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Influence of body temperature on food assimilation and locomotor performance in white-striped grass lizards, *Takydromus wolteri* (Lacertidae)

Xue-Jun Chen[a], Xue-Feng Xu[b], Xiang Ji[a,*]

[a] *School of Life Sciences, Hangzhou Normal College, Hangzhou, Zhejiang 310036, China*
[b] *Department of Biochemistry, Chuzhou Normal College, Chuzhou, Anhui 239012, China*

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Abstract

Influence of body temperature on food assimilation and locomotor performance was studied in adult white-striped grass lizards (*Takydromus wolteri*) from a population in Chuzhou (Anhui, Eastern China). Food passage time dramatically decreased with increase in body temperature within the range from 26°C to 34°C, and then nearly levelled at higher body temperatures. Lizards overall gained net mass at 26°C, 28°C and 30°C and lost mass at 32°C and 34°C. Daily production of faeces (mass-specific) was affected by body temperature and, when influence of variation in the total food energy intake was removed by an ANCOVA, lizards at 26°C were found to produce faeces that contained significantly lower energy as compared with those at higher body temperatures. The total energy of urates was affected by the total food energy intake, but an ANCOVA with the total food energy intake as the covariate showed that lizards at different body temperatures did not produce urates that differed in energy. Within the temperature range considered, daily production of urates (mass-specific), apparent digestive coefficient (ADC) and assimilation efficiency (AE) were not affected by body temperature, although both ADC and AE were apparently greater in lizards at 26°C. Both locomotor stamina and sprint speed increased with increase in body temperature within the range from 18°C to 30°C, and then decreased at higher temperatures. Inter-individual differences were a significant source of variation in locomotor performance. Except for ADC and AE, all traits examined were significantly affected by body temperature, although thermal sensitivities differed considerably among traits. Within the body temperature range considered, 26°C was the most suitable body temperature for somatic tissue growth, and 30°C was an optimal body temperature for locomotor performance.

Keywords: Reptilia; Lacertidae; *Takydromus wolteri*; Food passage time; Apparent digestive coefficient; Assimilation efficiency; Locomotor stamina; Sprint speed

1. Introduction

Body temperature may profoundly affect physiological and behavioural performances of reptiles. Extreme body temperatures are harmful and potentially lethal; however, within a certain range, moderate to relatively high body temperatures usually maximize performances (Huey, 1982; Huey and Kingsolver, 1989; Ji et al., 1995, 1996, 1997; Xu et al., 1999, 2001; Du et al., 2000). Reptiles that are active in the field tend to maintain relatively high and constant body temperatures mainly through behavioural thermoregulation, so that their performances can be expressed at high levels. However, for reptiles living in the environments lacking thermal gradients, behavioural thermoregulation is rather constricted,

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*Corresponding author. Tel.: +86-571-88082506; fax: +86-571-88804145.

E-mail addresses: chen-shl@163.com (X.-J. Chen), xuefxu@cztc.edu.cn (X.-F. Xu), xji@mail.hz.zj.cn (X. Ji).

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and variation in body temperature may largely mirror variation in ambient temperature (Wang and Xu, 1987). The thermally homogeneous environments where the temperature is uniform usually do not occur in nature but can be established in the laboratory by using constant temperature rooms, inside which a reptile's body temperatures can be controlled precisely at expected levels so that its behavioural and physiological performances corresponding to any given body temperature can be examined (Wang and Xu, 1987; Ji and Wang, 1990; Ji et al., 1993, 1995, 1996, 1997; Xu et al., 1999, 2001; Du et al., 2000).

In reptiles, food assimilation and locomotor abilities have clear ecological relevance: net energy gains through feeding mean somatic tissue growth and/or offspring production (Nagy, 1983), whereas locomotor abilities may be associated with individual fitness because of its importance for avoiding predators and enhancing foraging success (Pough, 1989; Bauwens et al., 1995; Miles et al., 1995; Braña and Ji, 2000; Ji et al., 2002). Thus, quantifying the thermal dependence of food assimilation and locomotor abilities is important. In this study, we investigate *Takydromus wolteri*, a small multiple-clutched oviparous insectivorous lacertid lizard mainly living in hilly areas covered by grasses and bushes (Chen, 1991). The species is geographically widespread; its distributional range covers some provinces in eastern (Jiangsu, Anhui and Jiangxi) and central (Hubei and Sichuan) China, north to the northeastern provinces of China, Korea and Russia (Southern Primorskiy Territory) (Chen, 1991; Zhao and Adler, 1993). We present data on several traits that are relevant to food assimilation and locomotor abilities and supposed to be influenced by body temperature, including: (1) food intake, (2) food passage time, (3) apparent digestive coefficient (ADC), (4) assimilation efficiency (AE), (5) locomotor stamina and (6) sprint speed. Our purposes are to contribute further data to the thermal biology of lizards in eastern China and to compare data generated from this study with those collected in other parallel studies.

2. Materials and methods

Adult *T. wolteri*, with snout-vent length (SVL) ranging from 44 to 61 mm, were collected by hand or noose in early May 2000 and 2001 from a population in Chuzhou (Anhui, Eastern China), where is the southern limit of its distributional range. The mean temperatures of the whole year, the hottest month (July) and the coldest month (January) in Chuzhou are approximately 14.5°C, 28.5°C and 1.8°C, respectively; the active season of *T. wolteri* there begins in late March and ends in early November (Chen, 1991). In the laboratory, large females are able to lay up to 4 clutches with 1–4 pliable-shelled eggs each per breeding season lasting from May to July (Chen, 1991; Pan and Ji, 2001).

The captured lizards were transported to our laboratory at Hangzhou Normal College, where sex was determined and mass and length were recorded to the nearest 1 mg and 0.01 mm, respectively. Prior to and between trials, lizards were randomly maintained 8–10 in each $600 \times 400 \times 300\,\text{mm}^3$ (length × width × height) glass terrarium, of which the bottom was filled with moist soil, grasses and debris. We fed lizards with mealworms (larvae of *Tenebrio molitor*) and water enriched with vitamins and minerals. We exposed lizards to a natural light cycle. The supplementary heating was provided by a 100 W light bulb suspended 15 cm above the terrarium floor, so that lizards had ample opportunities to regulate body temperatures within their voluntary range during the photophase and cool to air temperature when the lights were switched off. Individual lizards were measured only at a single temperature. Excepting for competing occasionally for food, we did not find any antagonistic interactions among lizards in the terraria. Body temperatures (cloacal, Tb) were taken using a WMZ-03 electronic thermometer (Shanghai Medical Instruments, China), which was calibrated with a standard thermometer. To improve the reliability of our measurements, we measured each lizard twice and considered the mean of the two readings as a lizard's body temperature.

2.1. Food passage time

The trials at 26°C, 28°C, 30°C, 32°C, 34°C, and 36°C were conducted in May 2000 and 2001, and the trial at 38°C was conducted in May 2001. All trials were conducted in a constant temperature room inside which the fluorescent tubes were on a 12 light: 12 dark cycle; lights were automatically switched on at 07:00 (Beijing time). Lizards were individually housed in a $200 \times 150 \times 250\,\text{mm}^3$ glass terrarium. We starved lizards at the test body temperature for 3 d prior to feeding, and then fed each lizard with two mealworms of which each had been marked by inserting a 3 mm blue plastic thread (diameter 0.2 mm) into the abdomen. We started trials at different temperatures at the same time (17:00) of day, and allowed all lizards to eat voluntarily marked mealworms, thereby avoiding force-feeding. All plastic threads were collected within a few minutes after being expelled, and the food passage time was defined as the lapsed time from swallowing to the first appearance of plastic threads.

2.2. Food intake and food assimilation

The trials at 28°C, 30°C, 32°C and 34°C were conducted between May and July in 2000 and 2001, and the trial at 26°C was conducted in the same season of 2001. All trials were conducted in constant temperature rooms as described above. Lizards were also individually housed in a $200 \times 150 \times 250\,\mathrm{mm}^3$ glass terrarium. We starved lizards at the test body temperature for 3 d to insure uniform post-absorptive states, and then fed them with mealworms and water *ad libitum*. We collected faeces and urates at least 5 times daily. Trials lasted for a minimum of 24 days to allow the accumulation of sufficient faeces and urates for accurate calorimetry. Initial body mass was recorded at the end of 3 d fast prior to feeding, and final body mass was recorded at the end of a 3 d fast which terminated each trial.

Faeces, urates and mealworms for each lizard were dried to constant mass at 65°C and weighed. Dried samples were burned in a WGR-1 adiabatic calorimeter (Changsha Instruments, China) and data were automatically recorded in a computer. The assimilation efficiency was calculated as $\mathrm{AE} = 100(I - F - U)/I$ (Kepenis and McManus, 1974; Ji and Wang, 1990; Ji et al., 1993), where I is the total energy consumed, F the energy in faeces and U the energy in urates. The apparent digestive coefficient was calculated as $\mathrm{ADC} = 100(I - F)/I$ (Harwood, 1979; Ballinger and Holscher, 1983; Waldschmidt et al., 1986).

2.3. Locomotor performance

Locomotor stamina was examined in May 2000 and at 9 body temperatures ranging from 18°C to 38°C (18°C, 23°C, 26°C, 29°C, 30°C, 32°C, 34°C, 36°C and 38°C). All trials were conducted in a $600 \times 400 \times 300\,\mathrm{mm}^3$ glass terrarium which was placed in a constant temperature room, and the sequence was randomized. We housed lizards ($N = 11$) in the room for 2 h prior to each trial, thereby insuring their body temperatures to be controlled at the test level. We kept chasing lizards until they refused to move because of fatigue. Locomotor stamina was defined as the lapsed time from being chased to refusing to move.

Sprint speed, which was defined as the speed in the fastest 50 cm interval selected by a computer software (see below), was examined in May 2001 and at 11 body temperatures ranging from 18°C to 38°C (18°C, 20°C, 22°C, 24°C, 26°C, 28°C, 30°C, 32°C, 33°C, 35°C and 38°C), the sequence being also randomized. All trials were conducted in a constant temperature room, and body temperatures were controlled in the same way as described above. We chased lizards ($N = 12$) down a $2000 \times 100 \times 150\,\mathrm{mm}^3$ racetrack with one side transparent, which allow lateral filmation with a Panasonic NV-DS77 digital video camera (Panasonic Co., Japan). Each lizard was run two times at each temperature with a minimum of 30 min rest between trials, and the tapes were later examined with a computer using MGI VideoWave III software (MGI Software Corp., Canada).

2.4. Statistical analyses

Individuals that refused to run 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 Arc-sine (for ADC and AE) and Log_e (for other traits when necessary) transformations were performed to achieve to the conditions for using parametric tests. Because preliminary analyses showed that there were no significant differences in all examined traits between both sexes and among individuals examined in different years, we pooled data for both sexes and for individuals examined in different years. We used one-way ANOVA to determine whether there were differences in food passage time, ADC and AE among temperature treatments. The same analysis was also used to determine whether there were differences in daily food intake, changes in body mass, daily production of faeces, daily production of urates, locomotor stamina and sprint speed among temperature treatments, because no linear relationships existed between these variable and individual size (mass). We used one-way ANCOVA (with total food energy intake as the covariate, thereby removing influence of variation in this variable) to determine whether lizards at different body temperature would differ in energy contents of faece and urates produced. We used two-way ANOVA (with body temperature and individual as the factors) to determine whether there were inter-individual differences in locomotor stamina and sprint speed. Descriptive statistics are presented as mean ±1 standard error, and the significance level is set at $\alpha = 0.05$.

3. Results

3.1. Food passage time and food assimilation

Food passage time was significantly affected by body temperature ($F_{6,135} = 48.91$, $P < 0.0001$), and it decreased dramatically with increase in body temperature within the range from 26°C to 34°C and then nearly levelled within the range from 34°C to 38°C (Fig. 1).

Lizards used for determination of food assimilation did not differ in initial body mass among temperature treatments ($F_{4,71} = 2.06$, $P = 0.096$). Mass changes were affected by body temperature ($F_{4,71} = 4.20$, $P < 0.004$), with lizards overall gaining net mass at 26°C, 28°C and 30°C and losing mass at 32°C and 34°C (Table 1). Daily food intake (mass-specific) was affected by body temperature ($F_{4,71} = 5.19$, $P < 0.001$), with lizards taking apparently more food at 26°C and 34°C than at the three intermediate body temperatures (Table 1). Daily production of faeces (mass-specific) was affected by body temperature ($F_{4,71} = 2.76$, $P = 0.034$), but this trait was significantly affected by food intake at each test temperature (Table 1). An ANCOVA with the total food energy intake as the covariate showed that lizards at different body temperatures produced faeces that differed in energy ($F_{4,70} = 3.07$, $P = 0.022$), with lizards at 26°C producing faeces that contained significantly lower energy as compared with those at other four higher body temperatures (Tukey's test, all $P < 0.04$). Within the temperature range examined, daily production of urates (mass-specific) ($F_{4,71} = 1.99$, $P = 0.105$), ADC ($F_{4,71} = 2.09$, $P = 0.091$) and AE ($F_{4,71} = 2.33$, $P = 0.064$) were not significantly affected by body temperature (Table 1), although both ADC and AE were apparently greater in lizards at 26°C Tb (Table 1). The total energy of urates was also affected by the total food energy intake at each test temperature, but an ANCOVA with the total food energy intake as the covariate showed that lizards at different body temperatures did not produce urates that differed in energy ($F_{4,70} = 1.81$, $P = 0.136$).

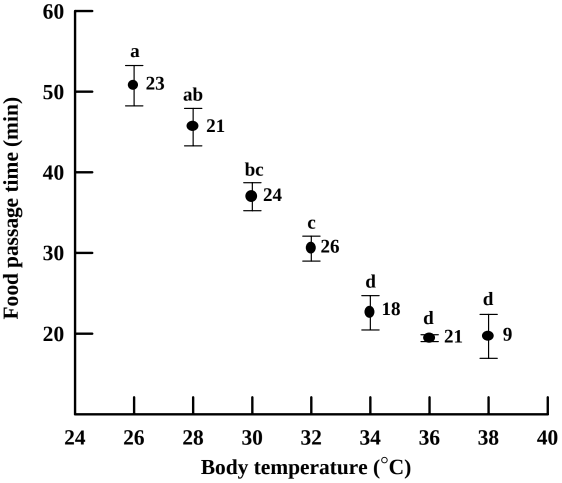

Fig. 1. Food passage time of *Takydromus wolteri* at different body temperatures. Data are expressed as mean ±1 standard error. Sample sizes are indicated in the figure. Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$; $a > b > c > d$).

3.2. Locomotor performance

Body temperature significantly affected locomotor stamina ($F_{8,90} = 5.36$, $P < 0.0001$) and sprint speed ($F_{10,121} = 15.00$, $P < 0.0001$). Locomotor stamina increased with body temperature within the range from 18°C to around 30°C, and then decreased at higher temperatures (Fig. 2). Sprint speed also increased with body temperature within the range from 18°C to 30°C, and then decreased at higher temperatures (Fig. 3). A two-way ANOVA confirmed that body temperature significantly affected locomotor stamina ($F_{8,80} = 12.59$, $P < 0.0001$) and sprint speed ($F_{10,110} = 19.34$, $P < 0.0001$), and it also revealed that inter-individual differences were a significant source of variation in both traits (locomotor stamina: $F_{10,80} = 13.14$, $P < 0.0001$; spring speed: $F_{11,110} = 15.00$, $P < 0.0001$).

4. Discussion

The mean values of food passage time corresponding to a given body temperature and the thermal sensitivity of the trait may differ considerably among species (Waldschmidt et al., 1986; Van Damme et al., 1991;

Table 1
Initial body mass, changes in body mass, daily food intake, daily production of faeces, daily production of urates, ADC and AE of adult *Takydromus wolteri*

Temperature (°C)	N	Initial body mass (g)	Changes in body mass (mg d^{-1})	Daily food intake (J g^{-1} d^{-1})	Daily production of faeces (J g^{-1} d^{-1})	Daily production of urates (J g^{-1} d^{-1})	ADC (%)	AE (%)
26	7	2.1±0.0.1 (1.9–2.4)	11.0^{a}±2.3 (2.7–28.3)	509.6^{a}±33.5 (368.0–602.9)	33.9^{b}±2.9 (27.8–49.5)	23.1±2.6 (15.6–34.5)	93.3±0.5 (91.8–94.8)	88.8±0.8 (86.1–91.7)
28	22	2.5±0.1 (1.9–3.3)	3.7^{b}±2.1 (−14.0–22.4)	451.3^{ab}±22.8 (288.1–777.1)	42.2^{ab}±3.1 (21.4–76.2)	26.2±1.7 (13.7–46.0)	90.5±0.6 (85.4–94.5)	84.6±1.0 (76.8–91.1)
30	17	2.6±0.1 (1.9–3.6)	3.6^{b}±1.8 (−14.8–15.8)	398.5^{b}±19.0 (244.4–583.3)	36.8^{ab}±2.9 (13.7–65.7)	21.4±1.5 (10.6–30.8)	90.7±0.5 (87.2–94.5)	85.2±0.7 (79.6–89.3)
32	14	2.7±0.1 (2.2–3.8)	−1.0^{bc}±2.6 (−18.7–13.8)	367.3^{b}±23.0 (233.3–548.2)	32.8^{b}±2.8 (14.2–52.2)	19.9±1.7 (10.8–32.3)	90.5±0.5 (87.5–94.9)	84.4±0.8 (79.7–89.8)
34	16	2.4±0.1 (1.9−3.0)	−3.8^{c}±2.0 (−24.1–10.0)	515.7^{a}±38.8 (339.3–818.5)	45.4^{a}±3.1 (22.8–68.2)	25.3±2.4 (11.7–45.9)	90.7±0.6 (85.9–94.6)	85.8±0.7 (79.9–90.6)

Data are expressed as mean ±1 standard error (range). ANOVA for all traits, and mean with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$; $a > b > c$).

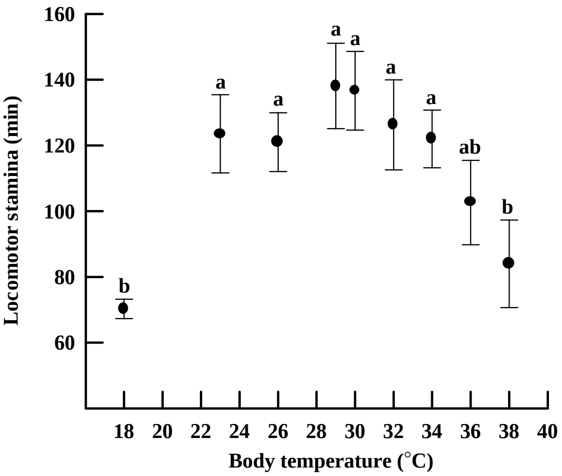

Fig. 2. Locomotor stamina of *Takydromus wolteri* ($N = 11$) at different body temperatures. Data are expressed as mean ±1 standard error. Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$; $a > b$).

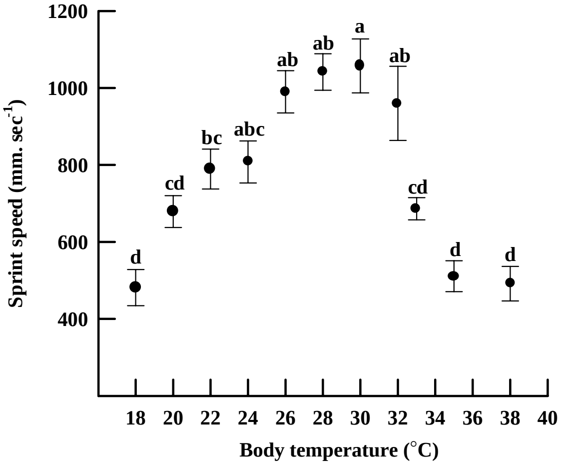

Fig. 3. Sprint speed of *Takydromus wolteri* ($N = 12$) at different body temperatures. Data are expressed as mean ±1 standard error. Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$; $a > b > c > d$).

Beaupre et al., 1993; Ji et al., 1995, 1996, 1997; Xu et al., 1999, 2001; Du et al., 2000), but no general patterns can be drawn at the time because of lack of data from more species. However, based on available data, three patterns of thermal dependence of food passage time can be drawn in lizards: (1) decreasing with increase in body temperature [*Uta stansburiana* (Waldschmidt et al., 1986); *Takydromus septentrionalis* (Ji et al., 1996)]; (2) decreasing with increase in body temperature at lower temperatures and being levelled at higher temperatures [*Eumeces chinensis* (Ji et al., 1995; Xu et al., 1999); *Sphenomorphus indicus* (Ji et al., 1997)]; (3) decreasing with increase in body temperature at lower temperatures and increasing at higher temperatures [*Lacerta vivipara* (Van Damme et al., 1991); *Sceloporus merriami* (Beaupre et al., 1993); *Eumeces elegans* (Du et al., 2000); *Eremias brenchleyi* (Xu et al., 2001)]. The thermal dependence of food passage time in *T. wolteri* seems to belong to Pattern 2, although food passage time of the species levels at a body temperature (34°C) higher that that reported for *E. chinensis* [adults: 30°C (Ji et al., 1995); juveniles: 26°C (Xu et al., 1999)] and *S. indicus* [adults: 30°C (Ji et al., 1997)]. The three patterns are evident, although they seem to be the same one (Pattern 1) within the range from low to moderate body temperatures. Patterns 2 and 3 show up in some species when lizards are tested at very warm temperatures (Van Damme et al., 1991; Beaupre et al., 1993; Ji et al., 1995, 1997; Xu et al., 1999, 2001; Du et al., 2000).

In this study, lizards at body temperatures ranging from 26°C to 30°C gained net mass, whereas lizards at body temperature higher than 32°C lost mass. This implies that there might be a pivotal point between 30°C and 32°C for energy balance in *T. wolteri*: lizards at body temperatures lower than this point are overall in a positive energy balance, and lizards at body temperatures higher than this point are in a negative energy balance. Among individuals whose body temperatures were lower than this point, lizards at 26°C gained much more mass than did those at 28°C and 30°C, largely because of their greater daily food intake, lower metabolic rate and apparently higher ADC and AE. This observation indicates that, similar to what observed in other lizards (e.g., Ji et al., 1993, 1995; Xu et al., 1999; Du et al., 2000), growth can be maximized in *T. wolteri* by shifting body temperatures to moderate levels. Lizards at 34°C, although took significantly more food daily than did those at 30°C and 32°C, lost more mass, largely because of their higher metabolic rates.

It is well known that the values of ADC and AE are influenced by activities of digestive enzymes, food passage time and type and amounts of food consumed (Andrews and Asato, 1977; Harwood, 1979; Beaupre et al., 1993; Witz and Lawrence, 1993). Within a certain range, increasing body temperature may increase activities of digestive enzymes but reduce exposure of food to enzymatic action because of the shortened food passage time (Harwood, 1979). It is this unique mechanism that results in thermal insensitivity of ADC and AE in many studied lizards, 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, influence of body temperature on ADC and AE was not statistically significant, but lizards at 26°C had noticeably greater values of ADC and AE (Table 1), largely because they produced faeces that contained lower energy as compared with those at other body temperatures. Lizards at other four higher body temperatures had almost the same ADC and AE (Table 1), suggesting that *T. wolteri* be still among the species of which ADC and/or AE are relatively less sensitive to variation in body temperature (Dutton et al., 1975; Waldschmidt et al., 1986; Ji and Wang, 1990; van Damme et al., 1991; Beaupre et al., 1993; Ji et al., 1993, 1995, 1996, 1997; Xu et al., 1999, 2001; Du et al., 2000). Moreover, *T. wolteri* is also similar to other typical insectivorous lizards in that ADC and AE are both much greater than those reported for herbivorous lizards (see Andrews and Asato, 1977).

As in other studied lizards [*L. vivipara* (van Damme et al., 1991); *E. chinensis* (Ji et al., 1995); *E. elegans* (Du et al., 2000); *E. brenchleyi* (Xu et al., 2001); *T. septentrionalis* (Ji et al., 1996)], *T. wolteri* exhibited great inter-individual differences in locomotor performance across the test body temperatures. The optimal body temperatures for locomotor stamina and sprint speed in *T. wolteri* are much consistent, because the maximum values of both traits occurred at nearly the same body temperature (30°C). Unfortunately, no comparable data on locomotor stamina are available for other species, so inter-specific comparisons cannot be made at this time. However, it seemed that locomotor stamina in *T. wolter* was not as thermally sensitive as expected, because lizards were able to express over 90% potential of this ability over a wide range of body temperatures (23–34°C; Fig. 2).

Compared with locomotor stamina, sprint speed was more thermally sensitive, because the body temperature range (26–32°C) over which lizards were able to express over 90% potential of this ability was narrower (Fig. 3). Our data show that the optimal body temperature for sprint speed is lower in *T. wolteri* (30°C) than in *E. chinensis* (34°C; Ji et al., 1995), *E. elegans* (34°C; Du et al., 2000), *E. brenchleyi* (32°C; Xu et al., 2001) and *T. septentrionalis* (32°C; Ji et al., 1996), but we are presently unable to give explanations for these differences. All of these species are very common in eastern China, but they differ, in various degrees, in habitat use, selected body temperature and thermal tolerance. The maximum sprint speed also differs considerably among species and, in our experience, lizards that differ in size, mass, morphology (and body shape), selected body temperature and habitat use may differ considerably in this trait (Ji et al., 1995, 1996; Du et al., 2000; Xu et al., 2001). In Chuzhou, *T. wolteri* and *T. septentrioanlis* are largely sympatric species that use similar habitats, although lizards of both species rarely appear simultaneously in the same perch and lizards of the former species are more often found in slightly wetter and shadier microhabitats (Chen, 1991). The maximum sprint speed (1057 mm s^{-1}/30°C Tb) of *T. wolteri* is greater that that (approximately 800 mm s^{-1}/32°C Tb) of *T. septentrioanlis*, but the range of body temperatures over which lizards were able to express over 90% potential of maximum sprint speed is very similar in both species [*T. wolteri*: 26–32°C; *T. septentrioanlis*: 27–33°C (Ji et al., 1996)].

Overall, except for ADC and AE, all traits examined in this study were significantly affected by body temperature, although thermal sensitivities differed considerably among traits. Within the temperature range considered, 26°C was the most suitable body temperature for somatic tissue growth and 30°C was an optimal body temperature for locomotor performance. Thus, our data add some evidence supporting the multiple optima hypothesis for the thermal dependence of behavioural and physiological performances in reptiles.

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