

THE ENERGETICS AND CARDIORESPIRATORY CORRELATES OF MAMMALIAN TERRESTRIAL LOCOMOTION

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Summary

Energy costs of locomotion in mammals can be predicted from running speed and body mass, with the minimum cost decreasing regularly with increasing mass ($M_b^{-0.30}$). The predictive value of this model is surprising, given the differences in gait and limb structure among mammals. The decrease in mass-specific cost cannot be explained by the work done in moving the limbs and the centre of mass, as animals of different sizes do the same amount of work to move a unit mass a unit distance. The magnitude of the muscle forces involved and the shortening velocity are more likely causes. Terrestrial mammals use a variety of gaits to minimise locomotory energy costs with a 'preferred speed' within each of those gaits correlating with the point of greatest economy. The maximum mass-specific energy cost during locomotion is about 10 times the resting level, but there is marked variation among species, especially between wild and domestic forms.

The total cost for locomotion in mammals lies between 1 and 6 % of the daily energy budget. Hopping is an energetically cheap way of moving in large animals and correlates with phase-locking of respiratory and limb frequencies. This form of coupling is also seen in most other mammals, especially at higher running speeds.

Comparison of the relative costs of running, flying and swimming for a given body mass shows a respective decrease, but each of these costs scales similarly with body size.

Introduction

"Upon the whole, the quantity of air breathed whilst I rode upon the engine, was just over 800 C.I. per min., whilst it was just under the same quantity in the 3d class. In the 2d class, the quantity breathed was about 700 C.I. per min., and the first class about 600 C.I. per min.: but once it was so low as 545 C.I. per min..... Riding in private carriages had a less effect than riding upon an omnibus, on account of their improved and easy construction."

This report, read by Edward Smith before the British Medical Association

Key words: locomotion, mammals, cardiorespiratory, energetics.

at Nottingham in 1859, documents one of the earliest attempts to define the metabolic cost of human activity. It was a wide-ranging study of respiratory minute volume and pulse rate associated with activities including rowing, walking at various speeds, carrying increasing weights, swimming and working on a vertical treadmill used as a punishment in prisons. In the latter case he had concluded in an 1857 report to The Royal Medical and Chirurgical Society that "the lives of prisoners are at the mercy of uneducated engineers". In another colourful account he estimated the respiratory volumes of various social strata including 'unoccupied gentlemen'. All of Smith's experiments were done on himself using a small, portable dry gas meter which he slung around his shoulders.

The first major comparative study of locomotory energetics appears to be that of the German physiologist Zuntz (1897), who measured the energy required for treadmill running in humans, horses and dogs. Later Coleman (1920) demonstrated a relationship between stride frequencies and cardiac frequencies, much of his data being recorded from species in the zoological gardens in London.

Our current knowledge of the scaling of metabolic requirements in mammals began with the work of Tucker (1970) and Taylor *et al.* (1970). In the latter study, individuals from six species, ranging in body mass from 21 g to 18 kg, were run on a motor-driven treadmill and their rates of oxygen consumption measured. The mass-specific metabolic rate was found to increase linearly with speed, the slope of the line describing this relationship being termed the incremental cost of transport. This parameter (C_t) has units such as $\text{l O}_2 \text{ kg}^{-1} \text{ s}^{-1}$ and thus represents the cost of transporting a unit of body mass over a unit distance. It has overcome the problem of comparing the locomotory energy requirements of animals with different resting rates of oxygen consumption.

Since this early work many authors have confirmed the validity of the model (e.g. Baudinette *et al.* 1976; Crompton *et al.* 1978; Fedak and Seeherman, 1979; Thompson *et al.* 1980). Taylor *et al.* (1982) pooled data from 66 mammalian species and found that the cost of transport decreases regularly with body mass:

$$C_t = 0.533M_b^{-0.316}, \quad (1)$$

where the cost of transport is in units of $\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$. (Here and elsewhere in this paper, M_b represents body mass in kilograms: other abbreviations are standard SI units).

This equation can be combined with one relating the extrapolated zero speed cost (the y-intercept of mass-specific oxygen consumption, \dot{V}_{O_2} , against speed):

$$\text{y-intercept} = 0.300M_b^{-0.303}, \quad (2)$$

to produce a single equation for predicting \dot{V}_{O_2}/M_b from body mass and speed:

$$\dot{V}_{O_2}/M_b = 0.533M_b^{-0.316}v + 0.300M_b^{-0.303}, \quad (3)$$

where \dot{V}_{O_2}/M_b is in units of $\text{ml O}_2 \text{ s}^{-1} \text{ kg}^{-1}$ and speed (v) is in m s^{-1} . Because the contribution from anaerobic metabolism was negligible in all the animals used

This derivation, multiplying the two constants by the energy equivalent of 1 ml of O_2 (20.1 J) permits the more useful expression:

$$E/M_b = 10.7M_b^{-0.316}v + 6.03M_b^{-0.303}, \quad (4)$$

where E/M_b has units of $W\ kg^{-1}$. The equation also includes data from 13 avian species, but members of no taxonomic order diverged from this general equation at the 95 % confidence level.

The predictive value of this model is surprising considering locomotor differences such as stance and bipedalism and variation among species in the position of the centre of mass of the limb. It also includes representatives from the three infra-classes of mammals. For any given body mass there is some variation in cost, but this is insignificant compared to the 17-fold increase seen between the largest and smallest species. Perhaps even more surprising is the later extension of the model to amphibians, reptiles and arthropods in which C_t has been found to vary as $M_b^{-0.31}$ (Full, 1989).

The establishment of the principle that large mammals are capable of moving a unit of body mass through a unit distance at a lower metabolic cost than small mammals has stimulated work in related areas. Recent studies have centred on the properties of muscle which underlie this scaling phenomenon, its ecological relevance, cardiorespiratory correlates and their scaling functions, and an examination of animals that may be exceptions to the general model. A detailed study of adaptive variation in cardiorespiratory function in relation to exercise has been the primary stimulus behind the concept of 'symmorphosis', a proposal that each structural entity in a functional sequence matches the overall requirements of the system (see Taylor and Weibel, 1981). Most recent studies have concentrated on running mammals but there have been some measurements of the energy requirements of mammals during flight and when swimming.

In the remainder of this review I will deal with these aspects in varying degrees of depth, first because of overlap with other reviews in this series (see Alexander, 1991; Goldspink, 1991), and second because, for some, there is still insufficient information to draw rigorous generalisations. I will develop the situation in kangaroos and wallabies more fully since they are the only large animals to have adopted hopping as their primary form of locomotion, and they provide an interesting exception to the scaling model discussed above.

Total mechanical energy changes in running mammals

The total mechanical energy of an animal during steady-state locomotion (E_{tot}) is the potential plus kinetic energy of the centre of mass, combined with the kinetic energy of the body and limbs relative to this centre of mass. This derivation excludes any contribution of elastic potential energy throughout the stride, a contribution that would be difficult to assess in the body as a whole. Perhaps the scaling of metabolic transport cost simply reflects the mechanical work performed

by the muscles in accelerating and decelerating the limbs and moving the centre mass of the body. This intuitively attractive hypothesis cannot be sustained. Using a combination of high-speed film and force platform measurements, Heglund *et al.* (1982) estimated the magnitude of E_{tot} in two chipmunks, a dog and a quail. Previous work by Cavagna and Kaneko (1977) provided comparable data for humans. The minimum mass-specific power required by the muscles to drive the oscillating energy requirements (E_{tot}/M_b) during running is described by:

$$E_{\text{tot}}/M_b = 0.478\nu^{1.53} + 0.685\nu + 0.072, \quad (5)$$

where E_{tot}/M_b has units of W kg^{-1} and ν is in m s^{-1} . The equation is independent of body size and there is no apparent nexus between mechanical work scaling and metabolic rate scaling of locomotion. Put simply, the muscles of mammals of various sizes perform work at the same rate in moving each unit of mass a given distance.

Biewener (1990) suggests that the lack of correlation between net mechanical work and the energy requirements of locomotion reflects the many functional roles of skeletal muscle. Although all muscle contractions use ATP, and therefore reflect oxygen consumption in the cycling of cross-bridges, the work performed by individual muscles may be positive in magnitude in the case of shortening, negative if the active muscle is lengthened, or zero if contraction is isometric. Certain muscle-tendon systems may also act as springs in order to store and recover elastic strain energy during a step cycle. Given this complexity in function from tissue that constitutes about 45 % of the body mass of a mammal, it is not surprising that mechanical work and metabolic cost do not show congruent scaling.

Two other major factors have been examined in the search for a link between body mass and energy cost. Studies have examined whether the metabolic cost of generating muscular force varies with speed and body mass in a manner parallel to the metabolic requirements of locomotion. To gain this information Taylor *et al.* (1980a) measured the increased cost in load-carrying for running rats, dogs, humans and horses. They found that oxygen consumption at a given speed increased in direct proportion to the relative increase in mass. Since the stride characteristics of the animals did not change with load-carrying, the magnitude of force generated per unit time (the tension-time integral of force) is most likely to be responsible for the increased total energy cost. Hence, the metabolic energy consumed by muscles in a running mammal at any speed varies systematically with the force exerted by those muscles. Using this information, and comparing Biewener's (1990) scaling of volume-specific muscle force ($M_b^{-0.29}$) to that of the cost of transport ($M_b^{-0.30}$), suggests that the magnitude and duration of force generation in muscle are ultimately responsible for locomotory cost scaling.

However, the rate at which muscle develops force, a consequence of stride frequency, may also be part of the explanation. The stride frequency of running animals decreases in a regular way with increasing body mass. Heglund and Taylor (1988) demonstrated that stride frequency at five 'equivalent speeds', such as the transition speed between gaits or the preferred speed within a gait, scale

Approximately to $M_b^{-0.21}$. It therefore follows, and has been demonstrated experimentally (see Close, 1972), that the skeletal muscles of large animals will develop force more slowly than those of small animals. This lower rate of a contraction-relaxation sequence will result in slower cycling of cross-bridges and lower rates of calcium flux, both resulting in the use of less metabolic energy to develop an equivalent amount of force (see Rall, 1986; Heglund and Cavagna, 1987).

The next logical step in the search for a causal link between gait variables and energy requirements was to normalise the rate of muscle force production by determining the metabolic cost per stride, per length of stride or per ground contact time. In a seldom-quoted paper, Gold (1973) put forward the simple proposal that all animals require the same quantity of energy to move a unit of body mass one stride at equivalent gaits. More recently, Strang and Steudel (1990) reported a high correlation between stride frequency and the energy cost to run at a given speed, and Heglund and Taylor (1988) determined the same relationship at five equivalent speeds. In the latter study the energy cost per kilogram per stride at an equivalent speed was independent of body mass in 16 species of wild and domestic mammals ranging from 16 g to 200 kg. However, the cost increased from $5.0 \text{ J kg}^{-1} \text{ stride}^{-1}$ at the preferred trotting speed to $9.4 \text{ J kg}^{-1} \text{ stride}^{-1}$ at the maximum speed for a sustained gallop. It follows that, since the higher stride frequencies of smaller animals require more rapid rates of generation and decay of muscle force, but that the cost per stride is the same, the required metabolic rate for locomotion will be driven by stride frequency.

Strang and Steudel (1990) have examined two kinematic variables that may contribute to locomotor cost, stride frequency and stride length. Their approach differs from previous studies in that they examine the rates at which these variables increase with speed, and employ a residual analysis rather than equivalent speeds to remove size-correlated effects. Their results indicate that, for a given species, the slope of the line relating metabolic cost with running speed can be predicted from those relating stride frequency and stride length with running speed. It is interesting that the lines relating metabolic cost and limb frequency with mass have non-overlapping 95 % confidence intervals, but the combined exponent for frequency and stride length is within the 95 % confidence limit of the exponent for transport cost.

When normalised for the duration of time the foot remains in contact with the ground, the metabolic cost per stride is independent of speed (Taylor and Heglund, 1982). Since this is the period over which the muscles are developing most of their force, this result again supports the view that differences in the rate of force production are the underlying cause of the scaling relationships.

There is little comparable material from other taxa to clarify the kinematic-energy relationship in running mammals. However, one group that is amenable to similar analysis, the insects, is remarkably similar to mammals in its energy and kinematic scaling (see Full *et al.* 1990). The energy cost per stride and the cost normalised for the time of ground contact in three insects approximated to the

value reported in mammals. Furthermore, insects, crustaceans and myriapods all follow the same scaling relationship for C_t as mammals.

The mechanisms underlying the scaling of mass-specific transport costs would seem to lie in changes in both force-dependent and time-dependent properties of muscle contraction (Biewener, 1990). It is possible that stride length contributes to this relationship, but the recruitment pattern of muscle fibres to achieve a longer stride is unresolved.

Another contributing factor to scaling energetics is the storage of elastic strain energy in muscle and tendon (see Alexander, 1991). There is evidence that large bipedal animals rely to a greater extent on elastic recovery than do smaller forms (Biewener *et al.* 1981), but a scaling relationship between mass and total elastic storage is not available.

Finally, although most of the work on scaling of locomotor costs has been done on mammals, the above generalisations also appear to hold for arthropods, amphibians, reptiles and birds. This combined data base includes animals that range over eight orders of magnitude in body mass, have fundamental differences in skeletal and gait arrangements and are both ectotherms and endotherms. It is therefore not surprising that the systematic decrease in the mass-specific cost of locomotion with increasing body size is not a reflection of the total mechanical work done by animals, but of the force-dependent and time-dependent properties within the conservative design of skeletal muscle.

Gaits and biomechanics of terrestrial locomotion in mammals

It is clear from the preceding discussion that the relationship between metabolic power requirements and mechanical power requirements for locomotion are still not completely understood. But what of the gaits and biomechanics involved in transmitting this mechanical power? In a recent review, Biewener (1990) addresses the mechanics of musculoskeletal design in animals and focuses on the safety factors relating to the stresses developed during locomotion. Skeletons from mammals ranging from mice to elephants have been used to compare the peak locomotor stresses of major long bones at the point of compressive failure. A safety factor of between two and four was found in all the animals considered, but poor locomotory performance, differential skeletal allometry, posture-related decreases in mechanical advantage and skeletal stiffness all contribute to this constant over a 3000-fold range in body mass. Safety factors for other biological materials seldom exceed a value of eight (Alexander, 1981).

Most mammals use gaits that approximate to a walk at slow speeds, followed by a trot and a gallop as speed increases. A second generalisation is that, as speed increases, stride length increases proportionally more than does stride frequency. The descriptive study of animal gaits has a long history (e.g. Muybridge, 1957), but only recently has the significance of why animals change gaits at particular speeds become clear. Intuitively, we may assume that gait changes occur in order to minimise the work done by locomotory muscles. The first demonstration of this

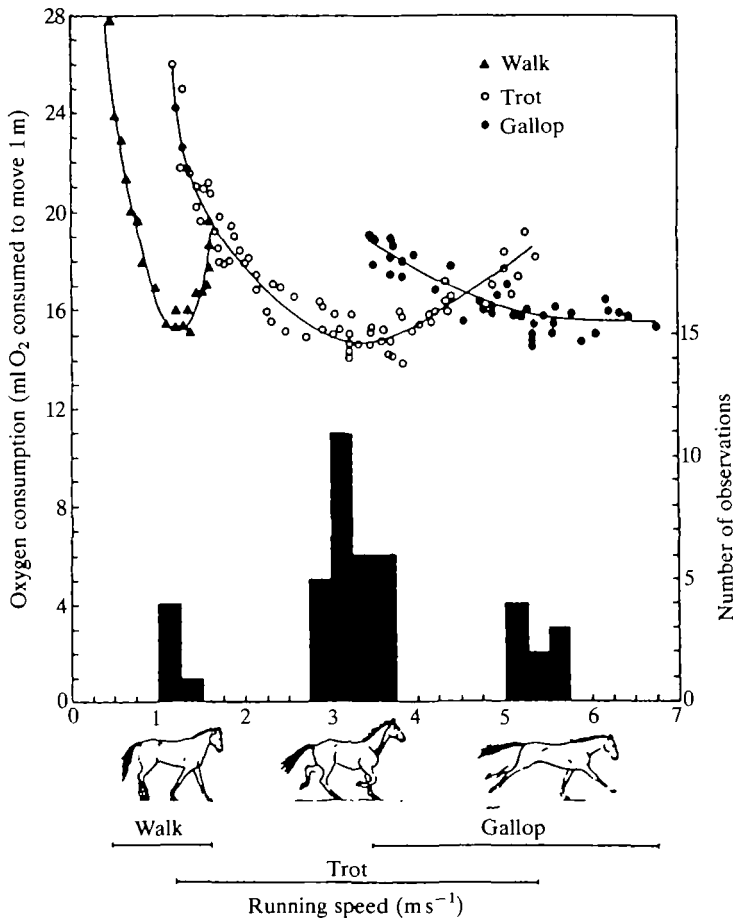


Fig. 1. Oxygen consumption of ponies using three gaits. The histograms show the frequencies of speeds spontaneously selected by one of the animals when running freely. (From Hoyt and Taylor, 1981. Reprinted by permission from Nature: Copyright 1981 MacMillan Magazines Ltd.)

came from experiments on horses that had been trained to extend their gaits beyond the normal point of change (Hoyt and Taylor, 1981). Energy use within each of three gaits increased curvilinearly, rather than linearly as data from most other mammals using natural gait transitions had previously shown. The speed at the minimal cost of transport within each gait corresponded to the spontaneously selected speed in an open field (Fig. 1). Optimum gait selection would therefore seem to permit a linear increase in metabolism with speed which approximates to a tangent to three curvilinear relationships.

An analogous situation is seen in humans. Adults walk at speeds ranging from 0.8 to 1.7 m s⁻¹, with about 1.0 m s⁻¹ being the most economical to cover a given distance. Above about 2 m s⁻¹ running takes over as being more economical than walking (see Margaria, 1976; Bornstein and Bornstein, 1976). Similarly, African

ungulates were observed by Pennycuik (1975) to use a narrow range of preferred speeds in their migrations across the African plains and it seems likely that such speeds correspond with the minimum cost of locomotion.

Given the similarities in the work rate of muscles and the skeletal safety factors from different-sized mammals, it would be interesting to know whether peak locomotory stresses were similar at preferred speeds. The only suggestion that this might be the case comes from a study of laboratory rats and kangaroo rats; animals of similar body mass but markedly different gaits (Perry *et al.* 1988). In both species the ankle extensor muscles developed similar levels of peak stress at their preferred speeds, despite the fact that the bipedal kangaroo rat showed a peak vertical acceleration per limb that was four times greater than that of the rat. In both animals the muscle stresses at the preferred speeds were only about one-third of the maximal isometric stress, and Biewener (1990) suggests that selection may have favoured a similar scope for the recruitment of muscle force between the preferred and maximal speeds.

From differing viewpoints, three recent reviews have examined gait characteristics and their control. The first, by English (1989), examines recent work on inter-limb coordination during locomotion and, in particular, the role of two ascending spinal cord systems. Two theoretical treatments have also recently become available. Optimisation criteria are used by Alexander (1989a) to argue that vertebrates adjust gait patterns so as to minimise power requirements at the current speed. In this study, interesting extrapolations are made concerning the design of robots. Whereas Alexander views gait changes as occurring when optimisation dictates an abrupt change in one or more variables (the mathematical concept of bifurcation), Schoner *et al.* (1990) suggest that gait transitions are non-equilibrium phase transitions accompanied by a loss of stability. This is a theoretical treatment, but several validations are included from human subjects. A detailed animal experiment to validate the model has not been attempted.

The ecological cost of transport

I now wish to diverge into an aspect of the field biology of mammals. So far we have discussed energetics and efficiency on a convenient mass-specific basis. There is no doubt that this approach has greatly helped in understanding comparative aspects of energetics and muscle performance. Where such an approach has been criticised is in its applicability to whole-animal foraging strategies. There would seem to be no reason to suggest that selection acts on mass-specific character states of animals, and yet such arguments have been implied in discussions of the evolutionary advantages of large body size. McNab (1971), Garland (1983) and Altmann (1987) have all commented on this problem and stressed the obvious point that animals live as intact individuals, not on a mass-specific basis.

This raises the question of how the energy required for locomotion should be compared among mammals of different body mass. Both Garland and Altmann have adopted similar approaches in evaluating locomotory costs relative to the

total maintenance costs of animals. Garland defines his 'ecological cost of transport' (ECT) as the percentage of an animal's daily energy expenditure that is devoted to transport costs. Estimates of daily energy expenditure (DEE), based on doubly-labelled water turnover and time-energy budgets are given as:

$$\text{DEE} = 800M_b^{0.71}, \quad (6)$$

where DEE is in units of kJ day^{-1} . Information on how far animals move per day (DMD) came from information on 76 species of mammals, and scales with body mass according to the equation:

$$\text{DMD} = 1.038M_b^{0.25}, \quad (7)$$

where DMD is in units of km day^{-1} . Combining these equations with that for the minimum cost of transport (Taylor *et al.* 1980a):

$$C_t(\text{J km}^{-1}) = 10\,678M_b^{0.70} \quad (8)$$

in the equation:

$$\text{ECT}(\%) = 100(\text{DMD} \times C_t)/\text{DEE}, \quad (9)$$

we obtain, for mammals:

$$\text{ECT} = 1.39M_b^{0.24} \quad (10)$$

and for carnivores alone:

$$\text{ECT} = 5.17M_b^{0.21}. \quad (11)$$

The analysis produces the surprising result that, for many mammals, daily transport costs are an insignificant part of the total daily energy budget. For example, ECT increases from values of less than 1 % for small animals to around 6 % in an elephant. There have been a few independent measures of ECT which, although generally higher than the predictions from the above equation, show similar values and a similar increasing trend with body mass. Altmann (1987) suggests that these calculated percentages suffer from a systematic underestimation in measurements of path lengths per day and from the non-inclusion of energy associated with changing speed and direction. This may apply to primates in particular.

Even with the latter reservation for some species, the 1–6 % range suggests that economy of locomotor energy is not a distinct advantage of large body size in mammals. We will not concern ourselves here with the details of this unresolved evolutionary problem. However, increased size permits an increase in running speed (see Garland *et al.* 1988) and, perhaps, an increase in foraging distance (Pennycuik, 1979; but see Altmann, 1987) and aerobic scope (see Bennett and Rubin, 1979). Altmann also adds the advantages of increasing the floristic diversity of foods and the chance of local concentrations of food, but points to the compounding factor of body size altering an animal's nutrient requirements and array of available foods.

While arguments based on mass-specific energy usage are useful heuristic tools in considering muscle and, as we shall see, cardiorespiratory function during locomotion, they are a potential fallacy when considering whole-animal energetics

from an ecological standpoint. The intrinsically selected character state which results in large mammals may not be energy *per se* but some function of foraging efficiency related to a specific environment.

The energetics of hopping mammals

A notable exception to the simple linear relationship between metabolic rate and the speed of locomotion in mammals occurs in large hopping species: wallabies and kangaroos of the family Macropodidae. All macropodid species have the ability to hop, including the tree kangaroos, which are primarily quadrupedal. The only other mammals that show this form of locomotion are desert rodents, although some high-latitude lagomorphs and some prosimians occasionally hop on their hindlegs. Dawson and Taylor (1973) trained two red kangaroos, *Macropus rufa*, to hop on a treadmill and measured rates of oxygen consumption. At slow speeds the animals moved 'pentapedally', using the tail for support as the two hindlimbs moved forward. At these speeds the animals spent more energy on locomotion than a quadrupedal mammal of equivalent body mass. However, when the animals began to hop at speeds around 1.8 m s^{-1} , rates of oxygen consumption were independent of speed and even fell slightly. Above 5 m s^{-1} a hopping kangaroo spends less energy than a quadruped of the same size. Given that the maximum speed of these animals is probably about 15 m s^{-1} , and provided that the line relating oxygen consumption and speed can be extrapolated, the energy savings associated with high-speed hopping are significant.

A similar relationship between speed and oxygen consumption has been shown for the smaller (5 kg) wallaby, *Macropus eugenii* (Baudinette *et al.* 1987). In this species, speeds above 2 m s^{-1} resulted in metabolic energy consumption becoming independent of speed but, while wearing a mask, the animals would not consistently hop faster than 5 m s^{-1} . This problem was recently overcome by the use of a transparent gas-sampling cone that was briefly lowered in front of an animal hopping at high speed. Oxygen consumption was calculated using the 'instantaneous' method (see Frappell *et al.* 1989) by back-calculating for the washout characteristics of the mask and tubing. Using this technique G. K. Snyder, R. V. Baudinette and P. B. Frappell (unpublished observations) were able to measure metabolic rates in animals moving at their maximum speeds of around 10 m s^{-1} (Fig. 2). Even at this speed the 'uncoupling' or independence of metabolism and speed was maintained. The animals were not at their maximum aerobic levels as blood lactate levels had not significantly increased above levels measured at rest.

In their original report on the energetics of hopping in kangaroos, Dawson and Taylor (1973) likened this form of locomotion to a bouncing ball or pogo stick, and suggested that elastic elements act to store gravitational and potential energy when the animal contacts the ground. As this anatomical spring recoils at take-off its energy is used in the next step. Evidence for this hypothesis comes from comparisons of oxygen consumption and mechanical energy changes in kangaroos

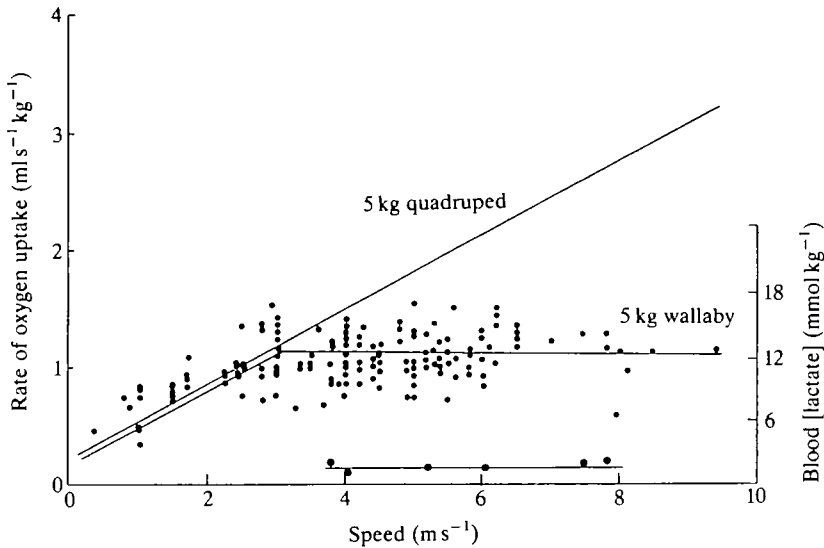


Fig. 2. Rates of oxygen consumption (small circles) and blood lactate levels (large circles) during locomotion in the tammar wallaby. Line for wallaby fitted by least-squares regression. (From R. V. Baudinette, G. K. Snyder and P. B. Frappell, unpublished results.) The predicted line for a 5 kg quadruped is from Taylor *et al.* (1982).

hopping across force plates (Alexander and Vernon, 1975; Cavagna *et al.* 1977) and from mechanical analysis of muscles and tendons (Bennet *et al.* 1986; Ker *et al.* 1986; Morgan *et al.* 1978). Dawson and Taylor's finding that oxygen consumption actually decreases a little at higher speeds is explicable if the degree of elastic storage increases with speed. In support of this view, Alexander and Vernon's (1975) force plate experiments show that the elastic mechanism is more effective at high speeds.

The idea that the percentage of energy stored in muscles and tendons would increase with hopping speed has been challenged by Griffiths (1989). In his experiments, the length and force generated by the gastrocnemius complex were telemetered from freely hopping wallabies (*Thylogale billardierii*) and correlated with electromyographs and filmed records. The results showed that at higher hopping speeds the tendon stretched and provided an energy store. However, the muscle itself was stretched beyond the predicted elastic level of the cross-bridges, resulting in energy absorption rather than the capacity for elastic recoil (see Rack and Westbury, 1974). The net result is that, even though elastic storage in tendons increases with speed, the percentage of energy stored and subsequently recovered by the complete muscle system does not increase.

It is tempting to regard kangaroos and wallabies as exceptional in the ability of their tendons to store and subsequently release stored strain energy. The role of elasticity in leg tendons has been examined in several other mammals, including monkey and deer (see Dimery *et al.* 1986). These species would appear to be more

specialised at storing energy because of the combination of exceptionally short muscle fibres and long tendons; the former are not seen in kangaroos (Alexander and Vernon, 1975).

Clearly there are discrepancies in the estimated amounts of energy stored by elastic structures in large hopping macropods. However, it is probable that at least one-third of the metabolic energy that the animals would otherwise need for locomotion is saved by using elastic energy stores.

Is energy usage independent of speed for smaller bipedal mammals? Thompson *et al.* (1980) trained two rat kangaroos (*Bettongia penicillata*) weighing 3 kg and three species of rodents to hop on a treadmill. In all these animals the rates of oxygen consumption increased linearly with speed, including the transition speed where movement changed from quadrupedal to bipedal. Similar results were found from another rat kangaroo, *Potoroos tridactylus* (D. S. Hinds, R. V. Baudinette and E. A. Halpern, unpublished observations) weighing about 1.5 kg. Dawson (1976) reported a plateau in oxygen consumption in the Australian desert rodent *Notomys cervinus*, but this may be an artefact because the animals were poorly trained (see Thompson *et al.* 1980). In support of this view, a related species, *Notomys alexis*, exhibits a linear relationship between oxygen consumption and speed (Baudinette *et al.* 1976).

The overall conclusion from the growing number of studies of small bipedal mammals is that hopping does not result in energy savings for mammals of less than about 3 kg in body mass. Comparing these data with those from the tammar wallaby suggests that at body masses of between 3 and 5 kg the energy advantage associated with hopping should become apparent.

What then are the selective advantages of bipedalism for small mammals? Biewener *et al.* (1981) compared the mechanical properties of the ankle extensor tendons and muscles of the kangaroo rat (*Dipodomys spectabilis*) with those of macropodid marsupials. *Dipodomys* has a poor capacity to store strain energy in tendons, which were square in cross-section compared with the strap-like dimensions of kangaroo tendons. Subsequently, Biewener and Blickhan (1988) compared the levels of acceleration achieved by kangaroo rats during vertical jumps of around 0.5 m with those measured during steady-state hopping and found that jumping produces three times the stress associated with hopping. The structure of the hindlimb of these animals is consistent with rapid acceleration rather than energy saving, and may aid in the avoidance of predators.

Scaling maximum aerobic capacity to body mass in mammals

Studies by Pasquis *et al.* (1970) and Lechner (1978) have shown that the maximum rate of oxygen consumption ($\dot{V}_{O_{2max}}$) is about 10 times resting metabolic rate and scales with body mass to about the 0.8 power. This work was extended by Taylor *et al.* (1980b) using eight domestic and 14 wild species of mammals, many of them large African species. $\dot{V}_{O_{2max}}$ was defined as a constant level of oxygen consumption as treadmill speed increased, with the resulting anaerobic glycolysis

Producing an accumulation of lactic acid. The wild animals used in the study showed little variability around the line:

$$\dot{V}_{O_{2\max}} = 1.94M_b^{0.79} \quad (12)$$

where $\dot{V}_{O_{2\max}}$ has units of ml s^{-1} .

This relationship shows a remarkable parallel with Kleiber's (1961) derivation for standard oxygen consumption ($\dot{V}_{O_{2\text{std}}}$):

$$\dot{V}_{O_{2\text{std}}} = 0.188M_b^{0.75} \quad (13)$$

and suggests a value around 10 for factorial scope. For domestic animals there was a marked variation between species; for example, dogs had a $\dot{V}_{O_{2\max}}$ 3.5 times greater than that of goats of the same body mass, and horses had the same factorial increase over cattle. Most wild animals fall within the range set by these domestic species.

The relationship of the minimum speed (v) where $\dot{V}_{O_{2\min}}$ is attained and body mass is not strong:

$$v = 2.34M_b^{0.122} \quad (r=0.45), \quad (14)$$

where v has units of m s^{-1} . Since the cow reaches its peak oxygen usage at about 4 m s^{-1} and the horse at a speed in excess of 10 m s^{-1} , both while galloping, this speed is clearly not an 'equivalent' or reference speed in terms of locomotory mechanics.

Cardiorespiratory function during locomotion

The concept of symmorphosis

The initial question posed in the study of Taylor *et al.* (1980b) discussed above was whether $\dot{V}_{O_{2\max}}$ would scale proportionally to $M_b^{0.75}$, like $\dot{V}_{O_{2\text{std}}}$, or to $M_b^{1.0}$, like the diffusing capacity of the lung. The latter proposal is consistent with the principle that close quantitative correlations exist between the flow rate of O_2 , in this case $\dot{V}_{O_{2\max}}$, and the structural parameters that determine such flows, in this case pulmonary diffusing capacity. Such correlations were not found and other size-dependent factors must be operating to confound a potentially simple scheme (see Weibel *et al.* 1981). In their second series of studies on this theme (see Wiebel *et al.* 1987 and following papers), attention was focused on the functional aspects of cardiorespiratory exchange rather than on structure. The study exploited the differences between 'athletic' dogs and horses and animals of lower $\dot{V}_{O_{2\max}}$ (goats and calves). We will not be concerned here with the detailed findings. However, Weibel and Taylor and their collaborators maintain their support for the concept of symmorphosis. They point to exceptions, such as the inbuilt redundancy in the lung, but stress that symmorphosis can only be expected to hold in structures that are malleable in development and meet the requirement of regulated morphogenesis.

The proposal that symmorphosis is '....a rather general principle of regulated economical construction which should apply to all levels of biological organisation'

has begun to attract the attention of those interested in evolutionary problems Garland and Huey (1987) completed a residual analysis on some of the original data used to test the theory and found few positive correlations between structural and functional indices. This is not a remarkable finding as Weibel and Taylor's original analysis admitted to some contradictions, especially in their original hypothesis that $\dot{V}_{O_{2max}}$ and pulmonary respiratory capacity scale congruently. More significant is the belief that symmorphosis may be an unlikely evolutionary outcome in that optimality may have no intrinsic selective value. This could arise, for example, as a consequence of conservative developmental constraints (see Burger, 1986; Garland and Huey, 1987).

There is also physiological evidence to challenge the premise of a matched series of components in an oxygen delivery system with no identifiable rate-limiting step. Dempsey *et al.* (1985) suggest that limits to the oxygen delivery system occur in pulmonary function in many species, and the oxidative capacity of muscle may be the limiting step to $\dot{V}_{O_{2max}}$ in goats (Jones *et al.* 1985).

Finally, there is the analysis of Wagner (1988), who proposes that the central factor determining $\dot{V}_{O_{2max}}$ is the rate of tissue diffusional O_2 transport from cellular haemoglobin to the mitochondria. The diffusion gradients that drive this process are determined by the secondary role of the circulation. It follows that a reduction in any of the secondary cardiorespiratory components must reduce the value of $\dot{V}_{O_{2max}}$, and the idea of a single rate-limiting step is not conceptually sound. Is this a corollary of symmorphosis?

In summary, the concept has heuristic value as a working hypothesis (Lindstedt and Jones, 1987), but is far from established as a new principle in biology. It is, however, a provocative idea, it forms the basis of many of the recent investigations into the cardiorespiratory correlates of locomotion, and it may be a common meeting ground for physiological and evolutionary theory.

Integration of locomotory and respiratory rhythms

The mammalian thorax has two primary mechanical functions, ventilation of the lungs, and body propulsion and support *via* the limbs. It is therefore not surprising that there is integration of these functions (Attenburrow, 1982; Bramble, 1986, 1989; Baudinette *et al.* 1987). Bramble and Carrier (1983) showed that galloping dogs, horses and jackrabbits took one breath per stride, and coined the term 'locomotory-respiratory coupling'. Slower symmetrical gaits such as trotting show a greater flexibility in entrainment and several coupling ratios are seen (Table 1). Running humans also fit this latter pattern and up to six different ratios may be employed, although a 2:1 locomotory respiratory pattern is most common in experienced runners (see also Loring *et al.* 1990). Hopping wallabies and flying bats appear to have no flexibility in respiratory coupling.

Several mechanisms have been proposed by which locomotory movements could drive breathing frequencies (see Alexander, 1989b; Bramble, 1989). The evidence for a neuronal 'command centre' has been reviewed by Eldridge *et al.*

Table 1. *Coupling of locomotory-respiratory patterns in mammals*

Species	Gait	Coupling ratios
Hare	Half bound	1:1, 1:2
	Gallop	1:1
Horse	Trot	1:1, 3:2, 2:1, 5:2
	Gallop	1:1
Dog	Trot	1:1 plus others?
	Gallop	1:1
Human	Run	3:2, 2:1, 5:2, 3:1, 7:2, 4:1 and possibly 1:1
Bat	Flight	1:1
Wallaby	Hopping	1:1
Tree kangaroo	Trot	1:1
Bettong	Hopping	1:1
Potoroo	Gallop	1:1
	Hopping	1:1

Modified from Bramble (1989) with additional data from Baudinette (1989).

(1985). The demonstration of respiratory phase-locking during mechanical ventilation in humans adds to this evidence (Graves *et al.* 1986). Such a centre would provide parallel output to locomotor and respiratory muscles and may receive afferent information from limb and joint mechanoreceptor or intercostal and pulmonary stretch receptors (see, for example, Waldrop *et al.* 1986). The idea of parallel and proportional output from a pontomedullary centre fits well with the concept of a dual parallel pump model for respiratory organisation (see Barnas *et al.* 1989). In such an arrangement one 'pump' serves both respiratory and structural roles and the second is devoted to respiration. A single neuronal control for such a system, in which proportional recruitment could be achieved at differing intensities, is an attractive idea.

Mechanical factors such as flexion of the back have been shown to drive the abdominal viscera and diaphragm in a cranio-caudal direction, thus compressing and expanding the lungs. Similarly, dynamic loading and subsequent compression of the thorax by forces transmitted through the forelimbs would couple expiration to forelimb substratum contact (see Bramble, 1989).

The simplest mechanism that could account for locomotory respiratory coupling is that of a 'visceral piston' (Bramble and Carrier, 1983). The potential for this mechanism is seen in the anatomy of the diaphragm, with a central tendon attached to the 'piston' of the liver. Details of the anatomy of this arrangement are provided by Bramble (1989) but, in summary, the viscera are free to move in the cranio-caudal direction and to force air from the posterodorsal pulmonary lobes.

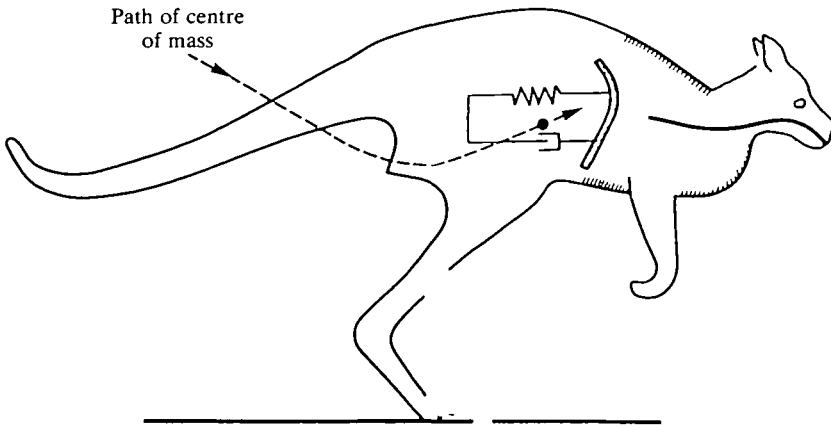


Fig. 3. A suggested visceral piston to drive respiration in hopping kangaroos. (From Baudinette, 1989, after Alexander 1987.) The abdominal viscera are represented by the resistance and dashpot symbols attached to the diaphragm.

Both Bramble (1986) and Alexander (1987) have suggested that the piston is a resonant system tuned to stride frequency.

A clear demonstration of the role of a visceral piston is associated with the simple hopping gait of the tammar wallaby (Baudinette *et al.* 1987). In these animals, stride frequencies is relatively constant at speeds between 1 and 9 m s^{-1} , and stride length is the primary determinant of speed increase. The frequencies of breathing and limb movement are coupled 1:1 at all hopping speeds and inspiration begins as the animal leaves the substratum and continues through about 26% of the hopping cycle (Figs 3 and 4). The proposal that ventilation during steady-state hopping is largely dependent on the action of a visceral piston is supported by the morphology of the diaphragm. The structure is of similar area to that of other mammals of the same body size, but is lighter and has a larger central tendon relative to muscle. Bramble (1983) has suggested that the disadvantage of a single coupling ratio between locomotory and respiratory frequencies is that increased oxygen demand could only be met by proportional increases in tidal volume. Therefore, a change in coupling ratio, such as that seen in humans, may be initiated by an approaching limit to tidal volume. This problem does not exist in wallabies. As discussed above, the storage of elastic strain energy has the effect of making oxygen demand independent of increasing speed, and tidal volumes and consequently minute volumes remain unchanged. Correlation of gait and respiratory frequencies has been observed in other macropods, including a quadrupedal tree kangaroo (Baudinette, 1989).

Alexander (1989*b*) has used a mathematical model to test the plausibility of this simple form of marsupial respiration. He concludes that such a mechanism could account for the experimental observations if the piston was tuned to the stride frequency. The alternative explanation, a system driven by flexion of the back, is not compatible because the phase relationships of leg and back movements differ.

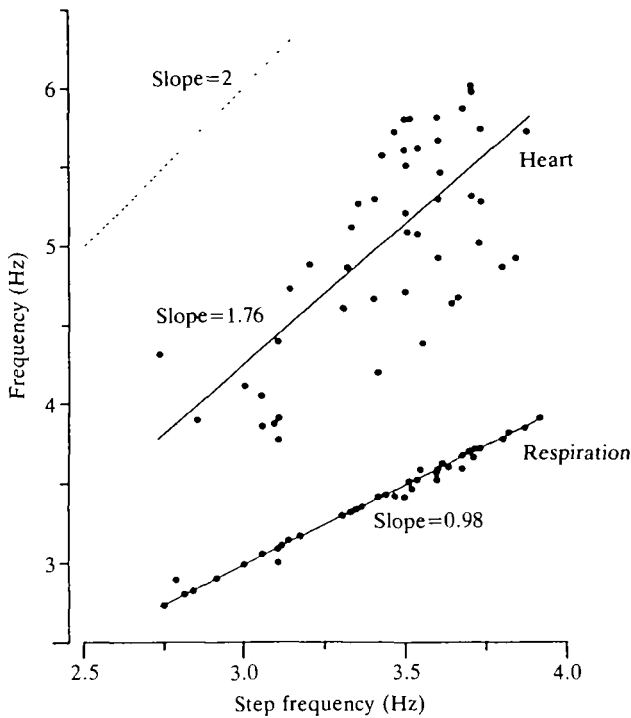


Fig. 4. Respiratory and cardiac frequencies plotted as a function of hopping frequencies in tammar wallabies (From Baudinette *et al.* 1987). The relationship between breathing frequency (y) and hopping frequency (x) is represented by the equation: $y=0.98x+0.04$ ($N=47$, $r=0.99$) and for heart rate (y) as a function of hopping frequency by $y=1.76x-1.02$ ($N=46$, $r=0.67$).

In applying his model to galloping horses the outcome is not as clear, but back-bending is judged to be the primary contributor to synchrony.

Coupling of locomotor and cardiac rhythms

During exercise, intramuscular pressure can rise to levels that exceed peak systolic pressures, and complete occlusion of blood vessels has been recorded at between 30 and 70 % of maximum voluntary contraction in human muscles (Sejersted *et al.* 1984). It is therefore reasonable to suggest that, to maximise perfusion of working muscle and to reduce cardiac work associated with after-loading, cardiac contraction should occur at the lowest point in the intramuscular pressure cycle. To achieve this condition, cardiac and locomotor frequencies would have to be phase-locked, with a short lag to accommodate the time for the pulse wave to reach the muscle.

Cardiac-locomotor coupling was first investigated by Coleman (1920), who showed a remarkable coincidence between the number of steps and the number of

heart beats in a variety of zoo animals. The same report details the phenomenon in human subjects but points to over-riding emotional factors if the body is not '...in erect, easy poise, and the attention steady but flexible'. Two recent investigations of coupling have been conducted, the first in the tammar wallaby by Baudinette *et al.* (1987) and the second in human subjects by Kirby *et al.* (1989).

Large hopping kangaroos would seem to be an ideal animal model for cardiac-locomotor coupling. In contrast to quadrupedal locomotion, hopping results in opposing sets of muscles acting synchronously. When the animal lands on the ground most of the muscles of both hindlimbs will be in an active state and vascular impedance will be high. We could expect that this would result in large, potentially damaging, excursions in arterial pressure and high levels of cardiac work if cardiac contraction were not coupled appropriately with the intramuscular pressure cycle. The conical body shape of the animals would tend to accentuate the problem further. Body size and shape are major determinants of arterial pressure pulse contours, and variation among species has been attributed to differences in wave reflection from muscle mass. Kangaroos have more marked secondary aortic wave reflections than any other species examined (Avolio *et al.* 1984). The narrow upper body, with its lack of locomotory muscles and relatively small brachiocephalic and subclavian arteries, provides insignificant pressure reflections compared to those from the lower body mass. The effect of this conical body shape can result in reflected pressure pulses that exceed peak systolic pressures.

Results from the tammar wallaby show that cardiac-locomotor phase-locking does not occur over speeds from 1 to 9 m s⁻¹ (Baudinette *et al.* 1987). The paradox is not resolved by recent results (R. V. Baudinette and B. J. Gannon, unpublished results) which demonstrate peak arterial pressures of around 24 kPa during hopping, levels commonly found in other mammals and birds during exercise. A full explanation of the mechanisms responsible for the dissipation of the postulated high pressures is not yet available, but we do know that the static compliance of the aorta in wallabies is much greater than in the rabbit, and that the walls of the vessel contain many more layers of elastin.

Using human subjects, Kirby *et al.* (1989) demonstrated coupling between stride and cardiac frequencies at one or more speeds in 18 of 25 subjects during treadmill exercise. To remove the possibility that coupling may be caused by vertical accelerations of the heart during running, the experiments were repeated on another 12 subjects using a bicycle ergometer. In this second group, coupling was found in at least two sampling periods from 10 subjects. The authors conclude that the results constitute '...no more than circumstantial evidence for a functionally significant relationship between heart rate and exercise', but nevertheless suggest that such coupling appears to be a normal physiological phenomenon and one that provides new insight with which to study endurance.

In humans there is evidence of cardiac-locomotor coupling at the fastest running speed. Since scaling relationships have been one of the themes of this review, it is interesting to examine how maximum heart rate and stride frequency scale with body mass. For quadrupeds ranging in body mass from 0.029 to 680 kg,

stride frequency per second (f_s) varies with mass according to the equation (Heglund and Taylor, 1988):

$$f_s = 4.70M_b^{-0.162}. \quad (15)$$

The maximum steady-state heart rate (f_H in units of beats s^{-1}) during treadmill exercise in 10 species of mammals ranging in mass from 0.032 to 67.1 kg scales as:

$$f_H = 6.25M_b^{-0.19}, \quad (16)$$

(Baudinette, 1978). A comparison of these equations suggests that 1:1 coupling at maximum stride and heart rates is more likely to occur in animals of large body mass; however, the exponents are similar enough to suggest that this coupling might occur in all but the smallest mammals.

The energy cost of running compared to flying and swimming

This review has been concerned with terrestrial locomotion, but there are analogies in gaits, elastic structures and scaling relationships that are apparent in swimming and flying mammals. Information is available on the flight energetics of several species of bats (see Thomas, 1975; Carpenter, 1986), and aerodynamic experiments in which vortices were visualised have suggested gait changes with flight in these animals (Rayner *et al.* 1986). There are no published studies on the role of storage of elastic strain energy in bat flight.

Studies of the energetics and mechanics of swimming have concentrated on fish, but data are available for several marine mammals. The area has been recently reviewed by Videler and Nolet (1990). Different gaits are employed by some fish depending on the mechanical conditions experienced but, apart from comment on human swimming styles and 'porpoising' in cetaceans, little quantitative information exists from mammals (see Alexander, 1989*a,b*). The elastic properties of tendons in the tails of two cetacean species have been examined by Bennett *et al.* (1987) and, in an apparent paradox, the structures appear to have compliance levels far in excess of the optimum. The conclusion is that elasticity in this case may increase energy costs associated with swimming. Elastic fibres under the blubber of whales have been suggested to act as energy-saving springs during swimming (Wainwright *et al.* 1985).

Since the seminal papers of Tucker (1970) and Schmidt-Nielsen (1972) there has been interest in the comparative power requirements of swimming, flying and running. Data are now available for about 40 swimming species, five of them mammals. The cost of transport for submerged swimmers (in units of J Nm^{-1}) and for surface swimmers decreases with body mass according to the equation (Videler and Nolet, 1990):

$$C_t = 0.33M_b^{-0.24}. \quad (17)$$

For running animals the equivalent equation from Taylor *et al.* (1982) is:

$$C_t = 1.09M_b^{-0.32}. \quad (18)$$

For flying animals the situation is not directly comparable in that the cost of

transport generally shows a parabolic relationship with speed (see Thomas, 1975). However, pooling the data from eight bat species with those reported from birds, Carpenter (1986) has scaled the minimum power input with body mass. On examining the relationships of mass-specific metabolic rates with speed, it seems that most species have minimum values at flying speeds around 8.5 m s^{-1} . Using this speed, a minimum cost of transport for flying animals (J Nm^{-1}) scales as:

$$C_t = 0.608 M_b^{-0.26}. \quad (19)$$

From these equations, and as pointed out in the earliest papers on comparative locomotory energetics (e.g. Schmidt-Nielsen, 1972), for a given body size, swimming, flying and running are ranked quite separately in their relative power requirements. The second generalisation that can be made is the similarity in scaling for all three modes of transport. In spite of the detailed mechanical and metabolic analyses of locomotion that are now available, our understanding of the reasons underlying these trends is incomplete.

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