

ENERGETIC COST OF LOCOMOTION AS A FUNCTION OF AMBIENT TEMPERATURE AND DURING GROWTH IN THE MARSUPIAL *POTOROUS TRIDACTYLUS*

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Summary

In the marsupial, the potoroo, multiple regression analysis shows that ambient temperature makes a minor (2%) contribution towards variation in oxygen consumption with speed. This suggests that the heat generated during running is substituted for heat which would otherwise have to be generated for temperature regulation. Maximum levels of oxygen consumption are also temperature-independent over the range 5–25°C, but plasma lactate concentrations at the conclusion of exercise significantly increase with ambient temperature. Adult potoroos show a linear increase in oxygen consumption with speed, and multiple regression indicates that the most significant factor affecting energy use during running is stride length. Juvenile potoroos have an incremental cost of locomotion about 40% lower than that predicted on the basis of body mass. The smaller animals meet the demands of increasing speed by increasing stride length rather than stride frequency, as would be expected in a smaller species. Our results show that juvenile potoroos diverge significantly from models based only on adult animals in incremental changes in stride frequency, length and the cost of transport, suggesting that they are not simply scaled-down adults.

Introduction

A model of locomotory energetics developed by Taylor *et al.* (1970) from six species of mammals permitted the metabolic cost of running to be predicted from speed and body mass. Since this initial derivation, Fedak and Seeherman (1979) have reported that the model applies to both bipedal and quadrupedal runners, and the data base has been extended to over 60 mammalian species, including ten marsupials (Taylor *et al.* 1982). The predictive value of the model is impressive given the differences in gait and limb morphology among the taxa included. The notable exclusions from the model are bipedal marsupials, in which the rate of energy consumption does not increase linearly with speed

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(see Baudinette, 1991), and mink, in which different linear equations apply to walking and running (Williams, 1983).

The model has stimulated work on other taxa, particularly invertebrates (see Full, 1989) because of its simplicity and its prediction that large endothermic vertebrates move a unit of body mass through a unit distance at lower energy cost than do small animals. It has also prompted questions about the relationship between net mechanical work and the energy requirements of locomotion, and the scaling considerations of muscle function within this nexus (see Biewener, 1990; Kram and Taylor, 1990).

Our study addresses two extensions of the model which have received little attention. It should follow from the prediction that small animals are less efficient than large ones on a mass-specific basis that, during growth, the mass-specific power to move a given distance should be greater in a young animal than in its parent. This appears not to have been tested. The second question we address is the effect of ambient temperature (T_a) on running energetics; specifically we determine the degree to which exercise-related thermogenesis can substitute for cold-induced thermogenesis at low ambient temperature. If metabolism during exercise is independent of ambient temperature, this substitution would be complete. This question does not imply two 'kinds' of heat, locomotory and non-locomotory in origin, rather it indirectly asks how much does insulation change during running.

The study uses an Australian marsupial, the potoroo *Potorous tridactylus* (Kerr, 1792), one of the smallest members of the family Macropodidae. A study of temperature regulation in the species showed a dependence on sweating from the tail at high ambient temperatures (Hudson and Dawson, 1975). The animal is an omnivore, formerly common over much of Australia but now largely restricted to Tasmania. Its natural habitat is wet sclerophyll forests, which encompass the range of temperatures used in the study.

Materials and methods

Six animals were trapped under National Parks of Tasmania permit in native grasslands adjacent to forested areas north of Hobart, Tasmania. They were transported to Adelaide where they were housed in an open, grassed enclosure and maintained on commercial dog food supplemented with a range of vegetables and wholemeal bread. Three of the animals had young, which were used in the study following their natural departure from the pouch. At the beginning of the experimental period the body mass of individual adult animals ranged between 831 and 1396g, with a mean of 1083.9 ± 83.8 g (S.E.). Over a period of three weeks the six adults and three juveniles were trained to run on a motor-driven treadmill, the characteristics of which have been described previously (Baudinette *et al.* 1987). The experiments were conducted in a constant-temperature room, regulated to within 1°C, at 5, 15 and 25°C for the adult group and at 25°C for the young animals. All experiments were conducted during the day, and a period of 2h was permitted for temperature acclimation.

Rates of oxygen consumption (\dot{V}_{O_2}), corrected for respiratory carbon dioxide, were determined using an open-flow system designed to meet the guidelines of a single-

chamber system as defined in Frappell *et al.* (1989). Respiratory gases were collected from light conical masks, formed from acetate sheeting, which were attached to the animals with a light rubber collar. Air was drawn through the masks at flow rates of $10\text{--}14\text{ l min}^{-1}$; metering of nitrogen gas around the extremities of the mask showed that these flows were sufficient to prevent loss of the respiratory gas. The flows were calibrated volumetrically (Brooks vol-u-meter) and by nitrogen dilution (Fedak *et al.* 1981). The flow through the primary circuit was sub-sampled at 100 ml min^{-1} , dried in a column of anhydrous CaSO_4 , and pumped through an O_2 analyser (Ametek, model S-3A) and a CO_2 analyser (Ametek, CD-3A). A running session was considered successful if the oxygen level maintained a steady state ($\pm 3\%$) over a 3-min period. At the conclusion of a run the animal was weighed and body temperature was taken with a fine thermocouple calibrated against a mercury thermometer traceable to a national standard.

Separately from the variable speed measurements, maximal metabolic rates were determined at 5, 15 and 25°C for the adult animals. This point was defined as the highest oxygen consumption attained even with continually increasing running speeds. The daily log of running speeds for each animal during earlier trials made the point relatively easy to define. In each animal, at the end of two of these runs, lactate levels were determined in venous blood taken from a lateral vessel in the tail. Immediately after collection, the blood samples were deproteinized with HClO_4 and spun in a centrifuge. The plasma was added to a mixture of 2.25 mmol l^{-1} NAD, 0.5 mol l^{-1} glycine-hydrazine buffer and 14 units of lactate dehydrogenase activity (Sigma 826A) and incubated for 30 min at 37°C . The absorbance changes were compared to standard concentrations of lactate in HClO_4 .

A capacitive transducer glued to shaven skin on the back of the animal was used to determine stride frequencies. A thin wafer of piezoelectric material was mounted at the end of a 1 cm support and sealed in a Perspex capsule filled with silicon grease to dampen the vibrations in the system. A light coaxial cable connected the transducer to a charge amplifier, the output of which was fed to a Gilson duograph recorder. To determine the phase lag of the system, the sensor was mounted adjacent to a microswitch above a rotating cam which could be driven at frequencies of up to 6 Hz. The output from the accelerometer and the microswitch were compared on a dual-beam oscilloscope. At frequencies of up to 4 Hz, the lag in the accelerometer was less than 5 ms. Gait descriptions were made from high-speed video records.

Mean values and standard errors of the mean are quoted throughout. Regressions for the data were determined by the method of least squares. Differences between slopes and intercepts of simple regressions were examined using analysis of covariance (Snedecor, 1956) and Student–Newman–Kuhl tests (Zar, 1984). Stepwise multiple regression was used to determine the relative contributions of various main factors on oxygen consumption, stride frequency and stride length. Factors examined included ambient temperature, running speed, stride length, stride frequency and, in the case of the young animals, body mass; interactions (e.g. temperature \times speed) were not examined. Only factors with a statistically significant effect (*t*-test with $P < 0.05$) are reported.

Results

Gait patterns during locomotion

Filmed records showed that the most common gait used on the treadmill by the animals was a bounding or galloping motion with the forelimbs contacting the surface asynchronously. Bipedal hopping was seen in some individuals during runs at higher speeds, but it was seldom maintained for more than 10 strides and there was no consistent pattern in its usage. Some of the animals were never seen to move bipedally.

Stride length increased linearly with running speed and contributed more to speed increases at higher speeds than did stride frequency (Fig. 1, Table 1). Temperature had no significant effect on the relationship of either stride length or stride frequency to speed; thus, the data in Fig. 1 are pooled at T_a values of 5, 15 and 25°C. Stride frequency rises steeply at speeds of up to 1.3 ms^{-1} and then less steeply at higher speeds. The relationship between stride frequency and speed across all speeds measured is best

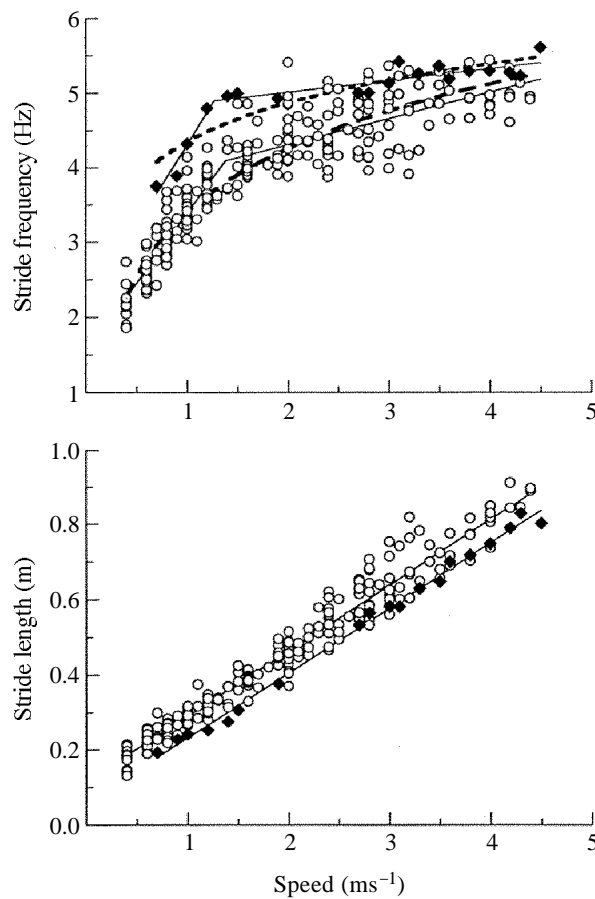


Fig. 1. Stride frequency and length as a function of treadmill speed in six adult potoroos of mean mass 1083.9g and in a 312g juvenile (filled symbols). Relationships between stride frequency and speed are statistically described by both a multiplicative line and by two lines (see Table 1 for details).

Table 1. Relationship of stride length ($mstride^{-1}$) and frequency (fs , $strides s^{-1}$) to speed (V , $m s^{-1}$) in juvenile (312g) and adult (1089 \pm s.e. 83.6g) potoroos

Equation number	Group	N	Equation	% <i>r</i> ²	S _{yx}	S _b	S _a	Mean V	Predicted at a speed of 2 m s ⁻¹	
Stride length (m)										
1	Juvenile	19	0.059+0.173 <i>V</i>	99.4	0.017	0.003	0.009	2.705	0.41	
2	Adult	226	0.116+0.174 <i>V</i>	96.2	0.037	0.002	0.005	1.882	0.46	
Slopes: <i>F</i> =0.027, <i>P</i> =0.863					Elevations: <i>F</i> =45.700, <i>P</i> <0.001					
Stride frequency (Hz)										
Multiplicative analysis										
3	Juvenile	19	4.319 <i>V</i> ^{0.161}	80.0	0.021	0.020	0.009	2.705	4.83	
4	Adult	226	3.282 <i>V</i> ^{0.349}	85.7	0.041	0.010	0.003	1.882	4.18	
Lower line									<i>I</i> - <i>V</i>	<i>I</i> - <i>fs</i>
5	Juvenile	4	2.126+2.171 <i>V</i>	92.2	0.161	0.446	0.431	0.950	1.27	4.89
6	Adults	95	1.503+1.886 <i>V</i>	80.8	0.278	0.095	0.086	0.855	1.37	4.09
Slopes: <i>F</i> =0.137, <i>P</i> =0.7136					Elevation: <i>F</i> =40.507, <i>P</i> =0.001					
Upper line										
7	Juvenile	15	4.694+0.157 <i>V</i>	63.9	0.120	0.003	0.109	3.173	5.01	
8	Adults	131	3.584+0.362 <i>V</i>	39.4	0.355	0.040	0.108	2.627	5.31	
Slopes: <i>F</i> =4.163, <i>P</i> =0.041										

Data for the juvenile were collected at 25°C; data for the adults were obtained at 5, 15, and 25°C and pooled since temperature had no significant effect on the relationships.

Stride frequency has been analysed both multiplicatively and using a two-line analysis where positioning of the lines was determined statistically (Yeager and Ultsch, 1989).

Velocity and stride frequency at the intersection of the two lines are given in the lower rows ($I-V$ and $I-fs$).

In this and other tables the symbol % r^2 denoted the coefficient of variation and S denotes the standard deviation of the subscripted variable: b (regression coefficient or slope), a (the intercept) and yx (the unexplained error in y).

described by a multiplicative equation (highest r^2). Two arithmetic lines were also fitted to the relationship of stride frequency to speed using the statistical technique of Yeager and Ultsch (1989) to position the lines optimally.

Stride characteristics of a small juvenile animal (312g) are distinctly different from those of the adults (1083g). Stride length of the juvenile was significantly less than that in the adults at all speeds, but the increase in length per unit increase in speed is statistically the same (Table 1, Fig. 1). Conversely, stride frequency in the juvenile is considerably higher than in the adult, particularly at low speeds. A transition in stride frequency in both the juvenile and adults occurs around 1.3 ms $^{-1}$; above this speed, the adults exhibit a steeper increase in frequency with increasing speed than does the juvenile.

Multi-factor analyses of the results from adults combined with the results from the single juvenile revealed that speed is the most important factor affecting both stride length and frequency; 96% of the variation in stride length is explained by its positive relationship to speed, while 84% of the variation in stride frequency is explained by its

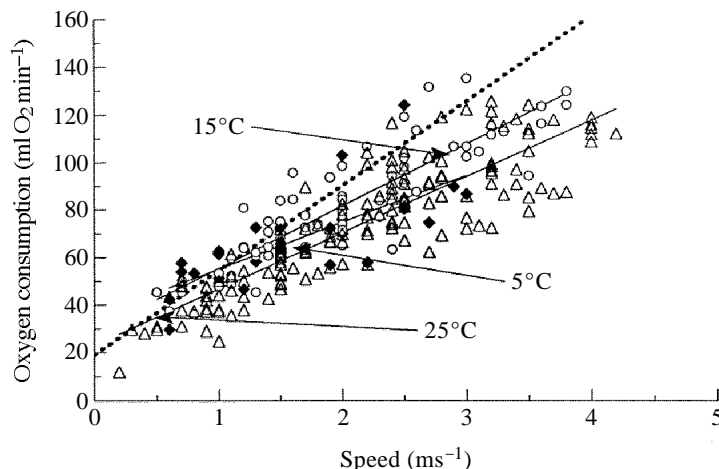


Fig. 2. The relationship of oxygen uptake to running speed in adult potoroos, of mean mass 1083g, at three ambient temperatures. Details of the simple regression lines relating the variables are shown in Table 2. The dashed line represents the predicted values for a 1083 g mammal from the equation of Taylor *et al.* (1982). The filled diamonds represent values taken at 5°C; circles, 15°C; triangles, 25°C.

multiplicative (log-log) relationship to speed. The second, though much less important, factor influencing stride length is the effect (negative) of stride frequency, which explains only an additional 1.8% of the variation in stride length. Conversely, the secondary effect upon stride frequency of stride length is much greater; stride frequency explains an additional 11.1% more of the variation in stride frequency than does speed alone. The third most important factor for stride length and frequency was the effect of mass, but in both cases it explains less than an additional 1% of the variation. Ambient air temperature does not significantly affect either stride length or frequency.

Rates of oxygen consumption as a function of ambient temperatures

Oxygen consumption for running adult animals increased linearly with the speed of locomotion at each of the three temperatures (Fig. 2, Table 2). The slopes of the lines are statistically indistinguishable. However, at the same speed, values of oxygen consumption at 5 and 15°C are statistically similar, and both are significantly greater than that at 25°C (elevations, Table 2). If we normalise the predicted oxygen consumption values at a speed of 2 ms⁻¹, by using the mean body temperatures during a run and a value for Q_{10} of 2, the new predictions at 5 and 15°C are 21 and 29% above that at 25°C.

To gain a measure of the relative contributions of speed (V) and air temperature (T_a) on $\dot{V}O_2$, a multiple regression equation has been derived relating these variables (Table 2). Within this linear model, changes in running speed account for 73%, and ambient temperature only a further 2%, of the variability in metabolic rate.

Rates of oxygen consumption as a function of body size

The relationship between oxygen consumption and running speed was determined for

Table 2. Oxygen consumption (\dot{V}_{O_2} , ml O_2 min $^{-1}$) of potoroos at varying treadmill speeds (V , m s $^{-1}$) for three different ambient temperatures (T_a , °C)

Equation number	T_a	N	Equation	% r^2	S_{yx}	S_b	S_a	Mean V	\dot{V}_{O_2} at 2 m s $^{-1}$	
									No	Q ₁₀
1	5°	27	35.525+19.666V	55.7	13.239	3.510	6.178	1.604	74.86	85.82
2	15°	68	29.246+26.228V	78.4	11.606	1.695	3.664	1.996	81.70	90.80
3	25°	156	23.081+23.652V	78.2	12.005	1.008	2.398	2.181	70.39	70.39
			Slopes: $F=1.786$, $P=0.168$		Elevation: $F=21.338$, $P<0.001$					

Elevational comparisons

5°C = 15°C, $q=2.437$, $P>0.05$ 5°C>25°C, $q=3.216$, $P<0.05^*$ 15°C>25°C, $q=9.172$, $P<0.05^*$

Equation number	N	Equation	S_a	S_v	S_T	S_{yx}	% r^2
Multi-regression – all							
4	251	37.1+24.1V–0.563 T_a	2.806	0.875	0.112	12.48	75.2
\dot{V}_{O_2} at 2 m s $^{-1}$							
		5°C, 82, 49 (no Q ₁₀)	15°C, 76.86, 85.42	25°C, 71.23, 71.23			

Statistics are given for simple regression equations relating \dot{V}_{O_2} to V at each temperature and for the multiple regression equation relating \dot{V}_{O_2} to both V and T_a .

Test statistics for differences between equations for each T_a are given (* denotes a significant difference). Predicted \dot{V}_{O_2} levels for each T_a were computed at 2 m s $^{-1}$ before and after normalization for the mean T_b measured at the 25°C run, assuming a Q₁₀ value of 2.

young potoroos from four body mass ranges (Fig. 3, Table 3). The slopes of the lines relating speed and \dot{V}_{O_2} in mass-specific units of ml O_2 s $^{-1}$ kg $^{-1}$ are significantly different among each of the mass classes. The slopes of the lines, in units of ml O_2 s $^{-1}$ m $^{-1}$, are compared with those predicted for the ‘cost of transport’ (Taylor *et al.* 1982). In each size class, the measured slope of the potoroo data is less than that predicted from the allometric equation, but the difference between observed and predicted values generally decreased with increasing body size. The y-intercept of the relationship between oxygen consumption and speed changes dramatically during growth. This is probably a reflection of higher mass-specific ‘resting’ metabolism in smaller animals.

Rates of oxygen consumption as a function of stride frequency and length

Even though metabolism was not measured simultaneously with stride frequency and length, it was possible to select oxygen consumption values collected at the same speeds as were used for stride determinations and in the same animals. This analysis provides an estimate of the effect of all factors including stride frequency and length on energy use.

The single most important factor affecting oxygen consumption in locomotion is stride length (Fig. 4). If only adult animals are included in the analysis, stride length accounted for 78.7% of the variation in oxygen consumption. Air temperature is the only other significant factor in this analysis and explains only an additional 2.8% of the variation in energy use. If the single juvenile animal is included in the analysis, stride length explains

58.5% of the variation in oxygen consumption and body mass accounts for an additional 19.8%. Stride frequency also has a significant effect when the juvenile is included, but it accounts for only an additional 1.6% of the variation in oxygen consumption. Although speed was included as a factor it had no effect on oxygen consumption in these analyses.

Maximal rates of oxygen consumption

Maximal rates of oxygen consumption, and the associated plasma lactate levels, were determined at all three ambient temperature (Table 4). Maximal levels of $\dot{V}O_2$, and the running speeds at which these occur, are independent of ambient temperature. However, the plasma lactate concentrations at the conclusion of the exercise significantly increased with increasing ambient temperatures.

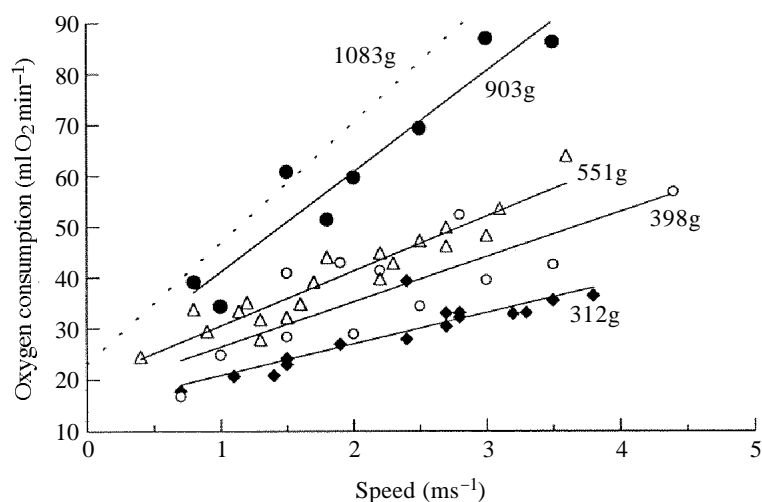


Fig. 3. Relationship of oxygen consumption to speed at 25°C for potoroos of differing body mass. The dashed line represents the equation relating the variables in an adult animal (equation 3 in Table 2); details of the simple regression equations represented by the other lines are given in Table 3.

Table 3. Relationship of mass-specific oxygen consumption ($\text{ml O}_2 \text{ s}^{-1} \text{ kg}^{-1}$) to treadmill speeds (V , m s^{-1}) at 25°C for three potoroos of different body masses

Equation number	Mass (g)	N	Equation	% r^2	S_{yx}	S_b	S_a	Mean V	Pre-dicted C_t	%P
1	312.5±5.6	17	0.803+0.323V	60.8	0.244	0.067	0.172	2.406	0.770	42
2	397.6±11.2	12	0.880+0.298V	74.4	0.194	0.055	0.136	2.250	0.713	42
3	551.2±4.7	20	0.565+0.345V	91.6	0.092	0.025	0.051	1.897	0.643	54
4	903.0±4.8	12	0.383+0.370V	89.6	0.128	0.051	0.113	2.013	0.550	67

The slopes of these relationships are the incremental cost of transport (C_t , $\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$); predicted values (%P) are based on the equation of Taylor *et al.* (1982).

%P=100×slope/predicted C_t .

Discussion

The literature is equivocal in defining whether the heat produced during locomotion is additive or substitutive to that required for temperature regulation below thermal neutrality. A recent analysis of the situation in birds (Marsh and Dawson, 1989) lists two studies in which the metabolic cost of running was measured as a function of air

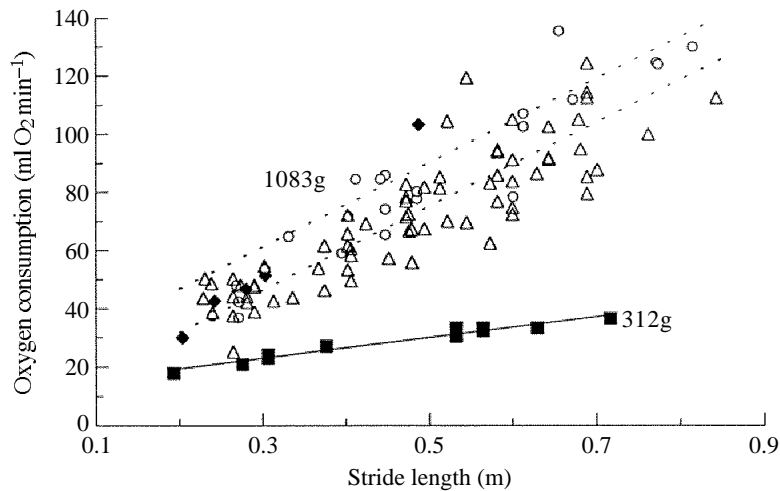


Fig. 4. Relationship of oxygen consumption to stride length in a juvenile (312g) potoroo running at an ambient temperature of 25°C and potoroo adults (1083g) running at 5°C ($N=5$, filled diamonds), 15°C ($N=20$, circles) and 25°C ($N=72$, triangles). Lines for the adults at 5°C (upper line) and 25°C (lower line) are based on multiple regression equations relating oxygen consumption to stride length (SL) and air temperature (C) ($=21.58+144.25SL-0.75C$, $N=97$, $r^2=0.81$, $S_a=5.25$, $S_{SL}=7.10$, $S_C=0.20$), where S is the standard error for the subscripted variable and a is the intercept. The line for the juvenile is based on a simple linear equation relating oxygen consumption to stride length ($=12.27+35.14SL$, $N=11$, $r^2=0.95$, $S_{yx}=1.25$, $S_a=1.16$, $S_b=0.47$; the symbols are explained in Table 1.

Table 4. Mean values (\pm standard error) of plasma lactate concentrations, maximal oxygen consumption and running speed, and initial body temperature (T_b) as a function of ambient temperature (T_a) in five adult potoroos during treadmill locomotion

T_a (°C)	Speed (m s ⁻¹)	Maximum $\dot{V}O_2$ (ml min ⁻¹)	[Lactate] (mmol l ⁻¹)	Initial T_b (°C)
5	3.08 \pm 0.35	90.02 \pm 8.19	11.12 \pm 1.21	34.6 \pm 0.2
15	3.33 \pm 0.17	95.73 \pm 9.43	14.23 \pm 2.13	35.4 \pm 0.2
25	3.93 \pm 0.29	98.30 \pm 10.99	18.71 \pm 2.11	36.7

The relationship between lactate (y) and temperature (T_a) is significant: $y=9.038+0.377T_a$ ($\%r^2=47.7$, $S_a=1.96$, $S_b=0.12$, $S_{yx}=3.56$).

There is no significant relationship between air temperature and oxygen consumption ($F_{[1,12]}=0.439$, $P=0.521$) or air temperature and speed ($F_{[1,12]}=4.35$, $P=0.06$).

$N=5$ for each measurement except for T_b at 25°C where $N=2$.

temperature. In one case, exercise thermogenesis was found to substitute for regulatory thermogenesis at low temperatures (Nomoto *et al.* 1983); in the second study the sources were additive (Pohl, 1969). In flying birds three of the four reported studies indicate that exercise thermogenesis aids temperature regulation. Two studies in flying hummingbirds are included in this sample. In *Amazilia fimbriata* heat substitution occurs at air temperatures down to 0°C (Hart and Berger, 1972), whereas in *Ocreatus underwoodii* the heat sources appear to be additive (Schuchmann, 1979). A recent study on the effects of temperature on the rates of oxygen consumption during diving in the tufted duck *Aythya fuligula* suggests that heat produced by muscle partially compensates for heat loss in cold water (Bevan and Butler, 1992). Substitution of thermoregulatory heat production by heat from working muscle during diving has also been shown in king penguins (Butler and Jones, 1992) and in Weddell seals (Kooyman *et al.* 1973).

The interaction of cold-induced and exercise thermogenesis in other mammals is not clear, and the older literature suggests variations among species (e.g. Wunder, 1970; Hart, 1971). However, in general, heat produced during locomotion in small mammals, especially rodents, appears to be additive rather than substitutive to heat associated with thermoregulation. One of the clearest apparent examples of this is a small marsupial, *Dasyuroides byrnei*, in which the energetic cost of running is inversely related to air temperature (MacMillen and Dawson, 1986). However, body temperatures are not reported in that study so it is not possible to correct for a Q_{10} effect. In the case of Merriam's chipmunk (Wunder, 1970), such a correction changed an apparently additive heat pattern to one of substitution, in that most of the measured increase in running cost at 5°C was due to the increase in body temperature. In the 4kg patas monkey, Mahoney (1980) has shown independence between oxygen consumption and air temperature during running over the range 0–55°C.

Our data clearly show that air temperature makes only a minor contribution towards variation in oxygen consumption with speed in the potoroo, particularly after correction for a Q_{10} effect. This indicates that the heat generated during running in the potoroo can be substituted for heat which would otherwise have to be produced for temperature regulation. Perhaps even more critical to this conclusion is our finding that maximal levels of oxygen consumption are also largely temperature-independent over the range 5–25°C.

Speculation on the control of the substitutive nature of temperature regulation in the potoroo may be of particular interest because of the role of sweating in these animals. Hudson and Dawson (1975) showed that at high ambient temperatures copious sweating occurred from the tail at rates about twice that reported in large mammals. This is unique among small mammals and results in their being able to dissipate the whole of their metabolic heat production at ambient temperatures above 35°C. As a corollary to this mechanism, lumped thermal conductance across the body surface is low compared to that of other mammals and there is a lessened dependence on respiratory heat loss. A system which is 'designed' to retain metabolic heat, but with a specialised sweating surface that can be used at high ambient temperatures, would seem consistent with the substitution of exercise-induced heat for thermoregulation at low ambient temperatures. There appears

to be no comparable information from other mammals in which the question of heat substitution has been addressed, and the matter remains speculative.

For both the smaller juvenile and larger adult potoroos, stride frequency initially rises steeply with increasing speed and then levels off (Fig. 1). The transitions in stride frequency occur at calculated speeds which are very close to the trot–gallop transition speeds predicted for animals of these sizes by the equation of Heglund and Taylor (1988). In the juvenile the observed speed is only 6% faster than predicted (1.27 vs 1.20 ms^{-1}); in the adult this observed transition occurs at a speed 13% lower than predicted (1.37 vs 1.57 ms^{-1}). Heglund and Taylor (1988) also recognise a ‘preferred gallop’, which they defined as the speed at the middle of the observed galloping speed range. The predicted preferred gallop speed for the adult potoroo (2.82 ms^{-1}) is near the middle of the observed range of adult potoroo speeds above the transition, but the predicted value for the juvenile is lower than that observed here (Fig. 1). The predicted speeds for the trot–gallop transition and preferred gallop can be used to compare locomotion characteristics of the smaller juvenile and larger adult potoroos with those of other quadrupeds (Table 5).

Stride characteristics of both the smaller and larger potoroos appear very similar to those predicted from body mass (Table 5). The stride frequency of the smaller juvenile is only 5% below that predicted at both the trot–gallop transition and preferred gallop speeds. In the adult the stride frequency is the same as predicted at the trot–gallop transition speed and only 5% higher at the preferred gallop speed.

The energetic costs incurred by the potoroos at these two speeds are less than predicted (Table 5). The deviation is greater at the faster speed; 25% less in both small and large potoroos. For the smaller juvenile, the cost is very similar to that predicted at the slower trot–gallop transition speed, but markedly reduced at the faster speed. In the adult, the cost is reduced at both speeds. For juvenile and adult, the energy cost per kilogram per stride is similar at the equivalent speeds and increases with increasing speed. Postulated reasons for these changes are discussed by Heglund and Taylor (1988) and Kram and Taylor (1990).

Typically, in smaller animals, the slope of the line relating stride length to speed is lower, while the slope of the line relating stride frequency to speed is greater, than that in larger animals (Strang and Steudel, 1990). This was not the case in the comparison of the juvenile and adult potoroo (Table 1, Fig. 1). The slope of the line relating stride length to speed, or incremental sstride^{-1} , of the smaller juvenile potoroo is the same as that observed for the adult (0.17, slopes, equations 1, 2, Table 1). This observed slope is higher than that predicted by the equation of Strang and Steudel (1990) for animals trotting on the basis of the body mass of both the juvenile (55%, predicted $0.11\text{ sstrides}^{-1}$) and the adult (24%, $0.14\text{ s stride}^{-1}$). The slope of the line relating stride frequency to speed, or incremental strides m^{-1} , of the juvenile is greater than that for the adult at speeds below the gait transition (equation 5 vs 6, Table 1; Fig. 1). The difference is less than predicted because the juvenile has a slope which is 25% lower than predicted ($2.93\text{ strides m}^{-1}$) and that of the adult is 13% higher than predicted ($1.67\text{ strides m}^{-1}$) from the equation of Strang and Steudel (1990).

Thus, the adult potoroo has slightly higher incremental $s\text{stride}^{-1}$ (24%) and strides m^{-1} (13%) than predicted for a trotting animal of the same body mass. Another way of expressing this is that a one unit increase in trotting speed results in the adult potoroo taking 24% longer to complete a single stride and expending 13% more strides per distance than predicted. Conversely, an incremental increase in trot speed results in the juvenile taking 55% longer to complete a stride with 26% fewer strides per distance than predicted.

Clearly, the juvenile is not operating simply like a scaled-down adult. The former meets the demands of increasing speed by increasing its stride length rather than its stride frequency, as would be expected for a small animal. This could be a characteristic of juvenile animals in general and could reflect increased flexibility and elasticity of immature animals or proportionally longer limbs.

As previously mentioned, the juvenile also has a markedly lower incremental cost of transport than that predicted on the basis of its body mass (Table 3); this reduction amounts to 42% of that predicted in the smallest juvenile examined (0.312kg). The incremental cost of transport in the adult (76% of predicted) is at the lower extreme for an animal of this body mass.

The allometric functions for the metabolic cost of running are based on a large number of species over a wide range of taxa and have proved robust in their applicability. What still remains unclear, however, is the reason for this regularity in scaling. It does not simply reflect the mechanical work performed by the muscles in accelerating and decelerating the limbs and moving the centre of mass of the animal, because the work performed by muscle in moving a unit mass over a fixed distance is mass-independent (Heglund *et al.* 1982a,b). Biewener (1990) comments that the lack of congruence between net mechanical work and the energy requirements for locomotion is not surprising given the many different roles of skeletal muscle in performing positive and negative work and its role in storing strain energy during isometric contraction. Other factors have been proposed to account for the regularity in function between body mass and the energetic cost of running. Magnitude, duration and rate of development of muscle force are prominent proposals (e.g. Strang and Steudel, 1990; Baudinette, 1991). The latter of these suggestions is most interesting. Close (1972) showed that skeletal muscles of large animals will develop force at a slower rate than those of small animals. A corollary of this is that the stride frequency of running animals at an equivalent speed, such as at a gait change, should scale inversely with body mass. In fact, Heglund and Taylor (1988) show that this frequency scales as $\text{mass}^{-0.15}$. This relationship has not been tested during growth. Is the rate of the muscle contraction-relaxation sequence species-specific or does it change during development? Our finding that growing potoroos diverge significantly in incremental changes in stride frequency, length and cost of transport from the model derived only from adult animals suggests that the rate of cycling of cross bridges in muscle, and the associated rates of calcium flux, may vary during growth in a different fashion from that seen in adult animals. It could also mean that the storage of elastic strain energy is greater in young animals. Because of the large change in body mass which occurs from the onset of locomotion until adulthood, precocial birds or some marsupial species may be good models with which to address these questions.

We conclude that heat produced during locomotion in the potoroo can largely substitute for heat that would otherwise be required for temperature regulation. We also show that immature potoroos diverge from the locomotory model derived for adult animals in that the increases in metabolic power required to meet speed increases are proportionally less than in adult mammals. Marsupials may prove a useful model for further investigations into the energy–work nexus involved in locomotion.

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