

## ENERGETICS OF BIPEDAL RUNNING

### I. METABOLIC COST OF GENERATING FORCE

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#### Summary

Similarly sized bipeds and quadrupeds use nearly the same amount of metabolic energy to run, despite dramatic differences in morphology and running mechanics. It has been shown that the rate of metabolic energy use in quadrupedal runners and bipedal hoppers can be predicted from just body weight and the time available to generate force as indicated by the duration of foot–ground contact. We tested whether this link between running mechanics and energetics also applies to running bipeds. We measured rates of energy consumption and times of foot contact for humans (mean body mass 78.88 kg) and five species of birds (mean body mass range 0.13–40.1 kg). We find that most (70–90%) of the increase in metabolic rate with speed in running bipeds can be explained by changes

in the time available to generate force. The rate of force generation also explains differences in metabolic rate over the size range of birds measured. However, for a given rate of force generation, birds use on average 1.7 times more metabolic energy than quadrupeds. The rate of energy consumption for a given rate of force generation for humans is intermediate between that of birds and quadrupeds. These results support the idea that the cost of muscular force production determines the energy cost of running and suggest that bipedal runners use more energy for a given rate of force production because they require a greater volume of muscle to support their body weight.

Key words: locomotion, energetics, bipedal, bird, muscle force.

#### Introduction

The question of whether more energy is required to run on two or four legs was addressed 100 years ago when Zuntz (1897) performed some of the first measurements of metabolic energy consumption in running animals. He found that horses used less energy than humans to move a unit body weight a unit distance, and he speculated that there might be an energetic benefit to moving on four legs rather than two. However, subsequent measurements of oxygen consumption in running dogs showed that these quadrupeds use more energy per unit body mass to move a given distance than both humans and horses. Zuntz (1897) noticed that this energy cost of transport in horses, dogs and humans was proportional not to limb number but to body mass and concluded that, per unit body weight, small animals use more energy to run a given distance than do large animals, regardless of limb number (Zuntz, 1897).

Energetic measurements from a diverse group of quadrupedal mammals have since established that the amount of energy required to move a unit body weight a unit distance (cost of transport  $E_{\text{trans}} W_b^{-1}$ ) decreases in direct proportion to body weight,  $W_b^{-0.31}$  (Taylor *et al.* 1982). Extrapolation from data for small bipedal runners initially suggested that large

bipeds might be exceptionally economical (Fedak *et al.* 1974), but this suggestion was not supported by subsequent measurements: ostriches and ponies of the same size use the same amount of energy to run (Fedak and Seeherman, 1979). In fact, the energy cost of transport follows the same allometric function for two- and four-legged vertebrates, as well as for invertebrates that run on six or more limbs (Full, 1989). Even within the same individual, the cost of running can be independent of the number of limbs – chimpanzees trained to run on either two or four legs show no difference in cost between the two gaits (Taylor and Rowntree, 1973).

It has been proposed that the energy cost of running is determined mainly by the cost of producing force to support body weight (Taylor *et al.* 1980; Taylor, 1985, 1994; Kram and Taylor, 1990). Kram and Taylor (1990) hypothesized that the high metabolic cost of running in small animals can be explained by a greater cost of producing force with faster muscle fibers. A mouse must take many fast steps to cover the same ground that a pony covers in one step, so its muscle fibers must turn on and off and develop force more quickly. These faster muscles require higher rates of cross-bridge cycling and  $\text{Ca}^{2+}$  pumping and use more ATP per gram of active muscle

(Barany, 1967; Rall, 1985; Rome, 1992). Kram and Taylor (1990) proposed that the energy used by each gram of active muscle in a running animal should be inversely proportional to the time available to produce force in each step, measured as the time for which an individual foot is in contact with the ground,  $t_c$ . The total volume of muscle that must be active to support body weight will also determine energy use; the scaling of muscle forces and fiber lengths suggests that active muscle volume is the same proportion of body weight in large and small mammals (Alexander *et al.* 1981; Biewener, 1990; Kram and Taylor, 1990). Across both speed and body size, metabolic rate in running and hopping mammals is directly proportional to body weight and the time available to produce force:

$$\dot{E}_{\text{metab}} = \frac{c W_b}{t_c}, \quad (1)$$

where  $\dot{E}_{\text{metab}}$  is the rate of energy consumption (W),  $W_b$  is body weight (N) and  $t_c$  is the time of individual foot contact (s). The 'cost coefficient',  $c$  ( $\text{JN}^{-1}$ ), expresses the proportionality between body-weight-specific energy cost and the rate of force generation. Animals take faster steps and have shorter times of foot contact as they run faster. Similarly, smaller animals must have higher rates of force development because their short legs take quicker steps. The same cost coefficient accurately predicted differences in metabolic energy cost from the time of foot contact across a fourfold range in running speed and a 4000-fold range in size in quadrupeds (Kram and Taylor, 1990).

We undertook the present study to determine whether the energetics of bipedal running could also be explained by the energetics of muscle force production. We hypothesized that the rate of energy use for bipedal runners would be the same proportion of body weight and inverse time of foot contact as observed for quadrupedal runners. In other words, we tested whether the 'cost coefficient' in equation 1 is the same for bipedal and quadrupedal runners. Several assumptions were made by Kram and Taylor (1990) when formulating the prediction of equation 1. First, it was assumed that the metabolic cost of swinging the limbs is negligible compared with the cost of supporting the body weight. Their second assumption was that during running muscles perform similar activities, i.e. operate over similar ranges of muscle shortening velocities ( $V/V_{\text{max}}$ ), irrespective of body size or running speed. Third, it was assumed that the volume of muscle active to produce force is proportional to body weight, i.e. that the muscle mass active to support body weight is the same fraction of body mass in all runners. If these assumptions are equally valid for bipedal and quadrupedal runners, their cost coefficients should be equivalent.

## Materials and methods

### Animals

The species, mean body weight and number of animals used are listed in Table 1. Birds were housed in outdoor coops or

Table 1. *Species, body weight and number of animals*

Species	$M_b$ (kg)	$W_b$ (N)	$N$
Northern bobwhite quail <i>Colinus virginianus</i> (L.)	0.13	1.3	3
Guinea fowl <i>Numida meleagris</i> (L.)	1.30	12.7	2
Wild turkey <i>Meleagris gallopavo</i> (L.)	5.30	51.9	3
Rhea <i>Rhea americana</i> (L.)	19.90	195.0	3
Emu <i>Dromaius novaehollandiae</i> (Latham)	40.10	393.0	1
Human <i>Homo sapiens</i> (L.)	78.88	773.1	4

$M_b$ , body mass;  $W_b$ , body weight.

pastures, with the exception of the quail which were housed in indoor pens. All birds were given food and water *ad libitum*. Humans were fit recreational runners.

### Kinematic measurements

The time of individual foot contact ( $t_c$ ) was measured from video recordings of treadmill running. Animals were recorded using either a NAC 200 high-speed video camera operating at 200 fields  $\text{s}^{-1}$  (guinea fowl, turkey, emu) or a Sony CCD-V701 camera operating at 60 fields  $\text{s}^{-1}$  (quail, rhea, human). Time of contact was determined by counting the number of frames during which the foot was on the ground. The largest error in measuring time of foot contact was 8% for rhea running at the fastest speed (0.213 s measured  $t_c$ , maximum 1/60 s error). At least 10 strides were analyzed for each animal at each running speed. Step length ( $L_c$ ), defined as the distance that the hip moves while the foot is on the ground, was calculated by multiplying running speed by the time of foot contact. Possible errors in this measure due to acceleration or deceleration were minimized by analyzing only those strides in which the animal maintained its forward position on the treadmill.

### Energy consumption and cost coefficient

All energetic and kinematic measurements were made while the animals ran on a motorized variable-speed treadmill. Birds were trained for approximately 20 min a day, 3 days a week for at least 6 weeks before measurements were made.

The rates of oxygen consumption ( $\dot{V}_{\text{O}_2}$ ) were determined using an open-circuit indirect calorimetry system (Fedak *et al.* 1981). Large animals wore loose-fitting masks, and small birds (quail and guinea fowl) ran inside small acrylic chambers. Room air was metered at constant rates through the chamber or mask, and a small sample of the collected gas was dried, scrubbed of  $\text{CO}_2$  and measured for  $\text{O}_2$  content using a Beckman F3 oxygen analyzer. Calibration with a known flow

rate of nitrogen allowed calculation of  $\dot{V}_{O_2}$  (Fedak *et al.* 1981). The system was found to be accurate to within  $\pm 2\%$ .

The rate of  $O_2$  consumption was measured continuously during each trial. We used measurements taken after a steady-state level of  $\dot{V}_{O_2}$  had been maintained for 5 min or more. Several measurements were made on different days and averaged. We used an energy equivalent of  $20.1 \text{ J ml}^{-1} O_2$  to convert measurements of oxygen consumption to energy consumption (Blaxter, 1989).  $\dot{E}_{\text{metab}}$  for a given running speed was defined as the metabolic rate minus the zero-speed ( $y$  intercept) rate. The cost coefficient was determined according to equation 1. The cost of transport was defined as the slope of the least-squares linear regression of  $\dot{E}_{\text{metab}} W_b^{-1}$  against speed.

## Results

### Bipedal energetics and speed

Rates of energy use ( $\dot{E}_{\text{metab}} W_b^{-1}$ ) and the inverse time of foot contact ( $1/t_c$ ) increased linearly with speed in each species (Fig. 1). The cost coefficient changed little with running speed, indicating that increases in metabolic cost were accurately predicted by changes in the foot contact time. To quantify the fraction of increase in metabolic rate for each species not accounted for by equation 1, we compared the increase in metabolic rate across the speed range measured with the increase predicted from equation 1 using the mean cost coefficient for all running speeds for that species. The residual (measured metabolic rate minus predicted metabolic rate) indicated the increase in metabolic rate not predicted by equation 1. Of the increase in metabolic rate, 70–90% could be explained by the increase in the rate of force generation across the speed ranges measured for all species. Both metabolic rate and the rate of force generation increased more rapidly with speed in smaller animals, resulting in similar cost coefficients across the entire size range for birds (Fig. 1; Table 2). Humans had a slightly lower cost coefficient than birds, with the exception of quail (Table 2).

### Bipedal energetics and size

To compare the metabolic cost per unit distance traveled and the rate of force generation as a function of body size, we can divide both sides of equation 1 by running speed to obtain:

$$E_{\text{trans}} W_b^{-1} = \frac{c}{L_c} \quad (2)$$

The left-hand side of the equation is the cost of transport ( $\text{J N}^{-1} \text{ m}^{-1}$ ) and  $L_c$  is the step length, defined here as the horizontal distance moved by the hip during foot contact. Because step length changes little with speed, we used a mean of the values for all speeds for each species (Table 2).  $E_{\text{trans}} W_b^{-1}$  and  $L_c$  averaged over the speed range measured can be used to compare different-sized bipeds and quadrupeds, irrespective of speed (Fig. 2; Table 2).

Larger animals used less energy to move a unit body weight a unit distance (Fig. 2). The cost of transport for birds was proportional to  $W_b^{-0.31 \pm 0.07}$  (slope and 95% confidence limits

of least-squares regression), a value very similar to previously reported values for bipeds and quadrupeds (Fedak and Seeherman, 1979; Taylor *et al.* 1982). Larger animals took longer steps than smaller animals, in proportion to their longer limbs ( $L_c \propto W_b^{0.36 \pm 0.13}$ ) (Fig. 2). The cost coefficient, the ratio of these two, did not change significantly with body weight

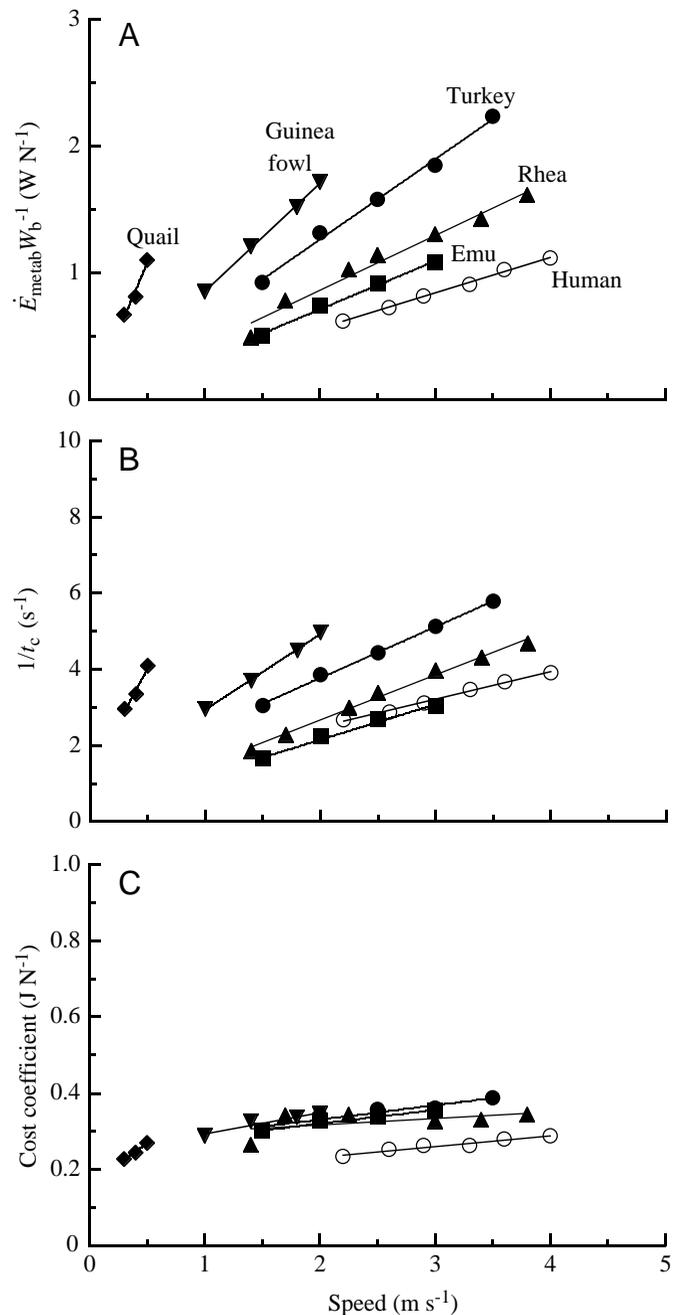


Fig. 1. Metabolic rate ( $\dot{E}_{\text{metab}} W_b^{-1}$ ) (A), the rate of force generation measured as the inverse of time of foot contact ( $1/t_c$ ) (B) and the 'cost coefficient', the ratio of these two variables (C) versus running speed. All least-squares regression lines shown were significant ( $P < 0.05$ ), with the exception of cost coefficient for quail ( $P = 0.070$ ) and rhea ( $P = 0.235$ ). Least-squares regression lines are, however, included for quail and rhea cost coefficient for ease of identification.

( $c \propto W_b^{0.05 \pm 0.06}$ ;  $F_{(1,3)} = 5.49$ ,  $P = 0.10$  for least-squares regression of log-transformed data) (Fig. 2).

#### Bipedal energetics compared with quadrupedal energetics

The metabolic cost of transport was similar in birds, humans and other mammals (Fig. 2A). Comparing animals of the same mass, the birds in this study had longer step lengths than the mammals studied by Kram and Taylor (1990) (Fig. 2B) (ANCOVA,  $P = 0.004$ ). Longer steps allow more time to generate force at a given running speed  $v$  ( $t_c = L_c/v$ ); thus, the longer step lengths of birds allow slower rates of force generation compared with mammals of similar body weight. The mean cost coefficient for birds ( $0.315 \pm 0.020 \text{ J N}^{-1}$ ) was 1.7-fold greater than that for mammalian quadrupeds and hoppers ( $0.183 \pm 0.020 \text{ J N}^{-1}$ ;  $P = 0.002$ , two-tailed  $t$ -test). Humans had a cost coefficient intermediate between the mean values for birds and the mammals studied by Kram and Taylor (Fig. 2C).

### Discussion

#### Speed, energy cost and the rate of force generation

We find that 70–90% of the increase in energy cost with speed in bipedal runners can be explained by the increase in rate of force generation. The direct proportionality between metabolic rate and  $1/t_c$  supports the theory that metabolic rate increases at higher speeds because faster, metabolically more expensive, muscle fibers must be recruited to produce force. Small but consistent increases in cost coefficient with speed in

Table 2. The mean and range of step lengths, cost of transport and cost coefficient

	<i>N</i>	Step length, $L_c$ (m)	Cost of transport, $E_{\text{trans}}W_b^{-1}$ ( $\text{J N}^{-1} \text{ m}^{-1}$ )	Cost coefficient, $c$ ( $\text{J N}^{-1}$ )
Bobwhite quail	3	0.114 ± 0.011 (0.101–0.122)	2.150 ± 1.910	0.246 ± 0.021
Guinea fowl	4	0.379 ± 0.030 (0.337–0.402)	0.854 ± 0.095	0.324 ± 0.026
Wild turkey	5	0.553 ± 0.047 (0.492–0.606)	0.632 ± 0.090	0.349 ± 0.031
Rhea	7	0.762 ± 0.026 (0.749–0.809)	0.431 ± 0.083	0.327 ± 0.028
Emu	4	0.928 ± 0.044 (0.905–0.990)	0.363 ± 0.105	0.331 ± 0.022
Human	6	0.935 ± 0.068 (0.824–1.024)	0.280 ± 0.022	0.262 ± 0.019

Cost coefficient and step length are the means ± s.d. for all running speeds.

Cost of transport is the slope ± 95% confidence interval for metabolic rate *versus* speed.

The range of step lengths measured is given in parentheses.

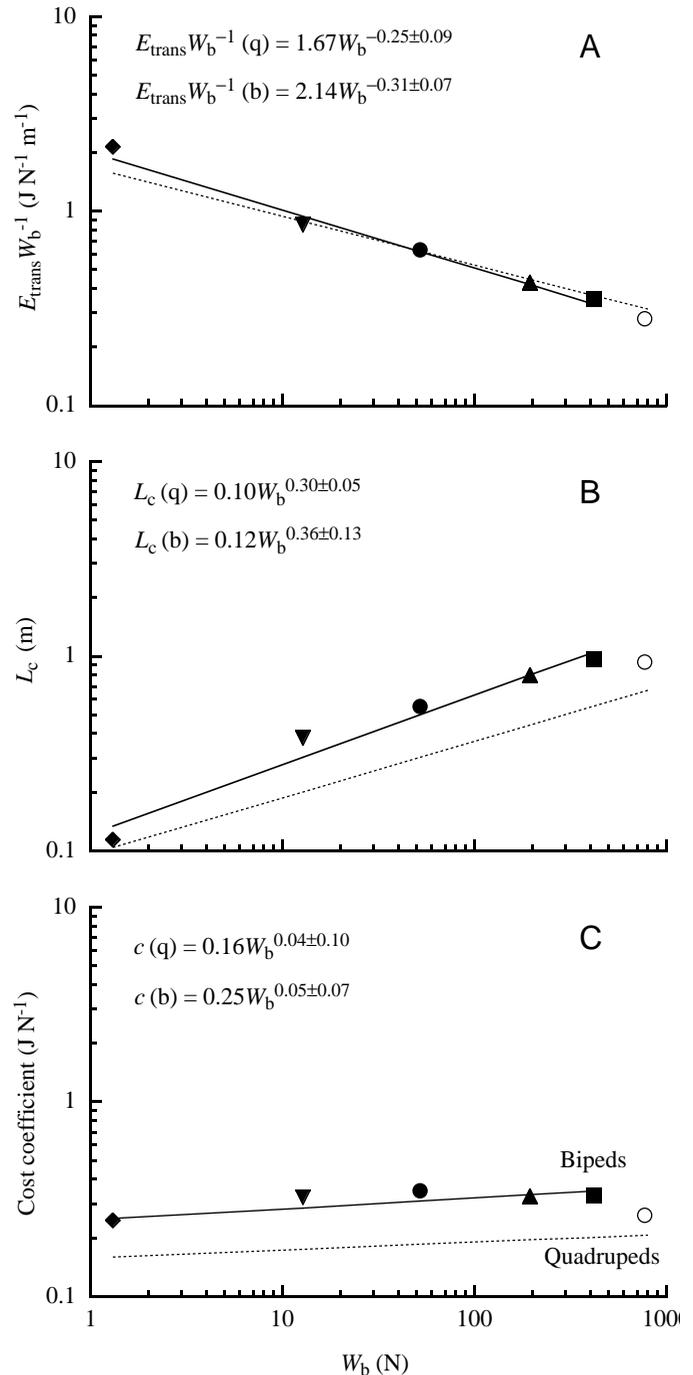


Fig. 2. (A) The amount of metabolic energy required to move a unit body weight a unit distance,  $E_{\text{trans}}W_b^{-1}$ , versus body weight.  $E_{\text{trans}}W_b^{-1}$  was measured from the slope of the linear regression of energy cost against speed. (B) Step length  $L_c$  versus body weight. Step length is the mean step length over the speed range measured for each species. (C) The cost coefficient versus body weight. Lines and equations were obtained by least-squares linear regressions of log-transformed data for the birds (b, solid lines), excluding the human data; the regression for other mammals (q, dotted lines) is taken from Kram and Taylor (1990). Regressions for  $E_{\text{trans}}W_b^{-1}$  and  $L_c$  were significant ( $P < 0.05$ ). Least-squares regressions for cost coefficient were not significant (mammals  $P = 0.23$ ; birds  $P = 0.10$ ), but the lines are shown for ease of comparison. Symbols as in Fig. 1.

bipedal runners demonstrate that other speed-related factors in addition to rate of force generation affect energy cost. For example, the systematic increase in cost coefficient in humans reveals that 30 % of the increase in energy cost across the speed range measured is not explained by the linear relationship between energy cost and rate of force generation of equation 1. Among the possible explanations for this increase in cost of force generation are a change in the relative shortening velocity of the muscles across speed or decreases in mean muscle mechanical advantage with running speed. If muscles were to operate on average at higher muscle shortening velocities  $V/V_{\max}$  as running speed increased, a greater cross-sectional area of muscle would have to be activated to provide the same force as a result of the force–velocity relationship of skeletal muscle (Roberts *et al.* 1997). Likewise, a poorer mechanical advantage would result in an increase in the cross-sectional area of muscle that would have to be active to support body weight. A greater active muscle cross-sectional area would mean an increase in active muscle volume, causing an increase in energy cost in addition to that predicted from changes in the rate of force generation.

Changes in the inverse time of foot contact with running speed are more closely correlated with changes in metabolic rate than other kinematic or mechanical variables that have been investigated. Stride frequency increases nearly linearly with speed in bipeds (Gatesy and Biewener, 1991), but quadrupeds running at fast speeds primarily increase stride length, with very little change in stride frequency (Heglund and Taylor, 1988). Thus, the energy cost per stride almost doubles from a preferred trotting speed to a preferred galloping speed (Heglund and Taylor, 1988). Time of foot contact decreases independently of stride frequency because the fraction of a stride during which a foot is in contact with the ground (duty factor) decreases continuously at higher running speeds (Biewener, 1983). Increases in metabolic rate with speed also appear to be poorly correlated with changes in mechanical work rate; mass-specific mechanical work rate increases curvilinearly with running speed, in contrast with the linear increase in metabolic rate (Heglund *et al.* 1982). However, it has also been proposed that the changes in metabolic rate with speed might be predicted from changes in mechanical work of muscle operating at a constant efficiency (Alexander, 1991).

#### *The cost of generating force and variation in cost coefficient*

Differences in the metabolic cost of transport across body weight in birds were closely correlated with differences in the time course of force development. For a given running speed, smaller bipeds take shorter steps, have shorter times of foot contact and presumably require faster, more metabolically expensive, muscle fibers to produce force quickly. For birds, metabolic rate is directly proportional to the rate of force development,  $1/t_c$ . However, compared with mammalian hoppers and quadrupedal runners, running birds use energy at nearly twice the rate for a given rate of force generation. The mean cost coefficient for birds was 1.7 times that of quadrupedal runners and hoppers, and the value for humans

was intermediate between those for other mammals and birds. Thus, our hypothesis that bipedal and quadrupedal runners have the same cost coefficient was refuted.

Previous measurements of cost coefficients suggest a pattern that is confirmed by the present observations for bipedal and quadrupedal runners: the rate of force development,  $1/t_c$ , accurately predicts changes in metabolic rate across speed, but the proportionality between  $1/t_c$  and weight-specific metabolic rate (the cost coefficient) can vary between species with dramatically different limb morphologies. The cost coefficient is constant across running speed for locomotor systems ranging from beetles, cockroaches and crickets (Full *et al.* 1990) to humans running on the level (Hoyt *et al.* 1994), uphill (Minetti *et al.* 1994) and on their hands (Glasheen and McMahon, 1995). It is also relatively constant as gravity or force is varied (Farley and McMahon, 1992; Taylor *et al.* 1980). However, the cost coefficient can differ between different modes of running or between animals with very different limbs, from  $0.95 \text{ JN}^{-1}$  for hand-running (Glasheen and McMahon, 1995) to  $0.316 \text{ JN}^{-1}$  for cricket locomotion and  $0.153 \text{ JN}^{-1}$  for beetle locomotion (Full *et al.* 1990).

What is the explanation for variation in the cost coefficient between animals with very different limb morphologies? During running, the rate of energy consumption will be proportional not only to the rate of energy use per gram of active muscle, but also to the total mass (or volume) of muscle active. As formulated, equation 1 assumes that the rate of energy use per gram of active muscle is proportional to  $1/t_c$  and that the mass of active muscle is a constant fraction of body mass, irrespective of running speed or animal size (Kram and Taylor, 1990). For mammalian quadrupeds, this assumption is supported by the allometry of muscle mechanical advantage and fascicle length. The scaling of muscle mechanical advantage indicates that the cross-sectional area of muscle that must be active on average to support the body (assuming equivalent active muscle stress) scales as  $W_b^{0.74}$  (Biewener, 1989). Muscle fascicle length scales as  $W_b^{0.26}$  (Alexander *et al.* 1981). Thus, active muscle volume, which is the product of muscle fascicle length and cross-sectional area, should be proportional to  $W_b^{1.0}$  (Biewener, 1990; Kram and Taylor, 1990). In addition, the observation that muscle mechanical advantage is constant across speed in running quadrupeds supports the assumption that the volume of active muscle required to support body weight is the same proportion of body weight at different running speeds (Biewener, 1990).

The greater cost coefficient of bipedal runners compared with that of quadrupeds may result from a greater volume of active muscle necessary to support body weight during running. Muscle mechanical advantage measurements comparable with those for quadrupeds are not available for bipedal runners. There is reason to expect that birds must use longer muscle fascicles to support their body: for a given body mass, running birds have legs that are almost twice as long as the legs of mammalian runners and hoppers (Fig. 3) (data from Alexander *et al.* 1979; Alexander, 1983). Kinematic studies suggest that differences in limb excursion angle explain little

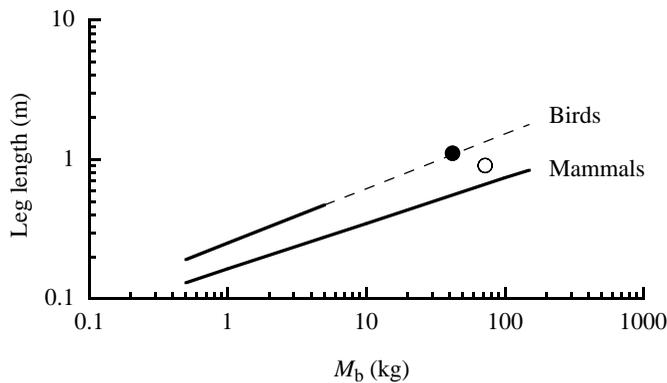


Fig. 3. Leg lengths ( $L_l$ ) of birds and mammals *versus* body mass ( $M_b$ ). Data for birds are calculated from the equation for galliformes given by Alexander (1983), extrapolated to the size of the largest ratites (dashed line). A data point for a single ostrich (filled circle) falls on this line (Alexander, 1983). The scaling of hind limb length (femur + tibia + metatarsus) for mammals is calculated from the allometric equations for a diverse selection of mammals given by Alexander *et al.* (1979), which exclude values for the metatarsals of artiodactyls. Human leg length (open circle) is the sum of tibia and femur lengths and is intermediate between the regression lines for birds and mammals. The equations are:  $L_l = 0.252M_b^{0.39}$  for birds (Alexander, 1983) and  $L_l = 0.164M_b^{0.327}$  for mammals (Alexander *et al.* 1979).

of the difference in step length; excursion angles are similar for quadrupeds and bipeds of the same body mass (comparing data from Gatesy and Biewener, 1991, for bipeds and Farley *et al.* 1993, for quadrupeds). Thus, birds have longer step lengths and times of foot contact primarily because they have longer legs. Human leg lengths are intermediate between those of quadrupeds and birds, as are their step lengths (Fig. 2). It is possible that the potential energetic benefits of longer legs and slower rates of force generation are offset by the higher cost of producing force with longer muscle fibers and increased active muscle volumes.

It has been proposed that differences in active muscle volume due to morphological differences in insect species with different locomotor specializations might explain the variation in their cost coefficients (Full *et al.* 1990). Other factors that may also contribute to differences in cost coefficient include differences in the relative shortening velocity ( $V/V_{\max}$ ) in active muscle or variations in the cost of swinging the limbs. However, the differences in limb morphology between mammalian quadrupeds, birds and humans are consistent with the suggestion that differences in active muscle volume explain some of the variation in energy cost. In the accompanying study (Roberts *et al.* 1998), measurements of muscle mechanical advantage and fascicle length in similarly sized bipedal and quadrupedal species, small dogs and wild turkeys, are used to compare the relative volume of muscle required for support during running.

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