Review

Biomechanical consequences of scaling

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Summary

To function over a lifetime of use, materials and structures must be designed to have sufficient factors of safety to avoid failure. Vertebrates are generally built from materials having similar properties. Safety factors are most commonly calculated based on the ratio of a structure's failure stress to its peak operating stress. However, yield stress is a more likely limit, and work of fracture relative to energy absorption is likely the most relevant measure of a structure's safety factor, particularly under impact loading conditions characteristic of locomotion. Yet, it is also the most difficult to obtain. For repeated loading, fatigue damage and eventual failure may be critical to the design of biological structures and will result in lower safety factors. Although area:volume scaling predicts that stresses will increase with size, interspecific comparisons of mammals and birds show that skeletal allometry is modest, with most groups scaling ($l \propto d^{0.89}$) closer to geometric similarity (isometry: $l \propto d^{1.0}$) than to elastic similarity ($l \propto d^{0.67}$) or stress similarity ($l \propto d^{0.5}$). To maintain similar peak bone and muscle stresses, terrestrial mammals change posture when running, with larger mammals becoming more erect. More erect limbs increases their limb muscle mechanical advantage (EMA) or ratio of ground impulse to muscle impulse ($r/R = \int G / \int F_m$). The increase in limb EMA with body weight ($\propto W^{0.25}$) allows larger mammals to match changes in bone and muscle area ($\propto W^{0.72-0.80}$) to changes in muscle force generating requirements ($\propto W^{0.75}$), keeping bone and muscle stresses fairly constant across a size range 0.04–300 kg. Above this size, extremely large mammals exhibit more pronounced skeletal allometry and reduced locomotor ability. Patterns of ontogenetic scaling during skeletal growth need not follow broader interspecific scaling patterns. Instead, negative allometric growth (becoming more slender) is often observed and may relate to maturation of the skeleton's properties or the need for younger animals to move at faster speeds compared with adults. In contrast to bone and muscle stress patterns, selection for uniform safety factors in tendons does not appear to occur. In addition to providing elastic energy savings, tendons transmit force for control of motion of more distal limb segments. Their role in elastic savings requires that some tendons operate at high stresses (and strains), which compromises their safety factor. Other 'low stress' tendons have larger safety factors, indicating that their primary design is for stiffness to reduce the amount of stretch that their muscles must overcome when contracting to control movement.

Key words: bone, muscle, tendon stress, elastic savings, safety factor.

Introduction

Scale effects on the biomechanical design of organisms depend strongly on the properties of the biomaterials of which they are built, requirements for avoiding failure over a lifetime of their use, and on physiological demands for performance over a range of activities. For animals and plants constructed of similar materials, geometrical effects on the scaling of biomechanical function predominate. For structural support, design requirements depend mainly on the operating stresses (σ; or strains, ε) that structural elements experience relative to their yield, or failure strength (Wainwright et al., 1976). The ratio of failure stress to peak functional, or operating, stress is most commonly used to define a structure's 'safety factor'. However, it is likely that lower safety factors based on yield stress more often apply to the functional integrity of a structure. Repeated loading characteristic of locomotion may also cause fatigue damage and eventual failure at stresses well below those that cause failure in a single or few loading cycles (Carter and Caler, 1983; Wang et al., 1995). For this reason, a structure's 'loading history' is important, in terms of design for an adequate safety factor, as well as for remodeling and repair (Carter, 1987). For the dynamic loading conditions of locomotion, it is also likely that the amount of strain energy

that must be absorbed during a loading cycle relative to the work of fracture of a material (e.g. bone or tendon) is the most critical determinant of a structure's safety factor. Because the distribution and amount of strain energy absorption in structural elements are difficult to measure during locomotion, energy absorption is not often used to evaluate a structure's safety factor relative to its mechanical use.

For skeletal support elements, such as animal limb bones, design to maintain an adequate safety factor and avoid failure over a lifetime of use is most critical. However, for elastic elements, such as tendons and ligaments, the capacity for strain energy savings to reduce muscle work and lower the energy cost of locomotion also has selective value. Consequently, a trade-off exits in the design of tendons for adequate strength *versus* achieving high-energy savings, which depends on the tendons experiencing high strains (strain energy per unit volume of material is $\propto \varepsilon^2$ or, equivalently, σ^2; Alexander, 1988; Biewener, 2003). Morphological evidence suggests that most tendons are designed to have high safety factors, in excess of what is required for effective strain energy savings and necessary strength (Ker et al., 1988). This indicates that maintaining sufficient stiffness (force/displacement) for control of length and thus, position and movement of limb segments, may be an overriding design requirement for many tendons. Such tradeoffs in functional design therefore can result in quite distinct operating stresses and safety factors.

In this article, I focus on the biomechanical consequences of scaling in the limbs of terrestrial vertebrates, principally birds and mammals, comparing design requirements for three locomotor elements: bones, muscles and tendons. While other structural elements (e.g. cartilage) are clearly of key importance to the biomechanical function of these animals, less is known about the scaling implications for the design of cartilage in the joints of small *versus* large animals. Although my focus is on vertebrate animals, general principles concerning design tradeoffs for differing functions likely apply broadly to other organisms. Scaling comparisons across vertebrate taxa also reflect my conviction that size effects predominate over historical evolutionary constraints with respect to their influence on skeletal design and interpretations that may be drawn from scaling patterns. Although historical constraints clearly underlie the biomaterials of which diverse groups of organisms are built, over this broad diversity body size varies enormously and, as a result, plays a dominant role.

Scale effects on the vertebrate skeleton

Because stress (and strain, which is proportional to stress based on a material's elastic modulus; (Biewener, 2003; Wainwright et al., 1976) depends on the ratio of force applied and transmitted over a certain cross-sectional area of a material ($\sigma = F/A$), peak functional stresses are predicted to increase with size. By geometric similarity (or isometry), in which all lengths (l) and diameters (d) of similar structural elements scale to the animal's weight, $l \propto d \propto \mathbf{W}^{1/3}$, stress is predicted to scale $\propto \mathbf{W}^{1/3}$, given that force scales $\propto \mathbf{W}^1$ and $A \propto \mathbf{W}^{2/3}$. This has profound

implications for how vertebrate animals are built and function, and in the terrestrial environment counter gravitational and inertial forces. Because of the strong increase in stress with size predicted by geometric similarity, early work dating from Galileo (Galilei, 1638) predicted that skeletal elements in different sized animals would exhibit strong positive allometry (i.e. becoming increasingly robust with size). McMahon (1973, 1975b) published two influential papers arguing that animals scale with elastic similarity ($l \propto d^{2/3} \propto \mathbf{W}^{1/4}$) to maintain similar elastic deformations under equivalent loading conditions. Although elastic similarity reduces the scaling effect of size on stress and strain, it predicts an increase: $\sigma \propto \mathbf{W}^{1/4}$ for axial stress and $\sigma \propto \mathbf{W}^{1/8}$ for stresses due to bending and torsion. Only under conditions of static stress similarity (McMahon, 1975b) can stress remain constant across size based on geometry alone.

Although ungulates, and bovids in particular (McMahon, 1975a), have limb bones that scale close to elastic similarity, over a much broader size range mammalian (Fig. 1) and avian taxa scale closer to geometric similarity (Alexander, 1979; Biewener, 1982; Maloiy et al., 1979; Selker and Carter, 1989), with the prediction that peak bone stresses scale $\propto \mathbf{W}^{0.28}$. Consistent with their geometrically similar form, mammals and birds of different size move in dynamically similar fashion (Alexander and Jayes, 1983; and see Alexander p. 1645, this issue) at equivalent points in gait. Nevertheless, because the fracture strengths of mammalian and avian bones are generally uniform (Biewener, 1982; Currey, 2002), measurements of
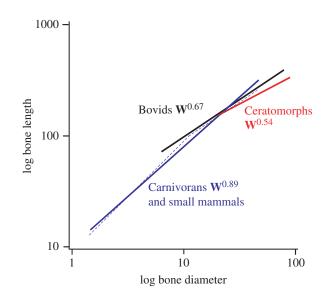

Fig. 1. Length–diameter scaling patterns of long bones from three groups of mammals: carnivorans (blue line: Bertram and Biewener, 1990), bovids (black line: McMahon, 1975a) and ceratomorphs (red line: Prothero and Sereno, 1982). Data for carnivorans exhibit differential allometry with smaller families scaling more closely to isometry and larger families closer to elastic similarity (reflected by light blue dashed lines). The larger carnivorans match the pattern for bovids, which scale with elastic similarity. Ceratomorphs scale with stronger allometry, close to stress similarity. Larger-sized bovids also exhibit this pattern. Adapted from Bertram and Biewener (1990, Fig. 5). Lines are based on least-squares regressions.

compressive stresses operating in the limb bones of chipmunks and ground squirrels during galloping in the range of –31 to –86 MPa (mean for both species: –57 MPa; Biewener, 1983) would predict (using $\sigma \propto W^{0.28}$) that no terrestrial mammals or birds should exist with similar ability to run and gallop at a size much greater than 20 kg in body mass, without exceeding a compressive fracture strength of –240 MPa (Currey, 2002)!

The presence of much larger land animals is likely best explained by either a reduction in locomotor ability at very large size or regular changes in limb posture and mechanical advantage that reduce the magnitude of muscle forces ($\mathbf{F_m}$) required to support weight-related ground reaction forces (Biewener, 1989, 1990). Although there is evidence (Alexander et al., 1977) that larger artiodactyls increase their relative limb support time (duty factor), which may help to reduce body weight related ground forces, this does not appear to be a general pattern within mammals and birds (Gatesy and Biewener, 1991).

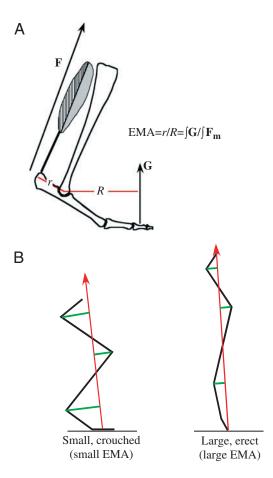By adopting more erect postures when they run, large

A

$EMA = r/R = \int\mathbf{G}/\int\mathbf{F_m}$

B

Small, crouched (small EMA)

Large, erect (large EMA)

Fig. 2. (A) Limb EMA defined as the ratio of extensor muscle moment arm (r) *versus* ground force moment arm (R), which over the period of limb support equals the ratio of ground force ($\mathbf{G}$) impulse *versus* muscle force ($\mathbf{F_m}$) impulse. (B) Effect of posture on limb EMA, showing that small animals with crouched postures have lower limb EMA (smaller 'R' moment arms: green bars) than larger animals with more erect postures.

mammals are able to reduce the moment arm (R) of the ground reaction force ($\mathbf{G}$) relative to the muscle's moment arm (r, Fig. 2). This decreases the magnitude of joint moments produced by the ground reaction force (=$R \times \mathbf{G}$), which are the principal moments that the muscles and bones of the limb must withstand during ground contact (moments due to segment inertia and segment weight are much smaller and most important during limb swing; Biewener, 2003). The 'external' moments produced by the ground force are counteracted by muscle moments, so that at each joint $F_m \times r = \mathbf{G} \times R$ (ignoring segment inertia and weight). By measuring changes in $\mathbf{G}$ and R at different instances in time during ground contact, and assuming a fixed agonist moment arm (r), weighted by the muscle agonists' fiber-areas, changes in muscle force required to support ground reaction moments can be determined. These are averaged over the period of limb support by determining the ratio of ground impulse ($\int\mathbf{G}$) to muscle impulse ($\int\mathbf{F_m}$), to calculate the agonist muscles' effective mechanical advantage (EMA) at a particular joint. By running with more upright postures, larger terrestrial mammals increase their effective limb's effective mechanical advantage (EMA=$r/R=\int\mathbf{G}/\int\mathbf{F_m}$), reducing the magnitude of muscle force transmitted to bone elements and tendons. Over a size range from mice to horses, when averaged for the major fore and hind limb joints, EMA scales $\propto W^{0.25}$ (Fig. 3A,B). Given that peak ground forces generally match changes in body weight ($\mathbf{G} \propto W^1$), this implies that weight-specific muscle forces ($\mathbf{F_m}/\mathbf{W}$) are expected to vary $\propto W^{-0.25}$. It also predicts that terrestrial mammals of different size produce the same force per unit gram (volume) of muscle recruited to support their body weight when running (Biewener, 1989). This follows from the fact that mammalian muscle fiber lengths generally scale $\propto W^{0.23}$ (Alexander et al., 1979), so that force per active muscle volume (= weight-specific force $\times$ fiber length) generally scales $\propto W^{-0.25} \times W^{0.23}$, or close to W^0. However, it is worth noting that muscle fiber-length and fiber-area scaling exponents can vary substantially between different muscle groups (Pollock and Shadwick, 1994), so that the scaling of muscle stress and force per unit volume within different muscles may also be expected to vary. The functional implications of such variation would be interesting to explore.

The scaling of mammalian limb EMA also matches the general scaling of force production observed by Marden and Allen (2002) (and see also Marden p. 1653, this issue) for both animate (muscle, myosin, dyenin, kinesin) and inanimate (winches and linear actuators) translational motors, as applied to dragonfly flight muscle (Schilder and Marden, 2004). Marden and Allen (2002) found that force output of animate and inanimate translational motors scales $\propto W^{0.67}$, but when the leverage (moment arm, r) of dragonfly flight muscles is measured, overall 'leveraged force output' of the dragonfly flight muscles to move their wings scales $\propto W^{1.0}$. Although this scaling pattern obeys geometric similarity (i.e. force $\propto W^{0.67}$ and $r \propto W^{0.33}$), it parallels closely the pattern of muscle force output and limb mechanical advantage observed for terrestrial mammals, which follow 3/4 and 1/4 power scaling.
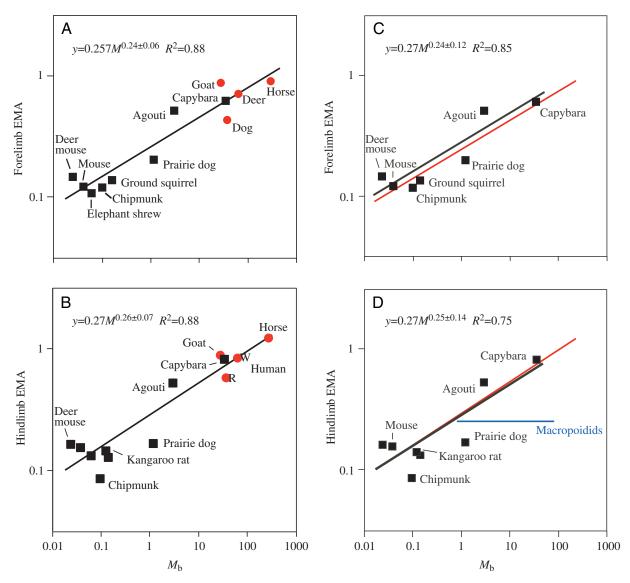
Fig. 3. (A) Forelimb and (B) hindlimb effective mechanical advantage (EMA) scaling for all mammalian species (original data reported in Biewener, 1989). Rodents are distinguished from other mammals by black squares. The lines are the least squares regressions for all species, except for the human data shown in (B). Human EMA during walking ('W') falls within the 95% confidence interval for all other mammals (not shown), but during running ('R') falls below (Biewener et al., 2004). (C,D) Forelimb and hindlimb EMA scaling of rodent species compared with the line for all mammals. No significant difference in scaling is observed for either limb; however, this is limited by the fact that the majority of mammalian species studied to date are rodents. Body mass (M_b; kg); Fore- and hind-limb EMAs (r/R); mean EMA = $M^{0.25}$.

Interestingly, in contrast to quadrupedal mammals that have been studied, which show little consistent change in limb EMA across speed and gait change (Biewener, 1989), human limb EMA significantly decreases from walking to running (Fig. 3B; Biewener et al., 2004). This results primarily from the knee being extended during walking *versus* flexed during running, consistent with the shift in limb mechanical function from pendular exchange of center of mass potential and kinetic energy during walking to spring-like energy savings during running (Cavagna et al., 1977). The lower limb EMA during running results in a fivefold increase in force by the knee extensors, compared with a twofold increase at the hip and no change at the ankle. It also correlates with the higher energy

cost of human running compared with walking (Margaria, 1976) and compared with quadrupeds of similar size (Taylor et al., 1970).

When rodents are compared (as a group) with mammals more generally there is no significant difference in EMA scaling (Fig. 3C,D). However, a limitation of this comparison is that most of the species (9 of 14) included in the 'mammal' line are rodents. When goats (*Capra hircus*) are compared with capybaras (*H. hydrochaeris*), and adjusted for the same size, goats have a significantly greater forelimb EMA (*P*<0.01) and greater overall (fore and hind) limb EMA (*P*<0.05) than capybaras. Whether artiodactyls, and ungulates as a group, have generally more erect postures than rodents remains to be

determined. A broader range of ungulates, particularly at smaller size, needs to be studied. A potential difficulty with this comparison is that capybaras are semiaquatic animals, which might be expected to affect their limb mechanics. As the largest rodent species, their values may disproportionately influence the regression line. However, the capybara values fall close to the line for rodent EMA scaling. When compared with values predicted based on least-squares regression of the other rodent species alone (capybara data excluded), the capybara hind limb EMA is 78% greater than predicted and the fore EMA is 5% lower than predicted.

Consequently, while general scaling effects of more erect posture on limb EMA to reduce bone and muscle stresses appear to apply within rodents and across mammals more generally, data for a broader diversity of land animals is needed to improve our understanding of how evolutionary ancestry may influence biomechanical constraints of scaling relative to other functional determinants of limb and skeletal form. For example, in a comparison of different sized macropoidids, Bennett and Taylor (1995) found that ankle EMA does not change with size (averaging 0.24), in contrast with the eutherian mammals discussed above (Fig. 3D). This appears to reflect selection favoring increased elastic energy savings (discussed below) in larger macropodids, at the risk of increased operating stresses in their hind limb tendons, bones and muscles. In addition, no data yet exist to compare avian bipeds across their size range in terms of limb EMA and whether a scaling pattern similar to terrestrial eutherian mammals emerges. In a study comparing skeletal allometry in different carnivoran families with that observed in bovids and certaomorphs, Bertram and Biewener (1990) found evidence for differential allometry across taxonomic groups at different sizes (Fig. 1). In contrast to carnivorans and other small to moderate-sized mammals (Bou et al., 1987; Christiansen, 1999), which scale generally close to geometric similarity, bovids display elastically similar scaling (McMahon, 1975b). Whereas, at extremely large size ceratomorphs scale with increasing skeletal robustness (Prothero and Sereno, 1982) close to static stress similarity (Fig. 1). These patterns of differential skeletal allometry within terrestrial mammals suggest different biomechanical and physiological constraints may apply between taxonomic groups that span different size scales. It is also the case that no study has examined whether ontogenetic changes in limb EMA occur within a species. Although size change during growth is often much less than across a diversity of related species, postural changes in limb loading could well play a role in terms of growth-related changes in skeletal form and function.

In recent studies of the ontogenetic growth and skeletal biomechanics of goats (Main and Biewener, 2004a) and emu (*Dromaius novaehollandiae*; Main and Biewener, 2004b), locomotor bone strains were found to increase in the goat radius and in the emu tibiotarsus (Fig. 4A,B) and femur (not shown) with growth and age, in contrast to the generally uniform peak strain patterns found in the chick tibiotarsus during growth (Biewener et al., 1986). This increase appears to result from isometric scaling of peak ground reaction forces (**G**) at different ages during growth relative to negatively allometric scaling of bone area and second moment of area in the goat radius and isometric scaling of bone geometry in the emu tibiotarsus (Fig. 4C,D) and femur (not shown). The finding of a relative thinning of the radius in goats and to a certain degree in the emu tibiotarsus and femur is surprising, but may be explained by the need of smaller young animals to run at relatively faster speeds to keep up with larger adults (Main and Biewener, 2004a). In an earlier study, Carrier (1983) found that jackrabbits (*Lepus californicus*) also exhibit negative ontogenetic growth allometry in the tibia and femur, which may offset the reduced mineralization (and stiffness) of their bone at an early age and small size. As no difference in mineralization has been found in goats and emu from 2 weeks of age to adult (Main and Biewener, 2004b), it would be interesting to know whether jackrabbit bone strains are maintained uniformly during growth as they are in the chicken tibiotarsus (Biewener et al., 1986). These results show how other factors (such as an ecological pressure for group movement to reduce predation risk in younger animals) may influence the biomechanics and scaling of ontogenetic growth in ways that may differ considerably from those found more broadly across species of different size. Additional studies of musculoskeletal growth trajectories in relation to locomotor performance are needed for a greater understanding of how such factors may interact with size to influence biomechanical design strategies during ontogenetic growth.

Scale effects on muscle function

The scaling of limb mechanical advantage in terrestrial eutherian mammals suggests that peak stresses developed by limb muscles at equivalent levels of physical activity are generally similar. This follows from the scaling of muscle force based on limb EMA $\propto \mathbf{W}^{0.75}$ (Biewener, 1989), which fairly closely matches the scaling of muscle cross-sectional area $\propto \mathbf{W}^{0.80}$, based on the results of Alexander et al. (1979). To date no study has formally tested the prediction that peak muscle stresses are size-invariant, but reported values of muscle stresses developed in various terrestrial species during moderate to strenuous activity to date generally support this conclusion (Table 1). Although peak muscle stresses vary fourfold, there is no significant correlation with the ratio of muscle area to tendon area: A_m/A_t; Fig. 5), or with body size. Much of the variation in peak muscle stresses reflects differences in measurement technique and differing performance of the animals studied (e.g. kangaroo rat hopping *versus* jumping, Table 1). In one study (Perry et al., 1988) that compared muscle stresses acting in the ankle extensors of quadrupedal rats (*Rattus norvegicus*) *versus* bipedal kangaroo rats (*Dipodomys spectabilis*) moving at their preferred speed and gait (rat gallops at 1.48 m s^{-1}; kangaroo rat hops at 1.46 m s^{-1}), similar peak muscle stresses (70 and 69 kPa) were found.

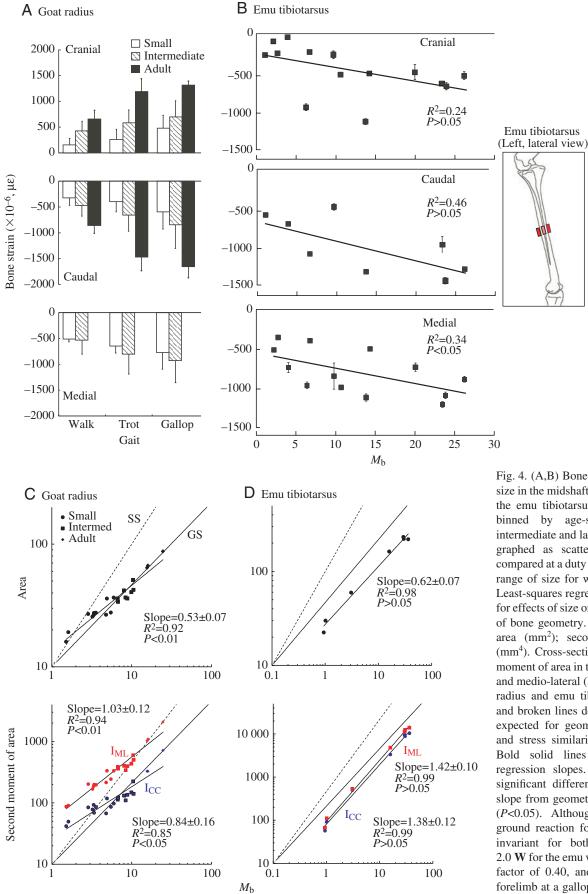Whereas *in vivo* methods provide direct measurements of

Fig. 4. (A,B) Bone strain *versus* age and size in the midshaft of the goat radius and the emu tibiotarsus. Data for goats are binned by age-size groups (small, intermediate and large). Data for emu are graphed as scatterplots, with animals compared at a duty factor of 0.40 over the range of size for which data are shown. Least-squares regression was used to test for effects of size on strain. (C,D) Scaling of bone geometry. Body mass (M_b; kg); area (mm^2); second moment of area (mm^4). Cross-sectional area and second moment of area in the cranio-caudal (I_{CC}) and medio-lateral (I_{ML}) directions in goat radius and emu tibiotarsus. Light solid and broken lines depict scaling relations expected for geometric similarity (GS) and stress similarity (SS), respectively. Bold solid lines show least-squares regression slopes. *P*-values test for a significant difference of the regression slope from geometrically similar scaling ($P<0.05$). Although not shown, peak ground reaction forces (**G**) were scale-invariant for both species, averaging 2.0 **W** for the emu when running at a duty factor of 0.40, and 1.5 **W** for the goat forelimb at a gallop.

Table 1. *Peak muscle and tendon stresses in terrestrial animals*

Species (mass, kg)	Muscle	σ_m (kPa)	σ_t (MPa)	A_m/A_t	Activity	Method	Reference
Horse (270)	Fore DDF	240	45	223	Galloping	Inv. dyn.	1
	Fore SDF	240	34	150			
	Gastrocnemius	245	28	114			
Human (75)	Triceps surae	151	50	167	Running (4 m s^{-1})	Inv. dyn.	2,3
	Quadriceps	255	–	–			
	Hip extensors	110	–	–			
	Triceps surae	101	33	167	High jump	Inv. dyn.	3
	Quadriceps	277	–	–			
	Hip extensors	120	–	–			
Goat (34)	SDF	58	7	110	Canter	*In vivo*	4
	Gastrocnemius	72	13	175			
Dog (36)	Triceps surae	245	84	296	Jumping	Inv. dyn.	5
Red kangaroo (6.6, juvenile)	Plantaris (SDF)	170	42	245	Hopping	Inv. dyn.	6
	Gastrocnemius	170	84	275			
Rock wallaby (6.6)	Triceps surae	279	39	147	Jumping	Inv. dyn.	7
		201	28		Hopping		
Tammar wallaby (4.8)	Plantaris (SDF)	262	37	189	Hopping	*In vivo*	8
	Gastrocnemius	227	34	150			
Cat (3.6)	Plantaris (SDF)	123	17	140	Trotting	*In vivo*	9*
	Gastrocnemius	73	8	109			
Kangaroo rat (0.12)	Triceps surae	297	33	120	Jumping	Inv. dyn.	10
Guinea fowl (1.3)	Digital flexor-IV	115	8	76	Jumping	*In vivo*	11
		130	9	–	Running		
	Lat. gastrocnemius	133	17	117	Jumping		
		40	5	–	Running		
Mallard duck (1.1)	Gastrocnemius	121	18	110	Running	*In vivo*	12
Frog (*Xenopus*) (0.10)	Plantaris longus	200	4	20	Swimming	*In vivo*	13

DDF, deep digital flexor; SDF, superficial digital flexor; Inv. dyn., inverse dynamics.

[1]Biewener (1998); [2]Ker et al. (1987); [3]Thorpe et al. (1998); [4]M. P. McGuigan, E. Yoo and A. A. Biewener (unpublished); [5]Alexander (1974); [6]Alexander and Vernon (1975); [7]C. P. McGowan and A. A. Biewener (unpublished); [8]Biewener and Baudinette (1995); [9]Herzog et al. (1993); [10]Biewener and Blickhan (1988); [11]Daley and Biewener (2003); [12]Biewener and Corning (2001); [13]C. Richards (unpublished).

*Stresses determined from *in vivo* forces recorded by Herzog et al. (1993) and cat tendon areas reported by Pollock and Shadwick (1994).

muscle–tendon stress, they are limited to muscles having sufficiently long tendons that enable direct measurements. By contrast, indirect methods based on inverse dynamics (linked-segment joint moment analysis that accounts for external, inertial and gravitational forces acting at a joint; e.g. Winter, 1990) and free-body analysis, rely on assumptions about muscle force distribution among muscle agonists. For more proximal joints (such as the hip and knee), such approaches also cannot resolve agonist muscle forces due to force transmission by two-joint muscles, resulting in an indeterminant condition. Nevertheless, the highly conservative nature of muscle contractile proteins and their organization in vertebrate skeletal muscle fibers (other than for differing distributions of muscle fiber type and associated mitochondrial and capillary densities for energy supply among different species that show important allometric patterns (Hoppeler et al., 1981a,b; Mathieu et al., 1981; Weibel, 1985), indicates that maximal stresses within the skeletal muscles of different sized animals are likely fairly constant.

However, if two species have differing capacities for increasing their locomotor performance beyond rest, peak muscle stresses at preferred levels of activity might also differ. In comparison to metabolic scope (see Bishop p. 1695, this issue), factorial scopes for muscle force and power output (for increased speed or acceleration) have not been examined across species. Species with a greater ratio of top speed to preferred speed might be expected to operate with lower stresses at their preferred speed of locomotor movement. Nevertheless, changes in limb mechanical advantage and relative limb length might offset such speed-related influences on peak muscle stress. In the case of large macropodids (kangaroos and wallabies), selection for effective tendon elastic energy savings favors higher operating stresses in the animal's tendons (Alexander, 1988; Bennett and Taylor, 1995). Stresses in the muscles of tammar wallabies determined from tendon force–buckle recordings (Biewener and Baudinette, 1995) are also quite high (227 to 262 kPa at 6 m s^{-1}) compared with peak muscle stresses found in other species, such as goats,
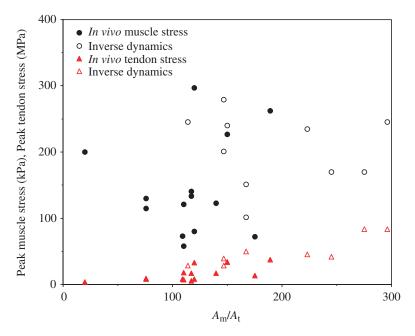
Fig. 5. Peak muscle (circles) and tendon (triangles) stresses plotted against the ratio of muscle to tendon area (A_m/A_t), based on measurements obtained from direct *in vivo* muscle–tendon force recordings (solid) and those calculated from ground reaction forces and/or kinematics using inverse dynamics (open). Note that the variation in tendon stress (>20-fold) greatly exceeds that of muscle stress (fourfold), which may be hidden by graphing both sets of data on the same graph. Least-squares regressions are shown for both sets of data. See Table 1 for values and sources. In contrast to peak muscle stresses (R^2=0.069, P>0.05), peak tendon stresses show a significant correlation with A_m/A_t (R^2=0.753, P<0.01).

domestic cats, guinea fowl and kangaroo rats, based on similar force–buckle recordings (Table 1). Kangaroo rat stresses are low during steady speed hopping but this allows them to increase muscle and tendon stresses dramatically when jumping. Muscle stresses in dogs and rock wallabies are similarly high during jumping, being in the range of peak isometric stress for skeletal muscle. Muscle stresses calculated to act in horses during steady speed trotting and galloping also reach high levels, which likely reflects their role in favoring tendon energy savings. It would be interesting to know how these stress levels compare with those developed when horses jump.

Before discussing biomechanical constraints on tendon design it is worth noting the important influence of size on the rate of muscle contraction and speed of limb movement. The rate of muscle shortening scales inversely with size ($\propto W^{-0.18}$; Rome et al., 1990) in a manner that is generally inversely related to limb length. This corresponds to the fact that larger animals move their limb more slowly than small animals to move at a given speed. As a result, when compared at equivalent speeds (trot–gallop transition speed, preferred trotting and galloping speeds) Heglund and Taylor (1988) found that stride frequency scales $\propto W^{-0.15}$, close to that predicted by the scaling of maximum shortening velocity. The higher stride frequencies, shorter ground contact times and faster muscle contraction rates

of smaller animals results in the use of more metabolic energy to generate a given amount of force to support their body weight (Kram and Taylor, 1990), which helps to explain their greater cost of transport compared with larger animals (Taylor et al., 1982; Taylor et al., 1970). As noted before, because of the scaling of limb EMA (Fig. 3; Biewener, 1989) quadrupeds of different size generally recruit the same volume of muscle per unit body weight, so changes in force do not account for the scaling of metabolic rate with speed and size.

Scale effects on tendon design and function

A structure's safety factor and its probability of failure depend not only on the average magnitude of loading to which it is subjected, but also on how variable such loads are over a period of use (Alexander, 1981). For a given median operating stress, a structure's risk of failure increases with more variable loading. As a result, structures subjected to more variable loads of a given median magnitude may be expected to have greater safety factors than structures subjected to more predictable loads. Whereas bones may experience a broad range of loads resulting from shifting limb orientation and muscle contractile patterns, the loads that tendons bear are limited by the strength of their muscles. Tendons simply needn't bear forces greater than the maximum their muscles can produce. This would suggest that tendons might operate with particularly low safety factors.

However, in a study of muscle–tendon architecture in different mammalian species, Ker et al. (1988) found that most mammalian tendons appear to be built with safety factors that likely exceed 8 or more, based on an estimated peak isometric force that their muscles can transmit (= 0.3 MPa isometric stress × the muscle's fiber area, A_m). Only highly specialized muscle–tendon systems, such as those found in the digital flexors of horses and other ungulates, and in kangaroos and wallabies, have such slender tendons that they would be expected to operate with safety factors as low as two to three. Ker et al. (1988) interpreted the greater than expected thickness of most mammalian tendons as reflecting a need to maintain adequate stiffness, rather than sufficient strength. The high safety factors of most tendons suggest that minimizing in-series compliance (stretch) of the tendon relative to the operating length range of the muscle's fibers may be of overriding importance. Reducing tendon compliance likely favors increased control of position and length change of the muscle–tendon unit as a whole. Therefore, control of limb segment movement, rather than strength and weight savings for an adequate safety factor, appears to be the critical design of these tendons.

By contrast, the 'high stress' tendons found in the distal limbs of ungulates, canids, macropodids, and other terrestrial
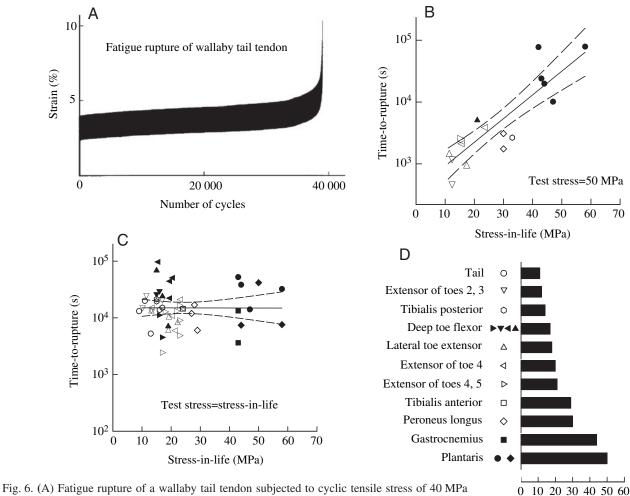
Fig. 6. (A) Fatigue rupture of a wallaby tail tendon subjected to cyclic tensile stress of 40 MPa at 5.3 Hz (from Wang et al., 1995). (B) Time of rupture for various wallaby tendons *versus* their 'stress in life' when subjected to a creep failure stress of 50 MPa (least-squares slope and 95% confidence intervals shown). (C) Time of rupture for various wallaby tendons when each tendon is subjected to its own 'stress in life', showing that all fail in about 5.5 h (least-squares regression slope and 95% confidence intervals shown). (D) Symbol key for the wallaby tendons tested to creep failure and their 'stress in life (= 0.3 MPa A_m/A_t). B–D are from Ker et al. (2000).

animals that make effective use of elastic energy savings, must operate with low safety factors. Indeed, the operating stresses in the tendons of wallabies and kangaroos during steady, preferred speed hopping (range: 32–84 MPa, Table 1; Alexander and Vernon, 1975; Bennett, 1987; Biewener and Baudinette, 1995; Ker et al., 1986) are generally high. This prevents these animals from achieving the factorial increase in tendon stress that smaller animals, such as heteromyid kangaroo rats, benefit from when jumping or accelerating to escape predation (Biewener and Blickhan, 1988). Rapid acceleration simply is not feasible or safe for animals that have evolved slender tendons for achieving effective elastic energy storage and return at preferred speeds of movement. The strong positive allometry of energy savings in macropodids $\propto W^{1.73}$ (Bennett and Taylor, 1995), which results (in part) from a size-invariant low ankle EMA, is evidence of this.

These results make clear that the design of tendons in terms of failure strength and loading predictability for ensuring a minimum, but adequate, safety factor is the exception rather than the rule. Instead, most tendons appear to have higher than expected safety factors, reflecting their need to be stiff enough for muscular control of position and movement. Other tendons specialized for elastic savings operate at much lower safety factors, but this likely limits the factorial increase in locomotor performance that these animals can achieve. As a result, peak tendon stresses vary much more (>20-fold) than stresses developed in muscles (Table 1) and, in contrast to peak muscle stresses, they exhibit a significant change with differences in muscle–tendon architecture (Fig. 5). Studies of the scaling of the Achilles tendon in mammals (Peterson et al., 1984; Pollock and Shadwick, 1994) indicate that Achilles tendon energy storage is also scale-dependent ($\propto W^{1.28}$) in quadrupedal mammals, but not as strong as in macropodids (Bennett and Taylor, 1995).

Fatigue damage in tendons and bones

Skeletal support tissues are subjected to repeated loading as

a consequence of locomotor activity. Because of this, they are liable to fatigue failure. Repeated cyclic loading can lead to fatigue damage accumulation, with the result that a structure, or the material of which it is built, fails at a stress that may be much lower than its failure stress for a single or very few cycles of loading (Ashby, 1999; Currey, 2002). Among other factors, the rate of damage accumulation depends on the number and frequency of loading cycles, as well as their stress magnitude and amplitude (and whether stresses reverse from compression to tension). Unless fatigue damage is repaired, cyclic loading will therefore reduce a structure's safety factor and eventually lead to its fatigue failure. However, because remodeling and repair are common features of many biological tissues, it has been generally believed that, except for extreme loading circumstances (such as those that new army recruits or elite athletes experience), failure resulting from fatigue damage may not be a significant feature of the mechanical design of most organisms.

Carter and colleagues (Caler and Carter, 1989; Carter and Caler, 1983; Carter and Hayes, 1976) carried out early work on the fatigue properties of mammalian compact bone and found that compact bone from various sources, tested under different loading conditions, generally fails from creep at faster rates when loaded at higher stresses, and when subjected to cyclic loading fails at >10^6 loading cycles for stress amplitudes in the range of 50–100 MPa. (Currey, 2002) discusses these data and speculates that a migrating animal might sustain this number of loading cycles over a period of month, but at much lower stress levels than those that operate during fast locomotion. Given that damage accumulation is likely to be repaired, it would appear that under only the most strenuous physical conditions is fatigue failure a problem for maintaining the structural integrity of a bone. It remains unclear if wild populations of animals undergoing natural activity patterns incur skeletal fatigue fractures.

In recent work Ker and colleagues (Ker et al., 2000; Wang and Ker, 1995; Wang et al., 1995) have examined the fatigue rupture of different types of tendons, based on cyclic loading and creep rupture under *in vitro* conditions (Fig. 6). They found that tendons fail after a surprisingly few loading cycles (40,000 or less) at test stresses (40 MPa) well below the failure stress of tendon (~100–120 MPa for a single loading cycle). When subjected to a constant stress that was 50% or less of their failure stress, the tendons also ruptured over fairly short periods of time. When 'low stress' tendons (e.g. tail and digital extensor tendons) of a wallaby were compared with 'high stress' tendons (e.g. plantaris and digital flexor tendons), Ker et al. found that the 'low stress' tendons failed over much shorter times (as low as 1 h or less) at a given test stress (50 MPa) than the 'high stress' tendons (up to 22 h; Fig. 6B). However, when each tendon was subjected to its 'stress-in-life' (calculated based on the peak isometric force that the tendon's muscle would transmit to the tendon = 0.3 MPa $\times$ A_m/A_t; see Table 1), Ker et al. found that the different tendons all failed at generally the same time: ~5.5 h under a constant creep load (Fig. 6C). Despite the apparently high safety factors of most tendons (Ker et al., 1986), the surprisingly short fatigue life of the different tendons suggests that the tendons, like bones, must undergo ongoing repair of damage that accumulates as a result of cyclic loading during locomotor activity. Otherwise, fatigue failure may result. It seems probable that under *in vivo* conditions, with the tendon cells alive and the local matrix biochemistry intact, damage would not accumulate at a rate as rapid as the *in vitro* tests suggest. Nevertheless, these dramatic results indicate that fatigue damage likely affects the safety factors of tendons and bones, and needs to be considered in relation to skeletal structures are loaded over longer periods of use.

Given the occurrence of fatigue damage, it seems likely that scaling effects on longevity that influence lifetime loading histories may affect the relative importance of design for fatigue failure in different sized animals. Many factors influence a species' lifespan, but in general larger animals live longer than small animals, with lifespan generally scaling $\propto W^{1/4}$ (Calder, 1984; and see Speakman p. 1717, this issue). This suggests that fatigue damage accumulation may be increasingly prevalent in larger, longer-lived animals. Small animals, such as rodents, with less determinant growth may also benefit from continued growth and modeling of their skeletal tissues, with the consequence that any damage resulting from repeated loading might be removed as an ongoing feature of growth. Because of this, larger animals may operate with smaller safety factors than small animals when fatigue damage over lifetime use is considered. However, the increased longevity of larger animals might be offset by the fact that they take fewer strides over a lifetime of activity (reflecting their longer limbs and lower stride frequency). Similar to the general scale invariancy of the number of lifetime heart beats and breaths, animals of different size may also, on average, take the same number of total steps in a lifetime, offsetting the possible size effect on fatigue failure.

One way to test this might be to compare the relative fracture incidence in natural populations of small *versus* large animals, with the prediction that smaller animals would suffer a lower incidence of limb bone fractures. Unfortunately, other than for certain primates, including humans, horses, and a few other vertebrate species, such data are difficult to obtain (Alexander, 1981), and other factors that affect safety factors (e.g. loading variability) are also are likely to complicate these comparisons and the interpretations that may be drawn from them.

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