ENERGETIC COST OF GENERATING MUSCULAR FORCE DURING RUNNING

A COMPARISON OF LARGE AND SMALL ANIMALS

By C. RICHARD TAYLOR, NORMAN C. HEGLUND, THOMAS A. McMAHON† AND TODD R. LOONEY

Museum of Comparative Zoology and †Division of Engineering and Applied Physics, Harvard University, Cambridge, MA 02138, U.S.A.

SUMMARY

The energetic cost of generating muscular force was studied by measuring the energetic cost of carrying loads in rats, dogs, humans, and horses for loads ranging between 7 and 27% of body mass.

Oxygen consumption increased in direct proportion to mass supported by the muscles, i.e.

$$\frac{\dot{V}_{O_2, L}/\dot{V}_{O_2}}{m_L/m} = 1 \cdot 01 \pm \text{S.D.} \pm 0 \cdot 017,$$

where $\dot{V}_{O_2, L}$ is the oxygen consumption of the animal running with a load, $\dot{V}_{O_2}$ is the oxygen consumption at the same speed without a load, m_L is the mass of the animal plus the load, and m is the mass of the animal.

Stride frequency, average number of feet on the ground over an integral number of strides, the time of contact of each foot relative to the other feet, and the average vertical acceleration during the contact phase were not measurably changed by the loads used in our experiments. From these observations we conclude that the average accelerations of the centre of mass of the animal are not changed by carrying the loads, and that muscular force developed by the animal increases in direct proportion to the load.

It follows that the rate of energy utilization by muscles of an animal as it runs along the ground at any particular speed is nearly directly proportional to the force exerted by its muscles.

The energetic cost of generating force over an interval of time ($\int F dt$) increases markedly with running speed.

An important consequence of the direct proportionality between increased oxygen consumption and mass of the load is that small animals expend much more energy to generate a given force at a given speed than large animals.

INTRODUCTION

This paper addresses the question of how muscles use energy as animals move along the ground at a constant speed. Most attempts to explain the energetics of terrestrial locomotion have assumed that the major energetic cost occurs when

muscles shorten and perform mechanical work (Fenn, 1930; Hill, 1950; Cavagna, Saibene & Margaria, 1964; McMahon, 1975; Alexander, 1976; Cavagna, Heglund & Taylor, 1977). Furthermore, it is generally assumed that the muscles perform this work at close to their maximal efficiency, which is though to be nearly the same for all vertebrate striated muscle (Hill, 1950; Alexander, 1973; Alexander & Goldspink, 1977). Recent studies scaling the mechanical work performed by running animals to body size indicate that these assumptions are not justified. Mass specific energy cost of locomotion varies as a regular function of body size (Taylor, Schmidt-Nielsen & Raab, 1970; Taylor, 1977), while mass specific mechanical work of locomotion is nearly independent of body size (Heglund, 1979; Heglund *et al.* 1979). For example, a 30 g mouse uses approximately 15 times as much energy to move each gram of its body a given distance along the ground as a 100 kg pony, but the mechanical work per unit mass which is necessary to keep each gram of its body moving at a constant speed is the same for the mouse and the pony. Thus it appears that the energy consumed by muscles of running animals is not used primarily for performing work.

If the amount of mechanical work performed by muscles does not determine the amount of energy they use when animals run at a constant speed, what are the other activities that the muscles are involved in that require energy? It is useful to think of muscles as 'biological machines' for converting chemical energy into force. If they shorten while generating force, they perform mechanical work (work = force × distance). However, during level running, the muscles of an animal generate force and consume energy not only while they are shortening, but also while they are being stretched (e.g., to slow the animal's fall and to reverse the direction of its limbs) and while their length remains constant (to stabilize the joints). Work is performed on the active muscle when it is stretched, and no work is done by the active muscle when its length does not change.

It seemed reasonable to postulate that the rate at which muscles of running animals consume energy might be related to the magnitude of the integral of force over the time during which it is developed during running. The area under the curve of muscle force *v.* time (the so-called tension-time integral) is commonly related to energy consumption in both isolated and *in situ* skeletal muscle experiments and in studies of heart muscle. The tension-time integral determines the rate of energy consumption for isometric muscular activities (Feng, 1931; Sandberg & Carlson, 1966).

We have been able to increase the force-time integral of the muscles of a running animal by known amounts while simultaneously measuring oxygen consumption. This enables us to determine the increments in energy utilization for known increments of force-time integral. We have applied this technique to animals over a nearly 3-orders of magnitude range of body mass.

<div style="text-align:center">MATERIALS AND METHODS</div>

Animals

Twenty six white rats (all male, average weight 274 g), two dogs (one male, average weight 27 kg and one female, average weight 23 kg), two humans (both males, average weights of 72 and 101 kg), and two horses (both females, average weights of 114 and

124 kg) were utilized in these experiments. The rats were housed in activity wheels and the other animals were exercised regularly before and during the experiments.

Training

All subjects were trained to run on the treadmill while carrying a load equal to between 20 and 30% of their body mass. Special harnesses were constructed for the horses, dogs and rats which allowed the load to be evenly distributed along the length of the back. The human subjects wore commercially available back packs with a metal frame. Lead shot packed in foam rubber was used for adjusting the load to the desired mass. The oxygen consumption at a given speed declined as the training progressed until it reached a constant value after a period of one to three weeks. A subject was considered to be trained once this constant value was obtained. Only data from trained subjects were used in this study.

Oxygen consumption

Rate of oxygen consumption was measured while subjects ran on a treadmill for 15 min without a load, followed by 15 min with a load, and another 15 min without a load. The loading conditions and the speeds used with each experimental animal under each condition are given in Table 1.

The rats ran in a plexiglass box which slid along the surface of the tread (analogous to a mask enclosing the entire animal) and the other animals all wore light-weight masks during measurement of oxygen consumption. Air was metered through the box or the masks at rates between 3 and 10 l/min (STP) for the rats and between 200 and 600 l/min (STP) for the dogs, humans and horses. The difference in oxygen concentration of dry air (dried with Drierite) entering and leaving the mask (Δ_{O_2}) was measured using a Beckman Model F-3 oxygen analyzer. Rate of oxygen consumption was calculated assuming an RQ of 0·80 using equation 1. RQ was measured in a number of experiments with each animal to ensure that this value was reasonable. The equation:

$$\dot{V}_{O_2} = \frac{\dot{Flow}_{mask}\,(\Delta_{O_2})}{0\cdot9581}, \tag{1}$$

was used to calculate $\dot{V}_{O_2}$ as described by Tucker (1968) for a similar system where $\dot{Flow}_{mask}$ is the flow out of the mask.

The rat chamber and mask were checked for leaks of exhaled air by decreasing the flow rate by 30% as the O_2 consumption was monitored. This procedure should increase the magnitude of any loss of exhaled air. No difference was found between the two measurements indicating that there were no leaks. The flow meters were calibrated daily by passing N_2 through the mask at a known rate and measuring the changes in oxygen concentration using the equation:

$$\dot{Flow}_{mask} = \frac{\dot{Flow}_{N_2}\,(0\cdot2094)}{\Delta_{O_2}}. \tag{2}$$

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

Three approaches were taken to determine whether acceleration of the animal changed when they carried loads: (1) stride frequency was measured under the same
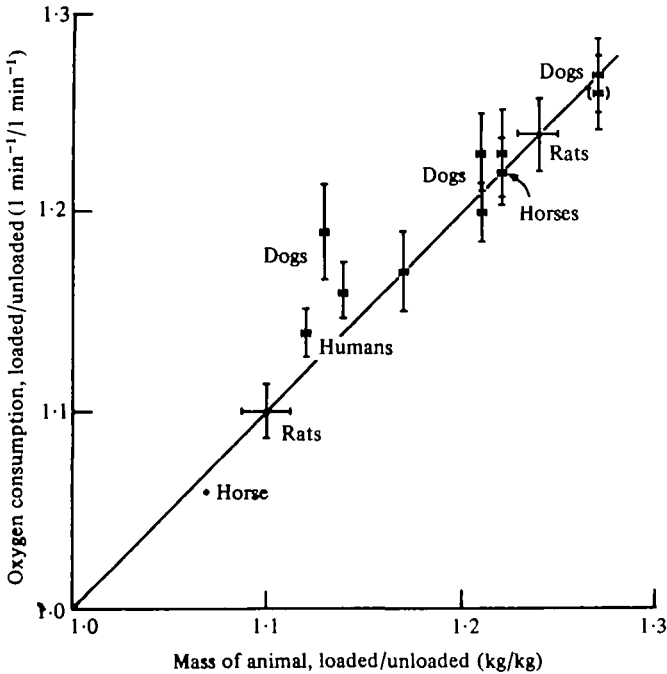
Fig. 1. Oxygen consumption ratio *v.* animal weight ratio loaded/unloaded. Each point represents the mean of a single running speed. The vertical bars represent $\pm$ 2 S.E. of the mean of the ratio of the oxygen consumption measured while the animal carried a load to its oxygen consumption when the animal ran at the same speed without a load. The horizontal bars represent ± 2 S.E. of the ratio of loaded to unloaded mass. The solid line is drawn to show direct proportionality of 1 between the two ratios. The parenthesis around the dog point at 1·27 represent identical results for this loading condition for two speeds.

speed and loading conditions as oxygen consumption; (2) time of contact of each foot relative to the other feet was measured while horses and dogs ran at a variety of speeds with and without loads (using high speed films); and (3) vertical accelerations of horses and dogs were measured at a variety of speeds and loading conditions (using an accelerometer attached to the back of the animals).

Stride frequency was determined three times for each experimental condition where oxygen consumption was measured. The interval for 25 strides was timed with a stopwatch.

Time of contact of each foot relative to the other feet was determined from cine films taken at 200 frames/s^{-1} with an Eclair GV-16 camera. The dogs and ponies were filmed from the side at an angle which enabled us to see their feet and the tread clearly. A clock that made 10 revolutions per second was placed in the field of view and served as a time calibration. Two dogs were filmed at three speeds (1·97, 2·54 and 3·91 m/s^{-1}) and four loading conditions (1·0, 1·16, 1·22 and 1·26 times body mass). One horse was filmed at two speeds (2·68 and 3·14 m/s^{-1}) and three loading conditions (1·0, 1·07, and 1·22 times body mass).

Both the vertical acceleration and its integral, the vertical velocity, were measured by mounting a linear accelerometer (Entran Model no. E6C-240-5D) on the backs of the dogs and horses just caudal to the scapula, in a position estimated to be above

Table 1. *Rate of oxygen consumption increased in direct proportion to the mass supported by the muscles of humans and three species of animals when they ran at a constant speed on a treadmill*

(This was found for all the speeds and loading conditions used in our experiments. Mass with (m_L) and without (m) a load and the rate of oxygen consumption with ($\dot{V}_{O_2}$) and without ($\dot{V}_{O_2,L}$) a load are given for four species at each of the tread speeds and loading conditions used in our experiments. Values are expressed as means ± standard error and n is the number of experiments.)

Animal	n	Speed (m/s)	m (kg)	m_L (kg)	m_L/m	$\dot{V}_{O_2}$ (l/min)	$\dot{V}_{O_2,L}$ (l/min)	$\dot{V}_{O_2,L}/\dot{V}_{O_2}$	$\dfrac{\dot{V}_{O_2,L}/\dot{V}_{O_2}}{m_L/m}$
White rat	12	0.52	0.270±0.010	0.297±0.010	1.10±0.006	0.0183±0.0003	0.0202±0.0002	1.10±0.007	1.00
	74	0.52	0.278±0.005	0.345±0.005	1.24±0.005	0.0191±0.0003	0.0237±0.0002	1.24±0.009	1.00
Dog	24	1.97	23.07±0.09	26.33±0.09	1.14±0.008	0.669±0.004	0.773±0.004	1.16±0.007	1.02
	24	1.97	22.58±0.07	27.31±0.07	1.21±0.0009	0.657±0.005	0.788±0.006	1.20±0.008	0.99
	24	1.97	22.59±0.07	28.68±0.07	1.27±0.0007	0.648±0.004	0.817±0.004	1.26±0.009	0.99
	12	2.61	22.34±0.13	25.26±0.13	1.13±0.0011	0.805±0.006	0.955±0.007	1.19±0.012	1.05
	12	2.61	22.78±0.11	27.50±0.11	1.21±0.0009	0.825±0.006	1.013±0.006	1.23±0.010	1.02
	12	2.61	22.91±0.10	29.00±0.10	1.27±0.0009	0.811±0.003	1.016±0.004	1.26±0.009	0.99
	12	3.89	22.73±0.07	26.52±0.07	1.17±0.0011	1.373±0.004	1.604±0.003	1.17±0.010	1.00
	12	3.89	21.79±0.09	26.52±0.09	1.22±0.0012	1.236±0.004	1.524±0.004	1.23±0.011	1.01
	12	3.89	22.29±0.10	28.35±0.10	1.27±0.0010	1.287±0.003	1.638±0.004	1.27±0.009	1.00
Human	28	2.92	86.63±2.86	97.41±2.78	1.12±0.0007	3.370±0.071	3.841±0.073	1.14±0.006	1.02
Horses	12	3.11	118.8±0.15	145.4±0.15	1.22±0.001	2.943±0.003	3.587±0.003	1.22±0.008	1.00
	1	2.69	100.0	106.9	1.07	1.729	1.835	1.06	0.99

Table 2. *Average number of feet on the ground over an integral number of strides as a function of load and tread speed*

Loading dogs and horses had little effect on average number of feet on the ground at a given speed. Values are means ± s.e. of 30 strides. Loads are expressed as the mean ratio of the mass of the animal plus the load (m_L) to the mass of the animal (m).

		Average number of feet on the ground				
Animal	Speed (m/s)	Unloaded ($m_L/m = 1\cdot00$)	7% load ($m_L/m = 1\cdot07$)	16% load ($m_L/m = 1\cdot16$)	22% load ($m_L/m = 1\cdot22$)	26% load ($m_L/m = 1\cdot26$)
Dogs	1·97	2·05 ± 0·007	—	2·07 ± 0·014	2·16 ± 0·022	2·11 ± 0·008
	2·61	1·95 ± 0·016	—	1·83 ± 0·015	1·83 ± 0·014	1·94 ± 0·011
	3·91	1·49 ± 0·014	—	1·54 ± 0·015	1·60 ± 0·19	1·59 ± 0·14
Horse	2·67	1·91 ± 0·016	1·89 ± 0·024	—	1·96 ± 0·025	—
	3·14	1·76 ± 0·017	1·75 ± 0·014	—	1·78 ± 0·021	—

Dog (unloaded)

3·89 m/s
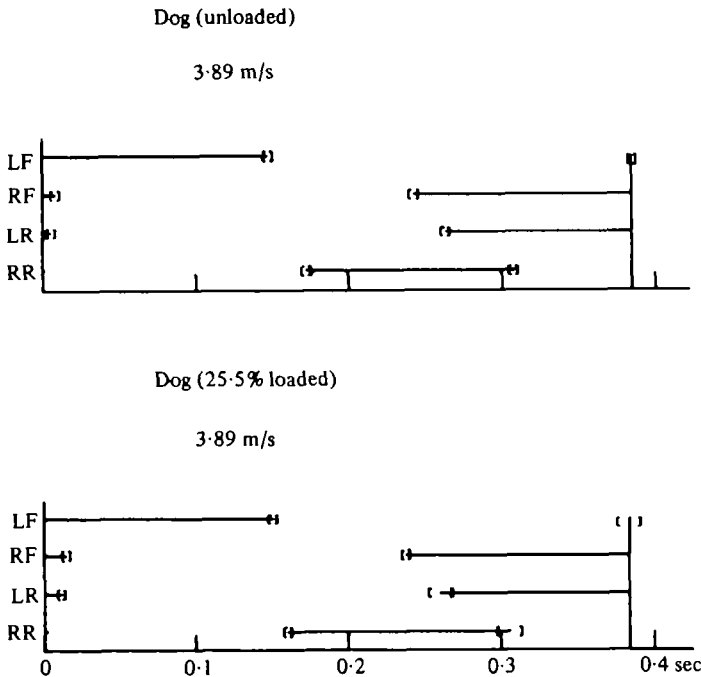

Dog (25·5% loaded)

3·89 m/s

Fig. 2. Footfall pattern of a dog carrying a load equal to 25·5% of its body mass is compared with the pattern of the same dog running without a load. Each pattern represents the average of 10 strides. The bars at the end of each solid line show the s.e. of the mean. Right and left forelimb and right and left hindlimb are shown as RF, LF, RR, LR, respectively. The loaded and unloaded patterns stayed the same in trained dogs and horses, even though the animals carried up to 26% of body weight on their backs in specially designed packs.

Table 3. *Stride period and average vertical acceleration during the supported phase*

Animal	Mass		Speed (m/s)	Stride period		Vertical acceleration during supported phase divided by gravity	
	Unloaded (kg)	Loaded (kg)		Unloaded (sec)	Loaded (sec)	Unloaded	Loaded
Horse	114·0	143·4	1·94, trot	0·635	0·665	1·443	1·471
			3.00, trot	0·563	0·575	1·756	1·753
			4·42, trot	0·454	0·461	2·072	2·033
			5·00, gallop	0·401	0·400	1·849	1·799
			5·78, gallop	0·417	0·380	1·944	1·955
			6.67, gallop	0·412	0·405	2·040	2·012
Dog	23·6	27·2	1·67, trot	0·539	0·537	1·598	1·658
			2·56, trot	0·459	0·461	1·896	1·859
			2·94, trot	0·442	0·442	1·920	1·939
			3.39, trot	0·403	0·407	2·136	2·145
			5·00, gallop	0·369	0·366	1·469	1·525
			7·78, gallop	0·341	0·323	1·908	1·799

the centre of mass. Continuous recordings were made using a Grass Instruments polygraph (Model 5 A).

RESULTS

Oxygen consumption increased almost in direct proportion to the mass supported by the muscles in all of our experiments, i.e. there was approximately a 10% increase in $\dot{V}_{O_2}$ when the load was equal to 10% of body mass, a 20% increase when the load was 20%, etc. (Fig. 1). This direct proportionality

$$\left(\frac{\dot{V}_{O_2, L}/\dot{V}_{O_2}}{m_L/m} \simeq 1 \right),$$

was found for trotting rats, trotting and galloping dogs, running humans, and trotting horses carrying loads ranging between 7% and 27% of their body mass (Table 1). The mean of the individual proportionality constants determined for each experimental condition was 1·01 ± S.D. 0·017.

There was no systematic change in stride frequency as a result of carrying these loads and the maximum difference between the loaded and unloaded frequency in any experiment was less than 1·5%.

The average number of feet supporting the animal over an integral number of strides decreased with increasing speed, but was not changed as a result of carrying load (Table 2). The time of contact of each foot relative to the other feet was also approximately the same when animals ran with and without a load. Fig. 2 demonstrates the absence of any effect of load on foot fall patterns under a 'worst case' situation in our experiments: it compares the foot fall patterns of a dog running at the heaviest loading condition and the highest speed used in our experiments with those of the dog running at the same speed without any load.

The average upward vertical acceleration during the time the feet were in contact with the ground measured using the accelerometer was approximately the same when the horses and dogs ran at the same speed with and without a load (Table 3).

The average ratio of vertical accelerations of the loaded/unloaded animal was 1·01 ± 0·01.

<div align="center">DISCUSSION</div>

We conclude from our results that the rate of energy utilization by the muscles of an animal as it runs along the ground at any particular speed is nearly directly proportional to the force exerted by its muscles. This conclusion follows from our finding that the increase in metabolic rate ($\Delta \dot{V}_{O_2}$) was directly proportional to the increase in mass supported by the muscles (Δm)

$$\Delta \dot{V}_{O_2} = k\Delta m, \tag{3}$$

if (1) the accelerations of centre of mass were the same in the loaded and unloaded animal; and (2) most of the energy was used by the muscles to maintain the forward speed and height of the centre of mass constant from stride to stride. Then using Newton's Law:

$$F = ma, \quad a = k', \tag{4}$$
$$\Delta F = k'\Delta m, \tag{5}$$

and combining equations (3) and (5)

$$\Delta F = k'' \dot{V}_{O_2}. \tag{6}$$

The first assumption seems justified. The absence of any effect of load in our experiments on the stride frequency, average number of feet supporting the animal, or average vertical acceleration indicate that accelerations of the centre of mass are approximately the same in the loaded and unloaded animal moving at the same speed.

The evidence in support of the second assumption is not as strong. Cavagna & Kaneko (1977) and Heglund (1979) have shown that the amount of energy required to accelerate the limbs relative to the centre of mass is about half of the amount required to sustain the speed and height of the centre of mass at the running speeds used in these experiments. In our experiments, the load was not distributed over the limbs of the animals and would not have increased the energy required to accelerate and decelerate the limbs relative to the centre of mass. However, a large part of the decreases in kinetic energy as the limbs decelerate appears to be sorted elastically and recovered on reacceleration, resulting in a small metabolic cost for movement of limbs. The evidence for this elastic storage comes from direct measurements of the increases in kinetic energy of the limb relative to the trunk (Heglund, 1979; Heglund *et al.* 1979) and metabolic energy consumed by the limb muscles (unpublished observations from our laboratory) as a function of speed. If the metabolic cost of moving the limbs relative to the centre of mass is small, then most of the energy consumed would appear to be used to sustain the speed and height of the centre of mass.

The rate at which the unloaded or loaded human or animal expended energy increased dramatically with speed. If the force exerted by the muscles on the centre of mass is broken down into its horizontal and vertical components, only the integral of the horizontal accelerating forces with time increases with increasing speed (Cavagna *et al.* 1977). The integral of vertical force exerted by the muscles on the centre of mass over a stride must remain the same at all speeds and equal to the weight of the animal plus any load in order for the animal's centre of mass to remain at the same

height from stride to stride. Because the integral of vertical force with time is nearly an order of magnitude greater than the integral of accelerating horizontal force with time (Cavagna *et al.* 1977), the integral of the total force exerted by the muscles on the centre of mass increases only slightly with increasing speed. We must conclude, therefore, that the energetic cost of generating force over time ($\int F dt$) increases with increasing speed.

Another important consequence of the direct proportionality between the increased oxygen consumption and mass of the load is that small animals use more oxygen and consume more energy to carry each gram of a load a given distance than large animals, just as they expend more energy to carry each gram of their own body mass a given distance. Thus the cost of generating muscular force at a given speed appears to increase dramatically with decreasing body size.

Our results do not distinguish between work and force, both should increase in the same proportion as a result of carrying a load. However, a plausible hypothesis can be formulated in terms of force that is consistent with our data, but not in terms of work, at least if we assume muscles are operating at close to their maximal efficiency.

The intrinsic velocity of active muscle fibres should increase both with increasing speed and with decreasing animal size at any particular speed (Hill, 1950; Close, 1972). It has been suggested (Alexander & Goldspink, 1977) that cost of generating force is is proportional to the rate at which the cross bridges between the actin and myosin cycle, and this rate increases in direct proportion to intrinsic velocity. If this is the case, it might explain the increase in energetic cost of generating force both at higher speeds and with decreasing body size. Although the experiments will be difficult, this is a testable hypothesis.

REFERENCES

ALEXANDER, R. McN. (1973). Muscle performance in locomotion and other strenuous activities. In *Comparative Physiology* (ed. L. Bolis, K. Schmidt-Nielsen and S. H. P. Maddrell). Amsterdam: North Holland.

ALEXANDER, R. McN. (1976). Mechanics of bipedal locomotion. In *Perspectives in Experimental Biology: Zoology* (ed. S. P. Davies). Oxford: Pergamon.

ALEXANDER, R. McN. & GOLDSPINK, G. (eds). (1977). *Mechanics and Energetics of Animal Locomotion.* London: Chapman and Hall.

CAVAGNA, G. A., HEGLUND, N. C. & TAYLOR, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R 243–R261.

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.

CLOSE, R. (1972). Dynamic properties of mammalian skeletal muscles. *Physiol. Rev.* **52**, 129–183.

FENG, T. P. (1931). The heat–tension ratio in prolonged tetanic contractions. *Proc. R. Soc.* B. **108**, 522–537.

FENN, W. O. (1930). Work against gravity and work due to velocity changes in running. *Am. J. Physiol.* **93**, 433–462.

HEGLUND, N. C. (1979). Size scaling, speed and the mechanics of locomotion. Ph.D. thesis, Harvard University, Cambridge, MA.

HEGLUND, N. C., CAVAGNA, G. A., FEDAK, M. A. & TAYLOR, C. R. (1979). Muscle efficiency during locomotion: How does it vary with body size and speed? *Fedn. Proc.* **38**.

HILL, A. V. (1950). The dimensions of animals and their muscular dynamics. *Sci. Progr., Lond.* **38**, 209.

KUSHMERICK, M. J. & PAUL, R. J. (1976). Relationship between initial chemical reactions and oxidative recovery metabolism for single isometric contractions of frog sartorius at 0 °C. *J. Physiol., Lond.* **254**, 711–727

MCMAHON, T. A. (1975). Using body size to understand the structural design of animals: quadrupedal locomotion. *J. appl. Physiol.* **39**, 619–627.

SANDBERT, J. A. & CARLSON, F. D. (1966). The length dependence of phosphorylcreatine hydrolysis during an isometric tetanus. *Biochem. Z.* **315**, 212–231.

TAYLOR, C. R. (1977). The energetics of terrestrial locomotion and body size in vertebrates. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley). London: Academic Press.

TAYLOR, C. R., SCHMIDT-NIELSEN, K. & RAAB, J. (1970). Scaling of energetic cost of running to body size in mammals. *Am. J. Physiol.* **219**, 1104–1107.

TUCKER, V. A. (1968). Respiratory physiology of house sparrows in relation to high-altitude flight. *J. exp. Biol.* **48**, 55–66.