

Scaling for stress similarity and distorted-shape similarity in bending and torsion under maximal muscle forces concurs with geometric similarity among different-sized animals

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SUMMARY

When geometric similarity, or isometry, prevails among animals of different sizes their form and proportions are similar. Weight increases as the cube of the length dimension, while cross-sectional areas increase as its square, so in load-bearing structural elements the stress, caused by the body weight, increases in direct proportion to the length dimension, both for pure axial loads and for transverse bending and torsional loads. On this account, large body sizes would be expected to set up compensatory selection on the proportions of supporting structures, making them disproportionately thicker as required to maintain similar, size-independent safety factors against breakage. Most previous scaling theories have assumed that the strength of support elements has evolved with respect to loads due to the body weight. But then, from the arguments above, a scaling principle different from the geometric similarity rule would be required in order for safety factors to remain similar among different-sized animals. Still, most comparable animals of ‘similar kind’ scale in accordance with the geometric similarity rule. Here, we instead argue that muscle forces cause much larger loads on structural support elements during maximum performance events (such as during prey capture or escape from predators) than do loads dictated by the body weight (such as during cruising locomotion), and that structural strength therefore might evolve with respect to maximal muscle forces rather than to the body weight. We explore how the transverse and longitudinal lengths of structural support elements must scale to one another, and to muscle transverse length, in order to satisfy each of the following, functionally based, similarity principles for support elements placed in bending, or in torsion, by maximal muscle forces during locomotion: (1) similarity in axial stress, or (2) in torsional shear stress, and (3) similarity in bent shape, or (4) in twisted shape. A dimensional relationship that satisfies all four conditions actually turns out to be the geometric similarity rule. These functional attributes may therefore help to explain the prevalence of geometric similarity among animals. Conformance of different-sized species with the geometric similarity principle has not been directly selected for as such, of course, but may have arisen as a by-product of adaptation in morphological proportions, following upon selection, in each separate species-lineage, for adequate and similar safety factors against breakage, and similar optimal distorted shapes, of structural support elements placed in bending, or in torsion, by maximal muscle forces.

Key words: allometry, distorted-shape similarity, geometric similarity, scaling under maximal muscle forces, stress similarity in bending and torsion.

INTRODUCTION

Geometric similarity has hitherto been mainly a descriptive term, denoting similar form among different-sized organisms, but with no functional connotation. Here, we explore functional relationships with locomotion in animals.

When geometric similarity, or isometry, prevails among animals of different sizes their form and proportions are similar. Weight increases as the cube of the length dimension, l^3 , while cross-sectional areas increase as its square, l^2 , so in structural support members the material stress (force per unit area), caused by the body weight, increases in direct proportion to the length dimension ($l^3/l^2=l$), and proportional to the 1/3 power of the body mass, both for pure axial loads and for transverse bending and torsional loads. On this account, large body sizes would be expected to set up compensatory selection on the proportions of supporting structures, making them disproportionately thicker as required to maintain similar, size-independent safety factors against breakage. Still, empirical data show that most comparable animals of ‘similar kind’ scale in accordance with the geometric similarity rule, except for bovids and a few other taxa of large mammals, which tend to have relatively stouter skeletal elements the larger they are (Alexander

et al., 1979; Alexander, 1983a; Biewener, 1983; Biewener, 1990; Christiansen, 1999; Economos, 1983; Garcia and daSilva, 2004; McMahon, 1975a). The departure from geometric similarity has been variously reported among mammals larger than 20 kg (Economos, 1983), larger than 50–100 kg (Christiansen, 1999) or larger than 100 kg (Bertram and Biewener, 1990).

During locomotion in terrestrial mammals, bending and torsional loads cause much larger material stress and deformation of structural support elements than do axial loads (Alexander, 1985a; Biewener, 1983; Biewener, 1991; Rubin and Lanyon, 1982; Rubin and Lanyon, 1984). This must be even more so for bird and bat wings (Figs 1 and 3), as evidenced by their musculo-skeletal geometry, mechanics and aerodynamics (Pennycuick, 1967; Pennycuick, 2008). It has also been confirmed experimentally in birds as well as in bats (Biewener and Dial, 1995; Swartz et al., 1992). So strength against bending and torsion must have been of first priority in the adaptation of structural support elements of terrestrial quadrupeds, birds and bats.

Most previous scaling theory has assumed that the strength and dimensions of supporting structures are adapted to loads proportional to the body weight, such as during cruising locomotion. But muscle forces during maximal locomotor performance must cause much

greater loads on supporting structures than do loads due to gravity. Supporting structures may therefore be more adapted to maximal muscle forces, and scale with respect to them rather than to the body weight. For that reason the scaling developed here emphasises loads caused by maximal muscle forces, such as during extreme manoeuvres.

Here, we derive four functionally based size-scaling principles for the relationships between muscle transverse length and the longitudinal and transverse lengths of structural support elements placed in bending, or in torsion, by maximal muscle forces during locomotion: (1) similarity in axial stress, or (2) in torsional shear stress, and (3) similarity in bent shape, or (4) in twisted shape. We explore how dimensions of muscles and load-bearing elements must scale to one another in order to fulfil these criteria. A dimensional relationship that satisfies all four conditions turns out to be the geometric similarity rule. These functional attributes may therefore explain the prevalence of geometric similarity among animals. The conflict between data and earlier scaling theory, based on body-weight-dictated loads, might be resolved by instead shifting focus to maximal muscle forces.

Morphology

Lever arm ratio

Fig. 1 shows a structural support element free to rotate about a joint at its left end. It is exposed to a muscle force F_m acting on moment arm L_m and to an opposing external reaction force F_{ext} acting on moment arm L . The external force F_{ext} that acts on the element from the environment arises in reaction to the out-force F_{out} , and is equal to it but opposite in direction. At moment equilibrium:

$$L_m F_m = L F_{ext}. \quad (1)$$

In Fig. 1, L_{bend} is the bending moment arm of force F_{ext} , taken with respect to some characteristic lengthwise position along the beam, i.e. at the same proportion of distance L from the line of action of force F_{ext} in different-sized animals. In Figs 1, 2 and 3 that position is chosen to be where the bending moment on the beam is largest, which is at the line of action of the muscle force F_m in Figs 1 and 3 but at the fulcrum in Fig. 2.

In those cases when the muscle moment arm L_m is a constant proportion of moment arm L of the external reaction force, L_{bend} is also proportional to L (Fig. 1), and the external force is directly proportional to the muscle force, regardless of animal size:

$$F_{ext} \propto F_m. \quad (2)$$

In bird wings the lever arm ratio L_m/L is constant regardless of body size (Janson, 1996). Therefore, the aerodynamic force acting on a particular feather at a characteristic spanwise position in the wing is also the same weight-independent proportion of the muscle force in different-sized birds (Fig. 3). This makes scaling straightforward. But in terrestrial mammals (Fig. 2) the lever arm ratio L_m/L_{bend} increases with increasing body size (Biewener, 1983; Biewener, 1989; Biewener, 1990; Biewener, 2005), which complicates scaling, as will be explained below.

Terrestrial mammals

Among terrestrial mammals the increase in stress in leg muscles and skeletal elements, which the foregoing argument suggests would follow from larger body weights of geometrically similar animals, is nearly eliminated by compensatory, size-related changes of limb posture and lever arm ratios (Alexander, 2003; Biewener, 1983; Biewener, 1989; Biewener, 1990; Biewener, 2005). Small mammals have a crouched locomotion posture with rather flexed limb joints

but the posture becomes increasingly more upright in larger mammals so that limb elements become more nearly aligned with the ground reaction force (Fig. 2). Very big terrestrial animals, like elephants, walk on rather straight legs, sometimes termed columnar legs, with the limb segments supposedly taking up a nearly columnar posture, a so-called graviportal adaptation (Hildebrand, 1985; Hildebrand and Hurley, 1985) – although locomotion in elephants does involve more limb flexion than traditionally thought (Ren et al., 2008; Hutchinson, 2009).

The straighter and more upright leg posture, following upon more open joint angles among larger mammals, aligns the leg more nearly with the ground reaction force and changes the direction of the muscle forces relative to the limb elements that they act upon. An effect of this is that with increasing body size there is a systematic increase in the ratio between the muscle moment arm and the moment arm of the ground reaction force, acting about leg joints. Larger mammals therefore gain larger ‘effective mechanical advantages’ (EMA) (Biewener, 1989; Biewener, 1990), also known as the ‘lever gear ratio’ (Grimmer et al., 2008; Williams et al., 2009). Biewener (Biewener, 1990) calculated EMA for 10 species ranging in size from a mouse to a horse, and later added another four species, including two bipeds – kangaroo rat and man [fig. 3 in Biewener (Biewener, 2005)]. EMA was measured during the middle third of the ground contact phase at the trot–gallop transition speed and averaged across all joints of forelimb and hindlimb, except the forelimbs of the two bipeds in the large sample. The speed of locomotion, and thus the type of gait, has negligible effect on the lever arm ratio. The EMA scales with body mass as $M_b^{0.26}$ in the sample of 10 species (Biewener, 1990) and as $M_b^{0.25}$ in the sample of 14 species [fig. 3 in Biewener (Biewener, 2005)]. It thereby violates one aspect of the geometric similarity rule, which requires that EMA is constant, and thus $\propto M_b^0$.

The lever arm ratio of mammal legs increases with increasing body weight because the muscle moment arm L_m increases more than expected from geometric similarity, as $M_b^{0.44}$ instead of $M_b^{0.33}$ (Biewener, 1990), whereas the moment arm L_{bend} of the ground reaction force increases less, as $M_b^{0.19}$ instead of $M_b^{0.33}$ (Fig. 2) (from $EMA = L_m/L_{bend} \propto M_b^{0.25}$, so $L_{bend} \propto M_b^{0.44}/M_b^{0.25} \propto M_b^{0.19}$). The moment arm of the muscle force thus scales more nearly as expected under geometric similarity (as 0.44 vs 0.33) than does the moment arm of the ground reaction force (as 0.19 vs 0.33). These various exponents – 0.25, 0.44 and 0.19 – have different effects on the scaling of bone and muscle stress depending on whether scaling is done with respect to body-weight-related locomotor forces or to maximal muscle forces, as will be explained below.

Birds

We know of no reports about any size-related variation in wing joint angles or in the ratio between muscle and out-force moment arms in birds and bats similar to the size-related changes in limb posture and lever arm ratio among terrestrial mammals. Here, we review results from a study of bird wings (Janson, 1996), showing that the ratio L_m/L between the moment arms of the pectoral muscle and the resultant aerodynamic force on the wing is nearly constant among different-sized birds (Fig. 1).

In order to enable a comparison between the lengths of the muscle moment arm and the moment arm of the external force, acting on the wing, the aerodynamic forces – distributed among all wing elements of area – must be added into a resultant force. And it may be thought of as acting at a hypothetical centre of pressure of the wing, located at such a spanwise position that the whole force exerts the same moment about the shoulder joint, as do the distributed

aerodynamic forces. When calculating the moment arm of the resultant aerodynamic force, the relative air velocity was assumed to be the same over the entire wingspan, as it is during gliding flight. And the profile lift coefficient was also taken to be the same along the entire wingspan. From this follows that the aerodynamic force on each element of area is proportional to the element's area. Areas can therefore be used as proxies, representing forces.

The entire wing, outstretched as during gliding flight, was divided up into 10–32 narrow chordwise strips, parallel to the axis of rotation of the wing–root joint and perpendicular to the leading edge of the wing (Fig. 3). The area of each strip was measured and multiplied by its distance from the shoulder joint, measured in the spanwise direction, parallel to the wing's leading edge. These products, representing the moment contributions from strips at different distances from the wing root, were then summed over the entire wing to obtain its first moment of area. The total area of the wing, representing the resultant aerodynamic force, multiplied by the sought-after distance L of the spanwise centre of pressure from the shoulder joint (Fig. 1), is equal to the sum, across all wing strips, of the product of strip area multiplied by its moment arm, i.e. the wing's first moment of area with respect to the wing–root joint (Pennycuick, 1967; Pennycuick, 2008).

The moment arm of the pectoral muscle and the moment arm of the resultant aerodynamic force of the wing, as well as their ratio L_m/L , were measured on 35 specimens of 21 bird species, ranging in size from a 10 g flycatcher, *Ficedula hypoleuca*, to a 1450 g Gooshawk, *Accipiter gentilis*. The moment arm of the pectoral muscle scales as $M_b^{0.46}$ ($R^2=0.93$) and that of the resultant aerodynamic force as $M_b^{0.40}$ ($R^2=0.86$), so the ratio between them scales with body mass as $M_b^{0.06}$ (Janson, 1996). We think this exponent is near enough to zero to let the lever arm ratio be treated as constant among different-sized birds. Then the external reaction force F_{ext} is proportional to the muscle force F_m (proportionality 2); a relationship that applies to the wing and flight feathers of birds whereas there are no such data available for bat wings.

Loads

Peak and maximal muscle forces

During locomotion the bending and torsional loads on structural support elements are determined by the muscle forces that are actually generated. A distinction must be made between the maximal force that a muscle can exert and the peak force, which is the largest, but not necessarily – and most often not – the maximal-possible muscle force generated during a locomotion cycle. It must be emphasised that, except for accidental impact forces, the largest bending and torsional forces that support elements can ever be exposed to during locomotion have upper limits set by maximal muscle forces.

For swimming and flying it is obvious that the fluid-dynamic reaction forces from water and air cannot exceed what the muscles can muster. For terrestrial locomotion similar limitations prevail. Limb joints are usually held somewhat flexed at touchdown, enabling flexural yield, and at least the forelegs are elastically suspended *via* the shoulder girdle. Both means of shock absorption prevent exceedingly large impact forces from arising.

Humans running across uneven ground adjust leg stiffness at touchdown to control the ground reaction force by varying muscle-controlled flexural yield of leg joints [Grimmer et al. who defined leg stiffness as the ratio between peak ground reaction force and maximum leg compression due to joint flexion during ground contact (Grimmer et al., 2008)]. At touchdown, tendons and ligaments produce resistance under elastic tensile yield, and muscles generate

force while being forcibly stretched (doing negative work), whereas elastic elements spring back and extensor muscles shorten against external resistance in the power phase, extending the leg (doing positive work), prior to take-off.

The impulse at touchdown (the integral of the transient impact reaction force with respect to the time for the brake) causes a loss of momentum (body mass multiplied by velocity), which is regained by means of an equally large impulse during the pushing phase before take-off. In running animals, and humans, the braking phase after touchdown has a shorter duration than the pushing phase before take-off. Therefore, the muscle force developed during the brake must be larger than that exerted during the longer-lasting push (Cavagna and Legramandi, 2009). This landing–takeoff asymmetry is consistent with the capacity of muscles to produce greater force while being forcibly stretched than when shortening.

The maximal force that muscles can exert for the control of joint flexion and girdle yield during the brake, after touchdown, thus gives the largest possible out-force. And this, in turn, sets an upper limit to the ground reaction force.

Were it not for muscle-controlled joint flexural yield and girdle suspension, ground impact forces would be determined directly and exclusively by the body weight (gravity and inertia), with no moderation by muscles. But with muscles in control, it is not a question of whether muscle forces or impact forces from the ground at touchdown are the most significant ones. Instead they are interrelated; it is the maximal muscle forces that determine, and set the upper limits to, the reaction forces from the ground. So safety factors against breakage may be expected to evolve with respect to maximal muscle forces, not only for swimming and flying but also for terrestrial locomotion.

We also distinguish between two alternative load domains, dependent on the mode of locomotion. The loads, produced by muscles, can either be (1) dictated by the body weight, or (2) they can be due to maximal muscle forces.

Cruising locomotion: body-weight-dictated loads

Cruising locomotion refers to steady locomotion at moderate and energy-efficient speed below the maximum (top) speed, and with no manoeuvres. It is what Biewener called ‘the preferred speed’, at which mammals operate with lower muscle and bone stresses than at top locomotor speed (Biewener, 2005). Cruising speed in flying animals may be ‘the minimum power speed’, which requires the least energy per unit time, or ‘the maximum range speed’, which requires the least energy per unit distance flown, enabling the animal to fly the longest distance for a given amount of energy, a likely choice for migration, even though there are other options depending on what will be achieved (Pennycuick, 1969; Pennycuick, 2008; Norberg, 1981; Hedenström and Ålerstam, 1995).

During steady cruising locomotion the magnitude of the peak external force F_{ext} that needs to be elicited from the ground, water or air is determined by the body weight and the mode of locomotion, with its associated duty factor, and the muscles have to exert a force F_m as required, given the lengths of the respective moment arms (Eqn 1). So even though the body weight determines the external reaction force, it is controlled and kept within limits by muscles. Because animals usually have spare muscle capacity in excess of what is required for cruising locomotion, the peak muscle force during a cruising locomotion cycle is less than the maximal force that the muscle can exert. Therefore, for each type of cruising locomotion the required peak external reaction force F_{ext} , occurring during a locomotor cycle, is dictated by some gait-characteristic and size-independent multiple of the animal's body weight, and it

is not limited by muscle capacity. The external force, multiplied by its moment arm, sets the value of the moment that the muscles have to set up by matching its force F_m to the muscle moment arm as required. Because the bending moment is dictated by the body weight, adaptations to loads that occur during cruising locomotion should cause dimensions and strength of structural support elements to scale with respect to the body weight.

Except for bone loads due to gravitational and inertial forces that act on the body during cruising locomotion, there are also loads due to the weight and inertia of legs or wings that are being cyclically accelerated. And these forces act on different moment arms than does the external reaction force. Even though moments due to the weight and inertia of leg segments are much smaller than the dominant body-weight-dictated moments, set by the ground reaction force and its moment arm (Biewener, 2005), muscles must nonetheless exert extra forces for accelerating the limbs during cruising locomotion.

In birds the lever arm ratio L_m/L is constant as required by geometric similarity (Fig. 1) (Janson, 1996), so during cruising locomotion the external reaction force is directly proportional to the muscle force, and the muscles must exert a force F_m , equal to $F_{ext}L/L_m$ (Eqn 1), which is proportional to the body mass M_b because F_{ext} is, so $F_{ext} \propto F_m \propto M_b$. During cruising locomotion, and if geometric similarity prevails, the bending moment $F_{ext}L (=F_m L_m)$ would scale as $M_b M_b^{1/3} \propto M_b^{1.33}$ and muscle stress as $M_b^{1/3}$ [from F_m /(muscle fibre cross-sectional area) $\propto M_b/M_b^{2/3} \propto M_b^{1/3}$].

In terrestrial mammals, the lever arm ratio L_m/L_{bend} scales as $M_b^{0.25}$, thus violating geometric similarity (Fig. 2) (Biewener, 2005). During cruising locomotion the external bending moment $F_{ext}L_{bend}$ dictates the moment $F_m L_m$ that muscles have to set up by matching its force F_m to the muscle moment arm L_m as required. The required muscle force $F_m (=F_{ext}L_{bend}/L_m)$ scales as $M_b/M_b^{0.25} \propto M_b^{0.75}$, as opposed to $M_b^{1.0}$ under geometric similarity, and the bending moment scales as $M_b^{1.19}$ (from $F_{ext}L_{bend} \propto M_b M_b^{0.19}$ or from $F_m L_m \propto M_b^{0.75} M_b^{0.44}$) as opposed to $M_b^{1.33}$ under geometric similarity (from $F_{ext}L_{bend} \propto M_b M_b^{1/3}$). Muscle fibre cross-sectional area scales as $M_b^{0.81}$ in terrestrial mammals (and as $M_b^{0.77}$ in Bovidae) [table 2-1 in Alexander (Alexander, 1985a)], so muscle stress scales as $M_b^{-0.06}$ (from $M_b^{0.75}/M_b^{0.81}$) (Biewener, 1990; Alexander, 2003) (and as $M_b^{-0.02}$ in Bovidae). During cruising locomotion in terrestrial mammals the ground reaction force is proportional to the body weight but muscle stress is nearly independent of body size, scaling as $M_b^{-0.06}$ rather than as $M_b^{0.33}$ under geometric similarity.

Maximal performance events: maximal muscle-force-dictated loads

Under certain circumstances, however, supporting structures may instead be subjected to maximal muscle forces. This may occur during events like a maximal jump, a fast start, top-speed locomotion and the tightest possible turn. Such behaviours are likely to occur during predator pursuit of prey and for capturing and bringing down prey, during escape manoeuvres of prey (Biewener, 2005), during fights over territory and mating opportunities, and during courtship display.

During tight manoeuvres the body need not only be balanced against gravity over a locomotion cycle but additional forces are required for linear and angular accelerations of the body and of limbs relative to the trunk. In such cases peak forces are larger than during cruising locomotion. To bear this out, consider a cheetah in a turning pursuit sprint at speeds of up to 104 km h^{-1} (Sharp, 1997), a falcon pulling out of an attack dive at speeds of up to 140 km h^{-1} (Alerstam, 1987) or a hummingbird (*Calypte anna*) pulling out of a 97 km h^{-1}

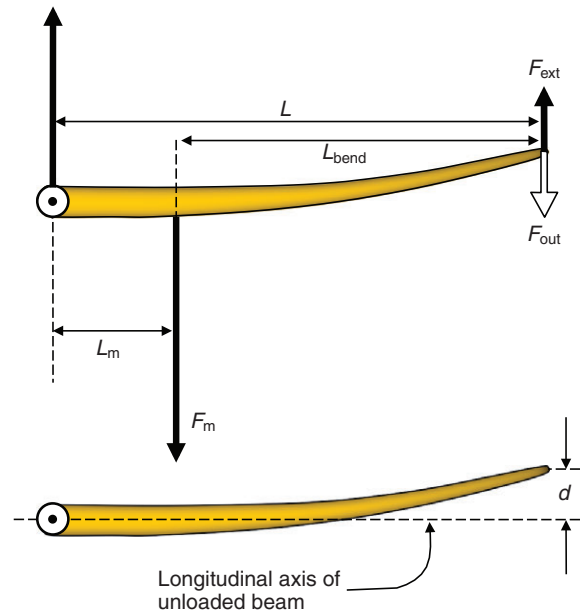


Fig. 1. Free-body diagram showing forces, in solid arrows, acting on a structural support element with the fulcrum at its left end. The layout shows a third class lever with the muscle force and external reaction force acting on the same side of the fulcrum. This is representative for skeletal elements of bird and bat wings, the shaft of flight feathers and the veins, acting like spars, in wings of some insects, like dragonflies (in downstroke). Regarding flight feathers, muscle force is transferred to them by means of the postpatagial tendon, running spanwise across and on top of the feather calami (bases), generating a force couple in the structures (follies) embedding the feather base, holding the feather down on the wing plane (Pennycuik, 2008). Locomotion may cause either of two alternative loads that must be distinguished. (1) In steady cruising locomotion the magnitude of the out-force, F_{out} (hollow arrow) is dictated by the body weight because it sets the value of the external force F_{ext} that needs to be elicited from the ground, water or air in reaction to F_{out} . Therefore, for each given type of cruising locomotion the loads on support elements are the same size-independent multiple of the animal's body weight. (2) When maximal muscle forces are exerted, such as during maximal locomotor performance, the out-force moment $F_{out}L$ is instead determined by the maximal muscle moment $F_m L_m$, so then the reaction force F_{ext} is not dictated by the body weight any longer. L_{bend} in Figs 1, 2, and 3 is the moment arm of the external reaction force F_{ext} with respect to the cross-section where the bending moment is largest and where failure is most likely to occur. F_{ext} acts on moment arm L_{bend} and bends the support element through distance d .

courtship display dive, experiencing $9g$ centripetal acceleration (Clark, 2009), which, incidentally, equals the breaking load of the pigeon humerus in both bending and torsional mode (Pennycuik, 1967; Pennycuik, 2008).

The success rate of predator attacks is generally rather low, and to cite one large study of raptors it was about 5–10% in *Accipiter* hawks and *Falco* falcons (Rudebeck, 1950; Rudebeck, 1951). There should thus be ample opportunities for selection to act on safety factors in relation to maximal muscle forces – for maximal locomotor performance – among predators and prey alike.

So here it is the other way around – when the muscle force F_m reaches its maximum attainable value, it becomes the independent variable. The maximal muscle force, multiplied by its moment arm about the joint, thus determines the moment of the reaction force F_{ext} from the ground, water or air, and the body weight does not determine F_{ext} (Fig. 1). And the value of the external reaction force

F_{ext} itself is not fixed; it will vary reciprocally with the length of its moment arm as required to match the muscle moment (Eqn 1). What matters is only that the muscle exerts its maximal force, so the locomotion mode and duty factor make no difference. Adaptations to bending and twisting moments that occur under maximal muscle forces should cause dimensions and strength of structural support elements to scale with respect to muscle fibre cross-sectional area instead of to the body weight.

When locomotor muscles exert their maximum force, which is what we emphasise here, the distinction between gravitational and inertial loads from the body and from the legs is of no concern for the loading of skeletal elements. This is because when a maximal muscle force acts on its muscle moment arm, it dictates the out-force moment, no matter what the length is of the moment arm that the external reaction force acts on, and no matter what the force is used for, i.e. regardless of how it may be split into components for support against gravity and for accelerating the body and the legs or wings. So when maximal muscle forces are exerted, they do not match any body-weight-dictated needs, and the out-force can only be as large as the muscle moment permits, given the length of the out-force moment arm. Therefore, so long as maximal muscle forces are exerted, scaling is not affected by how the out-force is used.

In birds the lever arm ratio L_m/L is constant (Janson, 1996), so the external reaction force is directly proportional to the muscle force ($F_{\text{ext}} \propto F_m$) during cruising locomotion as well as when maximal muscle forces are exerted. If geometric similarity prevails, the maximal muscle force F_m and the corresponding external reaction force F_{ext} would both scale as $M_b^{2/3}$ instead of as $M_b^{1.0}$ for the body-weight-dictated non-maximal muscle force, and the corresponding reaction force, in cruising locomotion. And the maximal bending moment during maximum performance events would scale as $M_b^{1.0}$ (from $F_m L_m \propto M_b^{2/3} M_b^{1/3}$) instead of as $M_b^{1.33}$ for the non-maximal, bending moment at cruising speed (from $F_{\text{ext}} L_{\text{bend}} \propto M_b M_b^{1/3}$). When maximal muscle force is developed, muscle stress is independent of body size and scales as M_b^0 .

We found earlier that during cruising locomotion in mammals the ground reaction force is dictated by the body weight and duty factor. The lever arm ratio L_m/L_{bend} is weight-dependent and scales as $M_b^{0.25}$ (Biewener, 1990). It determines the muscle force F_m required, which scales as $M_b^{0.75}$ (from $F_m \propto F_{\text{ext}} L_{\text{bend}} / L_m \propto M_b / M_b^{0.25}$). The moment $F_{\text{ext}} L_{\text{bend}}$ acting about limb joints scales as $M_b M_b^{0.19} \propto M_b^{1.19}$, which is rather different from $M_b^{1.33}$ under geometric similarity.

Not so when maximal muscle forces are developed. Regardless of how the moment arm L_{bend} of the external reaction force F_{ext} may change with animal size, the product $F_{\text{ext}} L_{\text{bend}}$ is dictated by the maximal muscle moment $F_m L_m$. Muscle fibre cross-sectional area scales as $M_b^{0.81}$ in terrestrial mammals [table 2-1 in Alexander (Alexander, 1985a)], so the muscle moment $F_m L_m$ (and thus also the external moment $F_{\text{ext}} L_{\text{bend}}$) scales as $M_b^{0.81} M_b^{0.44} \propto M_b^{1.25}$ instead of as $M_b^{2/3} M_b^{1/3} \propto M_b^{1.0}$ under geometric similarity and maximal muscle force. When maximal muscle force is exerted, muscle stress is independent of body size, $\propto M_b^0$, just as it almost is, $\propto M_b^{-0.06}$ (Biewener, 1990; Alexander, 2003), during cruising locomotion in terrestrial mammals. And under maximal muscle forces the ground reaction force ($F_{\text{ext}} \propto F_m L_m / L_{\text{bend}}$) is almost proportional to body mass, scaling as $M_b^{0.81} M_b^{0.25} \propto M_b^{1.06}$, very close to $M_b^{1.00}$ that holds for cruising locomotion.

As it thus turns out, the moment acting about limb joints in terrestrial mammals scales with body mass in nearly the same way regardless of whether loads are dictated by the body weight, giving $M_b^{1.19}$ (in contrast to $M_b^{1.33}$ for geometric similarity), or by maximal

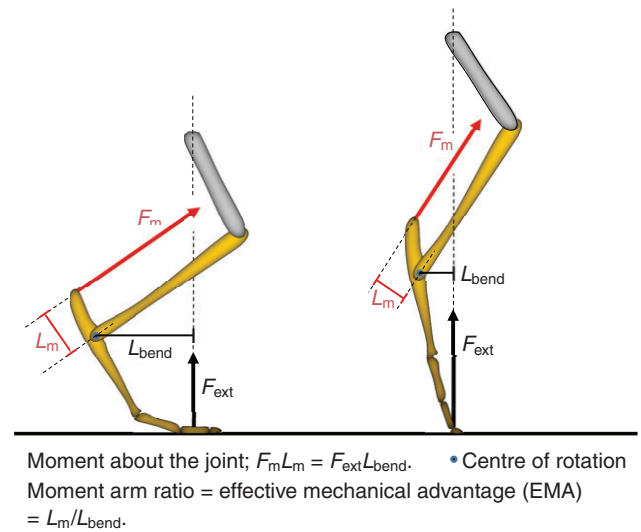


Fig. 2. Schematic diagram showing a first class lever with the muscle force and the external reaction force acting on either side of the fulcrum, formed by the ankle joint (or, analogously, by the elbow joint) of a small (left) and a large (right) mammal. It illustrates different ratios L_m/L_{bend} between the moment arms of the muscle and of the external reaction force, explored and elaborated by Biewener (see references below). The difference follows from a progressive shift from crouched to more upright locomotion postures in increasingly large mammals, whereby the limb elements become more nearly aligned with the ground reaction force F_{ext} , here taken to be vertical midway through the stride [following Biewener (Biewener, 1983)]. The diagrams are drawn to different scales and based on figs 1 and 8 in Biewener (Biewener, 1983), fig. 1 in Biewener (Biewener, 1989), fig. 3 in Biewener (Biewener, 1990) and fig. 2 in Biewener (Biewener, 2005). L_m , length of muscle moment arm; L_{bend} , length of bending moment arm; F_{ext} , external reaction force.

muscle forces, giving $M_b^{1.25}$ (in contrast to $M_b^{1.0}$ for geometric similarity). The ground reaction force in mammals scales as $M_b^{1.00}$ during cruising locomotion and as $M_b^{1.06}$ under maximal muscle forces (in contrast to $M_b^{1.00}$ and $M_b^{0.67}$, respectively, for geometric similarity). But for a given body mass, moments and ground reaction forces are always larger under maximal muscle forces than during cruising locomotion. The scaling similarities between moments ($M_b^{1.19}$ and $M_b^{1.25}$ as opposed to $M_b^{1.33}$ and $M_b^{1.0}$ for geometric similarity) and between ground reaction forces ($M_b^{1.00}$ and $M_b^{1.06}$ as opposed to $M_b^{1.00}$ and $M_b^{0.67}$ for geometric similarity) are due to the departure from geometric similarity in the ways that muscle fibre cross-sectional area and leg lever-arm ratio scale with body mass in terrestrial mammals. An effect of this is that bone axial stress due to bending will scale with body mass in almost identical ways regardless of whether loads are caused by non-maximal muscle forces, dictated by the body weight during cruising locomotion, or by maximal muscle forces during maximal locomotor performance, as will be shown below.

Duty factors

During steady locomotion the upward supporting force from the environment, as averaged over the time of an entire locomotion cycle, must equal the weight of the animal. The duty factor of a terrestrial animal is the fraction of the duration of a stride during which a foot is in ground contact and provides support against gravity. As mammals run faster they successively shift gait with ever decreasing duty factors. For flying animals the duty factor is the fraction of the time of a locomotion cycle during which lift is

elicited and provides weight support and thrust. Birds use different flight modes, such as continuous flapping, flap-gliding, hovering, etc. The reaction force from the environment varies in inverse proportion to the duty factor. So different gaits in terrestrial locomotion, and different flight modes, do elicit different peak loads during the support phase.

During cruising locomotion the body weight and duty factor dictate the ground, or air, reaction force in running and flying and thus sets the value of the muscle force that is required at different locomotion modes and cruising speeds. Alexander et al. found that the duty factor of freely running African ungulates scales with body mass as $M_b^{0.14}$ (Alexander et al., 1977). From treadmill studies of other mammals, Biewener (Biewener, 1983) got no change with size ($M_b^{0.006}$ at the trot-gallop transition speed, and from $M_b^{0.04}$ to $M_b^{0.02}$ at top galloping speed), nor did McMahon (McMahon, 1977), whereas Bennett (Bennett, 1987) got an opposite trend for kangaroos, $M_b^{-0.10}$. Because the reaction force from the environment varies in inverse proportion to the duty factor, the duty factor, when it varies with animal size, also affects the scaling of skeletal dimensions required to maintain a constant safety factor against breakage. This is when the body weight dictates the load, such as during cruising locomotion under less than maximal muscle forces.

But when maximal muscle forces are developed, which is what we emphasise here, they dictate the out-force moment. Then the ground reaction force can only be as large as the muscle moment permits, given the length of the out-force moment arm, and there is no matching of the out-force to the weight of the animal or to the mode of locomotion or to the duty factor. So under maximal muscle forces, the scaling of strength and dimensions, required to maintain a constant safety factor against breakage of support elements, would not be influenced by the mode of locomotion or the duty factor. When muscles exert maximal force the duty factor cannot be any lower, the animal cannot run any faster or make any more extreme manoeuvre, and the duty factor cannot affect the muscle force any longer.

Scaling premises

To recapitulate, during cruising locomotion the reaction force that needs to be elicited from the environment is dictated by the body weight, and for any given locomotion mode and duty factor is the same multiple of the body weight regardless of animal size. So the body-weight-dependent external reaction force determines the loads on support elements, and muscles produce the moment required. But for maximal locomotor performance, the muscles exert maximal force and the ground reaction force will be as it may, and is unaffected by the body weight, the mode of locomotion and duty factor. Then the muscles alone dictate the loads on support elements.

Most previous scaling theory has assumed that peak external forces during locomotion are proportional to the body weight (e.g. Biewener, 1983; Biewener, 1989; Biewener, 2005; Alexander, 2003), such as during cruising locomotion, as outlined above. By contrast, we emphasise maximal muscle forces – but also treat body-weight-dependent loads – in the derivations below of the scaling of proportions, required to maintain equal stress, and equal distorted shape, of structural support elements among different-sized animals.

Similarity criteria

We will consider four criteria of performance similarity (scaling rules) of structural load-bearing elements placed in bending, or in torsion, by maximal muscle forces among different-sized animals: (1) bending, or (2) twisting to similar axial stress or torsional shear stress, respectively, and (3) bending, or (4) twisting to similar distorted shapes. During animal locomotion, structural support

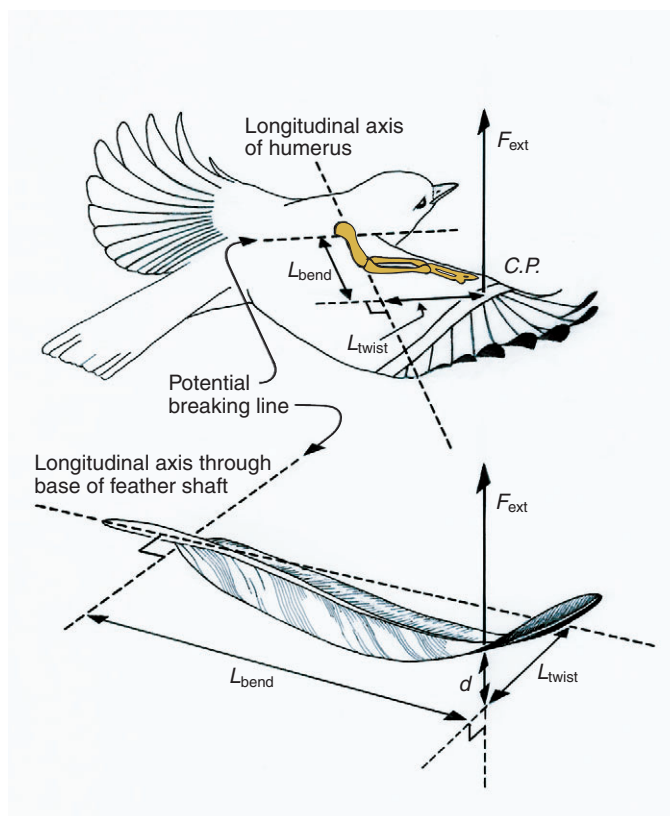


Fig. 3. Geometry of the wing and a primary wing feather of a bird in flight as examples of structures subjected to combined bending and torsional torques during locomotion. A streamwise strip element of the wing carries distributed aerodynamic pressure that is represented here by a resultant force F_{ext} , located at the strip's centre of pressure (*C.P.*). It acts on moment arms L_{bend} and L_{twist} , tending to bend and twist the humerus of the upper arm, and similarly for the shaft of the isolated primary flight feather (bottom). The moment arms L_{bend} and L_{twist} are functions of longitudinal lengths L of support structures. The total aerodynamic moment of the wing can be found by adding the sub-moments of all streamwise strips across the entire wing (using the distance of each strip from the shoulder joint, like L in Fig. 1). The potential breaking line of the humerus is where the bending moment is largest, which is outward of the wing joint where the pectoralis muscle inserts, as also shown experimentally by Pennycuik (Pennycuik, 1967; Pennycuik, 2008). The breaking point of the isolated primary feather (bottom) is taken to be just distal to its attachment in the wing where the spanwise, postpatagial tendon exerts pressure, holding the feather down on the wing plane (Pennycuik, 2008). The feather shaft curves backwards relative to the longitudinal, major axis through its base, and the front web is usually so narrow that the *C.P.*, which is located near the quarter-chord point, falls behind the shaft in a local chordwise strip across the feather. Therefore, the dynamic air pressure not only bends up the feather through distance d but also twists it in the nose-down sense, rotating it about the local shaft axis within each streamwise strip element, and also rotating it with respect to the major longitudinal axis through the base of the shaft. The aeroelastic bending and twisting behaviour of wings and feathers is essential for their aerodynamic efficiency (Norberg, 1972; Norberg, 1985; Norberg, 1994).

elements are often subjected simultaneously to both bending and twisting (Fig. 3) but we treat each component separately here.

We want to find how dimensional relationships (proportions) might need to change with increasing size for the respective similarity criterion to be fulfilled. To this end, two length scales are distinguished – one longitudinal and one transverse – and we explore

how they must scale to one another in structural support elements, and to muscle transverse length, under each similarity criterion.

Assumptions

As discussed above, there are different determinants of the moment about a joint depending on the kind of locomotion. During cruising locomotion the body weight and locomotion mode determine the required external reaction force, which, multiplied by its moment arm, determines the magnitude of the moment that muscles have to set up. The way the external moment arm scales with body mass therefore affects the scaling of the moment about the joint. By contrast, during maximal locomotor performance the maximal muscle force, multiplied by its moment arm, determines the moment about the joint, and the external reaction force will be as it may, dependent on its moment arm. Then the way the muscle moment arm scales with body mass affects the scaling of the moment about the joint. This distinction is essential in mammals, among which the moment arms of the muscle and of the external reaction force scale differently with body mass (Biewener, 1990) whereas different-sized birds have a constant moment arm ratio (Janson, 1996).

The elastic modulus E is a characteristic of the material, defined as its stress/strain ratio when exposed to a force. The mechanical strength of bone of birds and mammals and the elastic modulus of feather keratin are nearly independent of body size and taxonomy (except that failure stress of the humerus is lower in bats than in birds), so breaking stress and stiffness of the respective material are treated here as constant among different-sized animals of similar kind (Alexander, 1981; Biewener, 1982; Bonser and Purslow, 1995; Kirkpatrick, 1994; Maloij et al., 1979). We make the following additional assumptions: the cross-sectional shape of structural support elements is the same regardless of animal size; the maximal stress in muscles is independent of animal size, so the maximal muscle force is proportional to muscle fibre cross-sectional area (Hill, 1950; Alexander, 1985b; Biewener, 1989); and all deformation occurs within the linear, fully elastic, range of action of the material.

The last assumption needs some comment. During the most strenuous activities animals operate near the safety factor limit of their structural support elements but not near the breaking limit. The safety factors against breakage are 2–4 in mammal leg bones during strenuous activities (Rubin and Lanyon, 1984; Biewener, 1989; Biewener, 1990). Pennycuik examined the strength of the pigeon wing skeleton and estimated safety factors in bending and torsion during hovering (a flight mode so demanding that pigeons can keep it up for a few wing-beats only); he got between 5 and 6 for the humerus and between 4 and 5 for the radio-ulna (Pennycuik, 1967). Based on *in vivo* shear strain recordings in flying pigeons, Biewener and Dial reported a safety factor of 3.5 for the humerus loaded in bending and 1.9 in torsion (Biewener and Dial, 1995). Kirkpatrick estimated a mean safety factor of 2.2 for wing bones from 14 bird and bat species (Kirkpatrick, 1994), and Swartz et al. got safety factors about 3.9 for both bending and shear in megachiropteran wing bones (Swartz et al., 1992). So when structural support elements approach their safety factor limit they are likely to remain in their linear range of elastic response because the loads are only 1/6–1/2 of the breaking load.

Dimensional relationships for axial stress similarity of support elements placed in bending by maximal muscle forces

First, we explore how the transverse and longitudinal length dimensions of support elements must scale to one another, and to

muscle transverse length, in order to maintain equal axial stress in corresponding structural support elements placed in bending under maximal muscle forces. For slender beams, shear stress due to bending is negligible compared with axial stress, so it is ignored here.

The material axial stress σ at a transverse distance y from the neutral surface of a beam is:

$$\sigma = \frac{yM}{I} \quad (3)$$

(Nash, 1977; Alexander, 1983b; Niklas, 1992). M is bending moment, caused by a maximal muscle force, proportional to muscle cross-sectional area, and so to muscle transverse length squared, t_m^2 , acting on its moment arm L_m (Figs 1 and 2). And I is the second moment of area, which is a mathematical property of the geometry (size and shape) of the element's cross-section, obtained by multiplying each cross-sectional element area (like $z\delta y$ in Fig. 4) by the square of its distance from the neutral axis with respect to bending (like y in Fig. 4), and adding over the entire cross-section, so I is proportional to the fourth power of the transverse linear dimension t_s of the support element.

When the spatial relationships of corresponding support elements are similar among different-sized animals, axial stress scales with longitudinal and transverse lengths as:

$$\sigma \propto \frac{t_s t_m^2 l}{t_s^4} \propto \frac{t_m^2 l}{t_s^3} \quad (4)$$

Proportionality 4, and many of those following, look to have unbalanced dimensions on left and right sides but this is because we let area represent force because force is proportional to area in those cases.

From proportionality 4, axial stress due to bending under maximal muscle forces will be the same at the same relative, characteristic, cross-sectional position in corresponding support elements among different-sized animals when:

$$t_s^3 \propto t_m^2 l \quad (5)$$

The moment due to bending under maximal muscle forces increases as $t_m^2 l$ with increasing animal size. In order to maintain the same axial stress in structural support elements, and thus the same safety factor against breakage, their transverse dimension, such as the diameter, must increase as t_s^3 .

For a more intuitive derivation, consider a cross-section at the same relative position in corresponding, structural support elements among different-sized animals. Further consider a narrow cross-sectional element of area, z_1 wide and δy_1 thick, parallel with the neutral axis and located distance y_1 from it (Fig. 4). The cross-section is acted upon by an external, reaction, bending moment $F_{\text{ext}} L_{\text{bend}}$, set up by, and equal to, a moment $F_m L_m$ caused by a maximal muscle force F_m (Fig. 1). When the element area $z_1 \delta y_1$ is the same proportion of the cross-sectional area and is located at the same relative cross-sectional position in different-sized animals, and when the moment caused by all forces acting over the cross-section is in equilibrium with the bending moment, the axial force $f_{\text{axial},1}$, set up on that particular element of area, scales as:

$$f_{\text{axial},1} \propto \frac{F_{\text{ext}} L_{\text{bend}}}{y_1} \propto \frac{t_m^2 l}{t_s} \quad (6)$$

Axial stress in the strip area $z_1 \delta y_1$ therefore scales as:

$$\sigma = \frac{f_{\text{axial},1}}{z_1 \delta y_1} \propto \frac{t_m^2 l}{t_s t_s t_s} \quad (7)$$

which gives the condition for constant axial stress in proportionality 5.

When the lever arm ratio L_m/L is constant, as it is in birds, the length dimension l may refer to the length of the muscle moment arm L_m as well as to L_{bend} or the external moment arm L ; all three of which are linear functions of the longitudinal lengths of support elements in bird wings (Figs 1 and 3). But when the lever arm ratio varies with animal size, as it does in terrestrial mammals, l must instead refer exclusively to the length L_m of the muscle moment arm, given that muscles exert maximum force (Fig. 2).

Geometric similarity requires that $t_s \propto t_m \propto l \propto M_b^{1/3}$, and this fulfils the condition set out in proportionality 5, even though there are other conceivable solutions. In the special case of geometric similarity, maximal muscle forces thus generate identical axial stress at corresponding positions in structural support elements placed in bending, regardless of animal size ($\sigma \propto M_b^0$; from proportionality 7).

When instead the body weight dictates the external reaction force that must be elicited, as during cruising locomotion, the body mass M_b and the external moment arm determine the moment M and proportionalities 4 and 5 change to:

$$\sigma \propto \frac{M_b l}{t_s^3} \quad (8)$$

and

$$t_s^3 \propto M_b l, \quad (9)$$

where l may refer to the moment arm of the muscle as well as of the external force, given that the lever arm ratio L_m/L is constant, as in birds. When the lever arm ratio L_m/L_{bend} varies with animal size, as it does in mammals, l must refer to the length of the external moment arm L_{bend} (Fig. 2). Proportionality 9 specifies the conditions required to give the same stress among different-sized animals under loads proportional to the body mass (rather than to maximal muscle forces as in proportionality 5). In order to satisfy proportionality 9 the scaling relationships between the constituent variables must obviously be different from those required for proportionality 5; and proportionality 9 can be seen not to be compatible with geometric similarity, under which stress would increase as $M_b^{0.33}$ with increasing body mass (from proportionality 8).

If body mass M_b is taken to be proportional to generalised transverse and longitudinal body dimensions as $M_b \propto l t^2$, proportionality 9 gives $t \propto l^2$, which is the necessary condition for axial stress similarity under self-load or under loads proportional to the weight. This is the classic rule for stress similarity under self-load (McMahon, 1975b; McMahon, 1984). When it is applied to different-sized animals, their overall body proportions are taken to be as required for stress similarity, so that body volume, and hence body weight, are proportional to $l t^2$, and so to $l^2 \times l^2 = l^4$, and to $l^{1/2} t^2 = t^{5/2}$ (McMahon, 1975b; McMahon, 1984). Body-weight-dictated loads occur under static, resting conditions and during steady cruising locomotion but not during extreme manoeuvres when maximal muscle forces are exerted and determine the load.

The geometric similarity relationship $t \propto l$, obtained here for stress similarity under maximal muscle forces, thus contrasts with the classic rule for stress similarity under self-load, which requires that $t \propto l^2$ in order to give similar stress in different-sized structures placed in bending under loads proportional to the body weight.

Strain is the change in length, due to a force, divided by the initial length. When the elastic modulus E of support elements is the same among different-sized animals, identical axial stress due to bending gives rise to identical axial elastic strain, because $\text{strain} = \text{stress}/E$. So stress similarity and elastic-strain similarity are two characteristics of the same design principle (Alexander, 2003). This must not be confused with 'elastic similarity' in the sense used by McMahon

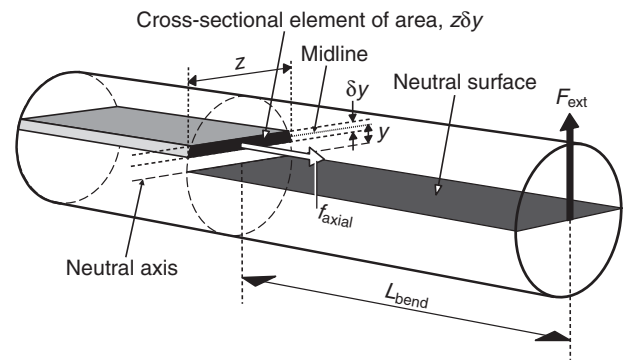


Fig. 4. Geometry of a structural support element, fixed at the left end and similar to that in Fig. 1 but exaggerated in width for clarity. It is placed in bending by an external force F_{ext} , acting on moment arm L_{bend} with respect to the internal cross-section shown, located at the same characteristic lengthwise position in different-sized animals. The neutral axis is the line where the neutral, zero-stress surface cuts the cross-section. The bending moment $F_{\text{ext}} L_{\text{bend}}$ causes the beam material, immediately to the left of the internal cross-section shown, to exert an axial compressive force f_{axial} on a cross-sectional strip element of area, with height δy and width z , located at a transverse distance y above the neutral surface. Bones and feathers are hollow but the beam is drawn solid to avoid undue complexity, and the force vectors are not drawn to the same scale.

(McMahon, 1975a; McMahon, 1984) and McMahon and Kronauer (McMahon and Kronauer, 1976), which is different. It means that different-sized structures bend in a geometrically similar way under their own weight, or under loads proportional to the weight (but not under maximal muscle forces), and requires that their transverse dimension scales with the longitudinal dimension as $t \propto l^{3/2}$ (derived below under 'Dimensional relationships for bent-shape similarity of support elements placed in bending by maximal muscle forces').

Test against empirical data

When testing theory against empirical data, here and elsewhere in the paper, it must be noticed that confidence limits are usually rather wide for scaling functions fitted to empirical data. Because of this uncertainty, small differences between scaling exponents are likely to be within the error limits, and so may not be real.

In order to test whether t_s , t_m and l actually scale to one another in such ways as to satisfy proportionality 5, one would ideally use direct, empirical, scaling relationships between t_s , t_m and l , where l is the functional length of the moment arm, which in terrestrial mammals differs in a size-dependent way from the actual physical length of the respective skeletal element because of progressively more upright leg postures in increasingly large mammals (Biewener, 2005). Unfortunately, such direct scaling data are not available, so we are left to use indirect relationships based on how the respective length dimension scales with body mass.

Proportionality 5 is satisfied when t_s , t_m and l maintain isometry among themselves, i.e. when they vary linearly to one another. But this does not require that they are also isometric with respect to the body mass, only that they scale to body mass with the same exponent. This possibility will now be examined.

Birds

Based on a study of 18 raptor species, Florén (Florén, 2006) showed that humerus length (l in proportionality 5) scales with body mass as $M_b^{0.41}$ ($R^2=0.925$), humerus diameter (t_s in proportionality 5) as $M_b^{0.39}$ ($R^2=0.970$), ulna length as $M_b^{0.41}$ ($R^2=0.901$) and ulna diameter

as $M_b^{0.35}$ ($R^2=0.945$). These exponents are somewhat larger than 0.33 for geometric similarity with respect to body mass but are quite similar, so length and diameter of wing skeletal elements are nearly isometric to one another. There seems to be no scaling data on flight muscle fibre cross-sectional area for birds but the mass of the pectoral muscle (wing depressor) scales as $M_b^{0.99}$ and thus shows perfect isometry with respect to body mass (Rayner, 1988). If muscle shapes are similar among different-sized birds, then flight muscle fibre cross-sectional area (t_m^2 in proportionality 5) would scale to body mass as $M_b^{2/3}$ (and t_m as $M_b^{1/3}$). Tentative muscle data thus indicate that the pectoral muscle cross-sectional diameter (t_m) is isometric with respect to body mass but deviates somewhat from isometry with respect to the length (l) and diameter (t_s) of wing skeletal elements.

Using these data, but $M_b^{0.46}$ for the muscle moment arm L_m (Janson, 1996), stress in the bird humerus, placed in bending by maximal muscle forces, would scale as $M_b^{0.67}M_b^{0.46}/M_b^{0.39 \times 3} = M_b^{0.04}$ (from proportionality 4) and humerus safety factor as $M_b^{0.04}$, whereas stress in the bird ulna would scale as $M_b^{0.67}M_b^{0.46}/M_b^{0.35 \times 3} = M_b^{0.08}$ and its safety factor as $M_b^{-0.08}$. Conversely, given the observed scaling of bone diameter and muscle moment arm, muscle cross-sectional diameter (t_m) would need to scale as $M_b^{(0.39 \times 3 - 0.46)/2} = M_b^{0.36}$, rather than as $M_b^{0.33}$ (tentatively deduced above), in order to satisfy proportionality 5 and give stress similarity in the humerus, whereas muscle cross-sectional diameter would need to scale as $M_b^{(0.35 \times 3 - 0.46)/2} = M_b^{0.30}$ for stress similarity in the ulna. So dimensions of the wing musculo-skeletal system in this bird sample conform fairly well with the requirements set out in proportionality 5 for stress similarity under maximal muscle forces.

Under body-weight-dictated loads (cruising flight) the body weight and the moment arm L in Fig. 1 determine the moment that muscles must set up. The moment arm L of the wing's resultant aerodynamic force scales as $M_b^{0.40}$ (Janson, 1996), so humerus stress would scale as $M_bM_b^{0.40}/M_b^{0.39 \times 3} = M_b^{0.23}$ (from proportionality 8) and safety factor as $M_b^{-0.23}$, whereas ulna stress would scale as $M_bM_b^{0.40}/M_b^{0.35 \times 3} = M_b^{0.35}$ and safety factor as $M_b^{-0.35}$. In order to achieve equal stress in the humerus under body loads in different-sized birds, humerus diameter would need to scale as $M_b^{1.40/3} = M_b^{0.47}$ (from proportionality 9) rather than as $M_b^{0.39}$ (observed; see above) but then humerus stress under maximal muscle forces would scale as $M_b^{0.67+0.46}/M_b^{0.47 \times 3} = M_b^{-0.28}$ (from proportionality 4). So skeletal stress is much more similar among different-sized birds under maximal muscle forces ($M_b^{-0.04}$ and $M_b^{0.08}$ for humerus and ulna) than under body-weight-dictated loads ($M_b^{0.23}$ and $M_b^{0.35}$). This suggests that adaptation of the wings' musculo-skeletal system has occurred with respect to maximal muscle forces rather than to body-weight-dictated loads. The skeletal data are from raptors, which have a high frequency of occurrence of maximal performance events for prey capture. They may therefore be expected to be especially adapted to withstand large aerodynamic loads.

Worcester measured wing primary feathers from 13 bird species of mixed taxonomy and found that feather length scales with body mass as $M_b^{0.30}$ and feather shaft diameter as $M_b^{0.37}$ (Worcester, 1996). With these data, axial stress in the feather shaft due to bending would scale as $M_b^{0.67+0.30}/M_b^{0.37 \times 3} = M_b^{-0.14}$ under maximal muscle forces (from proportionality 4), and as $M_b^{1+0.30}/M_b^{0.37 \times 3} = M_b^{0.19}$ under loads proportional to the body weight (from proportionality 8). So stress tends to be more similar under maximal muscle forces than under body loads also in primary feather shafts among different-sized birds, even though such small differences in absolute value between scaling exponents, based on empirical data, here and elsewhere, may be fortuitous because of the wide confidence limits of empirical scaling exponents.

Terrestrial mammals

During maximal locomotor performance the maximal muscle force and its moment arm dictate the moment about the joint. Muscle fibre cross-sectional diameter t_m scales as $M_b^{0.40}$ (from $M_b^{0.81}$ for t_m^2) [table 2-1 in Alexander (Alexander, 1985a)], muscle moment arm scales as $M_b^{0.44}$ (Biewener, 2005), and long bone diameter t_s scales as $M_b^{0.36}$ (Alexander et al., 1979). These scaling exponents differ somewhat from 0.33, required for geometric similarity with respect to body mass, but they are fairly similar, so t_s , t_m and l are not far from being isometric to one another, as would be required for the geometric-similarity solution of proportionality 5. Given the observed relationships (see above), bone stress due to bending under maximal muscle forces would nonetheless increase with increasing body size and scale as $M_b^{0.81}M_b^{0.44}/M_b^{0.36 \times 3} \propto M_b^{0.17}$ (from proportionality 4).

Under body-weight-dictated loads the body weight and the moment arm of the ground reaction force dictate the moment. The moment arm of the ground reaction force scales as $M_b^{0.19}$ and thus departs considerably from the observed scaling exponents 0.40 and 0.36 for cross-sectional diameter of muscle and bone (see above). Bone stress would then scale as $M_bM_b^{0.19}/M_b^{0.36 \times 3} \propto M_b^{0.11}$ (from proportionality 8). Alexander (Alexander, 2003) got bone stress $\propto M_b^{0.10}$ because he used $EMA = L_m/L_{bend} \propto M_b^{0.26}$ from Biewener (Biewener, 1989) whereas we use $\propto M_b^{0.25}$ from Biewener (Biewener, 2005), and this causes the moment arm of the ground reaction force to scale as $M_b^{0.19}$ here instead of as $M_b^{0.18}$. So even though the moment arm of the muscle force scales more nearly as expected under isometry (as $M_b^{0.44}$ vs $M_b^{0.33}$) than does the moment arm of the ground reaction force (as $M_b^{0.19}$ vs $M_b^{0.33}$), bone axial stress due to bending increases somewhat faster with increasing body mass under maximal muscle forces (as $M_b^{0.17}$) than under body-weight-dictated loads (as $M_b^{0.11}$). In order to achieve equal bone stress among different-sized mammals under body loads, bone diameter would need to scale as $M_b^{(1+0.19)/3} = M_b^{0.40}$ (from proportionality 9), rather than as $M_b^{0.36}$ (observed; see above), and then stress under maximal muscle forces would scale as $M_b^{0.81+0.44}/M_b^{0.40 \times 3} = M_b^{0.05}$ (from proportionality 4).

Geometric similarity would generate perfect bone stress similarity – stress $\propto M_b^0$ (from proportionality 4) – under maximal muscle forces whereas stress would scale as $M_b^{0.33}$ under body-weight-dictated loads (from proportionality 8). Because of the ways, in which moment arm lengths ($\propto M_b^{0.19}$ and $M_b^{0.44}$) and muscle fibre cross-sectional area ($\propto M_b^{0.81}$) deviate from isometry in terrestrial mammals, the scaling exponents for bone stress ($\propto M_b^{0.17}$ and $M_b^{0.11}$) become remarkably similar regardless of whether the bending moment is determined by maximal muscle forces, or by the body weight – and their respective moment arms. Both exponents are intermediate between those that would be caused by maximal muscle forces (M_b^0), and by body-weight-dictated loads ($M_b^{0.33}$), respectively, under perfect geometric similarity. So bone stress due to maximal muscle forces increases moderately fast with increasing body size, rather than remaining constant as it would under geometric similarity; $\propto M_b^{0.17}$ vs M_b^0 (from proportionality 4). However, bone stress due to body-weight-dictated loads increases much more slowly with increasing body size than it would under geometric similarity; $\propto M_b^{0.11}$ vs $M_b^{0.33}$ (from proportionality 8). The similar rates of increase in bone stress, caused by maximal muscle forces and by the body weight, respectively ($\propto M_b^{0.17}$ and $M_b^{0.11}$), mean that safety factors for both kinds of load decrease in parallel, at similar moderate rates ($\propto M_b^{-0.17}$ and $M_b^{-0.11}$), as body size increases. The ratio between the safety factors for each of the two kinds of load scales as $M_b^{0.06}$ and is thus nearly the same in different-

sized mammals. But bone stress due to maximal muscle forces is always larger, so animals operate with lower safety factors during maximal locomotor events than during cruising locomotion. The former mode might therefore be expected to have a larger impact on the selection of dimensions of the musculo-skeletal system. But among animals in general, cruising locomotion occurs much more frequently. For that reason, and because of the risk for material fatigue that the high incidence of cruising locomotion may incur, cruising locomotion may select for larger safety factors against breakage than do maximal performance events. This might help to explain why the mammalian musculo-skeletal dimensions change (scale) with animal size in such a way as to make bone stress increase in parallel, at about the same moderate rates, with increasing body weight for both kinds of load.

Based on strain gauge measurements, Rubin and Lanyon reported that peak axial force (not stress) in the tibia during high-speed running of five vertebrates, in sizes from turkey to elephant, scales as $M_b^{0.69}$ (Rubin and Lanyon, 1984). This is close to the empirical scaling $M_b^{0.72}$ for bone cross-sectional area in mammals [from $M_b^{0.36}$ for bone diameter in Alexander et al. (Alexander et al., 1979)], so bone axial stress would scale as $M_b^{0.69}/M_b^{0.72} \propto M_b^{-0.03}$. Bone stress would thus be similar during vigorous locomotion in different-sized species in this mixed sample of birds and mammals, entailing similar safety factors against breakage because the breaking stress of bone is nearly independent of animal size and taxonomy (Alexander, 1981; Biewener, 1982; Bonser and Purslow, 1995; Kirkpatrick, 1994; Maloiy et al., 1979).

A similar approach

Kokshenev (Kokshenev, 2003) and Kokshenev et al. (Kokshenev et al., 2003) reconsidered McMahon's elastic similarity scaling principle. Originally, McMahon (McMahon, 1975a; McMahon, 1975b) showed that the transverse and longitudinal dimensions of different-sized structures under self-load must scale to one another as $t \propto l^{3/2}$, and to the structure's mass as $t \propto M_b^{3/8}$ and $l \propto M_b^{1/4}$, in order for the structure to be elastically stable and resist buckling under the force of gravity. This is fine for structures like trees and other plants, as well as for their branches and twigs, when the dominant forces acting on them are due to gravity (McMahon and Kronauer, 1976; Norberg, 1988a; Norberg, 1988b). But Kokshenev (Kokshenev, 2003) argued, like we do in this paper, that skeletal elements of terrestrial mammals are adapted to maximal muscle forces during maximal effort locomotion, not to forces proportional to the gravitational force on the body (its weight), as during cruising locomotion, which has usually been assumed.

Kokshenev therefore modified McMahon's elastic similarity principle in two respects (Kokshenev, 2003). First, he derived the scaling required for structural support members to maintain elastic stability against buckling under near-axial compressive forces caused by maximal muscle forces. Because structural failure of animal skeletal elements is much more likely to occur under bending forces than under near-axial compressive forces, we do not consider this scaling rule any further here.

His second derivation concerns the scaling required to maintain equal safety factors against breakage of support elements placed in bending under maximal muscle forces, which is the loading mode most likely to cause animal support structures to break. So muscle-induced bending loads probably drive evolutionary adaptation of the geometry of muscles and skeletal elements, as we emphasise here. We will therefore review this scaling rule of Kokshenev, and show that it accords with the stress-similarity rule that we have given in proportionality 5.

Kokshenev (Kokshenev, 2003) did not show how bone and muscle dimensions must scale directly to one another, as we do (proportionality 5), but he did so indirectly by referring to their scaling relationships with respect to the body mass. Kokshenev (Kokshenev, 2003) and Kokshenev et al. (Kokshenev et al., 2003) presented the scaling principle, which gives stress similarity under bending by maximal muscle forces, as $3d-l=a$. Here d , l and a are scaling exponents in power functions relating bone diameter, bone length and muscle cross-sectional area to the body mass M_b . Working backwards, we therefore get $M_b^{3d}/M_b^l \propto M_b^a$ or $M_b^{3d} \propto M_b^a M_b^l$. If we refer instead directly to bone transverse length, bone longitudinal length and muscle transverse length – not to muscle cross-sectional area – and shift to the notation that we use, this scaling rule can be rewritten as $t_s^3 \propto t_m^2 l$, where the l here refers directly to bone longitudinal length, not to the exponent relating bone length to body mass as in Kokshenev's notation. The relationships between bone and muscle transverse lengths (t_s , t_m) and bone longitudinal length (l), implicit in Kokshenev's scaling rule for similar stress in corresponding support elements among different-sized animals, are thus identical to those given in our proportionality 5.

Dimensional relationships for shear stress similarity of support elements placed in torsion by maximal muscle forces

There is no information available, neither for birds nor for mammals, about how the ratio between the twisting moment arms of the muscle, and of the external reaction force, may vary with body size. If the twisting lever arm ratio is constant, the external twisting force F_{ext} is proportional to the muscle force F_m . The following scaling is based on that. Therefore, l may refer to either moment arm regardless of whether maximal muscle forces or the body weight determines the load. If, instead, the twisting lever arm ratio varies with animal size, l must refer to the length of the moment arm that determines the twisting moment.

When a shaft-like structural support element with a roughly circular cross-section is placed in torsion, the material shear stress τ at a distance r from the central axis of the shaft is:

$$\tau = \frac{rT}{J}, \quad (10)$$

where T is the twisting moment, and J is the polar second moment of area, a mathematical property of the geometry (size and shape) of the cross-section, obtained by multiplying each ring-shaped, concentric, cross-sectional element of area (like $2\pi r dr$ in Fig. 5) by the square of its distance from the central axis (like r in Fig. 5) and adding over the entire cross-section, so J is proportional to the fourth power of the transverse linear dimension (Nash, 1977).

The following treatment is analogous to the foregoing one for stress similarity in bending under maximal muscle forces and leads up to the same proportionalities 5 and 9. When the twisting moment is caused by a maximal muscle force it is proportional to muscle cross-sectional area multiplied by the force moment arm, L_{twist} , which is a linear function of the longitudinal lengths of structural support elements (Figs 3 and 5). When the spatial relationships of corresponding support elements are similar among different-sized animals, shear stress scales as:

$$\tau \propto \frac{t_s t_m^2 l}{t_s^4} \propto \frac{t_m^2 l}{t_s^3}. \quad (11)$$

Therefore, shear stress due to torsion will be the same at corresponding cross-sectional positions among different-sized

animals, entailing similar safety factors against breakage due to shear, when:

$$t_s^3 \propto t_m^2 l, \quad (12)$$

which is as for axial stress in proportionality 5. The twisting moment due to maximal muscle forces increases as $t_m^2 l$ with increasing animal size. In order to maintain the same shear stress in structural support elements, and thus the same safety factor against breakage, their transverse dimension, such as the diameter, must increase as t_s^3 .

For a more intuitive derivation, consider a cross-section at the same relative position in corresponding structural support elements among different-sized animals. Further consider a thin, cross-sectional ring of area $2\pi r_1 \delta r_1$ at radial distance r_1 from the geometric axis (Fig. 5). An external force F_{ext} , arising in reaction to a maximal muscle force, acts on a twist moment arm L_{twist} with respect to the geometric axis. When the ring-element area $2\pi r_1 \delta r_1$ is the same proportion of the cross-section and is located at the same relative cross-sectional position r_1 in different-sized animals, and when the reaction twisting moment, caused by all forces acting over the cross-section, is in equilibrium with the external twisting moment, the tangential, torsional shear force $f_{\text{shear},1}$ set up on that particular element area scales as:

$$f_{\text{shear},1} \propto \frac{F_{\text{ext}} L_{\text{twist}}}{r_1} \propto \frac{t_m^2 l}{t_s}. \quad (13)$$

Torsional shear stress in the characteristic cross-sectional ring-element area $2\pi r_1 \delta r_1$ therefore scales as:

$$\tau = \frac{f_{\text{shear},1}}{2\pi r_1 \delta r_1} \propto \frac{t_m^2 l}{t_s t_s t_s}, \quad (14)$$

which gives the condition set out in proportionalities 5 and 12.

Geometric similarity requires that $t_s \propto t_m \propto l \propto M_b^{1/3}$, and this fulfils the conditions in proportionalities 5 and 12, even though there are other conceivable solutions. In the special case when geometric similarity prevails, maximal muscle forces thus generate identical shear stress at corresponding positions in structural support elements subjected to twisting, regardless of animal size ($\tau \propto M_b^0$; from proportionality 14).

When instead the body weight dictates the external reaction force that must be elicited, as during cruising locomotion, the body mass M_b determines the twisting moment T , and proportionalities 14 and 12 change to:

$$\tau \propto \frac{M_b l}{t_s^3} \quad (15)$$

and:

$$t_s^3 \propto M_b l, \quad (16)$$

where proportionality 15 is analogous to proportionality 8, and proportionality 16 is as for axial stress similarity (proportionality 9). Proportionality 16 gives the conditions under which shear stress would be the same in different-sized animals under loads proportional to the body weight. In order to satisfy proportionality 16, the scaling relationships between the constituent variables must obviously be different from those required in proportionality 12; and proportionality 16 is not compatible with geometric similarity, under which shear stress would increase as $M_b^{0.33}$ with increasing body mass (from proportionality 15).

Taking body mass M_b to be proportional to generalised transverse and longitudinal body dimensions as $M_b \propto t^2 l$, proportionality 16 gives $t \propto l^2$, which is the condition for shear stress similarity in torsion under self-load, and the same as for

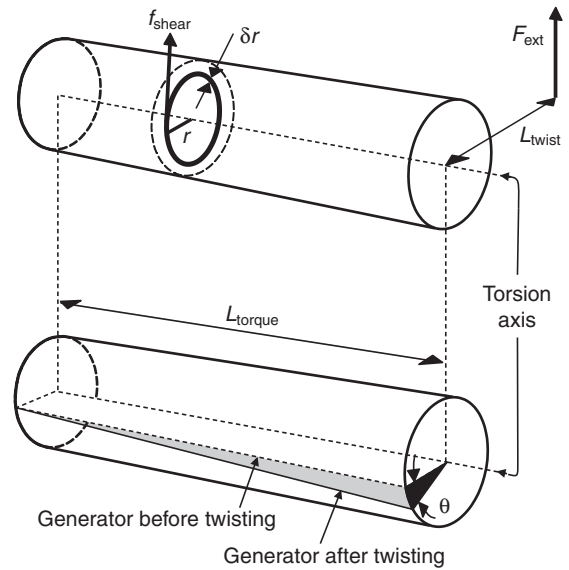


Fig. 5. Geometry of a structural support element with a circular cross-section placed in torsion by an external force F_{ext} that is applied at an axial distance L_{torque} from the fixed end to the left, and at a transverse distance L_{twist} off the central axis of the shaft. The twisting moment $F_{\text{ext}} L_{\text{twist}}$ causes the shaft material, immediately to the left of the internal cross-section shown, to exert a tangential, torsional shear force f_{shear} on a cross-sectional, ring-shaped element of area, with radial thickness δr , located at a radial (transverse) distance r from the central axis. The force vectors are not drawn to the same scale. The lower figure shows the angle θ through which the distal end of the shaft twists relative to the fixed end to the left when subjected to a torque.

axial stress similarity in bending under self-load. This contrasts with the relationship $t \propto l$ obtained here for shear stress similarity in torsion, due to maximal muscle forces, for the special case when geometric similarity prevails.

Dimensional relationships for bent-shape similarity of support elements placed in bending by maximal muscle forces

Fluid-elastic distortion of lifting and propulsive surfaces, like fins, wings and feathers, influences their function, as reviewed under a separate heading below. Flight feathers of birds, in particular the primaries that form the hand-wing, do bend and twist considerably during flight. The following scaling for similarity in bent shape (this section) and twisted shape (next section) is done with bird flight feathers in mind. The ratio between the bending moment arms of the pectoral muscle and of the wing's resultant aerodynamic force is constant among different-sized birds (Janson, 1996), so therefore any position-characteristic aerodynamic force is directly proportional to the muscle force – a condition we use in the following scaling.

When a slender beam is placed in bending, and given that the bending moment arm is at least 20 times longer than the beam diameter and 10 times the deflection distance, then, from beam theory, a bending force F_{ext} , acting on moment arm L_{bend} , causes the beam to deflect through distance d , as:

$$d = \frac{F_{\text{ext}} L_{\text{bend}}^3}{3EI}, \quad (17)$$

where E is the modulus of elasticity, I is the second moment of area of the cross-section of the beam and EI is its flexural stiffness (Figs 1 and 3) (e.g. Wainwright et al., 1976; Nash, 1977; Alexander, 1983b; Niklas, 1992).

The moment arm L_{bend} is a linear function of longitudinal lengths of structural support elements (Figs 1 and 3). When F_{ext} is set up in reaction to a maximal muscle force, the deflection distance d scales as:

$$d \propto \frac{t_m^2 l^3}{t_s^4}. \quad (18)$$

If corresponding support elements of different sizes bend to similar shapes, the ratio between the deflection distance d and the length of the bending moment arm L_{bend} is constant. From Eqn 17 and proportionality 18 relative bending, or bent shape, scales as:

$$\frac{d}{L_{\text{bend}}} = \frac{F_{\text{ext}} L_{\text{bend}}^3}{L_{\text{bend}} 3EI} \propto \frac{t_m^2 l^2}{t_s^4}, \quad (19)$$

so equal bent shape under maximal muscle forces requires that:

$$t_s^4 \propto t_m^2 l^2. \quad (20)$$

Geometric similarity requires that $t_s \propto t_m \propto l \propto M_b^{1/3}$, and this fulfils the condition set out in proportionality 20, even though there are other conceivable solutions. In the special case when geometric similarity prevails among different-sized animals, corresponding support elements placed in bending by moments, caused by maximal muscle forces, thus take the same bent shape regardless of animal size ($d/L_{\text{bend}} \propto M_b^0$; from proportionality 19).

If instead the body weight dictates the external reaction force, proportionalities 19 and 20 change to:

$$\frac{d}{L_{\text{bend}}} \propto \frac{M_b l^2}{t_s^4}, \quad (21)$$

and:

$$t_s^4 \propto M_b l^2. \quad (22)$$

Proportionality 22 gives the conditions under which different-sized feathers would bend to the same shape under loads proportional to the body weight. It is not compatible with geometric similarity, which would cause feather relative bending d/L_{bend} to increase as $M_b^{0.33}$ with increasing body mass (from proportionality 21).

If body mass M_b is taken to be proportional to generalised transverse and longitudinal body dimensions as $t_s^2 l$, proportionality 22 gives $t \propto l^{3/2}$, which is the necessary condition for similar bent shapes of different-sized structures, like cantilever beams, placed in bending under their own weight or under loads proportional to the weight. This is the classic rule of elastic similarity under self-load (McMahon, 1975b; McMahon, 1984; McMahon and Kronauer, 1976). When it is applied to different-sized animals, their overall body proportions are taken to be as required for elastic similarity, so that body volume, and hence body weight, are proportional to $l \times t^2$, and so to $(l \times l^{3/2 \times 2}) t^4$ and to $(t^{2/3} \times t^2) t^{8/3}$ (McMahon, 1975b; McMahon, 1984; McMahon and Kronauer, 1976). Body-weight-dictated loads occur under static, resting conditions and during steady cruising locomotion.

The geometric similarity relationship $t \propto l$, obtained here for bent-shape similarity under maximal muscle forces, thus contrasts with the classic rule of elastic similarity under self-load, which requires that $t \propto l^{3/2}$ in order to give similar bent shapes among different-sized structures placed in bending under loads proportional to the weight (McMahon, 1975b). Empirical data can be tested against proportionalities 19–22 to find out which kind of load that causes the most similar bent shapes among different-sized animals. This may indicate whether bending stiffness is adapted more nearly to loads determined by maximal muscle forces or by the body weight.

Worcester measured wing primary feathers from 13 bird species of mixed taxonomy and found that feather length scales with body mass as $M_b^{0.30}$ and feather shaft diameter as $M_b^{0.37}$ (Worcester, 1996). With these data, feather relative bending due to maximal muscle forces would decrease with increasing body weight as $M_b^{-0.21}$ ($M_b^{0.67+0.30 \times 2 - 0.37 \times 4}$, from proportionality 19) but increase as $M_b^{0.12}$ under loads proportional to the body weight ($M_b^{1.00+0.30 \times 2 - 0.37 \times 4}$, from proportionality 21). Wing primary feathers would thus bend to more similar shapes among different-sized birds under loads proportional to the body weight than under maximal muscle forces.

Dimensional relationships for twisted-shape similarity of support elements placed in torsion by maximal muscle forces

There is no information about how the ratio between the twisting moment arms of the pectoral muscle and of the wing's resultant aerodynamic force may vary with bird size (Figs 3 and 5). In the lack of such data, and because the ratio between the bending moment arms is nearly constant among different-sized birds (Janson, 1996), the ratio between the twisting moment arms is treated as constant here.

In a shaft-like support element that is subjected to a constant twisting moment T along a length L_{torque} , the angle θ through which one end of the shaft twists relative to the other is:

$$\theta = \frac{TL_{\text{torque}}}{GJ} \quad (23)$$

(Fig. 5) (Nash, 1977). When F_{ext} is caused by a maximal muscle force, T is proportional to muscle cross-sectional area, and so to muscle transverse length squared multiplied by the twisting moment arm L_{twist} , which is a linear function of the longitudinal lengths of structural support elements (Figs 3 and 5). The polar second moment of area, J , is proportional to the fourth power of the transverse length, and the shear modulus of elasticity, G , is shear stress over shear strain, here taken to be the same among different-sized animals. When the spatial relationships of corresponding support elements are similar among different-sized animals, the angle of twist scales as:

$$\theta \propto \frac{t_m^2 l l}{t_s^4}. \quad (24)$$

Therefore, the angle of twist is identical in corresponding structural support elements in different-sized animals when:

$$t_s^4 \propto t_m^2 l^2, \quad (25)$$

which is as for bent-shape similarity in proportionality 20.

In the special case when geometric similarity prevails among different-sized animals, corresponding support elements placed in torsion by maximal muscle forces thus take the same twisted shape ($\theta \propto M_b^0$; from proportionality 24).

If instead the body weight dictates the external reaction force, proportionalities 24 and 25 change to:

$$\theta \propto \frac{M_b l^2}{t_s^4}, \quad (26)$$

and:

$$t_s^4 \propto M_b l^2 \quad (27)$$

which is identical to proportionality 22.

Proportionality 27 shows the requirements for equal twisted shape under loads proportional to the body weight and is as for bent-shape similarity. This function is not compatible with geometric similarity, which would cause twist angle to increase as $M_b^{0.33}$ (from proportionality 26).

Effects of fluid-induced distortion of lifting and propulsive surfaces

Similarity in bent shape, or in twisted shape, may not be important with most skeletal elements because they deform rather little. The tibiofibula in the frog hindlimb bends only 2–3 deg in jumping, which is among the largest leg bone deformations reported hitherto (Calow and Alexander, 1973). Optimum stiffness for leg bones was modelled by Alexander et al. (Alexander et al., 1990), based on the premise that thin bones bend more so their muscles must shorten more and therefore need longer fibres and so must be heavier. Their optimisation criterion for bone thickness was minimisation of the combined mass of bone plus muscle. Here we take a different perspective and consider functional effects of fluid-induced changes in the shapes of lifting and propulsive surfaces.

The skin membrane of the bat hand-wing is supported, spread and tightened by very thin finger bones. The outer phalanges of the third digit, which alone form the distal part of the wing's leading edge, bend and twist especially much under the pull from the flight membrane [figs 6–10 in Norberg (Norberg, 1976) and figs 9.3a–e and fig. 11.15 in Norberg (Norberg, 1990)]. An effect of this flexibility is that transient forces from the wing membrane are smoothed out, reducing the risk of digit breakage and membrane rupture. In addition, because the distal part of the third digit bends strongly backwards, and also bends dorso-ventrally and twists, the wingtip pitches down in the down-stroke, up in the up-stroke, matching its angle of attack (below stall angle) to the steep incidence of the airflow due to the wing's flapping velocity. This is similar, in effect, to the nose-down twisting of the separated outer parts of the anterior-most primary feathers in bird wings in down-stroke (Fig. 3) (Norberg, 1985).

Fish fin rays deflect and bend under hydrodynamic loads, and the resulting fin deformation strongly improves propulsion efficiency (Zhu and Shoole, 2008). The aero-elastic bending and twisting behaviour of flight feathers in bird wings (Fig. 3) and tails give profound aerodynamic benefits (Norberg, 1985; Norberg, 1994). Insect wings are stiffened by veins, which act like spars. They bend and twist under aerodynamic and inertial loads in flight, and the resulting wing distortions enhance aerodynamic efficiency (Norberg, 1972; Ishihara et al., 2009; Miller and Peskin, 2009; Mountcastle and Daniel, 2009; Young et al., 2009).

Load-induced distortion of flexible, lifting and propulsive surfaces alters their hydrodynamic or aerodynamic characteristics, often to the effect that locomotor performance is improved, as reviewed above. Therefore, there must be strong selection on their fluid-elastic properties, which determine their behaviour in interaction with water or air. Some shapes obviously improve function more than others, so distorted shape may be expected to be similar among different-sized animals. Judging by photographs and films, the bending and twisting of fish fins, bird flight feathers and insect wings seem to be roughly similar in different-sized animals within each category.

Conclusion

The rationale for doing scaling analyses of locomotor organs is this. Relationships between linear dimensions, areas and volumes are prone to change with increasing body size, for pure geometrical reasons. Such scale effects influence function. If there is a fit between empirical data and a particular scaling relationship between different dimensions, as predicted from mechanical principles to enable similar functions in different-sized animals, then some insight has been gained about what functional demands and constraints that govern selection. Scaling analysis is therefore a powerful method for detecting what functions that drive the evolution of structure and form.

Geometric similarity has hitherto been mainly a descriptive term, denoting similar form among different-sized animals, but with no functional connotation. Here we have explored possible functional relationships with locomotion. We distinguished between the transverse t_s and longitudinal l length dimensions of structural support elements and scaled them to one another and to the muscle cross-sectional, transverse, length dimension t_m as required by each of four similarity principles. And this led to the identification of geometric similarity as a scaling principle that gives: (1) constant axial stress, (2) constant torsional shear stress, as well as (3) constant bent shape, and (4) constant twisted shape of corresponding structural support elements placed in bending, or in torsion, respectively, under maximal muscle forces. These functional attributes may therefore help to explain the prevalence of geometric similarity among animals.

The point that maximal muscle forces give rise to stress similarity among geometrically similar animals of different sizes is apparent from the following very simple argument. In geometrically similar systems of different size, the ratio of the stresses in two components – in this case a muscle and a bone – will be independent of size. If the maximum stress the muscle can exert is the same for all sizes of animal, the resulting bone stress will also be the same for all sizes. No other scaling rule, pertaining to muscles and bones alike, would have this effect, as is obvious from the conditions for stress similarity set out in proportionalities 5 and 12.

The dimensional requirements for stress similarity in bending and in torsion are identical (proportionalities 5 and 12) and those for distorted-shape similarity in bending and in torsion are also identical to each other (proportionalities 20 and 25), leaving two different similarity functions. Geometric similarity is compatible with both but there are other conceivable scaling relationships between t_s , t_m and l that would satisfy one or the other of proportionalities 5 (= proportionality 12) and 20 (= proportionality 25). Geometric similarity is the only principle, however, that muscles and bones can share in order to satisfy both functions. To see this, let $t_s \propto l^a$ and $t_m \propto l^b$, and insert this in proportionalities 5 (= proportionality 12) and 20 (= proportionality 25):

$$l^{3a} \propto l^{2b}l \quad (28)$$

$$l^{4a} \propto l^{2b}l^2 \quad (29)$$

From proportionality 28 we get $3a=2b+1$ and proportionality 29 gives $4a=2b+2$. Solving for a , and equating the results, we get $(2b+1)/3=(2b+2)/4$, which gives $b=1$. When inserted in proportionality 28 or proportionality 29 it gives $a=1$. So the geometric similarity relationship $t_s \propto t_m \propto l$ satisfies proportionality 5 (= proportionality 12) as well as proportionality 20 (= proportionality 25), and no other scaling rule would have this dual effect. Therefore, when geometric similarity prevails, bending (or twisting) of a structural support element by maximal muscle forces causes the same axial stress (or torsional shear stress) and the same bent shape (or twisted shape) in different-sized animals.

Whether safety factors against breakage, and optimal extents of distortion, of structural support elements evolve more nearly with respect to loads dictated by the body weight (during cruising locomotion), or by maximal muscle forces (during maximal performance events), will depend on the natural frequency of occurrence of the respective load. And this, in turn, dictates the size scaling function, such that stress in support elements, and their distorted shape, remain more similar among different-sized animals under one or the other of the two kinds of load.

In geometrically similar animals of different sizes, loads dictated by the body weight would cause bone stress to increase as $M_b^{0.33}$ (from

proportionality 8) whereas maximal muscle forces would generate perfect bone stress similarity, $\propto M_b^0$ (from proportionality 4). Stress generated by maximal muscle forces is always larger, so the ratio between bone stresses generated by maximal muscle forces and by the body weight decreases as $M_b^{0.33}$ with increasing body size.

Dimensions of the musculo-skeletal system of bird wings are fairly close to isometric. Based on available data, stress in the bird humerus, placed in bending under body-weight-dictated loads (cruising flight), would scale as $M_b^{0.23}$ (from proportionality 8), and safety factors as $M_b^{0.23}$, whereas stress due to bending under maximal muscle forces would scale as $M_b^{0.04}$ (from proportionality 4), and safety factors as $M_b^{0.04}$, which is close to predictions for geometric similarity and maximal muscle forces (M_b^0). So skeletal stress is much more similar among different-sized birds under maximal muscle forces than under body-weight-dictated loads. This suggests that adaptation of the wing musculo-skeletal system in birds has evolved with respect to maximal muscle forces rather than to body-weight-dictated loads. The skeletal data above are from raptors, which have a high frequency of occurrence of maximal performance events for prey capture, so they may be especially adapted to withstand large aerodynamic loads.

Based on available data for bird primary wing feathers, axial stress in the feather shaft due to bending would scale as $M_b^{0.19}$ under loads proportional to the body weight (from proportionality 8), and as $M_b^{0.14}$ under maximal muscle forces (from proportionality 4). So stress tends to be more similar under maximal muscle forces than under body loads also in primary feather shafts among different-sized birds, even though such small differences in absolute value between scaling exponents, based on empirical data, here and elsewhere, may be fortuitous because of the wide confidence limits of empirical scaling exponents.

In terrestrial mammals, skeletal dimensions are geometrically similar except among very large species. But leg muscles and moment arms depart from geometric similarity. Leg muscle fiber cross-sectional area scales as $M_b^{0.81}$, rather than as $M_b^{0.67}$ under isometry [table 2-1 in Alexander (Alexander, 1985a)]. And because of increasingly more upright leg postures in larger mammals, the moment arm of the muscle force scales as $M_b^{0.44}$ and the moment arm of the ground reaction force scales as $M_b^{0.19}$, rather than as $M_b^{0.33}$ for both under isometry (Biewener, 2005). An intriguing result of this departure from geometric similarity is that the scaling exponents for bone stress become remarkably similar regardless of whether the bending moment is determined by maximal muscle forces (stress $\propto M_b^{0.17}$), or by the body weight (stress $\propto M_b^{0.11}$) – and their respective moment arms. Both exponents are intermediate between those that would be caused by maximal muscle forces (stress $\propto M_b^0$) and by body-weight-dictated loads (stress $\propto M_b^{0.33}$) under perfect geometric similarity. So bone stress due to maximal muscle forces increases moderately fast with increasing body size, rather than remaining constant as it would under geometric similarity [as $M_b^{0.17}$ vs M_b^0 (from proportionality 4)]. However, bone stress due to body-weight-dictated loads increases much more slowly with increasing body size than it would under geometric similarity [as $M_b^{0.11}$ vs $M_b^{0.33}$ (from proportionality 8)].

The dimensions of the musculo-skeletal system in terrestrial mammals thus change (scale) with animal size in such a way as to cause a compromise that minimises departure from stress similarity for both kinds of load. The ratio between bone stresses caused by maximal muscle forces, and by the body weight, respectively, scales as $M_b^{0.17}/M_b^{0.11}=M_b^{0.06}$, and is thus almost identical among mammals of different sizes. The safety factor ratio varies in inverse proportion to stress and scales as $M_b^{-0.06}$. If selection favours a certain ratio between safety factors with respect to, respectively, maximal muscle

forces and body-weight-dependent loads, this could explain the similar scaling of stress – due to each of the two kinds of load – across different-sized mammals. Even though maximal muscle forces cause larger bone stress for any given body size, body-weight-dependent loads are much commoner, so this, together with the associated higher risk of bone-material fatigue that they may incur, might select for larger safety factors for body-weight-dependent loads. This might help to explain why the mammalian musculo-skeletal dimensions change (scale) with animal size in such a way as to make bone stress increase in parallel, at about the same moderate rates (as $M_b^{0.17}$ and $M_b^{0.11}$), with increasing body weight for both kinds of load.

Based on available data on bird feather dimensions, shaft relative bending would scale as $M_b^{0.21}$ under maximal muscle forces (from proportionality 19), and as $M_b^{0.12}$ under loads proportional to the body weight (from proportionality 21). Wing primary feathers would thus bend to somewhat more similar shapes among different-sized birds when loads are proportional to the body weight than when caused by maximal muscle forces but the latter load causes more bending for any given body size.

Selection acts to maximise individual fitness. This may occur indirectly *via* selection for optimisation of morphology and function. Adherence of different-sized animals to some particular scaling rule has not been directly selected for as such, of course, but may have arisen from adaptation in morphological proportions, occurring independently in each separate species-lineage. Conformance of different-sized species with the geometric similarity principle may thus have arisen as a by-product of selection for adequate and similar, size-independent, safety factors against breakage, and similar optimal, size-independent, distorted shapes of structural support elements placed in bending, or in torsion, by maximal muscle forces, as emphasised in this paper.

LIST OF SYMBOLS AND ABBREVIATIONS

<i>C.P.</i>	centre of aerodynamic pressure on a streamwise strip element of area of a wing or feather
<i>d</i>	deflection distance of a support element placed in bending
<i>E</i>	modulus of elasticity; the ratio stress/strain
<i>EI</i>	flexural stiffness
EMA	effective mechanical advantages
<i>F_{ext}</i>	external force set up in reaction to the out-force generated
<i>F_m</i>	muscle force
<i>F_{out}</i>	out-force
<i>f_{axial}</i>	internal axial force set up on a cross-sectional element of area $z\delta y$ in reaction to an external bending moment
<i>f_{shear}</i>	internal tangential torsional shear force set up on a ring-shaped cross-sectional element of area $2\pi r\delta r$ in reaction to an external twisting moment
<i>G</i>	shear modulus of elasticity; the ratio (shear stress)/(shear strain)
<i>I</i>	second moment of area of a cross-section
<i>J</i>	polar second moment of area of a cross-section
<i>L</i>	longitudinal length
<i>L_{bend}</i>	length of bending moment arm
<i>L_m</i>	length of muscle moment arm
<i>L_{torque}</i>	longitudinal length of a support element along which a torque is applied
<i>L_{twist}</i>	length of twisting moment arm
<i>l</i>	longitudinal length dimension
<i>M</i>	moment
<i>M_b</i>	body mass
<i>r</i>	transverse, radial moment arm of internal, tangential shear force f_{shear} acting on ring-shaped, cross-sectional element of area $2\pi r\delta r$ with respect to the central, torsion axis in a cross-section of a structural support element placed in torsion
<i>T</i>	twisting moment
<i>t</i>	generalised transverse length dimension
<i>t_m</i>	transverse length dimension of muscle

t_s	transverse length dimension of structural support element
y	transverse moment arm of internal axial force f_{axial} acting on cross-sectional element of area $z\delta y$ with respect to the neutral axis in a cross-section of a structural support element placed in bending
z	width of a cross-sectional element of area, parallel with the neutral surface
δr	width of cross-sectional ring-element of area with its centre on the geometric axis of a supporting element
δy	thickness of a cross-sectional element of area, measured perpendicular to the neutral surface
θ	angle of twist of a structural support element placed in torsion
σ	axial stress; axial force per unit cross-sectional area
τ	torsional shearing stress; shear force per unit cross-sectional area

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