# 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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### 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):

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

where $\dot{V}_{O_2}/M_b$ has the units ml $O_2$ s$^{-1}$ 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 ($\dot{E}_{metab}/M_b$) using the energetic equivalent of 1 ml $O_2$ = 20·1 J because the contribution of anaerobic glycolysis was negligible:

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

where $\dot{E}_{metab}/M_b$ 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 treadspeed*

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 tread 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, $M_b$:

$$Y = a.M_b b \tag{1}$$

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

$$\log Y = \log a + b.\log M_b \tag{2}$$

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:

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

(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 $N_2$ 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 $O_2$ 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 $N_2$ 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 $O_2$ of 0·2094, therefore each litre of $N_2$ displaced 209·4 ml of $O_2$. The fractional concentration of oxygen leaving the mask when $N_2$ was added ($F_E$) equalled:

$$F_E = \frac{0.2094\,(\dot{V}_{mask} - \dot{V}_{N_2})}{\dot{V}_{mask}}. \tag{4}$$

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

$$\dot{V}_{mask} = \frac{0.2094\,\dot{V}_{N_2}}{0.2094 - F_E}. \tag{5}$$

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
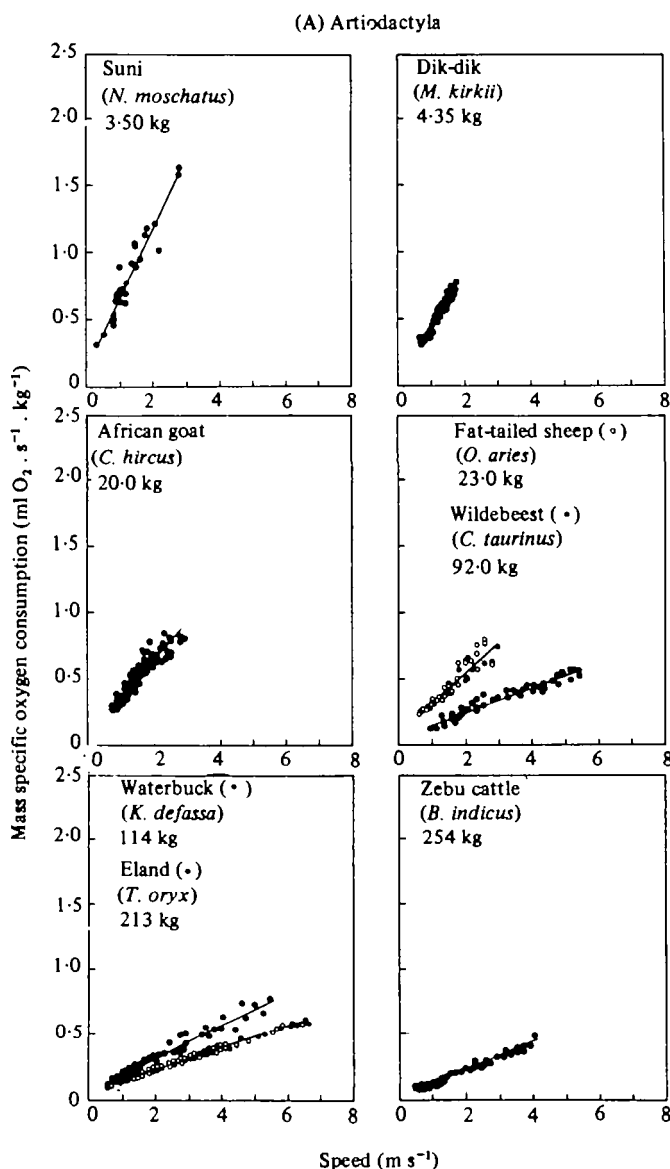
Fig. 1. For legend see page 8.

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
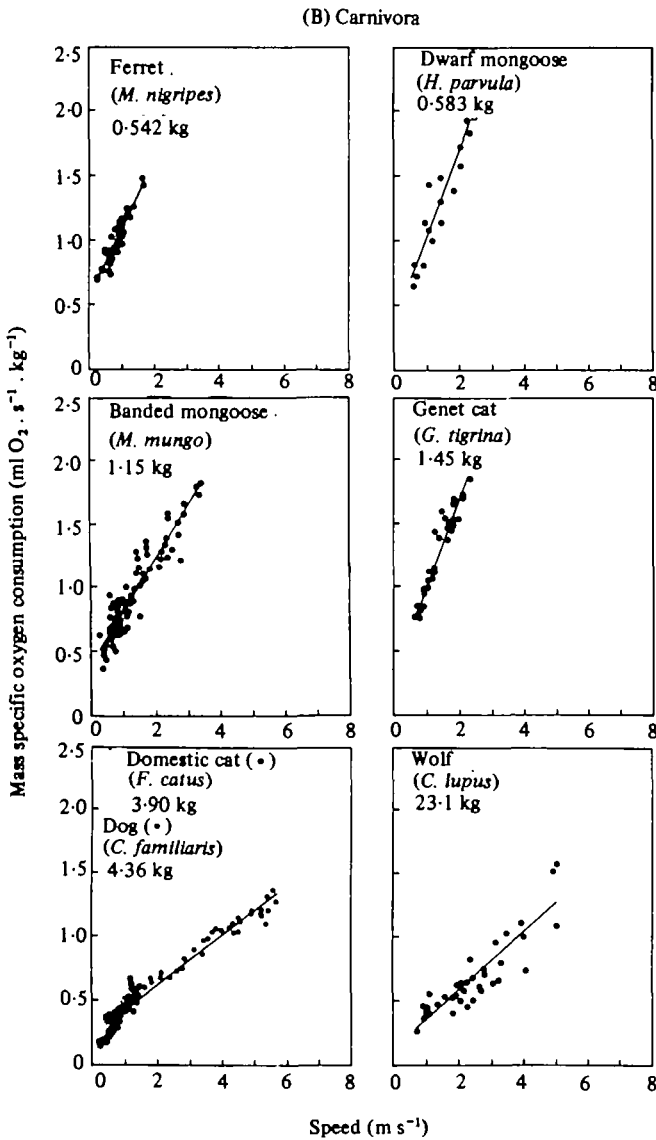
(B) Carnivora



Fig. 1. For legend see page 8.

Test Combinations and a Beckman u.v. Spectrophotometer (model 24). Fifty $\mu$l 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
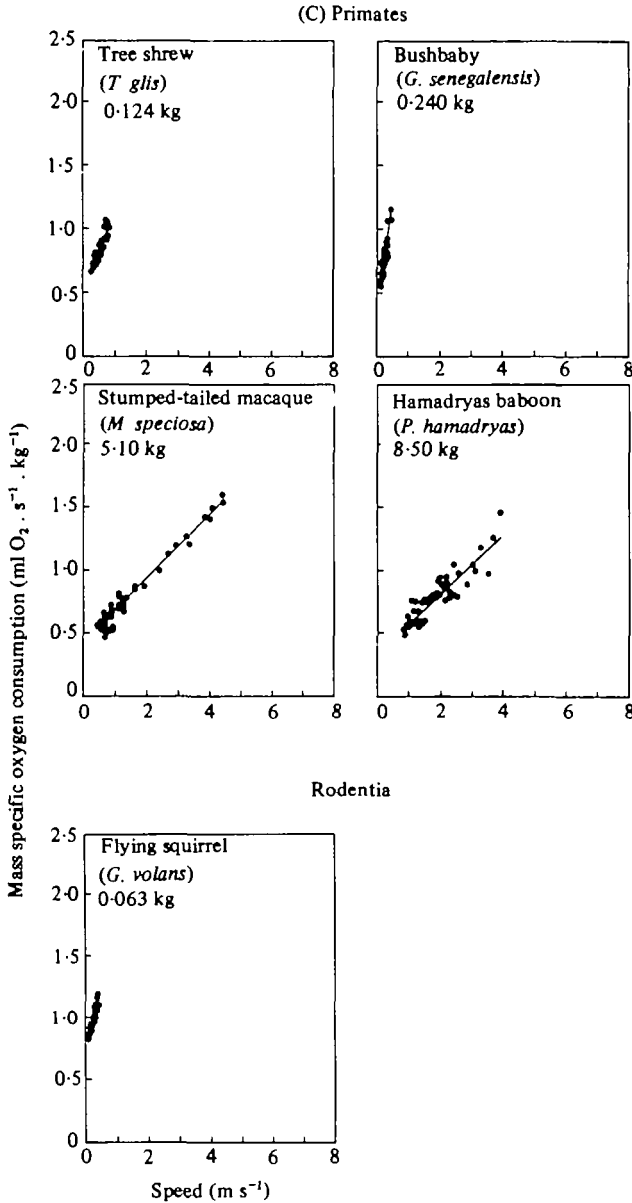
Fig. 1. Mass-specific oxygen consumption ($\dot{V}_{O_2}/M_b$) plotted as a function of speed for 8 species of artiodactyls (Fig. 1A), 7 species of carnivores (Fig. 1B), 4 species of primates and 1 species of rodent (Fig. 1C). $\dot{V}_{O_2}/M_b$ increased nearly linearly with speed. The contribution 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

$$\dot{V}_{O_2}/M_b = \text{slope.speed} + Y \text{ intercept.} \tag{6}$$

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

$$Y \text{ intercept} = 0.300\ M_b^{-0.303} \tag{7}$$

where $Y$ intercept has the units ml $O_2$ s$^{-1}$ 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

$$\text{slope} = 0.533\ M_b^{-0.316} \tag{8}$$

where the slope has the units ml $O_2$ m$^{-1}$ 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 $\dot{V}_{O_2}/M_b = Y$ intercept+slope.$v_g$, (where $\dot{V}_{O_2}$ is rate of oxygen consumption in ml $O_2$ s$^{-1}$, $M_b$ is body mass in kg, and $v_g$ 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: $\dot{V}_{O_2}/M_b = Y$ intercept+slope.$v_g$ | | | | | Reference |
|---|---|---|---|---|---|---|
| | $M_b$ (kg) | Y intercept, ml $O_2$/s kg | Slope, ml $O_2$/m kg | $r^2$ | Diff. (%) | |
| **MAMMALIA** | | | | | | |
| MONOTREMATA | | | | | | |
| Tachyglossidae | | | | | | |
| *Tachyglossus aculeatus* (Echidna) | 5·04 | 0·097 | 0·30 | 0·48 | −37·3 | Crompton *et al.* (1978) |
| | 1·69 | 0·86 | 0·45 | 0·77 | −66·6 | Edmeades & Baudinette (1975) |
| | 3·53 | 0·069 | 0·37 | 0·92 | −66·4 | Edmeades & Baudinette (1975) |
| MARSUPIALIA | | | | | | |
| Didelphidae | | | | | | |
| *Monodelphis domesticus* (Short-tailed opossum) | 0·068 | 0·44 | 1·69 | 0·72 | −4·08 | Oron *et al.* (1981) |
| *Didelphis virginianus* (American opossum) | 2·70 | 0·19 | 0·36 | 0·96 | −13·2 | Crompton *et al.* (1978) |
| Dasyuridae | | | | | | |
| *Sminthopsis crassicaudata* (Narrow-footed mouse) | 0·015 | 1·90 | 1·62 | 0·49 | 32·2 | Baudinette *et al.* (1976*a*) |
| *Antechinomys spenceri* (Hopping mouse) | 0·030 | 1·19 | 1·47 | 0·81 | 19·6 | Baudinette *et al.* (1976*a*) |
| *Antechinus flavipes* (Broad-footed mouse) | 0·034 | 1·56 | 1·77 | 0·42 | 51·3 | Baudinette *et al.* (1976*a*) |
| | 0·048 | 1·69 | 1·34 | 0·40 | 63·2 | Baudinette *et al.* (1976*a*) |
| *Dasyuroides byrnei* (Crested-tailed rat) | 0·12 | 0·79 | 0·84 | 0·71 | −2·38 | Baudinette *et al.* (1976*a*) |
| *Dasyurus viverrinus* (Native cat) | 1·12 | 0·68 | 0·43 | 0·62 | 32·9 | Baudinette *et al.* (1976*a*) |
| Phalangeridae | | | | | | |
| *Trichosurus vulpecula* (Brush-tailed possum) | 1·95 | 0·36 | 0·44 | 0·72 | 18·8 | Baudinette *et al.* (1978) |
| Macropodidae | | | | | | |
| *Bettongia penicillata* (Rat kangaroo) | 1·10 | 0·48 | 0·39 | 0·88 | −10·6 | Thompson *et al.* (1980) |
| *Setonix brachyurus* (Quokka) | 2·95 | 0·61 | 0·38 | — | 53·1 | Baudinette (1977) |
| *Macropus rufus* (Red kangaroo) | 23·0 | 1·14 | −0·026 | −0·40 | 5·6 | Dawson & Taylor (1973) |

| | | | | | | |
|---|---|---|---|---|---|---|
| **INSECTIVORA** | | | | | | |
| Tenrecidae | | | | | | |
| *Setifer setosus* (Setifer) | 0·12 | 0·10 | 0·68 | 0·88 | −69·1 | Crompton et al. (1978) |
| *Tenrec ecaudatus* (Tenrec) | 0·68 | 0·11 | 0·58 | 0·86 | −37·3 | Crompton et al. (1978) |
| Erinaceidae | | | | | | |
| *Erinaceus europaeus* (Hedgehog) | 1·05 | 0·13 | 0·46 | 0·83 | −36·6 | Crompton et al. (1978) |
| Macroscelididae | | | | | | |
| *Elephantulus rufescens* (Elephant shrew) | 0·060 | 0·54 | 1·65 | 0·79 | −0·83 | Oron et al. (1981) |
| Soricidae | | | | | | |
| *Suncus murinus* (Musk shrew) | 0·036 | 0·95 | 1·62 | 0·69 | 10·2 | Oron et al. (1981) |
| **PRIMATES** | | | | | | |
| Tupaiidae | | | | | | |
| *Tupaia glis* (Tree shrew) | 0·12 | 0·45 | 0·69 | 0·87 | −27·3 | New data |
| Lorisidae | | | | | | |
| *Galago senegalensis* (Bush baby) | 0·24 | 0·48 | 1·47 | 0·89 | 25·3 | New data |
| *Nycticebus coucang* (Slow loris) | 1·55 | 0·17 | 0·48 | 0·71 | −24·9 | Parsons & Taylor (1977) |
| | 0·88 | 0·28 | 0·68 | 0·85 | 2·04 | Parsons & Taylor (1977) |
| Cebidae | | | | | | |
| *Cebus albifrons* (Capuchin) | 3·34 | 0·42 | 0·28 | 0·81 | 10·6 | Taylor & Rowntree (1973) |
| *Ateles geoffroy* (Spider monkey) | 3·80 | 0·23 | 0·37 | 0·79 | 10·3 | Parsons & Taylor (1977) |
| Circopithecidae | | | | | | |
| *Macaca speciosa* (Stump-tailed macaque) | 5·10 | 0·43 | 0·25 | 0·97 | 8·03 | New data |
| *Papio hamadryas* (Hamadryas baboon) | 8·50 | 0·36 | 0·24 | 0·79 | 14·5 | New data |
| *Erythrocebus patas* (Patas monkey) | 3·80 | 0·35 | 0·25 | 0·59 | −10·9 | Mahoney (1980) |
| Pongidae | | | | | | |
| *Chimpanzee troglodytes* (Chimpanzee) | 17·5 | 0·22 | 0·25 | 0·92 | 35·6 | Taylor & Rowntree (1973) |
| Hominidae | | | | | | |
| *Homo sapiens* (Human) | 68·8 | 0·12 | 0·20 | — | 43·4 | Margaria et al. (1963) |

| CLASS<br>ORDER<br>Family<br>*Genus species*<br>(Common name) | $M_b$<br>(kg) | For equation:<br>$\dot{V}_{O_2}/M_b = Y$ intercept + slope$\cdot v_g$ | | $r^2$ | Diff.<br>(%) | Reference |
|---|---|---|---|---|---|---|
| | | *Y* intercept,<br>ml O$_2$/s kg | Slope,<br>ml O$_2$/m kg | | | |
| EDENTATA | | | | | | |
| Dasypodidae | | | | | | |
| *Dasypus novemcinctus*<br>(Armadillo) | 4·07 | 0·18 | 0·25 | 0·62 | −14·0 | Oron *et al.* (1981) |
| RODENTIA | | | | | | |
| Sciuridae | | | | | | |
| *Glaucomys volans*<br>(Flying squirrel) | 0·063 | 0·65 | 1·20 | 0·97 | −6·69 | New data |
| *Tamiasciurus hudsonicus*<br>(Red squirrel) | 0·25 | 0·64 | 0·78 | 0·48 | 20·5 | Wunder & Morrison (1974) |
| *Tamias striatus*<br>(Chipmunk) | 0·092 | 0·64 | 0·78 | 0·93 | −22·3 | Seeherman *et al.* (1981) |
| | 0·075 | 0·53 | 1·58 | — | 3·60 | Wunder (1970) |
| *Spermophilus tridecemlineatus*<br>(13-lined ground squirrel) | 0·21 | 0·56 | 0·64 | 0·91 | −15·3 | Fedak & Seeherman (1979) |
| *Spermophilus tereticaudus*<br>(Round-tailed ground squirrel) | 0·24 | 0·35 | 0·66 | — | −23·5 | Taylor *et al.* (1970) |
| *Ammospermophilus harrisii*<br>(Antelope ground squirrel) | 0·086 | 0·92 | 1·42 | — | 34·0 | Yousef *et al.* (1973) |
| Heteromyidae | | | | | | |
| *Dipodomys merriami*<br>(Merriam's kangaroo rat) | 0·041 | 0·49 | 2·01 | — | −16·6 | Taylor *et al.* (1970) |
| | 0·032 | 1·02 | 1·10 | 0·50 | −14·3 | Thompson *et al.* (1980) |
| | 0·031 | 0·94 | 5·30 | — | 81·4 | Yousef *et al.* (1970) |
| *Dipodomys spectabilis*<br>(Kangaroo rat) | 0·100 | 0·50 | 1·13 | — | −10·3 | Taylor *et al.* (1970) |
| *Dipodomys deserti*<br>(Desert kangaroo rat) | 0·104 | 0·90 | 0·66 | 0·85 | −8·83 | Thompson *et al* (1980) |
| Pedetidae | | | | | | |
| *Pedetes capensis*<br>(Spring hare) | 3·00 | 0·57 | 0·34 | 0·67 | 26·9 | Thompson *et al.* (1980) |
| Caicetidae | | | | | | |
| *Baiomys taylori*<br>(Pygmy mouse) | 0·0072 | 0·93 | 2·25 | 0·97 | −20·0 | Seeherman *et al.* (1981) |
| Muridae | | | | | | |
| *Mus musculus*<br>(White mouse) | 0·021 | 0·93 | 2·83 | — | 10·2 | Taylor *et al.* (1970) |
| | 0·030 | 0·71 | 2·07 | 0·81 | −2·09 | Taylor *et al.* (1972) |
| | 0·033 | 1·02 | 1·64 | 0·66 | 12·5 | Oron *et al.* (1981) |

| Species | | | | | | Reference |
|---|---|---|---|---|---|---|
| *Rattus norvegicus* (White rat) | 0·38 | 0·41 | 1·09 | — | 19·5 | Taylor et al. (1970) |
| | 0·21 | 0·55 | 0·97 | 0·95 | 10·8 | Seeherman et al. (1981) |
| *Notomys alexis* (Australian hopping mouse) | 0·027 | 0·89 | 1·96 | — | 7·13 | Baudinette et al. (1976b) |
| *Notomys cervinus* (Fawn hopping mouse) | 0·037 | 1·09 | 0·69 | 0·95 | −25·4 | Dawson (1976) |
| CARNIVORA | | | | | | |
| Canidae | | | | | | |
| *Canis familiaris* (Domestic dog) | 2·60 | 0·21 | 0·34 | — | −12·5 | Taylor et al. (1970) |
| | 4·36 | 0·24 | 0·19 | 0·99 | −33·2 | New data |
| | 18·0 | 0·18 | 0·17 | — | −2·87 | Taylor et al. (1970) |
| | 21·0 | 0·089 | 0·22 | 0·95 | 2·77 | Seeherman, H. J. (pers. comm.) |
| | 24·0 | 0·11 | 0·19 | — | −2·99 | Cerretelli et al. (1964) |
| *Lycaon pictus* (African hunting dog) | 8·75 | 0·19 | 0·33 | 0·98 | 22·8 | Taylor et al. (1971b) |
| *Canis lupus* (Wolf) | 23·1 | 0·13 | 0·23 | 0·80 | 15·9 | New data |
| Mustelidae | | | | | | |
| *Mustela nigripes* (Ferret) | 0·54 | 0·56 | 0·52 | 0·75 | 7·85 | New data |
| *Martes pennanti* (Fisher) | 3·25 | 0·21 | 0·40 | 0·96 | 6·01 | Powell, R. (pers. comm.) |
| | 5·16 | 0·28 | 0·31 | 0·92 | 10·8 | Powell, R. (pers. comm.) |
| Viverridae | | | | | | |
| *Helogale parvula* (Dwarf mongoose) | 0·58 | 0·36 | 0·67 | 0·80 | 4·28 | New data |
| *Mungos mungo* (Banded mongoose) | 1·15 | 0·41 | 0·42 | 0·89 | −4·51 | New data |
| *Genetta tigrina* (Genet cat) | 1·46 | 0·38 | 0·64 | 0·86 | 35·9 | New data |
| Felidae | | | | | | |
| *Felis catus* (Domestic cat) | 3·90 | 0·043 | 0·40 | 0·88 | −22·6 | New data |
| *Leo leo* (Lion)* | 27·5 | 0·15 | 0·30 | 0·92 | 54·4 | Seeherman et al. (1981) |
| | 53·5 | 0·00 | 0·36 | 0·96 | 69·0 | Chassin et al. (1976) |
| *Acinonyx jubatus* (Cheetah) | 39·0 | 0·20 | 0·14 | 0·93 | 2·67 | Taylor et al. (1974) |

| CLASS<br>ORDER<br>Family<br>*Genus species*<br>(Common name) | $M_b$ (kg) | For equation:<br>$\dot{V}_{O_2}/M_b = Y\text{-intercept} + \text{slope}. v_g$ | | $r^2$ | Diff. (%) | Reference |
| --- | --- | --- | --- | --- | --- | --- |
| | | Y intercept, ml O₂/s kg | Slope, ml O₂/m kg | | | |
| **PERISSODACTYLA** | | | | | | |
| Equidae | | | | | | |
| *Equus caballus* (Horse) | 107 | 0·039 | 0·15 | 0·96 | 15·3 | Fedak & Seeherman (1979) |
| **ARTIODACTYLA** | | | | | | |
| Suidae | | | | | | |
| *Sus scrofa* (Miniature pig) | 19·0 | 0·13 | 0·29 | 0·94 | 32·3 | Seeherman *et al.* (1981) |
| Bovidae | | | | | | |
| *Nesotragus moschatus* (Suni) | 3·50 | 0·17 | 0·52 | 0·93 | 26·8 | New data |
| *Madaqua kirkii* (Dik-dik) | 4·35 | 0·064 | 0·40 | 0·91 | −9·58 | New data |
| *Gazella gazella* (Desert gazelle) | 23·2 | 0·15 | 0·16 | 0·94 | −12·0 | Taylor *et al.* (1974) |
| *Connochaetes taurinus* (Wildebeest) | 92·0 | 0·069 | 0·092 | 0·90 | −24·6 | New data |
| *Kobus defassa* (Waterbuck) | 114 | 0·046 | 0·13 | 0·92 | 2·37 | New data |
| *Taurotragus oryx* (Eland) | 213 | 0·072 | 0·083 | 0·96 | −9·12 | New data |
| *Capra hircus* (African domestic goat) | 20·0 | 0·12 | 0·26 | 0·82 | 19·6 | New data |
| (U.S. domestic goat) | 28·0 | 0·089 | 0·18 | 0·95 | −7·25 | Taylor *et al.* (1974) |
| *Ovis aries* (Fat-tailed sheep) | 23·0 | 0·10 | 0·23 | 0·82 | 8·34 | New data |
| *Bos indicus* (Zebu cattle) | 254 | 0·026 | 0·096 | 0·94 | −7·58 | New data |
| **AVES** | | | | | | |
| **STRUTHIONIFORMES** | | | | | | |
| Struthionidae | | | | | | |
| *Struthio* (Ostrich) | 103 | 0·09 | 0·11 | 0·93 | −5·18 | Fedak & Seeherman (1979) |
| **RHEIFORMES** | | | | | | |
| Rheidae | | | | | | |
| *Rhea americana* (Rhea) | 22·0 | 0·11 | 0·34 | — | 51·8 | Taylor *et al.* (1971*a*) |

| | | | | | |
|---|---|---|---|---|---|
| **ANSERIFORMES** | | | | | |
| Anatidae | | | | | |
| *Anser anser* (Greylag goose)* | 3·81 | 0·14 | 0·72 | — | 46·8 | Fedak et al. (1974) |
| **TINAMIFORMES** | | | | | |
| Tinamidae | | | | | |
| *Nothoprocta pentlandi* (Tinamou) | 0·31 | 0·19 | 1·20 | — | −7·98 | Fedak et al. (1974) |
| **SPHENISCIFORMES** | | | | | |
| Spheniscidae | | | | | |
| *Aptenodytes forsteri* (Emperor penguin)* | 20·8 | 0·13 | 0·43 | 0·66 | 52·3 | Pinshow et al. (1977) |
| *Pygoscelis adeliae* (Adelie penguin)* | 3·89 | 0·26 | 0·76 | 0·88 | 77·4 | Pinshow et al. (1977) |
| *Eudyptula albosignata* (White-flippered penguin)* | 1·15 | 0·34 | 1·11 | 0·90 | 61·3 | Pinshow et al. (1977) |
| **GALLIFORMES** | | | | | |
| Phasianidae | | | | | |
| *Excalfactoria chinensis* (Painted quail) | 0·042 | 0·64 | 1·20 | — | −18·5 | Fedak et al. (1974) |
| *Colinus virginianus* (Bobwhite quail) | 0·19 | 0·39 | 0·90 | — | −11·6 | Fedak et al. (1974) |
| *Alectoris graeca* (Chukar partridge) | 0·49 | 0·42 | 0·69 | — | 6·25 | Fedak et al. (1974) |
| Numididae | | | | | |
| *Numida meleagris* (Guinea fowl) | 1·21 | 0·39 | 0·47 | — | 7·18 | Fedak et al. (1974) |
| Meleagrididae | | | | | |
| *Meleagris gallopavo* (Turkey) | 4·31 | 0·17 | 0·41 | — | 12·7 | Fedak et al. (1974) |
| **CHARADRIIFORMES** | | | | | |
| Charadriidae | | | | | |
| *Charadrius wilsonia* (Wilson's plover) | 0·018 | 0·67 | 1·85 | — | −23·7 | Fedak & Seeherman (1979) |
| **CUCULIFORMES** | | | | | |
| Cuculidae | | | | | |
| *Geococcyx californianus* (Road runner) | 0·29 | 0·61 | 0·59 | 0·73 | 4·06 | Fedak & Seeherman (1979) |

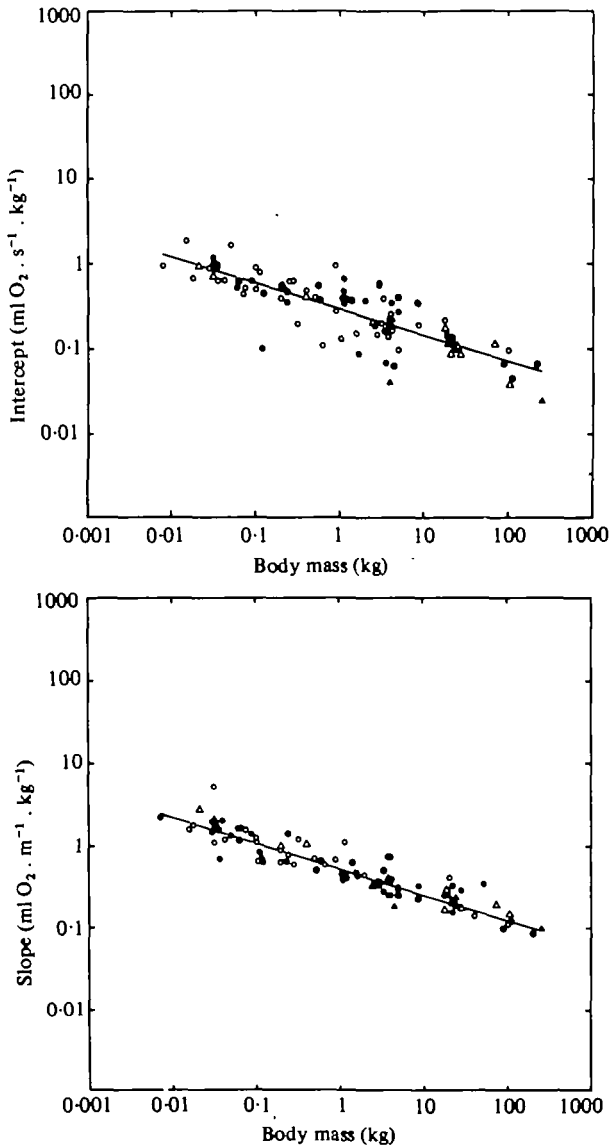* Data excluded from allometric equations, see text.

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:

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

(where $\dot{V}_{O_2}/M_b$ is the mass-specific oxygen consumption of an animal running at speed $v_g$). 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:

$$\dot{V}_{O_2}/M_b = 0\cdot533\,M_b^{-0\cdot316}.\,v_g + 0\cdot300\,M_b^{-0\cdot303} \tag{9}$$

where $\dot{V}_{O_2}/M_b$ has the units ml $O_2$ s$^{-1}$ kg$^{-1}$, $M_b$ is in kg, and $v_g$ 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 ($\dot{E}_{metab}/M_b$) 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:

$$\dot{E}_{metab}/M_b = 10\cdot7\,M_b^{-0\cdot316}.\,v_g + 6\cdot03\,M_b^{-0\cdot303} \tag{10}$$

where $\dot{E}_{metab}/M_b$ 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* $\dot{V}_{O_2}/M_b = aM_b\mathbf{b} + cM_b\mathbf{d}$. *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.

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# ENERGETICS AND MECHANICS OF TERRESTRIAL LOCOMOTION

## II. KINETIC ENERGY CHANGES OF THE LIMBS AND BODY AS A FUNCTION OF SPEED AND BODY SIZE IN BIRDS AND MAMMALS

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### SUMMARY

This is the second paper in a series examining the link between energetics and mechanics of terrestrial locomotion. In this paper, the changes in the kinetic energy of the limbs and body relative to the centre of mass of an animal ($E_{KE, tot}$) are measured as functions of speed and body size. High-speed films (light or X-ray) of four species of quadrupeds and four species of bipeds running on a treadmill were analysed to determine $E_{KE, tot}$. A mass-specific power term, $\dot{E}_{KE, tot}/M_b$ was calculated by adding all of the increments in $E_{KE}$ during an integral number of strides and dividing by the time interval for the strides and body mass. The equations relating $\dot{E}_{KE, tot}/M_b$ and speed were similar for all bipeds and quadrupeds regardless of size. One general equation for the rate at which muscle and tendons must supply energy to accelerate the limbs and body relative to the centre of mass seems to apply for all of the animals:

$$\dot{E}'_{KE, tot}/M_b = 0.478 \, v_g^{1.53}$$

where $\dot{E}'_{KE, tot}/M_b$ has the units W kg$^{-1}$ and $v_g$ is ground speed in m s$^{-1}$. Therefore, $\dot{E}'_{KE, tot}/M_b$ does not change in parallel with the mass-specific rate at which animals consume energy ($\dot{E}_{metab}/M_b$), either as a function of speed or as a function of body size.

## INTRODUCTION

The first paper in this series demonstrates two very general relationships about energetic cost of terrestrial locomotion in birds and mammals: (1) metabolic power increases nearly linearly with speed over a wide range of speeds; and (2) the cost to move a gram of body mass a given distance decreases as a regular function of increasing body mass (e.g. a 30 g quail or mouse uses approximately 13 times as much energy to move each gram of its body a given distance as a 100 kg ostrich or pony). This paper and the two that follow report attempts to find the physical mechanisms that underlie these empirical relationships.

It seems reasonable to assume that skeletal muscles are consuming most of the energy consumed by an animal moving across the ground, and that the muscles use this energy while generating force and performing mechanical work. We have measured the changes in mechanical energy which take place as animals move at a constant average speed as a function of speed and body size. For convenience of measurement we, like others before us (Fenn, 1930; Manter, 1938; Cavagna, Sabiene & Margaria, 1964; Clark & Alexander, 1975), have divided the energy changes into two components. In this paper we have measured the rate at which mechanical work must be supplied to accelerate the limbs and other parts of the body relative to the centre of mass during each stride as an animal runs ($\dot{E}_{KE, tot}$). In the next paper we have measured the rate at which mechanical work must be supplied to raise and accelerate the centre of mass during each stride ($\dot{E}_{CM, tot}$). The final paper discusses various ways these terms can be combined into a single term for the total rate at which mechanical work must be performed by the muscles ($\dot{E}_{tot}$).

Various authors have predicted from theoretical considerations how muscles use energy to sustain a constant average speed. Hill (1950), Gray (1968), and Hildebrand (1974) assumed that most of the energy required to sustain a constant average speed is used to move the limbs relative to the body. They predicted that energy changes should increase as some function between the square and the cube of speed.

It is also possible to predict how kinetic energy changes of the limbs per unit time will vary with body mass for any particular speed by using allometric analysis. A. V. Hill (1950), T. A. McMahon (1975), Alexander (1977) and Alexander, Langman and Jayes (1977) have developed arguments which predict that these energy changes per unit body mass and unit time will decrease with increasing body size in a manner that closely approximates the observed relationship between energy cost of locomotion and body size.

Direct measurements of kinetic energy changes of the limbs as a function of ground speed and as a function of body size are necessary to evaluate these arguments and predictions. Fenn (1930) and Elftman (1940) made such measurements on humans. This early work has been augmented by later studies of Ralston (1958), Ralston & Lukin (1969), Cavagna et al. (1964) and Cavagna & Kaneko (1977). All these authors found that the kinetic energy changes involved in moving limbs increase with the square of speed; and become large relative to metabolic energy delivered to the muscles at high speeds. There is relatively little information about kinetic energy changes of the limbs of animals other than humans. Manter (1938) computed these values for one walking step of a cat. Clark & Alexander (1975) and Alexander & Vernon (1975) estimated that the magnitude of these changes was small relative to metabolic energy input in quail and wallabies. All these measurements, however, were made at a single relatively low speed. We could find no measurements for kinetic energy changes over a wide range of speeds for any animal other than humans, and it seemed likely that humans would be atypical of most other animals because the mass of their leg is greater and located more distally than is usual for most birds and mammals.

## MATERIALS AND METHODS

### *Experimental approach*

Our approach for measuring the kinetic energy changes of limbs and body relative to an animal's centre of mass is outlined briefly to provide an overview, and then described in detail step by step.

(1) Seven species of animals were trained to run on motorised treadmills over a wide range of speeds.

(2) High-speed visible light or X-ray cine films were taken of the animals for 4–12 different tread speeds.

(3) Each animal was killed, frozen, and divided into 6 segments for bipeds and 9–11 segments for quadrupeds (including head, body and limbs). Each segment was treated as a rigid body. The mass, the position of the centre of mass relative to its end points, and its moment of inertia around its centre of mass were determined for each segment.

(4) Films of three to six strides of each animal for each speed were analysed to determine the frame-by-frame co-ordinates of the end points of each segment in the film plane (only limb segments on the side of the animal facing the camera were entered, the others were computed later). This information was stored in a computer for analysis.

(5) The position of the centre of mass of each segment and the angle of the segment relative to a fixed co-ordinate system were computed for each frame from the positional information. The position of the centre of mass of the whole animal was calculated from the position and masses of all the individual segments.

(6) Translational and angular velocities were computed relative to the centre of mass for each segment at the instant each frame was photographed.

(7) Kinetic energy of each segment relative to the centre of mass was calculated from its velocity, moment and mass for each film frame. Then kinetic energy of each segment was plotted as a function of time.

(8) Kinetic energy of the segments of each limb and kinetic energy of all the segments of the whole animal including the limbs were summed at each instant and plotted as a function of time as kinetic energy of a limb and of the entire animal by the computer.

(9) The increments in kinetic energy of each limb and of the whole animal including the limbs were summed over an integral number of strides and divided by the time interval for those strides to produce kinetic energy power terms for the limbs ($\dot{E}_{KE, limb}$) and the whole animal ($\dot{E}_{KE, tot}$).

(10) The functions relating the power required for kinetic energy changes and tread speed for the propulsive stroke, recovery stroke and the entire stride were calculated for one limb of each biped and one front and one hind limb for each quadruped.

(11) The function relating the power required for kinetic energy changes of all segments to tread speed was then calculated for each experimental animal.

### *Animals*

Four species of bipeds and three species of quadrupeds were used in this study. We selected species for which metabolic rate had been measured as a function of

Table 1. *Definition and properties of the individual segments into which the animals were divided for analysis of kinetic energy changes relative to the animal's centre of mass*

| Animal | Body mass (kg) | Height at shoulder (m) | Height at hip (m) | Segment | Mass of segment (kg) | Location of centre of mass | | Moment of inertia about the centre of mass (kg m²) |
|---|---|---|---|---|---|---|---|---|
| | | | | | | $P_1$ to $P_2$ (%) | Normal (%) | |
| Quail (*Excalfactoria chinensis*) | 0·0444 | 0·052 | | Foot | 0·0002 | 64 | 0 | $5·0 \times 10^{-8}$ |
| | | | | Lower leg | 0·0003 | 41 | 4 | $5·7 \times 10^{-8}$ |
| | | | | Middle leg | 0·0014 | 64 | 0 | $9·1 \times 10^{-8}$ |
| | | | | Upper leg | 0·0022 | 55 | 9 | $8·9 \times 10^{-8}$ |
| | | | | Trunk | 0·0318 | 43 | −7 | $1·1 \times 10^{-5}$ |
| | | | | Head | 0·0044 | 108 | −53 | $4·4 \times 10^{-7}$ |
| Guinea fowl (*Numida meleagris*) | 1·089 | | 0·21 | Foot | 0·010 | 61 | 0 | $2·7 \times 10^{-6}$ |
| | | | | Lower leg | 0·010 | 49 | 5 | $4·8 \times 10^{-6}$ |
| | | | | Middle leg | 0·055 | 63 | 2 | $4·6 \times 10^{-6}$ |
| | | | | Upper leg | 0·073 | 43 | 17 | $2·6 \times 10^{-5}$ |
| | | | | Trunk | 0·743 | 59 | 3 | $4·0 \times 10^{-3}$ |
| | | | | Head | 0·050 | 50 | 41 | $2·0 \times 10^{-5}$ |
| Wild turkey (*Meleagris gallopavo*) | 5·690 | | 0·42 | Foot | 0·036 | 67 | 6 | $2·1 \times 10^{-5}$ |
| | | | | Lower leg | 0·050 | 49 | 4 | $1·1 \times 10^{-4}$ |
| | | | | Middle leg | 0·337 | 68 | 3 | $9·8 \times 10^{-4}$ |
| | | | | Upper leg | 0·312 | 53 | 4 | $5·3 \times 10^{-4}$ |
| | | | | Trunk | 3·997 | 52 | 14 | $5·3 \times 10^{-2}$ |
| | | | | Head | 0·223 | 62 | 52 | $5·0 \times 10^{-4}$ |
| Ostrich (*Struthio camelus*) | 89·500 | | 1·21 | Foot | 0·872 | 59 | 14 | $3·6 \times 10^{-3}$ |
| | | | | Lower leg | 1·643 | 58 | −2 | $3·8 \times 10^{-2}$ |
| | | | | Middle leg | 7·203 | 73 | 4 | $1·47 \times 10^{-2}$ |
| | | | | Upper leg | 11·068 | 58 | 10 | $2·44 \times 10^{-1}$ |
| | | | | Trunk | 43·669 | 55 | 0 | $5·61 \times 10^{-1}$ |
| | | | | Head | 4·267 | 63 | 0 | 3·28 |
| Chipmunk (*Tamias striatus*) | 0·115 | 0·051 | 0·045 | *Foreleg* | | | | |
| | | | | Foot | 0·00024 | 50 | −7 | $1·6 \times 10^{-9}$ |
| | | | | Lower leg | 0·00130 | 55 | −1 | $1·1 \times 10^{-7}$ |
| | | | | Upper leg | 0·00270 | 54 | 3 | $1·2 \times 10^{-7}$ |
| | | | | Back foot | 0·00020 | 46 | 8 | $1·3 \times 10^{-9}$ |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Dog (*Canis familiaris*)** | 5·035 | 0·20 | 0·21 | | | | |
| | | | | *Hind leg* | | | |
| | | | | Lower leg | 0·0220 | 51 | 9 | 1·0 × 10⁻⁷ |
| | | | | Upper leg | 0·0640 | 72 | 0 | 5·4 × 10⁻⁷ |
| | | | | Front ⅓ trunk | 0·44 | 49 | 4 | 1·1 × 10⁻⁵ |
| | | | | Back ⅔ trunk | 0·28 | 51 | 3 | 9·3 × 10⁻⁶ |
| | | | | Head | 0·01730 | 15 | 17 | 2·2 × 10⁻⁶ |
| | | | | *Foreleg* | | | |
| | | | | Foot | 0·014 | 62 | −6 | 1·9 × 10⁻⁸ |
| | | | | Lower leg | 0·0138 | 62 | 11 | 1·6 × 10⁻⁶ |
| | | | | Middle leg | 0·054 | 59 | −2 | 3·5 × 10⁻⁶ |
| | | | | Upper leg | 0·1352 | 63 | 0 | 1·0 × 10⁻⁴ |
| | | | | Scapula | 0·1215 | 44 | 3 | 8·5 × 10⁻⁶ |
| | | | | *Hind leg* | | | |
| | | | | Foot | 0·0132 | 65 | −6 | 5·6 × 10⁻⁷ |
| | | | | Lower leg | 0·0193 | 52 | −5 | 8·7 × 10⁻⁶ |
| | | | | Middle leg | 0·0674 | 60 | −2 | 5·8 × 10⁻⁵ |
| | | | | Upper leg | 0·2275 | 55 | −8 | 2·1 × 10⁻⁴ |
| | | | | Trunk | 2·973 | 47 | −30 | 3·1 × 10⁻³ |
| | | | | Head | 0·7324 | 66 | −36 | 1·32 × 10⁻³ |
| **Horse (*Equus caballus*)** | 98·900 | 0·89 | 0·73 | | | | |
| | | | | *Foreleg* | | | |
| | | | | Hoof | 0·380 | 53 | −11 | 4·0 × 10⁻⁴ |
| | | | | Lower leg | 0·340 | 54 | 0 | 1·2 × 10⁻³ |
| | | | | Middle leg | 1·167 | 61 | 0 | 7·0 × 10⁻³ |
| | | | | Upper leg | 1·167 | 52 | −6 | 7·5 × 10⁻³ |
| | | | | Scapula | 2·404 | 42 | −4 | 2·0 × 10⁻³ |
| | | | | *Hind leg* | | | |
| | | | | Hoof | 0·393 | 55 | −9 | 3·9 × 10⁻⁴ |
| | | | | Lower leg | 0·631 | 56 | 0 | 2·1 × 10⁻³ |
| | | | | Middle leg | 2·077 | 62 | −4 | 1·3 × 10⁻³ |
| | | | | Upper leg | 0·643 | 74 | −16 | 5·7 × 10⁻³ |
| | | | | Trunk | 67·600 | 49 | −2 | 4·5 |
| | | | | Head | 11·900 | 91 | −32 | 2·8 × 10⁻¹ |

$P_1$ and $P_2$ for the segments of the bipeds are as follows: foot, tip of longest toe–distal end of tarsometatarsus; lower leg, distal end tarsometatarsus–intertarsal joint; middle leg, intertarsal joint–knee joint; upper leg, knee joint–hip; trunk, neck–body junction ($C_{12}$)–base of tail; head, tip of beak–neck/body junction ($C_{12}$)–base of tail. $P_1$ and $P_2$ for the segments of the dog and horse are as follows: (foreleg) foot/hoof, tip of longest toe/hoof–distal end of metacarpus; lower leg, distal end of metacarpus–carpal joint; middle leg, carpal joint–elbow joint; upper leg, elbow joint–humerus/scapula joint; scapula, humerus/scapula joint– midvertebral border; (hind leg) foot/hoof, tip of longest toe/hoof–distal end of metacarpus; lower leg, distal end of metacarpus–tarsal joint; middle leg, tarsal joint–knee joint; upper leg, knee joint–hip joint; trunk, tip 1st thoracic vertebra–base of tail; head, tip of nose–eye. In the chipmunk, the limbs were divided into fewer segments. $P_1$ and $P_2$ for the segments of the foreleg were: foot, tip of longest toe–carpal joint; lower leg, carpal joint–elbow joint; upper leg, elbow joint– scapula/humerus joint; back foot, tip of longest toe–tarsal joint. Segments of the hind leg were: lower leg, tarsal joint–knee joint; upper leg, knee joint–hip joint; head, angle of joint–atlas. The trunk was divided into front and back halves. $P_1$ and $P_2$ for these were: front ⅓ trunk, atlas–mid spine; and back ⅔ trunk, mid spine–hip joint, respectively.

speed (see the first paper of this series) and which spanned as large a range of body mass as was feasible. The bipeds included a 45 g Chinese painted quail (*Excalfactoria chinensis*); a 1·09 kg guinea fowl (*Numida meleagris*); a 5·70 kg turkey (*Meleagris gallopavo*); and a 90 kg ostrich (*Struthio camelus*). The quadrupeds included a 115 g chipmunk (*Tamias striatus*); a 5·0 kg dog (*Canis familiaris*); and a 98·9 kg pony (*Equus caballus*). All animals were trained to run on treadmills and were exercised regularly prior to the filming.

## Filming

Visible light films (16 mm Kodak 4X reversal, 360 ASA) of running animals were taken with an Eclair camera (model GV-16 with Angenieux Zoom lens f 9·5–95 mm). We used frame rates of 100–200 frames $s^{-1}$ and exposure times of 1/600 to 1/1200 s. The camera was positioned away from the animal to minimize parallax problems (7 m for larger and 3·5 m for smaller animals). The exact positions of the chipmunk's joints could not be resolved with the light films, so we used X-ray films. The X-ray films were taken with a Siemens model 150 G-3 medical X-ray cine apparatus (Kodak Plus X 16 mm film at 200 frames $s^{-1}$). The chipmunk ran about 80 cm from the X-ray source. The image intensifier receptor surface was 91 cm from that source. A rectangular array of 4 reference points known distances apart were placed on the Plexiglas side of the treadmills through which the filming (both light and X-ray) took place. The markers were positioned in such a way that they approximately framed the animal as it ran on the treadmill. We corrected for parallax using the known position of the cameras relative to the plane of the marker points and the plane in which the animal ran.

We tried to obtain as wide a range of speeds as we could for each species. We began to film after the animal had reached a constant average speed and was running smoothly in one position relative to the bed of the treadmill. A large number of strides were filmed at each speed. We selected 3–6 strides for analysis at each speed where the animal ran at a constant speed without any extraneous movement. We tried to obtain at least two speeds within each gait (walk, run in bipeds; walk, trot and gallop in quadrupeds). This was possible for all of the animals except the chipmunk, where we were able to obtain good films for only four speeds. A clock (1 ms resolution) was included in the field of view of the visible light films. The framing rate of the X-ray camera was determined using an oscilloscope connected to the film shutter in the camera.

## Mass and moments of segments

Each animal was killed, frozen and divided into a number of segments. The segments for each animal as defined by their distal and proximal end points, the mass of each segment, its percentage of total body mass and of total limb mass (for limb segment) are given in Table 1. The centre of mass of each segment was determined by hanging the frozen segment from a string, first from one end point and then from another point so that it was rotated by about 90° in the same plane as it appeared in the motion picture film. Photographs were taken of the segment in each orientation and a line was drawn along the supporting string in each photograph so that it extended through

Table 2. *The equation $\dot{E}_{KE, \text{limb}}/M_b = a.v_g b$ expresses the positive increments in kinetic energy per unit time of the leg calculated over an integral number of strides ($\dot{E}_{KE, \text{limb}}$ in watts) divided by body mass ($M_b$ in kg) as a function of average ground speed ($v_g$ in m s$^{-1}$)*

| | Propulsive stroke | | | Recovery stroke | | | Entire stride | | |
|---|---|---|---|---|---|---|---|---|---|
| | a | b | r² | a | b | r² | a | b | r² |
| Quail | 0·024 | 2·14 | 0·84 | 0·079 | 1·97 | 0·64 | 0·090 | 2·04 | 0·89 |
| Chipmunk | | | | | | | | | |
| Foreleg | 0·069 | 1·26 | 0·95 | 0·048 | 0·50 | 0·75 | 0·12 | 0·92 | 0·95 |
| Hind leg | 0·127 | 1·70 | 0·97 | 0·104 | 0·51 | 0·19 | 0·24 | 1·03 | 0·84 |
| Both legs | 0·199 | 1·53 | 0·99 | 0·154 | 0·52 | 0·45 | 0·36 | 1·00 | 0·89 |
| Guinea fowl | 0·018 | 2·62 | 0·95 | 0·081 | 1·47 | 0·98 | 0·085 | 1·64 | 0·96 |
| Turkey | 0·020 | 2·29 | 0·98 | 0·068 | 1·22 | 0·95 | 0·085 | 1·64 | 0·96 |
| Dog | | | | | | | | | |
| Foreleg | 0·040 | 2·59 | 0·97 | 0·155 | 1·09 | 0·89 | 0·218 | 1·60 | 0·99 |
| Hing leg | 0·041 | 2·35 | 0·99 | 0·127 | 0·95 | 0·94 | 0·182 | 1·50 | 0·98 |
| Both legs | 0·083 | 2·45 | 0·99 | 0·286 | 1·03 | 0·95 | 0·403 | 1·55 | 0·99 |
| Ostrich | 0·015 | 2·19 | 0·97 | 0·139 | 1·04 | 0·83 | 0·155 | 1·31 | 0·90 |
| Horse | | | | | | | | | |
| Foreleg | 0·0060 | 2·48 | 0·97 | 0·036 | 1·10 | 0·91 | 0·039 | 1·66 | 0·95 |
| Hind leg | 0·0068 | 2·58 | 0·97 | 0·040 | 1·17 | 0·91 | 0·047 | 1·68 | 0·98 |
| Both legs | 0·0129 | 2·54 | 0·97 | 0·078 | 1·14 | 0·94 | 0·085 | 1·67 | 0·98 |

The constants a and b have been calculated for data from one leg of bipeds, and from one foreleg, one hind leg and both legs of quadrupeds for the power stroke, recovery stroke and entire stride. They were obtained using a least-squares fit of data in a log-log form. During the power stroke, the limb moves backwards relative to the centre of mass and during the recovery stroke it moves forwards.

the segment. The photographs were superimposed and the point on the segment where the two lines crossed was taken as the projection of centre of mass in the cine film plane. The position of the centre of mass of each segment in Table 2 is expressed as a percentage of the distance from the first towards the second end point and as a percentage of that distance above or below the line connecting these two points.

To determine the moment of inertia about the centre of mass, the endpoint of a segment was attached to a stiff steel rod in a manner that allowed it to pivot about the attachment. The segment was then suspended from the rod and swung through a small arc about the pivot point. The frequency of the oscillation was determined to an accuracy of better than 1%. This procedure was repeated for each endpoint of the segment. The moment of inertia about the centre of mass ($I_0$) of the segment was calculated using the formula:

$$I_0 = I - mc^2 \tag{1}$$

where

$$I = \frac{t^2 mcg}{4\pi^2} \tag{2}$$

and $I$ is the moment about axis of suspension; $I_0$ is the moment about the centre of mass; $c$ is the distance between the axis of suspension and the centre of mass; $t$ is the period of oscillation; $m$ is the mass of the segment and $g$ is the acceleration of gravity. anter (1938) describes this method fully. This computation was done from each of

the two endpoints and the two moments were averaged. The difference between the two values was negligible for large animal segments and the head and body segments for the quail and chipmunk. For these small animals the differences between measurements increased as the size of the segments decreased (up to 55 % for the metacarpal/metatarsal segments of the chipmunk). Because the moments of the small segments are very small and because the segments rotate only slowly when the animal runs, errors in the calculated $I_0$ for these segments will cause insignificant errors in the final computation of total kinetic energy (total kinetic energy = rotational KE plus translational KE).

### $x$–$y$ coordinates of segments

The cine film was projected one frame at a time on a 19 × 14 cm screen of a Vanguard Motion Analyzer (Vanguard Instrument Co., Melville, N.Y.). The $x$ and $y$ co-ordinates of the end points were determined for each frame of the film by super-imposing the two cross-hairs of the analyser over the end point. These $x$–$y$ co-ordinates of the segment endpoints, reference points and the time for each frame were stored in a PDP-10 computer. Only the segment endpoints of the limb or limbs on the camera side of the body were entered directly. The endpoints of the limbs on the other side of the body were filled in by the computer. The positional changes on the segments of the equivalent far-side limb were assumed to be the same as for the camera side but out of phase. The phase relationships between the limbs were measured from the films. We were able to resolve the position of the following joints (as a percentage of the distance they moved during a stride) to better than: 1 % for the tip of the toe; 1 % for the carpal metatarsal joint; 2 % for the ankle; 10 % for the knee; 2 % for the hip; and 2 % for the body segments. These are 'worst case' errors for the smallest animals at the slowest speeds. We assumed that there was no motion in the $z$ plane. Films taken from above the animal indicated that movement in this plane was very small compared to movements in the $x$–$y$ plane.

### Position of centre of mass

Using the co-ordinates of the segment endpoints (entered from the film), together with the location of the centre of mass relative to these endpoints, the position of the centre of mass of each segment was calculated relative to the fixed co-ordinates defined by the reference points. The centre of mass of the whole animal for each frame was calculated from the position and masses of the individual segments.

### Kinetic energy of the body relative to the centre of mass, $E_{KE, tot}$

Translational velocities were computed from the change in the positions of each segment and the time that elapsed between the frames. A smooth curve was drawn through the position of the centre of mass of each segment for 5 frames as a function of time. The slope of the curve at the middle frame was taken as the instantaneous translational velocity of the centre of mass of that segment for that frame. The velocity of each segment relative to the centre of mass ($v_{s_i}$) was computed from the difference in the velocities of the centre of mass and the segment. The translational kinetic energy

f each segment ($E_{KE, trans i}$) relative to the centre of mass was calculated using the equation:

$$E_{KE, trans i} = \tfrac{1}{2} m_i v_{s_i}^2 \qquad (3)$$

The rotational kinetic energy of each segment was calculated from the angular velocity of the segment ($\omega_i$) as defined by its endpoints (using the same smoothing procedure) according to the equation:

$$E_{KE, rot i} = \tfrac{1}{2} I_{0_i} \omega_i^2 \qquad (4)$$

Total kinetic energy of each segment relative to the centre of mass ($E_{KE_i}$) was obtained by adding $E_{KE, trans i} + E_{KE, rot i}$ at each instant. We also added the $E_{KE i}$'s of all the segments of a leg at each instant to obtain a value for the kinetic energy of the entire limb relative to the centre of mass at any instant ($E_{KE, limb}$). Finally, we added the kinetic energy of all the segments of the entire body relative to the centre of mass (including our calculated values for the limbs on the far side of the animal) to obtain a value for the kinetic energy of the entire body relative to the centre of mass at each instant ($E_{KE, tot}$).

### Increments in kinetic energy relative to the centre of mass, $\dot{E}_{KE, tot}$

The kinetic energy of each segment, each leg and the total kinetic energy of the animal at each instant relative to the centre of mass were calculated directly by the computer for all strides at each speed. Then by adding all increments in relative kinetic energy for a segment of a limb or the whole animal that occurred during a stride, we calculated the total increase in kinetic energy that had to be supplied by muscles and tendons. Dividing this value by stride period gives a power term for relative kinetic energy increments for segments, limbs and whole animal for a particular speed.

### $\dot{E}_{KE, tot}$ as a function of speed

The procedure outlined above was repeated for 4–12 speeds for each animal. The power function relating $\dot{E}_{KE, tot}$ and speed was then calculated for the equation:

$$\dot{E}_{KE, tot} = \mathbf{a} . v_g \mathbf{b} \qquad (5)$$

(where $v_g$ is ground speed) using regression analysis on a logarithmic transformation trace from the horse, taken at the same speed, the oscillations in $E_{KE}$ in the propulsive

### $\dot{E}_{KE, tot}$ as a function of body size

We used the constants and exponents of the equations relating $\dot{E}_{KE, tot}$ and speed for the individual animals to determine how $\dot{E}_{KE, tot}$ changed as a function of body mass.

### RESULTS

Fig. 1 and 2 give examples of the computer plots of the relative kinetic energy of segments, limbs and whole animal which we obtained for each speed of each animal.
1 gives the computer plots of the relative kinetic energy (the sum of translational
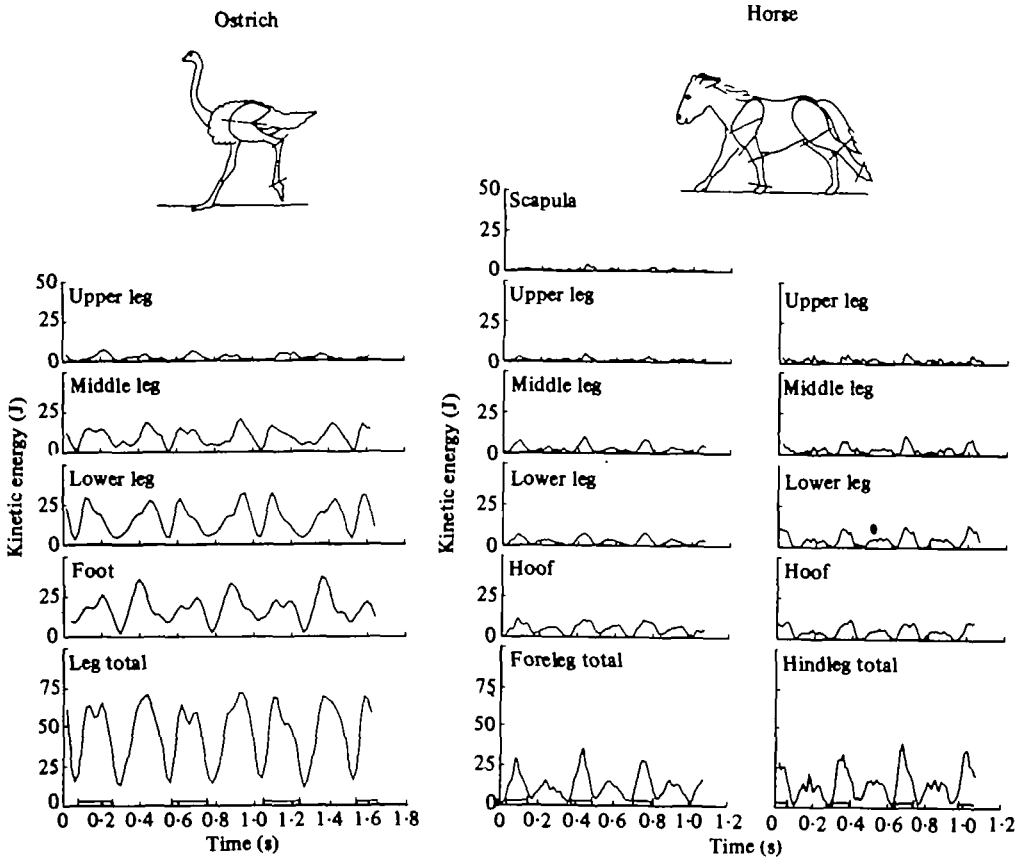
Fig. 1. Kinetic energy of limb segments and of the entire limb plotted as a function of time for three strides of a biped (ostrich) and a quadruped (horse). Body mass of both animals was about the same (~100 kg) and both were travelling at the same speed, 7·5 m s⁻¹. Lines are drawn across the limbs on the horse and ostrich at the top of the figure to indicate how we divided the limb into segments. The end points, mass, location of the centre of mass, and moment of inertia about the centre of mass are given for each segment in Table 1. The bottom tracing is the instantaneous sum of kinetic energy of all the segments of the limb. There are two peaks in kinetic energy of the limb during each stride: one during the propulsive stroke (when the limb moves backward relative to the centre of mass); and one during the recovery stroke (when the limb moves forward relative to the centre of mass). The period during which the foot makes contact with the ground (the stance phase) is indicated by a bar above the time axis of each limb. Similar plots were made over a range of speeds for seven species. The increments in kinetic energy of the limb (obtained by summing the kinetic energy of all the limb segments at each instant) during the propulsive stroke, the recovery stroke and the total stride were added and divided by the stride period to give the kinetic power term $\dot{E}_{KE,\,limb}$. Equations relating these power terms to speed are given in Table 2 for all species.

and rotational) of each segment ($E_{KE_i}$) and of the whole limb ($E_{KE,\,limb}$) vs. time for three strides for one limb of a biped (ostrich) and the front and hind limb on the same side of a quadruped (horse). Body mass of both animals was about the same ($\simeq$ 100 kg) and both ran at the same speed (7·5 m s⁻¹). The mass of each segment decreases as one moves distally along the limb (Table 1). However, because the distal segments move further during each stride, they reach higher velocities and in general (but not always) their kinetic energy goes through larger oscillations (Fig. 1). Relative kin
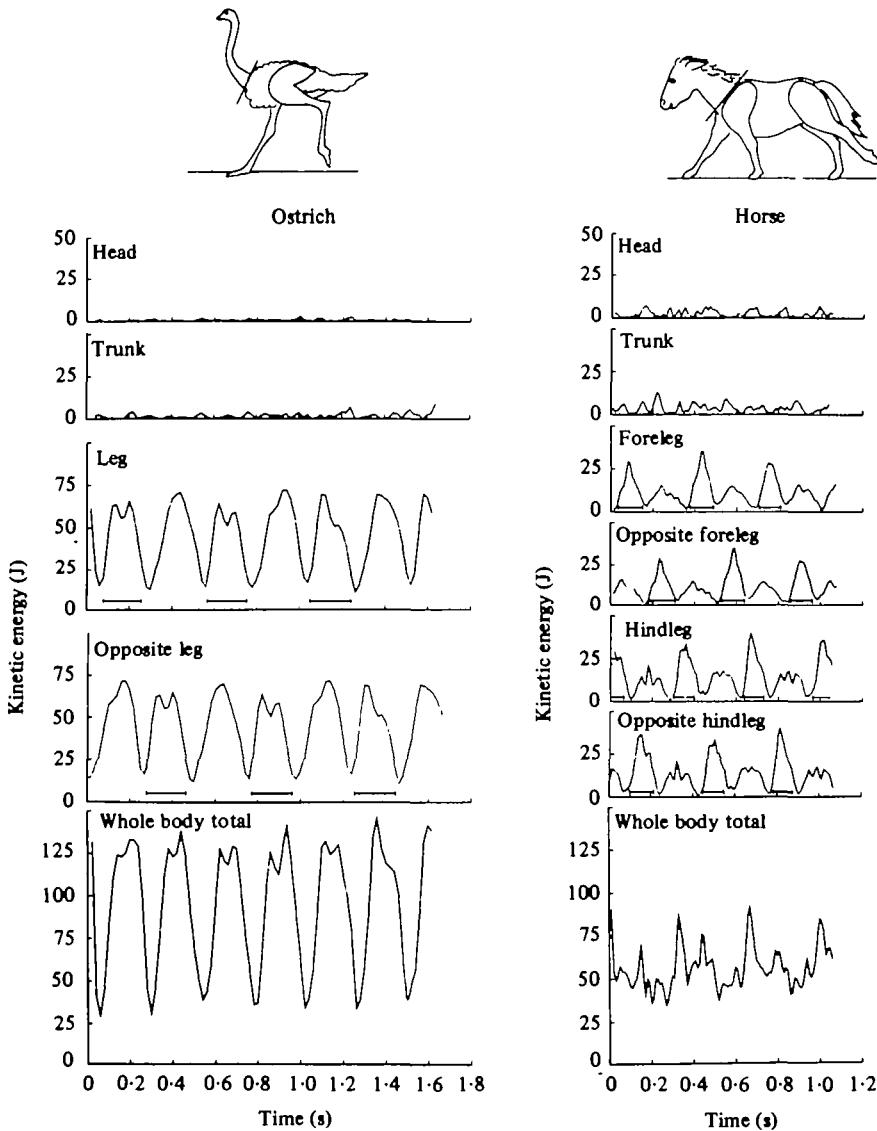
Fig. 2. Kinetic energy of head, trunk, each limb, and the entire animal plotted as a function of time for the three strides given in Fig. 1 of a biped (ostrich) and a quadruped (horse). The period during which each foot makes contact with the ground is indicated by a bar above the time axis of each limb. Similar plots were made over a range of speeds for seven species and $\dot{E}_{KM, tot}$ was calculated for each speed and is plotted as a function of ground speed in Fig. 3. The equations describing these plots are given in Table 4.

energy of the entire limb is also plotted as the sum of the kinetic energies of all the segments of the limb relative to the centre of mass at each instant.

During a stride, there are two oscillations of KE for each segment of the limb. One occurs during the propulsive stroke when the limb is moving backwards relative to the centre of mass. The other occurs during the recovery stroke when the limb moves forward relative to the centre of mass. It is common to divide the stride into a support

or stance phase when the feet are in contact with the ground (includes part of the propulsive stroke) and an aerial phase when no feet are in contact with the ground (includes the recovery stroke and part of the propulsive stroke). We have indicated the interval during which each foot is in contact with the ground, using a bar above the time axis in Figs. 1 and 2. The stance and aerial phases can be identified on Fig. 2 and compared to propulsive and recovery strokes.

In the $E_{KE}$ traces of the ostrich running at 7·5 m s$^{-1}$ in Figs. 1 and 2, the oscillations in $E_{KE}$ during the power and recovery strokes are similar in magnitude. In the $E_{KE}$ trace from the horse, taken at the same speed, the oscillations in $E_{KE}$ in the propulsive stroke of the foreleg and hind leg precedes and is much larger than that during the recovery stroke. The camera-side hind leg is about 90° out of phase with the foreleg at this speed of gallop. The $E_{KE}$ trace begins about halfway through the propulsive stroke, and is followed by the smaller $E_{KE}$ oscillations of the recovery stroke. At low speeds, the relative magnitude of the two oscillations for $E_{KE}$ for the propulsive and recovery strokes is reversed in the horse. Likewise, the $E_{KE}$ oscillations during the power stroke of the ostrich running at low speeds are much smaller than during the recovery stroke. This change in the relative magnitudes of the recovery and power strokes with speed was general for all the animals, as can be seen in the equations given in Table 2.

A power term, $\dot{E}_{KE, \text{limb}}$, has been calculated for the increments in relative kinetic energy which occur during each stroke and the entire stride (Table 2) as a function of tread speed for one leg of all the bipeds and a foreleg and a hind leg from the same side of all the quadrupeds. $\dot{E}_{KE, \text{limb}}$ for the propulsive stroke increases at a rate greater than the square of running speed for all the animals except the chipmunk. The $\dot{E}_{KE, \text{limb}}$ for the recovery stroke, however, increases at a much slower rate with increasing speed than for the propulsive stroke for all the animals except the quail, where the difference is not as great.

Fig. 2 gives the computer plots of the $E_{KE}$ of the trunk and head, and repeats the total KE for each of the legs (bottom tracings of Fig. 1). The bottom tracing was calculated by summing all of the $E_{KE}$'s. A mass-specific power term $\dot{E}_{KE, \text{tot}}/M_b$ was calculated by adding the increments in $E_{KE}$ during an integral number of strides and dividing by time interval for the strides and body mass. This procedure was carried out for each of speeds on each of the animals. The solid circles and solid line in Fig. 3 plots $\dot{E}_{KE, \text{tot}}$ for all the animals as a function of speed. The equations relating $E_{KE, \text{tot}}$ and ground speed for each of the animals are given in Table 3.

$\dot{E}_{KE, \text{tot}}$ calculated in this manner, although correct, does not provide a very good estimate of the rate at which muscles and tendons must provide energy to accelerate the limbs and body relative to the centre of mass (see discussion). A more reasonable estimate, $\dot{E}'_{KE, \text{tot}}$, is obtained by assuming that kinetic energy can be transferred between the segments of each leg, but not between different legs, or between the head and/or trunk. Values for $\dot{E}'_{KE, \text{tot}}$ calculated making these assumptions are given in the dashed lines in Fig. 3, and the functions relating these values and ground speed are given in parentheses in Table 3.

The equations relating $\dot{E}_{KE, \text{tot}}$ and $\dot{E}'_{KE, \text{tot}}$ and ground speed were independent of body mass. One general equation for the rate at which muscles and tendons must
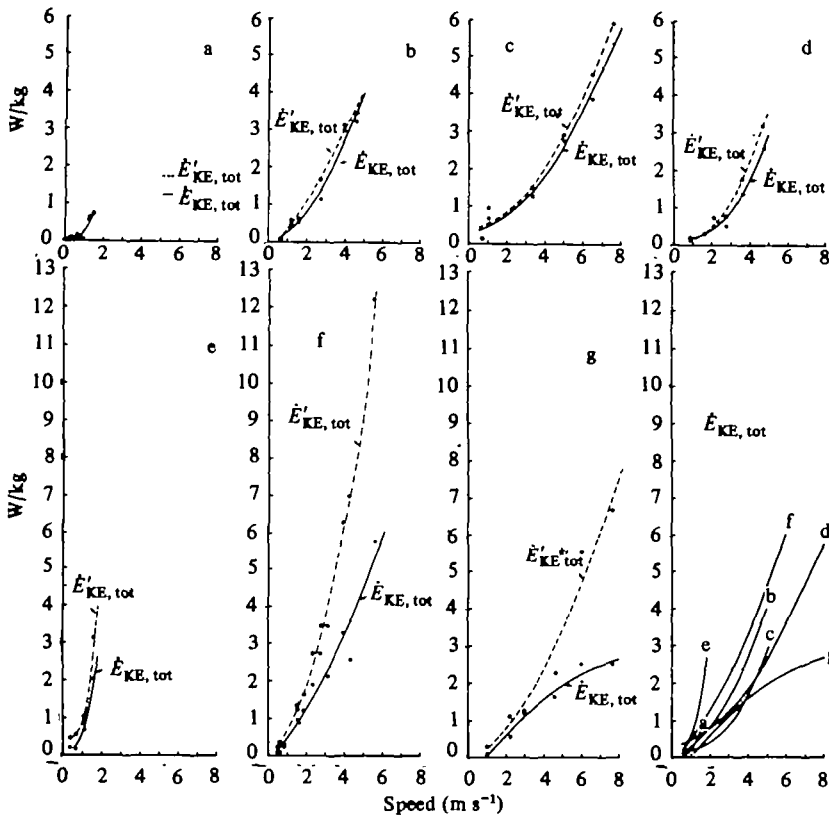
Fig. 3. $\dot{E}_{KE,\,tot}/M_b$ (W kg$^{-1}$) is plotted as a function of speed (m s$^{-1}$) for a series of bipeds and quadrupeds. The solid lines were obtained by adding the increments in kinetic energy of the whole body (as shown in the bottom tracing of Fig. 2) for three strides and dividing by the time for the three strides and the body mass of the animal. The dashed lines were obtained by determining the rate of increments in kinetic energy for each limb and the remaining segments separately and adding these powers. This latter method is a better indication of the increase in kinetic energy that would have to be supplied by muscles and tendons, because it represents the case where a decrease in kinetic energy in one limb would not cancel out an increase in another limb – i.e. no transfer from one limb to another – and it is not obvious to us how such exchanges could occur. The equations for these functions determined by method of least squares on a log-log transform of the data are given in Table 3. Animal key given in Fig. 4 legend.

supply energy to accelerate the limbs and body relative to the centre of mass seems to apply to all of the animals:

$$\dot{E}_{KE,\,tot}/M_b = 0.478\, v_g^{1.53} \qquad (6)$$

where $\dot{E}'_{KE,\,tot}/M_b$ has the units W kg$^{-1}$ and $v_g$ is ground speed in m s$^{-1}$.

## DISCUSSION

The purpose of this paper was to quantify the rate at which mechanical work must be supplied to accelerate the limbs and other parts of the body relative to the centre of mass during each stride as an animal moves along the ground. We hoped these data

Table 3. *The equation $\dot{E}_{KE,\,tot}/M_b = \mathbf{a}.v_g\mathbf{b}$ expresses the positive increments in kinetic energy per unit time (calculated over an integral number of strides) of the whole animal ($\dot{E}_{KE,\,tot}$ in watts) divided by body mass ($M_b$ in kg) as a function of average speed of locomotion ($v_g$ in m s$^{-1}$)*

| Animal | a | b | syx | S.D. slope | S.D. intercept | r² |
|---|---|---|---|---|---|---|
| Quail | 0·229 | 1·62 | 0·315 | 0·467 | 0·148 | 0·69 |
| | (0·448) | (1·75) | 0·237 | 0·352 | 0·111 | 0·83 |
| Chipmunk | 0·716 | 1·49 | 0·243 | 0·506 | 0·130 | 0·72 |
| | (1·26) | (1·24) | 0·171 | 0·356 | 0·091 | 0·79 |
| Guinea fowl | 0·241 | 1·74 | 0·11 | 0·150 | 0·064 | 0·96 |
| | (0·282) | (1·73) | 0·122 | 0·166 | 0·070 | 0·96 |
| Turkey | 0·151 | 1·66 | 0·127 | 0·214 | 0·092 | 0·92 |
| | (0·210) | (1·59) | 0·131 | 0·220 | 0·095 | 0·91 |
| Dog | 0·399 | 1·56 | 0·143 | 0·130 | 0·055 | 0·93 |
| | (0·658) | (1·161) | 0·047 | 0·043 | 0·018 | 0·99 |
| Ostrich | 0·376 | 1·25 | 0·202 | 0·211 | 0·129 | 0·87 |
| | (0·412) | (1·27) | 0·219 | 0·229 | 0·139 | 0·86 |
| Horse | 0·156 | 1·53 | 0·130 | 0·184 | 0·111 | 0·93 |
| | (0·285) | (1·53) | 0·089 | 0·127 | 0·076 | 0·97 |
| Human* | (0·230) | (1·93) | — | — | — | 0·94 |
| Average ± S.E. | 0·324 ± 0·075 | 1·55 ± 0·06 | | | | |
| | (0·478 ± 0·124) | (1·53 ± 0·10) | | | | |

The first set of values for a and b are for the equation calculated from the changes in kinetic energy of the entire body as a function of time; the values in parentheses represent a more realistic approximation of the power that has to be supplied by muscles and tendons to account for the observed increases in kinetic energy as discussed in the text. The r² values were obtained from the least-squares regression of data in log-log form.

* Data from Cavagna & Kaneko (1977) for running only.

would help us to understand the mechanisms that underlie the linear increase in metabolic rate as a function of speed of locomotion and the regular relationship between energetic cost of locomotion and body size.

### Kinetic energy changes as a function of speed

The simplest way in which the linear function between metabolic rate and speed of locomotion might be explained by our measurements of $E_{KE,\,tot}$ would have been if: (1) $\dot{E}_{KE,\,tot}$ increased linearly with increasing speed; (2) $E_{KE,\,tot}$ accounted for most of the energy consumed by the muscles; and (3) the muscles worked at close to their maximum efficiency in converting this energy into kinetic energy over the entire range of locomotion speeds (e.g. by recruiting muscle fibres with 'optimal' intrinsic velocities).

We, like Hill (1950), Hildebrand (1974) and Gray (1968), had anticipated that the kinetic energy increases of the limbs and body relative to the animal's centre of mass would increase as a function between the square and the cube of running speed. Instead we found that it increased as an average function of only the 1·55 power of speed (ranging between 1·25 for the ostrich and 1·74 for the guinea fowl (Table 3)). Our expectations were based on the assumption that the limb makes a reciprocal motion, i.e. retraces the same path in recovery and propulsive stroke with its veloc

Table 4. $\dot{E}_{KE,\,limb}/M_b$ (in watts/kg) for the propulsive and the recovery stroke calculated from the equation given in Table 2 for a horse and an ostrich at ground speeds of $1 \cdot 0 \text{ m s}^{-1}$ and $7 \cdot 5 \text{ m s}^{-1}$

| | $1 \cdot 0 \text{ m s}^{-1}$ | | $7 \cdot 5 \text{ m s}^{-1}$ | |
|---|---|---|---|---|
| | Propulsive stroke | Recovery stroke | Propulsive stroke | Recovery stroke |
| Ostrich | 0·015 | 0·014 | 1·24 | 1·13 |
| Horse | | | | |
| Foreleg | 0·006 | 0·036 | 0·89 | 0·33 |
| Hind leg | 0·007 | 0·040 | 1·23 | 0·89 |

going to zero relative to the centre of mass twice during each stride. The limb does not retrace the same path, and Fig. 1 and Fig. 2 show that neither kinetic energy of the limbs nor that of the whole animal relative to the centre of mass goes to zero during a stride.

$\dot{E}_{KE,\,limb}$ for the propulsive stroke and for the recovery stroke vary differently as a function of speed (Table 2). If one considers only the propulsive stroke (when the velocity of the foot must reach ground speed relative to the centre of mass), then an average $\dot{E}_{KE,\,limb}$ for each leg we have measured increases as a 2·2 power of speed. $\dot{E}_{KE,\,limb}$ for the recovery stroke, however, increases as the 1·1 power of speed. The path the limb follows during the propulsive stroke is determined by relative positions of the ground and trunk because the foot is in contact with the ground during the stance phase. The path the limb follows during the recovery stroke appears to minimise increases in limb velocity and its moment at high speeds (by greater limb joint flexion which moves the centre of the limb's mass closer to the body). The aerial phase allows more time for the recovery stroke relative to the propulsive stroke, and aerial phase becomes longer at higher speeds. This increase in aerial phase with increasing speed has also been reported by Cavagna, Heglund & Taylor (1977). Therefore the limb velocity can be much lower in the recovery than in the propulsive stroke.

The importance of the difference in exponents can be appreciated by comparing magnitudes of $\dot{E}_{KE,\,limb}$ during the propulsive and recovery stroke in an ostrich and a horse moving at $1 \text{ m s}^{-1}$ and $7 \cdot 5 \text{ m s}^{-1}$ (Table 4). $\dot{E}_{KE,\,limb}$ for the propulsive stroke increases by 82-fold for the ostrich and 148-fold for the foreleg and 180-fold for the hind leg of the horse with this 7·5-fold increase in speed. By contrast, $\dot{E}_{KE,\,limb}$ for the recovery stroke increases only 8-fold for the ostrich and 10-fold for the foreleg and 22-fold for the hind leg of the horse. $\dot{E}_{KE,\,tot}$ increases as the 1·55 power of speed because most of the increases in kinetic energy occur in the limbs, and combining the effects of the 2·22 exponent for the propulsive stroke and the 1·11 exponent for the recovery stroke yields a 1·55 exponent for the entire stride.

Our finding that $\dot{E}_{KE,\,tot}$ increases as a 1·55 power function of speed does not explain the linear increase in $\dot{E}_{metab}$ with speed. However, the relationship between $\dot{E}_{KE,\,tot}$ and speed is much closer to a linear function then we had anticipated when we began the study. Most animals can normally increase their speed by more than 10-fold over the range in speeds that they normally move. The relative increase in $\dot{E}_{KE,\,tot}$ for a
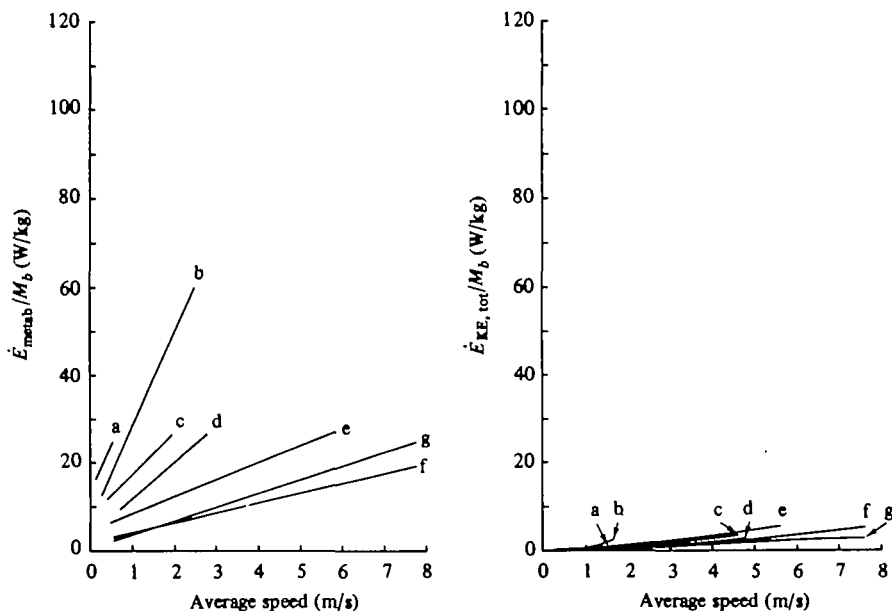
Fig. 4. Mass-specific metabolic rate $\dot{E}_{metab}/M_b$ (left graph) and rate of increments in kinetic energy $\dot{E}_{KE, tot}/M_b$ (right graph) are plotted as a function of speed. $\dot{E}_{metab}/M_b$ decreases dramatically with increasing body size while $\dot{E}_{KE, tot}/M_b$ does not change in any regular way with body size. Animal key: a, 42 g painted quail; b, 100 g chipmunk; c, 1·2 kg guinea fowl; d, 4·3 kg turkey; e, 5·0 kg dog; f, 103 kg ostrich; g, 107 kg horse.

10-fold increase in speed will be about 3·5 times as great as that for $\dot{E}_{metab}$ because of the difference between 1·55 and 1·00 in the exponents relating them to speed.

*Kinetic energy changes as a function of body size*

The second question we asked was whether $\dot{E}_{KE, tot}$ helped explain the regular decrease in energetic cost of locomotion with increasing size that has been presented in the first paper in this series. The answer is clearly no! The functions relating $\dot{E}_{KE, tot}$ and speed are independent of the body mass of the animal, while cost of locomotion varies as the $-0·3$ power of body mass. Fig. 4 plots both $\dot{E}_{metab}/M_b$ and $\dot{E}_{KE, tot}/M_b$ as a function of speed for each of our animals. $\dot{E}_{metab}/M_b$ increases much more rapidly with speed for small animals than for large ones, while $\dot{E}_{KE, tot}/M_b$ increases at about the same rates for all animals and the observed differences are independent of the size of the animal. $\dot{E}_{KE, tot}$ is small relative to $\dot{E}_{metab}$ over the entire range of speeds for small animals, amounting to less than 3% of $\dot{E}_{metab}$ at the lowest speeds and less than 7% for the highest speeds of quail, chipmunk, guinea fowl and turkey (Table 5). For the dog, ostrich and horse it was much larger relative to $\dot{E}_{metab}$ (because $\dot{E}_{metab}$ was much smaller) amounting for 1–10% at the lowest speeds and 15–30% at the highest.

Our values for $\dot{E}_{KE, tot}$ for 100 kg ostrich and horse are slightly smaller than those reported for 70 kg humans by Fenn (1930), Ralston & Lukin (1969) and Cavagna & Kaneko (1977). $\dot{E}_{KE, tot}$ is a minimum value for the increases in kinetic energy which

Table 5. *The ratio of* $\dot{E}_{KE, tot}$ *to* $\dot{E}_{metab} \times 100$ *at lowest and highest speeds used in our experiments*

| Animal | Low speed (m s$^{-1}$) | $\dfrac{\dot{E}_{KE, tot}}{\dot{E}_{metab}} \times 100$ | High speed (m s$^{-1}$) | $\dfrac{\dot{E}_{KE, tot}}{\dot{E}_{metab}} \times 100$ |
|---|---|---|---|---|
| Quail | 0·26 | 0·2–0·6 % (0·3–0·8 %) | 1·52 | 1·5–2·0 % (1·5–2·0 %) |
| Chipmunk | 0·37 | 1·6–3·0 % (3·1–5·8 %) | 1·60 | 5·3–6·4 % (8·1–9·8 %) |
| Guinea fowl | 0·66 | 0·7–1·2 % (0·7–1·3 %) | 4·60 | 4·8–5·3 % (5·1–5·6 %) |
| Turkey | 0·85 | 1·3–2·0 % (2·0–3·0 %) | 4·75 | 6·2–6·7 % (7·5–8·1 %) |
| Dog | 0·66 | 1·4–3·9 % (5·2–14·9 %) | 5·58 | 22·3–27·3 % (47·0–57·6 %) |
| Ostrich | 0·72 | 4·3–9·5 % (4·4–9·7 %) | 7·61 | 27·3–30·6 % (27·8–31·2 %) |
| Horse | 1·05 | 4·3–5·5 % (10·7–13·7 %) | 7·61· | 14·6–15·1 % (38·3–39·6 %) |

Two values of $\dot{E}_{metab}$ have been used to set reasonable limits for the metabolic rate of the muscles: total metabolic rate of the animal at a given speed and the increase in metabolic rate at a given speed over the values at extrapolated zero velocity. The rate of $\dot{E}'_{KE, tot}$ (which assumed kinetic energy can be transferred only within limbs but not between limbs or limbs and body) to $E_{metab}$ is also given (in parentheses).

must be supplied by muscular work and/or elastic recoil of muscles and tendons. It is a measure of the increments in kinetic energy within the animal. If the kinetic energy of one limb of a quadruped decreases at the same time kinetic energy of another limb increases by the same amount, then there would be no change in kinetic energy of the animal. No obvious mechanism exists for the exchange of kinetic energy between limbs and it seems likely that the decreases in the one limb are dissipated as heat or stored as elastic energy and the increases in the other are generated independently by the muscles or elastic recoil. For this reason we have calculated $\dot{E}'_{KE, tot}$ by assuming kinetic energy is transferred from one segment to another within each limb, but not from one limb to another. $\dot{E}'_{KE, tot}$ is plotted on Fig. 3 (dashed lines) and the equations relating it to speed are given in parentheses below those for $\dot{E}_{KE, tot}$ in Tables 3 and 5. $\dot{E}'_{KE, tot}$ differs dramatically from $\dot{E}_{KE, tot}$ only for galloping quadrupeds. This is because at these speeds the four limbs are out of synchrony. At the highest galloping speeds (which we were not able to obtain in these experiments) they return to synchrony. The assumption that there is no transfer in this situation doubles the rate at which energy would have to be supplied by muscles and/or elastic recoil at the highest speeds for the dog and horse. A very interesting point emerges from the measurements of $\dot{E}'_{KE, tot}$ at high speeds on humans and large animals. If there were no storage and recovery of energy in elastic elements, $\dot{E}'_{KE, tot}$ appears to account for all of the ATP being utilized by the muscles. This is because approximately $\frac{2}{3}$ of the energy contained in carbohydrates, lipids and/or proteins is lost as heat in the formation of ATP, leaving only $\frac{1}{3}$ of the energy being consumed available for muscles. ATP utilization by the muscles could not account for the work needed to supply $\dot{E}'_{KE, tot}$ Therefore we are forced to conclude that elastic recoil supplies a significant fraction of the increases in kinetic energy relative to the centre of mass when these animals

run at high speeds. However, we cannot be certain until we consider energy changes of the centre of mass. Energy exchanges are possible between the centre of mass and the parts of the body while a foot is in contact with the ground. The next two papers in this series consider the energy changes of the centre of mass, and the total energy changes of the animal as a function of speed and body size.

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# ENERGETICS AND MECHANICS OF TERRESTRIAL LOCOMOTION

## III. ENERGY CHANGES OF THE CENTRE OF MASS AS A FUNCTION OF SPEED AND BODY SIZE IN BIRDS AND MAMMALS

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### SUMMARY

This is the third in a series of four papers examining the link between the energetics and mechanics of terrestrial locomotion. It reports measurements of the mechanical work required ($E_{CM, tot}$) to lift and reaccelerate an animal's centre of mass within each step as a function of speed and body size during level, constant average speed locomotion. A force platform was used in this study to measure $E_{CM, tot}$ for small bipeds, quadrupeds and hoppers. We have already published similar data from large animals. The total power required to lift and reaccelerate the centre of mass ($\dot{E}_{CM, tot}$) increased nearly linearly with speed for all the animals. Expressed in mass-specific terms, it was independent of body size and could be expressed by a simple equation:

$$\dot{E}_{CM, tot}/M_b = 0.685\, v_g + 0.072$$

where $\dot{E}_{CM, tot}/M_b$ has the units of W kg$^{-1}$ and $v_g$ is speed in m s$^{-1}$.

Walking involves the same pendulum-like mechanism in small animals as has been described in humans and large animals. Also, running, trotting and hopping produce similar curves of $E_{CM, tot}$ as a function of time during a stride for both the small and large animals. Galloping, however, appears to be different in small and large animals. In small animals the front legs are used mainly for braking, while the back legs are used to reaccelerate the centre of mass within a stride. In large animals the front and hind legs serve to both brake and reaccelerate the animal; this difference in mechanics is significant in that it does not allow the utilization of elastic energy in the legs of small animals, but does in the legs of large animals.

## INTRODUCTION

The first paper in this series demonstrates two very general relationships about energetic cost of terrestrial locomotion in birds and mammals: (1) metabolic power increases nearly linearly with speed over a wide range of speeds; and (2) the cost to move a gram of body mass a given distance decreases as a regular function of in-

creasing body mass (e.g. a 30 g quail uses approximately 13 times as much energy to move each gram of its body a given distance as a 100 kg ostrich or pony). The second paper quantifies the kinetic energy changes of the limbs and body relative to the centre of mass as a function of speed and body mass. It shows that the mechanical power required to maintain these changes in kinetic energy increases as the 1·55 power of speed and is independent of body size.

This third paper considers a second component of the mechanical work required to sustain a constant average speed along the ground: the work required to lift and reaccelerate the centre of mass within a step, $E_{CM, tot}$. Locomotion at a constant average speed consists of a series of cycles (steps) during which the potential and kinetic energy of the centre of mass oscillates as the centre of mass rises, falls, accelerates and decelerates. These oscillations in energy have been measured over a wide range of speeds in man (Fenn, 1930; Elftman, 1940; Cavagna, Saibene & Margaria, 1963, 1964; Cavagna, Thys & Zamboni, 1976); in one step of a cat (Manter, 1938); in one step of a quail (Clark & Alexander, 1975); and in two hops of a wallaby (Alexander & Vernon, 1975). They have been found to constitute an important part of the mechanical work of locomotion in all these studies.

More than five years ago we began studies designed to find out how $\dot{E}_{CM, tot}$ varied as a function of speed and body mass. Our investigation had to be broken into two parts because the tool for measuring $\dot{E}_{CM, tot}$, a force platform, can only be used for a limited size range of animals. The first part of the study was carried out using a force platform that had originally been built for humans in Milan, Italy. It was suitable for studies of animals ranging in body mass from 3 to 100 kg. We studied $\dot{E}_{CM, tot}$ as a function of speed for a diversity of bipeds, quadrupeds and hoppers that fell within this size range (Cavagna, Heglund & Taylor, 1977). Then we designed and built a force platform that was suitable for small animals ranging in body mass from 30 g to 3 kg. This paper reports the experiments relating $\dot{E}_{CM, tot}$ and speed for small bipeds, quadrupeds and hoppers. We then utilize the data for $\dot{E}_{CM, tot}$ as a function of speed for both the small animals and the large animals to find out how it varies as a function of body mass.

## MATERIALS AND METHODS

### Experimental approach

We utilized two force platforms (one for animals greater than 3 kg and one for animals less than 3 kg) to quantify the vertical displacement and the horizontal and vertical speed changes of the animal's centre of mass as it moved along the ground at a constant average speed. The force platform measured the force exerted on the ground and resolved it into vertical and horizontal components. These forces were integrated to obtain horizontal and vertical velocities. The forces and velocities were recorded on a strip chart recorder. The velocity records were used to decide whether a particular experiment was acceptable for analysis of the energy changes of the centre of mass; we included only experiments where the animals moved at a constant average speed across the platform. Our criteria for inclusion of an experiment were: (1) records included one or more complete strides; (2) the sum of the increases in velocity (as measured by the integrators) was within 25 % of the sum of the decreases

in velocity in both the horizontal and vertical directions for an integral number of strides; and (3) no drift in the integrators during the period of analysis. For a typical chipmunk stride at 2·1 m s⁻¹, our 25 % limit amounted to a forward speed change of less than 1·5 % of the average forward speed.

For experiments that met our criteria, we carried out a second integration of the vertical forces to give the vertical displacement of the centre of mass. Then kinetic and gravitational energy changes of the centre of mass within a stride were calculated from the velocities and the displacement. Cavagna (1975) has described this technique in detail.

Theoretically, it might be possible to calculate the displacements and the speed changes of the centre of mass using the film analysis technique described in the previous paper. Practically, however, these displacements and speed changes were too small to be resolved accurately with the filming technique. For example, the centre of mass of a 170 g quail running at 2·6 m s⁻¹ typically went up and down only 7 mm and decelerated (and reaccelerated) only 0·07 m s⁻¹ within each step.

The mechanical work required to lift and reaccelerate the centre of mass was first measured as a function of speed of locomotion for individual animals. Then we used the equations relating the work necessary to accelerate and lift the centre of mass and speed to develop an equation which described how this work changed with body mass. Finally, we compared the equations for metabolic energy consumed with the work required to sustain a constant average speed of the centre of mass.

*Animals*

Two species of small bipedal runners, two species of small quadrupedal runners and two species of small bipedal hoppers were trained to run across the small force platform while we measured mechanical energy changes of their centre of mass. Measurements from two large bipedal runners, three large quadrupedal runners and two large bipedal hoppers had already been obtained on the large force plate, and these data have been reported (Cavagna *et al.* 1977).

We selected species in this study for which metabolic rate had been measured as a function of speed (see the first paper of this series) and which extended the range of body mass as much as was feasible. The bipedal runners included two 42–44 g Chinese painted quail (*Excalfactoria chinensis*) and three 150–180 g bobwhite quail (*Colinus virginianus*). Measurements had been made on the large plate for turkeys, rhea and humans, giving us a 2000-fold range in body mass for bipedal runners. The quadrupedal runners included two 80–100 g chipmunks (*Tamias striatus*) and one 190 g ground squirrel (*Spermophilus tridecemlineatus*). Measurements had been made on the large force plate for monkeys, dogs and ram, giving us a 1600-fold range in body mass for quadrupedal runners. The bipedal hoppers included one 37 g kangaroo rat (*Dipodomys merriami*) and three 100–140 g kangaroo rats (*Dipodomys spectabilis*). Measurements had been made on the large force plate for spring hares and kangaroos, giving us a size range 600-fold for bipedal hoppers.

*Force measurement*

In order to obtain measurements from small animals we constructed a smaller force platform suitable for measurements from animals ranging in body mass from 30 g to 3 kg. The small platform consisted of twelve mechanically distinct plates placed end to end in the middle of an 11 m runway. Each plate consisted of an aluminium honeycomb-panel surface (25 × 25 cm) with a sensing element at each corner. Each sensing element consisted of adjacent spring blades, one horizontal and one vertical, that were instrumented with metal-foil strain-gauges. The horizontally oriented spring blade was sensitive only to the vertical forces and the vertically oriented spring blade was sensitive only to the horizontal forces. Cross talk between the vertical and horizontal outputs of the force plate was less than 5 % in the worst case. The output of any particular plate was independent of where on the plate surface the force was exerted to within 3 %. The output of the platform was linear to within 1·5 % over the range of forces measured in these experiments. The natural frequency of oscillation of an unloaded plate was 170 Hz. The design of this force platform has been described in detail elsewhere (Heglund, 1979, 1981).

*Velocity of the centre of mass*

The horizontal force, and the vertical force minus the body weight, were each integrated (using an LM 208 op-amp with a 0·3 s R–C constant) to obtain continuous recordings of the velocity changes of the centre of mass. These recordings were entered directly into a microcomputer at 2 ms intervals using a 12-bit analog–digital converter. The remainder of these procedures were carried out by the microcomputer; complete schematics of the electronics and listings of the programs utilized in this analysis have been given elsewhere (Heglund, 1979).

In order to calculate the absolute vertical and horizontal velocity of the centre of mass, the constants of integration have to be evaluated. The integration constant for the vertical velocity was taken to be zero over an integral number of strides, that is, we assume that the height of the centre of mass was the same at the beginning and end of the strides that were analysed. The integration constant for the horizontal velocity is the average running speed during the period of integration. The average speed was measured by placing two photocells along the path of the force platform; the first photocell turned the integrators on and the second photocell turned the integrators off. The computer then calculated the integration constant (average speed) from the distance between the photocells and the time the integrators were on. The system was calibrated daily for each animal.

*Kinetic and gravitational potential energy of the centre of mass*

The kinetic energy due to the horizontal component of the velocity of the centre of mass ($E_H$) was calculated as a function of time (KE = $\frac{1}{2}M_b.v^2$, where $v$ is the horizontal velocity of the centre of mass). The vertical velocity of the centre of mass was integrated to obtain the vertical displacement of the centre of mass as a function of time. Multiplying the vertical displacement by the animal's body mass and the acceleration of gravity ($\Delta PE = M_b\,g\Delta h$) gave the gravitational energy changes of the centre of mass as a function of time. The instantaneous sum of the changes in potential

energy and the kinetic energy due to the vertical component of the velocity of the centre of mass gives the total changes in energy due to vertical position or movements of the centre of mass ($\Delta E_V$).

### Total energy of the centre of mass, $E_{CM,tot}$

The total energy of the centre of mass, $E_{CM,tot}$, was calculated as a function of time by summing the kinetic and gravitational potential energies of the centre of mass at the 2 ms intervals.

### The mechanical power required to maintain potential and kinetic energy of the centre of mass constant over a stride, $\dot{E}_{CM,tot}$

The average rate of increase in the total energy of the centre of mass, $\dot{E}_{CM,tot}$, was calculated by summing the increments in the $E_{CM,tot}$ curve over an integral number of strides and dividing by the time interval of those strides. This power had to be supplied by the muscles and tendons of the animal.

### $\dot{E}_{CM,tot}$ as a function of speed

The procedure outlined above was repeated for 7–38 speeds in each animal. The function relating $\dot{E}_{CM,tot}$ to speed was then calculated by linear regression analysis.

### $\dot{E}_{CM,tot}$ as a function of body size

We used the equations relating $\dot{E}_{CM,tot}$ to speed for the individual animals from this and the previous study (Cavagna *et al.* 1977) to develop an equation relating $\dot{E}_{CM,tot}$ to body mass.

### RESULTS

*Force, velocity and energy of centre of mass within a step*

*Walk.* The small quails (30 and 200 g) utilized the same walking mechanism as we had observed in larger animals (Cavagna *et al.* 1977) and humans (Cavagna *et al.* 1976). Fig. 1 shows force, velocity and energy records for a typical walking step of the quail. The changes in gravitational potential energy and kinetic energy due to the forward velocity of the animal are out of phase. Thus the decrease in kinetic energy that occurs as the animal slows during one part of the step is stored in gravitational potential energy as the centre of mass rises. This stored potential energy is recovered subsequently in the step as the animal reaccelerates and the centre of mass falls. This energy-saving mechanism is similar to an inverted pendulum or an egg rolling end over end.

Fig. 2 gives a quantitative measure of the energy savings resulting from this pendulum mechanism. As much as 75% of the energy changes that would have occurred had there been no transfer were recovered by this pendulum mechanism. Percentage recovery was calculated using the following equation:

$$\% \text{ recovery} = \frac{(\Sigma + \Delta E_H) + (\Sigma + \Delta E_V) - (\Sigma + \Delta E_{CM,tot})}{(\Sigma + \Delta E_H) + (\Sigma + \Delta E_V)} \times 100 \qquad (1)$$
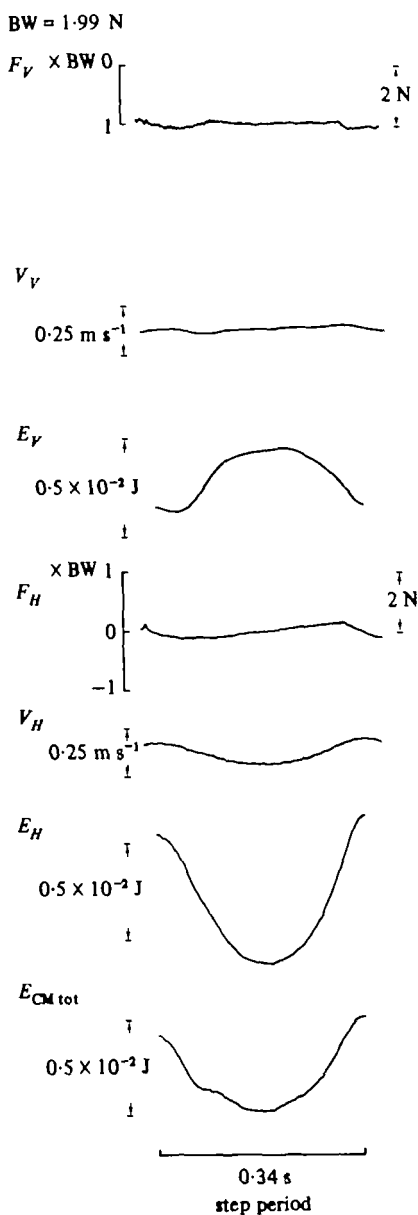
Fig. 1. *Walk.* One step of a 203 g (body weight = 1·99 N) bobwhite quail walking at 0·25 ms$^{-1}$ is analysed according to the procedure outlined in the text. The top curve, $F_V$, is the vertical force exerted by the animal on the force platform. The second curve is the vertical velocity change of the centre of mass, $V_V$, obtained by analog integration of the vertical force minus the animal's body weight. The third curve, $E_V$, is the sum of the kinetic energy of the centre of mass due to $V_V$ plus the changes in potential energy of the centre of mass; the potential energy changes are calculated by integrating the vertical velocity. The fourth curve, $F_H$, is the forward–aft horizontal force exerted by the animal on the force platform. The fifth curve, $V_H$, is the horizontal velocity change of the centre of mass, obtained by analogically integrating the horizontal force. The sixth curve, $E_H$, is the kinetic energy of the centre of mass due to its horizontal velocity, calculated from $V_H$ and the average forward speed of the animal (as measured by photocells, see text). The bottom curve, $E_{CM, tot}$ is the total energy change of the centre of mass of the quail, obtained by summing at each instant the $E_V$ and $E_H$ curves. Note that since the changes in $E_V$ and $E_H$ are out of phase, they tend to cancel when they are summed, resulting in smaller changes in $E_{CM, tot}$. $\dot{E}_{CM, tot}$ is calculated by summing all the increments in the $E_{tot}$ curve and dividing by the step period; the increments in the $E_{tot}$ curve are due to work done by the muscles and tendons.
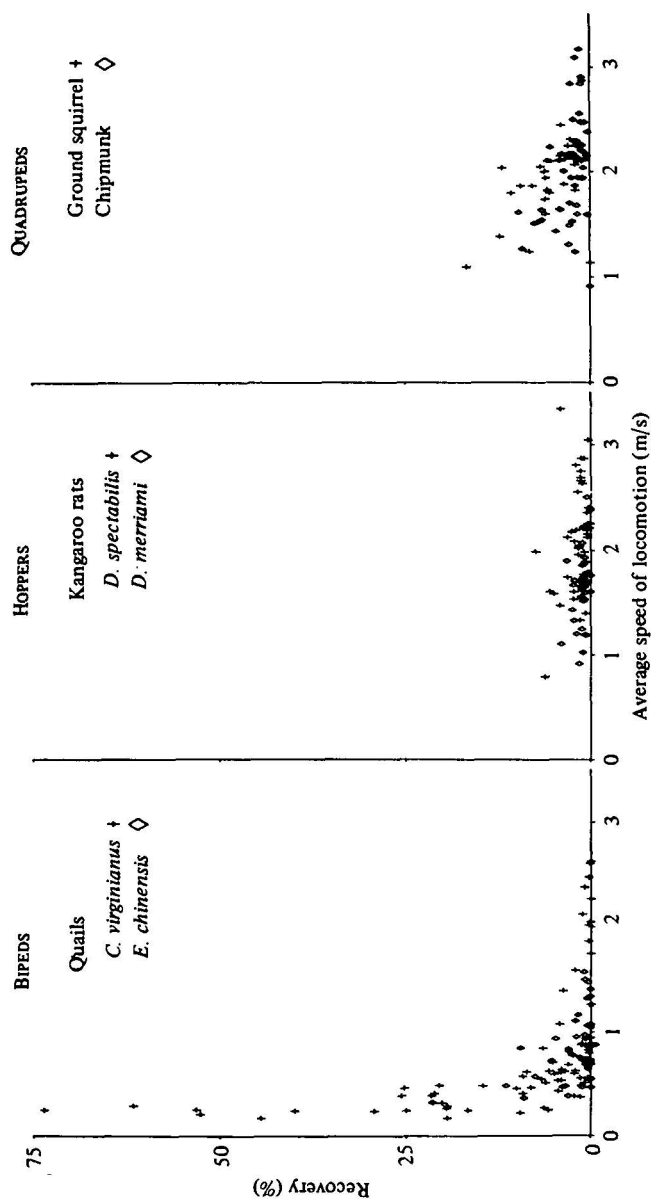
Fig. 2. Percentage recovery as a function of average speed of locomotion for small bipeds, hoppers and quadrupeds. Percentage recovery is the amount of energy that is transferred between the potential energy of the centre of mass and the kinetic energy due to the forward velocity of the centre of mass, expressed as a percentage of the energy changes that would have occurred had there been no transfer. Percentage recovery was high in walking quail, nearly zero in running quail and hopping kangaroo rats, and small in galloping ground squirrel and chipmunk.
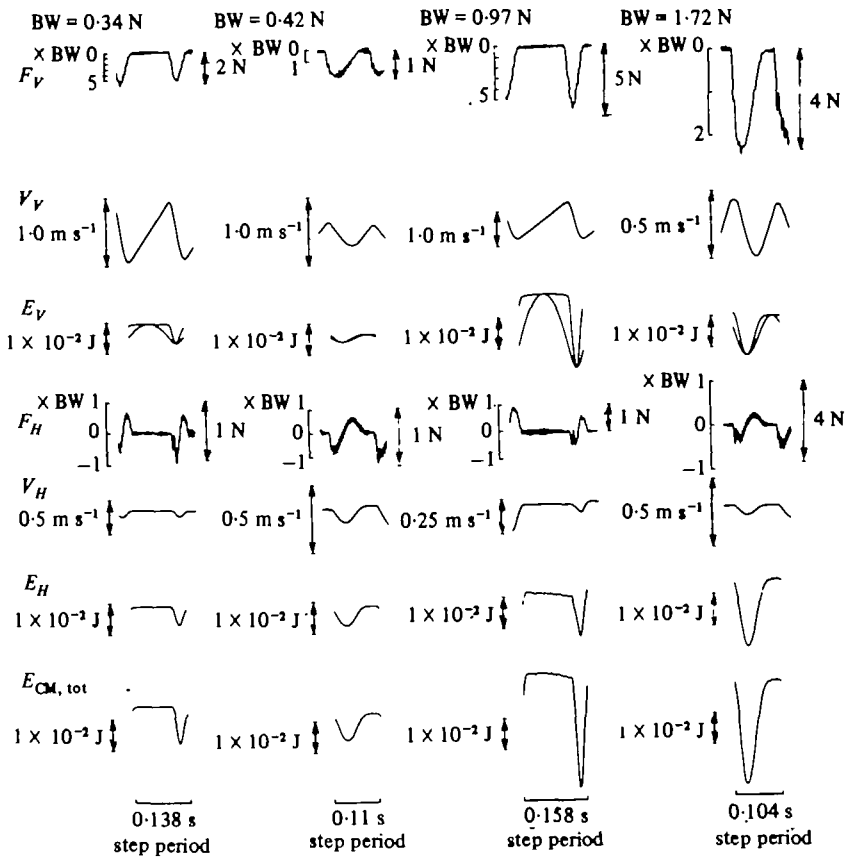
Fig. 3. Typical force, velocity and energy curves for the run or hop gait for small bipeds. The left column is one hop of a 35 g (body weight = 0·34 N) kangaroo rat hopping at 1·76 m s⁻¹; the second column is one step of a 43 g (body weight = 0·42 N) painted quail running at 1·04 m s⁻¹); the third column is one hop of a 99 g (body weight = 0·97 N) kangaroo rat hopping at 2·12 m s⁻¹; and the right column is one step of a 176 g (body weight = 1·72 N) bobwhite quail running at 1·75 m s⁻¹. The top row, $F_V$, is the vertical component of the resultant force exerted by the animal on the force platform; the peak vertical force was about 5–6 times body weight for the hopper, and 2–3 times body weight for the runners. The second row, $V_V$, is the vertical velocity of the centre of mass of the animal; this velocity goes from negative to positive as the animal's centre of mass goes up and down. The slope of the $V_V$ curve during free fall (when the $F_V$ = 0) is equal to the acceleration of gravity, 9·8 m s⁻². The third row, $E_V$, comprises two curves: the lower curve is the gravitational potential energy of the centre of mass; the upper curve is the sum of the gravitational potential energy of the centre of mass plus the kinetic energy of the centre of mass due to its vertical velocity. The two curves are equal twice during each stride: when the vertical velocity is zero because the centre of mass has just stopped going up before starting to go down; and when the vertical velocity is zero because the centre of mass has just stopped going down before starting back up. The top curve can be thought of as the total vertical energy of the centre of mass; note that it is constant during the aerial phase because gravitational potential energy is converted to kinetic energy during free fall. The fourth row, $F_H$, is the forward–aft horizontal component of the resultant force exerted by the animal on the force platform. There is initially a decelerating force as the animal lands with its leg(s) extended in front; this is followed immediately by an accelerating force as it subsequently takes off. The fifth row, $V_H$, is the horizontal velocity changes of the centre of mass; the horizontal velocity is constant during the aerial phase (air resistance is neglected), decreases upon landing and increases again during take-off. The sixth row, $E_H$, is the kinetic energy of the centre of mass due to the horizontal velocity changes. The seventh row, $E_{CM, tot}$, is the total energy of the centre of mass of the animal as

where $\Sigma + \Delta E_H$ is the sum of the positive increments in energy in the horizontal direction, $\Sigma + \Delta E_V$ is the sum of the positive increments in energy in the vertical direction and $\Sigma + \Delta E_{CM, tot}$ is the sum of the positive increments in total energy of the centre of mass that occur during a step. Percentage recovery in both quail falls rapidly with increasing speed to near zero at $1$ m s$^{-1}$. We were unable to train the chipmunk and ground squirrel to walk at the very low speeds necessary for the small animals to have an appreciable transfer of energy.

*Run or hop.* The small bipeds (quails) and hoppers (kangaroo rats) utilized a run or hop gait at speeds above $1$ m s$^{-1}$ similar to the gaits observed in larger animals (Cavagna *et al.* 1977) and humans (Cavagna *et al.* 1976). Fig. 3 gives force, velocity and energy records for a typical run or hop step for a 35 g kangaroo rat, a 43 g quail, a 99 g kangaroo rat and a 176 g quail. The changes in gravitational potential energy and kinetic energy due to the forward velocity of the animal are in phase. Thus the decrease in kinetic energy as the animal slows within a stride occurs almost simultaneously with the decrease in gravitational potential energy as the animal's centre of mass falls and little exchange can occur (Fig. 2).

The shape of mechanical energy curves are similar for a run, trot and hop, regardless of size of the animal or its mode of locomotion. The magnitude of the energy changes and the stride frequency, however, do change with body size. For example, $E_{CM, tot}$ during the step of a human running at a moderate speed is 80 J, and about 2·5 steps are taken each second. $E_{CM, tot}$ for a step of a bobwhite quail running at a moderate speed, by contrast, is only $4·5$ J $\times 10^{-2}$ and the quail takes 9·5 steps each second. We were unable to train the chipmunk and ground squirrel to move across the platform slowly enough to obtain good records for the trotting gait.

*Gallop.* The small quadrupeds (chipmunk and ground squirrel) galloped across the force platform over a wide range of speeds ($1$–$3$ m s$^{-1}$). The force, velocity and energy tracings obtained from these animals during a gallop (Fig. 4) are different from those we obtained from large animals (Cavagna *et al.* 1977). In each stride, the front legs decelerate the animal causing its kinetic energy to fall, and the rear legs reaccelerate the animal, causing its kinetic energy to increase. In the larger animals, both front and back legs decelerated and immediately reaccelerated the animal. Also, there was a significant transfer between gravitational potential energy and kinetic energy during the low-speed gallops of the larger animals, but not in the chipmunk and ground squirrel (Fig. 2).

### Energy changes of the centre of mass as a function of speed

Mass specific powers (W kg$^{-1}$) are plotted as a function of average speed in Fig. 5. Mass specific energy changes per unit time obtained from the vertical forces, $\dot{E}_V/M_b$, and horizontal forces, $\dot{E}_H/M_b$, and the total energy changes of the centre of mass,

a function of time; it is the instantaneous sum of the $E_V$ and $E_H$ curves. Note that since the $E_V$ and $E_H$ curves are in phase, there is little opportunity for energy transfer between them, and consequently the percentage recovery is very low in these gaits, as shown in Fig. 2. The sum of the increases in the $E_{CM, tot}$ curve divided by the step period gives $\dot{E}_{CM, tot}$, the average mechanical power required to maintain the observed oscillations in energy of the centre of mass.
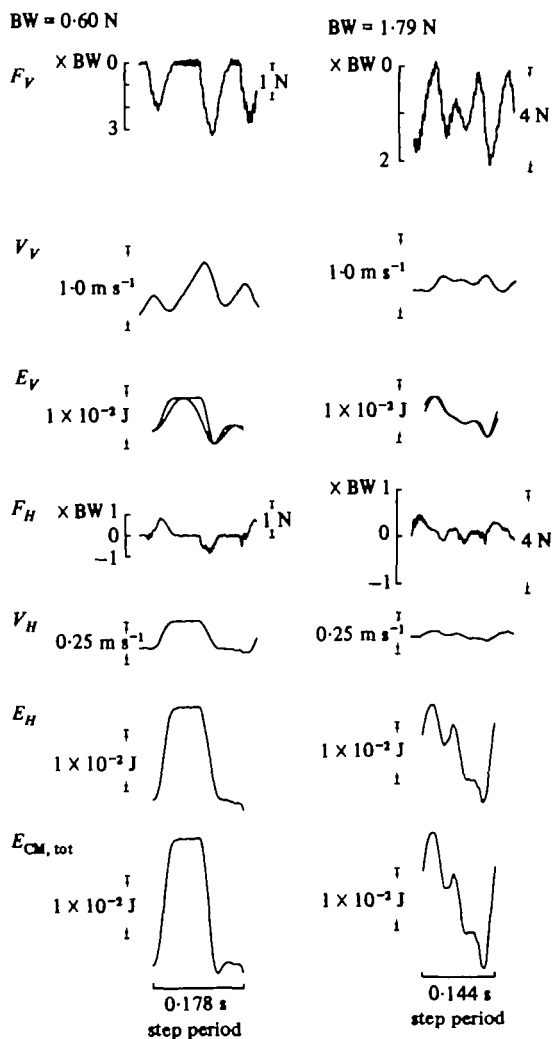
Fig. 4. Typical force, velocity and energy curves for one stride of a 61 g chipmunk (body weight = 0·6 N) galloping at 1·43 m s$^{-1}$ (left column) and a 182 g ground squirrel (body weight = 1·79 N) galloping at 1·6 m s$^{-1}$ (right column). Indications are the same as for Figs 1 and 3. The $E_{CM, tot}$ curve for the chipmunk reproducibly showed two aerial phases; one occurring at the highest $E_{CM, tot}$ achieved during the stride, and the other occurring at near the lowest. In the stride illustrated, the galloping chipmunk took off with a large upward and forward push of the rear legs (note the large increase in $E_V$ and $E_H$) resulting in the large increase in $E_{CM, tot}$. $E_{CM, tot}$ remains constant during the aerial phase, then decreases sharply when the animal lands on its front legs; this energy is absorbed in the muscles and tendons of the body. The front legs then give only a small forward push, resulting in only a slight increase in $E_{CM, tot}$, before the next aerial phase. Most of the energy absorbed in the front legs therefore must be dissipated as heat and then generated *de novo* by the rear legs as the cycle is repeated. However, if any of the energy absorbed by the animal during the large decrease in $E_{CM, tot}$ is stored in the muscles and tendons of the trunk, the animal may be able to recover this elastic strain energy as useful work during the subsequent simultaneous push of the rear legs and extension of the spine as the cycle is repeated. Careful analysis of the ground squirrel tracings shows that a similar situation exists; namely, primarily energy absorption by the front legs with very little positive work done by them as they push off, followed by an aerial phase, a small amount of energy absorption by the rear legs, and then a large amount of work done. The correspondence between the energy curves and footfall patterns of the animals was determined using film analysis.
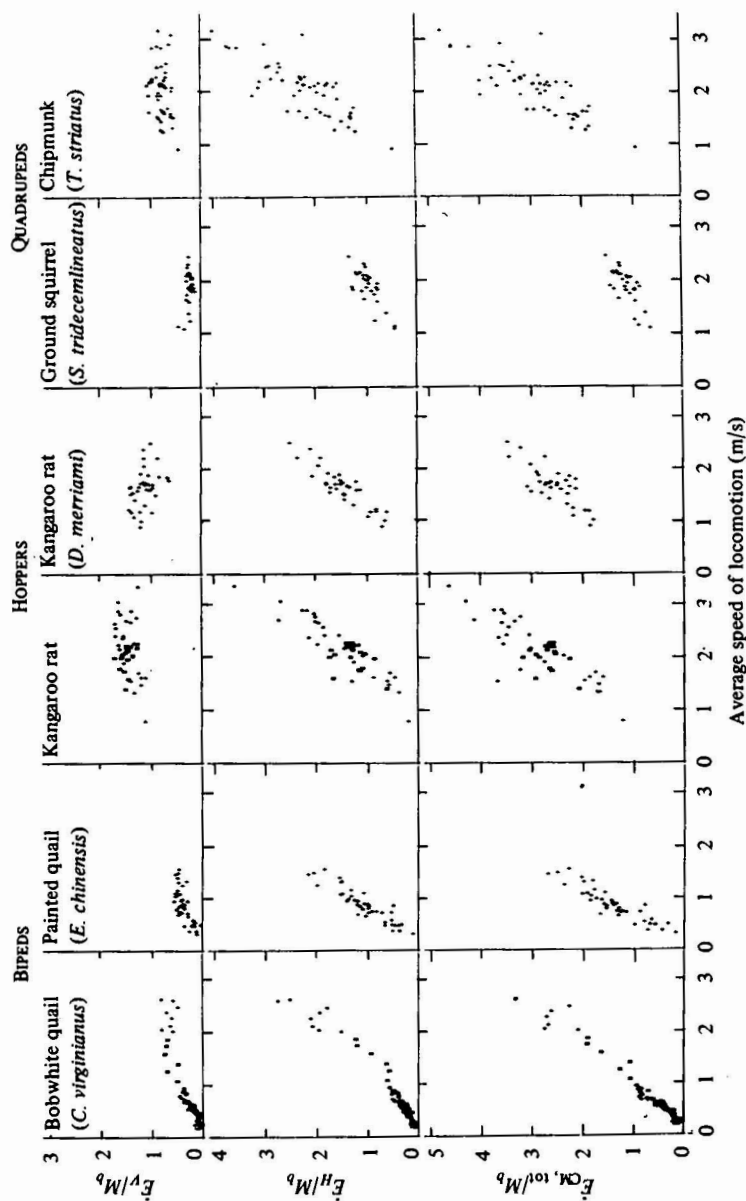
Fig. 5. The mass-specific mechanical power required to maintain the oscillations in energy of the centre of mass as a function of speed in six species of small animals. The top row, $\dot{E}_V/M_b$, is the average power required to maintain the oscillations in gravitational potential energy of the centre of mass. The second row, $\dot{E}_H/M_b$, is the average power required to maintain the oscillations in kinetic energy due to horizontal velocity changes of the centre of mass within a stride. The bottom row, $\dot{E}_{CM,tot}/M_b$, is the average power required to maintain the oscillations in the total kinetic and potential energy of the centre of mass. These values were calculated by summing the increments in the $E_V$, $E_H$ and $E_{tot}$ (Figs. 1, 3, 4) over an integral number of strides and dividing by the duration of the stride and body mass.

Table. 1. *The equations:* $\dot{E}_{CM, tot}/M_b = slope.v_g + Y\text{-}intercept$ *represents the sum of the increments in the total energy of the centre of mass per unit time over an integral number of strides* ($\dot{E}_{CM, tot}$) *divided by body mass* (kg) *as a function of speed* (*in* $m\ s^{-1}$) *for* 15 *species ranging in body mass from* 35 g *to* 73 kg. *The slope and intercept values were calculated by linear regression of the data in Fig.* 5, *or were taken from the literature. Average values were calculated from the slope and intercept values presented in the table.*

| | | | $\dot{E}_{CM, tot}/M_b =$ slope. $v_g$ + Y-intercept | | | Speed ranges | |
| | | | | | | | |
| Animal | $N$ | $M_b$ (kg) | Slope (J m$^{-1}$ kg$^{-1}$) | Y-intercept (W kg$^{-1}$) | $r^2$ | $v_g$ min (m s$^{-1}$) | $v_g$ max (m s$^{-1}$) |
|---|---|---|---|---|---|---|---|
| Kangaroo rat | 1 | 0·035 | 0·947 | 0·951 | 0·64 | 0·91 | 2·5 |
| Painted quail | 2 | 0·042 | 1·68 | −0·053 | 0·84 | 0·32 | 1·57 |
| Chipmunk | 2 | 0·098 | 1·28 | 0·235 | 0·64 | 0·91 | 3·16 |
| Kangaroo rat | 3 | 0·112 | 1·32 | 0·007 | 0·81 | 0·79 | 3·33 |
| Bobwhite | 4 | 0·175 | 1·57 | −0·372 | 0·80 | 0·17 | 2·63 |
| Ground squirrel | 1 | 0·186 | 0·470 | 0·21 | 0·54 | 1·1 | 2·45 |
| Spring hare* | 1 | 2·5 | 0·392 | 0·282 | 0·85 | 1·9 | 6·67 |
| Monkey* | 2 | 3·6 | 0·513 | −2·03 | — | 1·4 | 6·11 |
| Dog† | 1 | 5·0 | 0·279 | −0·7 | — | 1·0 | 7·2 |
| Turkey* | 2 | 7·0 | 0·398 | −0·450 | 0·91 | 1·9 | 5·0 |
| Dog† | 1 | 17·0 | 0·243 | 0·0 | — | 1·5 | 9·4 |
| Kangaroo* | 2 | 20·5 | 0·438 | 0·804 | 0·95 | 2·1 | 7·78 |
| Rhea* | 1 | 22·5 | 0·279 | 0·422 | 0·82 | 1·8 | 5·0 |
| Human‡ | 10 | 70 | 0·330 | 0·657 | 0·94 | 1·4 | 8·89 |
| Ram* | 2 | 73 | 0·136 | 1·112 | 0·39 | 1·1 | 3·47 |
| Average | | | 0·685 | 0·072 | | | |
| Standard deviation | | | ±0·525 | ±0·777 | | | |

* Data from Cavagna *et al.* 1977.
† Data recalculated from Cavagna *et al.* 1977 to include all gaits in each animal.
‡ Data from Cavagna *et al.* 1976.

$\dot{E}_{CM, tot}/M_b$, are plotted separately in Fig. 5. The divisions into vertical and horizontal power terms are useful in evaluating the relative amount of energy required to account for the height and speed changes of the centre of mass.

During a walk (walks were obtained only for the two quails), the vertical and horizontal power increased with increasing walking speed and are approximately equal in magnitude. This allows the relatively large transfer between kinetic and gravitational potential energy observed in Fig. 2. This is similar to what was observed in large animals and man during a walk (Cavagna *et al.* 1977; Cavagna *et al.* 1976). Because the details of the transfer have been discussed in these papers, we will not repeat them here.

During a run or hop and a gallop, the vertical power remained nearly constant over the entire range of speed, while the horizontal power increased. The magnitude of the vertical power was much greater in both the large and small hopping animals than in the running and galloping animals (Cavagna *et al.* 1977).

Total power required to lift and reaccelerate the centre of mass ($\dot{E}_{CM, tot}$) increased nearly linearly with speed for all of the animals in this study (Fig. 5), as it had for the larger animals in our previous study (Cavagna *et al.* 1977). The linear increase in tot
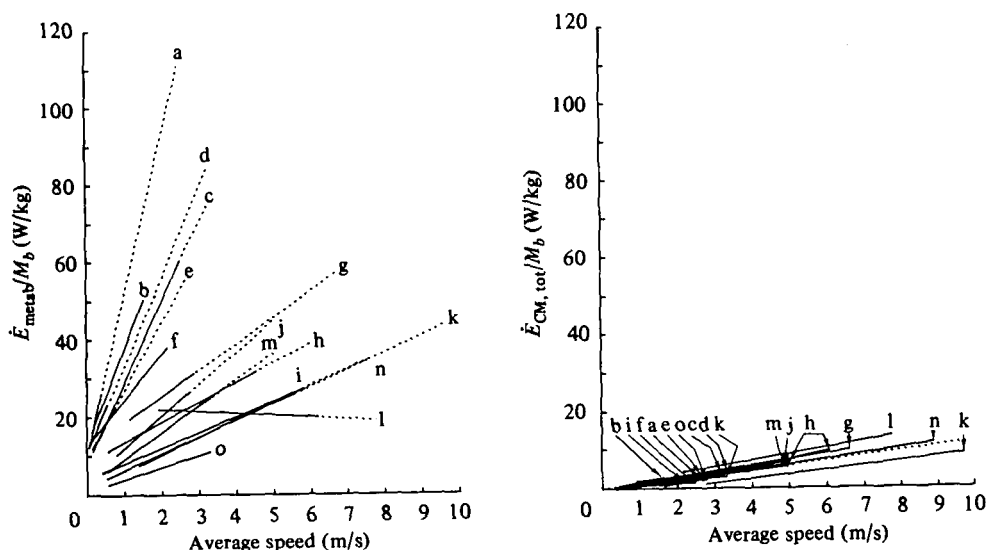
Fig. 6. Mass-specific metabolic rate, $\dot{E}_{metab}/M_b$, and mass-specific rate at which mechanical energy is required to reaccelerate and lift the centre of mass, $\dot{E}_{CM, tot}/M_b$ are plotted as a function of speed. $\dot{E}_{metab}/M_b$ decreases dramatically with increasing body size while $\dot{E}_{CM. tot}/M_b$ does not change in any regular way with body size. The dotted extensions of the $\dot{E}_{metab}/M_b$ lines refer to extrapolated data; the dotted $\dot{E}_{CM, tot}$ line is the average line as given in Equation 3 in the text. The animals are: a, 35 g Merriam's kangaroo rat; b, 42 g painted quail; c, 90 g chipmunk; d, 105 g kangaroo rat; e, 178 g bobwhite quail; f, 190 g ground squirrel; g, 2·5 kg spring hare; h, 3·6 kg monkey; i, 5·0 kg dog; j, 7·0 kg turkey; k, 17·5 kg dog; l, 20·5 kg kangaroo; m, 22·5 kg rhea; n, 70 kg human; o, 75 kg ram. Human data from Cavagna & Kaneko (1977).

power with speed makes it possible to express the relationship between total power and speed for each animal by a linear equation of the form:

$$\dot{E}_{CM, tot}/M_b = \text{slope.speed} + \text{Y-intercept} \qquad (2)$$

In Table 1 we have included the values for slope and Y-intercept (calculated using the method of least squares) together with the speed range over which measurements were made and the coefficient of determination for the linear regression ($r^2$) for both the small animals in this study and the large animals in our previous study (Cavagna *et al.* 1977).

*Energetic cost for lifting and reaccelerating the centre of mass as a function of body mass*

There are two components of the mechanical power expended to lift and re-accelerate the centre of mass (as there were with oxygen consumption): an extrapolated zero speed power (the Y-intercept) and an incremental power (the slope) (see equation 2). Both terms are constant for an individual animal because the relationship between $\dot{E}_{CM, tot}/M_b$ and speed is linear. Both terms are independent of body mass because the slope of the function relating each term of the equation to body mass is not significantly different from zero. Both the metabolic energy consumed ($\dot{E}_{metab}/M_b$) and $\dot{E}_{CM, tot}/M_b$ are plotted as a function of speed in Fig. 6. This figure clearly demon-

strates that the relationship between $\dot{E}_{metab}/M_b$ and speed changes dramatically with body size, while the relationship between $\dot{E}_{CM,tot}/M_b$ and speed does not.

We have obtained a single equation relating $\dot{E}_{CM,tot}/M_b$ and speed for all the animals by averaging the values for the Y-intercept and slope:

$$\dot{E}_{CM,tot}/M_b = 0.685 \cdot v_g + 0.072 \qquad (3)$$

where $\dot{E}_{CM,tot}/M_b$ has the units W kg$^{-1}$ and $v_g$ is in m s$^{-1}$. The standard deviations for the terms are given in Table 1.

## DISCUSSION

### Force, velocity and energy of the centre of mass within a step

Our data show that quail, like some large animals, utilize a pendulum-like energy conservation mechanism during a walk. Up to 70% of the energy is exchanged between kinetic and gravitational potential energy within a step. This is the same magnitude of exchange that was found in humans (Cavagna et al. 1976) and large animals (Cavagna et al. 1977). However, it was extremely difficult to obtain good walking records from small animals, and we were never able to obtain them from the chipmunks and ground squirrels. At slow speeds, small animals normally moved in a series of short bursts, alternating with stops, rather than at a constant speed.

During a run or hop small animals exhibit force and velocity patterns similar to those we observed for large animals. However, one major difference exists. At high speeds dogs, kangaroos and humans stored energy as elastic strain energy in the muscles and tendons when they landed and recovered some of this energy when they took off. This was demonstrated because the magnitude of energy changes of the centre of mass was greater than the metabolic energy consumed by the muscles (assuming muscles convert energy stored in carbohydrates, fats and proteins into work at a 25% efficiency). In the small animals, however, one could account for all of $\dot{E}_{CM,tot}/M_b$ with muscular efficiencies of less than 25%. Recent studies by Biewener, Alexander & Heglund (1981) show that the tendons of small kangaroo rats are relatively thicker than those of large kangaroos, and are too stiff to store large amounts of elastic energy. It seems possible, therefore, that large animals are able to utilize an elastic storage mechanism during a run or hop, but that small animals are not. This matter certainly merits more investigation.

The gallop of the small quadrupeds was quite different from the gallop of the large quadrupeds (Cavagna et al. 1977). The small animals landed on their front legs, decelerating the body, and then, after an interval (aerial phase), reaccelerated their body with their hind legs. In the larger animals, both front and hind limbs alternately decelerated and then reaccelerated the body during a stride. This means that elastic storage and recovery within the tendons and muscles of the limb would be possible for large animals but not for small animals. However, small animals did exhibit enormous spinal flexion during a gallop, and it might be possible for them to store energy elastically in the muscles and tendons of the back as the animal landed on its front limbs which could be recovered as it pushed off from its hind limbs. In addition, the large animals were capable of alternately storing and recovering significant

amounts of forward kinetic energy in gravitational potential energy at slow galloping speeds. Small animals do not appear to be able to utilize this energy-saving mechanism in a gallop.

*Energetic cost for lifting and reaccelerating the centre of mass as a function of speed and body mass*

$\dot{E}_{CM,tot}$ like $\dot{E}_{metab}$, increases nearly linearly with speed. Thus, $\dot{E}_{CM,tot}$ might provide an explanation of the linear increase in $\dot{E}_{metab}$ for individual animals if it were the major component of mechanical work performed by the animal's muscles. However, at the highest speeds achieved by the large animals, the rate at which muscles and tendons must supply energy to accelerate the limbs and body relative to the centre of mass, $\dot{E}'_{KE,tot}$, becomes equal to or greater than $\dot{E}_{CM,tot}$ and cannot be ignored (see Fedak, Heglund & Taylor, 1982). For this reason, consideration of the explanation of the linear increase in $\dot{E}_{metab}$ is left to the following paper when total mechanical energy is calculated. The relationship between $\dot{E}_{CM,tot}$ as a function of speed is nearly independent of body size as predicted by Alexander's mathematical models of running (Alexander, 1977; Alexander, Jayes & Ker, 1980). The increase in amplitude of the oscillations in energy of the centre of mass during a step with increasing body size appears to be nearly exactly compensated by a decrease in step frequency. Thus $\dot{E}_{CM,tot}/M_b$ does not help to explain the 10 to 15-fold changes in $\dot{E}_{metab}/M_b$ with body size observed in the first paper of this series.

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# ENERGETICS AND MECHANICS OF TERRESTRIAL LOCOMOTION

## IV. TOTAL MECHANICAL ENERGY CHANGES AS A FUNCTION OF SPEED AND BODY SIZE IN BIRDS AND MAMMALS

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### SUMMARY

This is the final paper in our series examining the link between the energetics and mechanics of terrestrial locomotion. In this paper the kinetic energy of the limbs and body relative to the centre of mass ($E_{KE, tot}$ of paper two) is combined with the potential plus kinetic energy of the centre of mass ($E_{CM, tot}$ of paper three) to obtain the total mechanical energy (excluding elastic energy) of an animal during constant average-speed locomotion. The minimum mass-specific power required of the muscles and tendons to maintain the observed oscillations in total energy, $\dot{E}_{tot}/M_b$, can be described by one equation:

$$\dot{E}_{tot}/M_b = 0.478 \cdot v_g^{1.53} + 0.685 \cdot v_g + 0.072$$

where $\dot{E}_{tot}/M_b$ is in W kg$^{-1}$ and $v_g$ is in m s$^{-1}$. This equation is independent of body size, applying equally as well to a chipmunk or a quail as to a horse or an ostrich. In marked contrast, the metabolic energy consumed by each gram of an animal as it moves along the ground at a constant speed increases linearly with speed and is proportional to $M_b^{-0.3}$. Thus, we have found that each gram of tissue of a 30 g quail or chipmunk running at 3 m s$^{-1}$ consumes metabolic energy at a rate about 15 times that of a 100 kg ostrich, horse or human running at the same speed while their muscles are performing work at the same rate. Our measurements demonstrate the importance of storage and recovery of elastic energy in larger animals, but they cannot confirm or exclude the possibility of elastic storage of energy in small animals. It seems clear that the rate at which animals consume energy during locomotion cannot be explained by assuming a constant efficiency between the energy consumed and the mechanical work performed by the muscles. It is suggested that the intrinsic velocity of shortening of the active muscle motor units (which is related to the rate of cycling of the cross bridges between actin and myosin) and the rate at which the muscles are turned on and off are the most important factors in determining the metabolic cost of constant-speed locomotion. Faster motor units are recruited as animals increase speed, and equivalent muscles of small animals have faster fibres than those of larger animals. Also, the muscles are turned on and off more quickly as an animal increases speed, and at the same speed a small animal will be turning muscles on and off at a much higher rate. These suggestions are testable, and future studies should determine if they are correct.

## INTRODUCTION

This is the fourth and final paper in our series examining the link between energetics and mechanics of terrestrial locomotion. Two experimental variables have been used throughout: speed and body size. The first paper quantified the metabolic energy consumed while animals ran at a constant speed; the second quantified the kinetic energy changes of the limbs and body relative to the centre of mass, $E_{KE,tot}$; and the third quantified the potential and kinetic energy changes of the centre of mass, $E_{CM,tot}$. This final paper combines the kinetic energy of the limbs and body relative to the centre of mass with the energy changes of the centre of mass to give the changes in total kinetic and gravitational potential energy of the animal during a stride, $E_{tot}$.

How do we combine $E_{KE,tot}$ and $E_{CM,tot}$ to obtain the total mechanical energy of the body? The total mechanical energy of a running animal can be described at any particular instant as the sum of the kinetic and gravitational potential energy of the centre of mass, $E_{CM,tot}$, plus the kinetic energy of elements of the body relative to the centre of mass $E_{KE,tot}$, plus the elastic strain energy (elastic potential energy) of the system, $E_{ES}$:

$$E_{tot} = E_{CM,tot} + E_{KE,tot} + E_{ES}. \qquad (1)$$

We have measured $E_{CM,tot}$ and $E_{KE,tot}$ independently as described in the second and third papers of this series. We know of no good way to measure $E_{ES}$ at this time. Therefore we will initially assume for the purpose of our measurements that elastic strain energy, $E_{ES}$, remains equal to zero throughout the stride.

If one neglects $E_{ES}$, then the only way animals can increase $E_{tot}$ as they move along the ground is by using their muscles to convert chemical energy into mechanical work. Limits can be set on the rate at which muscles must perform this mechanical work.

An upper limit is obtained by simply adding $\dot{E}'_{KE,tot}$ and $\dot{E}_{CM,tot}$. This would be the case if there were no transfer of energy between the two. Fenn (1930a, b), Cavagna, Saibene & Margaria (1964), Elftman (1966) and Cavagna & Kaneko (1977) have made this assumption in calculating $\dot{E}_{tot}$ for human locomotion.

A lower limit for $\dot{E}_{tot}$ is obtained by adding the values for $E_{KE,tot}$ and $E_{CM,tot}$ at each instant during a stride, summing all the increments of $E_{tot}$ over the stride and dividing by the time for the stride. This procedure has been used by Elftman (1944), Clark & Alexander (1975) and Alexander & Vernon (1975) for humans and animals. This value assumes complete transfers of energy between $E_{CM,tot}$ and $E_{KE,tot}$. No transfer can take place during the aerial phase of a stride. However, during the stance phase some exchange is possible. For example, when the foot lands, some of the decrease in energy as the centre of mass slows (a decrease in $E_{CM,tot}$) can be used to accelerate the limbs forward relative to the centre of mass (an increase in $E_{KE,tot}$). The minimum rate at which muscles must work to increase the mechanical energy of the body as humans or animals move at a constant speed falls within these limits.

In addition to performing work to increase $E_{tot}$ within a stride, muscles also perform work as antagonistic muscles work against each other and/or against friction as animals move along the ground at a constant speed. However, all these forms of work appear to be small in comparison with $E_{tot}$, and therefore can be ignored for the purpose of this study. Alexander & Vernon (1975) have calculated that the work by

antagonistic muscles could account for only 15 % of the total positive work performed by a kangaroo hopping at 5·5 m s$^{-1}$. The frictional losses have been shown to be small at all but the highest speeds in terrestrial locomotion (Pugh, 1971). For example, in humans, which present a large frontal area to the air during running, wind resistance accounts for less than 2 % of the total mechanical power expended at 2·8 m s$^{-1}$ and less than 8 % at 8·3 m s$^{-1}$ (calculated from Cavagna & Kaneko, 1977; and Hill, 1927). Work to overcome friction against the ground is zero unless the animal is slipping (e.g. running on sand).

Muscular efficiency can be calculated by dividing the rate at which the muscles perform work by the rate at which they consume chemical energy, $\dot{E}_{metab}$. If muscles perform work at some optimal efficiency, independent of speed, when animals move along the ground (Hill, 1950; Alexander & Vernon, 1975), then $\dot{E}_{tot}$ should vary in the same way with speed and body size as $\dot{E}_{metab}$ (i.e. it would be some constant fraction of $\dot{E}_{metab}$).

## MATERIALS AND METHODS

### *Experimental approach*

In order to calculate the limits for the rates at which muscles must supply energy to increase $E_{tot}$ within a stride, we reviewed all the measurements of $E_{KE, tot}$ and $E_{CM, tot}$ for each animal to find experiments where both had been measured at the same speed. Using these data, we calculated the lower limits for $E_{tot}$ by adding $E_{KE, tot}$ and $E_{CM, tot}$ at each instant during the stride. The upper limit for $E_{tot}$ was calculated for all the animals in which both $E_{KE, tot}$ and $E_{CM tot}$ were measured by simply adding the two.

### *Animals*

Measurements of $E_{KE, tot}$ and $E_{CM, tot}$ at the same speeds (within ±5 %) were available for: a 44 g painted quail (*Excalfactoria chinensis*), a 61 g chipmunk (*Tamias striatus*), an 89 g chipmunk and a 5·0 kg dog (*Canis familiaris*).

### *Methods*

For those strides were both $E_{KE, tot}$ and $E_{CM, tot}$ had been measured at the same speed, $E_{KE, tot}$ was divided into 50 parts per stride for 3 strides. Each part was averaged with the corresponding parts of the other strides to produce an average $E_{KE, tot}$ as a function of time for one stride. $E_{CM, tot}$ was also divided into 50 parts per stride for as many strides as were available at a given speed (1–3 strides). Then $E_{KE, tot}$ and $E_{CM, tot}$ were added for each of the 50 parts to generate $E_{tot}$ as a function of time for one stride. The increments in the $E_{tot}$ curve were summed and divided by the stride period in order to calculate the lower limit of $\dot{E}_{tot}$. To determine the upper limit of $\dot{E}_{tot}$ for the same strides, we simply added the values for $\dot{E}_{KE, tot}$ and $\dot{E}_{CM, tot}$.

### Upper and lower limits for $\dot{E}_{tot}$

The changes in $E_{KE, tot}/M_b$, $E_{CM, tot}/M_b$ and $E_{tot}/M_b$ during an averaged stride are presented in Fig. 1 for a low-speed (0·4 m s$^{-1}$) and a high-speed (1·5 m s$^{-1}$) stride of a quail; a high-speed stride of two chipmunks (1·2 and 1·6 m s$^{-1}$); and a high-speed (3·7 m s$^{-1}$) stride of a dog. The upper and lower limits for $\dot{E}_{tot}$ obtained from these strides are given in Table 1. The difference between the upper and lower limits ranged between 7·5 and 33·7 %. The difference was greatest during the high-speed gallops of the 89 g chipmunk and 5000 g dog; therefore, the magnitude of the difference appears to increase with speed and does not appear to change dramatically with the size of the animal.

### Upper limit for $\dot{E}_{tot}$ as a function of speed and body size

The upper limit for $\dot{E}_{tot}/M_b$ as a function of speed can be obtained by simply adding the equations for $\dot{E}_{KE, tot}/M_b$ and $\dot{E}_{CM, tot}/M_b$ for those individuals where both had been measured in the second and third papers of this series. Equations for $\dot{E}_{tot}/M_b$ as a function of speed obtained in this manner are given in Table 2 and plotted in Fig. 2 for painted quails, chipmunks, dogs, turkeys and humans.
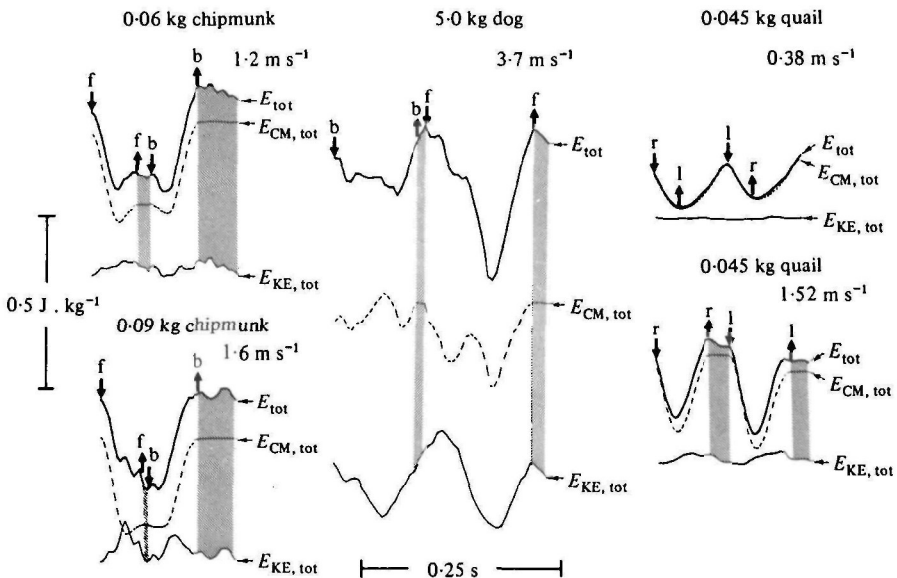


Fig. 1. Curves representing the average of three strides each for the $E_{KE, tot}$ (thin bottom lines), $E_{CM, tot}$ (middle dashed lines) and the instant-by-instant sum of the two, $E_{tot}$ (thick top lines). Curves shown are for one stride of a 60 g chipmunk galloping at 1·2 m s$^{-1}$ (upper left); a 90 g chipmunk galloping at 1·6 m s$^{-1}$ (lower left); a 5·0 kg dog galloping at 3·7 m s$^{-1}$; one stride (two steps) of a 45 g quail running at 0·38 m s$^{-1}$ (upper right); and one stride of the same quail running at 1·52 m s$^{-1}$. The shaded areas represent the aerial phases of the strides; the arrows pointing down labelled f, b, r, or l are for footdown for the front, back (quadrupeds), right or left (bipeds) feet, respectively. The arrows pointing up are for foot-up. The dashes in the $E_{CM, tot}$ curve are at 50 evenly spread intervals during the stride and show the 50 divisions into which each stride was divided (see text).

Table 1. *Upper and lower limits for the rates at which muscles must work to increase* $E_{tot}$ *within a stride as animals move along the ground at a constant speed (assuming no storage and recovery of elastic strain energy)*

| Animal | $M_b$ (kg) | Speed (m s$^{-1}$) | $\dot{E}_{tot, max}$ upper limit (W) | $\dot{E}_{tot, min}$ lower limit (W) | $\dfrac{\dot{E}_{tot, max} - \dot{E}_{tot, min}}{E_{tot, max}} \times 100$ (%) |
|---|---|---|---|---|---|
| Painted quail | 0·444 | 0·38 | 0·065 | 0·060 | 7·5 |
| (*Excalfactoria chinensis*) | | 1·52 | 0·116 | 0·100 | 13·0 |
| Chipmunk | 0·061 | 1·18 | 0·151 | 0·131 | 13·5 |
| (*Tamias striatus*) | | 1·60 | 0·283 | 0·188 | 33·7 |
| Dog (*Canis familiaris*) | 5·0 | 3·70 | 18·8 | 12·8 | 31·5 |

Table 2. *Equations for the mass-specific rate at which muscles must work to increase the kinetic and gravitational potential energy within a stride when animals move along the ground at a constant speed,* $\dot{E}_{tot}/M_b$ *in* $W\,kg^{-1}$

This equation assumes that no elastic storage and recovery of energy occurs. These equations were obtained by adding the equations for $\dot{E}_{KE,tot}/M_b$ and $\dot{E}_{CM\,tot}/M_b$ given in papers two and three. (See text for discussion of assumptions involved in these equations.)

$$\dot{E}_{tot}/M_b = \mathbf{a}v_g^{\mathbf{b}} + slope.v_g + intercept$$

| Animal | $M_b$ (kg) | a (J m$^{-1}$ kg$^{-1}$) | b | Slope (J m$^{-1}$ kg$^{-1}$) | Intercept (W kg$^{-1}$) |
|---|---|---|---|---|---|
| Painted quail | 0·043 | 0·448 | 1·75 | 1·68 | −0·053 |
| Chipmunk | 0·107 | 1·26 | 1·24 | 1·28 | 0·235 |
| Dog | 5·0 | 0·658 | 1·16 | 0·279 | −0·7 |
| Turkey | 6·4 | 0·210 | 1·59 | 0·398 | −0·45 |
| Human[1] | 70·0 | 0·230 | 1·93 | 0·33 | 0·657 |
| General equation (for all birds and mammals) | — | 0·478 | 1·53 | 0·685 | 0·072 |

[1] Data from Cavagna & Kaneko (1977) for running only.

A general equation relating the maximum limit for $\dot{E}_{tot}/M_b$ and speed for terrestrial locomotion can be obtained by adding the general equations for $\dot{E}'_{KE,\,tot}/M_b$ and $\dot{E}_{CM,\,tot}/M_b$ given in papers two and three of this series:

$$\dot{E}_{tot}/M_b = 0\cdot478 . v_g^{1\cdot53} + 0\cdot685 . v_g + 0\cdot072, \tag{1}$$

where $\dot{E}_{tot}/M_b$ is in W kg$^{-1}$ and $v_g$ is in m s$^{-1}$. This equation is independent of body size, applying equally as well to chipmunk and quail as to horse and ostrich.

## DISCUSSION

### $\dot{E}_{metab}$ *and* $\dot{E}_{tot}$ *as a function of speed and body mass*

In the first paper of this series it was found that the metabolic energy consumed by each gram of an animal as it moves along the ground at a constant speed increases linearly with speed and varies with $M_b^{-0\cdot3}$. In marked contrast, the total mechanical work performed by each gram of muscle to replace losses in kinetic and gravitational energy during each stride increases curvilinearly with speed and is independent of body mass (i.e. $M_b \propto_b^0$). If we compare different-sized animals running at the same
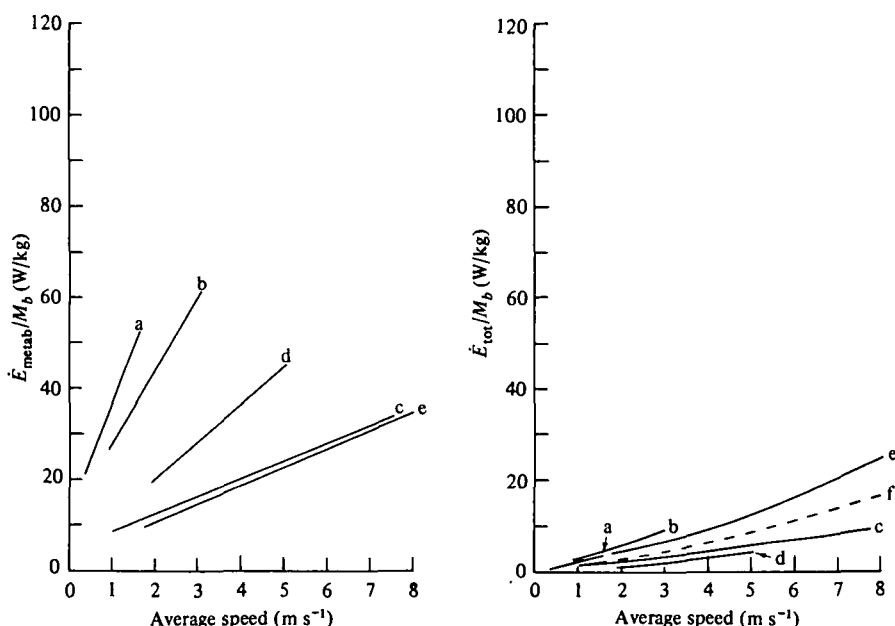
Fig. 2. *Left.* Mass-specific metabolic energy input, $\dot{E}_{metab}/M_b$ calculated from the general equation given in paper one of this series, is plotted as a function of running speed for the following animals: a, 43 g painted quail; b, 107 g chipmunk; c, 5·0 kg dog; d, 6·4 kg turkey; e, 70 kg human. The steady-state oxygen consumption per gram body mass of running animals increases nearly linearly with speed and decreases dramatically with increasing body size. *Right.* The total mass-specific mechanical power required to maintain the oscillations in kinetic and potential energy of the body as animals run at a constant average speed, $\dot{E}_{tot}/M_b$, is plotted as a function of speed. Although there is a fair amount of scatter in the data, the total power output does not appear to be size-dependent; the dotted line (f) shows the average total mechanical power output calculated by adding the general equations for $\dot{E}'_{KE,tot}/M_b$ and $\dot{E}_{CM,tot}/M_b$ given in papers two and three for a greater diversity of animals. $\dot{E}_{tot}/M_b$ increases curvilinearly with speed and is independent of size.

speed we find, for example, that each gram of a 30 g quail or chipmunk running at 3 m s$^{-1}$ consumes metabolic energy at a rate about 15 times that of a 100 kg ostrich, horse or human running at the same speed, while their muscles are performing work at about the same rate.

A. V. Hill (1950) made predictions based on dimensional arguments (see paper 1) that the mass-specific work per stride would be the same for large and small animals running at their top speed. By assuming that muscular efficiency was constant, he concluded that the mass-specific metabolic energy consumed per stride would also be the same for large and small animals. Measurements of $\dot{E}_{metab}/M_b$ and $\dot{E}_{tot}/M_b$ have not been made at top speed: however, Heglund, Taylor & McMahon (1974) have proposed that the trot–gallop transition speed is a 'physiologically equivalent' speed at which animals of different size can be compared.

In the first paper of this series, it was found that the amount of metabolic energy consumed per gram per stride at this equivalent speed was approximately the same for animals of different size, suggesting that Hill's logic and assumptions were correct. However, Hill seems to have arrived at the correct conclusions for the wrong reason

Table 3. *Energy consumed and mechanical work performed during a stride by each gram of large and small quadrupeds moving at a 'physiologically equivalent speed' (trot–gallop transition)*

Speed and stride frequency at the trot–gallop transition are calculated from the allometric equations given by Heglund, Taylor & McMahon (1974); the rate of energy consumption at this speed was calculated using the general equation for $\dot{E}_{metab}/M_b$ from the first paper of this series; and the rate at which muscles performed mechanical work was calculated using the general equation for $\dot{E}_{tot}/M_b$ in this paper.

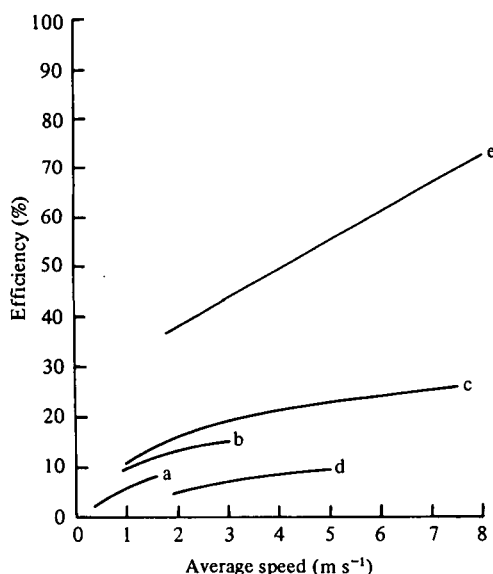| Body mass (kg) | Speed at trot–gallop transition (m.s⁻¹) | Metabolic energy consumed per kg J stride⁻¹ kg⁻¹ | Mechanical work performed per kg J stride⁻¹ kg⁻¹ | Efficiency (%) |
|---|---|---|---|---|
| 0·01 | 0·51 | 5·59 | 0·07 | 1·24 |
| 1·0 | 1·53 | 5·00 | 0·46 | 9·11 |
| 100 | 4·61 | 5·53 | 0·35 | 62·9 |



Fig. 3. Muscular efficiency, calculated as the ratio of total mechanical work production to metabolic energy input (as a percentage), as a function of running velocity for: a, 43 g painted quail; b 107 g chipmunk; c, 5·0 kg dog; d, 6·4 kg turkey; and e, 70 kg human. Efficiency increases with running speed and decreases with decreasing body size.

Although energy consumed by each gram of muscle per stride is independent of size at the trot–gallop transition speed, Table 3 shows that the mass-specific mechanical work performed per step is much smaller in the smaller animals, and as a result, the muscular efficiency (expressed as the ratio between $\dot{E}_{metab}$ and $\dot{E}_{tot}$, per cent) increases with increasing body size (Table 3 and Fig. 3). The highest efficiency observed in the 44 g quail was about 7 % while the efficiency of the 70 kg human reached 73 %. Therefore, we must conclude from our measurements that we cannot explain the changes in metabolic energy consumption observed with changing speed and body size simply by parallel changes in mechanical work performed by the muscles.

Our findings are in general agreement with those of Alexander and his colleagues (Alexander, 1977, 1980). Their calculations of muscular work are based upon measurement of the forces and displacements of the muscles during locomotion; work force × displacement. This is in contrast to our calculations of muscular work based upon measurements of the energy changes of the bodies of running animals; work ⩾ increments in total energy of the body. The technique used by Alexander has the advantage of giving an indication of elastic storage of energy, $\dot{E}_{ES}$, for both small and large animals, and puts a lower limit on the work done by antagonistic muscles upon each other. We arrive at similar results in spite of the difference in experimental procedure.

### Elastic energy: its importance in large animals

Because we were unable to measure elastic energy accurately, our measurements have assumed no storage of energy in, or recovery from, elastic elements. Yet the observed efficiencies of greater than 25 % for larger animals demonstrate that storage and recovery of elastic energy occurs and that it becomes very important when large animals move at high speeds. Vertebrate striated muscles are generally found to be capable of attaining efficiencies of about 25 % for performing positive work without a pre-stretch, i.e. without the help of elastic energy storage and recovery (Hill, 1950; Cavagna et al. 1964). These values have been obtained both in experiments on isolated muscles (Hill, 1939; Heglund & Cavagna, submitted) and whole animals (Margaria, 1976; Dickinson, 1929). Therefore, efficiencies of greater than 25 % can be interpreted as demonstrating that storage of energy in elastic elements occurs in one part of the stride and that this energy is recovered in another.

Although our values demonstrate the importance of storage and recovery of elastic energy in larger animals, they cannot confirm or exclude the use of elastic storage by small animals. It may be that the same relative amount of kinetic and gravitational energy is stored in elastic energy in small animals as in large, and that other factors are responsible for the higher rates of metabolic energy consumption by the muscles of smaller animals. However, a recent study by Biewener, Alexander & Heglund (1981) has shown that the tendons of small kangaroo rats are relatively thicker than those of the larger wallabies and kangaroos. As a result of the thicker tendons, the kangaroo rats store a much smaller fraction of the decrements in $E_{tot}$ when they land than has been observed in the larger animals (Alexander & Vernon, 1975). The size dependency of storage and recovery of elastic energy needs more study.

### How do muscles use the energy they consume?

It seems clear from these studies that the rate at which animals consume metabolic energy during locomotion cannot be explained simply by assuming a constant link between the metabolism and the positive mechanical work performed by their muscles (i.e. constant efficiency). Muscles are active, generate force and consume energy not only when they shorten and perform mechanical work (positive work), but also when their length is unchanged (zero work) as they stabilize joints, and when they are stretched (work is done on the active muscles, negative work). Perhaps it is simply the metabolic cost of generating force that, to a large extent, determines the rate of energy consumption. Recently, Taylor, Heglund, McMahon & Looney (1980

reported that the metabolic cost of generating muscular force in running animals increases linearly with speed and is proportional to $M_b^{-0.33}$ (in the same manner as energy cost of running).

Muscular force must be generated and decay more rapidly as an animal increases its speed. This is accomplished by recruiting muscle fibres which have more rapid rates of actin–myosin cross-bridge cycling. Since each cross-bridge cycle consumes a unit of energy, the increase in energy cost of locomotion with speed could be the result of the recruitment of faster fibres with faster cycling times.

Muscular force must also be generated and decay more rapidly in small animals than in large ones because the small animal takes more steps per unit time to move at the same speed (Heglund *et al.* 1974). Equivalent muscles of small animals have faster fibres with more rapid cross-bridge cycling rates than those of large animals (Close, 1972). This decrease in rate of cross-bridge cycling with increasing body size could help account for the scaling factof of $-0.3$ for the mass-specific energy cost of running.

Finally, there is evidence showing that the cost of pumping calcium by the muscles may be as high as 30 % of the total cost of an isometric twitch (Homsher, Mommaerts, Ricchiuti & Wallner, 1972). If this 'activation cost' were about the same for each contraction per gram of muscle, then the mass-specific rate at which energy would need to be supplied to activate the muscle, like the cost of force generation, would increase with speed and with body size in a manner paralleling stride frequency.

### CONCLUSIONS

We have found that the rate at which muscles of running animals perform mechanical work during locomotion does not provide a simple explanation for either the linear increase in metabolic rate with speed, or the regular change in cost of locomotion with body size. It seems likely that the energetic costs involved in generating force and activating the muscles may provide such a simple explanation, and we are currently investigating these possibilities.

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