

ENERGETICS AND MECHANICS OF TERRESTRIAL LOCOMOTION

I. METABOLIC ENERGY CONSUMPTION AS A FUNCTION OF SPEED AND BODY SIZE IN BIRDS AND MAMMALS

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(Received 28 May 1981)

SUMMARY

This series of four papers investigates the link between the energetics and the mechanics of terrestrial locomotion. Two experimental variables are used throughout the study: speed and body size. Mass-specific metabolic rates of running animals can be varied by about tenfold using either variable.

This first paper considers metabolic energy consumed during terrestrial locomotion. New data relating rate of oxygen consumption and speed are reported for: eight species of wild and domestic artiodactyls; seven species of carnivores; four species of primates; and one species of rodent. These are combined with previously published data to formulate a new allometric equation relating mass-specific rates of oxygen consumed (\dot{V}_{O_2}/M_b) during locomotion at a constant speed to speed and body mass (based on data from 62 avian and mammalian species):

$$\dot{V}_{O_2}/M_b = 0.533 M_b^{-0.316} \cdot v_g + 0.300 M_b^{-0.303}$$

where \dot{V}_{O_2}/M_b has the units $\text{ml O}_2 \text{ s}^{-1} \text{ kg}^{-1}$; M_b is in kg; and v_g is in m s^{-1} . This equation can be expressed in terms of mass-specific rates of energy consumption ($\dot{E}_{\text{metab}}/M_b$) using the energetic equivalent of $1 \text{ ml O}_2 = 20.1 \text{ J}$ because the contribution of anaerobic glycolysis was negligible:

$$\dot{E}_{\text{metab}}/M_b = 10.7 M_b^{-0.316} \cdot v_g + 6.03 M_b^{-0.303}$$

where $\dot{E}_{\text{metab}}/M_b$ has the units watts/kg.

This new relationship applies equally well to bipeds and quadrupeds and differs little from the allometric equation reported 12 years ago by Taylor, Schmid-Nielsen & Raab (1970). Ninety per cent of the values calculated from this general equation for the diverse assortment of avian and mammalian species included in this regression fall within 25% of the observed values at the middle of the speed range where measurements were made. This agreement is impressive when one considers that mass-specific rates of oxygen consumption differed by more than 1400% over this size range of animals.

INTRODUCTION

In this series of four papers we investigate the link between the energetics and the mechanics of terrestrial locomotion by measuring both the metabolic energy consumed and the mechanical energy changes that occur as birds and mammals move along the ground. We use two experimental variables throughout the study: speed and body size.

It is generally assumed that most of the energy consumed by the muscles of running animals is used in the transformation of chemical energy into mechanical energy (Hill, 1950; McMahon, 1975; Cavagna, Thys & Zamboni, 1976; Cavagna, Heglund & Taylor, 1977; Alexander, 1977; Alexander, 1980; Alexander, Jayes & Ker, 1980). A. V. Hill (1950) used dimensional analysis to predict how a variety of locomotory parameters, including rates at which muscles work and consume metabolic energy, change with body size. He limited his consideration to the peak performance of an animal moving at its top speed. He assumed that three properties were common to all vertebrate striated muscle, regardless of size: the maximal force developed per cross-sectional area; the maximum work performed by each gram of muscle during a contraction; and the maximum efficiency with which muscles convert chemical energy into mechanical work. His analysis predicted that large and small animals would reach the same top speed, and at that speed the muscles of small animals would be working and consuming energy at much higher rates. A simple way of summarizing Hill's logic is that each gram of muscle performs the same amount of work and consumes the same amount of energy during a step, but the small animals have to take many more steps to cover the same distance because of their shorter legs. Therefore when running at the same speed small animals should have higher stride frequencies and consume energy at higher rates.

Both of our experimental variables provide the potential for large changes in the rate of energy consumption. Aerobic metabolism of a running animal can be increased by about tenfold over resting rates. Also, mass-specific metabolic rates of animals running at the same speed vary by 10 to 15-fold over the size range of animals used in this study (Taylor, 1977). Tenfold differences in mass-specific metabolic rates should be large enough to overcome the uncertainties inherent in mechanical energy measurements and enable us to establish the link, if any, between metabolic and mechanical energy.

This first paper considers the metabolic energy consumed during terrestrial locomotion. More than 10 years ago, Taylor *et al.* (1970) developed a simple, empirically based equation that predicted the metabolic energy consumption by running mammals from two simple and easily measured parameters: speed and body mass. They found that metabolic cost of running increased linearly with speed over a wide range of speeds; and that this relationship between metabolism and speed varied as a regular function of body mass. Measurements were made on six species of mammals ranging from 21 g to 18 kg. The results of this study have been substantiated by many measurements on a variety of mammalian species (Taylor, 1977). Recently, Fedak & Seeherman (1979) have reported that the energy cost of locomotion is the same for bipeds and quadrupeds regardless of size. However, an important gap in the literature is a lack of measurements from large wild animals.

In this paper, we extend the data on energetic cost of locomotion to include: (1) a greater diversity of animals; (2) a greater range of running speeds from individual animals; and (3) a greater size range of animals. Then we calculate a revised allometric equation for energy cost of locomotion. We compare the metabolic rates calculated using the revised equation with the observed rates at the middle of the speed range obtained for each animal. Additionally, we formulate allometric equations for taxonomically related groups of animals (where the data base is sufficient) and compare these equations with the general equation for birds and mammals. This analysis should enable us to find out whether costs vary from group to group. The equations are used in the subsequent papers for comparison with similar equations describing mechanical energy changes within an animal.

MATERIALS AND METHODS

Experimental approach

Energy consumption as a function of treadmill speed

To obtain a reproducible relationship between rate of energy consumption and speed for animals running on a treadmill, we have: (1) used 'trained' animals; (2) made the measurements at each speed over a long enough interval to be certain that a steady-state oxygen consumption was achieved; and (3) ascertained that the energy was being derived primarily from aerobic metabolism over the entire range of speeds.

Training animals to run on the treadmill required a period of weeks to months, depending on the species and the individual animal. Two factors seemed important in the training. First, the animals were frightened when first introduced to the treadmill and did not run with normal gaits or stride frequencies at a given speed. Trained animals had the same gait and stride frequency for a given speed on the treadmill and on the ground. Second, the oxygen-consumption experiments required far greater endurance than would normally be required in nature. We have found that when a human or animal begins to tire, its oxygen consumption increases. As the training progressed, animals were able to run much longer without tiring, and oxygen consumption remained constant during the run. Rate of oxygen consumption (\dot{V}_{O_2}) was measured while the animals were being trained. We considered that the animals were trained once we were able to obtain reproducible values for \dot{V}_{O_2} at any speed.

To achieve a steady-state \dot{V}_{O_2} , we measured \dot{V}_{O_2} of the trained animals for 15–30 min at each speed. Frequently, \dot{V}_{O_2} was higher during the first 2–3 min of a run. We did not include these higher values, but used an average over the remainder of the run. We assumed these higher values were either the result of repayment of an anaerobic 'start-up cost' or due to an abnormal gait as the animal adjusted to the treadmill speed at the beginning of a run.

To ensure that all of the energy was being provided aerobically, R values ($\dot{V}_{CO_2}/\dot{V}_{O_2}$) were determined during the run, and blood lactate values were determined at the beginning and end of the runs at the highest speeds. We selected our top speeds so that R values were less than 1.0 and less than 1% of the total energy consumed could be attributed to anaerobic glycolysis on the basis of the energy derived from the lactic acid that accumulated during the run (Seeherman *et al.* 1981).

Energetic cost of locomotion as a function of body size

We used the equations relating energy consumption and speed for individual animals to develop allometric equations. Allometry is the study of how structures and/or functions vary with body mass. One calculates the power function which describes how a parameter, Y , changes with body mass, M_b :

$$Y = a.M_b^b \quad (1)$$

where the exponent b is called the scaling factor. It is convenient to use the logarithmic transformation

$$\log Y = \log a + b.\log M_b \quad (2)$$

in order to calculate regression coefficients and confidence intervals.

In order for allometry to yield meaningful results, both the range of body mass and the number of animals must be great enough to yield small 95 % confidence limits.

Animals

A review of existing data (Taylor, 1977) indicates that the principal gaps on energetic cost of locomotion are for large wild mammals. Therefore, we decided to take advantage of the diversity of large wild mammals living in Africa and carried out a major part of this work in Kenya. We obtained eight species of wild and domestic artiodactyls and three species of carnivores by capture or purchase. The wild artiodactyls in order of increasing body mass were: 2 suni (*Nesotragus moschatus*, av. body mass 3.50 kg); 2 dik-diks (*Madoqua kirkii*, av. body mass 4.35 kg); 2 wildebeest (*Connochaetes taurinus*, av. body mass 92.0 kg); 2 waterbucks (*Kobus defassa*, av. body mass 114 kg); and 2 elands (*Taurotragus oryx*, av. body mass 213 kg). The domestic artiodactyls in order of increasing body mass were: 2 African goats (*Capra hircus*, av. body mass 20.0 kg); 2 African sheep (*Ovis aries*, av. body mass 23.0 kg); 2 zebu cattle (*Bos indicus*, av. body mass 254 kg). We also obtained three species of the small carnivores. In order of increasing body mass they were: 3 dwarf mongooses (*Helogale pervula*, av. body mass 0.583 kg); 2 banded mongooses (*Mungos mungo*, av. body mass 1.15 kg); 2 genet cats (*Genetta tigrina*, av. body mass 1.46 kg). The bovids were housed in facilities provided by the East African Veterinary Research Organization at Muguga. Muguga is in the Kenya highlands and a little over 2000 m above sea level. The average barometric pressure at Muguga during these experiments was 787 mbar (590 Torr). The viverrids were housed at the University of Nairobi, in Nairobi. This is also in the Kenyan highlands and a little less than 2000 m above sea level. The average barometric pressure during these experiments was 835 mbar (626 Torr).

At our laboratory in the United States, we purchased four species of primates, one species of rodent, and four species of carnivores. The primates in order of increasing mass were: 3 tree shrews (*Tupaia glis*, av. body mass 0.124 kg); 3 bush babies (*Galago senegalensis*, av. body mass 0.240 kg); 3 stump-tailed macaques (*Macaca speciosa*, av. body mass 5.10 kg); and 2 hamadryas baboons (*Papio hamadryas*, av. body mass 8.50 kg). The rodent was the flying squirrel (3 individuals, *Glaucomys volans*, av. body mass 0.063 kg). The carnivores in order of increasing size were: 1 ferret (*Mustela nigripes*, av. body mass 0.542 kg); 2 domestic cats (*Felis catus*, av. body mass 3.90 kg).

2 domestic dogs (*Canis familiaris*, av. body mass 4.36 kg); and 2 wolves (*Canis lupus*, av. body mass 23.1 kg).

Methods

Rates of oxygen consumption and carbon dioxide production were measured simultaneously using an open-circuit system. The system has been described and diagrammed schematically in Seeherman *et al.* (1981). The mongooses, genet cats, tree shrews, bush babies, flying squirrel and domestic cats ran in plexiglass (perspex) boxes that slid on the surface of the tread (analogous to a mask enclosing the entire animal). The other animals wore lightweight masks for measurements of gas exchange. Air was metered through the boxes or masks at rates between 0.10 and 1.00 l s⁻¹ (STP) for the small animals and 1 and 40 l s⁻¹ (STP) for the larger animals. \dot{V}_{O_2} was calculated using eq. 3:

$$\dot{V}_{O_2} = \frac{\dot{V}_{\text{mask}}(F_I - F_E)}{0.9581} \quad (3)$$

(modified from Tucker (1968)), where \dot{V}_{O_2} is the oxygen consumption in l s⁻¹, \dot{V}_{mask} is the air flow rate through the mask or box in l s⁻¹, F_I is the mole fraction of oxygen entering the box or mask and F_E is the mole fraction leaving the box or mask, and 0.9581 is a constant assuming the R value is 0.8, F_I is 0.2094 and F_{H_2O} is zero. R values ($\dot{V}_{CO_2}/\dot{V}_{O_2}$) were measured in a number of experiments. They fell between 0.7 and 0.9 over the speed ranges for which data are reported.

Flow meters were calibrated daily by 'replacing the animal' in the box or mask with a tube into which N₂ was metered with a precision flowmeter at a known rate, \dot{V}_{N_2} . \dot{V}_{N_2} was selected so that it gave a change in O₂ concentration that was similar to that caused by the \dot{V}_{O_2} of the animal. The flow leaving the mask, \dot{V}_{mask} , was the same during the calibration and during the experiment. The N₂ flowing into the mask decreased the amount of room air that was being drawn into the mask. The room air had a fractional concentration of O₂ of 0.2094, therefore each litre of N₂ displaced 209.4 ml of O₂. The fractional concentration of oxygen leaving the mask when N₂ was added (F_E) equalled:

$$F_E = \frac{0.2094 (\dot{V}_{\text{mask}} - \dot{V}_{N_2})}{\dot{V}_{\text{mask}}} \quad (4)$$

Solving this equation for \dot{V}_{mask} yields:

$$\dot{V}_{\text{mask}} = \frac{0.2094 \dot{V}_{N_2}}{0.2094 - F_E} \quad (5)$$

The accuracy of the entire system was found to be better than $\pm 3\%$.

The face mask system gave 95% response in 1 min for a step reduction in the oxygen content of the air from 20.94 to 19.94%. The enclosed treadmill system gave a 95% time response in less than 2 min for the same step change in the oxygen content of the air.

Systems which utilize loose-fitting face masks require large flow rates in order to ensure that all expired air is collected. Increasing the flow should decrease the magnitude of any leak, and decreasing the flow should increase the magnitude of any leak. We found no difference in the rate of oxygen consumption when the flow rate was

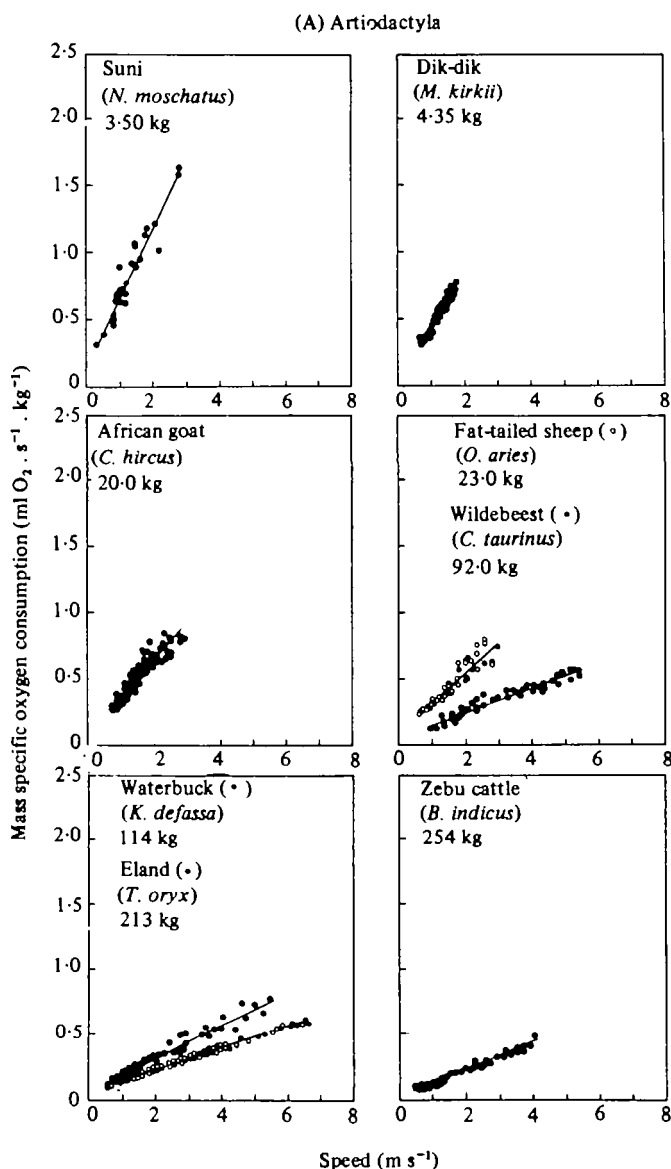


Fig. 1. For legend see page 8.

changed by 25% and were therefore confident that we were recovering all of the expired air.

Net rates of energy derived from anaerobic glycolysis (of the whole animal) were calculated from rates of change in lactate concentration in the blood during the runs by assuming a P/lactate ratio of 1.5 (Seeherman *et al.* 1981). Blood samples were obtained by cardiac puncture in the small animals and through catheters that had been chronically implanted in the external jugular vein in the larger animals. The lactate concentrations of blood samples were analysed using Boehringer Mannheim Lactate

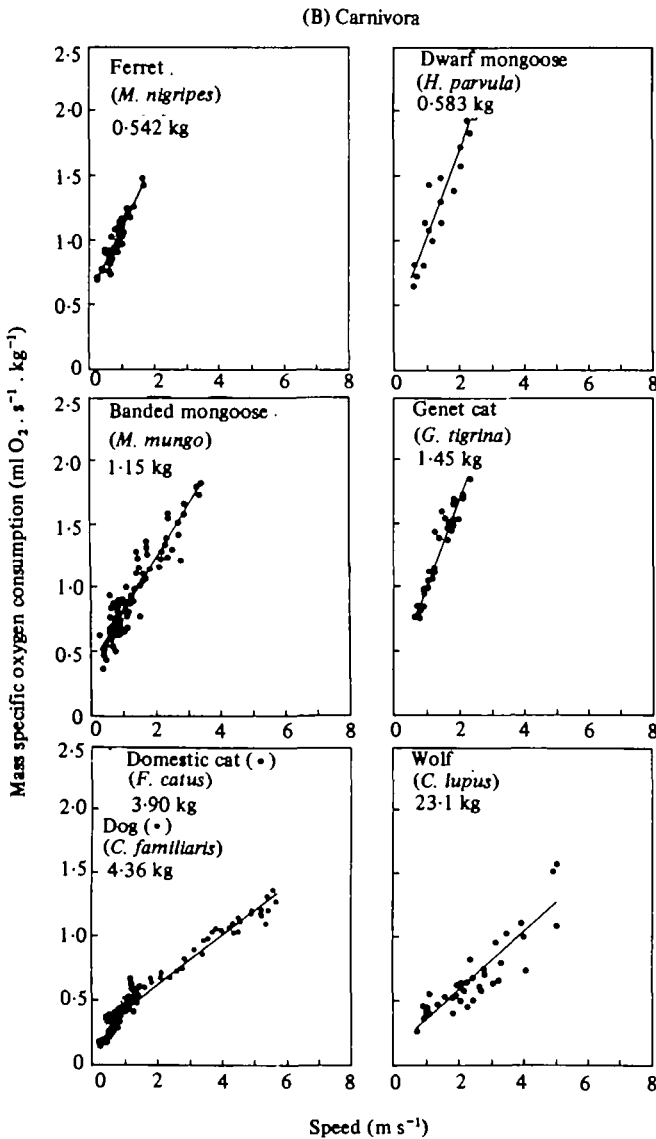


Fig. 1. For legend see page 8.

Test Combinations and a Beckman u.v. Spectrophotometer (model 24). Fifty μl samples of blood were used for the analysis with small animals and $\frac{1}{2}$ ml samples for the larger animals.

RESULTS

Oxygen consumption as a function of speed

Steady-state oxygen consumption of the 20 species investigated in this study increased linearly with tread speed over a wide range of speeds (Fig. 1 A–C). We found it convenient to use mass-specific oxygen consumption (rate of oxygen consumption

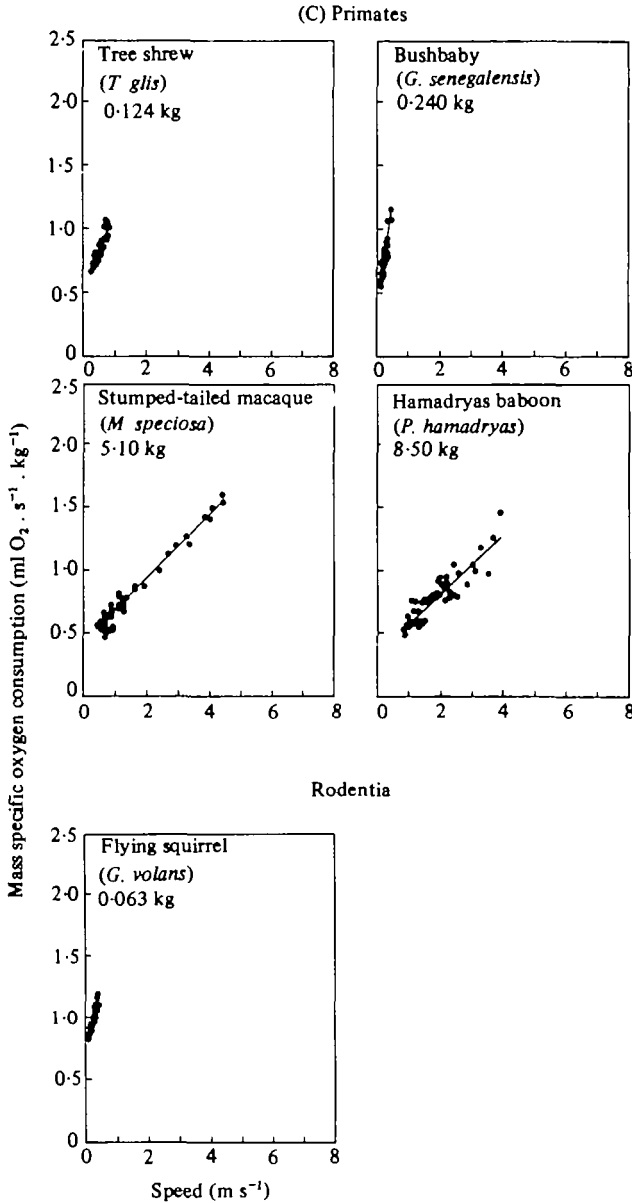


Fig. 1. Mass-specific oxygen consumption (\dot{V}_{O_2}/M_b) plotted as a function of speed for 8 species of artiodactyls (Fig. 1 A), 7 species of carnivores (Fig. 1 B), 4 species of primates and 1 species of rodent (Fig. 1 C). \dot{V}_{O_2}/M_b increased nearly linearly with speed. The contribution to energy consumption by anaerobic glycolysis was negligible over the speed ranges reported in this figure. The least-squares regression of the functions relating \dot{V}_{O_2}/M_b and speed are given for each of these species in Table 1.

divided by body mass) for comparing animals of different size because this enabled us to plot the data for the entire size range on the same co-ordinates.

The linear increase in oxygen consumption with speed makes it possible to express the relationship between oxygen consumption and speed for each animal by a linear equation of the form

$$\dot{V}_{O_2}/M_b = \text{slope} \cdot \text{speed} + Y \text{ intercept.} \quad (6)$$

In Table 1 we have included the values for the Y intercept and slope (calculated using the method of least squares) and the coefficient of determination for the linear regression (r^2). Table 1 groups the animals taxonomically, and includes data from 42 species taken from the literature in addition to the 20 species studied here.

Oxygen consumption accounted for the major part of the metabolic energy consumption over the range of speeds used in this study. At the maximum speeds reported in Table 1, R values were less than 1.0 and the rate of accumulation of lactate during the run accounted for less than 1% of the energy available from the oxygen consumption.

Energetic cost of locomotion as a function of body size

There are two components to the energetic cost of locomotion (measured as \dot{V}_{O_2}/M_b): an extrapolated zero speed cost (the Y intercept) and an incremental cost (the slope) (see equation 6). Both are constant for an individual animal because the relationship between energy consumption and speed is linear. However, both change with body size. Fig. 1(A–C) are organized in terms of increasing body mass for primates, carnivores, and artiodactyls. It is obvious from looking at these graphs that both the Y intercept and the slope decrease with increasing body size. This decrease is very general, being found among all the taxonomic groups of mammals and birds (Table 1).

Fig. 2 plots the Y intercept (top) and the slope (bottom) of the equations relating \dot{V}_{O_2}/M_b and speed against body mass on logarithmic co-ordinates. The solid points represent new data and the open points previously published data. Both visual comparison of the open and closed points, and linear regression analysis show there is no significant difference between the new data presented in this paper and the data in the literature. However, the new data reduces the 95% confidence intervals for the constants and the scaling factors. Therefore, we will limit our discussion of the allometric equations to those for the combined data.

The allometric equation for the Y intercept for all birds and mammals (except lion, red kangaroo and waddlers) was found to be

$$Y \text{ intercept} = 0.300 M_b^{-0.303} \quad (7)$$

where Y intercept has the units $\text{ml O}_2 \text{ s}^{-1} \text{ kg}^{-1}$ and M_b is in kg. The 95% confidence intervals for both the constant and the scaling factor were small (0.268–0.335 for the constant and -0.261 to -0.346 for the scaling factor).

The allometric equation for the slope for all birds and mammals combined (except lion, red kangaroo, and waddlers) was found to be

$$\text{slope} = 0.533 M_b^{-0.316} \quad (8)$$

where the slope has the units $\text{ml O}_2 \text{ m}^{-1} \text{ kg}^{-1}$ and M_b is in kg. The 95% confidence intervals for both the constant and the scaling factor were small (0.502–0.566 for the constant and -0.293 to -0.339 for the scaling factor).

The lion, red kangaroo and the waddlers (ducks, geese and penguins) were not included in our allometric equations because either their energy consumption did not increase linearly with speed over a wide range of speeds (lion and big red kangaroo: Chassin *et al.* 1976; Dawson & Taylor, 1973) or there was a large additional component to the energetics that was unique (waddlers: Pinshow, Fedak & Schmidt-Nielsen, 1977).

Table 1. *Energetic cost of locomotion for mammals and birds*

Data from the literature are combined with new data for 20 species reported in this paper to calculate a new allometric equation of the form $\dot{V}O_2/M_b = Y \text{ intercept} + \text{slope} \cdot v_o$, (where $\dot{V}O_2$ is rate of oxygen consumption in ml O_2 s⁻¹, M_b is body mass in kg, and v_o is speed in m s⁻¹). The percentage difference (% diff) between observed rates of oxygen consumption and the rate calculated using this new equation (equation 9 in text) are given for a speed at the middle of the speed range over which measurements were made.

CLASS ORDER Family Genus species (Common name)	For equation: $\dot{V}O_2/M_b = Y \text{ intercept} + \text{slope} \cdot v_o$				Diff. (%)	Reference
	M_b (kg)	Y intercept, ml O_2 /s kg	Slope, ml O_2 /m kg	r^2		
MAMMALIA						
MONOTREMATA						
Tachyglossidae						
<i>Tachyglossus aculeatus</i> (Echidna)	5.04 1.69 3.53	0.097 0.086 0.069	0.30 0.45 0.37	0.48 0.77 0.92	-37.3 -66.6 -66.4	Crompton <i>et al.</i> (1978) Edmeades & Baudinette (1975) Edmeades & Baudinette (1975)
MARSUPIALIA						
Didelphidae						
<i>Monodelphis domestica</i> (Short-tailed opossum)	0.068	0.44	1.69	0.72	-4.08	Oron <i>et al.</i> (1981)
<i>Didelphis virginianus</i> (American opossum)	2.70	0.19	0.36	0.96	-13.2	Crompton <i>et al.</i> (1978)
Dasyuridae						
<i>Sminthopsis crassicaudata</i> (Narrow-footed mouse)	0.015	1.90	1.62	0.49	32.2	Baudinette <i>et al.</i> (1976a)
<i>Antechinus spenceri</i> (Hopping mouse)	0.030	1.19	1.47	0.81	19.6	Baudinette <i>et al.</i> (1976a)
<i>Antechinus flavipes</i> (Broad-footed mouse)	0.034 0.048	1.56 1.69	1.77 1.34	0.42 0.40	51.3 63.2	Baudinette <i>et al.</i> (1976a) Baudinette <i>et al.</i> (1976a)
<i>Dasyuroides byrnei</i> (Crested-tailed rat)	0.12	0.79	0.84	0.71	-23.8	Baudinette <i>et al.</i> (1976a)
<i>Dasyurus viverrinus</i> (Native cat)	1.12	0.68	0.43	0.62	32.9	Baudinette <i>et al.</i> (1976a)
Phalangeridae						
<i>Trichosurus vulpecula</i> (Brush-tailed possum)	1.95	0.36	0.44	0.72	18.8	Baudinette <i>et al.</i> (1978)
Macropodidae						
<i>Bettongia penicillata</i> (Rat kangaroo)	1.10	0.48	0.39	0.88	-10.6	Thompson <i>et al.</i> (1980)
<i>Setonix brachyurus</i> (Quokka)	2.95	0.61	0.38	—	53.1	Baudinette (1977)
<i>Macropus rufus</i> (Red kangaroo)	23.0	1.14	-0.026	-0.40	5.6	Dawson & Taylor (1973)

INSECTIVORA						
Tenrecidae						
<i>Setifer setosus</i> (Setifer)	0.12	0.10	0.68	0.88	-69.1	Crompton <i>et al.</i> (1978)
<i>Tenrec ecaudatus</i> (Tenrec)	0.68	0.11	0.58	0.86	-37.3	Crompton <i>et al.</i> (1978)
Erinaceidae						
<i>Erinaceus europaeus</i> (Hedgehog)	1.05	0.13	0.46	0.83	-36.6	Crompton <i>et al.</i> (1978)
Macroscelididae						
<i>Elephantulus rufescens</i> (Elephant shrew)	0.060	0.54	1.65	0.79	-0.83	Oron <i>et al.</i> (1981)
Soricidae						
<i>Suncus murinus</i> (Musk shrew)	0.036	0.95	1.62	0.69	10.2	Oron <i>et al.</i> (1981)
PRIMATES						
Tupaiaidae						
<i>Tupaia glis</i> (Tree shrew)	0.12	0.45	0.69	0.87	-27.3	New data
Lorisidae						
<i>Galago senegalensis</i> (Bush baby)	0.24	0.48	1.47	0.89	25.3	New data
<i>Nycticebus coucang</i> (Slow loris)	1.55 0.88	0.17 0.28	0.48 0.68	0.71 0.85	-24.9 2.04	Parsons & Taylor (1977) Parsons & Taylor (1977)
Cebidae						
<i>Cebus albifrons</i> (Capuchin)	3.34	0.42	0.28	0.81	10.6	Taylor & Rowntree (1973)
<i>Ateles geoffroy</i> (Spider monkey)	3.80	0.23	0.37	0.79	10.3	Parsons & Taylor (1977)
Circopithecidae						
<i>Macaca speciosa</i> (Stump-tailed macaque)	5.10	0.43	0.25	0.97	8.03	New data
<i>Papio hamadryas</i> (Hamadryas baboon)	8.50	0.36	0.24	0.79	14.5	New data
<i>Erythrocebus patas</i> (Patas monkey)	3.80	0.35	0.25	0.59	-10.9	Mahoney (1980)
Pongidae						
<i>Chimpanzee troglodytes</i> (Chimpanzee)	17.5	0.22	0.25	0.92	35.6	Taylor & Rowntree (1973)
Hominidae						
<i>Homo sapiens</i> (Human)	68.8	0.12	0.20	—	43.4	Margaria <i>et al.</i> (1963)

CLASS ORDER Family Genus species (Common name)	For equation: $\dot{V}_{O_2}/M_b = Y \text{ intercept} + \text{slope} \cdot v_g$				r ²	Diff. (%)	Reference
	M_b (kg)	Y intercept, ml O ₂ /s kg	Slope, ml O ₂ /m kg				
EDENTATA Dasypodidae <i>Dasysus novemcinctus</i> (Armadillo)	4.07	0.18	0.25		0.62	-14.0	Oron <i>et al.</i> (1981)
RODENTIA Sciuridae <i>Glaucomys volans</i> (Flying squirrel) <i>Tamiasciurus hudsonicus</i> (Red squirrel) <i>Tamias striatus</i> (Chipmunk)	0.063 0.25 0.092 0.075	0.65 0.64 0.64 0.53	1.20 0.78 0.78 1.58		0.97 0.48 0.93 —	-6.69 20.5 -22.3 3.60	New data Wunder & Morrison (1974) Seeherman <i>et al.</i> (1981) Wunder (1970)
<i>Spermophilus tridecemlineatus</i> (13-lined ground squirrel) <i>Spermophilus tereticaudus</i> (Round-tailed ground squirrel) <i>Ammospermophilus harrisi</i> (Antelope ground squirrel)	0.21 0.24 0.086	0.56 0.35 0.92	0.64 0.66 1.42		0.91 — —	-15.3 -23.5 34.0	Fedak & Seeherman (1979) Taylor <i>et al.</i> (1970) Yousef <i>et al.</i> (1973)
Heteromyidae <i>Dipodomys merriami</i> (Merriam's kangaroo rat)	0.041 0.032 0.031	0.49 1.02 0.94	2.01 1.10 5.30		— 0.50 —	-16.6 -14.3 81.4	Taylor <i>et al.</i> (1970) Thompson <i>et al.</i> (1980) Yousef <i>et al.</i> (1970)
<i>Dipodomys spectabilis</i> (Kangaroo rat) <i>Dipodomys deserti</i> (Desert kangaroo rat)	0.100 0.104	0.50 0.90	1.13 0.66		— 0.85	-10.3 -8.83	Taylor <i>et al.</i> (1970) Thompson <i>et al.</i> (1980)
Pedetidae <i>Pedetes capensis</i> (Spring hare)	3.00	0.57	0.34		0.67	26.9	Thompson <i>et al.</i> (1980)
Caecetidae <i>Baiomys taylori</i> (Pygmy mouse)	0.0072	0.93	2.25		0.97	-20.0	Seeherman <i>et al.</i> (1981)
Muridae <i>Mus musculus</i> (White mouse)	0.021 0.030 0.033	0.93 0.71 1.02	2.83 2.07 1.64		— 0.81 0.66	10.2 -2.09 12.5	Taylor <i>et al.</i> (1970) Taylor <i>et al.</i> (1972) Oron <i>et al.</i> (1981)

<i>Rattus norvegicus</i> (White rat)	0.38 0.21	0.41 0.55	1.09 0.97	— 0.95	19.5 10.8	Taylor <i>et al.</i> (1970) Seeherman <i>et al.</i> (1981)
<i>Notomys alexis</i> (Australian hopping mouse)	0.027	0.89	1.96	—	7.13	Baudinette <i>et al.</i> (1976b)
<i>Notomys cervinus</i> (Fawn hopping mouse)	0.037	1.09	0.69	0.95	—25.4	Dawson (1976)
CARNIVORA						
Canidae						
<i>Canis familiaris</i> (Domestic dog)	2.60 4.36 18.0 21.0 24.0	0.21 0.24 0.18 0.089 0.11	0.34 0.19 0.17 0.22 0.19	— 0.99 — 0.95 —	—12.5 —33.2 —2.87 2.77 —2.99	Taylor <i>et al.</i> (1970) New data Taylor <i>et al.</i> (1970) Seeherman, H. J. (pers. comm.) Cerretelli <i>et al.</i> (1964)
<i>Lycan pictus</i> (African hunting dog)	8.75	0.19	0.33	0.98	22.8	Taylor <i>et al.</i> (1971b)
<i>Canis lupus</i> (Wolf)	23.1	0.13	0.23	0.80	15.9	New data
Mustelidae						
<i>Mustela nigripes</i> (Ferret)	0.54	0.56	0.52	0.75	7.85	New data
<i>Martes pennanti</i> (Fisher)	3.25 5.16	0.21 0.28	0.40 0.31	0.96 0.92	6.01 10.8	Powell, R. (pers. comm.) Powell, R. (pers. comm.)
Viverridae						
<i>Helogale parvula</i> (Dwarf mongoose)	0.58	0.36	0.67	0.80	4.28	New data
<i>Mungos mungo</i> (Banded mongoose)	1.15	0.41	0.42	0.89	—4.51	New data
<i>Genetta tigrina</i> (Genet cat)	1.46	0.38	0.64	0.86	35.9	New data
Felidae						
<i>Felis catus</i> (Domestic cat)	3.90	0.043	0.40	0.88	—22.6	New data
<i>Leo leo</i> (Lion)*	27.5 53.5	0.15 0.00	0.30 0.36	0.92 0.96	54.4 69.0	Seeherman <i>et al.</i> (1981) Chassin <i>et al.</i> (1976)
<i>Acinonyx jubatus</i> (Cheetah)	39.0	0.20	0.14	0.93	2.67	Taylor <i>et al.</i> (1974)

CLASS ORDER Family	Genus species (Common name)	For equation: $\dot{V}_{O_2}/M_b = Y\text{-intercept} + \text{slope} \cdot v_o$				r ²	Diff. (%)	Reference
		M _b (kg)	Y intercept, ml O ₂ /s kg	Slope, ml O ₂ /m kg				
PERISSODACTYLA								
Equidae								
	<i>Equus caballus</i> (Horse)	107	0.039	0.15		0.96	15.3	Fedak & Secherman (1979)
ARTIODACTYLA								
Suidae								
	<i>Sus scrofa</i> (Miniature pig)	19.0	0.13	0.29		0.94	32.3	Seeherman <i>et al.</i> (1981)
Bovidae								
	<i>Nesotragus moschatus</i> (Sumi)	3.50	0.17	0.52		0.93	26.8	New data
	<i>Madaqua kirkii</i> (Dik-dik)	4.35	0.064	0.40		0.91	— 9.58	New data
	<i>Gazella gazella</i> (Desert gazelle)	23.2	0.15	0.16		0.94	— 12.0	Taylor <i>et al.</i> (1974)
	<i>Connochaetes taurinus</i> (Wildebeest)	92.0	0.069	0.092		0.90	— 24.6	New data
	<i>Kobus defassa</i> (Waterbuck)	114	0.046	0.13		0.92	2.37	New data
	<i>Taurotragus oryx</i> (Eland)	213	0.072	0.083		0.96	— 9.12	New data
	<i>Capra hircus</i> (African domestic goat) (U.S. domestic goat)	20.0 28.0	0.12 0.089	0.26 0.18		0.82 0.95	19.6 — 7.25	New data Taylor <i>et al.</i> (1974)
	<i>Ovis aries</i> (Fat-tailed sheep)	23.0	0.10	0.23		0.82	8.34	New data
	<i>Bos indicus</i> (Zebu cattle)	254	0.026	0.096		0.94	— 7.58	New data
AVES								
STRUTHIONIFORMES								
Struthionidae								
	<i>Struthio</i> (Ostrich)	103	0.09	0.11		0.93	— 5.18	Fedak & Secherman (1979)
RHEIFORMES								
Rheidae								
	<i>Rhea americana</i> (Rhea)	22.0	0.11	0.34		—	51.8	Taylor <i>et al.</i> (1971a)

ANSERIFORMES					
Anatidae					
<i>Anser anser</i> (Greylag goose)*	3.81	0.14	0.72	—	46.8 Fedak <i>et al.</i> (1974)
TINAMIFORMES					
Tinamidae					
<i>Nothoprocta pentlandi</i> (Tinamou)	0.31	0.19	1.20	—	— Fedak <i>et al.</i> (1974)
SPHENISCIFORMES					
Spheniidae					
<i>Aptenodytes forsteri</i> (Emperor penguin)*	20.8	0.13	0.43	0.66	52.3 Pinshow <i>et al.</i> (1977)
<i>Pygoscelis adeliae</i> (Adelie penguin)*	3.89	0.26	0.76	0.88	77.4 Pinshow <i>et al.</i> (1977)
<i>Eudyptula albosignata</i> (White-flipped penguin)*	1.15	0.34	1.11	0.90	61.3 Pinshow <i>et al.</i> (1977)
CALLIFORMES					
Phasianidae					
<i>Excalfactoria chinensis</i> (Painted quail)	0.042	0.64	1.20	—	— Fedak <i>et al.</i> (1974)
<i>Colinus virginianus</i> (Bobwhite quail)	0.19	0.39	0.90	—	— Fedak <i>et al.</i> (1974)
<i>Alectoris graeca</i> (Chukar partridge)	0.49	0.42	0.69	—	6.25 Fedak <i>et al.</i> (1974)
Numididae					
<i>Numida meleagris</i> (Guinea fowl)	1.21	0.39	0.47	—	7.18 Fedak <i>et al.</i> (1974)
Meleagrididae					
<i>Meleagris gallopavo</i> (Turkey)	4.31	0.17	0.41	—	12.7 Fedak <i>et al.</i> (1974)
CHARADRIIFORMES					
Charadriidae					
<i>Charadrius wilsonia</i> (Wilson's plover)	0.018	0.67	1.85	—	— Fedak & Seeherman (1979)
CUCULIFORMES					
Cuculidae					
<i>Geococcyx californianus</i> (Road runner)	0.29	0.61	0.59	0.73	4.06 Fedak & Seeherman (1979)

* Data excluded from allometric equations, see text.

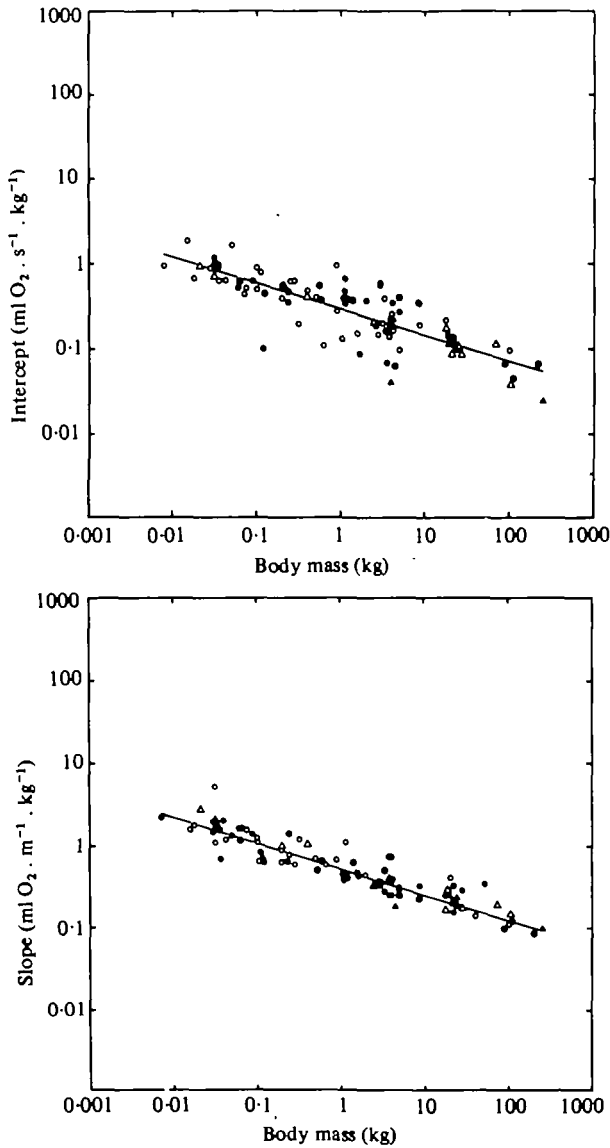


Fig. 2. The two components of energetic cost of locomotion are plotted as a function of body mass on logarithmic co-ordinates: Y intercept (top) and slopes (bottom) of the relationship:

$$\dot{V}_{O_2}/M_b = Y \text{ intercept} + \text{slope} \cdot v_r$$

(where \dot{V}_{O_2}/M_b is the mass-specific oxygen consumption of an animal running at speed v_r). The Y intercept is proportional to the -0.303 power of body mass and the slope proportional to -0.316 power. See equations (7) and (8) of the text for the allometric equations representing Y intercept and slope calculated by linear regression analysis from the data presented here. Open symbols represent data from the literature; closed symbols represent new data from this paper; circles represent data from wild species; and triangles represent laboratory/domestic species.

DISCUSSION

Oxygen consumption as a function of speed

The nearly linear increase in oxygen consumption as a function of speed observed in this study is in agreement with the findings of previous studies (Taylor *et al.* 1970; Taylor, 1977; Taylor, 1980). One of the reasons for initiating this series of studies was to find out whether the linear increase could be explained by the mechanical energy changes that occur within an animal. We will therefore defer the discussion of the linear increase to the subsequent papers where both metabolic and mechanical energies can be compared.

Energetics of locomotion as a function of size

The allometric functions for the Y intercepts (equation 7) and the slope (equation 8) can be combined into a single equation (see equation 6) for predicting \dot{V}_{O_2}/M_b from speed and body mass:

$$\dot{V}_{O_2}/M_b = 0.533 M_b^{-0.316} \cdot v_o + 0.300 M_b^{-0.303} \quad (9)$$

where \dot{V}_{O_2}/M_b has the units $\text{ml O}_2 \text{ s}^{-1} \text{ kg}^{-1}$, M_b is in kg, and v_o is speed in m s^{-1} .

This equation is very general. Table 2 compares the constants and scaling factors for both terms of the general equation for birds and mammals with various groupings of species: all mammals, all birds, all wild animals, all domestic animals, Marsupials, Insectivores, Artiodactyla, Carnivora, Rodentia, and Primates. None of the groups differed from the general equation at the 95 % level of confidence. The major difference is wider confidence intervals of the smaller groups because both the number of species and range in body mass are smaller.

How well does the general equation estimate the oxygen consumption observed for individual animals? For each of the species included in the regression analysis, we present the percentage deviation between the values calculated from the general equation and the observed value for the middle of the speed range for which oxygen consumption data were available. At the mid-speed, 90 % of the calculations for species included in the regression fall within 25 % of the observed value. This agreement is impressive when one considers that mass-specific oxygen consumption changes by more than 1400 % over this size range of animals.

It is convenient to express eq. 9 in terms of mass-specific rates of energy consumption ($\dot{E}_{\text{metab}}/M_b$) for comparison with rates of mechanical energy changes in the subsequent papers of this series. This conversion can be made using the energetic equivalent of 1 ml O_2 equals 20.1 J, because the contribution of anaerobic glycolysis was shown to be negligible:

$$\dot{E}_{\text{metab}}/M_b = 10.7 M_b^{-0.316} \cdot v_o + 6.03 M_b^{-0.303} \quad (10)$$

where $\dot{E}_{\text{metab}}/M_b$ has the units watts kg^{-1} .

Energy consumption per step at equivalent speeds

A. V. Hill's dimensional arguments outlined in the introduction of this paper predicted that, in mass-specific terms, muscles of small animals would be working and consuming energy at much higher rates than those of large animals.

Table 2. The coefficients, exponents and 95% confidence limits (in parentheses) of the functions relating $\dot{V}_{O_2}/M_b = aM_b^b + cM_b^d$, speed; where \dot{V}_{O_2}/M_b is in $ml\ O_2\ s^{-1}\ kg^{-1}$, M_b is in kg and speed is in $m\ s^{-1}$; r^2 is the correlation coefficient between either the log of the intercept (Fig. 2, top) or the log of the slope (Fig. 2, bottom) and $\log M_b$ for each group.

Animal group	Coefficient a	Exponent b	r^2	Coefficient c	Exponent d	r^2
All animals except waddlers, red kangaroos and lions	0.300 (0.268, 0.335)	-0.303 (-0.261, -0.346)	0.84	0.533 (0.502, 0.566)	-0.316 (-0.293, -0.339)	0.95
All mammals except lions and kangaroos	0.303 (0.268, 0.343)	-0.311 (-0.264, -0.357)	0.83	0.530 (0.496, 0.565)	-0.319 (-0.295, -0.344)	0.95
All birds except waddlers	0.279 (0.217, 0.358)	-0.246 (-0.149, -0.344)	0.90	0.566 (0.466, 0.688)	-0.285 (-0.208, -0.361)	0.95
All wild animals except waddlers, red kangaroos and lions	0.313 (0.275, 0.357)	-0.281 (-0.229, -0.333)	0.79	0.520 (0.485, 0.557)	-0.317 (-0.289, -0.345)	0.94
All domestic animals	0.272 (0.210, 0.352)	-0.336 (-0.255, -0.418)	0.91	0.603 (0.524, 0.694)	-0.333 (-0.289, -0.378)	0.97
Marsupials except red kangaroo	0.477 (0.323, 0.703)	-0.285 (-0.125, -0.445)	0.80	0.494 (0.423, 0.576)	-0.328 (-0.264, -0.391)	0.97
Insectivores	0.092 (0.017, 0.500)	-0.550 (-0.228, -1.33)	0.79	0.458 (0.244, 0.859)	-0.370 (-0.080, -0.660)	0.92
Artiodactyla	0.210 (0.093, 0.475)	-0.265 (-0.047, -0.483)	0.68	0.787 (0.552, 0.891)	-0.411 (-0.317, -0.506)	0.96
Carnivora	0.322 (0.202, 0.513)	-0.289 (-0.076, -0.521)	0.57	0.509 (0.417, 0.622)	-0.311 (-0.216, -0.407)	0.89
Rodentia	0.463 (0.352, 0.609)	-0.157 (-0.061, -0.254)	0.62	0.483 (0.313, 0.746)	-0.364 (-0.211, -0.517)	0.75
Primates	0.345 (0.256, 0.465)	-0.157 (-0.009, -0.305)	0.63	0.523 (0.405, 0.674)	-0.298 (-0.171, -0.424)	0.87

Table 3. *Energy consumed during a stride by each gram of body mass for quadrupeds of different size moving at a 'physiologically equivalent speed' (trot-gallop transition speed)*

Speed and stride frequency at the trot-gallop transition are calculated from the allometric equations given by Heglund, Taylor & McMahon (1974), and the rate of energy consumption at this speed was calculated using equation 10 in the text.

Body mass (kg)	Speed at trot- gallop transition (m s ⁻¹)	Stride frequency at trot-gallop transition (strides s ⁻¹)	Metab. energy consumed per kg per stride (J stride ⁻¹ kg ⁻¹)
0.01	0.51	8.54	5.59
1.0	1.53	4.48	5.00
100	4.61	2.35	5.53

The findings of this paper are in general agreement with Hill's predictions for how rates of energy consumption should change with size. Hill's analysis, however, was limited to top speed, which he used as an equivalent speed for comparing animals of different body size. Measurements of energy consumption at top speed are not available, but comparisons can be made for quadrupeds at the speed where they change gaits from a trot to a gallop. Heglund, Taylor & McMahon (1974) have proposed that this is a 'physiologically similar speed' for quadrupeds of different size. Both the speed at which quadrupeds change from a trot to a gallop, and the stride frequency at this speed, change in a regular manner with body mass and can be estimated using allometric equations given by Heglund *et al.* (1974). Table 3 gives the trot-gallop transition speed and the stride frequency at this speed calculated for a 10 g, 1 kg, and 100 kg animal using these equations. The amount of energy consumed at this speed was calculated using eq. 10, and cost per stride was obtained by dividing the rate of energy consumption by stride frequency. This analysis reveals that the amount of metabolic energy consumed per stride by each gram of muscle at this speed remains almost constant (5 J stride⁻¹ kg⁻¹) over a change in M_b of 4 orders of magnitude.

The finding that energy cost per stride by each gram of muscle at an equivalent speed is almost the same for large and small animals seems to indicate that Hill's logic is correct, i.e. the work performed per stride and the efficiency with which muscles perform this work are constant. We will return to this matter in the fourth and final paper of this series where it is possible to compare these assumptions with measurements of the rate at which mechanical work is performed by an animal's muscles as it runs at a constant average speed.

The essential part of this work depended on a field study on wild animals in Kenya. It would not have been possible without the support of various Kenyan authorities. We thank particularly the Kenyan Minister of Wildlife and Tourism for providing permits and for helping to obtain animals; Dr Walter Masiga, Director, East African Veterinary Research Organization, Muguga, Kenya, for making the excellent large animal facilities of his organization available to us for these studies. This study would not have been feasible without the most generous support of the School of Veterinary Medicine at the University of Nairobi; we thank the authorities of the University of Nairobi for all the encouragement and material help received during planning and execution of the study.

We thank Garth Ballantyne, Russ Baudinette, Daphne Cooke, Vaughn Langman, Timothy Lay, Victoria Rowntree, Emmett Schmidt, Howard Seeherman and Tom Shatten who all helped acquire the new data reported here.

We also gratefully acknowledge the excellent technical assistance received from Ms Gayle Kaufman and Ms Margaret McCutchin.

We finally acknowledge the financial support received for this study through the following grants: U.S. National Science Foundation (PCM75-22684 & PCM78-23319 to C. R. Taylor); National Institutes of Health (AM 18140 & AM 18123 to C. R. Taylor); National Geographic Society grant to C. R. Taylor; Guggenheim Foundation grant to C. R. Taylor; Nuffield Foundation grant to G. M. O. Maloij; Wellcome Trust grant to G. M. O. Maloij.

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