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Selected body temperature, thermal tolerance and thermal dependence of food assimilation and locomotor performance in adult blue-tailed skinks, *Eumeces elegans*

Wei-Guo Du*, Shui-Juan Yan, Xiang Ji

Department of Biology, Hangzhou Normal College, Hangzhou 310036, Zhejiang, People's Republic of China

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Abstract

1. Selected body temperature, thermal tolerance and influences of temperature on food assimilation and locomotor performance were studied in adult blue-tailed skinks, *Eumeces elegans*, from a population in Zhejiang, eastern China. 2. The selected body temperature (30.4°C) of males was on average 3.6°C higher than that of females (26.8°C). No between-sex differences in thermal tolerance were found, and the critical thermal minimum and the critical thermal maximum averaged 9.3 and 41.9°C, respectively. 3. The passage time decreased with increase in temperature within the range of 22 to 34°C and increased at higher temperatures. 4. The food intake generally increased with increase in temperature within the range of 22 to 30°C and decreased at higher temperatures. 5. The apparent digestive coefficient and the assimilation efficiency were both insensitive to temperature. 6. *Eumeces elegans* gained mass between 22 and 34°C, lost mass at 36°C and gained relatively more mass at temperatures around 26°C. 7. The sprint speed increased with increase in temperature within the range of 18 to 34°C, and decreased at higher temperatures. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Reptilia; Scincidae; *Eumeces elegans*; Selected body temperature; Thermal tolerance; Locomotor performance; Food assimilation

1. Introduction

It has been known that physiological and behavioural performances of reptiles are, in various degrees, dependent on their body temperatures. Whereas extreme body temperatures are damaging and potentially lethal, moderate to relatively high body temperatures usually maximize performances (Huey and Kingsolver, 1989). The optimal temperature and thermal sensitivity of different performances may differ considerably within and among species and, based on the "multiple optima hypothesis", no specific temperature maximizes all physiological and behavioural performances (Bustard, 1967; Lang, 1979; Pough, 1980; Huey, 1982; van Damme et al., 1991; Ji et al., 1995, 1996). Therefore, the voluntary range of body temperatures within which reptiles in nature tend to regulate may largely reflect a compromise for different performances. The body temperatures which field reptiles tend to maintain can be approximately estimated in the laboratory by measuring the body temperatures in a thermal gradient, although extrapolation of laboratory data to field populations should be made with caution (Litch et al., 1966; Avery, 1978).

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* Corresponding author. Tel.: +86-571-8082506.
E-mail address: herplab@public1.hz.zj.cn (W.G. Du).

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In reptiles, net energy gains through feeding mean somatic tissue growth and/or offspring production (Nagy, 1983), and speed may be associated with individual fitness because of its great importance for avoiding predators and enhancing foraging success (Pough, 1989; Bauwens et al., 1995; Miles et al., 1995). Thus, quantifying the effects of temperature on food assimilation and locomotor performance could be ecologically important.

The blue-tailed skink, *Eumeces elegans* (Scincidae), is a widely foraging, insectivorous lizard, widely distributed in southern provinces of China (Gu, 1990; Zhao and Adler, 1993). The maximum snout-vent length of *E. elegans* is approximately 105 mm (Gu, 1990). The skink is locally very abundant in Hangzhou (30° 16′N, 120° 9′E), Zhejiang, eastern China, where Wang (1964, 1966) studied activity pattern, food habits, habitat selection and reproduction of the species 30 years ago. Here, we (1) present some basic data on thermal biology, (2) quantify the effects of temperature on food assimilation and locomotor performance, (3) compare data with those reported for other lizard species and (4) add support for the multiple optima hypothesis associated with selected body temperature.

2. Materials and methods

All individuals used in this study were adults, with snout-vent length ranging from 67.56 to 96.10 mm. Animals were collected during the breeding season (May–June) 1998 from a population in Hangzhou. Skinks were returned to our laboratory at Hangzhou Normal College, where sex was determined and mass and length were recorded to the nearest 0.001 g and 0.05 mm, respectively. Prior to and during intervals of experiments, skinks were randomly maintained, 6–8 in each 120 × 60 × 40 cm (length × width × height) terrarium, which was filled with soil, grasses, blocks of wood and stones. Skinks were fed mealworms (larvae of *Tenebrio molitor*) and given water ad libitum. We exposed skinks to a natural light cycle. The supplementary heating was provided by a 100 W light bulb suspended 15 cm above the terrarium floor so as to allow skinks to regulate body temperatures within their voluntary range during the photophase and cool to air temperature when the lights were switched off. Males were used in all trials and females were used only for the trials of selected body temperature and thermal tolerance because of the male-biased sex ratio (males:females = ∼5:1).

2.1. Selected body temperature and thermal tolerance

To avoid possible interactions between experiments, we conducted each experiment at intervals of a week. The sequence was selected body temperature (T_{sel}), critical thermal minimum (CT_{min}) and critical thermal maximum (CT_{max}) determinations. Prior to each experiment, skinks were maintained in a constant-temperature room at 28°C for 24 h to allow habituation to the starting temperature. Because no formal acclimation was employed in this study, skinks were considered acclimatized to semi-natural conditions in the laboratory.

Selected body temperature was determined in a 100 × 50 × 30 cm glass terrarium. Two light bulbs (total 1000 W) suspended above one end created a thermal gradient ranging from 14 to 70°C (2 cm above the terrarium floor). Skinks were moved from the cool side into the terrarium at 07:30 when the lights were automatically switched on. Because there might be diel variation in T_{sel} (Hutchsion, 1976), to insure our data was more comparable to those from other lizard species collected by us, we began all our measurements at 15:00 and ended within 2 h. Body temperatures (cloacal, T_{b}) of active skinks in the gradient were taken using a WMZ-03 electronic thermometer (Shanghai Medical Instruments). To address the reliability of our measurements, we measured each skink twice on two consecutive days and considered the mean of the two readings as a skink's body temperature. Efforts were made to make the two readings at approximately the same time on the two days. We used the mean of all readings of body temperature as T_{sel} (Ji et al., 1995, 1996, 1997).

Critical thermal maximum and critical thermal minimum were determined in a LRH-250A incubator (Guangdong Medical Instruments). Experiments were conducted between 10:00 and 15:00. Skinks were heated or cooled from 28°C at the rate of 0.25°C per min. During the experiments, we observed the behaviour of the skinks through a window in the incubator. The body temperatures associated with a transient loss of righting response (the testing animals did not respond to intense stimulation and could not turn back when being turned over) at upper and lower thermal limits were used as endpoints for $\mathrm{CT}_{\mathrm{max}}$ and $\mathrm{CT}_{\mathrm{min}}$ (Ji et al., 1995, 1996, 1997).

2.2. Food intake, passage time and food assimilation

All trials were conducted in constant-temperature rooms. Skinks were randomly divided into eight groups; each group was placed in 22, 24, 26, 28, 30, 32, 34 and 36°C constant-temperature rooms. The fluorescent tubes and room lighting were on a 12 h light:12 h dark cycle; lights were automatically switched on at 07:30. Skinks were individually housed in a 20 × 15 × 20 cm glass terrarium. Three days prior to feeding for faeces collection, skinks were starved at the test temperature to insure uniform post-absorptive states. Trials lasted for a minimum of 9 days to allow the accumulation of sufficient faeces and urates for accurate calorimetry. Final body mass was recorded at the end of a 3 day fast which terminated each test period.

We marked mealworms by inserting a 3 mm blue plastic thread (diameter 0.2 mm) into their abdomen, and then allowed skinks to eat voluntarily a single marked mealworm. This allowed us to feed marked mealworms to skinks without force-feeding. Unmarked mealworms and water were then provided ad libitum. We collected faeces and urates at least six times daily and more frequently during the first days so that the plastic threads could be collected within a few minutes after being expelled. Passage time was defined as the lapsed time from swallowing to appearance of plastic threads, and additional data on this trait were collected at 38°C.

Faeces, urates and mealworms were dried to constant mass at 65°C and weighed. Subsamples were burned in a GR-3500 adiabatic calorimeter (Changsha Instruments) and energy densities were obtained. The assimilation efficiency (AE) was calculated as $AE = (I - F - U)/I \times 100\%$ (e.g., Kepenis and McManus, 1974; Ji and Wang, 1990; Ji et al, 1993), where I = total energy consumed, F = energy in faeces and U = energy in urates. The apparent digestive coefficient (ADC) was calculated as $ADC = (I - F)/I \times 100\%$ (e.g., Brody, 1945; Harwood, 1979; Ballinger and Holscher, 1983; Waldschmidt et al., 1986; van Damme et al., 1991).

2.3. Locomotor performance

Locomotor performance was tested at constant temperatures ranging from 18 to 40°C, the sequence being randomized. Body temperatures were controlled by placing skinks in an incubator at the corresponding temperature for at least 3 h prior to each trial. Locomotor performance was assessed by chasing the skinks down a 200 × 10 × 15 cm racetrack with one side transparent, which allows lateral filming with a video camera (Panasonic VX7). It was always the first author who chased the skinks, thereby standardizing the stimulus. Each skink was run two times at each temperature with a minimum of 30 min rest between trials, and the video tapes were later examined for sprint speed in the fastest 50 cm interval.

2.4. Statistical analyses

Individuals that refused to eat or died during the course of trials were excluded from analysis. All data were tested for normality (Kolmogorov–Smirnov test) and homogeneity of variances (F-max test), and transformed when necessary to achieve the conditions for using parametric tests. We precluded using ANCOVA to analyze data, because no linear relationships existed and a significant fraction of variances could be due to inter-individual differences that were preserved across test temperatures. We used one-way ANOVA to determine whether there were differences in food intake, food passage time, ADC, AE, changes in body mass and sprint speed among temperature treatments. Mann–Whitney U-test was used to test differences in T_{sel}, CT_{min} and CT_{max} between male and female *E. elegans*, because normality assumptions were not met.

Table 1
The selected body temperature, the critical thermal maximum, and the critical thermal minimum (°C) of adult *Eumeces elegans*

	T_{sel}			
	Males	Females	CT_{min}	CT_{max}
Mean	30.4	26.8	9.3	41.9
N	20	15	42	20
SE	0.5	0.4	0.1	0.1
Range	25.0–34.2	24.9–29.1	8.0–10.9	40.1–42.4

3. Results

There was a significant difference in T_{sel} between male and female *E. elegans* (Mann–Whitney U-test, $P < 0.05$), and T_{sel} of males was on average 3.6°C higher than that of females (Table 1). We did not find

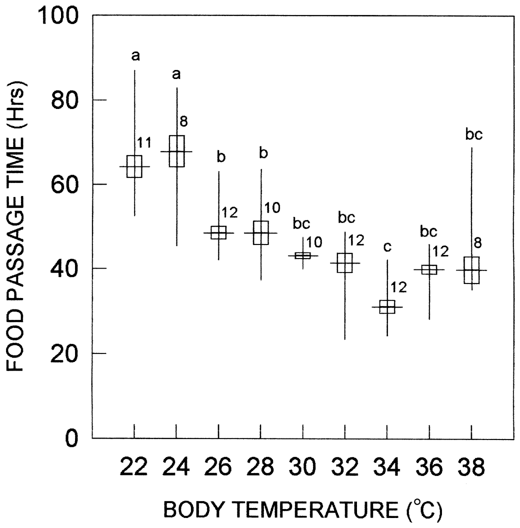

Fig. 1. Passage time of *Eumeces elegans* at different temperatures. Data are expressed as mean ± 1 standard error. Sample sizes are indicated in the figure. Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$).

Table 2
Initial body mass, body-mass change, food intake, ADC and AE of adult *Eumeces elegans*[a]

T(°C)	N	Initial body mass (g)	Body-mass gain (mg d^{-1})	Food intake (J d^{-1} g^{-1})	ADC (%)	AE (%)
22	11	12.6 ± 1.4	$22.0^{bc}\pm15.9$	$359.6^{d}\pm37.6$	$89.5^{b}\pm0.9$	82.9 ± 1.0
		(7.1–22.4)	(−53.0–82.4)	(194.0–541-0)	(82.1–93.8)	(75.33–87.56)
24	9	10.1 ± 1.1	$151.2^{a}\pm30.1$	$466.6^{cd}\pm67.1$	$92.4^{a}\pm0.4$	87.0 ± 0.5
		(5.4–15.9)	(32.5–326.6)	(163.5–743.4)	(89.5–93.3)	(83.6–88.9)
26	14	11.3 ± 1.0	$178.1^{a}\pm24.6$	$835.7^{ab}\pm81.4$	$90.9^{ab}\pm0.4$	84.3 ± 0.4
		(6.8–17.4)	(64.6–417.3)	(367.9–1335.3)	(88.8–93.8)	(81.8–87.4)
28	12	11.8 ± 1.2	$168.2^{a}\pm13.9$	$804.7^{ab}\pm57.8$	$90.6^{ab}\pm0.5$	84.6 ± 0.6
		(7.0–21.7)	(90.7–233.1)	(461.6–1085.0)	(87.9–93.4)	(81.6–88.0)
30	13	12.2 ± 0.8	$156.1^{a}\pm30.3$	$976.7^{a}\pm73.4$	$90.9^{ab}\pm0.5$	83.9 ± 0.8
		(7.6–17.6)	(−123.9–255.3)	(550.2–1441.8)	(86.1–92.8)	(76.7–86.4)
32	12	14.8 ± 1.13	$106.1^{ab}\pm28.9$	$718.96^{ab}\pm75.29$	$90.47^{ab}\pm0.53$	83.7 ± 0.7
		(10.0–23.9)	(−92.8–240.4)	(316.4–1156.3)	(86.9–94.5)	(79.6–89.0)
34	12	8 ± 0.7	$87.3^{ab}\pm24.6$	$696.90^{bc}\pm56.11$	$89.67^{b}\pm0.57$	81.7 ± 0.8
		(11.7–19.0)	(−104.5–182.8)	(417.5–896.5)	(86.6–93.2)	(77.0–86.4)
36	11	14.5 ± 0.7	$-69.5^{c}\pm26.5$	$269.69^{d}\pm30.54$	$90.8^{ab}\pm0.5$	82.5 ± 0.9
		(10.6–18.8)	(−157.8–101.2)	(112.0–437.3)	(88.6–94.7)	(79.9–86.5)

[a] Data are expressed as mean ± 1 standard error (range). Mean with different superscripts differ significantly (Tukey's test, $\alpha=0.05$).

between-sex differences in CT_{max} and CT_{min} between males and females (Mann–Whitney U-test, both $P > 0.05$), so we pooled data for both sexes (Table 1).

Temperature significantly affected passage time ($F_{7,85}=21.59$, $P < 0.001$), food intake ($F_{7,85}=15.01$, $P < 0.001$) and mass change ($F_{7,85}=10.03$, $P < 0.001$). The passage time generally decreased with increase in temperature within the range of 22 to 34°C, and then increased at higher temperatures (Fig. 1). The food intake generally increased with increase in temperature within the range of 22 to 30°C, and then decreased at higher temperatures (Table 2). *Eumeces elegans* gained mass between 22 and 34°C and lost mass at 36°C. When taking food intake into account, we found that skinks actually gained more mass at the temperatures around 26°C (Table 2).

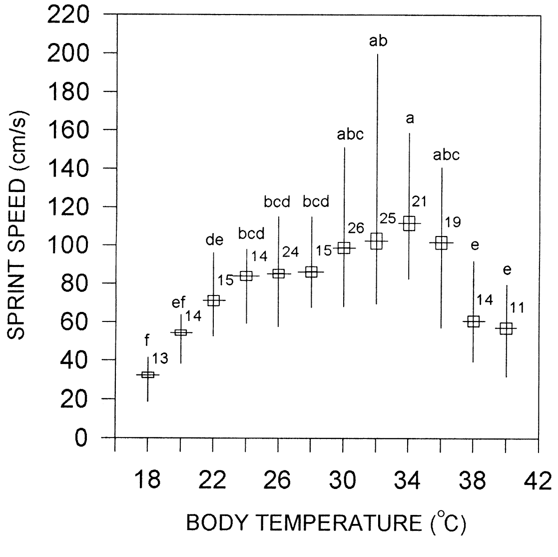

Fig. 2. Locomotor performance (sprint speed) of *Eumeces elegans* at different temperatures. Data are expressed as mean ± 1 standard error and range. Sample sizes are indicated in the figure. Means with different superscripts differ significantly (Tukey's test, $\alpha=0.05$).

The influence of temperature on ADC, although statistically significant ($F_{7,85}=2.23$, $P < 0.05$), was actually very slight (Table 2). We did not find a significant influence of temperature on AE ($F_{7,85}=1.43$, $P > 0.05$) (Table 2).

Temperature significantly affected locomotor performance of *E. elegans* ($F_{11,199}=26.07$, $P < 0.001$). The sprint speed increased with temperature within the range of 18 to 34°C, and then decreased at higher temperatures (Fig. 2).

4. Discussion

Because T_{sel}, CT_{max} and CT_{min} can be influenced by many external and internal factors (see Hutchison, 1976), application of standard techniques to different species or a particular species is of importance for data comparisons. Such comparisons could be of importance for revealing among species differences in T_{sel}, CT_{max} and CT_{min} and seasonal shifts and age or geographic variation in these variables within a particular species. Data collected by us over the past few years using the same methods have indicated that lizards that differ in habitat use exhibit different T_{sel}, CT_{max}

and CT_{min} (Ji et al., 1995, 1996, 1997). For example, lower T_{sel} (25.7°C), CT_{max} (37.6°C) and CT_{min} (3.1°C) recorded in *Sphenomorphus indicus* largely mirror its habit of living in shady places where both air and substrate temperatures are generally lower (Ji et al., 1997).

One interesting finding in this study is that females selected lower body temperatures in the thermal gradient than did males. One possible explanation of this difference is that female and male adults differ in thermal requirements during the breeding season. Female *E. elegans* retain eggs for an appreciable period and, as seen in some other *Eumeces* females, guard eggs (Wang, 1966; de Fraipont et al., 1996). Because reptilian embryos developing at lower and/or moderate temperatures usually produce larger, heavier, or well-performed young (Packard and Packard, 1988; Burger, 1990; van Damme et al., 1992), it could be important for female *E. elegans* to shift body temperatures to lower points favoring embryonic development. In the study, the sex ratio of the captured adult *E. elegans* was highly male-biased (males:females = ∼5:1). Such a biased sex ration could not be true in nature, but reflected the difference in activity pattern (and hence thermal requirements) between male and female adults, because the sex ratios in juveniles and the adults captured in the fall did not differ from the equality (1:1) (Du, unpubl. data). In addition, selecting lower body temperatures could be also important for postpartum females to recover their condition, as our data show that *E. elegans* apparently gained more net energy at the temperatures around 26°C (Table 2).

To date three patterns of the thermal dependence of passage time have been found in lizards: (1) decreasing with increase in temperature (*Uta stansburiana*—Waldschmidt et al., 1986; *Takydromus septentrionalis*—Ji et al., 1996); (2) decreasing with increase in temperature at lower temperatures and being leveled at higher temperatures (*Eumeces chinensis*—Ji et al., 1995; *Sphenomorphus indicus*—Ji et al., 1997); (3) decreasing with increase in temperature at lower temperatures and increasing at higher temperatures (*Lacerta vivipara*, van Damme et al., 1991; *Sceloporus merriami*—Beaupre et al., 1993). The thermal dependence of passage time in *E. elegans* seems to belong to Pattern 3.

Reptiles at higher temperatures should take more food because of the increased metabolic rate, whereas food intake in this study was greatest at 30°C and generally increased with increase in temperature within the range of 22 to 30°C and then decreased at higher temperatures. This implies that it could be more expensive for *E. elegans* to be active at temperatures higher than 30°C.

The values of ADC and AE are determined by activities of digestive enzymes, passage time and type and amount of food consumed (Andrews and Asato, 1977; Harwood, 1979; Beaupre et al., 1993; Witz and Lawrence, 1993). Within a certain temperature range, activities of digestive enzymes increase with temperature but shortened passage time at higher temperatures may reduce exposure of food to enzymatic action (Harwood, 1979). This unique mechanism may, in some degrees, results in thermal insensitivity of ADC and AE, although the amount of unavailable energy in food, which is dependent on the amount and type of food consumed, may also appreciably modify the values of ADC and AE. In this study, the influence of temperature on ADC was statistically significant, but the differences among temperature treatments were actually very slight. We therefore conclude that ADC in *E. elegans* is also insensitive to temperature. This conclusion is similar to that drawn by many investigators in other insectivorous lizards (e.g., Dutton et al., 1975; Waldschmidt et al., 1986; van Damme et al., 1991; Beaupre et al., 1993; Ji et al., 1995, 1996, 1997). The thermal insensitivity of AE in *E. elegans* is similar to the results reported for *E. Chinensis* (Ji et al., 1995; Xu et al., submitted), adult *T. septentrionalis* (Ji et al., 1996), *S. indicus* (Ji et al., 1997) and *Gekko japonicus* (Ji and Wang, 1990). However, the thermal dependence of AE did occur in some other species or group of lizards, e.g., *Sceloporus olivaceus* (Dutton et al., 1975), *S. merriami* (Beaupre et al., 1993) and juvenile *T. septentrionalis* (Ji et al., 1993). AE characteristically exhibited decreased AEs at higher temperatures presumably due to the increased production of urates.

Eumeces elegans exhibited great inter-individual differences in locomotor performance across the test temperatures. Such great inter-individual differences have been reported for other lizard species (e.g., *L. vivipara*, van Damme et al., 1991; *E. chinensis*, Ji et al., 1995; *T. septentrionalis*, Ji et al., 1996). Sprint speed in *E. elegans* was greatest at 34°C, which is the same as that (34°C) reported for *E. Chinensis* (Ji et al., 1995) but slightly higher than that (32°C) reported for *T. septentrionalis* (Ji et al., 1996).

In summary, ADC and AE in *E. elegans* were both insensitive to temperature, and other functions examined, including passage time, food intake, body-mass change and sprint speed, exhibited strong thermal sensitivities and differed in their optimal temperatures. Thus our data add support for the multiple optima hypothesis about the thermal dependence of behavioural and physiological performances in reptiles.

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