

## Review

# Models and the scaling of energy costs for locomotion

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### Summary

To achieve the required generality, models designed to predict scaling relationships for diverse groups of animals generally need to be simple. An argument based on considerations of dynamic similarity predicts correctly that the mechanical cost of transport for running [power/(body mass  $\times$  speed)] will be independent of body mass; but measurements of oxygen consumption for running birds and mammals show that the metabolic cost of transport is proportional to (body mass)<sup>-0.32</sup>. Thus the leg muscles seem to work more efficiently in larger animals. A model that treats birds as fixed wing aircraft predicts that the mechanical power required for flight at the maximum range speed will be proportional to (body mass)<sup>1.02</sup>, but the metabolic power is found to be proportional to (body mass)<sup>0.83</sup>; again, larger animals seem to have more efficient muscles. A model that treats hovering hummingbirds and insects as helicopters

predicts mechanical power to be approximately proportional to body mass, but measurements of oxygen consumption once again show efficiency increasing with body mass. A model of swimming fish as rigid submarines predicts power to be proportional to (body mass)<sup>0.5</sup> $\times$ (speed)<sup>2.5</sup> or to (body mass)<sup>0.6</sup> $\times$ (speed)<sup>2.8</sup>, depending on whether flow in the boundary layer is laminar or turbulent. Unfortunately, this prediction cannot easily be compared with available compilations of metabolic data. The finding that efficiency seems to increase with body mass, at least in running and flight, is discussed in relation to the metabolic energy costs of muscular work and force.

Key words: cost of transport, running, flight, swimming, efficiency, body mass.

### Introduction

In this paper I look at the scaling of the energy costs of locomotion, and ask whether we can explain what we observe. The explanations must depend on mathematical models. If we cannot formulate a convincing model that predicts a scaling rule reasonably accurately, we have failed to explain the rule. The reverse is unfortunately not true; a model that predicts a scaling rule correctly does not guarantee that our explanation is correct, because several models may predict the same rule.

My interest here is in widely applicable scaling rules; for example in rules that will predict the scaling of running over the range from small rodents to elephants, or of flight from sparrows to swans. Mice are not scale models of elephants, and do not move like tiny elephants, and sparrows are not miniature swans. The models will have to be very general, incorporating little specific anatomical or kinematic detail. Conveniently, this implies that they will be simple. Many simple models of running, swimming and flight were presented at the first Scaling Conference (Pedley, 1977), on which this paper builds.

In the decades preceding the first Scaling Conference, measurements of metabolic rate during locomotion had been greatly facilitated by the introduction of methods using

treadmills (Taylor et al., 1970), wind tunnels (Tucker, 1968) and water tunnels (Brett, 1964). Allometric exponents relating the measured energy cost of locomotion to body mass had been calculated by Taylor et al. (1970) for running; by Tucker (1970) for running and flight; and for swimming by Schmidt-Nielsen (1972). Allometric equations in more recent papers are referred to in later sections of this one.

Because muscles do not work with uniform efficiency, it is much more difficult to devise a model that predicts the metabolic energy cost of locomotion than one that predicts mechanical work. In contrast, oxygen consumption (and hence metabolic power) can be measured directly, whereas determination of mechanical work in locomotion generally involves calculations subject to a good deal of uncertainty. Thus comparisons between theoretical and observed energy costs are not easy. It is the metabolic cost of locomotion, rather than the mechanical work, which is important for the animal's energy budget.

### Dynamic similarity

I will refer frequently to the concept of dynamic similarity

(see, for example, Alexander, 2003). Two bodies are geometrically similar if one could be made identical to the other by multiplying all its linear dimensions by the same factor  $\lambda$ . By an extension of the same idea, two motions are dynamically similar if they could be made identical by multiplying all linear dimensions by a factor  $\lambda$ , all times by a factor  $\tau$ , and all forces by a factor  $\phi$ . For example, the motions of two pendulums of different lengths, swinging through the same angle, are dynamically similar. Strict dynamic similarity requires geometric similarity.

Two systems can only have dynamically similar motion in particular circumstances. If gravitational forces are important, ratios of (gravitational force/inertial force) must be the same for the two systems, at corresponding stages of their motions. For this to be possible, the systems must be moving with equal Froude numbers [ $\text{speed}^2/(\text{gravitational acceleration} \times \text{length})$ ]. A fuller explanation of this point can be found in Alexander (2003). In calculating a Froude number, any length characteristic of the systems may be used; for example, leg length is generally used in discussions of running. If viscous forces are important, dynamic similarity is conditional on equality of ratios of viscous forces to inertial forces, which requires equal values of the Reynolds number ( $\text{speed} \times \text{length} \times \text{fluid density}/\text{viscosity}$ ). For dynamic similarity of vibrating systems, the Strouhal numbers ( $\text{frequency} \times \text{length}/\text{speed}$ ) must be equal. Froude, Reynolds and Strouhal numbers are dimensionless. Other dimensionless numbers define conditions for dynamic similarity, in systems for which other kinds of forces are important.

### Running

Because gravitational forces are important, dynamic similarity in walking and running is possible only between animals travelling with equal Froude numbers. Alexander (1977) plotted relative stride length (stride length/leg length) against the square root of Froude number, for ostriches and various mammals, and found that all the points lay near a single line. Alexander and Jayes (1983) showed in more detail that mammals of different sizes, running with equal Froude numbers, tend to dynamic similarity: they use the same gait, similar relative stride lengths and duty factors, and exert similar patterns of force on the ground. There are some discrepancies (notably, rodents and other small mammals, which run with their legs more bent than larger mammals, and take relatively longer strides at the same Froude number), but the predictions of dynamic similarity hold reasonably well. Biewener (1989) pointed out that larger mammals need to run on straighter legs than small ones, to avoid excessive bone and muscle stresses. Birds of different sizes, running at equal Froude numbers, also tend to move in dynamically similar fashion, with discrepancies due to the largest birds keeping their legs straighter (Gates and Biewener, 1991).

Some of the energy that mammals and birds would otherwise need for running is saved by tendons that store and then return elastic strain energy, in the course of a step.

Alexander (1988) pointed out that, for dynamic similarity in running, animals should be elastically similar; in other words, forces proportional to their body weights should cause equal strains (fractional length changes). Bullimore and Burn (2004) showed that this presents a problem, because tendon has the same elastic modulus in mammals of all sizes. Elastically similar structures undergo equal strains (change of height/height) when loaded with their own weight. Structures with equal elastic moduli loaded with their own weight, however, undergo strains in proportion to the stress, which is (weight/cross sectional area). If they are geometrically similar, their weights are proportional to  $(\text{length})^3$  and their cross-sectional areas to  $(\text{length})^2$ . Therefore elastic similarity, between mammals of different sizes whose tendons have equal elastic moduli, is inconsistent with strict dynamic similarity. Bullimore and Burn (2004) went on to show that the size-related changes in posture that Biewener (1989) had shown to be necessary to avoid excessive stresses in large mammals, also made approximate elastic similarity possible.

For animals running in dynamically similar fashion, all forces are proportional to body weight and all velocities to the speed of running. Thus mechanical power is proportional to (weight  $\times$  speed), and the mechanical cost of transport [power/(mass  $\times$  speed)] is independent of body mass. Alexander (1977) showed that cost of transport was independent of mass for specific models of walking and running.

Taylor et al. (1982) showed for a wide range of mammals and birds that the metabolic power required for running was linearly related to speed. They subtracted the intercept at zero speed (representing the metabolic rate while standing still) to obtain the net power required for running. They found that the net metabolic cost of transport was proportional to body mass ( $M_b$ )<sup>-0.32</sup>. Fig. 1 shows that the same relationship also fits data from reptiles, amphibians and arthropods (Full, 1989). Calculations based on force plate records and films of a smaller sample of birds, mammals and arthropods showed, however, that the mechanical cost of transport was independent of body mass (Heglund et al., 1982; Full and Tu, 1991), as predicted by the dynamic similarity model.

The efficiency with which the muscles perform the work required for running is the work divided by the metabolic energy cost. Fig. 1 seems to show that large runners are more efficient than small ones; that the efficiency of running is approximately proportional to  $M_b^{0.3}$ . The mechanical costs shown in Fig. 1, however, ignore the savings made by elastic mechanisms, leading to the impossible prediction (by extrapolation) of efficiencies greater than 100% for animals of the size of elephants. The apparent increase of efficiency with increasing body size could be misleading if savings by elastic mechanisms are proportionately larger in larger animals. Apparent efficiencies calculated from the data of Fig. 1 are 17 times greater for 100 kg runners than for 10 g runners. It seems most unlikely that any difference in the effectiveness of elastic mechanisms, between runners of different sizes, is large enough to account for that. We must conclude that the muscles

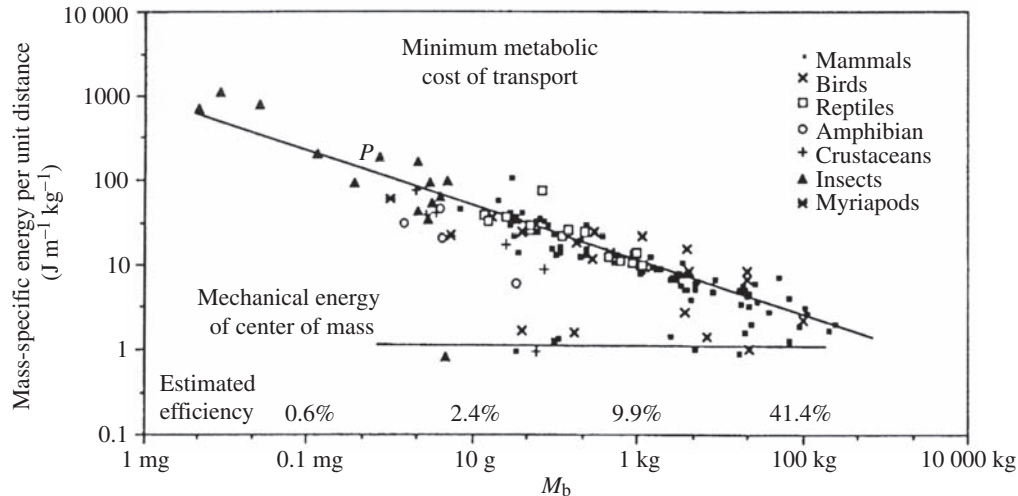


Fig. 1. Graphs of cost of transport against body mass  $M_b$  for running animals. The upper line shows the net metabolic cost, and the lower one the mechanical cost (ignoring fluctuations of internal kinetic energy, and energy saving by elastic mechanisms). On the horizontal axis, 0.1 mg should read 0.1 g. From R. J. Full: Mechanics and energetics of terrestrial locomotion: bipeds to polypeds. In *Energy Transformations in Cells and Organisms* (ed. W. Wieser and E. Gnaiger), pp. 175-182. Stuttgart: Thieme. Reprinted by permission.

of larger runners do indeed perform work with higher efficiency. Before discussing this further, we will ask whether the same is true for other modes of locomotion.

### Flight

Flying insects, birds and bats use their wings to drive air downward, exerting on the air a downward force that balances body weight. In fast forward flight, the speeds of the beating wings relative to the body are low compared to the speed of the body relative to the air. In slow and hovering flight, the reverse is true. We can make rough estimates of mechanical energy costs by modelling fast fliers as fixed-wing aircraft (following Pennycuik, 1969, with modifications) and slow fliers as helicopters (Weis-Fogh, 1973). The cruising flight of birds, bats and large insects such as locusts is fast in this sense. Hummingbirds and many insects hover, and even in cruising flight the wings of small insects move much faster than their bodies; their flight is slow, in the sense used in this paragraph.

Flow over the wings of aeroplanes and the rotors of helicopters is steady, in the sense that velocities remain constant. In contrast, flow over a flapping wing is unsteady. Aerodynamic forces acting in unsteady systems cannot be predicted accurately by equations for steady flow. Consequently, calculations based on steady aerodynamics, of the power required for flapping flight, are subject to error (Ellington, 1995; Rayner, 1995b). The greater the distance travelled by the wing in a single beat, expressed as a multiple of its chord length, the less serious are these errors likely to be. Thus they are likely to be less serious in fast flight, than in slow flight or hovering. In this paper, which requires only rough answers, I tolerate the errors for the sake of simplicity.

I will consider fast flight first. The power  $P$  required for flight by a fixed-wing aircraft is the sum of two components.

The induced power is required to give kinetic energy to the air that is driven downwards to counteract gravity. The profile power is required to overcome the drag due to the viscosity of the air in the boundary layer, and to give kinetic energy to the air that is drawn forward in the wake. The power needed to overcome the drag on the body (parasite power) is sometimes calculated separately, but here I include it in the profile power:

$$\text{Total power} = \text{profile power} + \text{induced power}$$

$$P = [(\rho v^3 C_0 A / 2) + (2k M_b^2 g^2 / \pi \rho v \alpha)] \quad (1)$$

(see, for example, Alexander, 2003). In this equation,  $\rho$  is the density of the air,  $v$  is the speed,  $C_0$  is the zero-lift drag coefficient,  $A$  is the wing area,  $k$  is the induced drag factor,  $M_b$  is body mass,  $g$  is the gravitational acceleration and  $\alpha$  is the aspect ratio (the ratio of wing span to the mean chord; the chord is the distance between the front and rear edges of the wing). As speed increases, the induced power falls and the profile power increases.

Two optimum speeds can be defined: the minimum power speed at which the total power  $P$  is least, and the maximum range speed at which the energy required to travel unit distance ( $P/v$ ) is least. These speeds can be obtained from Equation 1 by calculus (see, for example, Alexander, 1996). Textbooks of aerodynamics usually treat the zero-lift drag as constant, as it would be if the flight of different-sized animals were dynamically similar. Dynamic similarity would, however, require animals to fly at equal Reynolds numbers, that is at speeds inversely proportional to their linear dimensions; a moth with a 10 mm wing chord would have to fly ten times as fast as a bird with a 100 mm chord. That would generally not be the case, so we must take account of differences in  $C_0$ . All but the largest and fastest birds fly with Reynolds numbers  $Re$  below  $10^6$ , at which  $C_0$  is expected to be approximately

proportional to  $1/\sqrt{Re}$  and so to  $1/\sqrt{(\text{chord} \times \text{speed})}$ . For example, pigeon wings have a chord of about 12 cm. When the bird flies fast at  $15 \text{ m s}^{-1}$ , their Reynolds number is only 120 000.

A calculation of the maximum range speed, taking account of this dependence of  $C_0$  on  $Re$ , yields:

$$\text{Maximum range speed} \propto M_b^{4/7} / A^{1/2} \alpha^{5/14} \quad (2)$$

and

$$\text{Power at maximum range speed} \propto M_b^{10/7} / A^{1/2} \alpha^{9/14} \quad (3)$$

Rayner (1988) found that for birds, excluding hummingbirds, wing area is approximately proportional to  $M_b^{0.72}$  and wing span to  $M_b^{0.39}$ . Hence chord (=area/span) is proportional to  $M_b^{0.33}$  and aspect ratio to  $M_b^{0.07}$ . By substituting these proportionalities into Equations 2 and 3 we obtain:

$$\text{Maximum range speed} \propto M_b^{0.18} \quad (4)$$

and

$$\text{Power at maximum range speed} \propto M_b^{1.02} \quad (5)$$

Rayner's calculations (Rayner, 1995a), which took account of the vortex structure of the wake, gave maximum range speed proportional to  $M_b^{0.14}$  and power to  $M_b^{1.10}$ . Observed cruising speeds of birds increase with body mass (Pennycuick, 1997), but the correlation is too weak for a quantitative comparison with the calculated exponents for maximum range speed. These exponents for estimated mechanical power are very different from the exponent for measured metabolic power; Rayner (1995a) found that the metabolic power used in bird flight was proportional to  $M_b^{0.83}$ . As for running, the efficiency of flight increases with body mass (Fig. 2).

Until recently, calculations of the mechanical power required for animal flight depended on mathematical models (often more sophisticated than those presented here). There were no more direct estimates until Biewener et al. (1992) measured the forces exerted by the flight muscles of flying birds, using a strain gauge bonded to the humerus. Powers determined by this method (see especially Dial et al., 1997) agree reasonably well with the results of mathematical modelling (Alexander, 1997b).

Now we have to consider hovering. The rotating blades of a helicopter, and the beating wings of a hovering animal, drive air downwards. The power required for this can be estimated as:

$$\text{Induced power} = \sqrt{(M_b^3 g^3 / 2\pi\rho r^2)} \propto \sqrt{(M_b^3 / r^2)}, \quad (6)$$

where  $r$  is the radius of the rotor (equivalent to wing length in animals) and the other symbols have the same meanings as before (see Alexander, 2003). Wing length is proportional to  $M_b^{0.53}$  in hummingbirds (Rayner, 1988) and to  $M_b^{0.42}$  in euglossine bees (Casey et al., 1985). In both cases, larger animals are not geometrically similar to small ones, but have relatively longer wings. With these exponents we get:

$$\text{Induced power for hovering} \propto M_b^{0.97}$$

and

$$\text{Induced power for hovering} \propto M_b^{1.08} \quad (7)$$

for hummingbirds and bees, respectively. Rayner's vortex

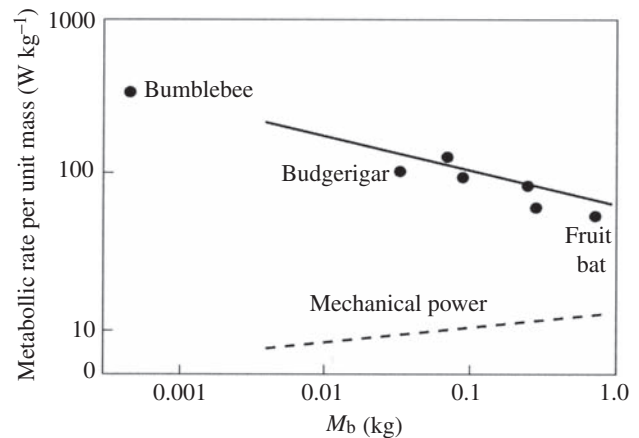


Fig. 2. Mass-specific metabolic rates in flight, plotted against body mass  $M_b$ . The unlabelled points refer to birds. The regression line has been calculated from data for 38 species, of which only a few are represented by points. The broken line shows estimates of mechanical power, based on data for 34 species. Both lines are based on equations in Rayner (1995a). From Alexander (1995), with permission.

theory of hovering (Rayner, 1979) treats the aerodynamics more realistically than the simple helicopter approximation, but gives similar predictions of induced power.

As for fixed wing aircraft, the power requirements of helicopters include profile power as well as induced power. For well-designed rotors, profile power is expected to be about proportional to induced power, so the exponents in Equation 7 should apply to total aerodynamic power as well as to induced power.

Hovering animals may incur yet another power requirement, which does not arise for helicopters. This is known as the inertial power, to distinguish it from the aerodynamic (induced plus profile) power. At the beginning of each stroke the wings and an 'added mass' of air that moves with them are given kinetic energy, which they lose at the end of the stroke. If this energy were small compared to the kinetic energy given to the air, it could be transferred to the air in the later part of the stroke, while the wings were decelerating. In fact, for hovering hummingbirds and insects, the inertial power is commonly as large or larger than the aerodynamic power (see Alexander, 2003). In many insects, some or all of the kinetic energy may be stored in elastic structures at the end of the stroke, and recovered in the next stroke. Elastic structures of optimal stiffness could in principle supply all the inertial power, leaving the muscles to supply only the induced and profile power.

The kinetic energy given to two wings at the start of a stroke is  $I\omega^2$ , where  $I$  is the moment of inertia of one wing. If the wing beat frequency is  $f$ , the mean power required to supply this energy (twice in each wing beat cycle) is  $2fI\omega^2$ . I will assume that each wing beats through an angle  $\pi$  during a half cycle of duration  $1/2f$ , making the mean angular velocity  $2\pi f$ . For simplicity, I assume that the stroke is made with constant angular velocity. Thus the inertial power is given by:



$$\text{Inertial power} = 2fI(2\pi f)^2 = 8\pi^2 f^3 I. \quad (8)$$

Each wing beat of a hovering animal adds a vortex ring to the wake of moving air below it. For dynamic similarity between animals of different sizes, the spacing of the rings should be proportional to wing length. Alexander (2000) pointed out that this implies equal Strouhal numbers, which in turn implies that the wing beat frequency should be proportional to  $\sqrt{M_b}/r^2$ . I showed that it is indeed approximately proportional to  $\sqrt{M_b}/r^2$ , both for hummingbirds and for euglossine bees. Thus:

$$\text{Inertial power} \propto M_b^{3/2} I / r^6. \quad (9)$$

Weis-Fogh's data for Lepidoptera, Hymenoptera and Diptera (Weis-Fogh, 1973) show that wing moment of inertia is approximately proportional to  $M_b^2$ , and wing length to  $M_b^{0.4}$ . With these proportionalities, Equation 9 gives inertial power proportional to  $M_b^{1.1}$ . The exponent is approximately the same as the one estimated above for aerodynamic power for bees. Weis-Fogh's moments of inertia refer only to the wing itself, ignoring the added mass of air, but this has probably had little effect on our calculated exponent. Ellington (1984) found that the added mass was about the same proportion of wing mass (0.4) for a bee, a wasp and a moth.

Casey (1981) compared metabolic rates of hovering sphinx moths with model-based estimates of mechanical power. The models gave induced power proportional to  $M_b^{1.07}$  and profile power proportional to  $M_b^{1.08}$ . Measured metabolic powers were proportional to  $M_b^{0.77}$ . If inertial power requirements were taken care of by elastic storage, muscle efficiency was approximately proportional to  $M_b^{0.3}$ . Casey and Ellington (1989) made similar comparisons for hovering euglossine bees. They found that metabolic power was proportional to  $M_b^{0.58}$ , and efficiency to  $M_b^{0.51}$  or  $M_b^{0.47}$ , for no elastic storage and perfect elastic storage, respectively. These data for moths and bees refer to fairly narrow ranges of body mass (about one order of magnitude in each case), so the exponents could not be determined very precisely, but it seems clear that for hovering insects, as for running animals and flying birds, efficiency increases with body mass.

### Swimming

In this simple analysis, I will estimate the power required for swimming by fish as if they were rigid submarines. This approach underestimates the power by a factor of about 3, for reasons discussed by Webb (1992). This factor changes only a little with Reynolds number, in experiments with the same fish swimming over a wide range of speeds. As the Strouhal numbers of swimming fish vary little with size and speed (see Alexander, 2003), the factor can be expected to be the about same for different-sized fish swimming at the same Reynolds number. The same conclusion seems to follow from the computational fluid dynamics model of Schultz and Webb (2002). The following discussion is concerned with the scaling of power rather than with absolute values, so would not be affected by a size-independent factor.

Animals develop the thrust required to propel them through water by driving some of the water backwards. The power required for swimming is the sum of parasite power, required to overcome the drag on the body; induced power, required to give kinetic energy to the water driven backwards; and inertial power, required to give kinetic energy to body parts that are accelerated at the beginning of each stroke. For an animal or other body travelling at speed  $v$  through water of density  $\rho$ :

$$\text{Parasite power} = 0.5\rho A v^3 C_D, \quad (10)$$

where  $A$  is the total surface area of the body and  $C_D$  is the drag coefficient based on total area. For well-streamlined bodies such as most fish, whales and squid, the drag coefficient is proportional to  $Re^{-0.5}$  at Reynolds numbers ( $Re$ ) up to about  $10^6$ , and to  $Re^{-0.2}$  at higher Reynolds numbers. The change in exponent is due to flow in the boundary layer changing from laminar to turbulent as the Reynolds number passes  $10^6$ . Small fish swim in the laminar range, and whales generally in the turbulent range. Medium-sized fish span the transition; for example, a 0.5 m fish swimming at  $2 \text{ m s}^{-1}$  would have a Reynolds number of  $10^6$ . Reynolds number is proportional to  $v l$ , where  $l$  is the length of the body. Thus for laminar flow:

$$\text{Parasite power} \propto A v^{2.5} / l^{0.5}$$

and for turbulent flow:

$$\text{Parasite power} \propto A v^{2.8} / l^{0.2}. \quad (11)$$

Cetaceans ranging from small dolphins to blue whales have lengths proportional to  $M_b^{0.34}$ , very close to geometric similarity (Economos, 1983). Fish of different sizes also tend to be close to geometric similarity (Peters, 1983). For geometrically similar animals,  $A$  is proportional to  $M_b^{0.67}$  and  $l$  to 0.33, so that for laminar flow:

$$\text{Parasite power} \propto M_b^{0.5} v^{2.5}$$

and for turbulent flow:

$$\text{Parasite power} \propto M_b^{0.6} v^{2.8}. \quad (12)$$

Swimmers can develop the thrust they need by driving small volumes of water backward at high speed, or large volumes at low speed. The latter requires less induced power. The ratio [parasite power/(parasite power + induced power)] is known as the Froude efficiency. It is close to 1.0 for two of the species studied by Wardle et al. (1995), and 0.75 for the third (see Alexander, 2003, for the method of calculation). For these fish, and presumably also for other fish and for whales, induced power is much smaller than parasite power and can be ignored in this simple analysis. Squids swimming by jet propulsion operate at lower Froude efficiencies, so induced power could not be ignored in discussions of them. Inertial power may be substantial in swimming dolphins and tunas, mainly due to the mass of water that oscillates with the tail rather than to the mass of the tail itself, but may be supplied in part by tendon elasticity rather than muscle action (Blickhan and Cheng, 1994; Alexander, 1997a).

Yates (1983) defined a coefficient of thrust:

$$\text{Coefficient of thrust} = \frac{(\text{metabolic rate} - \text{resting rate})}{(0.5\rho Av^3)}. \quad (13)$$

If Equation 10 held and muscle efficiency were constant, the coefficient of thrust would be a constant multiple of the coefficient of drag which, as we have seen, is a function of Reynolds number. Yates analysed Brett's data for salmon (Brett, 1965), plotting thrust coefficient against Reynolds number for fish of different sizes. Large salmon swim at higher ranges of Reynolds number than small ones but, if efficiency had been constant, the data for all sizes of salmon should have lain on the same line on this graph. They did not lie on the same line; larger fish had higher thrust coefficients at the same Reynolds number, seeming to show that larger fish were less efficient. This contrasts with the finding that larger running and flying animals are *more* efficient. Yates (1983) recognised, however, that the data probably suffered from two sources of error. At low speeds the fish may have behaved erratically, using more energy than would have been needed for steady swimming. At high speeds, some of their metabolism was probably anaerobic, and would have been missed by the measurements of oxygen consumption. Thus the thrust coefficients for slow swimming were probably misleadingly high, and those for fast swimming too low, for each fish. Correction for this would make the thrust coefficients lie more nearly along a single line. We cannot exclude the possibility that the swimming muscles of different-sized fish work with different efficiencies, but there is no evidence of larger fish being more efficient.

### Efficiency

Previous sections have shown that, at least for running and flight, muscles do the work of locomotion more efficiently in larger animals. Kram and Taylor (1990) tried to explain this observation for running. They ignored the metabolic cost of doing work, and considered only the cost of exerting the force required to counteract gravity. They assumed that muscles work over the same ranges of the force–velocity relationship, irrespective of speed and body size; faster muscle fibres would be recruited at higher running speeds, and smaller animals (whose feet remain on the ground for shorter times) would need faster muscles than large ones. These assumptions led them to the hypothesis:

$$\text{Metabolic power} \propto (\text{body weight}) / (\text{foot contact time}). \quad (14)$$

They measured foot contact time and oxygen consumption for mammals of a wide range of sizes, running at a wide range of speeds, and found excellent agreement with the hypothesis. Roberts et al., (1998) found similar agreement for running birds. Herr et al. (2002) modelled a selection of mammals, ranging from a chipmunk to a large horse. For each model they simulated running at a range of speeds, and showed that Kram and Taylor's hypothesis (Kram and Taylor, 1990) successfully predicted the metabolic cost of transport of the real animal.

Because models of particular species were used, rather than a general model of variable size, this study threw only limited light on scaling principles.

Kram and Taylor did not discuss the physiological basis for their hypothesis in detail. The metabolic rate of an active muscle is not a function solely of the force it is currently exerting, but depends also on the rate at which its length is changing; for any given force, the metabolic rate is greater when the muscle is shortening and less when it is being stretched (fig. 1b in Alexander, 2002). In every step, leg muscles are first stretched (doing negative work) and then shorten (doing positive work). Suppose that an active leg muscle has a metabolic rate  $x$  times the isometric rate. Then if the corresponding muscle in a different-sized animal is working at the same point in its force–velocity curve, it also is expected to have a metabolic rate  $x$  times its isometric rate. If the leg muscles of different-sized animals work over the same range of their force–velocity curves, as Kram and Taylor assumed, their metabolic rates (averaged over a stride) may be equal multiples of the rate in isometric contraction. It would be interesting to have experimental confirmation of the assumption. Kram and Taylor (1990) also assumed that strain rates of muscles should be inversely proportional to ground contact time. This implies that equal strains should occur, in the leg muscles of different-sized animals. Again, experimental confirmation would be welcome.

The following calculation highlights a possible problem with the assumption of equal strains. The mechanical cost of transport [ $\text{work}/(M_b \times \text{distance})$ ] is about the same for runners of all sizes (Heglund et al., 1982), and stride lengths in similar gaits are proportional to  $M_b^{0.38}$  (Heglund et al., 1974). Hence the work required for a stride is proportional to  $M_b^{1.38}$ . The work performed in a stride is (muscle stress  $\times$  muscle strain  $\times$  muscle volume). Muscle stress in similar gaits is proportional to  $M_b^{-0.06}$ , and muscle mass and volume are proportional to  $M_b^{1.03}$  (Biewener, 1989, 1990). If strains are independent of body mass, the (positive and negative) work performed by the muscles should be approximately proportional to  $M_b^{0.97}$ , which does not match the observed proportionality of work to  $M_b^{1.38}$ .

In flight, as in running, muscles have to exert forces to counteract gravity. It is therefore reasonable to ask whether Kram and Taylor's hypothesis successfully predicts metabolic power for flight. For foot contact time we can substitute the duration of a wing beat, which is inversely proportional to frequency:

$$\text{Metabolic power} \propto M_b \times \text{wing beat frequency}. \quad (15)$$

For forward flight, frequency is proportional to  $M_b^{-0.26}$  (Rayner, 1995a), giving predicted metabolic power proportional to  $M_b^{0.74}$ , not too far from the observed proportionality of  $M_b^{0.83}$ . For hovering euglossine bees, wing beat frequency is proportional to  $M_b^{-0.27}$ , giving predicted metabolic rate proportional to  $M_b^{0.73}$ , which is higher than the observed proportionality of (in this case)  $M_b^{0.58}$  (Casey and Ellington, 1989). Kram and Taylor's hypothesis (Kram and

Taylor, 1990) works reasonably well for bird flight, but less well for bees.

### Conclusions

I have based this paper on very simple, long-established models. There is scope for using more modern modelling approaches; for example, because fish of different sizes are often close to geometric similarity, it would not be too difficult to use computational fluid dynamics to investigate the scaling of swimming energetics. However sophisticated the methods, the models must be kept conceptually simple, and the need for anatomical and kinematic data must be kept to a minimum, if the generality required for broad scaling studies is to be preserved.

The most urgent need, however, in studies of the scaling of energy costs in locomotion, is for better understanding of the relationship between mechanical work and metabolism. Some studies of locomotion have attempted to model this relationship (Minetti and Alexander, 1997; Anderson and Pandey, 2001; Sellers et al., 2003), but this approach has not been used in scaling studies. It might, indeed, be premature to apply this approach to the scaling of energy costs, until it has a sounder foundation in muscle physiology. The problem is that, as used in the cited papers, it uses data from isotonic contractions to estimate energy costs in work loops. Hill's Equation, derived from isotonic experiments, does not predict forces in work loops well (Askew and Marsh, 1998), and we do not know whether the equations for metabolic rate work well for work loops.

### List of symbols

$A$	wing area (flight) or total surface area (swimming).
$C_0$	zero-lift drag coefficient
$C_D$	drag coefficient
$f$	frequency
$g$	gravitational acceleration
$I$	moment of inertia
$k$	induced drag factor
$l$	length
$M_b$	body mass
$Re$	Reynolds number
$r$	radius of a helicopter rotor
$v$	speed
$\alpha$	aspect ratio
$\lambda, \tau, \phi$	factors for length, time and force, in dynamically similar motions
$\rho$	density of air (flight) or water (swimming)
$\omega$	angular velocity

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