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BODY TEMPERATURE, THERMAL TOLERANCE AND INFLUENCE OF TEMPERATURE ON SPRINT SPEED AND FOOD ASSIMILATION IN ADULT GRASS LIZARDS, *TAKYDROMUS SEPTENTRIONALIS*

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Abstract—1. We studied in field and laboratory experiments several aspects of the thermal biology of adult lacertid lizards (*Takydromus septentrionalis*).

2. The selected body temperature and the critical thermal maximum averaged 30.0 and 42.3°C, respectively; the critical thermal minimum of males and females averaged 3.9 and 5.9°C, respectively.

3. The lizards in May exhibited lower and more variable active body temperatures than did the lizards in July, because of lower and more variable air and substrate temperatures in May.

4. The sprint speed generally increased with body temperature within the range of 17 to 32°C and decreased at temperatures >32°C.

5. Within the range of 26 to 36°C, body temperature influenced food assimilation primarily by affecting the food passage time, whereas it only slightly affected the daily food consumption, the apparent digestive coefficient and the assimilation efficiency. The food passage time decreased with increasing body temperature. Copyright © 1996. Elsevier Science Ltd.

Key Word Index: Reptilia; Lacertidae; *Takydromus septentrionalis*; selected body temperature; $CT_{\max}$; $CT_{\min}$; sprint speed; food passage time; food intake; food assimilation

INTRODUCTION

Many investigators, particularly in the U.S.A. and Europe, have presented a large quantity of data on thermal biology of lizards. While theories on this topic are getting more and more mature, we feel that more attention should be given to Asian lizards because available data on them have been extremely limited. As a part of our herpetological research in Zhejiang, East China, over the past 6 years, we have collected data on the thermal biology of five lizard species. We consider our work merely as a starting point, especially given that China, with 152 recognized species of lizards, is very abundant in such animals (Zhao and Adler, 1993).

Takydromus septentrionalis (Lacertidae) is a small (adult snout-vent length 55–78 mm; mass 2.9–8.1 g), widely foraging diurnal insectivore. Adult males and females are similar in average snout-vent length (SVL), but males have larger heads than females of similar SVL, except approaching the size at sexual maturity (Ji *et al.*, 1993a). The lizard is oviparous with distinct annual reproductive and activity cycles, and is widely distributed in southern China, north to Jilin and west to Gansu (Zhao and Adler, 1993). It is commonly called the grass lizard, reflecting its habit of spending much of its active time on grasses and shrubs. *Takydromus septentrionalis* is one of the best-known species of endemic lizard in China. Sexual dimorphism and reproduction (Ji *et al.*, 1993a; Liu, 1939; Wang, 1966), activity patterns and home range (Ji *et al.*, 1989, 1994; Wang, 1964), embryonic metabolism (Ji, 1992; Wang *et al.*, 1989), metabolism of adults (Wang and Xu, 1987) and food assimilation of juveniles (Ji *et al.*,1993b) have been previously studied. Here, we present data on the thermal biology of adult *T. septentrionalis*, involving (1) active body temperatures measured in the field in May and July, (2) selected body temperature (T_{sel}), critical thermal maximum ($CT_{\max}$) and critical thermal minimum ($CT_{\min}$) measured in the laboratory, and (3) the

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possible thermal dependence of sprint speed, food passage time and food assimilation.

MATERIALS AND METHODS

Field study

Our field work was conducted during 12–25 May 1993 and 18–29 July 1994 on five islets (Liuheng, Xiazhi, Taohua, Dengbu and Zhujiajian) in Putuo county, Zhoushan Islands (29°32′–31°04′N, 121°30′–123°25′E), Zheijiang, East China. Over the past 20 years, the annual air temperature, relative humidity and precipitation in this area have averaged 15.4–16.6°C, 71–80%, and 850–1367 mm, respectively (Zhoushan Science and Technology Committee). Our data were collected from 06:30–18:30 (Beijing time), covering almost the entire daily active period of the lizards at that season of the year. We randomly walked the study plots and captured adult lizards by hand. Body temperatures (cloacal, T_b) were obtained from active lizards using a RC-95 quick-reading electronic thermometer (Jinhua Instruments). Air (T_a, 2 cm above substrate) and substrate (T_s) temperatures were taken with the same thermometer at the site where a lizard was captured.

T_{sel}, CT_{max} *and* CT_{min}

On 25 May 1994 we transported 38 adult lizards (15 males, 23 females) from Xiushan Island (30°11′N, 122°9′E) to Hangzhou Normal College. Mean (±SE) SVLs and masses (M) were: males: SVL = 67.6 ± 0.6 mm, M = 6.1 ± 0.3 g; females: SVL = 64.2 ± 0.5 mm, M = 5.0 ± 0.2 g. The sexes were housed separately 5–6 to each glass cage (40 × 30 × 30 cm), which was filled with soil, blocks of wood, stones and grasses. Mealworms (larvae of *Tenebrio molitor*) and water were provided *ad libitum*. To prevent possible interactions between experiments, we conducted experiments at intervals of 7 days. Prior to each experiment, all lizards were kept in a constant-temperature room at 28°C for 48 h. The photoperiod of the room was 12 light:12 dark; lights were switched on 07:30.

T_{sel} was determined in a 220 × 90 × 60 cm plastic cage. Three light bulbs (total 1000 W) suspended above one end created a gradient of air temperatures (2 cm above substrate) ranging from 14 to 70°C. Lizards were moved into the cage at 07:30 when the lights were switched on. Because of the possibility of diel variations in T_{sel}, we began all our measurements at 15:00 and ended within 2 h. Body temperatures of active lizards were taken using the same thermometer as that in the field. To address the reliability of our measurements, we measured each lizard twice on 2 consecutive days. Efforts were made to make the two measurements fall within the same period (no more than 1 h) of the 2 days. We considered the mean of the two readings as the lizards' body temperature in the thermal gradient. We used the mean of all T_b recordings in the thermal gradient as the selected body temperature.

CT_{max} and CT_{min} were determined in a LRH-250A incubator (Guangdong Medical Instruments). Experiments were conducted between 10:00 and 15:00. Lizards 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 lizards. The body temperatures associated with a transient loss of righting response (LRR) at upper and lower thermal limits were used as CT_{max} (Lowe and Vance, 1955) and CT_{min} (Ji *et al.*, 1995), respectively. Two lizards not fully recovering from the CT_{max} experiment were excluded from analyses. The two lizards died 2 days after the experiment.

Thermal dependence of sprint speed

During late June–early July 1994, we randomly selected lizards (males:females = 1:1) from 210 individuals collected from Xiushan Island in early June 1994 to test the thermal dependence of sprint speed. No females which would oviposit within 2 weeks were used. SVLs varied from 58.7 to 69.4 mm, and masses from 3.1 to 7.6 g. The sequence was randomized (26, 24, 28, 30, 17, 34, 40, 36, 20, and 38°C). Prior to the experiment at each temperature, lizards had been kept at the test temperature for 24 h. We began the experiment at each temperature at 15:00. To standardize the stimulus, it was always the first author who chased the lizards down a racetrack (200 × 15 × 15 cm). Running times were measured by six sets of photocells positioned at 25 cm intervals along the track. Each lizard was run daily three times at each temperature. From the three trials, we selected the fastest 25 cm track interval, used as an estimate of maximum sprint speed at that temperature. We excluded from analyses any lizards which broke their tails during the experiment. We connected data points, constructed a minimum convex polygon (van Berkum *et al.*, 1986) and then estimated the width of the 80% performance breadths (TPB_{80} = body temperature range over which speed is at least 80% of its maximum).

Food passage time and food assimilation

We conducted this study in June 1994. Lizards (males:females = 1:1) were collected from the same site as those used for determination of sprint speed and divided into six groups; each group was placed in 26, 28, 30, 32, 34 and 36°C constant-temperature rooms, respectively. The fluorescent tubes and room

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

	T_{sel}	CT_{max}	CT_{min}	
			Male	Female
Mean	30.0	42.3	3.9	5.9
SE	0.3	0.1	0.1	0.2
N	38	36	15	21
Range	26.0–33.5	40.5–43.5	3.0–4.5	4.0–7.0

lighting were on a 12 light:12 dark cycle; lights were switched on at 07:30. Each lizard was housed in a 19 × 19 × 12 cm glass cage, fasted for 3 days at the test temperature, and then weighed and measured. These measurements were recorded as initial body mass and SVL. The test period at each temperature was 12 days. Final body mass was recorded at the end of a 3 day fast which terminated each test period.

Before the lizards were allowed to feed, we marked mealworms by inserting a 3 mm red plastic thread (diameter 0.2 mm) into their abdomen, and force-fed these mealworms to the lizards. Unmarked mealworms and water were then provided *ad libitum*. We collected faeces and urinary waste (mainly uric acid) at intervals of 15 min and separated them carefully. Faeces were examined with a stereomicroscope until the appearance of plastic threads. The food passage time was defined as the time from swallowing to the first appearance of plastic threads in the faeces.

All of the materials used for caloric determination were dried to constant mass in an oven at 65°C, and dry masses were recorded. Ash-uncorrected caloric values of mealworms, faeces and urinary waste were determined using a GR-3500 adiabatic calorimeter (Changsha Instruments Factory). Titrations of residuals were performed to correct for nitrogenous waste. The assimilation efficiency (AE) was calculated as: $AE = (I - F - U)/I \times 100\%$, where I = total calories ingested, F = calories in faeces, and U = calories in urinary waste (Ji and Wang, 1990; Kepenis and McManus, 1974); the apparent digestive coefficient (ADC) was calculated as $ADC = (I - F)/I \times 100\%$ (Ballinger and Holscher, 1983; Harwood, 1979; Waldschmidt *et al.*, 1986).

RESULTS

T_{sel}, CT_{min}, CT_{max} *and active body temperature*

We found no significant differences in T_{sel} and CT_{max} between males and females (Mann–Whitney U-test, both $P > 0.05$), but males had a significantly greater ability to tolerate extremely cold temperatures, exhibiting a significantly lower mean CT_{min} than did females (Mann–Whitney U-test, $P < 0.05$) (Table 1). T_{sel} and CT_{max} averaged 30.0 and 42.3°C, respectively; CT_{min} of males and females averaged 3.9 and 5.9°C, respectively.

We found no significant difference in mean body temperature between active males and females in the field (Mann–Whitney U-test, $P > 0.05$), so we pooled data for both sexes. A two-way ANOVA revealed that the variances of T_b, T_a and T_s in May differed significantly from the corresponding ones in July (T_b–$F_{76,139} = 1.56$, T_a–$F_{76,139} = 1.78$, T_s–$F_{76,139} = 2.02$; all $P < 0.05$). In May, active lizards in the open field were exposed to lower and greater variable thermal conditions, and hence exhibited lower and more variable body temperatures than did the lizards in July (Table 2).

Thermal dependence of sprint speed

Males and females did not differ significantly in sprint speed (Mann–Whitney U-test, $P > 0.05$), so we pooled the data for both sexes. The sprint speed increased with body temperature within the range of 17–32°C and decreased at higher temperatures (Fig. 1). The sprint speed varied considerably among individuals at each test temperature.

Food passage time and food assimilation

Mealworms fed to *T. septentrionalis* averaged 63.4% water and had a mean ash uncorrected caloric value of 5760.3 cal g^{-1} dry mass. We found no significant differences in food passage time and food assimilation between males and females (Mann–Whitney U-test, all $P > 0.05$), so we pooled the data for both genders. We evaluated calorimetrically the faeces collected at different temperatures, finding that there were slight differences in caloric values ($F_{5,60} = 2.93$, $P < 0.05$) (Table 3). The energy content of urinary waste remained almost unchanged

Table 2. Body, air and substrate temperatures (°C) recorded in the field in May and July

	May			July		
	T_b	T_a	T_s	T_b	T_a	T_s
Mean	28.3	23.7	24.5	32.4	29.4	29.9
SE	0.5	0.4	0.4	0.2	0.2	0.2
N	77	77	77	140	140	140
Range	19.5–36.3	16.9–32.0	16.9–31.6	27.4–38.5	26.4–38.0	26.4–40.5

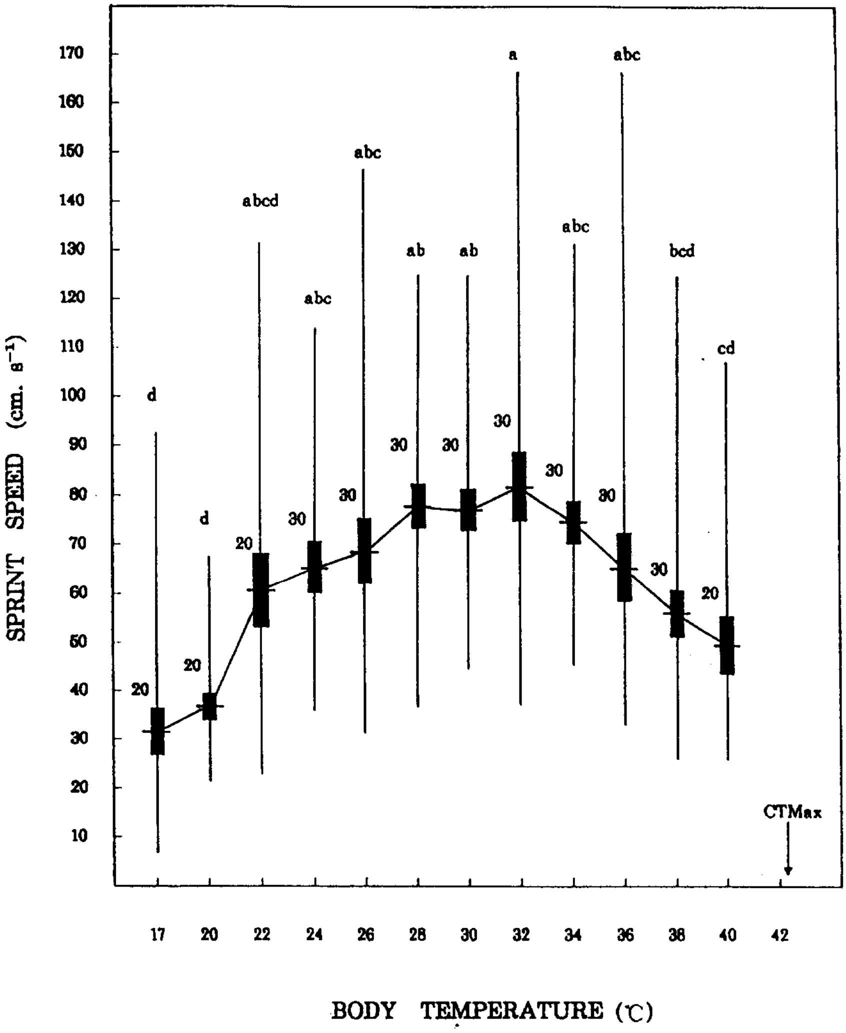

Fig. 1. The sprint speed of adult *Takydromus septentrionalis* at several body temperatures. Data are expressed as mean ± SE and range. Sample sizes are indicated in the figure. Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$).

across the test temperatures, with a mean of 2551.7 cal g^{-1} dry mass. Within the range of test temperatures, food passage time (FPT) decreased with body temperature ($FPT = 103.4 - 2.2T_b$, $r = -0.98$, $F_{1,4} = 104.05$, $P < 0.001$) (Fig. 2). No statistically significant differences in daily food intake occurred among lizards at different temperatures ($F_{5,60} = 1.10$, $P > 0.05$) (Table 4). Temperature had apparently slight but statistically significant effects on the ADC ($F_{5,60} = 327.04$, $P < 0.001$) and the AE ($F_{5,60} = 153.49$, $P < 0.001$). The maximum ADC (93.6%) and AE (89.1%) both occurred at 30°C (Table 4).

Table 3. Faecal calories (cal g^{-1} dry mass) of the adult *Takydromus septentrionalis* maintained in constant-temperature rooms

T (°C)	N	Mean	SE	Range
26	12	4238.1	23.0	4116.4–4329.4
28	12	4434.0	39.2	4266.6–4628.6
30	11	4221.6	31.6	4063.3–4353.4
32	8	4325.4	51.9	4179.2–4466.7
34	12	4410.1	101.7	4121.6–4809.3
36	11	4219.6	51.7	4068.4–4478.7

DISCUSSION

Takydromus septentrionalis are poor at physiological thermoregulation, because their body temperatures are almost the same as the corresponding ambient temperatures when they are placed in a constant-temperature room in which the temperature is uniform and behavioural thermoregulation is under strict control (see Wang and Xu, 1987). However, under natural conditions or provided a thermally diverse habitat in the laboratory, *T. septentrionalis* can increase their body temperature and

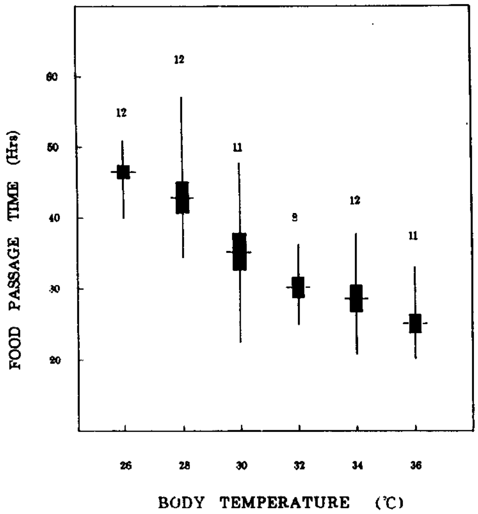

Fig. 2. Food passage time of adult *Takydromus septentrionalis* at several body temperatures. Data are expressed as mean ± SE and range. Sample sizes are indicated in the figure.

maintain it at a relatively constant level, primarily through behavioural adjustments. Severe weather conditions (e.g. extreme cold or heat) strongly prevent this lizard from achieving body temperatures within its preferred range (Ji *et al.*, 1994). During May and June, lizards avoided being active in the open field when the mean air temperature of the day was below 15°C or greater than 30°C (Ji *et al.*, 1994). Being active is important for *T. septentrionalis* in mate acquisition, foraging and thermoregulation, but they usually reduced their activity or remained motionless in grass clumps, crevices and other refuges during the period when the costs of maintenance and/or behavioural thermoregulation were presumably high.

A low mean body temperature and a greater variance in T_b in May were primarily due to lower and more variable air and substrate temperatures in May, suggesting that lizards in this month were more passive to ambient temperatures. The greater discrepancies between mean T_b and mean T_a and between mean T_b and mean T_s in May implied that during this month *T. septentrionalis* would expend more energy on thermoregulation than did the lizards in July, when ambient temperatures were higher and relatively constant.

It is well known that T_{sel}, CT_{max} and CT_{min} are influenced by many external and internal factors (see Hutchison, 1976). However, from our point of view, it is possible to compare T_{sel}, CT_{max} and CT_{min} from different species and then reveal the differences in these aspects among species or within species which differ in activity pattern, habitat utilization, geographical distribution, etc. Before doing this, we found it important to standardize the methods and procedures of experiments. We made efforts to reduce the possible influences of some of the above factors by keeping different lizard species under the same conditions as mentioned above and then measuring their T_{sel}, CT_{max} and CT_{min} during the same period. Data collected in the same way described here showed that there were obvious interspecific differences in T_{sel}, CT_{max} and CT_{min} among the three most common diurnal lizard species in Zhejiang: *Takydromus septentrionalis*, the brown skink *Sphenomorphus indicus* (T_{sel} 25.7°C, CT_{max} 37.6°C, CT_{min} 3.1°C; Ji *et al.*, submitted) and the Chinese skink *Eumeces chinensis* (T_{sel} 31.2°C, CT_{max} 42.1°C, CT_{min} 6.9°C; Ji *et al.*, 1995). The three species differ in habitat use and activity patterns (Wang, 1964), and hence exhibited obvious differences in T_{sel}, CT_{max} and CT_{min}. What should be pointed out here is that the end-point used by us for CT_{max} was the loss of the righting response (LRR) (Lowe and Vance, 1955) not the onset of

Table 4. Initial body mass, food intake, ADC and AE of adult *Takydromus septentrionalis*

T (°C)	N	Initial body mass (g)	Food intake (cal g^{-1} day^{-1})	ADC (%)	AE (%)
26	12	5.4 ± 0.3	188.3 ± 13.0	91.5 ± 0.6^{ab}	86.2 ± 0.9^{b}
		(4.0–8.1)	(108.6–268.9)	(88.4–92.3)	(81.2–90.0)
28	12	5.2 ± 0.2	195.4 ± 10.2	91.4 ± 0.5^{b}	86.5 ± 0.6^{ab}
		(4.8–6.6)	(139.7–266.5)	(88.0–93.9)	(82.1–89.2)
30	11	5.6 ± 0.3	206 ± 39.1	93.6 ± 0.5^{a}	89.1 ± 1.0^{a}
		(3.7–7.8)	(74.3–486.8)	(91.5–95.8)	(84.5–93.4)
32	8	5.5 ± 0.2	151.6 ± 14.3	91.9 ± 0.8^{ab}	87.0 ± 1.3^{ab}
		(4.8–6.6)	(99.6–228.1)	(88.6–94.7)	(82.1–91.9)
34	12	5.6 ± 0.3	160.1 ± 16.5	93.2 ± 0.3^{ab}	87.8 ± 0.6^{ab}
		(3.9–7.6)	(69.0–228.6)	(91.7–95.5)	(85.5–93.0)
36	11	5.4–0.3	169.7 ± 9.0	93.2 ± 0.5^{ab}	88.6 ± 0.8^{ab}
		(4.0–7.1)	(135.9–245.2)	(90.4–95.1)	(84.5–92.0)

Data are expressed as mean ± SE (range). Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$).

spasms (OS) (Cowles and Bogert, 1944). Several investigators have pointed out that LRR occurs at a lower temperature (0.5–1.5°C) than OS (e.g. Hutchison, 1961; Hutchison and Maness, 1979). Further studies will be conducted to check the temperature difference between LRR and OS in *T. septentrionalis*.

One interesting finding in this study was that the mean $CT_{\min}$ of male *T. septentrionalis* was lower than that of females; however, the explanation for this difference is unknown at present.

Several studies have demonstrated individual consistency in sprint speed (Bennett, 1980; Garland, 1985; Huey and Dunham, 1987; Huey and Hertz, 1984; van Berkum *et al.*, 1989), but studies demonstrating an obvious individual difference in sprint speed have been limited. Our results, as in the lacertid lizard *Lacerta vivipara* (van Damme *et al.*, 1991) and *E. chinensis* (Ji *et al.*, 1995), showed great individual variances in sprint speed that were preserved across experimental temperatures. The optimal temperature for sprint speed of *T. septentrionalis* is at or near 32°C, which is higher than its selected body temperature and is similar to that recorded in some temperate lizards. In the field, approximately 84% of T_b readings in May and 94% of T_b readings in July for adult *T. septentrionalis* were within the TPB_{80} (24–36°C), approximately 16% of T_b readings in May fell below this range and 6% of T_b readings in July were above this range. This means that most lizards in May and July were active at T_bs that enabled them to run quickly.

Previous studies generally showed an influence of temperature on food passage time (Harwood, 1979; Ji *et al.*, 1995; van Damme *et al.*, 1991; Waldschmidt *et al.*, 1986). In these studies, lizards were held to various ranges of temperature, thus we have difficulties in comparing the data reported here with those for other species. However, the result that the food passage time of *T. septentrionalis* decreased with body temperature was apparently similar to that reported for the iguanid lizard *Uta stansburiana* (Waldschmidt *et al.*, 1986). In *E. chinensis*, Ji *et al.* (1995) found that the food passage time decreased linearly with body temperature within the temperature range of 24–30°C and then was obviously maintained unchanged at higher temperatures. In *L. vivipara*, van Damme *et al.* (1991) reported that the food passage time decreased with body temperature within the temperature range of 20–32.5°C, but became noticeably long at 35°C, at which temperature the lizard was near its $CT_{\max}$.

The lower variation in ADC as a function of temperature is similar to that reported for several insectivorous lizards, e.g. the rusty lizard *Sceloporus olivaceus* (Dutton *et al.*, 1975), *U. stansburiana* (Waldschmidt *et al.*, 1986), *L. vivipara* (van Damme *et al.*, 1991) and *E. chinensis* (Ji *et al.*, 1995). Harwood (1979), however, found that the ADCs in the western fence lizard *Sceloporus occidentalis*, the western whiptail lizard *Cnemidophorus tigris* and the southern alligator lizard *Gerrhonotus multicarinatus* generally increased with body temperature. The low variation in the AE is similar to the results reported in the few studies measuring AE of lizards, including juvenile *T. septentrionalis* (Ji *et al.*, 1993b), the gecko *Gekko japonicus* (Ji and Wang, 1990) and *E. chinensis* (Ji *et al.*, 1995). In juvenile *T. septentrionalis* at 28, 30 and 32°C, Ji *et al.* (1993b) found that the AE was impaired at 32°C, because lizards at this temperature, when given a certain amount of food (mealworms), had not only the highest defecated material production but also the highest weight-specific calories of faeces. Changes in ADC and AE with body temperature presumably involve the thermal sensitivity of enzymes, because the maximum enzymatic activity is believed to be characteristically associated with an optimal temperature and pH (Harwood, 1979). Although the activity of digestive enzymes generally increases with temperature within a certain range of temperature, lizards at lower temperatures might maintain relatively normal ADC and AE by increasing food residency time, which would prolong the exposure of food to enzymatic action. The longer food passage time at low temperatures reported here and in other papers may support this assumption.

The assimilation efficiencies of adult *T. septentrionalis* were similar to those of juveniles at 28 and 30°C, but significantly greater than those of juveniles at 32°C (see Ji *et al.*, 1993b). In contrast to juveniles in which the AE was impaired at 32°C, adults maintained normal ADC and AE even at 36°C.

In summary, all functions examined in *T. septentrionalis* differ in their optimal temperatures and thermal sensitivities. Thus our results support the multiple optima hypothesis (Bustard, 1967; Huey, 1982; Ji *et al.*, 1995; Lang, 1979; Pough, 1980; van Damme *et al.*, 1991), which suggests that no specific temperature can maximize all physiological and behavioural traits. Among these functions, food passage time and sprint speed were strongly affected by temperature and the thermal sensitivities of these two traits were more obvious than the others. Within the range of experimental temperatures, temperature only slightly affected ADC, AE and food consumption, although its effects on the former two traits were statistically significant.

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REFERENCES

Ballinger R. E. and Holscher V. L. (1983) Assimilation efficiency and nutritive state in the striped plateau lizard, *Sceloporus virgatus* (Sauria: Iguanidae). *Copeia* **1983,** 838–839.

Bennett A. F. (1980) The thermal dependence of lizard behaviour. *Anim. Behav.* **28,** 752–762.

Bustard H. R. (1967) Activity cycle and thermoregulation in the Australian gecko *Gehyra variegata. Copeia* **1967,** 753–758.

Cowles R. B. and Bogert C. M. (1944) A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Mus. nat. Hist.* **83,** 265–296.

Dutton R. H., Fitzpatrick L. C. and Hughes J. L. (1975) Energetics of the rusty lizard *Sceloporus olivaceus. Ecology* **56,** 1378–1387.

Garland T., Jr (1985) Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis. J. Zool., Lond.* **207,** 425–439.

Harwood R. H. (1979) The effect of temperature on the digestive efficiency of three species of lizards, *Cnemidophorus tigris, Gerrhonotus multicarinatus* and *Sceloporus occidentalis. Comp. Biochem. Physiol.* **63A,** 417–433.

Huey R. B. (1982) Temperature, physiology, and the ecology of reptiles. In *Biology of the Reptilia*, Vol. 12 (Edited by Gans C. and Pough F. H.), pp. 25–91. Academic Press, London.

Huey R. B. and Dunham A. E. (1987) Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami. Evolution* **41,** 1116–1120.

Huey R. B. and Hertz P. E. (1984) Is a jack-of-all-temperatures a master of none? *Evolution* **38,** 441–444.

Hutchison V. H. (1961) Critical thermal maxima in salamanders. *Physiol. Zool.* **34,** 92–125.

Hutchison V. H. (1976) Factors influencing thermal tolerances of individual organisms. In *Thermal Ecology* 11. *Proc. 2nd SREL Thermal Ecology Symposium* (Edited by Esch G. W. and McFarlane R. W.), pp. 10–26. U.S. National Technical Information Service, Oak Ridge, TN.

Hutchison V. H. and Maness J. D. (1979) The role of behavior in temperature acclimation and tolerance in ectotherms. *Amer. Zool.* **19,** 367–384.

Ji X. (1992) Storage and utilization of energy and material in eggs of two lizard species, *Gekko japonicus* and *Takydromus septentrionalis. Comp. Biochem. Physiol.* **102A,** 783–788.

Ji X., Gu H. Q. and Tang Y. W. (1993a) Further ecological observations on the grass lizard *Takydromus septentrionalis* during its breeding season (Abstract). In *Proceedings of the First Asian Herpetological Meeting* (Edited by Zhao E. M., Chen B. H. and Papenfuss T. J.), p. 342, Huangshan, China, 1992. China Forestry Press, Beijing.

Ji X., Ma W. and Wang P. C. (1989) Study on home range of the lizard *Takydromus septentrionalis* during reproduction period. *J. Hangzhou Coll.* **89(6),** 60–63.

Ji X., Tang Y. W. and Hong W. X. (1994) Further observations on activity pattern and home range of the grass lizard *Takydromus septentrionalis* during the breeding season. *Acta Zool. Sinica* **40,** 207–210.

Ji X. and Wang P. C. (1990) The effect of temperature on food intake and assimilation efficiency of the gecko *Gekko japonicus. J. Hangzhou Normal Coll.* **90(6),** 90–94.

Ji X., Zheng X. Z., Xu Y. G. and Sun R. M. (1995) Several aspects of the thermal biology of the skink *Eumeces chinensis. Acta Zool. Sinica* **41,** 268–274.

Ji X., Zhou W. H., He G. B. and Gu H. Q. (1993b) Food intake, assimilation efficiency and growth of juvenile lizards *Takydromus septentrionalis. Comp. Biochem. Physiol.* **105A,** 283–285.

Kepenis V. and McManus J. J. (1974) Bioenergetics of young painted turtles, *Chrysemys picta. Comp. Biochem. Physiol.* **48A,** 309–317.

Lang J. W. (1979) Thermophilic response of the American alligator and the American crocodile to feeding. *Copeia* **1979,** 48–59.

Liu C. C. (1939) Notes on the life history and breeding habit of *Takydromus septentrionalis. Pekin Nat. Bull.* **14,** 35–42.

Lowe C. H. and Vance J. H. (1955) Acclimation of the critical thermal maximum of the reptile *Urosaurus ornatus. Science* **122,** 73–74.

Pough F. H. (1980) The advantages of ectothermy for tetrapods. *Am. Nat.* **115,** 92–112.

van Berkum F. H., Huey R. B. and Adams B. A. (1986) Physiological consequences of thermoregulation in a tropical lizard (*Ameiva festiva*). *Physiol. Zool.* **59,** 464–472.

van Berkum F. H., Huey R. B., Tsuji J. S. and Garland T., Jr (1989) Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard *Sceloporus occidentalis* (Baird and Girard). *Funct. Ecol.* **3,** 97–105.

van Damme R., Bauwens D. and Verheyen R. F. (1991) The thermal dependence of feeding behaviour, food consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. *Funct. Ecol.* **5,** 507–517.

Waldschmidt S. R., Jones S. M. and Porter W. P. (1986) The effect of body temperature and feeding regime on activity, passage time, and digestive coefficient in the lizard *Uta stansburiana. Physiol. Zool.* **59,** 376–383.

Wang P. C. (1964) Studies on the ecology of four species of lizards in Hangzhou I. *J. Chin. Zool.* **6(2),** 70–76.

Wang P. C. (1966) Studies on the ecology of four species of lizards in Hangzhou II. *Acta Zool. Sinica* **18,** 170–185.

Wang P. C., Ji X. and Ma W. (1989) Oxygen consumption of *Takydromus septentrionalis* eggs and hatchlings. In *Current Herpetology in East Asia* (Edited by Matsui M., Hikida T. and Goris R. C.), pp. 49–53. The Herpetological Society of Japan, Kyoto.

Wang P. C. and Xu H. F. (1987) The influence of ambient temperature on body temperature and heat energy metabolism of *Takydromus septentrionalis. Acta Herpetol. Sinica* **6(2),** 10–15.

Zhao E. M. and Adler K. (1993) *Herpetology of China,* 521pp. Society for the Study of Amphibians and Reptiles, Oxford, OH.