

ENERGETICS AND MECHANICS OF TERRESTRIAL LOCOMOTION

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

N. C. HEGLUND, M. A. FEDAK, C. R. TAYLOR AND G. A. CAVAGNA*

*Museum of Comparative Zoology, Harvard University, Old Causeway Road,
Bedford, MA 01730, USA and*

**Istituto di Fisiologia Umana, dell'Universita di Milano, Milano, Italy*

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 $W \text{ kg}^{-1}$ 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} :

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

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 (1930*a, 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 $E_{\text{KE, tot}}$ and $E_{\text{CM, tot}}$ 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 $E_{\text{KE, tot}}$ and $E_{\text{CM, tot}}$ at each instant during the stride. The upper limit for E_{tot} was calculated for all the animals in which both $E_{\text{KE, tot}}$ and $E_{\text{CM, tot}}$ were measured by simply adding the two.

Animals

Measurements of $E_{\text{KE, tot}}$ and $E_{\text{CM, tot}}$ at the same speeds (within $\pm 5\%$) 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 where both $E_{\text{KE, tot}}$ and $E_{\text{CM, tot}}$ had been measured at the same speed, $E_{\text{KE, tot}}$ 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 $E_{\text{KE, tot}}$ as a function of time for one stride. $E_{\text{CM, tot}}$ was also divided into 50 parts per stride for as many strides as were available at a given speed (1–3 strides). Then $E_{\text{KE, tot}}$ and $E_{\text{CM, tot}}$ 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 $\dot{E}_{\text{KE, tot}}$ and $\dot{E}_{\text{CM, tot}}$.

RESULTS

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.

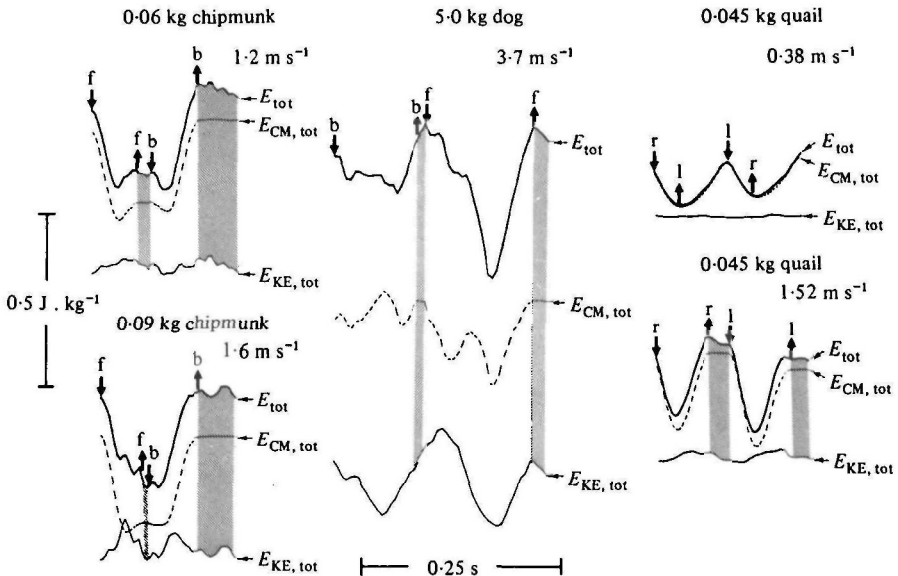


Fig. 1. Curves representing the average of three strides each for the $E_{KE, tot}$ (thin bottom lines), $E_{CM, tot}$ (middle dashed lines) and the instant-by-instant sum of the two, E_{tot} (thick top lines). Curves shown are for one stride of a 60 g chipmunk galloping at 1.2 m s^{-1} (upper left); 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 \dot{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)	$\frac{\dot{E}_{tot, max} - \dot{E}_{tot, min}}{\dot{E}_{tot, max}} \times 100$ (%)
Painted quail (<i>Excalfactoria chinensis</i>)	0.444	0.38	0.065	0.060	7.5
Chipmunk (<i>Tamias striatus</i>)	0.061	1.52	0.116	0.100	13.0
Dog (<i>Canis familiaris</i>)	5.0	1.18	0.151	0.131	13.5
		1.60	0.283	0.188	33.7
		3.70	1.8.8	1.2.8	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.)

Animal	M_b (kg)	$\dot{E}_{tot}/M_b = a v_g^b + \text{slope} \cdot v_g + \text{intercept}$			
		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:

$$\dot{E}_{tot}/M_b = 0.478 \cdot v_g^{1.53} + 0.685 \cdot v_g + 0.072, \tag{1}$$

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 $M_b^{-0.3}$. 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. $M_b \propto v_g^0$). If we compare different-sized animals running at the same

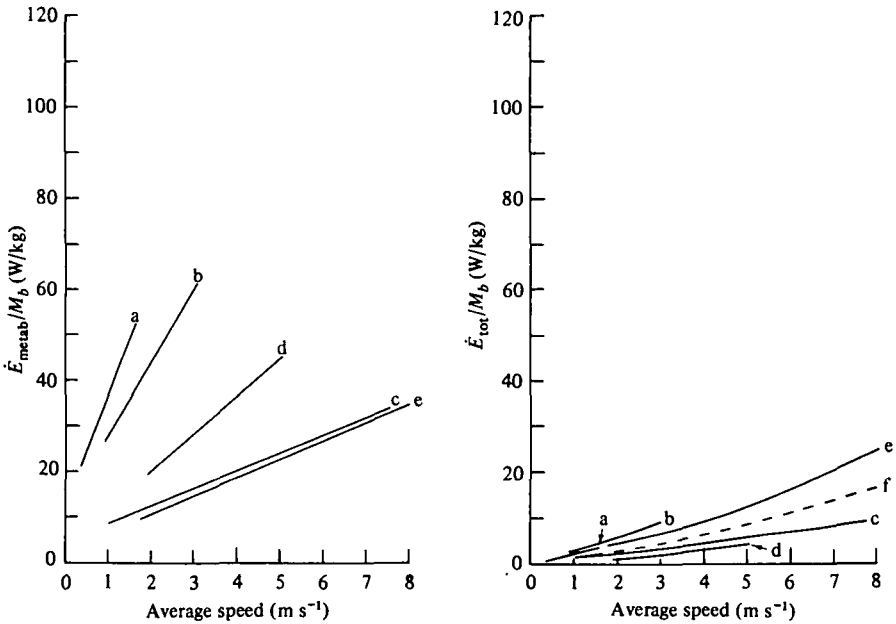


Fig. 2. *Left.* Mass-specific metabolic energy input, \dot{E}_{metab}/M_b calculated from the general equation given in paper one of this series, is plotted as a function of running speed for the following animals: a, 43 g painted quail; b, 107 g chipmunk; c, 5.0 kg dog; d, 6.4 kg turkey; e, 70 kg human. 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 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 $\dot{E}_{\text{metab}}/M_b$ 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

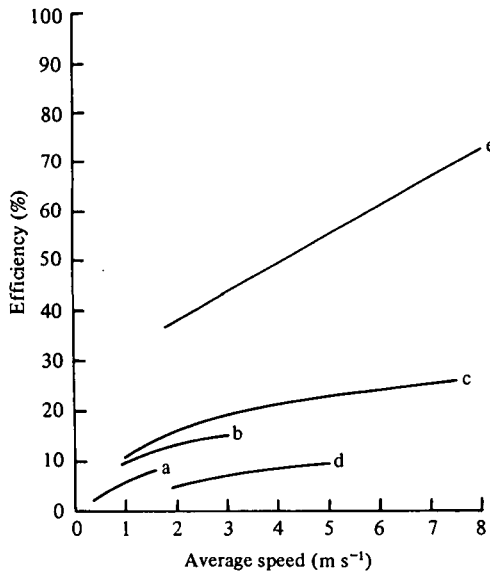


Fig. 3. Muscular efficiency, calculated as the ratio of total mechanical work production to metabolic energy input (as a percentage), as a function of running velocity for: a, 43 g painted quail; b, 107 g chipmunk; c, 5.0 kg dog; d, 6.4 kg turkey; and e, 70 kg human. Efficiency increases with running 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 \times 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 \geq 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 factor 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.

This work was supported by NSF grants PCM 75-22684 and PCM 78-23319, NRS training grant 5 T 32 GM 07117 and NIH post-doctoral fellowship 1 F 32 AM 06022.

REFERENCES

- ALEXANDER, R. MCN. (1977). Terrestrial locomotion. In *Mechanics and Energetics of Animal Locomotion* (ed. R. McN. Alexander & G. Goldspink). London: Chapman & Hall.
- ALEXANDER, R. MCN. (1980). Optimum walking techniques for quadrupeds and bipeds. *J. Zool., Lond.* **192**, 97-117.
- ALEXANDER, R. MCN. & VERNON, A. (1975). The mechanics of hopping by kangaroos (*Macropodiade*). *J. Zool., Lond.* **177**, 265-303.
- BIEWENER, A. A., ALEXANDER, R. MCN. & HEGLUND, N. C. (1981). Elastic energy storage in the hopping kangaroo rats (*Dipodomys spectabilis*). *J. Zool., Lond.* (in the Press).
- CAVAGNA, G. A. & KANEKO, M. (1977). Mechanical work and efficiency in level walking and running. *J. Physiol., Lond.* **268**, 467-481.
- CAVAGNA, G. A., SAIBENE, F. P. & MARGARIA, R. (1964). Mechanical work in running. *J. appl. Physiol.* **19**, 249-256.
- CLARK, J. & ALEXANDER, R. MCN. (1975). Mechanics of running by quail (*Coturnix*). *J. Zool., Lond.* **176**, 87-113.

- CLOSE, R. I. (1972). Dynamic properties of mammalian skeletal muscles. *Physiol. Rev.* **52**, 129-197.
- DICKINSON, S. (1929). The efficiency of bicycle pedalling, as affected by speed and load. *J. Physiol. Lond.* **67**, 242-255.
- ELFTMAN, H. (1944). Skeletal and muscular systems: structure and function. In *Medical Physics* (ed. O. Glasser). Chicago: Year Book Publishers.
- ELFTMAN, H. (1966). Biomechanics of muscle with particular application to studies of gait. *J. Bone Joint Surg.* **48 A**, 363-377.
- FENN, W. O. (1930a). Frictional and kinetic factors in the work of sprint running. *Am. J. Physiol.* **92**, 583-611.
- FENN, W. O. (1930b). Work against gravity and work due to velocity changes in running. *Am. J. Physiol.* **93**, 433-462.
- HEGLUND, N. C. & CAVAGNA, G. A. Oxygen consumption, mechanical work and efficiency in isolated muscle (submitted).
- HEGLUND, N. C., TAYLOR, C. R. & MCMAHON, T. A. (1974). Scaling stride frequency and gait to animal size: mice to horses. *Science, N. Y.* **186**, 1112-1113.
- HILL, A. V. (1927). The air resistance to a runner. *Proc. R. Soc. B* **102**, 380-385.
- HILL, A. V. (1939). The mechanical efficiency of frog muscle. *Proc. R. Soc. B* **127**, 434-451.
- HILL, A. V. (1950). The dimensions of animals and their muscular dynamics. *Sci. Prog., Lond.* **38**, 209-230.
- HOMSHER, E., MOMMAERTS, W. F. H. M., RICCHIUTI, N. V. & WALLNER, A. (1972). Activation heat, activation metabolism and tension related heat in frog semitendinosus muscles. *J. Physiol., Lond.* **220**, 601-625.
- MARGARIA, R. (1976). *Biomechanics and Energetics of Muscular Exercise*, p. 76. Oxford: Clarendon Press.
- PUGH, L. G. C. E. (1971). The influence of wind resistance in running and walking and the efficiency of work against horizontal or vertical forces. *J. Physiol., Lond.* **213**, 255-276.
- TAYLOR, C. R., HEGLUND, N. C., MCMAHON, T. A. & LOONEY, T. R. (1980). Energetic cost of generating muscular force during running: a comparison of large and small animals. *J. exp. Biol.* **86**, 9-18.