

EFFECT OF LIMB MASS AND ITS DISTRIBUTION ON THE ENERGETIC COST OF RUNNING

BY M. J. MYERS AND K. STEUDEL

Department of Zoology, University of Wisconsin, Madison, WI 53706, U.S.A.

Accepted 3 October 1984

SUMMARY

Functional morphologists have traditionally regarded cost of locomotion as an important influence on the design of locomotor structures. If cost of locomotion is an important constraint in the natural selection of these structures, it should be possible to show that animals differing in limb morphology also differ in their locomotor costs. In previous experiments on three species of cursorial mammals differing considerably in limb structure, no such differences were detected. Since the factors that determine the rate of energy consumption of a running animal are not well understood, we felt that the effect of limb morphology on cost could best be examined in a system in which only the inertial properties of limbs were varied while other factors remained constant. Consequently, we have measured changes in the rate of energy consumption of running human subjects produced by artificial alterations in limb inertial properties. Other variables that might influence cost have been controlled. We found that the cost of adding a given mass to the limbs is significantly greater than adding it to the centre of mass and that this effect becomes more pronounced as the limb loads are moved distally. Thus a clear effect of limb mass and its distribution on cost of locomotion has been demonstrated.

INTRODUCTION

Based on biomechanical considerations, functional morphologists have long regarded limb morphology as a significant influence on the energetic cost of locomotion in terrestrial animals (e.g. Howell, 1944; Smith & Savage, 1956; Hildebrand, 1962; Gray, 1968). These arguments assume that the work performed by muscles in moving the limbs forward and backward during a stride constitutes a substantial part of the total metabolic cost of running. Accordingly, for a given body mass, speed and gait, the smaller and more proximally distributed an animal's limb mass, the less kinetic energy required to accelerate and decelerate the limbs, and thus, the lower the cost of locomotion. However, Taylor *et al.* (1974) found no detectable differences in cost of locomotion between three species (cheetah, goat and gazelle) of similar body mass and limb length, yet decidedly different limb morphology. These

results have been interpreted to mean that the cost of accelerating and decelerating limbs during running is negligible (e.g. Taylor *et al.* 1974; Goldspink, 1977; Williams, 1983). If this interpretation is correct, some basic tenets of animal limb design theory must be discarded.

The factors which determine the rate of energy consumption of an animal as it runs are not well understood. It is reasonable to postulate that a complex function of many variables – both structural (e.g. body mass, limb mass, limb moment-of-inertia, limb centre of mass, limb length) and functional (e.g. speed, stride frequency, mode of locomotion, path of limb movement, intrinsic muscle velocity) – is involved. Consequently, in order to make a rigorous study of the effect of limb morphology on cost of locomotion we felt it was necessary to use a system in which only the inertial characteristics of limbs were varied, while other factors which might affect locomotor energetics were held constant.

To achieve this we have measured changes in rates of oxygen consumption of running humans as the result of alterations in limb mass, centre of mass and moment-of-inertia. Other variables which might influence rates of energy consumption have been controlled. Our experimental design has permitted us to discriminate the effect of loads on the cost of raising and accelerating the centre of mass from their effect on the cost of accelerating and decelerating the limbs.

MATERIALS AND METHODS

Subjects and training programme

Four human subjects (3 males and 1 female), similar in mass (range: 62–74 kg) and age (range: 18–24 years), and in good physical condition, were trained to run on a treadmill at a speed of 2.68 m s^{-1} under five different loading conditions: no load; a 3.6 kg load around the waist; and a 1.8 kg load around each upper thigh, each upper shank or each ankle. Runs without loads were used as a control condition in that rates of energy consumption for loaded runs were expressed as a percentage increase over the average cost of the unloaded runs of each test session. This procedure minimized variation in rates of energy consumption both between different test sessions for each subject and between different subjects. The purpose of the waist-loading condition was to provide a measure of the effect of a 3.6 kg load on the cost of raising and accelerating the centre of mass. The waist was chosen as the location of the load since calculations based on the equations of Clauser, McConville & Young (1969) showed that the waist was a reasonable approximation of the centre of mass of our subjects. This value was later subtracted from costs of limb-loaded runs in order to discriminate the effect of the load on the cost of raising and accelerating the centre of mass from its effect on the cost of moving the limbs relative to the centre of mass. Loading of the limbs at the three limb positions served to alter the inertial properties (mass, centre of mass and moment-of-inertia) of the limb and limb segments to various extents.

Loads were applied to subjects by means of specially constructed canvas weight belts, with lead shot sewn in pockets evenly distributed along the length of the belt. The waist-weight belt was fastened to subjects by laces at the front. Limb-weight belts

were wrapped around the limbs and taped so that loads were symmetrically distributed. All loads were firmly fastened in order to minimize extraneous movement, but were not so tight as to affect performance.

In an attempt to keep limb, and centre of mass, movements and accelerations the same for all loading conditions, subjects were instructed to maintain a constant stride frequency, achieved with the aid of a metronome, during all runs. The frequency for each subject was that which they found most comfortable while running without weights at the treadspeed used in the experiment. To determine whether a constant stride frequency was maintained by each subject, measurements of stride frequency were made from videotapes of each run, using a stopwatch to time the interval for 20 strides.

Rate of oxygen consumption for a given subject and loading condition decreased during the training period until a constant value was reached. A subject was considered to be trained when constant oxygen consumption values had been attained for all loading situations. The period of training lasted from 1 to 2 weeks, depending upon the subject. All data used in this study were taken after subjects had achieved the trained state.

Oxygen consumption measurements

Test sessions began and ended with a run without a load; in between were two to three runs, each with the load applied at a different point. Rate of oxygen consumption (\dot{V}_{O_2}), rate of carbon dioxide production (\dot{V}_{CO_2}), and the respiratory quotient (RQ) were determined for all runs using a Beckman metabolic measurement cart, an automated open-circuit system which contains the Beckman OM-11 (oxygen) and LB-2 (carbon dioxide) rapid response gas analysers, and has an accuracy of $\pm 2\%$. The gas analysers were calibrated just prior to each test session using a standard gas of known concentration. Subjects breathed through a Hans Rudolph low-resistance breathing valve, held in place by a plastic headframe. Noseclips were worn so that all expired air had to pass through the breathing valve. Expired air was collected continuously throughout each run. At 1-min intervals the system calculated \dot{V}_{O_2} (STPD), \dot{V}_{CO_2} (STPD), and RQ from measurements of fraction of oxygen in expired air (F_{EO_2}), fraction of carbon dioxide in expired air (F_{ECO_2}), and volume of dry air (dried with Drierite) expired, taken during the time interval. \dot{V}_{O_2} was calculated using the equation:

$$\dot{V}_{O_2} = \left[\dot{V}_E \frac{(1 - F_{EO_2} - F_{ECO_2})}{(1 - F_{IO_2})} F_{IO_2} \right] - \dot{V}_E \cdot F_{EO_2}, \quad (1)$$

(see Lamb, 1978), where \dot{V}_E is the minute ventilation expired, and F_{IO_2} is the fraction of oxygen in the inspired room air (0.2094). \dot{V}_{CO_2} was calculated using the equation:

$$\dot{V}_{CO_2} = \dot{V}_E (F_{ECO_2} - F_{ICO_2}), \quad (2)$$

(see Lamb, 1978), where F_{ICO_2} is the fraction of carbon dioxide in the inspired room air (0.0003).

Runs continued until \dot{V}_{O_2} values levelled off, between 8 and 15 min into the run, signalling that steady-state had been reached. RQ values ($\dot{V}_{CO_2}/\dot{V}_{O_2}$) were always less than 1.0, indicating that virtually all of the energy being consumed during steady-state exercise was provided aerobically (Taylor, Heglund & Maloiy, 1982).

Due to the possibility of subtle differences in energetic cost between the various loading conditions, several aspects of the experiment were designed to maximize precision.

(1) Calculations of the rate of oxygen consumption (equation 1) were made using the actual fractions of CO_2 and O_2 in the expired air, rather than assuming an average respiratory quotient (RQ) of 0.80. This was possible because the system being used contained both CO_2 and O_2 gas analysers.

(2) Mass-specific rates of oxygen consumption (in $ml O_2 \text{ min}^{-1} \text{ kg}^{-1}$) were converted to equivalent mass-specific rates of energy consumption (in $J \text{ min}^{-1} \text{ kg}^{-1}$) based on the calculated RQ for that time interval, rather than using the conversion factor associated with an RQ of 0.80.

(3) Mass-specific rates of energy consumption for runs with loads were expressed as percentage increases over the average mass-specific rate of energy consumption of the two runs in the unloaded condition, which began and ended each test session. Consequently, each subject served as his own control for each test session, permitting a more powerful statistical analysis of the data.

Estimation of changes in limb kinetic energy

Cost increases (over waist-loaded runs) of limb-loaded runs should reflect increases in the amount of kinetic energy (E_k) expended in moving the limbs backward and forward during a stride. Verification of this point would have required determining the oscillations in limb E_k for the various loading conditions of our experiment from films or videotapes. This exceeded the scope of the present study. However, two approaches were taken to estimate, albeit crudely, the changes in limb E_k produced by loads at the three limb positions.

The first approach was based on a simple model in which the entire limb is assumed to rotate at the proximal joint as a rigid compound pendulum whose kinetic energy is the sum of its translational and rotational kinetic energy,

$$E_k = \frac{1}{2}mv^2 + \frac{1}{2}I_o\omega^2, \quad (3)$$

where m is the mass of the limb, v is the linear velocity of its centre of mass relative to the centre of mass of the body, ω is the angular velocity of the limb, and I_o is the moment-of-inertia about its centre of mass. Since for a rotating rigid body:

$$v = \omega r, \quad (4)$$

where r is the distance from the point of rotation to the centre of mass of the body, and

$$I = I_o + mr^2, \quad (5)$$

-) where I is the moment-of-inertia about the point of rotation, this model allows us to rewrite equation 3 as:

$$E_k = \frac{1}{2}I\omega^2. \quad (6)$$

According to this model of the rotating limb, increases in limb I would result in proportional increases in E_k , since ω was approximately the same for all runs of a subject (see below). Thus, the increase in limb E_k due to addition of a mass M at a distance d from the proximal joint is proportional to Md^2 , the increase in limb I .

As an estimate of E_k changes due to limb loads, the percentage increase in limb I for each loading position was calculated for a 65-kg human male, the average body mass of the males in this study. Since no data on total limb I were available, unloaded limb I was calculated using the equation for the moment-of-inertia of a uniform rod about a perpendicular line through one end:

$$I = \frac{1}{3}ml^2 \quad (7)$$

(e.g. Tipler, 1976), where m is unloaded limb mass and l is limb length. Limb mass was estimated from the equations of Clauser *et al.* (1969) and l was the average limb length of our male subjects. The increase in limb I due to loads, Md^2 , was calculated for each of the three limb positions. These values were then used to calculate the percentage increase in limb I , and thus limb E_k , for each loading situation.

The second approach to estimating the effect of loads on limb E_k was based on a modelling of the limb as a series of linked rigid segments between which transfers of energy occur. According to this model, the kinetic energy required to move the limbs is the sum of the kinetic energy changes of the limb segments, taking into account transfers of energy between segments.

Using reasoning analogous to the preceding argument for the entire limb, it can be shown that the kinetic energy oscillations of limb segments should increase in proportion to the increase in limb segment I . This relationship is exact for the thigh segment, since v is equal to ωr (equation 4). Changes in limb segment I are not as good an estimator of the changes in kinetic energy expended for the shank segment, since the linear velocity of the centre of mass of the shank (v) is equal to the sum of shank ωr and the linear velocity of the knee (Fenn, 1930).

Limb segment I values were estimated for a 65-kg male from regression equations for thigh and shank segments developed by Chandler *et al.* (1975), based on the dissection of six male cadavers. To determine the extent to which the 1.8 kg loads increased the I of the segments to which they were attached, under the various loading conditions, the moment-of-inertia of the load about the proximal joint of the segment was calculated. A 1.8-kg weight belt was fastened to a free-swinging metal rod, which was suspended at one end, and the swing period of the rod-plus-weight belt was measured. This was done with the weight belt positioned at a distance from the pivot point that corresponded with the distances of the loads from the proximal joints of the segments in the three limb-loading positions; approximately 10 cm for the upper thigh

and upper shank situations, and approximately 35 cm from the pivot for the ankle-loading condition. The I of the rod (I_r) and the rod-plus weight belt (I_{r+w}) were calculated using the equation:

$$I = t^2 m_s g r_s / 4\pi^2, \quad (8)$$

(see Tipler, 1976), where t is the swing period of the system, m_s is the mass of the system, g is the acceleration due to gravity, and r_s is the distance from the point of suspension to the centre of mass of the system. The I of the weight belt at each position was found by subtracting I_r from I_{r+w} . These values were then used to calculate the percentage increase in limb segment I , for all three loading positions, as an estimate of the increase in kinetic energy required to move the limb segment.

RESULTS

The rate of energy consumption (\dot{E}) for each subject under each of the four loading situations – waist, upper thigh, upper shank and ankle – is given in Table 1, expressed as an average percentage increase over the \dot{E} in unloaded runs. In all subjects, runs with loads at the waist showed the smallest increases in cost. The inter-subject average increase in cost for waist-loaded runs was 3.7%. All limb loadings resulted in greater increases in cost than when the same mass was carried at the waist; the cost increasing as the position of the loads became more distal.

The percentage increase in \dot{E} was significantly different in limb-loaded and waist-loaded runs, for all limb-weighting conditions, using the Student's t -test for paired comparisons (Table 2). The inter-subject averages (\bar{D}) for the difference in cost between limb- and waist-loaded runs were 5.8%, 8.8% and 20.7% for runs with upper thigh, upper shank and ankle weights, respectively. Comparisons of upper shank and upper thigh, ankle and upper thigh, and ankle and upper shank, also yielded statistically significant differences in percentage increase in \dot{E} .

Stride frequency for each subject was approximately the same in all runs, whether loaded or unloaded. The maximum difference in stride frequency between any two

Table 1. Rate of energy consumption, \dot{E} ($J \min^{-1} kg^{-1}$), under various loading conditions expressed as average percentage increase (\pm standard error) over unloaded runs

	W(%)	T(%)	S(%)	A(%)
Subject 1	4.9 \pm 0.74	13.0 \pm 1.15	15.7 \pm 0.65	28.8 \pm 0.65
Subject 2	2.8 \pm 0.74	6.8 \pm 0.25	9.0 \pm 0.92	20.2 \pm 1.60
Subject 3	4.3 \pm 0.46	9.4 \pm 0.55	11.0 \pm 1.40	25.8 \pm 0.25
Subject 4	2.6 \pm 1.02	8.6 \pm 1.40	14.1 \pm 0.15	22.7 \pm 0.65
Inter-subject average	3.7 \pm 0.42	9.4 \pm 0.92	12.1 \pm 1.01	24.3 \pm 1.27

Loading conditions: waist (W), upper thigh (T), upper shank (S), ankle (A).

Table 2. Differences between pairs of loading conditions in percentage increase in rate of energy consumption

	T - W	S - W	A - W	S - T	A - S	A - T
Subject 1	8.1	10.8	23.9	2.7	13.1	15.8
Subject 2	4.0	6.2	17.4	2.2	11.2	13.4
Subject 3	5.1	6.7	21.5	1.6	14.8	16.4
Subject 4	6.0	11.5	20.1	5.5	8.6	14.1
\bar{D}	5.8	8.8	20.7	3.0	11.9	14.9
$s\bar{D}$	0.9	1.4	1.4	0.9	1.3	0.7
*Level of significance	0.01	0.01	0.001	0.05	0.005	0.001

*Significance levels determined using the *t*-test for paired comparison of treatments, $H_0: \bar{D} = 0$.
Loading conditions: waist (W), upper thigh (T), upper shank (S), ankle (A).

runs of a subject was 3.0%; the maximum difference between any two runs of a subject in the same test session was 1.8%.

The percentage increases in the moment-of-inertia of the entire limb about the proximal joint (I) produced by limb loads were calculated to be 1%, 18% and 39% for loads at the upper thigh, upper shank and ankle positions, respectively (Table 3).

The percentage increases in segment I due to limb loads were 3% for the thigh segment, as the result of upper thigh loads, and 18% and 179% for the shank segment, resulting from loadings at the upper shank and ankle positions, respectively (Table 3).

DISCUSSION

The purpose of this study was to determine the effect of changes in limb mass and its distribution on the energetic cost of running. Two aspects of our experimental design permitted potentially confounding variables to be controlled.

Table 3. Estimated percentage increase in limb and limb segment I due to loads at three positions along the limb

	Limb I			Limb Segment I		
	Unloaded (g cm ⁻²)	Loaded (g cm ⁻²)	Increase (%)	Unloaded (g cm ⁻²)	Loaded (g cm ⁻²)	Increase (%)
Upper thigh load	2.8×10^7	2.82×10^7	1	3.0×10^6	3.1×10^6	3
Upper shank load	2.8×10^7	3.3×10^7	18	1.1×10^6	1.3×10^6	18
Ankle load	2.8×10^7	3.9×10^7	39	1.1×10^6	3.1×10^6	179

(1) Body mass and limb mass, moment-of-inertia and centre of mass were artificially altered for each subject. This permitted us to measure the effects of the various loads on a physiologically and anatomically constant system and to assess how much of the observed effect of a load is due to its position rather than its contribution to total mass carried.

(2) Subjects were able to maintain a constant stride frequency across all runs. Increases in the rate of energy consumption (\dot{E}) can be attributed solely to load-induced increases in the inertial properties of the body and limbs only if the accelerations of the centre of mass of the body and of the limbs are demonstrated to be approximately the same for all runs, loaded or unloaded. Accelerations of our subjects' centres of mass can be considered approximately equal in all runs, since other workers have found accelerations of the centre of mass to vary little from loaded to unloaded runs (at a single speed) when stride frequency is constant (Taylor, Heglund, McMahon & Looney, 1980). Given that treadspeed, stride frequency, and hence stride length, were the same for all runs, it seems reasonable to assume that the limb movements, velocities and accelerations of each subject were relatively consistent across all runs, regardless of the loading situation.

If the increases in \dot{E} associated with carrying a given mass were determined solely by the amount of the load, and independent of the position of the load, there should have been no detectable differences in \dot{E} between the various loading conditions of our experiment. This was not the case. Location of the load near the body's centre of mass (as in the waist-loaded condition) resulted in significantly lower increases in \dot{E} than when the same mass was located along the limbs. Presumably, this is because the limbs move forward and backward relative to the centre of mass, so that addition of the load to the limbs would increase both the total mass to be carried, and thus the mechanical energy expended in raising and accelerating the centre of mass, and the oscillations in kinetic energy of the limbs relative to the centre of mass. Our results comparing the cost of adding a given mass near a subject's centre of mass with that of adding it to the subject's limbs show that the latter is between 1.5 and 5.5 times more costly.

Measurements of the mechanical work involved in accelerating and decelerating the limbs relative to the trunk in running humans (Cavagna & Kaneko, 1977) show that, at the running speed used in our experiment, the kinetic energy changes of the limbs account for approximately one-third of the total work done during a stride. Assuming that the energetic cost of the mechanical work performed by muscles comprises a substantial fraction of the total cost of running, this finding means that differences in limb morphology which alter the kinetic energy changes of the limbs can result in significant differences in the cost of running. Our data support this conclusion.

Furthermore, the kinetic energy changes associated with moving limbs increase as the square of running speed in humans (Cavagna & Kaneko, 1977) and as the 1.53 power of running speed in other animals (Fedak, Heglund & Taylor, 1982), while the mechanical energy used in raising and accelerating the centre of mass in both humans (e.g. Cavagna, Thys & Zamboni, 1976) and other animals (Heglund, Cavagna & Taylor, 1982) increases linearly with running speed. Thus, the kinetic energy changes

involved in moving limbs comprise an increasingly larger fraction of the total mechanical work of a stride as speed increases. The effect of a given limb morphology on cost of running would therefore be expected to increase with increasing speed.

According to our data, the relationship between the effect of limb loads on \dot{E} and the position of the load along the limb is not a simple one. Functional morphologists have often argued that an animal's limb musculature should be concentrated proximally and lightened distally for maximal locomotor economy. One conceptual model for this expectation views the entire limb as a rigid compound pendulum rotating from the proximal joint. Under this model, the increases in limb I produced by the various limb loads (Table 3) are proportional to the increases in the kinetic energy expended in limb acceleration and deceleration. The pattern of these increases does not parallel that of the increases in cost of running for the three loading situations (Table 2), as the average percentage increase in the cost of upper shank loads was much closer to that of upper thigh loads than to that of ankle loads. According to this simple model of limb energetics, the increased cost of limb-loaded runs cannot be explained by the increased kinetic energy changes of the limbs.

During running, the limbs are seldom straight, but instead assume a series of different configurations throughout a stride. Consequently, a more detailed model of limb energetics considers the limb as a series of linked, rigid segments between which transfers of energy occur (e.g. Cavagna & Kaneko, 1977; Fedak *et al.* 1982; Williams & Cavanagh, 1983). The kinetic energy expended in limb movement will therefore depend both on the kinetic energy changes of individual segments and the extent of transfers of energy between segments. Because of the complexity of this model, it was impossible to estimate the effect of the various limb loads on the total kinetic energy required for limb movement. However, the increased oscillations in limb segment E_k associated with limb loads have somewhat crudely been estimated by increases in limb segment I (Table 3). The pattern of these increases is consistent with that of the increases (over waist-loaded trials) in cost of running for the three loading conditions (Table 2), although the percentage increase in segment I, and thus segment E_k , as the loads are moved distally is greater than the percentage increase in cost. Although these results do not conclusively demonstrate that the observed increases in the cost of limb-loaded runs result from changes in limb segment E_k , they do suggest the importance of limb segment morphology and interaction in determining limb energetics.

Our finding that the distribution of mass significantly affects the cost of running in humans is in general agreement with the expectations of functional morphologists regarding limb design and cost of locomotion. It is at odds, however, with the results of the cheetah-goat-gazelle comparison by Taylor *et al.* (1974), in which an effect of limb morphology on cost of locomotion was not detected. This discrepancy may be due to a variety of factors, such as the substantial intra-animal error in their oxygen consumption data, making any differences more difficult to detect, or to differences in gait between their subjects, a point not controlled in that study.

On the other hand, our results were based on artificially produced differences in limb morphology, which cannot be applied indiscriminately to the locomotor

mechanics and energetics of animals which differ naturally in limb morphology. One question might be whether the changes in inertial properties produced by our limb loads were of the same magnitude as observable differences in the limb inertial properties of animals. The percentage difference in forelimb segment I between two dogs of similar mass was found to be 116% for the upper foreleg segment and 317% for the lower foreleg (unpublished laboratory data). These natural differences in segment I are considerably greater than those produced by the limb loads of our experiment.

Another difference between our experimental design and those involving a natural system was our control of gait. Each subject's stride frequency was kept constant in our trials, so that the results do not include any synergistic effects of gait and limb morphology on locomotor energetics. The extent to which gait might mitigate the effects of limb morphology on cost of locomotion remains to be investigated.

In conclusion, our data show that the cost of adding mass to the limbs is substantially greater than adding it to the centre of mass. This result is explicable only if the cost of accelerating and decelerating the limbs during running is an important aspect of the total cost of locomotion.

We would like to thank Dr C. R. Taylor for his encouragement and helpful criticisms of the manuscript. We are also grateful to Dr F. J. Nagle for allowing us to use the University of Wisconsin Biodynamics Laboratory for our experiments, and to Patricia Painter and Jay Rusek for technical assistance.

REFERENCES

- CAVAGNA, G. A. & KANEKO, M. (1977). Mechanical work and efficiency in level walking and running. *J. Physiol., Lond.* **268**, 467–481.
- CAVAGNA, G. A., THYS, H. & ZAMBONI, A. (1976). The sources of external work in level walking and running. *J. Physiol., Lond.* **262**, 639–657.
- CHANDLER, R. F., CLAUSER, C. E., MCCONVILLE, J. T., REYNOLDS, H. M. & YOUNG, J. W. (1975). Investigation of the inertial properties of the human body. *AMRL Tech. Rept.* 74–137. Ohio: Wright-Patterson Air Force Base.
- CLAUSER, C. E., MCCONVILLE, J. T. & YOUNG, J. W. (1969). Weight, volume, and center of mass of segments of the human body. *AMRL Tech. Rept.* 69–70. Ohio: Wright-Patterson Air Force Base.
- FEDAK, M. A., HEGLUND, N. C. & TAYLOR, C. R. (1982). 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. *J. exp. Biol.* **97**, 23–40.
- FENN, W. O. (1930). Frictional and kinetic factors in the work of sprint running. *Am. J. Physiol.* **92**, 583–611.
- GOLDSPIK, G. (1977). Energy cost of locomotion. In *Mechanics and Energetics of Animal Locomotion*, (eds R. McN. Alexander & G. Goldspink), pp. 153–167. London: Chapman & Hall.
- GRAY, J. (1968). *Animal Locomotion*. New York: Norton.
- HEGLUND, N. C., CAVAGNA, G. A. & TAYLOR, C. R. (1982). 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. *J. exp. Biol.* **97**, 41–56.
- HILDEBRAND, M. (1962). Walking, running and jumping. *Am. Zool.* **2**, 151–155.
- HOWELL, A. B. (1944). *Speed in Animals*. Chicago: University of Chicago Press.
- LAMB, D. R. (1978). *Physiology of Exercise*, pp. 77–79. New York: Macmillan Publishing Co., Inc.
- SMITH, J. M. & SAVAGE, R. J. G. (1956). Some locomotory adaptations in mammals. *J. Linn. Soc. (Zool)* **42**, 603–622.
- TAYLOR, C. R., HEGLUND, N. C., MCMAHON, T. A. & LOONEY, T. R. (1980). Energetic cost of generating muscular force during running. *J. exp. Biol.* **86**, 9–18.

- TAYLOR, C. R., HEGLUND, N. C. & MALOY, G. M. O. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. exp. Biol.* **97**, 1–21.
- TAYLOR, C. R., SHKOLNIK, A., DMI'EL, R., BAHARAV, D. & BORUT, A. (1974). Running in cheetahs, gazelles and goats: energy cost and limb configuration. *Am. J. Physiol.* **227**, 848–850.
- TIPLER, P. A. (1976). *Physics*, pp. 314, 369. New York: Worth Publishers, Inc.
- WILLIAMS, K. R. & CAVANAGH, P. R. (1983). A model for the calculation of mechanical power during distance running. *J. Biomechanics* **16**, 115–128.
- WILLIAMS, T. M. (1983). Locomotion in the North American mink, a semi-aquatic mammal. II. The effect of an elongate body on running energetics and gait patterns. *J. exp. Biol.* **105**, 283–295.

