

a fluid layer, and against drag when it moves through air or water. Finally, we have seen how muscle and tendon properties can be adjusted to minimize the metabolic costs of oscillatory movements. I had to add a note of warning at the end of the discussion of oscillatory movements, because advances in muscle physiology are needed to enable us to do the calculations properly, as I explained at the end of Chapter 2.

Chapter Four

Consequences of Size Differences

DOMESTIC CATS and lions are very different in size, but they are similar in shape and move in similar ways. Both walk to go slowly, trot at intermediate speeds, and gallop to go fast. Small minnows and large salmon are similar in shape and make similar movements when they swim. Both hummingbirds and vultures fly by beating their wings.

There are important differences as well as similarities between the movements of animals of different sizes. In each of their gaits, lions run faster than cats and take longer strides, at a lower stride frequency. Minnows make more tail beats per second than salmon, and hummingbirds beat their wings at higher frequency than vultures. Hummingbirds hover but vultures cannot. Vultures soar and hummingbirds do not.

These examples suggest that we should want to understand how the structure of animals and their patterns of movement depend on body size. In this chapter I try to establish some of the basic principles that will be useful in the later chapters in which I discuss particular modes of locomotion. You will find further discussion of the consequences of size differences in McMahon and Bonner (1983), Schmidt-Nielsen (1984), and Brown and West (2000).

4.1. GEOMETRIC SIMILARITY, ALLOMETRY, AND THE PACE OF LIFE

Two shapes are geometrically similar if one could be made identical to the other by multiplying all length dimensions by the same factor. For example, a triangle with sides 3, 4, and 5 cm long is geometrically similar to one with sides of 6, 8, and 10 cm.

Imagine two animals that are geometrically similar to each other, one a precise half-scale model of the other. The larger one is twice as long as the smaller and has twice the circumference, so has $2 \times 2 = 4$ times the surface area. It is twice as long, twice as wide, and twice as high as the smaller one, so has $2 \times 2 \times 2 = 8$ times the volume and (if the animals are made of the same materials) eight times its mass. More generally, geometrically similar animals (or other objects) have areas proportional to

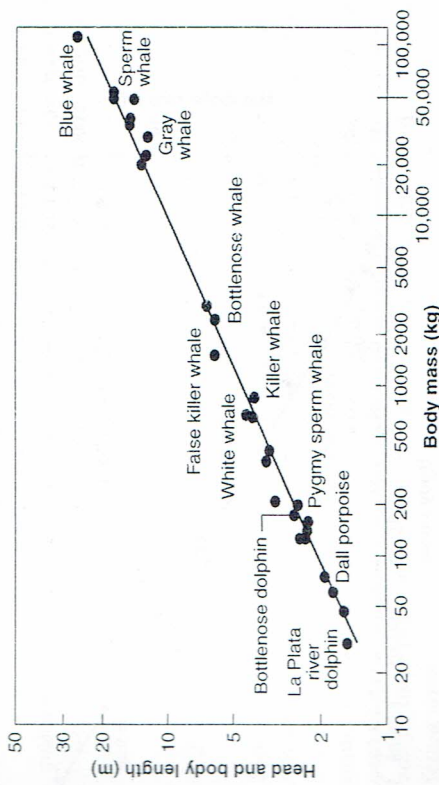


Fig. 4.1. A graph on logarithmic coordinates of length against body mass for whales. The slope of the regression line is 0.34. From Economos (1983).

(length)² and volumes proportional to (length)³; and if they are made of the same materials they have masses also proportional to (length)³. This implies that lengths are proportional to (mass)^{1/3} and areas to (mass)^{2/3}.

This suggests that when we analyze relationships between body dimensions in animals of different sizes we may expect to find that our data can be approximated by equations of the form

$$y = ax^b \quad (4.1)$$

where y is a body dimension (perhaps length or area), x is another (perhaps volume or mass), and a and b are constants. Equations like this are called allometric equations. By taking logarithms of both sides of Equation 4.1, we get

$$\log y = \log a + b \log x \quad (4.2)$$

implying that a graph of $\log y$ against $\log x$ should be a straight line of gradient b . The allometric equation that best fits a set of data can be found by regression of the logarithms of the data. Least-squares (model 1) regression, or reduced major axis (model 2) regression may be the more appropriate, depending on the nature of the data and the purpose for which the equation is required (Rayner 1985a).

Figure 4.1 is a graph of length against body mass for whales. Distances along the axes are proportional to the logarithms of length and mass, not to length and mass themselves. Thus, the distance along the horizontal

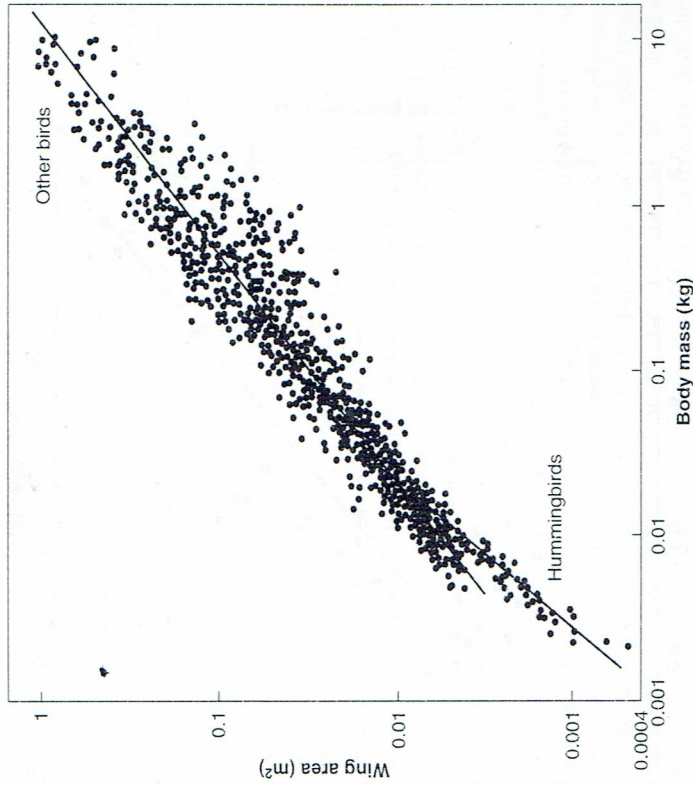


Fig. 4.2. A graph on logarithmic coordinates of wing area against body mass for birds. The slopes of the lines, fitted by reduced major axis regression, are 1.09 for hummingbirds and 0.72 for other birds. From Rayner (1987).

axis from 10 to 100 kg is the same as the distances from 100 to 1000 kg, and from 1000 to 10,000 kg. Drawn like this, the graph is equivalent to a graph of $\log(\text{length})$ against $\log(\text{mass})$. The equivalence of a graph on logarithmic coordinates, like this, and a graph of logarithms is made explicit in Fig. 4.3, which has a scale of logarithms at the bottom and a logarithmic scale at the top. If whales of different sizes were geometrically similar to one another, their lengths would be proportional to (body mass)^{1/3}, and all the points in Fig. 4.1 would lie on a line of slope 1/3. The slope of the line is actually 0.34, almost exactly as predicted.

In contrast, in Fig. 4.2 wing area is plotted against body mass for birds, again on logarithmic coordinates. If birds of different sizes were geometrically similar to each other, all the points would lie on a line of slope 2/3. In fact, the points form two lines of different slopes. The smallest birds are hummingbirds. The points for them (filled circles) are scattered around a

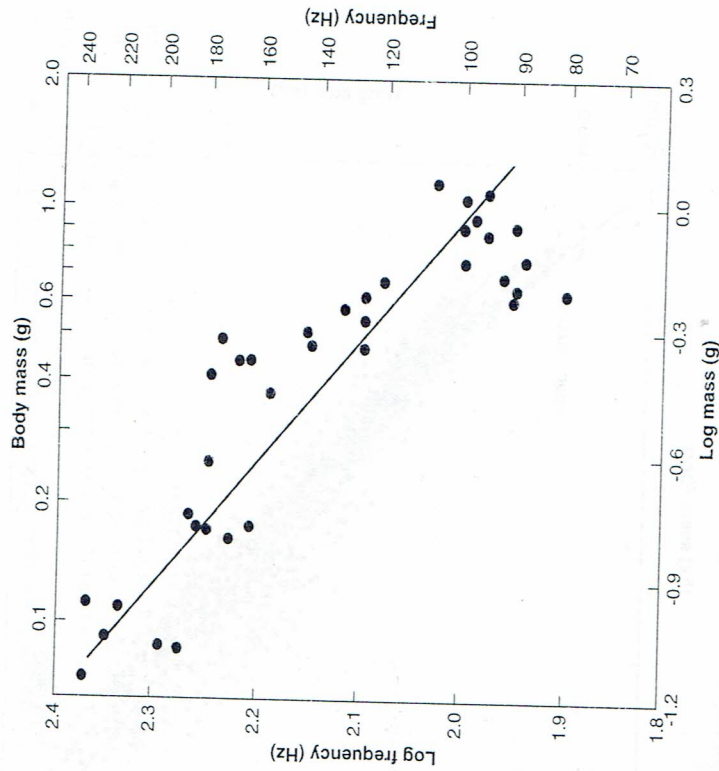


Fig. 4.3. A graph of the logarithm of wing beat frequency against the logarithm of body mass for engulssine bees. Scales of frequency and mass are also shown. From Casey et al. (1985).

line of slope 1.09, and the points for other birds around a line of slope 0.72. Both these slopes are significantly greater than the predicted slope of $2/3$, showing that the wing areas of large birds are generally larger than they would be, if large birds were geometrically similar to small ones. Notice, however, that the points in Fig. 4.2 are quite widely scattered above and below the lines. This reflects differences between the birds' area of life. For example, 10-kg vultures have wings of about twice the area of those of 10-kg albatrosses.

As well as being useful for describing how the dimensions of animals' bodies are related to body mass, Equation 4.1 is also often useful for describing how the rates of animal movements and of physiological processes are related to body size. Figure 4.3 shows that wing beat frequencies of a group of species of bees tend to be proportional to $(\text{body mass})^{-0.35}$. Again there is a good deal of scatter about the line.

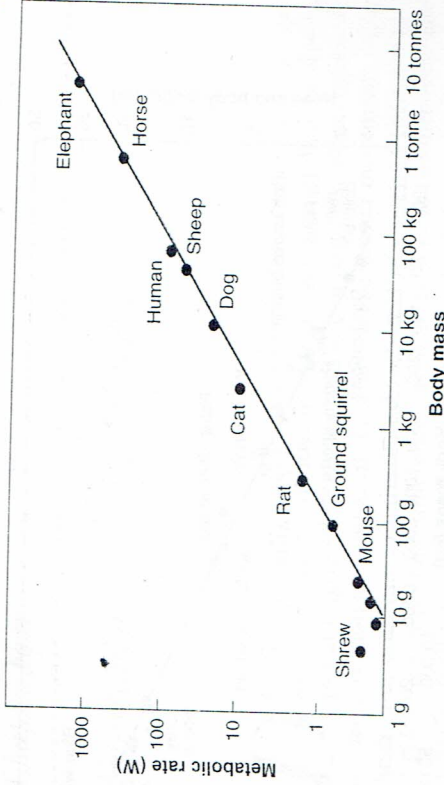


Fig. 4.4. A graph of logarithmic coordinates of resting metabolic rate against body mass for mammals. From Alexander (1999).

Figure 4.4 shows that the resting metabolic rates of mammals tend to be proportional to $(\text{body mass})^{0.76}$. This is just one example of a general tendency: the resting metabolic rates of similar animals of different sizes tend to be about proportional to $(\text{body mass})^{3/4}$ (Peters 1983). Maximum active metabolic rates of similar animals also tend to be roughly proportional to $(\text{body mass})^{3/4}$. For example, Taylor et al. (1981) found that the maximum rates of oxygen consumption while running, of mammals ranging from mice to cattle and elands, were proportional to $(\text{body mass})^{0.81}$.

If the metabolic rates of animals are proportional to $(\text{body mass})^{3/4}$, metabolic rates per unit mass are proportional to $(\text{body mass})^{-1/4}$. This fits in with a general tendency for the frequencies of animal movements to be about proportional to $(\text{body mass})^{-1/4}$ and for the times required for biological processes to be about proportional to $(\text{body mass})^{1/4}$. For example, the gestation periods of mammals are about proportional to $(\text{body mass})^{0.24}$ and their heart beat frequencies to $(\text{body mass})^{-0.25}$ (Peters 1983). If the energy used in each repetition of a movement (for example, a stride or a heart beat) is proportional to body mass, and the frequency of repetition is proportional to $(\text{body mass})^{-1/4}$, the rate at which energy is used will be proportional to $(\text{body mass})^{3/4}$.

However, there are some marked deviations from the general rule. Figure 4.3 has shown us that the wing beat frequencies of bees tend to be proportional to $(\text{body mass})^{-0.35 \pm 0.06}$ (95% confidence limits), and Heglund et al. (1974) found that the galloping stride frequencies of mammals are proportional to $(\text{body mass})^{-0.14}$ (confidence limits not calculated).

West et al. (1997) have tried to explain why metabolism and other biological processes tend to proceed at rates proportional to (body mass)^{-1/4}. Their theory seems to have great explanatory power, but does not fully satisfy me, as I have explained elsewhere (Alexander 1999).

4.2. DYNAMIC SIMILARITY

Lions are much larger than domestic cats and take fewer strides per second, but apart from that the movements of a galloping lion are very like those of a galloping cat. Large salmon beat their tails at lower frequencies than minnows, but may leave similar patterns of eddies in their wake. The concept of dynamic similarity will help us in comparisons like these and will enable us to make generalizations about the movements of animals of different sizes.

Two shapes are geometrically similar if one could be made identical to the other by multiplying all lengths by some factor λ . By an extension of the same kind of thinking, two motions are dynamically similar if one could be made identical to the other by multiplying all lengths by a factor λ , all times by a factor τ and all forces by a factor ϕ . As an example of dynamically similar motion, think of two pendulums of different lengths swinging through the same angle.

What does dynamic similarity imply? If all lengths are multiplied by λ and all times by τ , all velocities must be multiplied by λ/τ and all accelerations by λ/τ^2 . Newton's second law of motion tells us that force equals mass multiplied by acceleration, so if all forces are multiplied by ϕ , all masses must be multiplied by $\phi/(\lambda/\tau^2) = \phi\lambda/(\lambda/\tau)^2$. In other words,

$$\begin{aligned} \text{Ratio of masses} &= \frac{\text{Ratio of forces} \times \text{Ratio of lengths}}{\text{Ratio of velocities}^2} \\ \frac{\text{Ratio of masses} \times (\text{Ratio of velocities})^2}{\text{Ratio of forces} \times \text{Ratio of lengths}} &= 1 \end{aligned} \quad (4.3)$$

This tells us that for two motions to be dynamically similar, the following condition must be satisfied. Let m_1 , m_2 be corresponding masses in the two motions (for example, the masses of corresponding parts of two animals' bodies); let v_1 , v_2 be corresponding velocities (for example, the velocities of corresponding body parts at corresponding stages of the motion); let F_1 , F_2 be corresponding forces (for example, peak forces on the feet) and let l_1 , l_2 be corresponding lengths (for example, stride lengths). If the motions are dynamically similar,

$$\frac{m_1 v_1^2}{F_1 l_1} = \frac{m_2 v_2^2}{F_2 l_2} \quad (4.4)$$

Both motions must have the same value of $m v^2 / F l$.

This must be true for all the kinds of forces that are important for the motion. Suppose, for example, that gravitational forces are important, as they are for running mammals. The force F exerted by gravity on a mass m is $m g$, where g is the gravitational acceleration. Thus, $m v^2 / F l = v^2 / g l$. When gravity is important, motions can be dynamically similar only if they have equal values of $v^2 / g l$, a quantity that is called a Froude number.

This rule helps us to predict the speeds at which terrestrial animals change gaits. Quadrupeds walk at low speeds, trot at intermediate speeds, and gallop at high speeds. Walking, trotting, and galloping are markedly different patterns of movement, as every horse rider knows, and as the descriptions in Section 7.2 will show. Alexander and Jayes (1983) formulated the hypothesis that quadrupeds tend where possible to move in dynamically similar ways, which implies, among other things, that they will change gaits at equal Froude numbers. We took v to be running speed and l to be leg length (or, more precisely, the height of the hip joint from the ground in normal standing). We analyzed film of a wide variety of mammals ranging in size from small rodents to rhinoceros and concluded that in almost every case the change from trotting to galloping was made at a Froude number between 2 and 3. Our data seem also to show that the changes from walking to trotting in quadrupeds, from walking to running in humans, and from shuffling to hopping in kangaroos are all generally made at Froude numbers between about 0.3 and 0.8.

So far, we have assumed that gravitational forces are important. Now we will consider instead motions, such as swimming, in which viscous forces are important. Figure 3.2B showed a plate of area A moving with velocity v over a layer of thickness d of a fluid of viscosity η . Equation 3.7 told us that the force required to drive this motion is $\eta A v / d$. In dynamically similar motions, corresponding areas are proportional to the squares of corresponding lengths l^2 , and corresponding thicknesses must be proportional to l . Thus, forces are proportional to $\eta l v$. Also, the masses of corresponding regions of fluid are proportional to ρl^3 , where ρ is the density of the fluid. Thus, $m v^2 / F l$ (Equation 4.4) is proportional to $(\rho l^3 v^2) / (\eta l v)$. The quantity $\rho l v / \eta$ is called a Reynolds number. Motions in which viscosity is important can be dynamically similar only if their Reynolds numbers are equal.

The fluids that will concern us most in our discussions of locomotion are air and water. To calculate Reynolds numbers in them we need to know values of η / ρ , the quantity that is known as kinematic viscosity. For air at

20°C at a pressure of one atmosphere, it is $1.5 \times 10^{-5} \text{ m}^2/\text{s}$; and for freshwater or seawater at 20°C it is $1.0 \times 10^{-6} \text{ m}^2/\text{s}$ (Denny 1993).

Reynolds numbers will appear in our discussions both of swimming and of flight. For example, fluid flow in the boundary layer around a streamlined body of length l traveling at velocity v becomes turbulent if the Reynolds number $\rho v l / \eta$ rises above about 2×10^6 , causing an abrupt increase of drag. We will need to know the range of Reynolds numbers involved when we discuss the drag that acts on swimming dolphins (Section 14.4).

We have considered motions in which gravitational forces are important and ones in which viscous forces are important, and turn now to elastic forces. A force $S \Delta l$ is needed to stretch a spring of stiffness S by an amount Δl (Equation 3.4). In dynamically similar motions, extensions Δl will be proportional to lengths l , so forces will be proportional to $S l$. Thus, $m v^2 / Fl = m v^2 / S l^2$, and the condition for dynamic similarity (Equation 4.4) is that the motions being compared must have equal values of $m v^2 / S l^2$. The natural frequencies of vibration of spring-mass systems are proportional to $(S/m)^{0.5}$, so this implies that the motions must have equal values of $v^2 / f^2 l^2$, where f is the natural frequency of the system; hence, they must have equal values of $f l / v$, which is called the Strouhal number. The reduced frequency referred to in many discussions of animal swimming and flight is simply 2π times the corresponding Strouhal number.

Strouhal numbers are applicable to cyclic motions in general, whether or not elastic forces are important. Consider two dynamically similar motions that repeat in regular cycles. All times in one of them are τ times corresponding times in the other, and all lengths are λ times corresponding lengths. Thus, frequencies are proportional to $1/\tau$ and velocities to λ/τ . It follows that $f l / v$ is proportional to $(1/\tau)\lambda/(\lambda/\tau)$; in other words, it is constant. Any two dynamically similar cyclic motions must have equal Strouhal numbers. I will show in Section 11.1 that hovering hummingbirds of different sizes beat their wings at frequencies that make their Strouhal numbers about equal.

Froude numbers, Reynolds numbers, and Strouhal numbers are all dimensionless; they have no units. However, it is essential when calculating them to use a consistent system of units. The easiest way to do this is to express everything in SI units: lengths in meters (not millimeters or kilometers), times in seconds, masses in kilograms, forces in newtons, etc.

4.3. ELASTIC SIMILARITY AND STRESS SIMILARITY

McMahon (1973) suggested that animals and plants of different sizes should be built in such a way as to deform under gravity in geometrically similar ways; gravity should cause equal strains in corresponding parts of

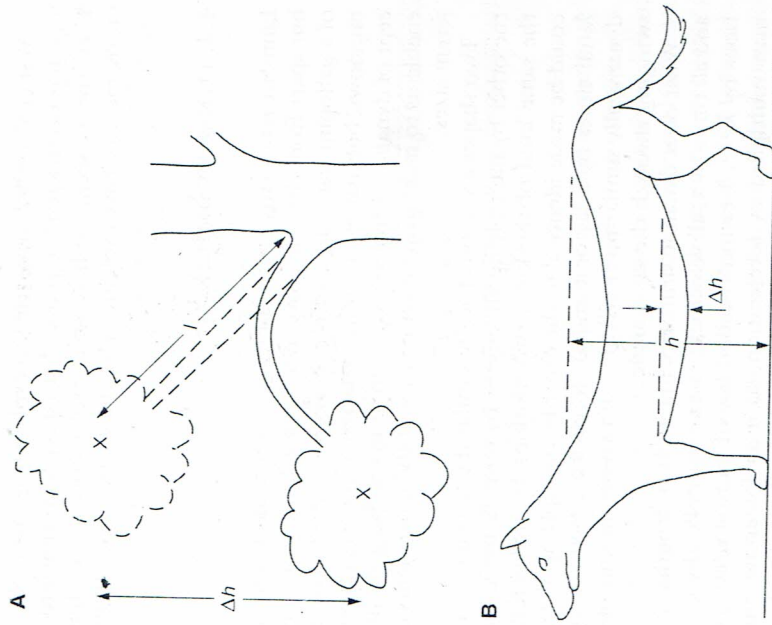


Fig. 4.5. Diagrams of (A) a branch and (B) a mammal, showing elastic deformations due to gravity. Broken outlines show their shapes as they would be in the absence of gravity.

their bodies. For example, Fig. 4.5A shows a branch of length l that bends elastically under its own weight, depressing its end by Δh . The theory of elastic similarity predicts that branches of different sizes will have equal values of $\Delta h/l$.

The theory is an attractive one for trees. Gravity is one of the principal forces they have to withstand (the other is drag exerted on them by wind). Less energy is needed to grow a thin branch than to grow a thick one of equal length, but too thin a branch will bend so much that its leaves are not well positioned to receive sunlight. It seems likely that the optimum compromise would result in branches of different sizes being elastically similar. McMahon and Kronauer (1976) published evidence that branches of different sizes are indeed proportioned so as to be, more or less, elastically similar.

The theory is less attractive for animals. McMahon (1975) applied it to the leg bones of mammals, but elastic deformation of leg bones is not a problem in any mammal known to me. McMahon (1973) also applied it to the trunks of mammals, arguing that these should be proportioned so as to sag under gravity in geometrically similar ways, with equal values of $\Delta h/h$ (Fig. 4.5B).

Geometrically similar structures have lengths and diameters proportional to (body mass)^{1/3}, but McMahon showed that his theory predicted that leg bones and trunks should have lengths proportional to (mass)^{1/4} and diameters proportional to (mass)^{3/8}. This would make them relatively shorter and stouter in larger animals. He found good agreement with these predictions, both for the leg bones of Bovidae (cattle and antelopes [McMahon 1975]) and for the chests of Primates (McMahon 1973). However, in other groups of mammals (Alexander 1979a), and especially in smaller mammals (Economos 1983), leg bones scale more nearly as predicted for geometric similarity.

Because leg bones bend only by amounts that seem trivial, I am inclined to think their proportions more likely to depend on the need to be strong enough, than on the need to be stiff enough. We will examine a theory along these lines shortly.

The theory of elastic similarity seems more promising for structures that undergo substantial elastic deformations in life, for example, the leg tendons of mammals. Consider two mammals of different sizes that run in dynamically similar ways, and suppose that their leg tendons stretch to equal strains. Dynamic similarity implies forces proportional to body weight, so forces proportional to body weight would be causing similar elastic deformations; the animals would have to be elastically similar. However, we will see in Section 7.4 that the leg tendons of kangaroo rats do not stretch to the same strains as those of kangaroos, when they hop like kangaroos.

Biewener (1989, 1990) shifted the emphasis, in discussions of mammal leg design, from elastic strain to stress. He suggested that forces proportional to body weight should set up equal stresses in the skeletons and muscles of mammals of different sizes; mammals of different sizes should show stress similarity. In animals built of the same materials, equal stresses imply equal elastic strains, so stress similarity and elastic similarity are two aspects of the same design principle. The difference of viewpoint is nevertheless important. There was no obvious reason why the tiny elastic strains that occur in leg bones should be expected to be the same in animals of different sizes, but there is a clear reason why we might expect to find equal stresses. Bones must be strong enough to withstand the forces that act on them. Leg bones of different sized mammals are built of essentially the same material, capable of withstanding the same stress.

Figure 4.6A represents an imaginary one-legged terrestrial animal that will help us to work out how stress similarity might be possible. A vertical force equal to the animal's weight mg acts on the foot, exerting a moment $mg l \sin \theta$ about the joint halfway up the leg. The muscle has cross-sectional area A and has a moment arm r about the joint, so when it exerts a stress σ the force is $A\sigma$ and the moment about the joint is $A\sigma r$. Balancing the moments about the joint gives

$$\begin{aligned} A\sigma r &= mg l \sin \theta \\ \sigma &= \frac{mg l}{Ar} \sin \theta \end{aligned} \quad (4.5)$$

If animals of different sizes were geometrically similar, A would be proportional to (body mass)^{2/3}, l and r would be proportional to (body mass)^{1/3}, and θ would be constant; stresses in a 3000-kg elephant would be ten times as high as in a 3-kg rabbit.

How could animals be built to avoid this unacceptable result? I will make two assumptions. The first of these is that muscle mass is the same proportion of body mass in animals of all sizes. I assume this because muscles make up so large a proportion of body mass in mammals of all sizes that there can be little scope for increase. For example, a blacktail jackrabbit (*Lepus californicus*) was found to have 46% muscle in its body (Grand 1977). Secondly, I assume that the fascicles of the muscles have lengths proportional to the moment arm r . This implies that if the fascicles of different-sized animals shorten by the same fraction of their length, they will move the joint through the same angle. Together, these two assumptions imply that Ar is proportional to the volume, and hence the mass, of the body. Hence, from Equation 4.5, the stress in the muscle is proportional to $l/\sin \theta$.

This tells us that one way of making muscle stress the same in animals of different sizes would be to keep l constant, but that would not be feasible; the legs of an elephant could not be made as short as those of a rabbit. Alternatively, θ could be made smaller in larger animals. This seems to be the case. Larger mammals generally do stand and run on straighter legs than small ones. Elephants hold their legs straighter than rabbits.

Let us look at the terms in Equation 4.5 and see how they actually scale. Biewener (1989) made measurements of the extensor muscles of the principal limb joints of mammals ranging in size from mice to horses. He described $r/(l \sin \theta)$ as the effective mechanical advantage of a muscle and found that it was about proportional to $m^{0.26}$, where m is body mass. Alexander et al. (1981) dissected mammals ranging from shrews to an elephant and found that limb muscles generally had cross-sectional areas about proportional to $m^{0.8}$. Hence, by Equation 4.5, muscle stresses should

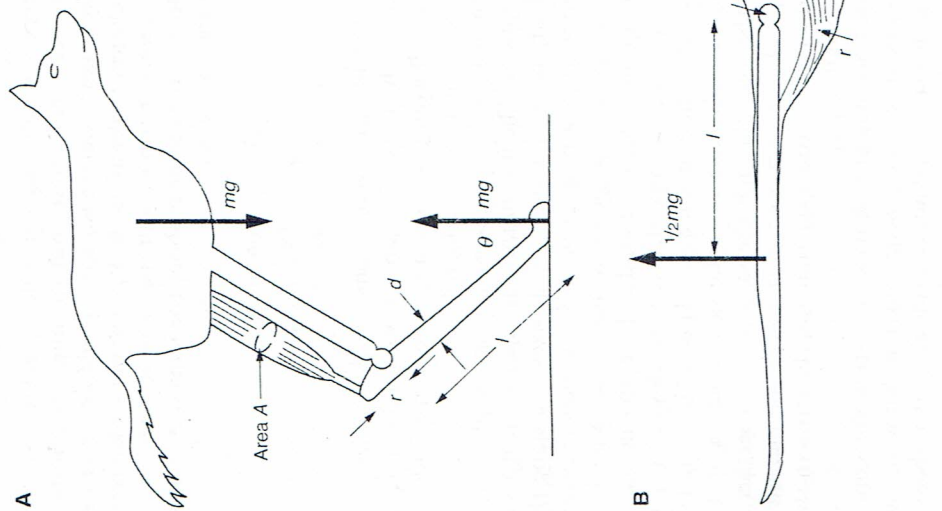


Fig. 4.6. Diagrams of (A) a terrestrial animal, represented as having only one leg, and (B) a flying animal seen in front view. These diagrams are used in a discussion of the stresses in bones and muscles of animals of different sizes.

be about proportional to $m/(m^{0.8}m^{0.26}) = m^{-0.06}$, they should be somewhat smaller in larger animals. The straightness of their legs is more than adequate to explain how large mammals can be supported by their leg muscles.

Now consider how bones should be built to ensure that they are strong enough to support animals of all sizes. The force mg on the foot (Fig. 4.6A) has an axial component $mg \cos \theta$ along the length of the lower leg

bone and a transverse component $mg \sin \theta$ at right angles to it. The axial component compresses the bone along its length and the transverse component bends it. Calculations of the stresses in limb bones in locomotion tell us that the transverse components of force generally give rise to much larger stresses than the axial components (Rubin and Lanyon 1982). This should not surprise us; long, slender structures such as bones or sticks are more easily broken by bending than by axial compression. For this reason, we will consider only stresses due to transverse forces.

The transverse component of force in Fig. 4.6A exerts bending moments on the lower leg bone, which increase from zero at the distal end of the bone to a maximum value of $mg l \sin \theta$ close to the joint. The peak stress in a cross section of a bent beam (or a bent bone) is Bending moment/Section modulus. Section modulus is a quantity that depends on the diameter and shape of the cross section; for cross sections of the same shape, it is proportional to (diameter)³ (Alexander 1983). Thus, the peak stress in the bone is proportional to $(mg l / d^3) \sin \theta$. If animals of different sizes were geometrically similar to each other, l and d would both be proportional to $m^{0.33}$ and θ would be constant, so the stress would be proportional to $m^{0.33}$. Either rabbits would have bones far stronger than necessary, or elephants would fracture their bones when they tried to stand.

Just as we found for muscles, the tendency for larger mammals to stand and run on straighter legs helps to avoid excessive stresses in bones. We have already seen that $r/(l \sin \theta)$ is about proportional to (body mass)^{0.26}. Biewener (1990) found that muscle moment arms r tend to be proportional to $m^{0.44}$, making $l \sin \theta$ proportional to $m^{0.44} / m^{0.26} = m^{0.18}$. Alexander, Jayes et al. (1979a) found that the diameters of mammal leg bones are generally about proportional to $m^{0.36}$. Thus, $(mg l / d^3) \sin \theta$ is expected to be proportional to $m m^{0.18} / (m^{0.36})^3 = m^{0.10}$. Bone stress should be proportional to $m^{0.10}$, implying that it should increase with animal size, but not by nearly as much as if mammals of different sizes were geometrically similar.

These arguments suggest that muscle stresses in standing animals should decrease slowly with increasing body size, in proportion to $m^{-0.06}$, and that bone stresses should increase slowly, in proportion to $m^{0.10}$. There is too much uncertainty about both exponents for us to be confident that either is different from zero, so our conclusion should probably be simply that bone and muscle stress change far less with changing body size than they would if mammals of different sizes were geometrically similar.

We have been thinking of the weight of the body as the load on an animal's legs. This is correct for standing, but much larger forces act on feet in running and jumping. For example, the peak forces on the feet of a galloping greyhound were four times as high as when it was standing still (Bryant et al., 1987). The two hind feet of bushbabies (*Galago moholi*)

taking off for a jump together exerted a force of up to 13 times body weight (Günther et al. 1989).

The faster an animal runs, the lower the duty factor (the fraction of the duration of the stride for which each foot is on the ground). The force exerted on the ground, averaged over a complete stride, must match body weight, so the lower the duty factor, the larger the forces that must be exerted while the foot is on the ground, fast running requires large forces. Alexander et al. (1977) filmed African ungulates, ranging from small gazelles to giraffes, galloping fast in their natural habitat. We found that duty factors were about proportional to (body mass)^{0.14}, implying that the forces exerted by the larger animals were smaller multiples of body weight. In contrast, Bennett (1987) filmed kangaroos of different sizes hopping fast and found that duty factors were proportional to (body mass)^{-0.10}, implying that the forces on the feet of larger kangaroos were larger multiples of body weight. I do not know which group is more typical of mammals in general. However, the very largest terrestrial mammals, rhinoceros and elephants, are less athletic than smaller ones, presumably because their legs are not strong enough to exert such large multiples of body weight. Elephants neither gallop nor jump. The lowest duty factor that I have observed for an elephant (0.49 [Alexander 1979b]) is much higher than the duty factors of around 0.2 that Alexander et al. (1977) observed for small antelopes galloping fast.

Flying animals as well as running ones have to support their own weight. A flying bird of weight mg requires an upward lift $mg/2$ on each wing (Fig. 4.4B). This lift is distributed along the length of the wing, but the moment it exerts about the shoulder is the same as if the whole force acted at the center of pressure, at a distance l from the wing base. Thus, the moment is $mg/2 \cdot l$. It must be balanced by the pectoralis muscle, which has cross-sectional area A and moment arm r , and exerts stress σ . Hence,

$$\sigma = \frac{mgl}{2Ar} \quad (4.6)$$

The argument that we used in our discussion of Equation 4.5 tells us that if birds of different sizes were geometrically similar, muscle stress would be proportional to $m^{0.33}$, stresses would be ten times as high in a 10-kg swan as in a 10-g tit. Birds of different sizes are not geometrically similar. Wingspan, and therefore the length l , tends to be proportional to $m^{0.39}$ (Rayner 1987), but that deviation from geometric similarity makes the problem worse rather than better. Not enough seems to be known about the scaling of bird wings and wing muscles to tell us how muscle stresses actually scale in birds of different sizes.

This chapter has introduced the concepts of geometric similarity, dynamic similarity, elastic similarity, and stress similarity. These concepts

will be very helpful when we compare the structure and movements of animals of different sizes, but it is important to remember that no animal is a precisely scaled model of another. We may discuss what the consequences would be if animals were, for example, geometrically similar or moved in dynamically similar ways, but the similarity is never exact. The chapter has also explained some dimensionless numbers that will be important when we compare the locomotion of animals of different sizes.