THERMAL DEPENDENCE OF SPRINT PERFORMANCE OF THE LIZARD *SCELOPORUS OCCIDENTALIS*

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SUMMARY

Sprint velocity of the lizard *Sceloporus occidentalis* was maximal at preferred body temperature (T_b, 35°C). Mean running velocity (V_R) and stride frequency (f) at this temperature were 3.23 ± 0.7 (mean $\pm$ S.E.M.) $m s^{-1}$ and $15.6 \pm 0.3 s^{-1}$, respectively. V_R and f did not change significantly when T_b was raised to 40°C. At T_b values between 25 and 35°C the thermal dependencies of V_R ($Q_{10} = 1.23$) and f ($Q_{10} = 1.12$) were quite low. At T_b values below 25°C the thermal dependence of these factors increased markedly. Stride length (L_S) was independent of T_b from 15 to 40°C. Lizards with a T_b of 10°C were largely incapacitated, and V_R, f and L_S were all greatly reduced. Comparisons with measurements of the contractile properties of skeletal muscle of this species suggest that stride frequency is limited by the twitch contraction time at temperatures below 23°C. At higher temperatures, sprint performance is nearly independent of the thermal effects on the muscles.

INTRODUCTION

Variable body temperatures of ectothermic vertebrates influence most aspects of their biology, including locomotor performance. In recent years research on thermal effects on locomotion has shifted emphasis from an examination of extreme temperatures that cause locomotor incapacitation (Brattstrom, 1965; Huey, 1982) to an investigation of the thermal effects on performance at intermediate temperatures that allow relatively normal locomotor activity (Huey & Stevenson, 1979; Bennett, 1980; Huey, 1982, 1983; Marsh & Bennett, 1985). Lizards have provided a particularly useful group of animals in which to examine the thermal effects on performance. This usefulness stems both from their ecological diversity, which provides the opportunity to relate laboratory measurements to ecological specialization (Huey, 1983), and from the relative ease with which repeatable measurements of both sustainable and burst activity can be obtained (see Bennett, 1980).

Depending on the activity performed and the temperatures experienced, loco-motion may be influenced by thermal effects on a variety of systems, e.g. cardio-vascular, respiratory, nervous and/or skeletomuscular. The investigations described here emphasize the possible relationships between thermal effects on the time-dependent properties of skeletal muscle (Marsh & Bennett, 1986) and locomotor performance in short burst runs (sprints) by an iguanid lizard *Sceloporus occi-dentalis*. In iguanids the skeletal muscles of the limbs appear to be primarily specialized for this type of locomotion, for approximately 80–90 % of the fibres in most muscles are of the fast-twitch glycolytic fibre type (Putnam, Gleeson & Bennett, 1980; Gleeson & Harrison, 1986).

In previous studies (Bennett, 1980; Marsh & Bennett, 1985), we have shown that sprint running performance of the iguanid *Dipsosaurus dorsalis* is at least partially uncoupled from thermal effects on the contractile speed of skeletal muscle at body temperatures between 25 and 40°C. This conclusion was reached because of the substantially lower Q_{10} of running velocity and stride frequency as compared to the Q_{10} values of the time-dependent isometric or isotonic contractile properties. We suggested that, over this range of temperatures, stride frequency is determined by some other factor with a low thermal dependence, such as elastic storage of energy. At body temperatures below 25°C, however, *Dipsosaurus* has a high thermal dependence of locomotor performance ($Q_{10} > 3$). This greater thermal dependence at low temperatures appeared to be primarily due to a prolongation of the state of activation of the muscle fibres. Consequently, the time taken to contract and relax the skeletal muscles may directly limit the maximum stride frequency attainable at low body temperatures. Such findings, if substantiated for other species, are important both for what they reveal about the mechanisms determining performance during high-speed running, and also for their ecological significance. The existence of an inflection in the temperature *versus* performance curves would be a major deter-minant of the thermal performance breadth (Huey & Stevenson, 1979; Huey, 1982) for sprint locomotion.

MATERIALS AND METHODS
Animals

Adult *Sceloporus occidentalis* of both sexes were collected in Orange County, CA, under a California scientific collector's permit to AFB and maintained in the laboratory for less than 1 week before use. Prior to the experiments they were housed in cages allowing behavioural thermoregulation and fed crickets and mealworms *ad libitum*. Lizards were collected in early July and had a mean body mass of $12\cdot3 \pm 0\cdot8$ g and snout–vent length of $67\cdot3 \pm 1\cdot3$ mm (mean $\pm$ S.E.M., $N = 10$).

Running experiments

Sprint running performance was assessed using essentially the methods of Marsh & Bennett (1985). During runs of approximately 3 m animals were filmed from above with a super-8 movie camera. Framing rates were measured on each roll of film by

filming a stopwatch and were approximately $65 s^{-1}$ when the lizards' body temperatures were 20°C and above and $34 s^{-1}$ at lower body temperatures. Following each run, body temperature was measured cloacally with a Schultheis small animal thermometer. Animals were run in the morning and afternoon on six successive days. Disturbance of the animals prior to the runs was minimized by housing them in individual containers in a controlled temperature cabinet. The approximate body temperatures (T_b) used in successive experiments were 35, 15, 30, 10, 25, 30, 25, 20, 35, 40 and 5°C.

Because the animals varied in how well they 'cooperated' during these measurements, we rated the runs subjectively at the time of filming. Runs were classified as: excellent, animal ran the entire length of the track with no stimulation; good, animal required some stimulation during the run but covered large segments of the track apparently at full speed; fair, animal stopped and started many times, often hitting the sides of the track, but usually progressed the entire length of the track; poor, animal refused to walk or run without continual stimulation and often appeared not to be taking full strides. One animal refused to run in two of the trials and was judged to be 'fair' or 'poor' in all of the other trials. Another individual was judged to be 'fair' or 'poor' in 7 of 10 trials. These two animals were excluded from the statistical analysis presented in Results. Inclusion of the data from these animals lowers the mean running velocity and increases the variance for all parameters, but does not substantially alter any of the analyses. The other eight animals performed in the 'good' or 'excellent' categories almost exclusively except when running with a T_b of 10°C. Maximal running velocity (V_R) was estimated from frame counts and the marks on the track and was defined as the fastest velocity maintained for at least three strides. The stride frequency (f) and stride length (L_S) reported are the average values maintained over the same portion of the run.

Means reported in the text are presented ± 1 S.E.M. Because the performance data were recorded on the same animals at the different temperatures, we analysed these data with a two-way analysis of variance (see Sokal & Rohlf, 1981, p. 348). This method allows the variance due to the effect of temperature to be partitioned from that due to variation among individuals.

RESULTS

In analysing data on the running performance of *Sceloporus occidentalis*, we concentrated on the data from eight animals with runs judged almost exclusively to be 'excellent' or 'good' (see Materials and Methods), as we consider these runs to be a better representation of physiological capacities at various T_b values. The inclusion of data from two additional animals that behaved poorly resulted in a small change in the mean values of V_R, f and L_S (Fig. 1), but did not change substantially any of the analyses or conclusions presented below. At 10°C, no runs were judged to be 'good' or 'excellent'. This qualitative change in performance appears to be due to the incapacitating effects of low T_b on locomotion.
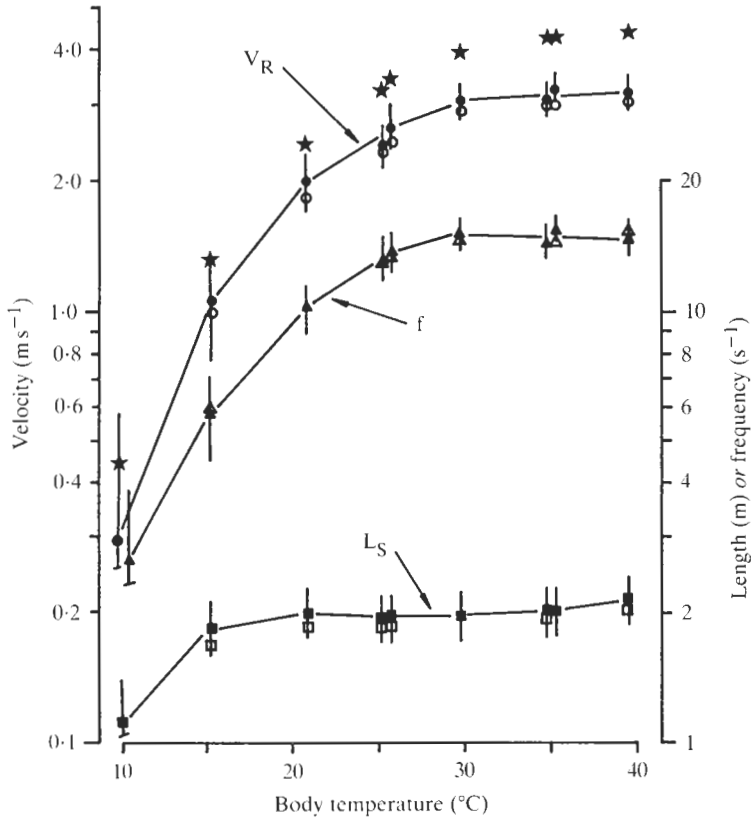
Fig. 1. Relationships between body temperature (T_b) and maximal velocity (V_R, ●, ○), stride frequency (f, ▲, △) and stride length (L_S, ■, □) during 3-m sprint runs by the lizard *Sceloporus occidentalis*. Closed symbols are the mean values for the eight animals used in the statistical analyses (see Materials and Methods). Vertical bars represent comparison intervals based on minimum significant differences calculated by the T-method (see Results). Means are significantly different ($P < 0.05$) if their respective comparison intervals do not overlap. Open symbols are the means for all animals used in the trials, including two animals that were consistently poor runners. Stars indicate the fastest V_R values recorded at each temperature. Vertical scales are logarithmic.

In two-way analysis of variance, variation among individuals accounted for a significant portion of the variance for all parameters measured, but a far greater portion of the variance was attributable to the effect of temperature (Table 1). As an aid to interpreting the variation in performance among the various temperatures, we calculated the minimum significant differences (MSD) using the T-method (Sokal & Rohlf, 1981). Comparison intervals based on this statistic are plotted in Fig. 1. To group means that were not significantly different, we used the SS–STP method (Sokal & Rohlf, 1981). Mean L_S of animals with T_b values from 15 to 40°C averaged 0.196 ± 0.007 m and did not vary significantly. This parameter dropped significantly at a T_b of 10°C compared to the mean value at any other temperature ($P < 0.01$), corresponding to the markedly abnormal running behaviour at the lower T_b. Mean V_R and f were highest at 35°C, 3.23 ± 0.22 m s^{-1} and 15.6 ± 0.3 s^{-1}, respectively

Table 1. *Two-way analysis of variance results for data on running performance of Sceloporus occidentalis*

Variable	Source of variation	df	Sums of squares	F	P
Running velocity	Individuals	7	8·84	8·23	<0·001
	Temperature	6	63·97	69·55	<0·001
	Error	42	6·44		
Stride frequency	Individuals	7	62·54	3·62	<0·005
	Temperature	6	1281·90	86·48	<0·001
	Error	42	103·76		
Stride length	Individuals	7	0·026	3·98	<0·005
	Temperature	6	0·060	10·98	<0·001
	Error	42	0·040		

Table 2. *Thermal dependence expressed as Q_{10} of running velocity (V_R) and stride frequency (f) during burst runs by the lizard Sceloporus occidentalis*

Body temperature interval (°C)	Q_{10}	
	V_R	f
35–40	0·99	0·90
30–35	1·12	1·02
25–30	1·38	1·26
20–25	1·90	2·10
15–20	3·05	2·54
10–15	12·53	4·82

(Fig. 1). The thermal dependence of these parameters is quite low over the range of T_b from 25 to 40°C (Table 2). Using analysis of variance, no significant effect of temperature on V_R or f is demonstrable at 25°C and above. Temperature has a significant effect on performance below 25°C, and the calculated Q_{10} value increases to 1·9 or above (Table 2).

The performance of the animals proved to be very repeatable. Duplicate measurements on separate days at T_b values of 25 and 35°C resulted in similar values for V_R, f and L_S (Fig. 1).

DISCUSSION

In short burst runs (sprints) *Sceloporus* attains the highest mean velocity when its T_b is 35°C, which is the preferred T_b of this species (Brattstrom, 1965). As in other small lizards examined to date (Bennett, 1980; Christian & Tracy, 1981; Hertz, Huey & Nevo, 1982, 1983; Marsh & Bennett, 1985), *Sceloporus* shows a low thermal dependence of running performance over a broad range of temperatures above and below the temperature at which performance is optimal. At 25°C, V_R is 80% of the value at 35°C. Below 25°C, the thermal dependence of sprint velocity increases, a phenomenon also noted in *Dipsosaurus* (Marsh & Bennett, 1985).
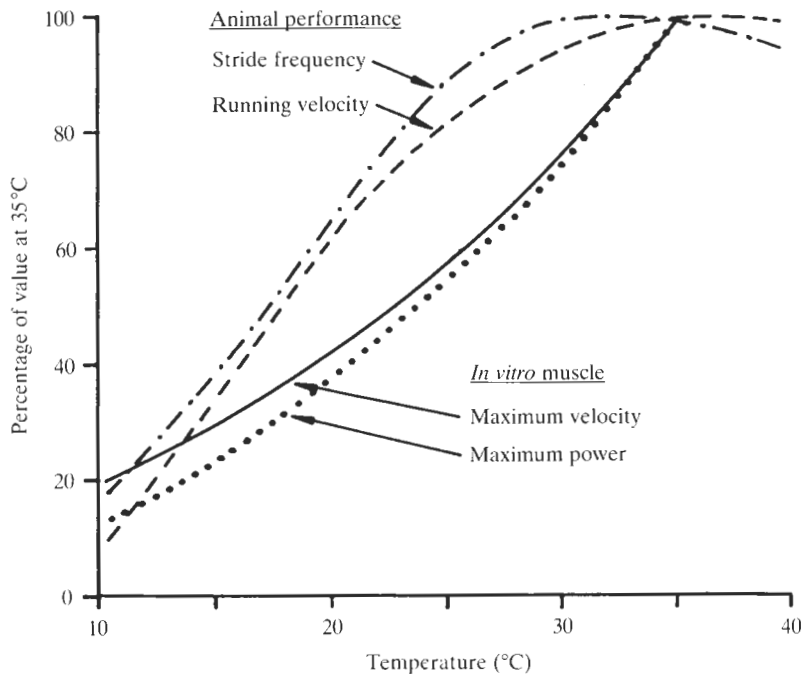
Fig. 2. Summary of the effects of temperature on sprint running performance and on the isotonic contractile properties of fast-twitch glycolytic skeletal muscle in the lizard *Sceloporus occidentalis*. Contractile data are from Marsh & Bennett (1986).

The question addressed here is the extent to which the thermal dependence of locomotor performance derives from the effects of temperature on the muscles used in running. The hindlimbs of iguanid lizards are primarily composed of fast-twitch glycolytic fibres (Putnam *et al.* 1980; Gleeson & Harrison, 1986), and presumably these fibres power primarily the burst type of locomotion examined in the present study. Evidence from previous studies of isometric contractile properties indicates that the iliofibularis has similar contractile properties to the larger locomotor muscles such as the gastrocnemius (Putnam & Bennett, 1982). We assume, therefore, that the properties of the fast glycolytic fibres from this muscle are representative of the muscles used by the animals in our behavioural experiments. In a companion study (Marsh & Bennett, 1986), we have examined the contractile properties of the fast-twitch glycolytic region of the iliofibularis muscle from *Sceloporus occidentalis*.

The low thermal dependence of running performance of *Sceloporus* above 25°C does not have a parallel in either the isometric or isotonic contractile properties (Marsh & Bennett, 1986). The velocity of shortening has a Q_{10} of 1·8 from 15 to 35°C (Fig. 2). Due to the small influence of temperature on tetanic tension, the predicted power output has a similar thermal dependence over most of this temperature range (Fig. 2). Clearly, as was the case with the lizard *Dipsosaurus* (Marsh & Bennett, 1985), some process operable *in vivo* during running must serve to mitigate the effects of temperature on the contractile properties of the muscles. We concluded in

this earlier study that the low thermal dependence of sprint running is probably not determined by temperature-induced changes in fibre recruitment, as has been suggested for low-speed walking in lizards (Rome, 1982) and slow swimming in fish (Rome, Loughna & Goldspink, 1985). We suggested instead that elastic storage and recovery of energy in muscles and/or tendons is a likely candidate for a thermally independent process occurring during sprint running. According to this mechanism, energy stored in elastic elements in one portion of the stride could be recovered and provide part of the power required to maintain velocity. In a running animal, the integrated value of the impulsive ground-reaction force determines the contact time and take-off velocity, which help determine stride frequency. The peak force possible during ground contact is presumably almost thermally independent due to the low temperature dependence of maximal muscle stress (Marsh & Bennett, 1985, 1986). If the presence of elastic elements in series with the muscles blunts the effects of temperature on the shape of the ground-reaction impulse, the result should be a small effect of temperature on the stride. Perhaps arguing against this hypothesis is evidence that elastic storage and recovery of energy is insignificant in small mammals (Biewener, Alexander & Heglund, 1981), and, by analogy, might not be expected to play a large role during running in small lizards. An additional possible mechanism for enhancing locomotor performance is suggested by the data of Cavagna, Mazzanti, Heglund & Citterio (1985), who describe a non-elastic potentiation of muscle performance following stretch. This mechanism may have been a factor in earlier experiments that documented a low thermal dependence of power output during post-stretch releases of frog skeletal muscle (Cavagna, Citterio & Jacini, 1981). Further understanding of the mechanistic basis for the low thermal dependence of lizard running may have to await a more complete knowledge of the patterns of muscle contraction during running, and effective modelling of these contractions *in vitro*.

Although the isotonic or isometric properties of the muscles do not determine directly the zone of low thermal dependence, the lower limit of this zone may be set by thermal effects on the muscles. We suggested previously (Marsh & Bennett, 1985) that this limit was set in *Dipsosaurus* by the effects of temperature on the duration of the state of activation following a single stimulus. The time course of twitch contractions appears to be primarily related to how fast the state of activation declines following a single stimulus (see Hoyle, 1983). Based on evidence from earlier studies on frog muscle (Jewell & Wilkie, 1960) and our data on lizard muscles, we used the time from onset of force to 50 % relaxation (t_C) as an approximate measure of the duration of the state of activation. During running a lizard must contract and relax its muscles in the time required for half of a stride ($\frac{1}{2}t_S$). Otherwise there would be interference between the antagonistic muscles that power the propulsive and return strokes of the stride. Fig. 3 shows t_C and $\frac{1}{2}t_S$ for *Sceloporus* plotted as a function of temperature. At high temperatures, t_C is considerably shorter than $\frac{1}{2}t_S$ and the muscles could be activated in short tetani without limiting t_S. As temperature is lowered the difference between the times lessens due to the high thermal dependence
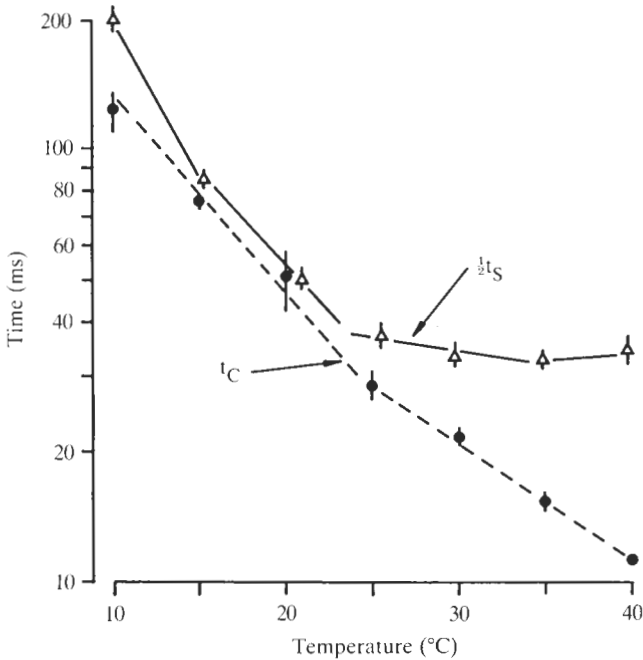
Fig. 3. Effects of temperature on the twitch contraction time (t_C = time from onset to 50 % relaxation) and on the time required for half of a stride ($\frac{1}{2}t_S$) during sprint running in the lizard *Sceloporus occidentalis*. Values plotted as mean ± 1 S.E.M. Contractile data are from Marsh & Bennett (1986). Vertical scale is logarithmic.

of t_C. The curves approach one another at approximately 23 °C, below which the thermal dependence of t_S increases. These data are fully consistent with those collected on *Dipsosaurus* and strengthen the conclusion that the time course of the twitch response limits stride frequency and hence sprint speed at low T_b.

Huey and coworkers have emphasized the use of thermal performance breadth in assessing the adaptation of ectotherms to temperature (Huey & Stevenson, 1979; Huey, 1982). Thermal performance breadth is defined as the range of temperatures over which an animal can maintain a certain percentage (e.g. 80 %) of its maximal performance. Assuming that a temperature-independent capacity for rapid escape is important for lizards under natural conditions, a wide thermal performance breadth would be favoured by natural selection. Such wide performance breadths exist in iguanid lizards but are limited by the effects of low temperature on the kinetics of twitch contractions. Further exploration of the role of muscle kinetics in determining locomotor performance of ectotherms will aid the formulation of predictions regarding the limits of thermally related adaptations.

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