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ENERGETIC COST OF RUNNING WITH DIFFERENT MUSCLE TEMPERATURES IN SAVANNAH MONITOR LIZARDS

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SUMMARY

The purpose of this study was to determine whether the energetic cost of locomotion was independent of muscle temperature, or if it tripled with a 10 °C increase in temperature, like the cost of generating isometric force in isolated muscle preparations. For a given running speed of Savannah Monitor lizards, the energetic cost of locomotion (the difference between running and resting metabolism) was the same when muscle temperature was 28·5 °C as when it was 38 °C. It was also found that stride frequency and posture did not change with temperature, indicating that the average force exerted by the lizards' muscles during locomotion at the two temperatures was the same. This suggests that the cost of generating force *in vivo* is independent of temperature. Several possible explanations of the apparent difference between *in vivo* and *in vitro* muscle energetics are discussed.

INTRODUCTION

It has been proposed that it is the energetic cost of generating muscular force (as opposed to the cost of performing mechanical work) which determines the energy cost of locomotion (Taylor *et al.* 1980; Heglund *et al.* 1982). Since the energetic cost of generating isometric force *in vitro* increases approximately threefold for each 10 °C increase in temperature, during a train of closely spaced contractions similar to those that might occur during locomotion (Kushmerick & Paul, 1976, 1977; L. C. Rome & M. J. Kushmerick, in preparation), one might expect that the energetic cost of locomotion would also have a Q_{10} of 3. However, it has been reported that the cost of locomotion in lizards is independent of their body temperature (Moberly, 1968; Dmi'el & Rappaport, 1976; John-Alder & Bennett, 1981). The purpose of this study was to test carefully whether the energetic cost of locomotion of lizards was independent of muscle temperature, and if so, to see if this finding could be explained by changes in stride frequency and posture.

MATERIALS AND METHODS

Animals

Savannah Monitor lizards (*Varanus exanthematicus*) were selected for these experiments because they could be trained to run steadily on a treadmill over a large range of body temperatures at speeds at which the energy they consumed was derived aerobically (Gleeson *et al.* 1980). Four lizards were captured in Kenya and air freighted to USA. They were housed in pairs in bath tubs and placed on a 12:12 light cycle with access to heat lamps during the daytime. They were fed live mice at a rate which allowed them to gain weight slowly during the studies. The animals were trained to run on the treadmill 1–2 months before measurements were begun.

Procedure

The energetic cost of locomotion (i.e. the sum of aerobic and anaerobic contributions) and stride frequency were measured in running lizards, at a muscle temperature of 28·5 and 38 °C. The rate of aerobic metabolism was calculated from measurements of the rate of oxygen consumption ($\dot{V}_{O_2}$) and the rate of anaerobic metabolism was calculated from the rate of lactate accumulation. To achieve uniform muscle temperatures the lizards were kept 12–15 h at the experimental temperature before each experiment.

The running speeds and muscle temperatures were selected so that metabolism was primarily aerobic, thus enabling the most accurate measure of the energetic cost of locomotion. The lizards would not run steadily below a certain minimum speed, which varied among individuals. These minimum speeds were used in the experiments because metabolic rate increased at higher ones. Aerobic capacity of these lizards is known to increase with body temperature (Bennett, 1978). In these experiments 28·5 °C was used because it was found to be the lowest temperature where the lizards' running metabolism was primarily aerobic, as indicated by $R(\dot{V}_{CO_2}/\dot{V}_{O_2})$ values less than or equal to 1.

Aerobic metabolism

'Steady-state' $\dot{V}_{O_2}$ was measured during running and rest. The criteria for 'steady-state' running $\dot{V}_{O_2}$ measurements were that: (1) the animal ran steadily for at least 10 min and (2) $\dot{V}_{O_2}$ did not change by more than 10% during this period of time. The $\dot{V}_{O_2}$ measurement was never taken within the initial 5 min of the experimental run, and often not within the first 40 min. The criteria for resting $\dot{V}_{O_2}$ were that: (1) the animal was inactive for at least 1 h prior to the measurement; and (2) $\dot{V}_{O_2}$ did not change by more than 15% over the 30 min measurement period.

$\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were measured using an open-flow system (see Fig. 1*a*). The lizard wore a loosely fitted mask constructed from clear lightweight plastic. Air from the room was drawn through the mask at a flow rate of 10–15 l/min. The lizard was placed in a plexiglass cage in a darkened environmental room for the resting measurements and air was drawn through at a reduced rate (2 l/min). The flow rate used under each condition was demonstrated to be sufficient to capture all the animal's exhaled air by decreasing the flow rate by 30% while $\dot{V}_{O_2}$ was monitored. If there had been

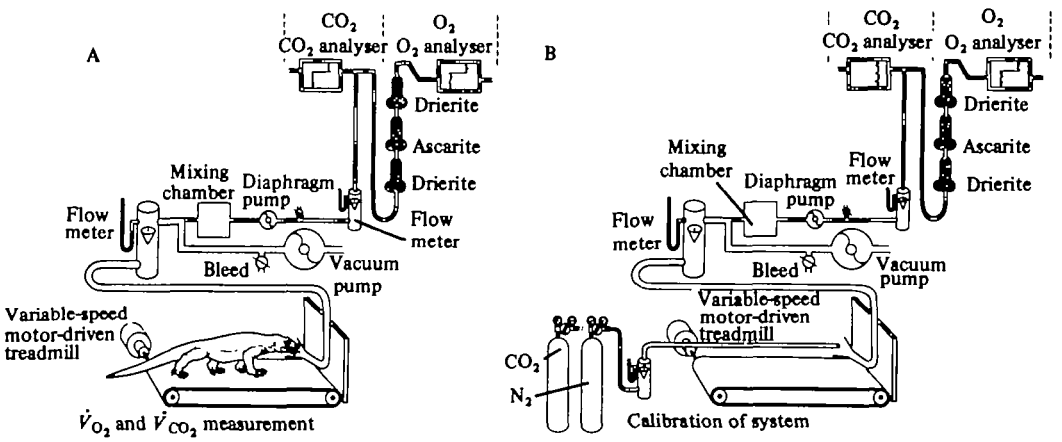

Fig. 1. Measurement of $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ and calibration of the system. (A) A negative pressure–open flow system was employed to measure $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$. The lizard wore a loose-fitting plastic mask during running. Room air as well as all of the animal's exhaled gases were pulled through the mask by the vacuum pump. An aliquot of this flow first passed through a mixing chamber that integrated the transient concentration changes caused by individual breaths. The aliquot was then divided and either passed directly to the CO_2 analyser or through Drierite and Ascarite to remove H_2O and CO_2, and then to the O_2 analyser. The $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ result in a decrease in the O_2 concentration and an increase in the CO_2 concentration measured as relative concentration changes by the respective analysers.

(B) The system was calibrated for the $\dot{V}_{O_2}$ measurement by nitrogen dilution. While keeping the system flow rate the same as it was during the $\dot{V}_{O_2}$ measurement, N_2 was bled into the mask at a known rate ($\dot{V}_{N_2\,cal}$), resulting in a deflexion of the O_2 analyser ($\Delta_{O_2\,cal}$). $\Delta_{O_2\,cal}$ is used in Equation 1 to calculate $\dot{V}_{O_2}$. The system was calibrated for the $\dot{V}_{CO_2}$ measurement, in a similar fashion, by switching tanks and flowing CO_2 into the mask at a known rate ($\dot{V}_{CO_2\,cal}$). The resulting deflexion of the CO_2 analyser ($\Delta_{CO_2\,cal}$) was used in Equation 2 to calculate $\dot{V}_{CO_2\,cal}$.

leaks in the system, this should have increased the loss of the animal's exhaled air. No difference in $\dot{V}_{O_2}$ was observed, with the reduction of flow indicating that there were no leaks.

$\dot{V}_{O_2}$ was calculated using the procedure described by Fedak, Rome & Seeherman (1981). This involved metering N_2 into the mask or cage (Fig. 1*b*) at a known rate ($\dot{V}_{N_2\,cal}$) while keeping the total flow of air through the system the same as that used during the experiments. The N_2 replaced an equal volume of air (which contained 20·94% O_2) that would otherwise have flowed into the system, and thereby reduced the oxygen concentration of the gas leaving the mask. The resulting change in output voltage ($\Delta_{O_2\,cal}$) of the paramagnetic O_2 analyser (Beckman F-3) was linearly proportional to the difference in O_2 concentration between room air and the gas leaving the mask during calibration, and was used, along with that measured during the experiment ($\Delta_{O_2\,exp}$), to calculate $\dot{V}_{O_2}$ by the following formula:

$$\dot{V}_{O_2} = \frac{0{\cdot}2094 \times \dot{V}_{N_2\,cal}}{0{\cdot}79} \times \frac{\Delta_{O_2\,exp}}{\Delta_{O_2\,cal}}. \quad (1)$$

In these experiments a value of 0·79 was used in the denominator instead of the 0·80 used in equation 11*c* of Fedak, Rome & Seeherman (1981) because the change in oxygen concentration in these experiments was approximately 0·001 instead of the 0·01 assumed in the derivation of equation 11*c*. All values are reported s.t.p. The accuracy of the technique was ±3%.

R value

R was calculated as the ratio of average $\dot{V}_{CO_2}$ to the 'steady-state' $\dot{V}_{O_2}$. The $\dot{V}_{CO_2}$ measuring system was calibrated in a similar way to the $\dot{V}_{O_2}$ measuring system. CO_2 was metered into the mask at a known rate ($\dot{V}_{CO_2\,cal}$) causing a change in CO_2 concentration measured as a voltage change ($\Delta_{CO_2\,cal}$), of the linear output of the CO_2 analyser (Infrared Industries). $\dot{V}_{CO_2}$ of the animal was calculated from the changes in output voltage measured during the experiment ($\Delta_{CO_2\,exp}$) by the following formula:

$$\dot{V}_{CO_2} = \dot{V}_{CO_2\,cal} \times \frac{\Delta_{CO_2\,exp}}{\Delta_{CO_2\,cal}}. \tag{2}$$

Anaerobic metabolism

Anaerobic energy consumption was estimated by measuring difference in blood lactate between the beginning and the end of the runs. Blood samples were taken by cardiac puncture and assayed using Boehringer Manneheim Single Vial Lactate Kits. The accuracy of the lactate assay was within 5%. The anaerobic contribution to the energetic cost of running (ATP derived from lactate production/ATP derived from oxygen consumption) was estimated as shown in Equation 3.

$$\frac{\text{ATP-lactate}}{\text{ATP-O}_2} = \frac{\left[\text{lact}_{run}\text{-lact}_{rest}\left(\frac{\text{moles}}{\text{l blood}}\right)\right]\left(\frac{1\text{ l blood}}{0{\cdot}83\text{ l H}_2\text{O}}\right)\left(\frac{0{\cdot}71\text{ l H}_2\text{O}}{\text{kg}}\right)[M_b\text{ (kg)}]\left(\frac{1{\cdot}5\text{ moles ATP}}{\text{mole lact}}\right)}{\text{O}_2\text{ (moles)}\left(\frac{6\text{ moles ATP}}{\text{mole O}_2}\right)}. \tag{3}$$

The total moles of lactate produced during the run were estimated by subtracting an average resting lactate concentration (lact_{rest}) from the lactate concentration measured at the end of the run (lact_{run}) and by assuming that blood is 83% H_2O (Seeherman, 1977) and total body water volume is 71% of body weight (Kleiber, 1975). The ATP derived was estimated by multiplying the total lactate production by 1·5 moles ATP/mole lactate (numerator, Equation 3). The ATP derived from oxygen consumption was estimated by multiplying the total oxygen consumed during the run by 6 moles ATP/mole O_2 (denominator, Equation 3).

Temperature

Muscle temperature was measured with thermocouples (0·06 cm O.D.) implanted in the muscle, using a Wescor TH60 thermometer. The thermocouples were calibrated before and after each experiment against a standard thermometer to within 0·2 °C.

Table 1. *Mass specific rates of oxygen consumption during running and rest, the anaerobic contribution to the cost of running, and stride frequency during running at two muscle temperatures*

Lizards were run at a fixed speed at muscle temperatures of approximately 38 and 28·5 °C. For each individual, the means of the rate of oxygen consumption during running (n = 5–8 measurements) and rest (n = 3–5 measurements); the anaerobic contribution to the cost of running (n = 2–4 measurements); and stride frequency (4–12 measurements) are reported at each muscle temperature with 95 % confidence limits. The cost of locomotion was calculated by subtracting the mean rate of oxygen consumption during resting from that during running. It is reported with 95 % confidence limits calculated using the standard formula for the difference of two means of unpaired data (Walpole & Myers, 1972). The anaerobic contribution to the cost of running (ATP derived from lactate production/ATP derived from oxygen consumption) was determined from lactate accumulation experiments and calculated by Equation 3 in text. (M_b = body mass; v = run speed; 95 % confidence limits are in parentheses.)

	Muscle temperature, T (°C)	Cost of running, $\dot{V}_{O_2\,run}/M_b$ (ml.s^{-1}.kg^{-1})		Cost of resting, $\dot{V}_{O_2\,rest}/M_b$ (ml.s^{-1}.kg^{-1})		Cost of locomotion $\dot{V}_{O_2\,run}/M_b$–$\dot{V}_{O_2\,rest}/M_b$ (ml.s^{-1}.kg^{-1})		Anaerobic contribution $\frac{ATP_{lactate\ production}}{ATP_{oxygen\ consumption}}$		Stride frequency, f (Strides.s^{-1})	
Lizard 1	37·9	0·196	(0·185, 0·208)	0·036	(0·029, 0·043)	0·160	(0·148, 0·172)	0·02	(−0·07. 0·11)	0·70	(0·69, 0·71)
(M_b = 2·2 kg)	28·6	0·186	(0·174, 0·198)	0·014	(0·012, 0·015)	0·172	(0·160, 0·185)	0·04	(0·01, 0·08)	0·71	(0·69, 0·73)
(v = 0·22 m.s^{-1})											
Lizard 2	38·0	0·234	(0·221, 0·247)	0·041	(0·035, 0·046)	0·193	(0·180, 0·207)	0·01	(−0·02, 0·05)	0·73	(0·71, 0·74)
(M_b = 1·8 kg)	28·3	0·199	(0·180, 0·217)	0·015	(0·012, 0·019)	0·183	(0·165, 0·202)	−0·01	(−0·06, 0·05)	0·74	(0·72, 0·76)
(v = 0·25 m.s^{-1})											
Lizard 3	38·0	0·304	(0·274, 0·334)	0·046	(0·042, 0·051)	0·258	(0·228, 0·288)	0·02	(−0·02, 0·06)	1·11	(1·08, 1·14)
(M_b = 1·2 kg)	29·0	0·255	(0·244, 0·265)	0·019	(0·014, 0·025)	0·236	(0·255, 0·246)	−0·01	(−0·03, 0·02)	1·13	(1·11, 1·15)
(v = 0·35 m.s^{-1})											
Lizard 4	37·8	0·182	(0·164, 0·200)	0·031	(0·026, 0·036)	0·151	(0·133, 0·170)	0·02	(−0·03, 0·06)	0·78	(0·75, 0·80)
(M_b = 1·4 kg)	28·4	0·167	(0·146, 0·190)	0·017	(0·015, 0·018)	0·151	(0·129, 0·173)	−0·03	(−0·05, 0·00)	0·78	(0·75, 0·81)
(v = 0·235 m.s^{-1})											

Table 2. *The temperature dependence of the cost of locomotion and stride frequency*

The cost of locomotion (cost of running-cost of resting) and stride frequency were measured at muscle temperatures of approximately 38 and 28·5 °C. For each animal the R_c (cost of locomotion at 38 °C/cost of locomotion at 28·5 °C) and the R_f (stride frequency at 38 °C/stride frequency at 28·5 °C) are reported with 95% confidence limits calculated using Fiellers' theorem (Finney, 1979) for the ratio of two means of unpaired data. The means R_c and R_f for the four animals are reported with 95% confidence limits (in parentheses).

	$R_c = \frac{\text{cost of locomotion at 38 °C}}{\text{cost of locomotion at 28·5 °C}}$		$R_f = \frac{\text{stride frequency at 38 °C}}{\text{stride frequency at 28·5 °C}}$	
Lizard 1	0·93	(0·85, 1·02)	0·99	(0·96, 1·01)
Lizard 2	1·05	(0·95, 1·17)	0·98	(0·95, 1·02)
Lizard 3	1·09	(0·96, 1·25)	0·98	(0·95, 1·00)
Lizard 4	1·00	(0·85, 1·18)	0·99	(0·96, 1·03)
Savannah Monitors ($n = 4$)	1·02	(0·91, 1·13)	0·98	(0·97, 1·00)

Muscle temperature was found to be within 0·2 °C of cloacal temperature after the first 5 min of exercise. Therefore only cloacal temperature was routinely measured because it was less traumatic for the animal.

Stride frequency

Stride frequency was measured by visually counting the number of strides during a timed interval.

RESULTS

The energetic cost of locomotion ($\dot{V}_{O_2}$ during running $-\dot{V}_{O_2}$ during rest) with muscle temperatures of 28·5 °C was not significantly different from the cost at 38 °C (Table 1) For each lizard, the ratio of the cost at 38 °C to that at 28·°C was close to unity (Table 2), and thus the cost of locomotion in Savannah Monitor lizards is independent of muscle temperature over the range of temperatures studied. Table 1 also shows that most of the energy consumed by the lizards under the experimental conditions was obtained by aerobic metabolism. The anaerobic contribution in these experiments was quite small, the largest being 4% in Lizard 1, running with a muscle temperature of 28·5 °C. Consistent with this finding, R values were equal to or less than 1 for all the lizards at both temperatures.

Stride frequency at a given speed was also independent of muscle temperature over the range studied (Tables 1 and 2). Also, no visually apparent differences were observed in the posture or limb movements during running at the two temperatures.

DISCUSSION

The observation that the energetic cost of locomotion is independent of muscle temperature, while the cost of generating isometric force in isolated muscle approximately triples with a 10 °C increase in temperature appears paradoxical. It is unlikely that this paradox can be explained by a difference in the average force ($\bar{F}$) generated by the muscles at the two temperatures. In order to explain the net cost of locomotion

remaining constant while the cost of generating force ($\dot{V}_{O_2}/\bar{F}$) triples, the average force ($\bar{F}$) generated by the muscles at 38 °C would have to be reduced to one-third that generated at 28·5 °C. Although muscle force has not been measured directly, there is strong evidence that muscle force is nearly independent of muscle temperature.

First, the average force exerted by the ground on the animal ($\bar{F}_{\text{ground}}$) is independent of temperature. The forces exerted by the ground on the animal can be resolved into two components; the horizontal force ($F_{\text{h-ground}}$) that decelerates and then reaccelerates the animal in the forward direction during each stride, and the vertical force ($F_{\text{v-ground}}$) that decelerates and reaccelerates the animal vertically during each stride. Calculations performed on force-plate data gathered by other authors (N. C. Heglund, personal communication; Cavagna, Heglund & Taylor, 1977; Alexander, 1980) show that the average vertical ground force ($\bar{F}_{\text{v-ground}}$) is 5–100-fold larger than the average of the absolute magnitude of horizontal ground force ($|\bar{F}_{\text{h-ground}}|$) for a variety of walking animals (quail, man, rhea, ram, dog and tortoise). Since $\bar{F}_{\text{v-ground}}$ is equal to the animal's body weight and is thus independent of temperature, it is fair to conclude that the average of the total force exerted by the ground on the animal ($\bar{F}_{\text{ground}}$) must also be nearly independent of running temperature.

In addition it was found that the lizards ran with approximately the same stride frequency, posture, and limb positions at both temperatures. Thus it seems likely that the moments around the joints and thus the forces generated by the limb muscles were also independent of temperature. These observations also suggest that the lizards' muscles shortened at the same velocities at both temperatures.

It therefore appears that the cost of generating force in a locomoting lizard is independent of temperature. One can envisage three explanations of this apparent departure from the energetics of isometric contractions found in isolated frog muscle (Kushmerick & Paul, 1976, 1977; L. C. Rome & M. J. Kushmerick, in preparation).

First, in contrast to frog muscle, the cost of generating isometric force in isolated lizard muscle might be independent of temperature. This seems unlikely, because the findings that the intrinsic velocity of shortening of isolated muscles from the lizard *Dipsosaurus dorsalis* increased with a Q_{10} of 1·9 between 20 and 40 °C (Marsh, Putnam & Bennett, 1981), and that the cost of generating isometric force is related to the intrinsic velocity of shortening in a greater than first-order manner (Hill, 1938; Feng, 1931; Hill & Woledge, 1962; Woledge, 1968), suggest that the cost of generating force in isolated lizard muscle should increase markedly with temperature.

Secondly, different numbers of fibres could be used at different temperatures or, thirdly, different types of fibres could be used. These latter two explanations are possible because in contrast to the isolated muscle experiments, where all fibres are stimulated, during locomotion only a small percentage are active (i.e. 35–65% in the rat elbow and ankle extensors during running at 0·5 m/s; Armstrong & Taylor, 1982).

If during locomotion muscles were primarily performing shortening contractions, and the muscles generated the same forces while shortening with the same velocities at the two temperatures, then the cost of generating force may have been independent of temperature. This argument is based on a quantitative analysis of the mechanics and energetics of shortening muscle. The cost of generating force (rate of energy liberation per cross-section/force per cross-section) is a function of both muscle shortening

velocity and temperature. The nature of this relationship can be calculated by the Hill equations (Hill, 1964), that describe both the rate of energy liberation per cross-section ($\dot{E}/cm^2$) and force generation per cross-section (F/cm^2) as a function of shortening speed, if the temperature dependence of the mechanical and energetic properties of the muscle are known. As an example, in 3 cm long isolated frog sartorius muscles at 0 °C, Hill (1938) found that the isometric force was approximately 15·7 N/cm^2, the maximum speed of shortening was approximately 4 cm/s, and the maintenance heat rate was approximately 0·039 W/cm^2. Assuming the appropriate Q_{10}s for these parameters (Hill, 1938; Hill & Woledge, 1962), these values would be 17·2 N/cm^2, 8·8 cm/s and 0·118 W/cm^2 respectively, at a 10 °C higher temperature. Under isometric conditions, the cost of generating force would be about threefold lower in the cold muscle (0·0025 W/N), than in the warm muscle (0·0069 W/N). As shortening velocity increases, however, the cost of generating force in the cold muscle increases more rapidly than that in the warm, and thus at a shortening velocity of 1·5 cm/s, they would both be equal to 0·035 W/N, and at faster shortening velocities the cost of generating force of the cold muscle would exceed that of the warm muscle. At a shortening velocity of 1·5 cm/s, the $\dot{E}/cm^2$ is twofold higher in the warm muscle than in the cold (0·307 W/cm^2 compared to 0·145 W/cm^2), and the F/cm^2 is twofold higher as well (8·6 N/cm^2 compared to 4·1 N/cm^2). For the sake of argument, if we assume that the properties of the lizards' muscles at the two running temperatures were identical to those described above, and that the lizards' muscles shortened at 1·5 cm/s, the lizard would only need to use one-half the cross-sectional area of muscle at the higher temperature that it used at the low temperature in order to generate the same force. Thus, although the $\dot{E}/cm^2$ at the high temperatures would be twofold larger, the total rate of energy liberation during running would be the same. The applicability of these arguments to the case of lizard locomotion cannot be determined without further information concerning the mechanics and energetics of lizard muscle and the speed at which the lizards' muscles shorten during locomotion.

If, on the other hand, muscles were primarily performing isometric contractions during locomotion, then approximately the same cross-section of muscle must have been used at both temperatures and the cost of generating isometric force could have been kept constant only by utilizing different muscle fibre types at different temperatures. Lizard muscle is heterogeneous, containing fast and slow fibres (Marum & Armstrong, 1978) as well as tonic fibres (Proske & Vaughan, 1968). These different muscle fibre types probably differ greatly in their cost of generating isometric force (Hill, 1950). It is possible that by utilizing the relatively high-cost fibres at the low temperature and the relatively low-cost fibres at the high temperature, the absolute cost of generating isometric force in both the warm and cold muscle might have been the same. Experiments performed to distinguish between the last two possible explanations would give further insight into what type of contractions muscles perform during locomotion.

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