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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

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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 $\dot{W}_{\mathrm{INT}}$ 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:

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

where $\dot{W}_{\mathrm{INT}}$ 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 $\dot{W}_{\mathrm{INT}}$ 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 $\dot{W}_{\mathrm{INT}}$ 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 $\dot{W}_{\mathrm{INT}}$, 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 $\dot{W}_{\mathrm{INT}}$ produced by the limb loads based on the equations of Fedak *et al.* (1982) will underestimate the change in $\dot{W}_{\mathrm{INT}}$ 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 $\dot{W}_{\mathrm{INT}}$ 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 $\dot{W}_{\mathrm{INT}}$ increases faster with speed than does $\dot{C}_{\mathrm{INT}}$. 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 $\dot{C}_{\mathrm{INT}}$ with velocity similar to that seen for $\dot{W}_{\mathrm{INT}}$ with velocity, I have compared the fit of the relationship between $\dot{C}_{\mathrm{INT}}$ 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 $\dot{C}_{\mathrm{INT}}$ shows a significant relationship to speed. In addition, I have made direct comparisons between $\dot{V}_{\mathrm{O_2}}$ values for limb-loaded trials and $\dot{V}_{\mathrm{O_2}}$ 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 $\dot{C}_{\mathrm{INT}}$ across a series of speeds with estimations of the increases in $\dot{W}_{\mathrm{INT}}$ 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 $\dot{V}_{\mathrm{O_2}}$ in a series of animals at a series of speeds. The analogous ratios in the present experiment are the ratio of $\dot{C}_{\mathrm{INT}}$ at the highest and lowest running speed for each animal to the ratio of estimates of $\dot{W}_{\mathrm{INT}}$ at the highest and lowest running speed for each animal. If these values are similar – that is, if the proportional increase in $\dot{C}_{\mathrm{INT}}$ is similar to the proportional increase in $\dot{W}_{\mathrm{INT}}$ – 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.

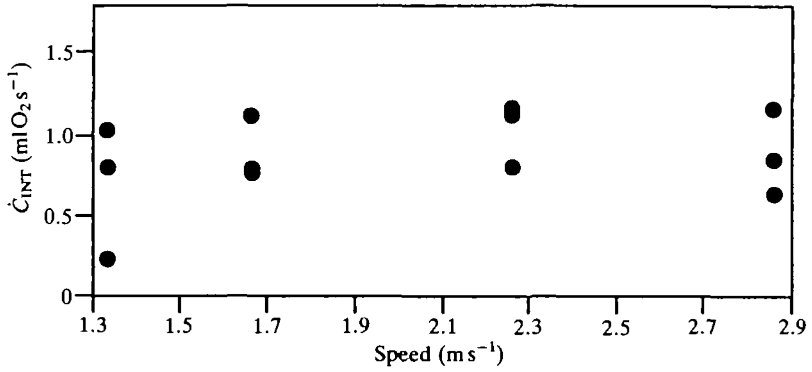

Fig. 1. The cost of the increased internal work produced by 0.77 kg mass added to the limbs as a function of speed. The symbols present the values of C_{INT} for all 12 trials from dog 2.

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

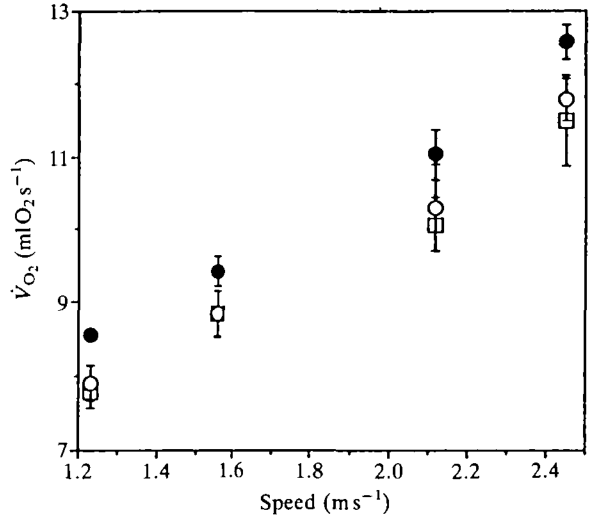

Fig. 2. Average values for the energetic cost of locomotion ($\dot{V}_{O_2}$) for each of the three loading conditions for dog 1. Closed circles represent limb loaded data, open circles represent back loaded data and open squares represent the control condition. (N=3 for each data point.) Bars represent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

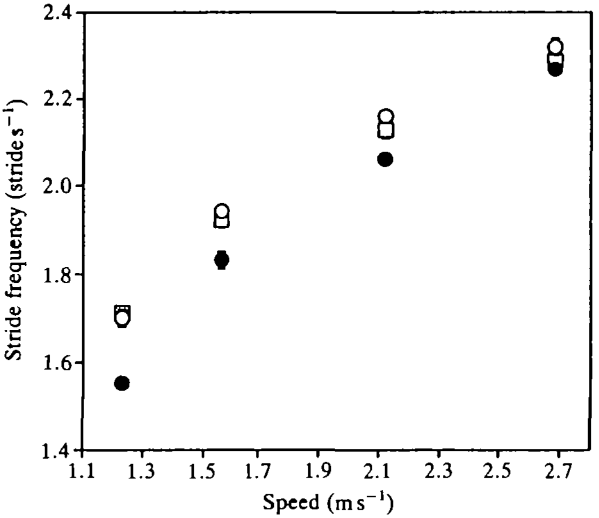

Fig. 3. Average values for stride frequency under each of the three loading conditions for each speed for dog 2. Closed circles represent limb loaded data, open circles represent back loaded data and open squares represent the control condition. (N=3 for each data point.) Bars represent S.E.M.

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. $N=3$).

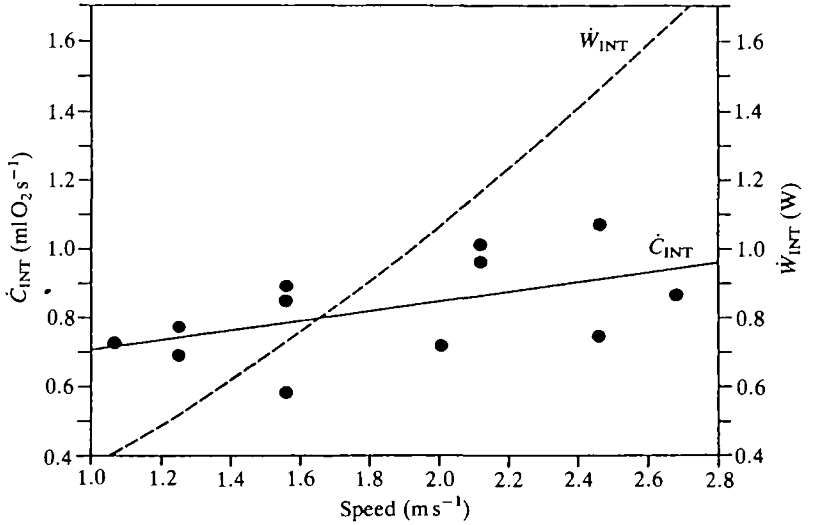

Fig. 4. The increase in internal work per unit time produced by 0.77 kg mass added to the limbs ($\dot{W}_{INT}$) compared to the actual energetic cost of the increased work ($\dot{C}_{INT}$). The curve represents the predicted values for the increase in internal work due to the loads (W) based on the 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 $\dot{W}_{\mathrm{INT}}$ with the observed values for $\dot{C}_{\mathrm{INT}}$ resulted in the same conclusion. Values for the increase in $\dot{W}_{\mathrm{INT}}$ 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 $\dot{C}_{\mathrm{INT}}$ 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 ($\dot{C}_{\mathrm{INT}}$) being a very small proportion of total cost or from a decoupling of $\dot{C}_{\mathrm{INT}}$ from the amount of internal work ($\dot{W}_{\mathrm{INT}}$) 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 $\dot{V}_{\mathrm{O}_2}$ 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 $\dot{C}_{\mathrm{INT}}$. 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 ($\dot{C}_{\mathrm{EXT}}$) keeps pace with the increase of external work itself ($\dot{W}_{\mathrm{EXT}}$). 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 $\dot{C}_{\mathrm{EXT}}$ 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, $\dot{C}_{\mathrm{EXT}}$ increases with velocity to an extent very similar to that predicted from the external work equations. Thus, both $\dot{C}_{\mathrm{EXT}}$ and $\dot{W}_{\mathrm{EXT}}$ 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 $\dot{W}_{\mathrm{EXT}}$ and $\dot{C}_{\mathrm{EXT}}$ 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 $0\,\mathrm{m\,s^{-1}}$.

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 ($\mathrm{m\,s^{-1}}$)	$\dot{W}_{\mathrm{EXT_H}}/\dot{W}_{\mathrm{EXT_L}}$	$\dot{C}_{\mathrm{EXT_H}}/\dot{C}_{\mathrm{EXT_L}}$
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

$\dot{C}_{\mathrm{EXT_H}}$ 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).

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

$\dot{W}_{\mathrm{EXT_H}}$ is the estimated external work done to move the added mass at the highest test speed.

$\dot{W}_{\mathrm{EXT_L}}$ 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.

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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:

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

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

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

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

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

where M and M_l 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:

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

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_l. In this case:

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

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

References

ALEXANDER, R. MCN. (1984). Elastic energy stores in running vertebrates. *Am. Zool.* **24**, 85–94.

ALEXANDER, R. MCN., DIMERY, N. J. AND KER, R. F. (1985). Elastic structures in the back and their role in galloping in some mammals. *J. Zool., Lond.* **207**, 467–482.

ATCHLEY, W. R., GASKINS, G. T. AND ANDERSON, D. (1976). Statistical properties of ratios. I. Empirical results. *Syst. Zool.* **25**, 137–148.

BENNETT, M. B., KER, R. F. AND ALEXANDER, R. MCN. (1989). Elastic strain energy storage in the feet of running monkeys. *J. Zool., Lond.* **217**, 469–475.

BLICKHAN, R. AND FULL, R. J. (1987). Locomotion energetics of the ghost crab. II. Mechanics of the centre of mass during walking and running. *J. exp. Biol.* **130**, 155–174.

CAVAGNA, G. A., HEGLUND, N. C. AND TAYLOR, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **268**, 467–481.

CAVAGNA, G. A. AND KANEKO, M. (1977). Mechanical work and efficiency in level walking and running. *J. Physiol., Lond.* **268**, 467–481.

CAVAGNA, G. A., SAIBENE, F. P. AND MARGARIA, R. (1964). Mechanical work in running. *J. appl. Physiol.* **19**, 249–256.

CAVANAGH, P. R. AND KRAM, R. (1985). The efficiency of human movement – a statement of the problem. *Med. Sci. Sports Exer.* **17**, 304–308.

DAWSON, T. J. AND TAYLOR, C. R. (1973). Energetic cost of locomotion in kangaroos. *Nature* **246**, 313–314.

FEDAK, M. A., HEGLUND, N. C. AND 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.

FUKUNAGA, T., MATSUO, A., YUASA, K., FUJIMATSU, H. AND ASAHINA, K. (1980). Effect of running velocity on external mechanical power output. *Ergonomics* **23**, 123–136.

GARLAND, T. (1983). The relation between maximal running speed and body mass in terrestrial mammals. *J. Zool., Lond.* **199**, 157–170.

GARLAND, T., JR, GEISER, F. AND BAUDINETTE, R. V. (1988). Comparative locomotor performance of marsupial and placental mammals. *J. Zool., Lond.* **215**, 505–522.

GOLDSPINK, G. (1977). Mechanics and energetics of muscle in animals of different sizes with particular reference to the muscle fiber composition. In *Scale Effects in Animals Locomotion* (ed. T. J. Pedley), pp. 37–55. New York: Academic Press.

GOSLOW, G. E., JR, SEEHERMAN, H. J., TAYLOR, C. R., MCCUTCHIN, M. N. AND HEGLUND, N. C. (1981). Electrical activity and relative length changes of dog limb muscles as a function of speed and gait. *J. exp. Biol.* **94**, 15–42.

GREGOR, R. J., ROY, R. R., WHITING, W. C., LOVELY, R. G., HODGSON, J. A. AND EDGERTON, V. R. (1988). Mechanical output of the cat soleus during treadmill locomotion: *in vivo vs in situ* characteristics. *J. Biomechanics* **21**, 721–732.

HEGLUND, N. C. AND CAVAGNA, G. A. (1985). Efficiency of vertebrate locomotory muscles. *J. exp. Biol.* **115**, 283–292.

HEGLUND, N. C., CAVAGNA, G. A. AND 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.

HEGLUND, N. C., FEDAK, M. A., TAYLOR, C. R. AND CAVAGNA, G. A. (1982). Energetics and mechanics of terrestrial locomotion. IV. Total mechanical energy changes as a function of speed and body size in birds and mammals. *J. exp. Biol.* **97**, 57–66.

HEGLUND, N. C. AND TAYLOR, C. R. (1988). Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *J. exp. Biol.* **138**, 301–318.

HEGLUND, N. C., TAYLOR, C. R. AND MCMAHON, T. A. (1974). Scaling stride frequency and gait to animal size: mice to horses. *Science* **186**, 1112–1113.

HILDEBRAND, M. (1966). Analysis of the symmetrical gaits of tetrapods. *Folio Biotheoretica* **6**, 1–22.

HILDEBRAND, M. (1980). The adaptive significance of tetrapod gait selection. *Am. Zool.* **20**, 255–267.

MARTIN, P. E. (1985). Mechanical and physiological responses to lower extremity loading during running. *Med. Sci. Sports Exer.* **17**, 427–433.

PERRY, A. K., BLICKHAN, R., BIEWENER, A. A., HEGLUND, N. C. AND TAYLOR, C. R. (1988). Preferred speeds in terrestrial vertebrates: are they equivalent? *J. exp. Biol.* **137**, 207–219.

PIERRYNOWSKI, M. R., WINTER, D. A. AND NORMAN, R. W. (1980). Transfers of mechanical energy within the total body and mechanical efficiency during treadmill walking. *Ergonomics* **23**, 147–156.

ROBERTSON, D. G. E. AND WINTER, D. A. (1980). Mechanical energy generation, absorption and transfer amongst segments during walking. *J. Biomechanics* **13**, 845–854.

STEUDEL, K. (1990). The work and energetic cost of locomotion. I. The effects of limb mass distribution in quadrupeds. *J. exp. Biol.* **154**, 273–285.

STEUDEL, K. AND STRANG, K. T. (1987). A simple explanation for the allometry of cost of locomotion. *Am. Zool.* **27**, 125A.

STRANG, K. T. AND STEUDEL, K. (1990). Stride frequency and stride length as co-determinants of the cost of transport and its scaling. *J. Zool., Lond.* (in press).

TAYLOR, C. R. (1985). Force development during sustained locomotion: a determinant of gait, speed and metabolic power. *J. exp. Biol.* **115**, 253–262.

TAYLOR, C. R., HEGLUND, N. C. AND MALOIY, 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., HEGLUND, N. C., MCMAHON, T. A. AND LOONEY, T. R. (1980). Energetic cost of generating muscular force during running. *J. exp. Biol.* **86**, 9–18.

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

WILLIAMS, K. R. (1985). The relationship between mechanical and physiological energy estimates. *Med. Sci. Sports Exer.* **17**, 317–325.

WILLIAMS, K. R. AND CAVANAGH, P. R. (1983). A model for the calculation of mechanical power during distance running. *J. Biomechanics* **16**, 115–128.

WINTER, D. A. (1979). A new definition of mechanical work done in human movement. *J. appl. Physiol.* **46**, R79–R83.