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# Relatively low upper threshold temperature in lizards from cool habitats

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## Abstract

We used the slender forest skink (*Scincella modesta*) as a model animal to test for the hypothesis that the upper threshold of incubation temperature is relatively low in lizards using shaded (and thus, cool) habitats. Eight gravid females were collected in early May 2005 from a population in Hangzhou, Zhejiang (eastern China). All females laid a single clutch of 7–13 eggs between mid-May and early June. Eggs were incubated at 24, 28 and 30 (±0.2) °C. None of eggs incubated at 30 °C hatched. Eggs incubated at 24 and 28 °C differed in incubation length but not in hatching success. The incubation length at 24 and 28 °C averaged 22.3 and 20.3 days, respectively. Hatchlings from eggs incubated at 24 and 28 °C did not differ in all examined morphological traits, but hatchlings from eggs incubated at 28 °C performed apparently worse in the racetrack than did their counterparts from eggs incubated at 24 °C. The temperature of 28 °C is close to the upper thermal threshold for successful embryonic development in *S. modesta*. Compared to other oviparous lizards using open (and thus, warm) habitats, the upper thermal threshold and the range of optimal temperatures for embryonic development are both lower in *S. modesta*. Our study supports the previous conclusion that species living in thermally different habitats may differ in the upper thermal threshold and the range of optimal temperatures for embryonic development.

*Keywords:* Reptilia; Scincidae; *Scincella modesta*; Egg; Incubation; Hatching success; Morphological phenotype; Locomotor performance

## 1. Introduction

Temperature is one of the most important environmental factors that may induce phenotypic variation in ectothermic vertebrates (Johnston et al., 1996; Deeming, 2004). Temperature-induced variation in morphological, physiological and behavioral traits is widespread in reptiles and can explain a substantial portion of within population phenotypic variation (e.g. Webb and Cooper-Preston, 1989; Burger, 1991, 1998; Shine et al., 1997; Braña and Ji, 2000; Ji et al., 2003; Deeming, 2004). In reptiles that temperatures maximizing the rate of embryonic development often do not maximize hatchling phenotypes and, thus, providing optimal temperatures for developing embryos may have beneficial consequences for hatchling fitness. Unlike viviparous females that have the potential to provide optimal temperatures for developing embryos through thermoregulation, oviparous females cannot control over thermal environments for their eggs (Wapstra et al., 2004). Nest-site selection is an efficient strategy adopted by oviparous females to buffer the adverse effects of extreme ambient temperatures on embryos developing during the period from oviposition to hatching (Shine and Harlow, 1996; Shine et al., 1997). However, in species where females deposit eggs in shallow nests, eggs are actually exposed to the general surrounding thermal environments. Previous studies strongly suggest that oviparous reptiles living in thermally different habitats or geographic regions may differ considerably in the upper thermal threshold and the range of temperatures optimal for embryonic development. For example, the upper thermal threshold and the range of optimal temperatures for embryonic development are both lower in species [e.g. *Deinagkistrodon acutus* (five-paced pit-viper) and

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*Xenochrophis piscator* (checkered keelback)] using cool habitats than in species using warm habitats [e.g. *Elaphe carinata* (king ratsnake), *Naja atra* (Chinese cobra), *Eumeces chinensis* (Chinese skink) and *Takydromus septentrionalis* (northern grass lizard)] (Lin and Ji, 1998, 2005; Ji and Du, 2001a, 2001b; Ji and Zhang, 2001; Ji et al., 2001).

The slender forest skink (*Scincella modesta*) studied here is a small sized [to 55 mm snout-vent length (SVL)] oviparous diurnal sincid lizard that is widely distributed in the eastern and center provinces of China (Zhao and Adler, 1993). Despite the fact that it is taxonomically and zoogeographically well-known, the biology and ecology of this species remain almost unknown. Adult *S. modesta* are morphologically so similar to juvenile *Sphenomorphus indicus* (a medium sized sympatric viviparous skink) that they are often regarded wrongly as juveniles of the latter species. The slender forest skinks typically live in deeply shaded forests where ambient temperatures are rarely higher than 30 °C even in the hottest months, and is therefore ideally suited to testing the hypothesis that the upper threshold of incubation temperature is relatively low in species using shaded habitats. The upper threshold of incubation temperature for *S. modesta* was determined by comparing data on hatching success, morphological phenotypes and locomotor performance of hatchlings derived from egg incubated at different constant temperatures.

## 2. Materials and methods

We collected eight gravid females by hand in early May 2005 from a population in Hangzhou (30 °16′N, 120 °12′E), Zhejiang (eastern China), and brought them to our laboratory at Hangzhou Normal College, where they were individually housed in 20 × 15 × 20 cm (length × width × height) glass cages with 5 cm depth moist soil, small pieces of clay tiles, grasses and a 20-W spotlight mounted in each cage to allow thermoregulation during the daytime (0700–1900 h). These cages were placed in a room where air temperatures were never higher than 24 °C. Skinks were fed mealworms (larvae of *Tenebrio molitor*) and water enriched with vitamins and minerals ad libitum.

All eggs were collected, measured (for length and width), weighed and numbered within 2 h after being laid, thereby avoiding any uncertainty about the initial egg mass due to loss or gain of water. The viability of freshly laid eggs was judged by the presence of an embryonic disc using a spotlight. Post-oviposition females were measured (for SVL and tail length) and weighed, and were then released to the site where originally collected.

One freshly laid egg from each of the eight clutches was dissected for identification of embryonic stage at oviposition, according to the classical criteria proposed by Dufaure and Hubert (1961). The remaining eggs were systematically incubated at 24, 28 and 30 (±0.2) °C, such that eggs from single clutches were distributed almost equally among treatments. One plastic container (16 × 10 × 80 cm) was used to hold all the eggs in a given temperature treatment. The containers holding eggs 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. Eggs were half-buried in the substrate, with the surface near the embryo being exposed to air inside the container. We weighed containers every other day and, if necessary, added distilled water to compensate for small evaporative losses and water absorption by the eggs, thereby maintaining the potential of the substrate constant.

When eggs were found to have pipped, we moved them individually into covered glass jars (100 ml), thereby assuring accurate identification of emergent young. The incubation length, measured as the number of days to pipping, was recorded for each egg. Wet body mass, SVL and tail length were taken for each hatchling. A total of 49 hatchlings were used to evaluate the effects of incubation temperature on locomotor performance and morphological traits. Because locomotor performance is highly sensitive to changes in body temperature in reptiles, we conducted all trials at the body temperature of 28 °C, which was controlled by placing hatchlings in an incubator at the correspondent temperature for approximately 30 min prior to testing. Locomotor performance was assessed by chasing the hatchlings along a 2-m racetrack with one side transparent, which allowed lateral filming with a Panasonic NV-DS77 digital video camera. Each hatchling was run two times with a 30-min rest between the two successive trials. Five hatchlings refused to run, and were therefore excluded from analyses. The tapes were later examined with a computer using MGI VideoWave III software (MGI Software Co., Canada) for sprint speed in the fastest 15-cm interval and the maximal distance traveled without stopping (hereafter the maximal length). After examination of locomotor performance, one hatchling from each of the eight clutches was randomly selected and was killed by freezing to −15 °C for later collection of morphological data, and the remaining hatchlings were released to the site where their mothers were collected. Morphological measurements taken for each killed hatchling included: SVL, tail length, head length (from the snout to the anterior edge of tympanum), head width (taken at the posterior end of the mandible), fore- (humerus plus ulna) and hind-limb (femur plus tibia) length, tympanum length and eye length.

All data were tested for normality using the Kolmogorov–Smirnov test, and for homogeneity of variances using Bartlett's test. $\text{Log}_e$ transformations were performed when necessary to satisfy the assumptions for using parametric tests. We used linear regression analysis, one-way analysis of variance (ANOVA) and one-way analysis of covariance (ANCOVA) to analyze the corresponding data, when the assumptions of parametric analyses were met. We used *G*-test to examine if hatching success differed between temperature treatments. Throughout this paper, values are presented as mean ± SE, and the significance level is set at $\alpha = 0.05$.

## 3. Results

Females ($N = 8$) laid a single clutch of pliable-shelled eggs between mid-May and early June. Clutch size ($r = 0.92$, $F_{1,6} = 33.21$, $P < 0.001$) and clutch mass ($r = 0.92$, $F_{1,6} = 32.46$, $P < 0.001$) were both positively correlated with female SVL (Fig. 1), and egg size was not ($r = 0.62$, $F_{1,6} = 3.75$, $P = 0.101$). Clutch size and egg mass averaged 10.5 (SE = 0.8; range = 7–13) eggs and 106.6 (SE = 4.6; range = 93.8−127.7) mg, respectively. Of the eight embryos identified at oviposition, seven were at Stage 31 and one at Stage 32 in the Dufaure and Hubert's (1961) developmental series.

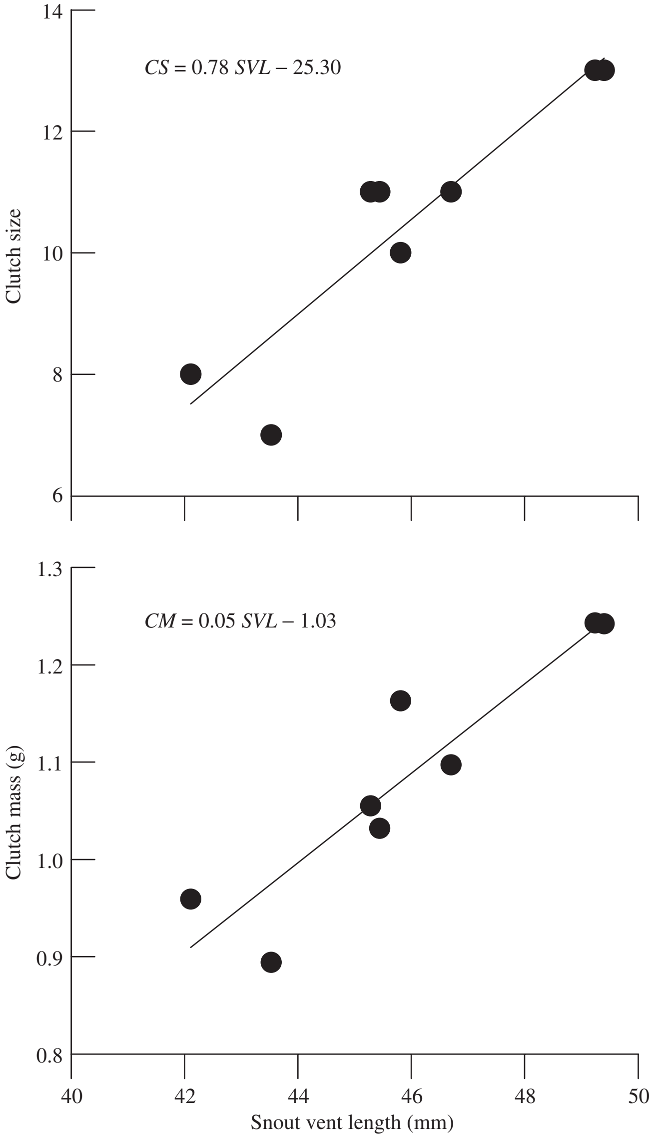

Fig. 1. The liner regressions of clutch size and clutch mass on female SVL in the slender forest skink, *Scincella modesta*.

### 3.1. Hatching success, incubation length and morphological traits of hatchlings

Eggs incubated at the three temperatures did not differ from each other in initial mass ($F_{2,21} = 0.06$, $P = 0.941$). None of the eggs incubated at 30 °C hatched, but hatching successes at the two lower temperatures were extremely high (Table 1). Eggs incubated at 24 and 28 °C differed in incubation length (ANOVA, $F_{1,14} = 25.40$, $P < 0.0002$), but not in hatching success ($G = 0.16$, df = 1, $P > 0.50$) (Table 1). The mean incubation length was shortened by 2 days from 24 to 28 °C (Table 1).

In each of the two temperature treatments yielding viable hatchlings, hatchling SVL was positively correlated with initial egg mass (both $P < 0.05$), and the remaining examined morphological traits were all positively correlated with hatchling SVL (all $P < 0.05$). Hatchlings from eggs incubated at 24 and 28 °C did not differ in all examined morphological traits (Table 2).

### 3.2. Locomotor performance of hatchlings

Neither sprint speed nor the maximal length was correlated with hatchling SVL presumably due to the limited range of hatchling SVL (both $P > 0.05$), so we used ANOVA with incubation temperature as the factor to analyze data. Hatchlings from eggs incubated at 24 °C ran faster than did their counterparts from eggs incubated at 28 °C ($F_{1,14} = 5.60$, $P = 0.033$); the maximal length was apparently greater in hatchlings from eggs incubated at 24 °C than in those from eggs incubated at 28 °C, but the difference was not significant ($F_{1,14} = 4.72$, $P = 0.054$) (Fig. 2).

## 4. Discussion

As reported for numerous other reptiles, thermal environments experienced by *S. modesta* embryos affect hatching success, incubation length and locomotor performance of hatchlings. Eggs could not be incubated at 30 °C, indicating that the upper threshold for successful embryonic development must be lower than this level in *S. modesta*. Within the range from 24 to 28 °C, incubation temperature significantly affected locomotor performance but not morphological phenotypes of hatchlings, with hatchling from eggs incubated at 28 °C performing apparently worse in the racetrack than did their counterparts from eggs incubated at 24 °C (Fig. 2). These results suggest that the temperature of 28 °C is close to the upper thermal threshold for successful egg incubation in *S. modesta* and that eggs incubated at the temperatures higher than this level must have dramatically increased adverse effects on hatching success as well as hatchling phenotypes.

The upper threshold of temperatures having detectable adverse effects on egg incubation is lower in *S. modesta* than in those reported for other species of lizards using

Table 1
Effects of incubation temperature on duration of incubation and hatching success

| Temperature (°C) | Incubated eggs | Hatching success (%) | Incubation length (days) |
|---|---|---|---|
| 24 | 33 | 97.0 (32/33) | 22.3 ± 0.4 (20.1–23.3) |
| 28 | 19 | 94.7 (18/19) | 20.3 ± 0.2 (19.6–21.0) |
| 30 | 24 | 0 (0/24) | — |

Data on duration of incubation are expressed as mean ± SE (range).

Table 2
Morphological phenotypes of hatchling slender forest skinks derived from eggs incubated at 24 and 28 °C

| | Temperature (°C) | | *F* values |
|---|---|---|---|
| | 24 | 28 | |
| *N* | 8 | 8 | |
| Initial egg mass (mg) | 106.0 ± 5.1 (94.0–129.7) | 107.8 ± 5.9 (93.7–134.0) | $F_{1,14} = 0.06$, $P = 0.815$ |
| Snout-vent length (mm) | 18.2 ± 0.3 (17.3–19.8) | 17.9 ± 0.2 (16.8–19.0) | $F_{1,13} = 1.71$, $P = 0.214$ |
| Tail length (mm) | 21.8 ± 0.5 (20.1–23.9) | 21.6 ± 0.4 (20.2–23.4) | $F_{1,13} = 1.40$, $P = 0.258$ |
| Wet mass (mg) | 108.7 ± 5.4 (93.5–133.9) | 109.9 ± 2.6 (100.6–121.2) | $F_{1,13} = 2.46$, $P = 0.141$ |
| Dry mass (mg) | 19.1 ± 1.0 (16.4–24.3) | 18.2 ± 0.4 (17.3–20.6) | $F_{1,13} = 0.02$, $P = 0.891$ |
| Head length (mm) | 4.54 ± 0.06 (4.33–4.78) | 4.49 ± 0.04 (4.37–4.72) | $F_{1,13} = 0.0006$, $P = 0.982$ |
| Head width (mm) | 2.95 ± 0.05 (2.78–3.17) | 2.86 ± 0.02 (2.79–2.96) | $F_{1,13} = 1.94$, $P = 0.187$ |
| Forelimb length (mm) | 3.75 ± 0.07 (3.52–0.07) | 3.76 ± 0.03 (3.63–3.88) | $F_{1,13} = 4.55$, $P = 0.053$ |
| Hindlimb length (mm) | 4.59 ± 0.08 (4.28–4.97) | 4.57 ± 0.07 (4.36–4.85) | $F_{1,13} = 0.58$, $P = 0.459$ |
| Tympanum diameter (mm) | 0.75 ± 0.01 (0.71–0.80) | 0.75 ± 0.01 (0.72–0.81) | $F_{1,13} = 0.34$, $P = 0.568$ |
| Eye diameter (mm) | 1.61 ± 0.02 (1.51–1.71) | 1.65 ± 0.02 (1.54–1.72) | $F_{1,13} = 4.62$, $P = 0.051$ |

Data are expressed as mean ± SE (range). *F* values of ANOVA (for initial egg mass, hatchling) or ANCOVAs (for hatchling SVL with initial egg mass as the covariate, and for the remaining variables with hatchling SVL as the covariate), and significance levels are indicated in the table.

more open habitats such as *Calotes versicolor* (oriental garden lizard: 33 °C; Ji et al., 2002b), *E. chinensis* (32 °C; Ji and Zhang, 2001; Ji et al., 2002a), *E. elegans* (blue-tailed skink: 33 °C; Du et al., 2003), *Podarcis muralis* (common wall lizard: 32 °C; Ji and Braña, 1999; Braña and Ji, 2000), *T. septentrionalis* (32 °C; Lin and Ji, 1998) and *T. wolteri* (white-striped grass lizard: 33 °C; Pan and Ji, 2001). These comparisons provide evidence that lizards differing in habitat use may have different upper thermal thresholds for embryonic development. Our claim that the upper threshold of incubation temperature is lower in species using shaded (and thus, cool) habitats than in species using opened (and thus, warm) habitat can be also supported by data collected from snakes. For example, prolonged exposure of eggs to 30 °C substantially increases embryonic mortality in snakes using relatively cool habitats such as *D. acutus* (Lin and Ji, 2005) and *X. piscator* (Ji et al., 2001), whereas incubating eggs at 30 °C has no detectable adverse effects on hatchling phenotypes in snakes using relatively warm habitats such as *Dinodon rufozonatum* (red-banded wolf snake; Ji et al., 1999; Zhang and Ji, 2002), *E. carinata* (Ji and Du, 2001a), *N. atra* (Ji and Du, 2001b), *Ptyas korros* (gray ratsnake; Du and Ji, 2002), *P. mucosus* (mucous ratsnake; Lin and Ji, 2004) and *Rhabdophis tigrinus lateralis* (red-necked keelback; Chen and Ji, 2002).

The incubation length at 24 °C is surprisingly shorter in *S. modesta* (22.3 days) than in other two species of skinks also common in Hangzhou, *E. chinensis* (41.7 days; Ji and Zhang, 2001) and *E. elegans* (44.1 days; Du et al., 2003), with the embryonic stage at oviposition varying from 31 to 33. The mean incubation length is shortened only by 2 days from 24 to 28 °C in *S. modesta*, but by approximately 17 days in *E. chinensis* (Ji and Zhang, 2001; Ji et al., 2002a) and 19 days in *E. elegans* (Du et al., 2003). These differences indicate that the ecological advantages, such as increased growth period prior to the first winter, decreased chance of microbial contamination and decreased mechanical damage due to the decreased incubation length at the change-over from incubating eggs at 24–28 °C, are negligible in *S. modesta* but could be important in *E. chinensis* and *E. elegans*. Because the temperature of 28 °C has noticeable adverse effects on *S. modesta* embryos (as indicated by the impaired locomotor performance of hatchlings), we therefore conclude that temperatures optimal for *S. modesta* embryos should be lower than 28 °C. However, in all aforementioned species of lizards using more opened habitats, the temperature of 30 °C still falls within the range of temperatures optimal for embryonic development (Lin and Ji, 1998; Ji and Zhang, 2001; Pan and Ji, 2001; Ji et al., 2002a, b; Du et al., 2003).

Reproducing females of oviparous reptiles respond to cool habitats such as deeply shaded forests in two different ways: providing relatively warm temperatures for developing embryos by increasing the length of egg retention or

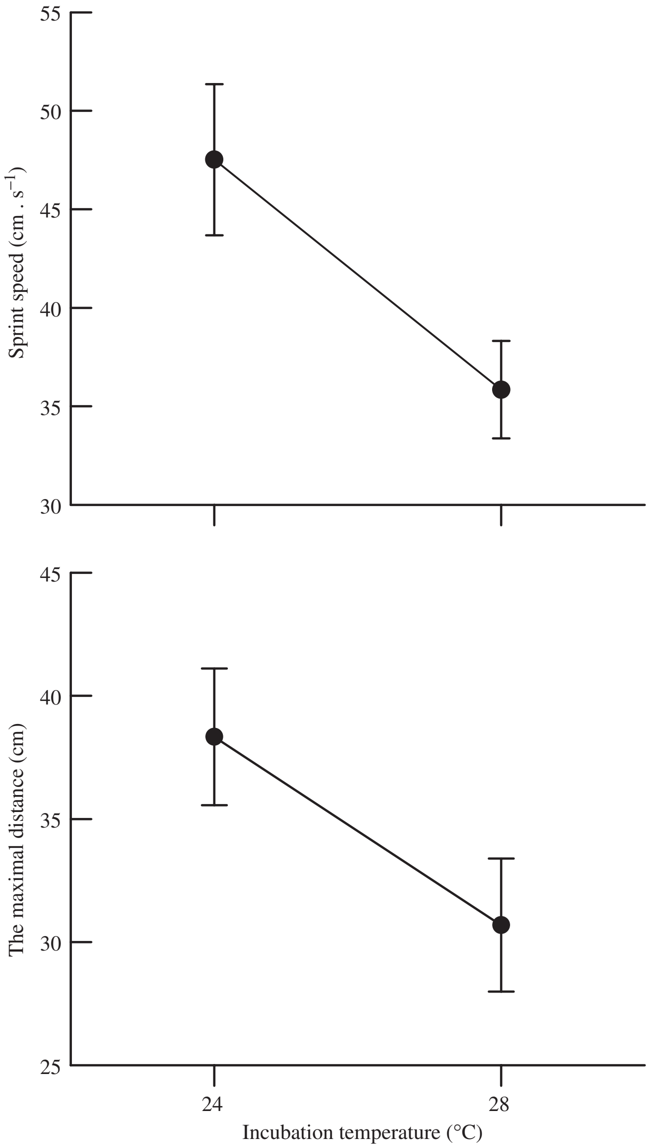

Fig. 2. Locomotor performance of hatchling slender forest skinks derived from eggs incubated at 24 and 28 °C. Data from single clutches ($N = 8$) are blocked by the clutch, and are expressed as mean ± SE.

nest-site selection (Shine, 1999), or shifting temperatures optimal for embryonic development to low levels (Ji et al., 2001; Lin and Ji, 2005). It is unlikely that reproducing females of *S. modesta* are able to provide warmer temperatures for developing embryos by thermoregulation (during the period of egg retention) or selecting warmer nests for eggs for two reasons. First, behavioral thermoregulation can be rather constrained in the habitats occupied by *S. modesta*, primarily because of the lack of pronounced spatial and temporal variation of thermal flux. Second, *S. modesta* is among species of lizards laying eggs in shallow nests inside which temperatures largely match the general surrounding temperatures in habitats (Huang, 1998). Thus, as in other reptiles using relatively cool habitats (Ji et al., 2001; Lin and Ji, 2005), temperatures optimal for embryonic development shift to low levels in *S. modesta*, primarily as a consequence of the adaptive response to cool thermal environments in shaded forestry habitats.

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