range of incubation temperatures producing larger and well-performed *Pelodiscus sinensis* (Trionychidae) hatchlings by incubating eggs in different thermal environments. *P. sinensis* is a soft-shelled turtle that is widely distributed in the central and southern provinces of China and south-eastern Asia (Zhao and Adler, 1993). The turtle is commercially important, and is cultured and harvested by local people for food. We incubated our eggs under 9 constant (ranging from 23°C to 34°C) and one fluctuating (varying from 22.3°C to 32.8°C) temperature regimes. We fixed the lower level of constant temperature at 23°C and the upper level at 34°C, because both temperatures are, respectively, close to the lower and upper limits of temperatures experienced by eggs in natural nests where they were collected.

2. Materials and methods

In late July 1998 and 1999, we obtained a total of 391 freshly laid eggs produced by 42 females from a hatchery in the vicinity of Hangzhou, Zhejiang, eastern China. All eggs were transported to our laboratory at Hangzhou Normal College, where they were numbered, measured for the diameter to the nearest 0.1 mm and weighed to the nearest 1 mg. The viability of eggs was judged by the presence of a white patch (indicative of fertilization) on the shell surface and the external characteristics of the eggshell. We incubated the majority of eggs ($N = 361$) at nine constant temperatures (23°C, 24°C, 26.5°C, 27°C, 28°C, 30°C, 32°C, 33°C and 34±0.3°C) in vermiculite-filled plastic containers ($250 \times 180 \times 70\,\mathrm{mm}^3$ (length × width × height)) within LRH-250G incubators (Guangdong Medical Instruments, China), and the remaining eggs ($N = 30$) within a chamber ($600 \times 600 \times 300\,\mathrm{mm}^3$) buried (300 mm below the ground surface) in the backyard of our laboratory. Temperatures inside the chamber varied temporally and were taken four times daily at 0600, 1200, 1800 and 2200 h (Beijing time) (Fig. 1). Eggs from single clutches were distributed as equally as possible among temperature treatments. Our eggs were laid by a large number of females ($N = 42$), so the family (clutch) effects were negligible or could be substantially averaged out in this study. We did not replicate our experiments at each temperature with different incubators due to logistic reasons. This shortcoming might lead our results subject to the putative incubator effects (Hurlbert, 1984), but the potential problems with our experimental design, if present, were less important for two reasons: First, the incubators by which we used to incubate eggs were all of the same model and were calibrated prior to the experiment with a standard thermometer. Second, the same incubators were used in our previous studies on other species of reptiles, and data generated were repeatable (e.g., Ji et al., 1999, 2002a; Ji and Zhang, 2001; Zhang and Ji, 2002).

Our experience with incubating *P. sinensis* eggs indicates that variation in incubation hydric conditions

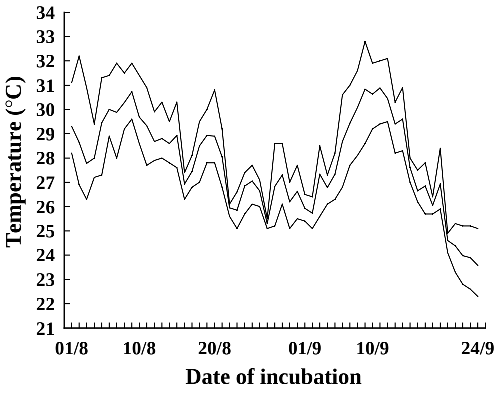

Fig. 1. Temporal changes in daily minimal, maximal and mean temperatures experienced by the *P. sinensis* eggs incubated at fluctuating temperatures.

over a wide range (from 0 to −220 kPa) does not modify phenotypes of hatchlings, so we set water potential of the incubation substrate at −12 kPa (2 g water/1 g vermiculite; Lin and Ji, 1998; Ji and Braña, 1999) for all temperature treatments. The containers holding eggs were covered with a perforated plastic membrane to retard water loss. Eggs were half-buried in the substrate throughout the course of incubation, with the white patch being always kept upward. We weighed containers daily and, if necessary, added water to the vermiculite to compensate for small evaporative losses, thereby maintaining the substrate moisture constant. We moved the containers among shelves in the incubator daily according to a predetermined schedule to minimize any effects of thermal gradients inside the incubator.

Upon emergence, each hatchling was measured for carapace width and weighed for wet body mass. Hatchlings derived from eggs incubated at constant temperatures ranging from 24°C to 33°C and fluctuating temperatures were tested for locomotor performance. We developed all trials within 1 h after hatching at the body temperature of 30°C, which was controlled by placing hatchlings in an incubator at 30°C for 30 min prior to testing. We chased each hatchling around a round racetrack (diameter = 600 mm; track width = 80 mm) for at least 1 min, and recorded its performance with a Panasonic VX7 video camera. Videotapes were later examined for sprint speed in the fastest 30 mm interval, maximal distance in a dash (hereafter maximal length), traveling length in the first 30 s (hereafter traveling length), and number of stops in the first 1000 mm (hereafter number of stops).

To test for the influence of incubation temperature on early growth, we maintained a part of hatchlings from incubation temperatures of 26.5°C, 30°C, 32°C and 34°C under identical conditions for 45 days. Hatchlings were housed, 15–20 of them, in individual glass cages ($500 \times 300 \times 300\,\mathrm{mm}^3$) with 200 mm depth water. Pieces of tiles and layers of plastic plates were moved into the cages to provide hatchlings shelters. We controlled water temperature constant at 29 ± 0.5°C, fed hatchlings commercial food (energy density = 15.4 kJ/g) ad libitum, and weighed them on 45 days since hatching.

All data were tested for normality using Kolmogorov–Smirnov test and for homogeneity of variance using Bartlett's test prior to further statistical analysis, and Log_e transformations were performed when necessary to meet the assumptions of parametric analyses. Because eggshell mass differed considerably among clutches (Du and Ji, 2001), we compared sizes (carapace width) and masses of hatchlings from different incubation thermal environments using one-way ANCOVA with eggshell-free initial egg mass (initial egg mass—hatched eggshell) as the covariate, thereby removing influence of variation in egg size. We used an ANCOVA with hatchling mass as the covariate to test for effects of temperature on locomotor capacity of hatchlings, and one-way analysis of variance (ANOVA) to test for other hatchling traits that are not related to the egg size or hatchling size. Tukey's multiple comparisons were used to test for

Table 1
Duration of incubation and hatching success of *Pelodiscus sinensis* eggs incubated in different thermal environments

Thermal environments	Temperature (°C)	Incubated eggs	Duration of incubation (d)	Hatching success (%)
Constant temperatures	23	50	97.2 ± 0.4 (92.9–101.5)	44.0 (22/50)
	24	23	88.6 ± 0.1 (88.4–88.7)	82.6 (19/23)
	26.5	38	66.1 ± 0.4 (61.6–70.9)	84.2 (32/38)
	27	32	63.4 ± 0.2 (61.0–66.2)	96.9 (31/32)
	28	30	56.3 ± 0.3 (53.8–57.8)	90.0 (27/30)
	30	71	45.7 ± 0.2 (42.5–49.8)	85.9 (61/71)
	32	60	42.0 ± 0.2 (40.4–44.9)	81.7 (49/60)
	33	38	40.4 ± 0.2 (40.0–44.9)	86.8 (33/38)
	34	19	39.4 ± 0.3 (38.9–42.5)	73.7 (14/19)
Fluctuating temperatures	27.8	30	56.8 ± 0.3 (54.4–60.1)	90.0 (27/30)

Values for duration of incubation are expressed as mean ± SE (range).

differences among hatchlings from different incubation thermal environments.

3. Results

Initial egg mass was not a significance source of variation in incubation length for all eggs incubated in different thermal environments (all $P > 0.05$). Duration of incubation varied considerably among temperature treatments (ANOVA-$F_{9,301} = 4426.6$, $P < 0.0001$), and it decreased nonlinearly as temperature increased (Table 1). For example, for every 2°C increase in temperature from 24°C to 34°C, the incubation length decreased averagely 22.5, 9.8, 10.6, 3.7 and 2.6 days, respectively (Table 1). The incubation length of eggs incubated at fluctuating temperatures (mean = 27.8°C, varying from 22.3°C to 32.8°C) was very close to that of eggs incubated at 28°C (Table 1). Hatching success differed significantly among temperature treatments (G-test, $G = 23.46$, $df = 9$, $P < 0.01$), with eggs incubated at lowest (23°C) and highest (34°C) temperatures exhibiting noticeably lower hatching success (23°C: 44.0%; 34°C: 73.7%) than did those incubated at intermediate temperatures (81.7–96.9%).

Eggs incubated at different temperatures produced hatchlings that differed in both body mass (ANCOVA-$F_{9,273} = 5.67$, $P < 0.0001$) and carapace width (ANCOVA-$F_{9,273} = 7.56$, $P < 0.0001$), with those incubated at 23°C producing the smallest hatchlings (both carapace width and body mass). Hatchlings derived from eggs incubated at constant temperatures ranging from 24°C to 34°C and fluctuating temperatures did not differ from each other in carapace width (Fig. 2). Eggs incubated at fluctuating temperatures apparently produced the heaviest hatchlings, which were significantly heavier than those derived from eggs incubated at 24°C, 33°C and 34°C (Fig 2). Hatchlings derived from eggs incubated at constant temperatures ranging from 24°C to 34°C did not differ from each other in body mass (Fig. 2).

Incubation thermal environments significantly affected locomotor performance of hatchlings (Sprint speed: ANCOVA-$F_{5,110} = 9.40$, $P < 0.0001$; Maximal distance: ANCOVA-$F_{5,110} = 3.94$, $P < 0.01$; Traveling distance: ANCOVA-$F_{5,110} = 6.46$, $P < 0.0001$; Number of stops: ANCOVA-$F_{5,110} = 4.71$, $P < 0.001$). Within the temperature range considered (24–33°C, including fluctuating temperatures), hatchlings from 24°C performed more poorly in the racetrack than did those from higher incubation temperatures (Fig. 3).

Hatchling size (both carapace width and body mass) on 45 day since hatching were not related to hatchling size at hatching for all temperature treatments (all $P > 0.05$), so we used ANOVA to analyze data on early growth. The analysis showed that hatchlings from different incubation temperatures differed considerably in early growth rate (Carapace width: ANOVA-$F_{4,61} = 6.02$, $P < 0.001$; body mass: ANOVA-$F_{4,61} = 7.57$, $P < 0.0001$), with hatchlings from 26.5°C grew significantly faster than did those from 34°C (Fig. 4).

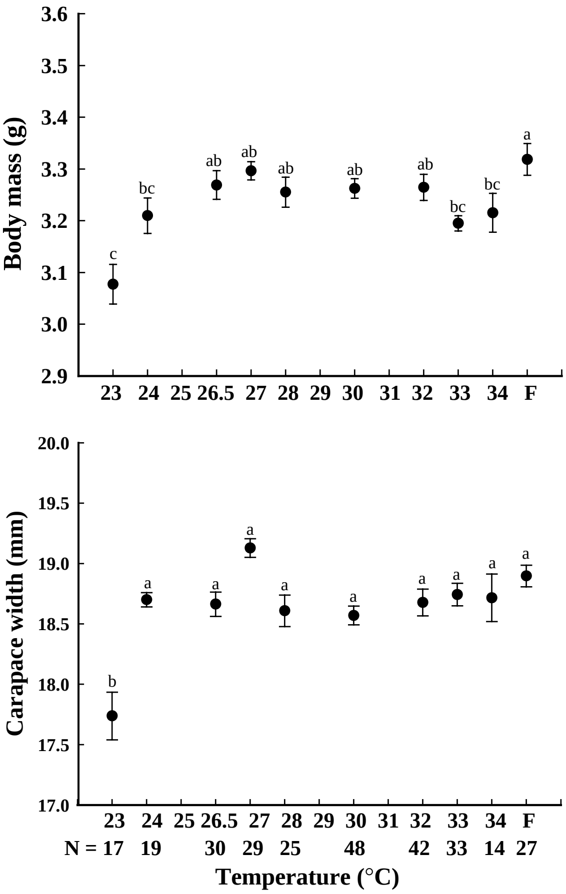

Fig. 2. Influence of incubation thermal environments on body mass and carapace width of hatchling *P. sinensis*. Values are expressed as mean ± SE. Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$).

4. Discussion

Incubation thermal environments affect all aspects examined in this study, including hatching success, incubation length, and size, locomotor performance and early growth of hatchlings. Hatching success dramatically deceased when eggs were incubated at 23°C, and it x also apparently decreased when eggs were incubated at 34°C (Table 1). Based on these observations, two conclusions can be drawn: (1) 23°C and 34°C are, respectively, close to the lower and upper limits of incubation temperatures yielding viable *P. sinensis* hatchlings; (2) exposure of *P. sinensis* eggs to temperatures

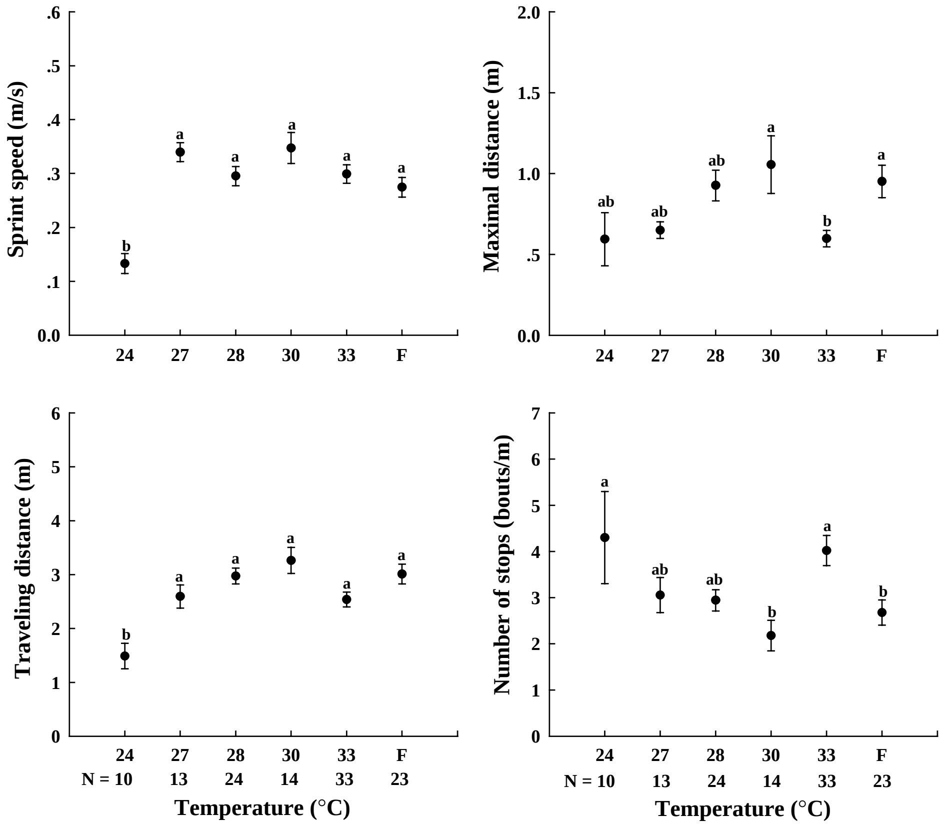

Fig. 3. Influence of incubation thermal environments on locomotor performance of hatchling *P. sinensis*. Values are expressed as mean ± SE. Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$).

lower than 23°C or higher than 34°C for a prolonged period is lethal to incubating eggs.

The incubation lengths are consistent with those at the same temperatures reported by Choo and Chou (1987) in Singapore, but the temperature range within which hatching success is higher than 80% is wider in this study (24–33°C vs. 25–31°C) presumably because of intra-specific geographic variation in thermal tolerance of embryos. In a recent work on egg incubation of Chinese skinks (*Eumeces chinensis*), Ji et al. (2002a) documented that the range of suitable incubation temperatures was wider in eggs from a higher latitudinal population than in those from a lower latitudinal population. This finding has an implication of eggs from higher latitudes being able to tolerate more severe thermal environments as an adaptation to the greater amplitude of temporal variation in temperature in higher latitudes.

As what observed in many other reptiles (e.g., Gutzke and Packard, 1987; Gutzke et al., 1987; Packard et al., 1989; Burger, 1990; van Damme et al., 1992; Lin and Ji., 1998, Ji and Du, 2001a, b), *P. sinensis* eggs incubated at moderate temperatures produce larger hatchlings than do those incubated at low (<24°C) or high (>33°C) temperatures (Fig. 2). The differences in hatchling size among temperature treatments primarily mirror influence of thermal environments on embryonic expenditure of energy during incubation (Du and Ji, 2001; Ji and Du, 2001a, b; Ji and Zhang, 2001; Ji et al., 2002b). *P. sinensis* embryos at low or high temperatures have been proved to cost more energy to complete development (Du and Ji, 2001), so it is not surprising that eggs incubated low or high temperatures produce smaller hatchlings.

Hatchling size is considered to be an important determinant of fitness in many reptiles, and larger size may have several advantages (Van Damme et al., 1992; Galán, 1996; Braña and Ji, 2000; Ji et al., 2002b). For example, larger hatchlings are more successful in hunting prey and avoiding predators (Webb, 1986; Sinervo and Adolph, 1989; Ji and Zhang, 2001), and may have prior access to limited resources and better chances to survive the first active season and winter (Fox, 1978; Ferguson et al., 1982; Ferguson and Fox, 1984; Garland et al., 1990). Thus, the smaller *P. sinensis* hatchlings derived from eggs incubated at low and high temperatures may have an implication of lower fitness at least in their first post-hatching days as compared with larger hatchlings from moderate incubation temperatures.

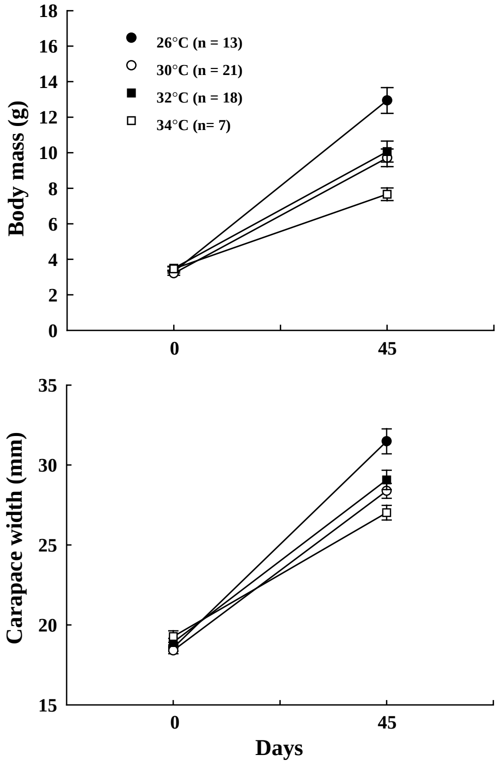

Fig. 4. Influence of incubation thermal environments on early growth of hatchling *P. sinensis*. Values are expressed as mean ± SE.

Hatchlings incubated at 24°C performed more poorly in the racetrack, whereas hatchlings incubated at 34°C performed more poorly in early growth. These results suggest that the temperature range for producing well-performed hatchlings be narrower than the range from 24°C to 34°C when *P. sinensis* eggs are incubated at constant temperatures. In this study, well-performed hatchlings were also larger in size and mass. Thus, our data add evidence supporting the conclusion that larger hatchling size is an indicative of higher fitness (Van Damme et al., 1992; Galán, 1996; Braña and Ji, 2000; Ji et al., 2002b).

Incubating eggs at fluctuating temperatures may well mimic the situation occurs in natural nests, and is therefore ecologically more meaningful (Cagle et al., 1993; Shine et al., 1997a, b). In this study, the range of fluctuating temperatures varied from 22.3°C to 32.8°C (mean = 27.8°C), so eggs incubated under this temperature regime once experienced low temperatures at which embryonic mortality would be high and smaller and poorly performed hatchlings would be produced (Fig. 1). However, eggs incubated at fluctuating temperatures exhibited high hatching success (Table 1) and produced larger and well-performed hatchlings as well (Fig. 2). These results support the conclusion that exposure of eggs to adversely low temperatures for a short period may not increase embryonic mortality and modify hatchling phenotypes (Sexton and Marion, 1974; Overall, 1994; Shine and Harlow, 1996; Andrews et al., 1997). The incubation length of eggs incubated at fluctuating temperatures is very parallel to that of eggs incubated at the constant temperature of 28°C (Table 1), indicating that the rate of embryonic development may not be accelerated or retarded when eggs are incubated at fluctuating temperatures. Overall, the most noticeable advantage of incubating eggs at the fluctuating temperature regime designed in this study is to widen the temperature range yielding larger and well-performed hatchlings, and the most noticeable disadvantage of incubating eggs at constant temperatures is to restrict temperatures yielding larger and well-performed hatchlings to a narrower range. However, no evidence available in this study supports the predication that reptilian embryos developing at constant temperatures would have adverse effects on their survival and development (e.g., Gorman and Hillman, 1977; Beuchat and Ellner, 1987).

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