THE WORK AND ENERGETIC COST OF LOCOMOTION

I. THE EFFECTS OF LIMB MASS DISTRIBUTION IN QUADRUPEDS

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Summary

Does limb design influence the cost of locomotion in quadrupedal mammals? If not, morphologists must dismiss the economy of locomotion from consideration when assessing the adaptive factors shaping limb structure. Several studies have recently used externally applied loads to demonstrate a relationship between limb mass distribution and energy costs in human subjects. It is not clear whether a similar correlation would hold for quadrupeds, given their very different gaits. The present study addresses this question by measuring the rate of oxygen consumption in domestic dogs running on a treadmill with mass added either to the limbs or to the back. Trials with no additional mass were used as a control. The use of externally applied loads has the advantage of allowing limb mass to be altered in a system in which other aspects of physiology that might influence cost of locomotion are held constant. The cost of adding mass to the limbs in dogs was found to be significantly greater than that of adding it at the center of mass. Limb mass distribution does affect the cost of locomotion in quadrupeds. A comparison of the results from a variety of studies in which the energetic cost of adding external loads has been measured in animals across a wide size range suggests a qualitative difference in the factors determining the cost of locomotion in large and small animals.

Introduction

Locomotion is a critical aspect of the biology of any animal, yet the adaptive constraints associated with it are not well understood. Discussions of the selective forces likely to be acting on locomotor structures in mammals have focused on three major factors: mechanical resistance to the stresses induced by locomotion (McMahon, 1973; Lanyon and Baggott, 1976; Lanyon, 1981; Alexander, 1981, 1984; Biewener *et al.* 1983), generation of speed and/or power (Smith and Savage, 1955; Alexander, 1977; Steudel, 1981) and determination of the energetic cost of locomotion (Howell, 1944; Gray, 1968; Taylor *et al.* 1974; Alexander, 1982).

The significance of the last of these factors – the energetic cost of locomotion – has been seriously questioned as an important force shaping the evolution of limb structure as a result of a study in which no difference in cost was detected in three

species, cheetah, goat and gazelle, that differ substantially in limb morphology (Taylor *et al.* 1974). As a consequence, many workers have ruled out selection for energetic efficiency as an important design constraint on animal limb structure (Fleagle, 1979; Hurst *et al.* 1982; Williams, 1983). Other workers (Hildebrand and Hurley, 1985; Hildebrand, 1988), however, have resisted this conclusion.

To determine whether a controlled experiment could detect a difference in cost in response to differences in limb mass distribution, Myers and Steudel (1985) studied human subjects with externally applied loads. Their design allowed limb mass and its distribution to be altered in a system in which other factors that might influence locomotor energetics, such as differences in locomotor physiology and daily fluctuations within a subject, were minimized. The results showed a consistent, statistically significant, increase in the cost of locomotion when mass was added to the legs of a subject compared with the results when the same mass was added at the waist. Thus, it became clear that experimental alterations of limb mass and its distribution affect locomotor cost, at least in bipedal humans. Other experiments on human subjects have documented similar increases in cost as a result of externally applied limb loads (e.g. Martin, 1985; Claremont and Hall, 1988).

It is not clear, however, whether these results can be generalized to non-human locomotion (Cavanagh and Kram, 1985). The results of the comparative study of cost in the cheetah, goat and gazelle (Taylor *et al.* 1974) would seem to imply that they cannot. The bipedal gait of humans produces substantially different kinematic patterns from those of quadrupeds, with potentially different capacities for the storage and recovery of elastic strain energy and/or the transfer of energy between body segments or between kinetic and potential energy. Furthermore, humans do not show the pronounced morphological modifications of their limbs characteristic of many cursorial quadrupeds of similar mass. To date there has been no analogous experiment to determine whether the cost of locomotion in quadrupeds varies with differences in limb loading.

To remedy this situation, the present study measures changes in the energetic cost of locomotion of domestic dogs produced by experimentally adding mass either to the limbs or to the body center of mass. As in the experiment on human subjects (Myers and Steudel, 1985), this design allows experimental control of many variables other than limb inertia that might influence cost. The results of this study are used to evaluate the earlier conclusion that limb mass distribution has no apparent effect on the cost of locomotion.

The metabolic impact of adding mass to animals of different size in this and other studies are compared in order to investigate the scaling of the relationship between the mechanical work of locomotion and its energetic cost.

Materials and methods
Experimental approach
Three adult male dogs (20.0, 20.9 and 26.8 kg) were trained to run on a treadmill

at $1.56\,\mathrm{m\,s^{-1}}$, a slow trot, under three different loading conditions. In all trials the dogs wore a commercially available dog harness around their shoulders and specially constructed Neoprene casings on all four limbs. The two experimental conditions involved adding 0.77 kg of lead either to the dog's harness or distributed equally on the four limbs. The casings were positioned so that the mass was added at the level of the radius and ulna on the forelimb and at the level of the metatarsals on the hindlimb. All loads were firmly attached to minimize extraneous movement, but were not so tight as to cause the animals any detectable discomfort. Runs in which the animals wore the harness and the casings with no added mass were used as a control. The purpose of the trials with the mass added to the harness was to provide a measure of the effect of a 0.77 kg mass affecting only the work done to raise and reaccelerate the center of mass of the body. Addition of mass to the limbs increased not only the total mass raised and reaccelerated, but also the work done to move the limbs relative to the center of mass.

The object of this experimental design was to alter the mass and inertia of the limbs to an extent similar to that which might occur during the evolution of a less cursorial locomotion, without producing any concomitant changes in limb length (which would be likely to change stride length and frequency), intrinsic speed of contraction of locomotor muscles, the capacity of the limbs to store energy elastically, and so forth. The fact that naturally evolved differences in limb mass and moment of inertia are likely to be accompanied by changes in these and other factors that may influence cost of locomotion make such natural variation unsuitable for investigating the specific effect of mass distribution on cost.

The training period in which the animals were accustomed to the treadmill, the weighting system and an open-circuit respiratory gas analysis system lasted 4 months. The rate of oxygen consumption ($\dot{V}_{O_2}$) under the various loading conditions gradually declined over the training period. The animals were considered trained when the $\dot{V}_{O_2}$ values for each animal under each test condition no longer decreased with training. All data used in the analysis were taken after the animals had reached the trained state.

Measurement of oxygen consumption

Rates of oxygen consumption ($\dot{V}_{O_2}$) were measured using an Applied Electrochemistry S-3A/1 oxygen analyzer in an open-circuit system. The animals wore loose-fitting masks through which room air was pulled at rates of $120–150\,\mathrm{l\,min^{-1}}$. I initially tested for leaks by bleeding nitrogen directly on to all joints while monitoring the fractional concentration of oxygen in the air being pulled through the system. Any leaks were revealed by a drop in the readings on the oxygen analyzer and could then be effectively sealed. To test for leaks in the overall system with the animal in place, oxygen consumption was monitored while the flow rate was decreased by 10 %. This fluctuation in flow rate did not change observed rates of oxygen consumption under equivalent conditions, indicating that all expired air was being recovered.

The analyzer and flow meters were calibrated at the beginning and end of every test session using the one-step N_2 dilution technique described by Fedak *et al.* (1981), which has been found to be accurate to better than $\pm 3\%$. A small stream of the expired gases was removed from the main flow downstream from the flow meter and diverted through Ascarite and Drierite to the oxygen analyzer for continuous monitoring of its fractional concentration of oxygen. Runs continued until values leveled off, between 7 and 20 min into a run, signalling that a steady state had been achieved. $\dot{V}_{O_2}$ values for the last three successful runs for each dog under each of the three test conditions were used for data analysis.

Estimation of changes in limb inertial properties

These experiments tested whether an increase in limb mass produced an increase in the cost of locomotion when other physiological variables were held constant. To evaluate the significance of any increase in $\dot{V}_{O_2}$, it is useful to assess the extent to which the limb loads alter the inertial properties of the limbs.

Based on the work–energy theorem (e.g. Halliday and Resnick, 1981), the internal work of locomotion, i.e. the work done to move the body segments relative to the center of mass, can be considered approximately equal to the sum of the changes in kinetic energy (E_{ke}) and potential energy (E_{pe}) of the body segments. The body can be treated as a series of linked, rigid segments between which energy can be exchanged. At any instant the total energy change of the body is equal to the sum of the changes in E_{ke} and E_{pe} of its segments. The E_{ke} of each segment is the sum of its translational and rotational components (Cavagna and Kaneko, 1977; Fedak *et al.* 1982),

$$E_{ke} = (1/2)Mv^2 + (1/2)I_o\omega^2 , \qquad (1)$$

where M is the mass of the segment, v is the linear velocity of its center of mass relative to the center of mass of the body, ω is its angular velocity and I_o is the moment of inertia of the segment about its center of mass. The potential energy of a segment is expressed as:

$$E_{pe} = Mgh , \qquad (2)$$

where g is the acceleration due to gravity and h is the vertical displacement of the center of mass of the segment.

The relevance of these equations is that they indicate which morphological parameters affect internal work. Mass is an important aspect of potential energy and translational kinetic energy, while the moment of inertia about the center of mass is important because of its role in defining rotational energy as indicated above. Also relevant is the distance between the point of rotation and the center of mass (d) because:

$$v = \omega d . \qquad (3)$$

The moment of inertia about the proximal point of rotation (I_p) is a good first approximation of limb mass and its distribution because it is defined as a

combination of the three aspects of work or energy that are determined morphologically.

$$I_p = I_o + Md^2 . \tag{4}$$

It would be feasible to calculate the average effective I_p of limbs across a series of individuals or species by filming the animals, documenting the position of the segments at each instant, determining the mass, center of mass and moment of inertia of each segment, and combining this information into an estimation of average limb I_p for a stride. This approach, however, suffers from a major disadvantage. The effective limb I_p calculated by this method will differ within an individual as its speed changes and between individuals and species as a result of variation in both morphology and gait kinematics. It therefore confounds changes in I_p produced by morphological alterations with changes in I_p produced by kinematic variation. Because limb inertial characteristics and gait kinematics may vary independently and are both of interest, it seems advisable to describe the morphological component of I_p in a way that is independent of variation in gait.

Consequently, the effect on limb mass distribution of the loads added to the distal limb segments has been estimated by calculating I_p as though the limb was a single rigid body arranged with segments extended – a single, standardized configuration. The alteration in I_p produced as a result of the addition of mass at a measured distance from the proximal point of rotation (the shoulder or hip joint) was calculated as described below. Estimation of limb moment of inertia based on particular segment configurations has also been used by Jayes and Alexander (1982).

Limb moments of inertia about the point of rotation have been determined experimentally for a sample of 12 dead dogs on which total body mass and a series of variables describing limb morphology have also been measured (K. Steudel and M. J. Myers, in preparation). Limb length was found to be an excellent predictor of limb inertia in the forelimb and the hindlimb, which both have coefficients of determination (r^2) of 0.97. These regression equations were used to estimate unloaded limb moments of inertia for the three dogs used in this study based on measurements of their limb lengths.

The moment of inertia of the load about the proximal joint of the limb (I_p) was determined experimentally by fastening the 0.19 kg loads (the amount added to the casings on each limb) to a free-swinging metal rod, which was suspended at one end. The swing period of the rod plus load was determined in a series of tests with the load positioned at distances from the pivot equivalent to the distances of the load from the proximal joint in the forelimbs and hindlimbs of each of the three dogs. The swing period of the rod alone was also measured. The moments of inertia for the rod (I_r) and for the rod plus load combination (I_{r+l}) were calculated using the equation:

$$I_p = t^2 mgd/4\pi^2 , \tag{5}$$

(Tipler, 1976), where t is the swing period of the system, m is the mass of the system, g is the acceleration due to gravity, and d is the distance from the pivot

point to the center of mass of the system. The moments of inertia of the load itself at the various distances from the pivot were calculated by subtracting I_r from each I_{r+1}. These values were then used to calculate the absolute and percentage increases in limb moment of inertia produced by the loads for each limb of each dog, modelling the limb as a single rigid body.

All trials were videotaped at $200 \, \text{frames} \, \text{s}^{-1}$ using a NAC high-speed video camera. Stride frequency was measured for each trial by counting the number of fields per stride and averaging over 10 strides. Knowing the tape speed allowed conversion to strides per minute.

Results

Rates of oxygen consumption for unloaded dogs were similar to those observed by previous investigators. Expected $\dot{V}_{O_2}$ values calculated from data reported by Taylor *et al.* (1970) for an 18 kg dog were slightly higher than those obtained here, while expected values calculated from data reported by Cerretelli *et al.* (1964) for a 24 kg dog were slightly lower.

$\dot{V}_{O_2}$ values for each subject under each of the three loading conditions are given in Table 1. In all subjects, trials with limb loads produced significant increases in cost compared with back-loaded runs and control runs ($P<0.001$, $N=6$, two-tailed t-test). There was no significant difference between back-loaded trials and control runs ($P=0.344$).

That the effect of the loads was similar in the three dogs tested can be verified using analysis of variance (ANOVA) with $\dot{V}_{O_2}$ as the dependent variable and dog and loading condition as independent variables. Both dog and loading condition had significant individual effects on $\dot{V}_{O_2}$ ($P<0.001$), but there was no significant interaction ($P=0.472$). This indicates that, although the dogs differed in $\dot{V}_{O_2}$ (due substantially to differences in their mass), they did not differ in the nature of their $\dot{V}_{O_2}$ responses to the loads.

The estimated limb moments of inertia about the proximal joint for the loaded and unloaded limbs of the three dogs are shown in Table 2. The addition of the

Table 1. *Rate of oxygen consumption of limb-loaded, back-loaded and unloaded dogs running at 1.56 m s^{-1}*

	N	Body mass (kg)	$\dot{V}_{O_2 \text{control}}$ (ml O$_2$ s^{-1})	$\dot{V}_{O_2 \text{back}}$ (ml O$_2$ s^{-1})	$\dot{V}_{O_2 \text{limb}}$ (ml O$_2$ s^{-1})
Dog 1	3	26.8	8.84±0.07	8.83±0.31	9.52±0.20
Dog 2	3	20.9	8.36±0.21	8.30±0.23	9.25±0.32
Dog 3	3	20.0	6.64±0.24	6.16±0.22	7.49±0.13
Average		22.6	7.95±0.35	7.76±0.43	8.72±0.33

Values are mean±S.E.

Table 2. *Estimated limb moments of inertia (I_p) about the proximal joint and increases in limb moments of inertia due to added loads*

| | Dog 1 | | Dog 2 | | Dog 3 | |
	Forelimb	Hindlimb	Forelimb	Hindlimb	Forelimb	Hindlimb
I_p unloaded (g cm^2)	5.78×10^5	9.95×10^5	3.86×10^5	5.66×10^5	4.19×10^5	4.59×10^5
I_p loaded (g cm^2)	6.88×10^5	12.44×10^5	4.86×10^5	7.76×10^5	5.20×10^5	6.42×10^5
% increase	19	25	26	37	24	40

loads, representing between 2.9 and 3.9 % increases in body mass, produced increases in moment of inertia of between 19 and 26 % in the forelimb and between 25 and 40 % in the hindlimb.

The dogs responded to the limb loads with a small decrease in stride frequency. The stride frequencies observed in the limb-loaded trials were significantly lower than those in control ($P<0.001$) or back-loaded trials ($P<0.002$). No significant difference was observed between stride frequencies in back-loaded and control trials ($P=0.432$). Stride frequency in the limb-loaded trials averaged 103.8 strides min^{-1} (s.e.$=2.24$, $N=9$), 96 % of that seen in both the control (average$=$ 107.74 strides min^{-1}, s.e.$=2.57$, $N=9$) and back-loaded (average$=108.34$ strides min^{-1}, s.e.$=3.07$, $N=9$) trials.

Discussion

The effect of mass distribution on $\dot{V}_{O_2}$

The addition of 0.77 kg of mass (2.9–3.9 % of body mass) to the limbs of the dogs produced increases in $\dot{V}_{O_2}$ that are qualitatively similar to those obtained in analogous experiments on human subjects. In the current experiments, the average 3.5 % increase in mass produced by the limb loads increased $\dot{V}_{O_2}$ by an average of 9.9 % over control values. In human subjects, the addition of a mass equivalent to 1.4–5.4 % of body mass resulted in increases in $\dot{V}_{O_2}$ of between 5.4 and 12.1 % (Myers and Steudel, 1985; Martin, 1985; Claremont and Hall, 1988). Thus, increasing limb moment of inertia by using externally applied loads produces generally similar effects on cost in bipedal humans and quadrupedal dogs.

In the present study, the dogs showed a decrease in stride frequency with limb loading. The various experiments involving limb loads on human subjects have reported dissimilar effects of the loads on stride frequency. Martin (1985) reported a slight reduction in stride frequency, similar to that seen in these dogs, but Claremont and Hall (1988) noted the opposite – a slight increase in stride frequency in their limb-loaded human subjects.

The observation that the relatively small amount of mass added in the present experiments did not produce a detectable effect on $\dot{V}_{O_2}$ when added to the back is

consistent with previous findings. Taylor *et al.* (1980) measured the effect on $\dot{V}_{O_2}$ of adding mass equivalent to 22 % and 27 % of body mass to the backs of dogs traveling at three different speeds. Calculation of the expected effect on $\dot{V}_{O_2}$ of adding 0.77 kg of mass to the backs of dogs based on the data of Taylor *et al.* (1980) indicates that the expected increase would be of the order of 0.5 ml $O_2 s^{-1}$, within the range of experimental error. Cureton *et al.* (1978) found that the addition of a load equal to 10 % of body mass to the backs of human subjects did not have a significant effect on $\dot{V}_{O_2}$. Nielsen *et al.* (1982) found that even a 25 % increase in mass obtained with back loads did not produce a significant effect on $\dot{V}_{O_2}$ in ants.

Are the experimental changes in limb moment of inertia induced in this study of a magnitude that one might reasonably expect to see within natural populations? Limb moments in domestic dogs of similar body mass have been shown to vary by 3.4-fold in the hindlimb and 4.0-fold in the forelimb of domestic dogs of similar body mass (K. Steudel and M. J. Myers, in preparation). Owing to artificial selection, domestic dogs show greater morphological variation than will be found in most natural populations. Yet even dogs of the same breed (beagle) and similar mass showed 2.6-fold variation in moment of inertia in the hindlimb and 3.1-fold in the forelimb. Thus, the vastly smaller changes in limb moments produced in this study, between 19 and 40 %, seem well within the range likely to be available for natural selection. This is especially true because measurement of I_p with the limb segments extended will tend to magnify the percentage change in I_p produced by the loads because it assesses I_p when the added mass is at its most distant from the proximal point of rotation.

The influence of mass distribution on daily energy budget

That the addition of 0.77 kg (3–4 % of body mass) to the limbs of trotting dogs produced a 7–22 % increase in the rate of oxygen consumption while a similar load on the back produced no detectable effect demonstrates that mass distribution influences locomotor cost. But will these increased locomotor costs influence the total energy budget of an animal to such an extent that they create significant selection for more economical limb design?

Garland (1983) has estimated that the ecological cost of transport (the percentage of an animal's daily energy budget allotted to locomotion) should be approximately 10 % for dogs of this size. The mass added in the present experiments would, therefore, increase the daily energy budget by approximately 1 %. Could such an increment in an organism's energy budget result in effective selection pressure?

I know of no studies that answer this question directly. That small changes in locomotor efficiency are detected and responded to by animals is suggested by data on the cost of locomotion in ponies. Rigorous training of the experimental animals coupled with data collection under very controlled conditions allowed Hoyt and Taylor (1981) to detect curvilinearity of the relationship between $\dot{V}_{O_2}$ and speed within gaits. The deviation from linearity was slight ($r^2=0.98$), implying only slightly lower cost to move a given distance when moving at speeds near the

midpoint of a gait range. Nevertheless, animals allowed to move freely selected speeds within each gait near the energetically optimal speed (Hoyt and Taylor, 1981).

Furthermore, several recent studies, albeit in completely different systems, suggest that energetic effects of very small magnitude can result in significant selection pressures. For example, Cowan and Farquhar (1977) found that time-varying adjustments of stomatal conductance in plants quantitatively match those predicted by an optimization model, and yet increase photosynthesis by only 2 % relative to a pattern of constant stomatal conductance. Givnish (1986) showed that leaf branching angles in the forest herb *Podophyllum* match the quantitative predictions of a model for minimum support costs, even though the variation in those costs within ±5° of the predicted and observed angle is considerably less than 1 % of the total biomass allocated to leaf, stem and vein tissue. Furthermore, Lande (1976) has shown that very weak selection (two selective deaths per million individuals per generation) can account for the evolutionary changes in paracone height and ectoloph length in the evolution of equids.

It should also be noted that Altmann (1987) has recently questioned the adequacy of the estimates of the distance moved daily on which Garland (1983) based estimates of the amount of energy allocated to locomotion as a percentage of the total. Altmann suggests that the energy required for locomotion might be several times higher than implied by the data on the ecological cost of transport quoted above. It seems, therefore, that variations in the cost of locomotion resulting from modest changes in limb mass distribution, such as those used in the present experiments, could indeed be the subject of selection to minimize daily energetic expenditures.

The influence of mass distribution on the duration of exercise

The economy of locomotion may also be important if energetically less efficient limbs limit the duration of a bout of exercise to such an extent that the probability of successful prey capture or predator escape is reduced. In situations where a substantial component of the energy needed for locomotion comes from anaerobic sources, a discrete, localized stockpile of ATP, creatine phosphate and muscle glucose will be depleted at a rate dependent on the intensity of the exercise. Less economical locomotion would tend to deplete these stores more rapidly, leading to an earlier onset of fatigue. High-intensity locomotion, such as that involved in prey capture or predator escape, may involve a substantial anaerobic component. This may result in animals with less economical locomotion being restricted to behavioral strategies that limit the duration of a bout of intense exercise. Alternatively, behavioral strategies that result in short bouts of exercise may allow less economical limb design. Certainly lions, which capture prey after a long stalk and short rush (Kruuk and Turner, 1967), have heavier limbs and higher locomotor costs (Chassin *et al.* 1976) than cheetahs, which capture prey after longer chases (Taylor *et al.* 1974), an observation consistent with this interpret-

Table 3. *Proportional changes in mean rates of oxygen consumption produced by limb loads compared to proportional changes in mass*

	$\dfrac{M+M_L}{M}$	$\dfrac{\dot{V}_{O_2L}}{\dot{V}_{O_2}}$	$\dfrac{\dot{V}_{O_2L}/\dot{V}_{O_2}}{(M+M_L)/M}$
Dog 1	1.03	1.07	1.04
Dog 2	1.04	1.11	1.07
Dog 3	1.04	1.13	1.09

M is the mass of the unloaded animal, M_L is the mass of the load, $\dot{V}_{O_2L}$ and $\dot{V}_{O_2}$ are the rates of oxygen consumption of the loaded and unloaded animal, respectively.

ation. More data are required, however, before this argument can be seriously evaluated.

The allometry of the effects of artificial loads on $\dot{V}_{O_2}$

Taylor *et al.* (1980) analyzed their data on back loads by comparing the proportional increase in $\dot{V}_{O_2}$ with the proportional increase in mass. Table 3 shows the results of an analogous approach to the limb load data from the present study. The proportional increase in $\dot{V}_{O_2}$ for a given proportional increase in mass is generally similar across dogs and speeds. The ratio $(\dot{V}_{O_2,L}/\dot{V}_{O_2})/((M+M_L)/M)$, where M is the mass of the animal, M_L is the mass of the load and $\dot{V}_{O_2,L}$ is the rate of oxygen consumption of limb-loaded animals, averages 1.06 (± 0.02, $N=9$) from the limb load data in the present study. This is significantly different (Student's t-test, $P<0.05$) from the average of 1.01 for dogs running with back loads sufficiently large to produce an effect on $\dot{V}_{O_2}$ (Taylor *et al.* 1980).

Although the double ratio tends to minimize the contribution of the increase in $\dot{V}_{O_2}$ due to the loads and the mass of the load by adding these effects to the unloaded values and then dividing by the unloaded value, it is useful for comparisons among species that differ widely in body size. Fig. 1 summarizes the results from a variety of studies in which varying amounts of mass were added to the limbs or backs of animals with a wide range of body mass. The line indicates the values that would be seen if the proportional increase in $\dot{V}_{O_2}$ were directly proportional to the proportional increase in mass. It is apparent that adding mass to the limbs produces increases in $\dot{V}_{O_2}$ that fall consistently above this line. Several studies in which loads have been added to the backs of animals have produced a range of results. The results of Taylor *et al.* (1980) from rats, dogs, humans and horses all fall on or near the 1:1 line, as do the back loading data on humans from Myers and Steudel (1985). When very large loads (1.5–1.9 times body mass) were added in human subjects, however, $\dot{V}_{O_2}$ increased faster than mass, producing values that fell above the 1:1 line (data from Soule *et al.* 1978). Very small animals, however, such as hermit crabs (Herreid and Full, 1986) and ants (Nielsen *et al.* 1982), showed a different pattern. In these animals, adding substantial load increased $\dot{V}_{O_2}$, but the increase was not proportional to the increase in mass (Herreid and Full, 1986). Thus, it appears that, at very small body sizes, an
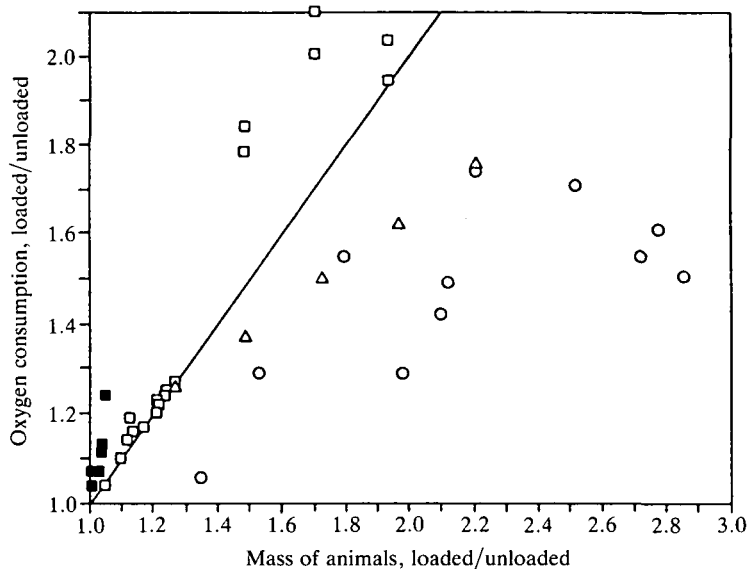
Fig. 1. Oxygen consumption (loaded/unloaded ratio) *versus* the loaded/unloaded ratio of masses summarizing the results of several studies that have used external loads to alter the mechanical work of locomotion. Solid squares represent studies in which mass has been added to the limbs (present study, Myers and Steudel, 1985; Martin, 1985). Open symbols represent data in which mass has been added on animal's backs. Squares represent data on mammals from Taylor *et al.* (1980) and from Soule *et al.* (1978); triangles represent data on ants from Nielsen *et al.* (1982); and circles represent data on hermit crabs (Herreid and Full, 1986).

increase in the total work done in locomotion produced by increasing mass does not cause proportionate increases in cost, while a substantial linkage between increase in work and increase in cost holds for larger animals. Similarly Taylor *et al.* (1972) found that increasing work by making animals run up and down inclines produced negligible effects on cost in small animals (mice) but very substantial effects in large animals (chimpanzees). Again, the relationship between cost and work observed in large animals is not apparent in small animals. These observations suggest that there may be a qualitative difference between large and small animals in the factors underlying the energetic cost of locomotion.

In conclusion, increases in limb mass result in substantially greater increases in cost than those that occur when the same amount of mass is added on the trunk. The magnitude of this effect is similar in quadrupedal dogs and bipedal humans. Comparison of the effects on cost of back loads on species showing a wide range of body size suggests substantial differences in the response of large and small animals.

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THE WORK AND ENERGETIC COST OF LOCOMOTION

II. PARTITIONING THE COST OF INTERNAL AND EXTERNAL WORK WITHIN A SPECIES

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Summary

Previous studies have shown that large animals have systematically lower mass-specific costs of locomotion than do smaller animals, in spite of there being no demonstrable difference between them in the mass-specific mechanical work of locomotion. Larger animals are somehow much more efficient at converting metabolic energy to mechanical work. The present study analyzes how this decoupling of work and cost might occur. The experimental design employs limb-loaded and back-loaded dogs and allows the energetic cost of locomotion to be partitioned between that used to move the center of mass (external work) and that used to move the limbs relative to the center of mass (internal work). These costs were measured in three dogs moving at four speeds.

Increases in the cost of external work with speed parallel increases in the amount of external work based on data from previous studies. However, increases in the cost of internal work with speed are much less (<50 %) than the increase in internal work itself over the speeds examined. Furthermore, the cost of internal work increases linearly with speed, whereas internal work itself increases as a power function of speed. It is suggested that this decoupling results from an increase with speed in the extent to which the internal work of locomotion is powered by non-metabolic means, such as elastic strain energy and transfer of energy within and between body segments.

Introduction

The energetic cost of locomotion has been shown to vary in a strongly size-dependent manner. Larger animals have systematically lower mass-specific costs of locomotion (see Taylor *et al.* 1982 for a summary of available data). A probable explanation for this pattern lay in differences in mechanical efficiency: larger animals had lower costs because they did less work in moving 1 g of their mass for a given time or distance. Experimental results, however, have contradicted this interpretation. This study looks at how this decoupling of work and cost can occur.

The mechanical work done per unit time in locomotion (in watts) is divided into

external work ($\dot{W}_{EXT}$, that done to raise and reaccelerate the center of mass of an animal) and internal work ($\dot{W}_{INT}$, that of accelerating and decelerating individual body segments relative to the center of mass). Heglund *et al.* (1982) reported a linear relationship between external work per unit time and velocity within each of 14 species tested. However, they found no systematic decrease in mass-specific external work per unit time with increasing body size that would explain the scaling of cost. Since cost shows an approximately linear relationship to velocity within an individual (Taylor *et al.* 1982), as does $\dot{W}_{EXT}$, there is considerable similarity between these two in their response to changes in velocity within an animal, perhaps even a causal linkage. Such a linkage may break down interspecifically owing to scaling of physiological and morphological determinants of locomotion.

This linkage is absent, however, for internal work and cost even within an individual. Fedak *et al.* (1982) found that the internal work done per unit time increased as a power function of speed within a species and showed no tendency to decrease in larger animals. This curvilinear relationship between $\dot{W}_{INT}$ and velocity (Cavagna and Kaneko, 1977; Fedak *et al.* 1982; Winter, 1979) coupled with the linear relationship between total cost and velocity (Taylor *et al.* 1982) could be interpreted in two ways. Taylor *et al.* (1980) argued that the results of their back-loading experiments were explicable only if the contribution of internal work to the total cost of locomotion was very small, possibly as a result of the use of elastic strain energy to power this aspect of locomotion. Alternatively, the cost of internal work may be substantial but increase with speed at a much slower rate than would be predicted from the increase in work itself; that is, the cost of internal work may be decoupled from the amount of internal work across a range of speeds.

These two possibilities can be discriminated through direct measurement of the cost of internal work within individual animals across a series of speeds. The present study develops a method of partitioning the metabolic cost of internal work from that of external work through the addition of artificial loads either at the center of mass or on the limbs. This technique is then used to estimate the relative magnitudes of the effects on cost of increases in internal and external work and to determine the pattern of variation with speed in the cost of internal work.

Materials and methods

Experimental approach

Three adult male dogs (body mass: 20, 20.9 and 26.8 kg) were trained to run on a treadmill at four speeds between 1.07 and 2.68 m s^{-1} under three different loading conditions. The speeds used differed somewhat among the three subjects. The lowest test speed was the highest speed at which each dog consistently used a walking gait; the highest test speed was the highest speed at which each dog could locomote comfortably while wearing the limb loads. For all dogs the latter was within the trot range. The remaining two test speeds were intermediate. The

experimental conditions involved adding 0.77 kg of lead either to a harness or distributed equally to the four limbs. Details of the harness and loads and of the training are given in Steudel (1990).

Measurement of oxygen consumption

Rates of oxygen consumption ($\dot{V}_{O_2}$) were measured using the open-circuit system described in Steudel (1990). $\dot{V}_{O_2}$ values for the last three successful runs for each dog under each of the 12 test conditions were used for data analysis.

All values of $\dot{V}_{O_2}$ in this study are given in $ml\,O_2\,s^{-1}$. To avoid the difficulties associated with the statistical treatment of ratios (see Atchley *et al.* 1976), I have not followed the widespread approach of dividing $\dot{V}_{O_2}$ values by body mass to obtain mass-specific values. Instead, differences in body size between the subjects are treated as a component of the between-subject variation.

All trials were videotaped at $200\,frames\,s^{-1}$ using a NAC high-speed video camera. Stride frequency was measured for each trial by counting the number of fields per stride and averaging over 10 strides. Knowing the tape speed allows conversion to strides per second.

Partitioning the costs of internal and external work

The position of the mass on the harness was very close to the center of mass of the animal and, therefore, affected external work ($\dot{W}_{EXT}$) while leaving internal work ($\dot{W}_{INT}$) virtually unchanged. Consequently, the cost of the increased external work ($\dot{C}_{EXT}$) produced by a load of this mass can be determined by subtracting the control $\dot{V}_{O_2}$ value for a given dog at a given speed from the $\dot{V}_{O_2}$ value for the same dog at the same speed running with a back load.

The cost of increased internal work ($\dot{C}_{INT}$) can be closely approximated by subtracting the $\dot{V}_{O_2}$ values for trials in which the 0.77 kg mass was added to the back from the $\dot{V}_{O_2}$ values obtained when the same mass was added to the limbs, again separately for each dog and each running speed.

I do not contend that adding mass on the trunk affects external work with no effect whatsoever on internal work or that adding mass to the limbs affects internal work with no change in external work. Rather, I argue that the back loads produce a small increase in external work while having a negligible impact on internal work, and that, similarly, the limb loads produce a substantial increase in internal work, while having a very small effect on external work.

Because the position of the center of mass of an animal oscillates slightly during locomotion as a result of changes in the position of body segments, a stationary load cannot be fixed precisely at the center of mass. The consequent changes in the relative positions of the center of mass of the trunk segment and the total body center of mass will result in some change in internal work. Given, however, the small mass of the loads and the fact that the vertical oscillations of the center of mass over a stride are of the order of a few centimeters (Cavagna *et al.* 1977; Fukunaga *et al.* 1980), the magnitude of the effect on internal work seems likely to be extremely small.

Because the total mass of the loads was between 2.9 and 3.9 % of body mass, the effect of their addition to the limbs of a stationary animal on the position of the center of mass should be modest. Moreover, the oscillations of the limbs during locomotion will not greatly alter the position of the center of mass. Because the gaits used by the dogs in this study, the walk and the trot, are both symmetrical (Hildebrand, 1966, 1980), the footfalls of the two hindfeet and two forefeet are evenly spaced in time. Consequently, the forward shift in the center of mass that would be produced by the forward placement of one limb of a pair will be approximately balanced by the backward shift in the center of mass produced by the more posterior placement of the other limb. Thus, the increase in external work produced by limb loads over the external work produced by back loads should not be very great, nor should any such effect show a strong relationship with speed because the dogs used symmetrical gaits at all speeds tested. Thus, attributing the increases in cost observed in limb-loaded trials over the costs from back-loaded trials to increases in $\dot{W}_{INT}$ seems justified.

Estimation of the mechanical work of locomotion

The rate of increase of mass-specific internal work has been shown to be independent of body size but closely related to velocity, as described by the following equation:

$$\dot{W}_{INT}/M = 0.478v^{1.53}, \tag{1}$$

where $\dot{W}_{INT}$ is the internal mechanical work done per unit time, M is body mass in kg and v is ground speed in $m\,s^{-1}$ (Fedak et al. 1982). This equation can be used to calculate a minimum estimate of the change in internal work that should be produced by adding 0.77 kg of mass to the limbs of an animal at the different speeds used in the experiments.

The minimal increments in $\dot{W}_{INT}$ due to the 0.77 kg limb loads that should be observed across the velocity range tested for each dog were calculated from the results of Fedak et al. (1982) based (i) on the relationship between $\dot{W}_{INT}$ and velocity observed for their 5 kg dog and (ii) on their summary equation (given above) based on data from seven species. The internal work done by each dog at each running speed was estimated by substituting the treadmill speed for that trial for v, calculating $\dot{W}_{INT}$, and then multiplying the result by 0.77 kg to estimate the effect of a load of that size on internal work.

Calculating the change in $\dot{W}_{INT}$ produced by the limb loads based on the equations of Fedak et al. (1982) will underestimate the change in $\dot{W}_{INT}$ actually produced by the loads. In unloaded animals, an increase in mass will be distributed across many body segments. This is the situation described by the equations of Fedak et al. (1982). With artificial loads, only the mass of the loaded segment changes. Martin (1985) has shown that it is only the mechanical work done to move the loaded segment that is altered as a result of added loads. Fedak et al. (1982) noted that the kinetic energy of the distal limb segments generally goes through greater oscillations than that of more proximal segments, because the distal

segments move further during a stride and reach higher velocities. Consequently, the addition of mass to distal segments will tend to have a greater effect on total internal work than if the same mass was more dispersed.

More importantly for the arguments given here, using the equations of Fedak *et al.* (1982) should also underestimate the magnitude of the increase with speed in work due to the loads. Because the substantial contribution of the distal segments to internal work results from their velocities at a given speed of locomotion being greater than that of more proximal segments (Fedak *et al.* 1982), the enhancement of limb velocity that occurs with increased running speed will tend to produce a larger effect on the kinetic energy of distal segments as compared to more proximal segments that have higher masses but lower velocities. Consequently, the effect of the loads being localized on the distal extremities, rather than spread evenly across the body, should result in actual increases in $\dot{W}_{INT}$ with speed being larger than the baseline values estimated here.

In summary, using the equations of Fedak *et al.* (1982) to estimate the changes in the mechanical work of locomotion produced in these experiments by the limb loads biases the results against the conclusion reported below, that $\dot{W}_{INT}$ increases faster with speed than does $\dot{C}_{INT}$. This approach to the estimation of internal mechanical work is, therefore, a conservative one, given the conclusions that are drawn below.

Statistical analysis

To determine whether there is evidence for a curvilinear increase in $\dot{C}_{INT}$ with velocity similar to that seen for $\dot{W}_{INT}$ with velocity, I have compared the fit of the relationship between $\dot{C}_{INT}$ and speed to the same relationship with logarithmic transformations to see if the exponential model produced by the transformation results in a better fit. Both relationships have also been tested to see if $\dot{C}_{INT}$ shows a significant relationship to speed. In addition, I have made direct comparisons between $\dot{V}_{O_2}$ values for limb-loaded trials and $\dot{V}_{O_2}$ values from back-loaded and control trials using regression analysis and analysis of variance (ANOVA).

Another approach involves direct comparisons of the observed increases in $\dot{C}_{INT}$ across a series of speeds with estimations of the increases in $\dot{W}_{INT}$ across the same series of speeds. Taylor *et al.* (1980) compared the ratios of loaded and unloaded mass with the ratios of loaded and unloaded $\dot{V}_{O_2}$ in a series of animals at a series of speeds. The analogous ratios in the present experiment are the ratio of $\dot{C}_{INT}$ at the highest and lowest running speed for each animal to the ratio of estimates of $\dot{W}_{INT}$ at the highest and lowest running speed for each animal. If these values are similar – that is, if the proportional increase in $\dot{C}_{INT}$ is similar to the proportional increase in $\dot{W}_{INT}$ – a clear association between internal work and its cost is indicated. A lack of proportionality between these ratios, however, would indicate a decoupling of internal work and its cost.

Results

The rates of oxygen consumption for each of the three subjects under each of the

three loading conditions (control, back loading and limb loading) at each of four test speeds are given in Table 1. Results from analysis of covariance (ANCOVA) indicate that the addition of 0.77 kg of mass to the limbs produces a consistent increase in $\dot{V}_{O_2}$ at all four speeds that is statistically highly significant. ANCOVA with $\dot{V}_{O_2}$ as the dependent variable, dog and loading condition as independent variables and velocity as a covariate showed that loading condition had a significant effect on $\dot{V}_{O_2}$ ($P < 0.001$). Least significant difference tests of the difference between mean values for each paired combination of the weighting conditions showed that the back loads did not produce a significant increase in $\dot{V}_{O_2}$ over the control condition, whereas the limb loads produced a significant increase over both back loads and control.

Since there was no significant difference between the $\dot{V}_{O_2}$ values produced under the back-loading and control conditions, in subsequent analyses the cost of internal work was measured as the $\dot{V}_{O_2}$ with limb loads minus the control $\dot{V}_{O_2}$. Since the $\dot{V}_{O_2}$ values for limb-loaded and control dogs that are subtracted to produce each estimation of $\dot{C}_{INT}$ were measured on the same day in the same test session, these values for $\dot{C}_{INT}$ contain less experimental error than those calculated by subtracting back-loaded $\dot{V}_{O_2}$ values.

The cost of internal work does not increase with speed at nearly the rate at which internal work itself increases. Least-squares regression analyses of $\dot{C}_{INT}$ *versus* speed are not significantly different from zero. This is true when the analysis is done on the untransformed data and also when the data have been logarithmically transformed to test the exponential model. Not only do the data fail to support the hypothesis that $\dot{C}_{INT}$ increases curvilinearly with speed, they show no evidence of any increase with speed. The cost of increasing internal work is significant, but the magnitude of this effect appears to be independent of speed (Fig. 1).

Table 1. *Mean rate of oxygen consumption for each of three dogs under the three loading conditions at each of four speeds*

		$\dot{V}_{O_2}$ (ml O$_2$ s^{-1})			
		Fast walk	Slow trot	Medium trot	Fast trot
Control	Dog 1	7.78±0.21	8.84±0.07	10.07±0.37	11.50±0.62
	Dog 2	7.11±0.10	8.36±0.21	9.64±0.29	10.78±0.12
	Dog 3	5.35±0.39	6.64±0.24	7.63±0.23	9.06±0.09
Back load	Dog 1	7.91±0.23	8.83±0.31	10.30±0.59	11.78±0.28
	Dog 2	7.24±0.25	8.30±0.23	9.43±0.29	10.28±0.08
	Dog 3	5.67±0.34	6.16±0.22	7.62±0.30	9.06±0.25
Leg load	Dog 1	8.55±0.02	9.42±0.20	11.03±0.34	12.57±0.23
	Dog 2	7.80±0.19	9.25±0.32	10.65±0.23	11.64±0.12
	Dog 3	6.08±0.22	7.49±0.13	8.35±0.19	9.81±0.08

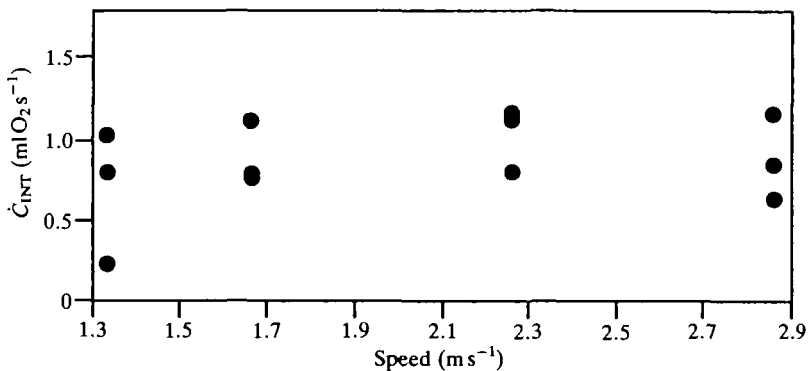Values are mean for the last three successful trials±S.E.

Fig. 1. The cost of the increased internal work produced by 0.77 kg mass added to the limbs as a function of speed. The symbols present the values of $\dot{C}_{INT}$ for all 12 trials from dog 2.

Other statistical approaches confirm this result. The observed rate of *linear* increase in the cost of locomotion with speed was not significantly greater in the limb-loaded trials than in the controls. Fig. 2 shows the $\dot{V}_{O_2}$ values obtained for each speed and loading condition for one of the animals. The results of least-squares regression analysis of $\dot{V}_{O_2}$ against speed for each dog and each loading condition are given in Table 2. For dogs 1 and 2, the slopes for the limb-loaded trials are larger than for control or back-loaded trials, but in neither case was this difference significant at $P<0.05$. In dog 3, the slope for the limb-loaded trials was nearly identical to that for the control runs.

This same conclusion is indicated by the results of ANOVA with $\dot{V}_{O_2}$ as the dependent variable, and dog, weighting condition and speed as the independent variables. Treating speed as a discrete variable rather than as a covariate allows one to test for the significance of an interaction between weighting condition and speed. If the effects of the loads are different at different speeds, as would be

Table 2. *Descriptive statistics, slope (α), y-intercept and coefficient of determination (r^2), for the least-squares regression equations for the relationship between rate of oxygen consumption ($ml\,O_2\,s^{-1}$) and speed ($m\,s^{-1}$) for each of the three dogs and for the pooled sample for the three loading conditions*

	Control			Back load			Limb load		
	α	y	r^2	α	y	r^2	α	y	r^2
Dog 1	2.93±0.83	4.13	0.86	3.11±0.83	3.95	0.87	3.26±0.54	4.37	0.95
Dog 2	2.49±0.42	4.23	0.94	2.07±0.46	4.86	0.90	2.61±0.55	4.87	0.92
Dog 3	2.63±0.51	2.49	0.93	2.52±0.66	2.66	0.87	2.62±0.36	3.28	0.96
All dogs	2.79±0.68	3.41	0.67	2.64±0.75	0.60	3.68	2.93±0.69	3.98	0.69

Values of α are mean±S.E., $N=12$.

expected if $\dot{C}_{INT}$ follows $\dot{W}_{INT}$, one should find a significant interaction. This interaction term is not significant ($P=0.579$).

Analysis of the stride frequency data showed that the dogs responded to the addition of limb loads with a small but significant ($P<0.05$) drop in the rate at
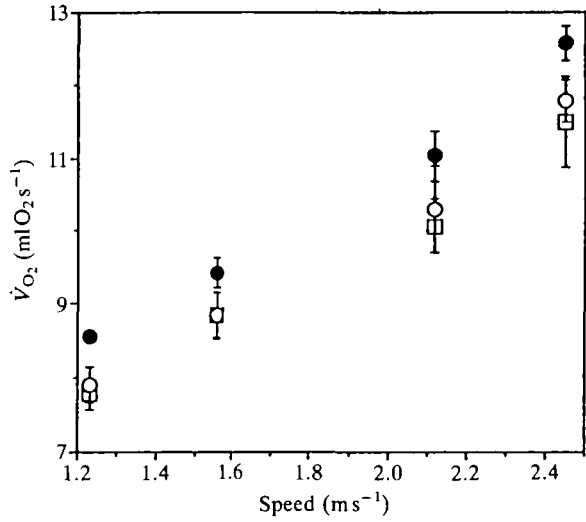

Fig. 2. Average values for the energetic cost of locomotion ($\dot{V}_{O_2}$) for each of the three loading conditions for dog 1. Closed circles represent limb loaded data, open circles represent back loaded data and open squares represent the control condition. ($N=3$ for each data point.) Bars represent S.E.M.
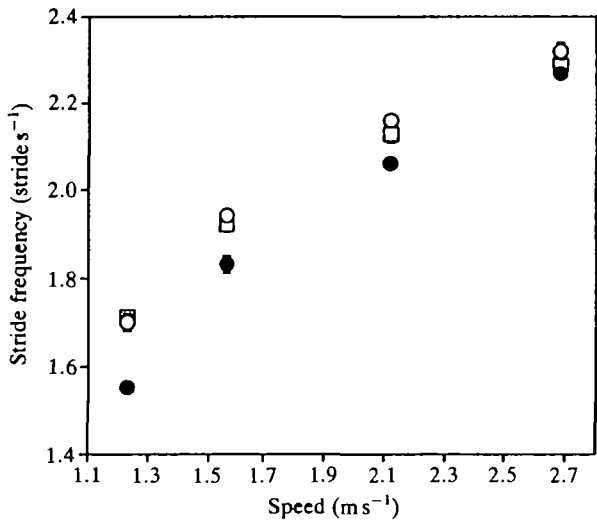

Fig. 3. Average values for stride frequency under each of the three loading conditions for each speed for dog 2. Closed circles represent limb loaded data, open circles represent back loaded data and open squares represent the control condition. ($N=3$ for each data point.) Bars represent S.E.M.

Table 3. *The proportional change in internal work with speed as a result of the addition of a load of 0.77 kg to the limbs compared to the observed proportional change in the cost of that work*

	Speed range (m s^{-1})	$\dot{W}_{INT_H}/\dot{W}_{INT_L}$	$\dot{C}_{INT_H}/\dot{C}_{INT_L}$
Dog 1	1.25–2.46	2.8 (2.88)	1.2 (1.4)
Dog 2	1.25–2.60	3.2 (3.29)	2.4 (1.2)
Dog 3	1.07–2.46	3.6 (3.67)	1.8 (1.0)

$\dot{W}_{INT_H}$ is the estimated internal work (in watts) needed to move the 0.77 kg mass at the highest running speed tested, while $\dot{W}_{INT_L}$ is the equivalent statistic at the lowest running speed, both based on the summary equation in Fedak *et al.* (1982).

The value in parentheses is the same statistic computed using the Fedak *et al.* (1982) equation for a 5 kg dog.

$\dot{C}_{INT_H}$ is the mean incremental cost of carrying the 0.77 kg mass on the legs over that of carrying it at the center of mass for the highest running speed tested.

$\dot{C}_{INT_L}$ is the equivalent statistic for the lowest speed tested.

The value in parentheses is the same statistic except that it expresses the incremental cost of carrying the mass on the limbs over the control condition.

The differences between the proportionate increases in work and in cost are significant at $P<0.03$ (two-tailed *t*-tests. $N=3$).
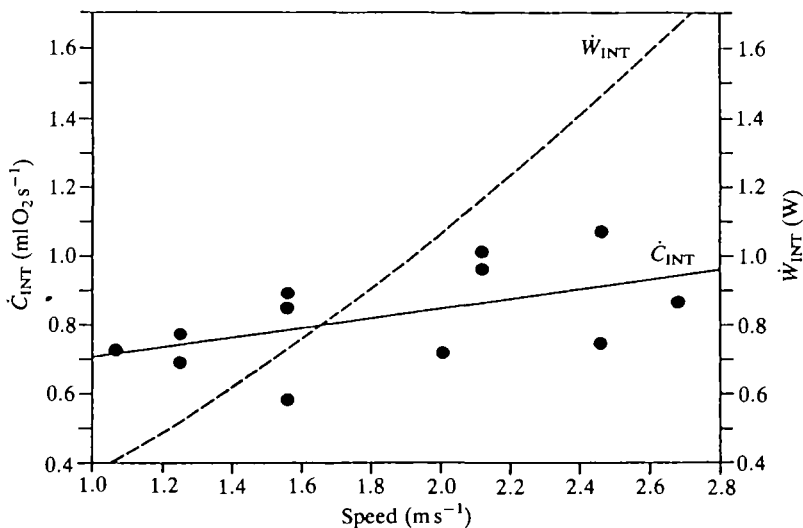

Fig. 4. The increase in internal work per unit time produced by 0.77 kg mass added to the limbs ($\dot{W}_{INT}$) compared to the actual energetic cost of the increased work ($\dot{C}_{INT}$). The curve represents the predicted values for the increase in internal work due to the loads (W) based on the summary equation in Fedak *et al.* (1982). Each symbol represents the average $\dot{V}_{O_2}$ value for a limb-loaded trial at a given speed minus the average $\dot{V}_{O_2}$ value for the control trial at the same speed for a given dog.

which they cycled their limbs (Fig. 3). This result, however, does not affect the conclusions about the rate of increase in the cost of internal work with speed. When stride frequency was regressed on speed, separately for each dog and weighting condition, the resulting slopes were not significantly different from one another at $P=0.05$. Thus, while the dogs responded to the limb loads by reducing stride frequency compared to back-loaded or control trials, the rate of increase of stride frequency with speed was not significantly different.

A direct comparison of the expected increases in $\dot{W}_{INT}$ with the observed values for $\dot{C}_{INT}$ resulted in the same conclusion. Values for the increase in $\dot{W}_{INT}$ for the velocity range tested in each dog predicted from data on a 5 kg dog and from the summary equation of pooled data (Fedak *et al.* 1982) can be seen in Table 3 along with the observed values for $\dot{C}_{INT}$ across the same velocity ranges. In all three dogs, the increase in cost is approximately half the increase that would be predicted from the increase in work. These differences are significant at $P<0.03$ (two-tailed t-tests, $N=3$). Again, these data show no evidence of a curvilinear increase in the cost of internal work with increasing velocity. This result is shown graphically in Fig. 4.

Discussion

The cost of internal work as a function of speed

These experiments were designed to determine how the variation of internal work with velocity within a species can be so different from the variation of cost with velocity within a species. As indicated above this dissimilarity could result either from the cost of internal work ($\dot{C}_{INT}$) being a very small proportion of total cost or from a decoupling of $\dot{C}_{INT}$ from the amount of internal work ($\dot{W}_{INT}$) across velocities. The latter possibility is the only one consistent with the results reported here. The cost of increasing internal work is substantially greater than that of increasing external work at all speeds tested, but the enhancement of this effect that would be expected at higher speeds does not occur.

This mitigation of cost at higher speeds implies that at such speeds the ability of the organism to use non-metabolic means to power internal work is enhanced. This is exactly the pattern that would be expected if the storage and recovery of elastic strain energy were an important interface between internal work and cost. While many aspects of the role of elastic strain energy in enhancing locomotor economy are poorly understood, it is widely believed that elastic mechanisms become increasingly effective at higher speeds. Dawson and Taylor (1973) reported an actual decline in $\dot{V}_{O_2}$ with increasing speed in hopping kangaroos, suggesting that elastic recoil paid for increasing amounts of work as speed increased. Heglund and Cavagna (1985), working on isolated muscle preparations, found that the effect of a prestretch on muscle efficiency increased with contraction rate. Gregor *et al.* (1988) have documented *in vivo* changes in time to peak force at three speeds in the cat, showing the increased opportunity for elastic storage with increasing velocity. Furthermore, they were able to demonstrate

enhanced generation of force and power output for a given shortening velocity in *in vivo* compared with *in situ* data at their higher speeds of locomotion, which they interpreted as the result of elastic storage *in vivo*.

Although most workers expect elastic mechanisms to become more important at higher speeds, a wide range of opinions exist concerning the likelihood that elastic mechanisms are important in mitigating $\dot{C}_{INT}$. Fedak *et al.* (1982) concluded that elastic recoil supplies a significant fraction of internal kinetic energy, especially at high speeds, based on comparisons of their estimates of internal work and published data on metabolic cost (Taylor *et al.* 1982). Alexander (1984) was persuaded by these arguments that elastic mechanisms should save internal work, but found that the possible mechanisms for these savings seemed 'unlikely to be very effective'. Subsequently, Alexander *et al.* (1985) presented data that make a convincing case for the importance of elastic structures in the back as a means of powering internal work. These arguments, however, apply only to galloping. Goslow *et al.* (1981) found muscle activity patterns consistent with the storage and recovery of elastic strain energy in the limbs in both trotting and galloping dogs. This occurred both in the stance phase and at the end of the swing phase and into the recovery stroke. Furthermore, Bennett *et al.* (1989) estimated that elastic strain energy stored in the hind foot could account for about 12.5 % of the cost of half a stride in trotting monkeys. The extent to which this value might change with increasing velocity is not known.

The results obtained here unequivocally indicate that some mechanism for powering internal work that supplements the muscular contribution becomes increasingly important at higher speeds. Thus, it seems very likely that the storage and recovery of elastic strain energy in muscles and tendons is important in supplying energy for internal work. Energy stored and recovered in the muscular and associated tendon complexes of the limbs described by Goslow *et al.* (1981) and Bennett *et al.* (1989) is especially likely to be involved at these speeds.

The cost of external work as a function of speed

Do these artificial loading experiments tell us anything about the role of non-metabolic mechanisms, such as elastic storage, in driving external work? Since the relatively small mass added in the present experiments did not produce a statistically significant effect when added at the center of mass, the data collected here do not indicate whether the cost of increasing external work ($\dot{C}_{EXT}$) keeps pace with the increase of external work itself ($\dot{W}_{EXT}$). Previous experiments, however, have measured the cost of locomotion in dogs running with and without back loads amounting to 21 and 27 % of body mass (Taylor *et al.* 1980). These data allow $\dot{C}_{EXT}$ to be calculated in a manner analogous to the internal work calculations made above. In this case the relevant statistic is cost with the back loads minus cost at the same velocity with no load. The appropriate calculations were carried out for both the 21 and the 27 % increases in mass. The results can then be compared with the expected increases in external work due to loads of that size based on equations given in Heglund *et al.* (1982). Data from Heglund *et al.*

(1982) were used to calculate expected increases in external work in two ways: (i) based on the relationship between work to move the center of mass and velocity observed in a 17 kg dog and (ii) based on their equation summarizing the results for that same relationship over all 14 species.

As can be seen from Table 4, $\dot{C}_{EXT}$ increases with velocity to an extent very similar to that predicted from the external work equations. Thus, both $\dot{C}_{EXT}$ and $\dot{W}_{EXT}$ are closely linked to velocity and apparently to one another within an individual. This empirical result is not at all surprising given the observation that both cost of locomotion and the work needed to move the center of mass have been shown to increase linearly with speed (Taylor et al. 1970, 1982; Heglund et al. 1982).

Thus, there is no evidence of a mitigation of the cost of external work with increasing speed. If elastic savings mechanisms become increasingly important at higher speeds and if these savings could be applied to increases in external work, one would not expect to see such a direct response of cost to work across speeds. This argument, however, is not conclusive. The direct proportionality described above for $\dot{W}_{EXT}$ and $\dot{C}_{EXT}$ will hold whenever two variables have linear relationships to a third variable with y-intercepts near zero. If the extent of elastic effects in saving external work showed a similar linear increase with speed and a zero intercept, this could result in a reduction of the observed slope for cost versus speed, a retention of the near-zero intercept and, hence, a retention of the direct proportion to cost. Thus, a role for elastic storage in mitigating external work can neither be confirmed nor ruled out by these results. If present, however, it must conform to the pattern just described – the effect must increase linearly with speed and be near zero at $0 \, m \, s^{-1}$.

As indicated above, Taylor et al. (1980) thought it necessary to assume that the direct proportionality of the change in cost to the change in mass produced by their back loads implied that most of the energetic cost of locomotion was allocated to

Table 4. *The proportionate increase in external work with speed due to the addition of load of 22 or 27% of body mass to the backs of dogs compared to the proportionate cost of that increased external work*

Test condition	Speed range $(m \, s^{-1})$	$\dot{W}_{EXT_H}/ \dot{W}_{EXT_L}$	$\dot{C}_{EXT_H}/ C_{EXT_L}$
21% increase in mass	1.97–3.89	1.9 (1.97)	2.2
27% increase in mass	1.97–3.89	1.9 (1.96)	2.06

$\dot{C}_{EXT_H}$ is the mean incremental cost of adding mass (equivalent to either at 21 or a 27% increase in body mass) to the backs of dogs at the highest test speed over a control with no added mass based on data in Taylor et al. (1980).
$\dot{C}_{EXT_L}$ is the equivalent statistic calculated for the lowest speed tested.
$\dot{W}_{EXT_H}$ is the estimated external work done to move the added mass at the highest test speed.
$\dot{W}_{EXT_L}$ is the estimated external work done to move the added mass at the lowest test speed.
The work estimates are based on the summary equation given in Heglund et al. (1982).
The number in parentheses is the same statistic based on their data for a 5 kg dog.

external work. The Appendix contains a mathematical argument concluding that the change in cost should be proportional to the change in external work as a fraction of *total* work, making no assumptions about the relative proportions of internal and external work. The result described here, that increasing internal work produces a substantial impact on cost, thus becomes readily explicable. The addition of external loads to either the limbs or the back alone does not produce an estimate of the relative importance of external and internal work in determining cost. This assessment can only be made using comparisons of the relative costs of limb loads to back loads.

The role of energy transfers in mitigating cost

Transfers of energy between body segments or between the kinetic and potential energy of the center of mass are also thought to be an important energy-saving mechanism (Cavagna *et al.* 1977; Pierrynowski *et al.* 1980; Robertson and Winter, 1980; Williams and Cavanagh, 1983). The efficiency of such transfers has been shown to vary with speed in walking humans (Cavagna *et al.* 1964). Current data on running speeds, however, are inadequate to determine the relationships between speed and the savings due to energy transfers. If the efficiency of such transfers increases with increased running speeds, it is possible that this could be another mechanism that preferentially mitigates internal work.

Implications for the scaling of total locomotor costs

Although adding mass to the limbs of an animal results in substantial, statistically significant increases in $\dot{V}_{O_2}$ across a range of speeds, the slope of the $\dot{V}_{O_2}$ *versus* speed relationship – the cost of transport – is unaltered (see Table 2 and Fig. 2). Species differences in limb mass distribution should not, therefore, emerge in studies of the cost of transport. Rather, the effect of limb morphology becomes apparent in comparisons of the absolute cost of locomotion or the mass-specific cost of locomotion at a given velocity.

The observation that the mechanical work of locomotion does not show a pattern of interspecific scaling that could be driving the scaling of the energetic cost of locomotion has caused interest to shift elsewhere for the determinants of cost (Heglund *et al.* 1982; Taylor, 1985; Steudel and Strang, 1987; Blickhan and Full, 1987; Heglund and Taylor, 1988; Strang and Steudel, 1990). Research on human locomotion, however, continues to search for a linkage between the mechanical work and the energetic cost of locomotion, attributing the lack of a perfect correspondence between the two to imprecise measurement and, especially, to imprecise understanding of the interface provided by elastic storage and energy transfers (Winter, 1979; Fukunaga *et al.* 1980; Williams and Cavanagh, 1983; Williams, 1985; Cavanagh and Kram, 1985). Perhaps what one sees is a substantial relationship between work and cost within a species, modulated by the storage and

recovery of elastic strain energy and transfers of energy, that breaks down when interspecific comparisons are made.

A variety of physiological and morphological factors might contribute to such a situation. Allometric variation in the intrinsic contraction rate of muscles (Goldspink, 1977; Taylor *et al.* 1980) or in the stride frequencies necessary to achieve a given velocity are two possibilities (Steudel and Strang, 1987; Heglund and Taylor, 1988). A third possibility is that larger mammals run at higher speeds, at which internal work becomes large relative to external work. Even though the relationship between internal work and speed is independent of mass (Fedak *et al.* 1982), the contribution of internal work to total work will be dependent on mass if running speed is dependent on mass.

Mass-dependence of running speeds is demonstrated by the scaling of speed at the trot–gallop transition as $M^{0.24}$ (Heglund *et al.* 1974). This gait transition is often regarded as a 'physiologically similar speed', useful for comparisons across species (Heglund *et al.* 1974; Heglund and Taylor, 1988; Perry *et al.* 1988). Garland (1983) reported a less pronounced scaling of maximal running speed of $M^{0.165}$. The maximum speed at which $\dot{V}_{O_2}$ has actually been measured for each species scales as $M^{0.20}$, which is similar to the scaling of maximal aerobic speed, $M^{0.19}$ (Garland *et al.* 1988).

The results described here indicate that the increased internal work produced at higher speeds does not exact a comparable increase in cost. This may be an important factor mitigating cost in larger animals.

In conclusion, the *cost* of increasing internal work does not increase as a power function of speed in a manner comparable to the *amount* of increase in internal work. Rather, the cost of increased limb mass is the same at all speeds tested. Consequently, differences in limb morphology will not be reflected in measurements of the cost of transport, but rather in measurements of the total cost of running at a given speed.

The decoupling of internal work from its energetic cost strongly implies the existence of some buffer between these parameters that becomes increasingly effective at higher speeds. The storage and recovery of elastic strain energy and the transfer of energy within and between body segments are two obvious candidates for such a buffer. The fact that larger animals more commonly run at the higher speeds at which the cost of internal work is mitigated might account, in part, for their lower energetic costs of locomotion.

Appendix

If the ratio of loaded to unloaded cost is a function of loaded to unloaded work, then:

$$\frac{\dot{V}_{O_{2,L}}}{\dot{V}_{O_2}} = \frac{W_{E,L} + W_I}{W_E + W_I}, \tag{A.1}$$

where $\dot{V}_{O_{2,L}}$ is the rate of oxygen consumption in the loaded animal, $\dot{V}_{O_2}$ is the rate of oxygen consumption in the unloaded animal, $W_{E,L}$ is external work in the loaded animal, W_E is external work in the unloaded animal and W_I is internal work, which in the Taylor *et al.* (1980) design is the same with and without the back loads. Since:

$$\text{work}(W) = \text{mass}(M) \times \text{acceleration}(a) \times \text{distance}(d)$$

and the kinematics of locomotion did not change in response to the back loads, we can rewrite equation A.1 as:

$$\frac{\dot{V}_{O_{2,L}}}{\dot{V}_{O_2}} = \frac{(M + M_1)ad + W_I}{Mad + W_I},$$

where M is the mass of the unloaded animal and M_1 is the mass of the load. Rearranging:

$$\frac{\dot{V}_{O_{2,L}}}{\dot{V}_{O_2}} = 1 + \frac{M_1 ad}{Mad + W_I} = 1 + \frac{\Delta W_E}{W_E + W_I} \tag{A.2}$$

The empirical results from the back-loading experiments suggested that:

$$\frac{\dot{V}_{O_{2,L}}}{\dot{V}_{O_2}} = k \left(\frac{M + M_1}{M} \right), \tag{A.3}$$

where M and M_1 retain the symbolism assigned above (which differs from the conventions in Taylor *et al.* 1980) and k is a constant. In the results of Taylor *et al.*, $k = 1$. Combining equations A.2 and A.3 yields:

$$k \left(1 + \frac{M_1}{M} \right) = 1 + \frac{\Delta W_E}{W_E + W_I} = \frac{\dot{V}_{O_{2,L}}}{\dot{V}_{O_2}}.$$

Thus, the result that the ratio of loaded to unloaded mass is directly proportional to the ratio of loaded to unloaded $\dot{V}_{O_2}$ also predicts that the ratio of masses is proportional to the ratio of the change in external work to *total* work. No assumption about the relative contribution of internal and external work is involved.

A similar argument can be made for the limb-loaded data holding W_E constant and increasing W_I by M_1. In this case:

$$k \left(1 + \frac{M_1}{M} \right) = 1 + \frac{\Delta W_I}{W_E + W_I} = \frac{\dot{V}_{O_{2,L}}}{\dot{V}_{O_2}}.$$

In the back-loading experiments $k = 1$, and the limb-loading results produced a value for k of 1.06.

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