

The thermal dependence of food assimilation and locomotor performance in southern grass lizards, *Takydromus sexlineatus* (Lacertidae)

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Abstract

We collected southern grass lizards, *Takydromus sexlineatus*, from a population in Shaoguan (Guangdong, southern China), and used adult males and non-reproductive females to study the thermal dependence of food assimilation and locomotor performance. We did not find sex differences in selected body temperature (T_{sel}), critical thermal minimum (CT_{Min}) and critical thermal maximum (CT_{Max}). T_{sel} measured on a laboratory thermal gradient was 31.5°C; CT_{Min} and CT_{Max} averaged 6.4°C and 42.2°C, respectively. Within the range from 24°C to 36°C, food passage time, daily food intake, daily production of faeces, apparent digestive coefficient (ADC) and assimilation efficiency (AE) were affected by body temperature, and daily production of urates was not. Food passage time decreased with increase in body temperature within the range from 24°C to 34°C, and then increased at higher body temperatures. Lizards at 32°C and 34°C took more food than did those at higher or lower body temperatures. When influence of variation in the total food intake was removed by an ANCOVA, lizards at 36°C produced faeces containing significantly higher energy as compared with those at body temperatures lower than 32°C. Energy in urates did not differ among lizards at different body temperatures, when removing the influence of variation in total food intake by an ANCOVA. Lizards at 36°C had apparently lower ADC and AE than did those at body temperatures lower than 34°C, mainly because they produced faeces with higher energy contents. Sprint speed increased with increase in body temperature within the range from 20°C to around 32°C, and then decreased at higher body temperatures. Inter-specific comparison among three species of *Takydromus* lizards occupying different latitudinal (climatic) ranges reveal that (1) the maximal sprint speed is greater in *T. wolteri* and *T. sexlineatus* than in *T. septentrionalis*, (2) the optimal body temperature for sprint speed decreases with increase in latitude, and (3) the thermal sensitivity of sprint speed is more pronounced in species occupying lower and higher latitudinal ranges.

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1. Introduction

Body temperature affects not only all physiological processes but also behavioral performances that are

directly linked to them (Huey and Stevenson, 1979; Huey, 1982; Bennett, 1980; Angilletta et al., 2002a, b). Unlike endotherms that stabilize body temperature at great energetic costs, thereby preventing it from fluctuation, reptiles and other ectotherms are subject to daily and seasonally fluctuations in body temperature because thermal interactions between the animal and its environment may cause temporal variation in body temperature. As moderate to relatively high body

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temperatures usually maximize physiological processes, reptiles should consequently maintain relatively high and constant body temperatures through thermoregulation (Huey, 1982; Huey and Kingsolver, 1989; Angilletta et al., 2002b). Most reptiles regulate their body temperatures behaviorally by exploiting environmental heat, although physiological thermoregulation may also be important (Cowles and Bogert, 1944; Avery, 1982; Bartholomew, 1982). Given that no specific body temperature maximizes all processes (Pough, 1980; Huey, 1982; Van Damme et al., 1991; Ji et al., 1995, 1996), the body temperature that reptiles attempt to maintain through thermoregulation largely reflects a compromise of optimal body temperatures for different processes (Hutchison, 1976; Stevenson et al., 1985; Braña, 1993). The set point of thermoregulation can be estimated by the selected body temperature measured on laboratory thermal gradients, and the optimal body temperatures for individual processes can also be estimated under controlled thermal conditions so that the level of performance corresponding to any given body temperature can be determined (e.g., Wang and Xu, 1987; Van Damme et al., 1991; Bauwens et al., 1995; Ji et al., 1995, 1996, 1997; Angilletta, 2001; Angilletta et al., 2002a; Chen et al., 2003).

Body temperature has a pronounced impact on the energy balance and the resulting net energy gains of reptiles, and it also exerts a controlling influence on locomotor performance. Net energy gain through feeding contributes to somatic growth and offspring production. Locomotor performance is also associated with individual fitness due to its importance in predator avoidance and foraging success (Nagy, 1983; Pough, 1989; Bauwens et al., 1995; Ji et al., 1995, 1996; Miles et al., 1995; Ji and Zhang, 2001; Zhang and Ji, 2002), quantifying the thermal dependence of feeding, digesting and locomotor capabilities is ecologically important. Previous studies on Chinese lizards showed that the general patterns of thermal dependence for these functional capabilities are similar among and within species: above the lower limit of thermal tolerance, these capabilities increase with increasing body temperature, reach a plateau at optimal body temperatures, and then decrease at higher body temperatures, up to the upper limit of thermal tolerance, at which functional capabilities cease (Ji and Wang, 1990; Ji et al., 1995, 1996, 1997; Xu et al., 1999, 2001; Du et al., 2000; Chen et al., 2003). Here, we present data on thermal tolerance, selected body temperature and several thermally sensitive traits that are relevant to food assimilation and locomotor performance collected in southern grass lizards, *Takydromus sexlineatus*. Our purposes are: (1) adding new data on a lizard species whose thermal biology is unknown; (2) comparing data from different species of lizards (*Takydromus* lizards in particular) to draw some general conclusions; (3) discussing how some of the

inter-specific differences may be adaptive to the different climatic conditions faced by each species.

2. Materials and methods

2.1. Animals

Takydromus sexlineatus is a small [up to 60 mm snout-vent length (SVL)] multiple-clutched oviparous lacertid lizard; its distributional range covers southern China (including Hainan, Hong Kong and Yunnan), India (Assam) through Burma and Thailand to Vietnam, south to Indonesia (Sumatra, Java and Borneo) (Zhao and Adler, 1993). In the laboratory, large females are able to lay up to 5 clutches with 1–4 eggs each clutch per breeding season lasting from April to July.

Lizards were collected in mid-April 2000 and 2001 from a population in Shaoguan (Guangdong, southern China), approximately 1.5 months after winter dormancy. The captured lizards were transported to our laboratory in Hangzhou, where they were individually sexed, weighed and measured. We palpated adult females (45–60 mm SVL) to assess their reproductive conditions, and allowed reproductive females to lay eggs in the laboratory so that female reproductive characteristics (e.g., clutch size, egg size, seasonal shifts in clutch size and egg size, annual fecundity, and the trade-off between clutch size and egg size) could be determined. Lizards used in this study were adult males and non-reproductive females. Prior to the experiment and during intervals of trials, lizards were randomly maintained 8–10 in each 600 × 400 × 300 mm (length × width × height) glass terrarium, of which the bottom was filled with moist soil and grasses. 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 60 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.

2.2. Selected body temperature and thermal tolerance

Because extreme body temperatures are harmful and potentially lethal, we first determined selected body temperature (Tsel) and then thermal tolerance (critical thermal minimum, CTMin; critical maximum, CTMax). To avoid possible interactions between trials, we conducted each trial at intervals of 1 week. No formal thermal acclimation was employed but, prior to each trial, lizards were maintained at 28°C for 24 h to allow habituation to the starting temperature.

Selected body temperature was determined in $1000 \times 500 \times 300$ mm glass terrarium that was placed in a constant temperature room of which the ambient temperature was controlled at 18°C . Two light bulbs (total 500 W) suspended above one end of the terrarium created a photothermal gradient ranging from 18°C to 60°C (20 mm above the terrarium floor) during the photophase, and the light cycle was 14L:10D. Lizards were moved from the cool end into the terrarium at 07:00 h (Beijing time) when the lights were automatically switched on. Because there might be diel variation in Tsel, we began measurements at 15:00 h and ended within 2 h, thereby making our data more comparable to those collected by us from other species of lizards in the same manner (Ji et al., 1995, 1996, 1997; Xu et al., 1999, 2001; Du et al., 2000; Chen et al., 2003). Body temperatures (cloacal, Tb) of active lizards were taken using a WMZ-03 electronic thermometer (Shanghai Medical Instruments, China), which was previously calibrated with a standard thermometer. To address the reliability of our measurements, we measured each lizard twice on two consecutive days and considered the mean of the two readings as a lizard's body temperature.

Thermal tolerance was determined in an LRH-250G incubator (Guangdong Medical Instruments, China). Experiments were conducted between 10:00 and 15:00 h. Lizards were cooled or heated from 28°C at the rate of 0.25°C per minute and more slowly when temperatures inside the incubator were lower than 10°C or higher than 35°C . During the experiments, we observed the behavior of lizards through a small window in the incubator. The body temperatures associated with a transient loss of righting response (lizards did not respond to intense stimulation and could not turn back when being turned over) at lower and upper limits of thermal tolerance were used as the endpoints for CTMin and CTMax (Ji et al., 1995, 1996).

2.3. Food passage time and food assimilation

Lizards, divided into seven groups, were moved into seven constant temperature rooms, thereby by controlling their mean body temperatures at 24°C , 26°C , 28°C , 30°C , 32°C , 34°C and 36°C . A given lizard was used only at one temperature. The fluorescent tubes in constant temperature rooms were on a 12L:12D cycle, and the lights were automatically switched on at 07:00 h. Lizards were individually housed in a $200 \times 150 \times 250$ mm glass terrarium. We starved lizards for 3 d prior to feeding to insure uniform post-absorptive states, and then fed each lizard with two marked mealworms of which each had been marked by inserting a 3 mm blue plastic thread (diameter 0.2 mm) into the abdomen. We allowed all lizards to eat voluntarily the marked mealworms, thereby avoiding force-feeding; we

subsequently fed them mealworms and water ad libitum. Faeces and urates were collected at least 5 times daily. 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 appearance of the first plastic thread. Trials lasted from 24 days at the highest test temperature (36°C) to 36 days at the lowest test temperature (24°C) 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. We burned dried samples in a WGR-1 adiabatic calorimeter (Changsha Instruments, China), and downloaded data in a computer. The assimilation efficiency was calculated as $AE = (I - F - U)/I \times 100\%$ (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 $ADC = (I - F)/I \times 100\%$ (Waldschmidt et al., 1986).

2.4. Locomotor performance

We measured locomotor performance immediately after returning lizards to the laboratory. Spring speed, defined as the speed in the fastest 50 cm interval, was examined at 10 body temperatures ranging from 20°C to 38°C , the sequence being randomized (30°C , 22°C , 28°C , 34°C , 20°C , 26°C , 36°C , 24°C , 38°C and 34°C). We conducted all trials in a constant temperature room, and housed lizards in the room for 2 h prior to each trial, thereby insuring their body temperatures to be controlled at the test level. We chased lizards down the length of a 2-m racetrack with one side transparent, which allow lateral filming with a Panasonic NV-DS77 digital video camera. The tapes were later examined with a computer using MGI VideoWave III software (MGI Software Co., Canada). Each lizard was run two times at one temperature per day with a minimum of 30 min rest between trials, and was given 48 h to rest between temperatures.

2.5. Statistical analyses

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. We pooled data for both sexes, because preliminary analyses showed that there were no differences in all examined traits between both sexes. One-way ANOVA, one-way ANCOVA and linear regression

analysis and Tukey's test (multiple comparisons) were employed to analyze corresponding data. Prior to testing for differences in adjusted means, the homogeneity of slopes was checked. Throughout this paper, descriptive statistics are presented as mean \pm 1 standard error, and the significance level is set at $\alpha = 0.05$.

3. Results

3.1. Tsel, CTMin and CTMax

Lizards in the laboratory thermal gradient had an ample opportunity to regulate body temperature within their voluntary range. Body temperatures of active lizards ($N = 38$) varied from 28.1°C to 33.9°C, with the mean (indicative of Tsel; Ji et al., 1996) being 31.5°C and the median 31.7°C. CTMin varied from 4.9°C to 8.4°C (Mean = 6.4°C, $N = 34$), and CTMax from 40.7°C to 43.2°C (Mean = 42.2°C, $N = 15$). The central 80% of all preferred temperature readings, an estimate of the preference zone for behavioral thermoregulation (Bauwens et al., 1995), included the values within the range from 29.4°C to 33.5°C.

3.2. Food passage time, food intake and food assimilation

Lizards differed in initial body mass among temperature treatments ($F_{6,85} = 5.70$, $P < 0.0001$), mainly because lizards at 30°C and 36°C were heavier than those at 26°C and 28°C (Table 1). Individual variation in all examined traits was found within each temperature treatment, but none of the traits was correlated with initial body mass.

Food passage time was affected by body temperature ($F_{6,84} = 13.14$, $P < 0.0001$), and it generally decreased with increase in body temperature within the range from 24°C to 34°C and then increased at 36°C (Table 1). Daily food intake (mass-specific) was affected by body temperature ($F_{6,85} = 8.93$, $P < 0.0001$), with lizards at 32°C and 34°C taking apparently more food than did those at other lower and higher temperatures (Table 1). Daily production of faeces (mass-specific) was affected by body temperature ($F_{6,85} = 8.60$, $P < 0.0001$), and the trait was significantly affected by daily food intake within each temperature treatment (All $P < 0.05$). An ANCOVA with the total food intake as the covariate showed that lizards at different body temperatures produced faeces that differed in energy contents ($F_{6,84} = 2.58$, $P = 0.024$), with lizards at 36°C producing faeces that contained significantly higher energy as compared with those at body temperatures lower than 32°C (Tukey's test, all $P < 0.02$). Within the temperature range examined, daily production of urates (mass-specific) were not affected by body temperature ($F_{6,85} = 1.29$, $P = 0.269$) (Table 1).

Table 1
Daily food intake, daily production of faeces, daily production of urates, ADC and AE of *Takydromus sexlineatus* at different temperatures

| Temperature (°C) | N | Initial body mass (g) | Food passage time (h) | 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 (%) |
|------------------|----|-------------------------|---|--|--|--|--|--|
| 24 | 8 | 2.0 \pm 0.1 (1.4–2.5) | 52.1 ^a \pm 4.8 (41.8–75.8) | 346.1 ^{bc} \pm 37.0 (221.5–505.1) | 35.1 ^{bc} \pm 3.5 (22.1–49.3) | 24.9 \pm 1.6 (21.1–35.6) | 89.7 ^a \pm 0.6 (86.7–91.2) | 82.0 ^{ab} \pm 1.3 (74.9–86.2) |
| 26 | 11 | 1.8 \pm 0.1 (1.2–2.4) | 51.5 ^a \pm 5.5 (39.7–96.3) | 367.0 ^{bc} \pm 26.5 (235.5–560.9) | 41.2 ^{bc} \pm 3.0 (30.7–65.5) | 24.3 \pm 2.6 (11.8–44.4) | 88.7 ^a \pm 0.5 (84.6–90.3) | 82.1 ^{ab} \pm 0.8 (76.7–85.3) |
| 28 | 11 | 1.9 \pm 0.1 (1.3–2.6) | 27.2 ^b \pm 3.9 (18.7–47.7) | 304.9 ^c \pm 20.5 (203.0–425.1) | 30.2 ^c \pm 1.9 (22.8–40.4) | 23.2 \pm 1.8 (13.7–32.6) | 90.0 ^a \pm 0.4 (87.8–91.6) | 82.3 ^{ab} \pm 0.7 (76.9–85.0) |
| 30 | 21 | 2.5 \pm 0.1 (1.8–3.1) | 17.4 ^b \pm 2.0 (17.0–46.5) | 388.6 ^{bc} \pm 27.0 (206.8–621.1) | 40.5 ^{bc} \pm 3.1 (18.4–67.7) | 24.5 \pm 1.5 (13.7–40.3) | 89.6 ^a \pm 0.3 (85.5–91.5) | 82.7 ^a \pm 0.6 (76.5–87.4) |
| 32 | 15 | 2.2 \pm 0.1 (1.5–2.7) | 29.6 ^b \pm 2.3 (19.2–42.6) | 501.9 ^{ab} \pm 27.2 (315.1–748.6) | 55.8 ^{ab} \pm 5.6 (24.3–104.4) | 25.3 \pm 2.8 (12.1–53.0) | 89.1 ^a \pm 0.8 (84.0–95.3) | 84.1 ^a \pm 1.0 (77.7–91.3) |
| 34 | 12 | 2.1 \pm 0.1 (1.5–3.2) | 22.0 ^b \pm 2.4 (12.0–40.1) | 618.1 ^a \pm 52.9 (344.4–922.3) | 88.8 ^a \pm 12.0 (25.9–155.1) | 36.5 \pm 5.0 (10.7–65.4) | 86.1 ^{ab} \pm 1.2 (80.0–92.5) | 80.4 ^{ab} \pm 1.5 (72.4–89.8) |
| 36 | 14 | 2.3 \pm 0.1 (1.9–3.1) | 27.2 ^b \pm 2.3 (15.0–43.9) | 425.1 ^{bc} \pm 37.2 (175.7–637.9) | 61.9 ^{ab} \pm 7.9 (26.1–133.4) | 25.8 \pm 3.0 (12.0–48.2) | 84.2 ^b \pm 2.1 (70.2–93.3) | 77.2 ^b \pm 3.1 (56.3–90.2) |

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

Both ADC ($F_{6,85} = 4.64$, $P < 0.0004$) and AE ($F_{6,85} = 2.50$, $P = 0.028$) were affected by body temperature (Table 1), with lizards at 36°C having apparently lower ADC and AE than those at body temperatures lower than 34°C (Table 1). The total energy of urates was also associated with the total food intake within each temperature treatment, but an ANCOVA with the total food intake as the covariate showed that lizards at different body temperatures did not produce urates that differed in energy contents ($F_{6,84} = 1.60$, $P = 0.158$).

3.3. Locomotor performance

Sprint speed was affected by body temperature ($F_{9,165} = 13.04$, $P < 0.0001$), and it generally increased with increase in body temperature within the range from 30°C to around 32°C, and then decreased at higher temperatures (Fig. 1). The optimal body temperature for sprint speed of *T. sexlineatus*, which was estimated by the midpoint of the body temperature range within which a lizard ran at more than 95% of its maximum speed (Bauwens et al., 1995; Ji et al., 1995, 1996), was at or near 34°C. The body temperature range within which a lizard ran at more than 80% of its maximum speed was 29–36°C (Fig. 1).

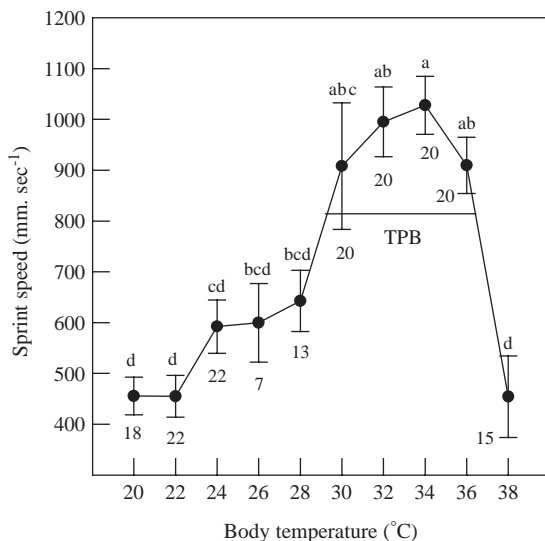


Fig. 1. Sprint speed of *Takydromus sexlineatus* at different body temperatures. Data are expressed as mean \pm 1 standard error. Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$; $a > b$). Sample size for each test temperature is indicated in the figure. The horizontal line indicates the thermal-performance breadth (TPB_{80} , Van Berkum, 1986).

4. Discussion

Tsel, CTMin and CTMax are widely used in studies of thermal biology of reptiles, and the three commonly examined traits are all affected by numerous internal and external factors (Hutchison, 1976). Tsel have generally used a single Tsel for a population of animals (e.g., Ji et al., 1995, 1996; Shine and Madsen, 1996; Dorcas and Peterson, 1991) and is thought to represent the body temperature at which numerous processes function at an optimal level (e.g., Hutchison, 1976; Van Damme et al., 1991; Hertz et al., 1993; Christian and Weavers, 1996; Blouin-Demers et al., 2000; Angilletta et al., 2002b). Temporal, spatial and individual variation in Tsel has been reported for numerous species of reptiles (e.g., Gatten, 1974; Ellner and Karasov, 1993; Christian and Bedford, 1995; Andrews, 1998). Thus, Tsel cannot be considered as a fixed trait of a species (Hutchison, 1976). However, in our previous experience with determining Tsel of lizards, data collected from different species in the same manner are not only comparable but also ecologically meaningful.

Based on available data, we conclude that lizards using shaded habitats select lower body temperatures on a laboratory thermal gradient as compared with those using opened habitats. For example, brown skinks (*Sphenomorphus indicus*) are collected from a population in Hangzhou select body temperatures averagely at 25.7°C, largely because they use forestry habitats, where ambient temperatures are rarely higher than 30°C even in the hottest months (from June to August). On the contrary, lizards using more opened habitats such as Chinese skinks (*Eumeces chinensis*; Ji et al., 1995), blue-tailed skinks (*E. elegans*; Du et al., 2000), multiple-lined skinks (*Mabuya multifasciata*; Ji et al., unpubl. data), sand lizards (*Eremias brenchleyi*; Xu et al., 2001) and northern grass lizards (*Takydromus septentrionalis*; Ji et al., 1996) select body temperatures averagely at 31.2°C, 30.4°C, 31.4°C, 33.7°C and 30.0°C, respectively. Similar to other *Takydromus* lizards, *T. sexlineatus* in the field spends a lot of its active time on grasses and shrubs opened to direct sunshine, and therefore select body temperatures higher than those using shaded habitats.

Inter-specific comparisons reveal that lizards using different habitats and occupying different geographic (climatic) regions differ in both CTMin and CTMax. Overall, CTMin is greater in lizards using warmer habitats or living in warmer localities, and CTMax is greater in lizards using opened habitats. For example, CTMin reported for *E. chinensis* (6.3°C; Ji et al., 1995), *E. elegans* (9.3°C; Du et al., 2000), *M. multifasciata* (9.1°C; Ji et al., unpubl. data) are greater than that for *T. septentrionalis* (3.9°C for males and 5.9°C for females; Ji et al., 1996) and *E. brenchleyi* (3.3°C; Xu

and Ji, 2000), largely because the former species live in lower latitudinal (and hence warmer climatic) regions.

CTMax is lower in *S. indicus* (37.6°C; Ji et al., 1997) than in *E. chinensis* (42.3°C; Ji et al., 1995), *E. elegans* (41.9°C; Du et al., 2000), *M. multifasciata* (41.0°C; Ji et al., unpubl. data), *T. septentrionalis* (42.3°C; Ji et al., 1996) and *E. brenchleyi* (43.6°C; Xu and Ji, 2000), indicating that *S. indicus* has a lower ability to tolerate high temperatures due to its use of shaded habitats. CTMin (6.4°C) and CTMax (43.2°C) are both noticeably great in *T. sexlineatus*, mainly because the species geographically occupies warm regions and uses opened habitats in the field.

The mean values of food passage time corresponding to a given body temperature and the thermal sensitivity of the trait differ considerably among species (Waldschmidt et al., 1986; Van Damme et al., 1991; Beaupre et al., 1993; Ji et al., 1995, 1996, 1997; Xu et al., 1999, 2001; Du et al., 2000; Chen et al., 2003) and, based on available data, three patterns of thermal dependence of food passage time have been found in lizards studied: (1) decreasing with increase in body temperature [*Uta stansburiana* (Waldschmidt et al., 1986); *T. septentrionalis* (Ji et al., 1996)]; (2) decreasing with increase in body temperature at lower temperatures and being leveled at higher temperatures [*E. chinensis* (Ji et al., 1995; Xu et al., 1999); *S. indicus* (Ji et al., 1997); *T. wolteri* (Chen et al., 2003)]; (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); *E. elegans* (Du et al., 2000); *E. brenchleyi* (Xu et al., 2001)]. The thermal dependence of food passage time in *T. sexlineatus* seems to belong to Pattern 3. Thus, each of the three *Takydromus* lizards studied by us interestingly belongs to one of the three different patterns, and a negative exponential fit on original data further supports this conclusion (Fig. 2). However, questions remain to be answered for these lizards are: (1) whether the three patterns are not different but actually the same one simply because of the artifact of the range of temperatures used? (2) Whether there is also a pivotal point in *T. septentrionalis* and *T. wolteri* above which food passage time increases with increase in body temperature? If the answers to the two questions are “Yes”, then the pattern of the three *Takydromus* lizards should be Pattern 3, but the position of the pivotal point would be certainly different among species.

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 due to the shortened food passage time (Har-

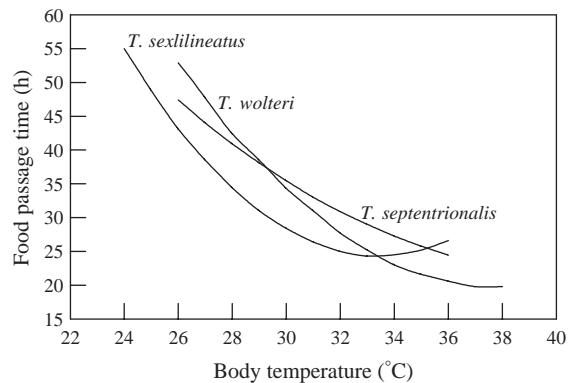


Fig. 2. Food passage time in *Takydromus* lizards (*T. sexlineatus*, *T. wolteri* and *T. septentrionalis*) as a function of body temperature. The curves are generated from a negative exponential fit on the original data reported in this study and by Ji et al. (1996) and Chen et al. (2003).

wood, 1979; Waldschmidt et al., 1986; Van Damme et al., 1991; Ji et al., 1995, 1996, 1997; Du et al., 2000; Xu et al., 1999, 2001; Chen et al., 2003). This unique mechanism results in the thermal independence of ADC and AE over a wide range of body temperatures 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 very pronounced, but only lizards at 36°C had noticeably lower values of ADC and AE (Table 1), largely because they produced faeces that contained higher-energy contents as compared with those at lower body temperatures. Lizards at other six lower body temperatures had almost the same ADC and AE (Table 1), suggesting that *T. sexlineatus* is also a species whose digestive performance is 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; Chen et al., 2003).

Inter-individual differences in locomotor performance were first reported by Bennett (1980) and later by other authors for numerous species of lizards, such as *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) and *T. wolteri* (Chen et al., 2003). *Takydromus sexlineatus*, as in other lizards studied, also exhibited great inter-individual differences in sprint speed within each test temperature (Fig. 1). The optimal body temperature for sprint speed in *T. sexlineatus* is at or near 34°C, which is higher than that reported for *E. brenchleyi* (32°C; Xu et al., 2001) but almost the same as that for

E. chinensis (34°C; Ji et al., 1995) and *E. elegans* (34°C; Du et al., 2000).

When comparing our data with the other two species of *Takydromus* lizards, we found that the maximal sprint speed, the optimal body temperature for sprint speed and the thermal sensitivity of sprint speed differ among species (Fig. 3). The maximal sprint speed is greater in *T. wolteri* and *T. sexlineatus* than in *T. septentrionalis* (ANOVA followed by Tukey's multiple comparisons, both $P < 0.01$) but it does not differ between *T. wolteri* and *T. sexlineatus* (Fig. 3), partly because these species differ in body size and morphological traits (e.g., limb length and tail length) throughout their size range (Lin and Ji, 1998; Xu and Ji, 2000; Zhang and Ji, 2000; Pan and Ji, 2001). The optimal body temperature for sprint speed is highest in *T. sexlineatus*, intermediate in *T. septentrionalis* (32°C; Ji et al., 1996) and lowest in *T. wolteri* (30°C; Chen et al., 2003). This finding is interesting, because it implies a geographic shift in optimal body temperature for sprint speed as an evolutionary consequence of adaptation to different climatic environments (Fig. 4). Of the three species of *Takydromus* lizards, *T. septentrionalis* is endemic to China, and its distributional range overlaps north with

T. wolteri and south with *T. sexlineatus*. Lizards occupying northern (colder) regions find it relatively difficult to maintain high and stable body temperatures, because of thermal constraints imposed by local environments (Fig. 4), or missed opportunities associated with thermoregulation. Thus, a geographic shift in optimal body temperature from high to low levels with increase in latitude might be a strategy adopted by lizards to perform more effectively.

The range of body temperatures within which a lizard expresses over 80% of its maximum speed (TPB₈₀, Van Berkum, 1986) differs among the three species of *Takydromus* lizards [7°C (29–36°C) for *T. sexlineatus*; 12°C (24–36°C) for *T. septentrionalis*; 8°C (25–33°C) for *T. wolteri*] (Fig. 3). This finding is also interesting,

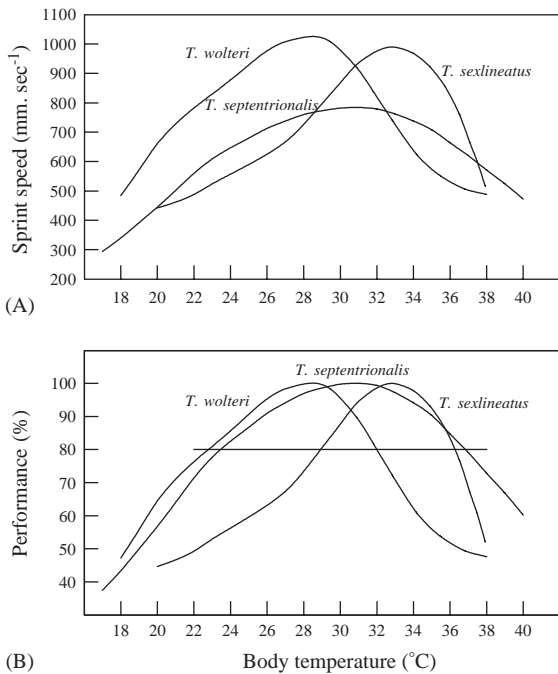


Fig. 3. Sprint speed in *Takydromus* lizards (*T. sexlineatus*, *T. wolteri* and *T. septentrionalis*) as a function of body temperature. The curves in the upper plot are generated from a fit of least squares on the original data reported in this study and by Ji et al. (1996) and Chen et al. (2003), and the curves in the lower plot are generated from the percentages of the maximal speed. The horizontal line indicates the thermal-performance breadth (TPB₈₀, Van Berkum, 1986).

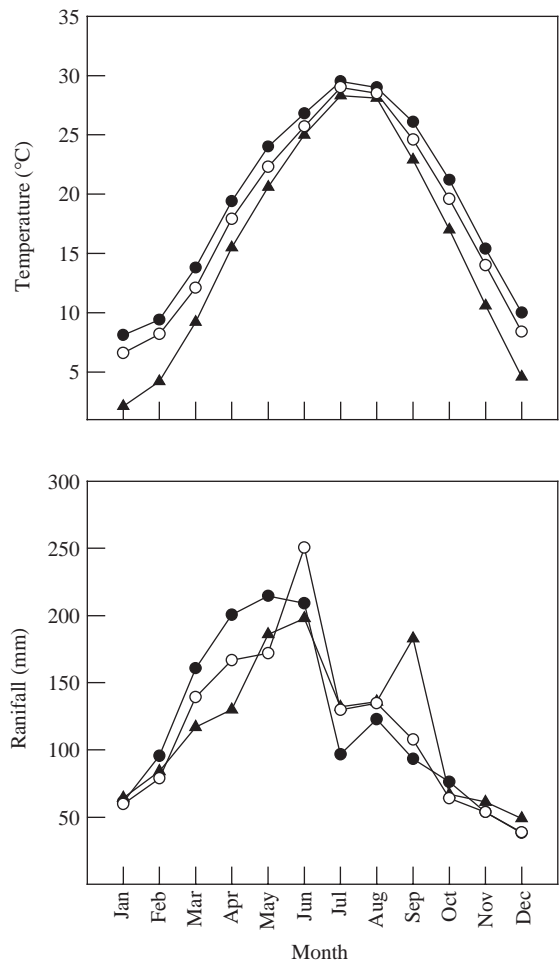


Fig. 4. Monthly mean air temperatures and monthly mean rainfall for 1980–2000 at the three localities (courtesy of the Provincial Bureaus Meteorology of Zhejiang, Guangdong and Anhui), from which *Takydromus* lizards were collected. ○: Lishui (*T. septentrionalis*); ●: Shaoguan (*T. sexlineatus*); ▲: Chuzhou (*T. wolteri*).

because it suggests that sprint speed may be thermally more sensitive in lizards occupying lower and higher latitudinal ranges. Among-species differences in thermal breadths of locomotor performance have been reported for European lacertid lizards, with TPB_{80} varying from 4.5°C in *Podarcis atrata* to 11.5°C in *Psammodromus algirus* and *Acanthodactylus erythrurus* (Bauwens et al., 1995). However, the causes resulting in these differences remain unknown.

Because TPB_{80} differs among congeneric species of lizards whose distributional regions are different, we predict that a species ranking on environmental temperatures in its habitat should be positively correlated with its ranking for the optimal temperature of locomotor speed. Given that the mean value and the stability of ambient temperatures vary temporally and geographically, we also predict that lizards occupying different latitudinal regions should differ in the length of active time or season within which they can express their locomotor capacities at relatively high levels.

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