

Scaling of Terrestrial Support: Differing Solutions to Mechanical Constraints of Size

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Terrestrial animals and plants span an enormous size *range*, and yet even distantly related groups are constructed of similar materials (e.g., bone, wood, muscle, and tendon). As with many physiological processes, evolutionary and ontogenetic changes in size impose constraints of scale on the mechanical design and function of skeletal support systems that are built of materials having similar properties. Adequate design requires that the capacity of skeletal **elements** (and muscles) for force transmission safely exceeds the levels required for biological support and movement. This is the case when the force transmitted per unit cross-sectional area of the material, defined as a mechanical stress ($= F/A$, e.g., N/mm^2), does not exceed the material's strength (the maximum stress that the material can withstand before **failure**). Clearly, larger structures can support larger forces more safely. The important design consideration, however, is whether changes in force requirements are matched by comparable changes in tissue cross-sectional area in order to keep maximal stresses and, thus, safety factors (defined as failure stress/peak functional stress) constant as size changes. Scale-invariant features (bone strength, timber strength, and peak muscle stress), therefore, require size-dependent changes in other features if the functional integrity of support systems is to be maintained over a broad size range (see also Li this volume). What are the features of terrestrial skeletal support systems that vary in a regular way with changes in size,

and are these scale-dependent features ones that operate across different size ranges and obey general biological scaling laws?

Because the forces acting on a structure are likely to vary in proportion to the organism's weight and, hence, are proportional to its volume (αV), stress is predicted to increase with size due to the disproportionate scaling of volume versus area (V/A). This also implies a scale-dependent increase in tissue strain (defined as the deformation of the tissue under mechanical load divided by its unloaded length, or dl/L). Stress (σ) and strain (E) are related by the elastic modulus (E) of the material, so that for linearly elastic materials, $\sigma = E\varepsilon$. Isometric, or geometrically similar, scaling predicts that larger animals and plants are subjected to greater stresses and strains, which should increase $\alpha M^{1/3}$. For organisms built of similar materials this suggests a drastic reduction in safety factor at larger sizes. Consequently, geometrically similar organisms likely face major constraints for meeting the force requirements of support and movement on land with the evolution of large body size. In order to avoid an increase in tissue stress and strain, and an increased probability of mechanical failure (which results directly from excessive tissue strain), larger organisms must either scale with strong allometry, restrict their size range or functional capacity, or evolve a means for reducing weight-specific forces to match the mass-specific decrease in tissue cross-sectional area.

In this chapter, I explore how different-sized terrestrial mammals achieve generally similar safety factors. The scaling of muscle mass and area, which limits locomotor stress capacity and underlies musculoskeletal design, may be linked to the $3/4$ power scaling of metabolic energy supply for force generation. However, in contrast to arguments that a single set of scaling laws may explain the design architecture of respiratory and vascular supply networks (see Brown et al. this volume) associated with the $3/4$ power scaling of metabolism, I argue that similar safety factors are achieved in the mammalian musculoskeletal system by differing solutions to mechanical constraints of size. Further, I examine whether similar constraints operate over different size ranges within these animals. In particular, is peak stress relative to tissue strength the limiting constraint at all sizes? I also discuss how differing design constraints may also operate at different scales of size within a single individual, by examining the branching architecture of a tree. Finally, I consider how musculoskeletal scaling to, maintain similar stress matches observed scaling patterns of whole-body and leg spring stiffness (Farley [12]).

1 SIZE-RELATED CHANGES IN LOCOMOTOR POSTURE AND MUSCLE MECHANICAL ADVANTAGE

Despite the constancy of their material properties, the skeletal and muscular systems of terrestrial mammals scale near isometry, or with only slight positive allometry over much of their size range ($> 10^4$) [1, 2, 7]. Because of this, adjustments of bone and muscle architecture are insufficient to maintain sim-

ilar locomotor stress. In order to achieve comparable safety factors, terrestrial mammals, ranging in size from 0.1 to 300 kg body mass, have evolved size-dependent changes in limb posture [8]. A shift from crouched postures at small sizes to more upright postures at large sizes enables a reduction in the ratio of muscular force to ground reaction force (α body weight, W) by increasing the effective mechanical advantage ($EMA = r/R$) of limb muscles (Figure 1). This size-related shift in limb posture during terrestrial locomotion means that muscle forces do not scale proportionally to body weight but, rather, scale $\alpha W^{0.73}$. For example, whereas muscular forces (F) developed in a chipmunk at a gallop are 10 times the ground reaction force (G), they are nearly equal to the

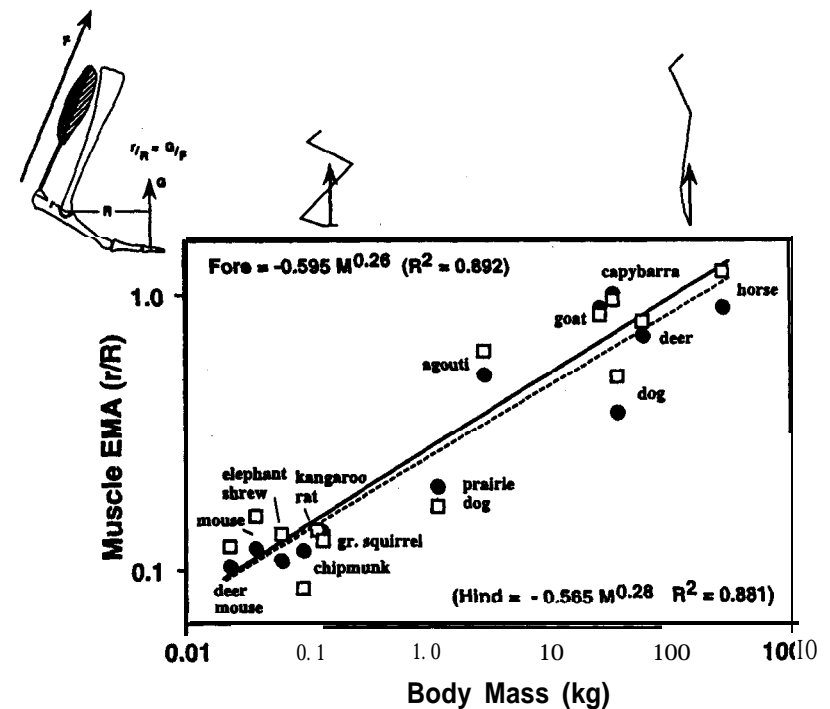


FIGURE 1 Scaling of posture-related muscle mechanical advantage ($EMA = r/R$, depicted in the upper left inset) in terrestrial mammals plotted against body mass on logarithmic coordinates. Least-squares (L-S) regression equations for forelimb and hindlimb show a similar pattern with the combined scaling of muscle $EMA \propto M^{0.27}$ (which implies muscle force $F \propto M^{0.73}$). Changes from crouched locomotor postures in small mammals to more upright postures in larger mammals explains the similarity of peak bone and muscle stress in different-sized species.

TABLE 1 Allometric and theoretical scaling relationships of bone and muscle stress, in terrestrial mammals.

	Area	Force	Stress	Reference
Bone	$\alpha M^{0.72}$	$\alpha M^{0.73}$	$\alpha M^{0.01}$	Biewener [7, 8]
Muscle	$\alpha M^{0.79}$	$\alpha M^{0.73}$	$\alpha M^{-0.06}$	Alexander et al. [1] and Biewener [8]
Theoretical	$\alpha M^{3/4}$	$\alpha M^{3/4}$	αM^0	

ground force exerted by a horse. By increasing limb mechanical advantage and reducing mass-specific muscle forces over this size range, terrestrial mammals are able to maintain nearly equivalent bone and muscle stresses (Table 1). This is supported by the observation of similar stresses (and strains) within the long bones of different-sized mammals [9, 26].

2 IS THERE A THEORETICAL BASIS FOR A LINK BETWEEN THE BIOMECHANICS OF MUSCLE SCALING AND ENERGY SUPPLY?

These empirical observations suggest the possibility that the scaling of muscle forces ($M^{3/4}$) over a considerable portion of the size range of terrestrial mammals may be related to the more general $3/4$ power scaling of metabolic and transport processes (see Table 1 and Brown et al. this volume). Because the mechanical properties of vertebrate skeletal muscle are generally scale invariant (i.e., constant stress and strain), muscle force generating requirements must scale proportional to scale-dependent changes in muscle fiber cross-sectional area, which is achieved through the scaling of limb posture and muscle mechanical advantage. Evidence that the cost of force generation by skeletal muscles during locomotion largely determines the scaling of energy cost in different-sized mammals [18, 29] indicates a metabolic link to the scaling of muscle force. Because the muscles of different-sized mammals generate similar forces per unit volume (the decrease in mass-specific force is offset by the longer fibers of larger animals), the cost of generating muscle force appears to depend mainly on the rates of force development and muscle shortening. With their slower stride frequencies ($\alpha M^{-0.15}$) [15] and longer periods of limb support, larger animals expend less energy than small animals to support a given weight of their body while running. Consequently, the scaling of metabolic cost of transport and maximum aerobic capacity [28] scales close to $M^{3/4}$ (empirical range: $\alpha M^{0.70}$ to 0.080). This suggests that the aerobic rate of ATP supply and the amount of ATP consumed by the muscles to move a given distance are matched to the biomechanical requirements of muscle force generation, at least for mammals ranging from 0.1 to 300 kg in

size. Do similar mechanisms apply more generally across the full size range of terrestrial mammals?

3 STRESS-SIMILARITY SCALING AT GIANT SIZE: POSITIVE SKELETAL ALLOMETRY

Economos [11] suggests that different scaling relationships and, by implication, mechanical constraints may apply to large versus small terrestrial mammals (which he has estimated to occur at about 20 kg body mass). Consistent with this, but at a larger size, posture-related changes in limb mechanical advantage at sizes above 300 kg body mass appear to be constrained, such that positive allometric changes in skeletal shape are required to maintain adequate safety factors in extremely large terrestrial species. In a study comparing the scaling of different-sized carnivoran families with previous studies of bovids [20] and ceratomorphs (rhinos, tapirs, and their fossil relatives) [24], John Bertram and I [6] found evidence that, over different size ranges, these groups of terrestrial mammals exhibit differing allometric scaling (Figure 2), with ursids closely matching the elastically similar scaling ($L\alpha D^{0.67}$) [19] observed within bovids. As a larger size group, ceratomorphs scale with stronger positive allometry, close to static stress similarity ($L\alpha D^{0.5}$) [19]. At smaller sizes, carnivorans and small bovids scale closer to geometric similarity ($L\alpha D$). The increasingly more robust scaling within larger sized groups of terrestrial mammals, particularly within ceratomorphs, is also likely associated with reductions in locomotor performance (maximum speed and maneuverability); however, other than for largely anecdotal evidence [14] constraints on locomotor performance at extremely large sizes remain to be demonstrated. It is the case that elephants are unable to trot or gallop [13, 16] and their maximum running speed is considerably less than fleet bovids and cursorial carnivores, but measurements of limb mechanical advantage have not yet been made for these terrestrial giants.

4 GEOMETRIC SCALING AT SMALL SIZE: A CONSTRAINT OF STIFFNESS VERSUS STRENGTH?

In most cases, limits on physiological and mechanical performance are generally analyzed in terms of the effect of a size increase, rather than a consideration of the implications of an (evolutionary) size **decrease**. Choosing the particular size from which scale-dependent changes are considered is equally important. In an evolutionary context, the reference size for considering scale effects should be the size of the basal ancestral group from which the group evolved. For eutherian mammals this would be in the range of 0.1 to 1.0 kg. What are the consequences when a lineage of animals or plants evolve to

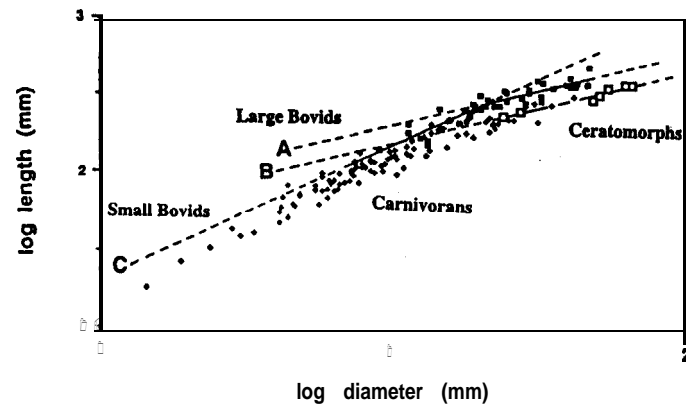


FIGURE 2 Differential scaling of tibial dimensions (length versus anteroposterior diameter on logarithmic coordinates) in bovids (small closed squares [20]), carnivorans (small crosses [6]) and ceratomorphs (open squares [24]). Small bovids (L-S slope = 0.89, $r = 0.90$) and small carnivorans (mustelids, procyonids, and viverrids: L-S slope = 0.85, $r = 0.98$) scale similarly, with only slight allometry; whereas, large bovids (L-S slope = 0.48, $r = 0.83$) and large carnivorans (ursids and felids: L-S slope = 0.70, $r = 0.95$) scale with strong allometry, approaching the extremely robust scaling observed for ceratomorphs (L-S slope = 0.47, $r = 0.98$). All regressions are significant at $p < 0.01$. L-S regression was used to compare the data from the three studies. The large-bovid line (A) parallels the ceratomorph line (B) but with a higher intercept, indicating their longer tibiae. The largest carnivoran species closely overlap the ceratomorph regression. From Bertram and Biewener [6]. Printed with permission from Wiley-Liss, Inc., a division of John Wiley & Sons, Inc.

smaller size? In terms of mechanical stress, geometric scaling as well as elastically similar scaling predict a decrease in stress with decreasing size (Figure 3). This results from decreases in weight-related forces that exceed reductions in bone, muscle, and tendon cross-sectional area. Consequently, smaller geometrically similar animals can also be expected to have relatively greater limb stiffness. That is to say, the structural elements of the limbs of smaller animals are likely to undergo smaller deflections for their size compared with the limb elements of larger animals. The nearly geometric scaling of small to medium-sized mammalian taxa (weighing 0.03 to 30 kg) suggests, therefore, that stiffness of support elements, and their effect on overall limb stiffness, may be the limiting design constraint rather than strength (i.e., peak stress).

Why is stiffness important? One property of muscles that is strongly affected by stiffness is their force-length relationship. All skeletal muscles exhibit an optimal range of length (L_{opt}) over which they can exert maximal force. Due to actin-myosin filament overlap, a muscle's ability to generate force is

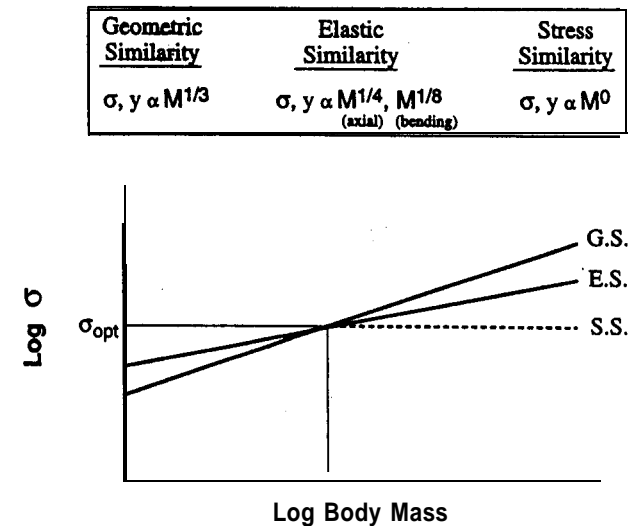


FIGURE 3 Theoretical logarithmic scaling of musculoskeletal stress (σ) versus body mass for the three similarity models: geometric (G.S.), elastic (E.S.), and static stress (S.S.). Only for S.S. does stress remain constant with change of size. For both G.S. and E.S., stress (and deflection of bone elements, y) scales with body mass, according to the above relationships (E.S. and S.S. relationships are based on McMahon [19]). For a given optimum stress (σ_{opt}) at a given mass, evolutionary decreases in body size according to G.S. or E.S., suggest reduced stress, increased stiffness, and increased safety factor. Evolutionary or ontogenetic size increases, on the other hand, predict increased stress, reduced stiffness, and reduced safety factor. These scaling trends suggest that, whereas peak stress and safety factor (i.e., strength) are important at large size, stiffness may be the key design constraint at small size.

greatly reduced at long lengths ($> 20\%$ of L_{opt}) and at short lengths ($< 20\%$ of L_{opt}). Consequently, the operating length of a muscle must be matched to the length of its fibers. If the tendons and bones of the limb become too slender relative to the forces that they must transmit, their resulting deflections might require excessive length change of the muscles' fibers, placing the muscles at a disadvantage for effective control of limb motion [25]. In most cases, the thickness of mammalian tendons seems to be disproportionately large relative to the forces that the tendon's muscle can exert, such that many tendons operate with safety factors in the range of 8-10 [17]. This suggests that stiffness can be as important a design constraint as strength. Geometric scaling to smaller body size is consistent with this observation.

While evolutionary decreases in size, at least within mammalian taxa, appear to be generally rare (the notable exception being insular island popu-

lations), interpretations of the importance of stiffness versus strength as constraints on mechanical design depend critically on what body size stress is considered to be “optimal” for the dimensions of the organism (σ_{opt} , Figure 3). Although no attempt is made here to define σ_{opt} , Alexander et al. [3] have defined an optimal bone stiffness in relation to bone stress, as that which would minimize the combined weight of bone and muscle in the limb at a peak stress of 70 MPa. Their analysis, however, does not consider scale effects of size. In the case of an evolutionary increase in size within a lineage (Cope’s rule; see Stanley [27] and Alroy [4]), therefore, stiffness may be the limiting constraint at small size, with a shift to strength (and safety factor) as the lineage evolves to larger size along a geometrically similar trajectory. In order to distinguish this, it would be necessary to demonstrate a reduction in safety factor from what would be considered an “excessive” value at small size, which is not an easy task.

5 DIFFERENTIAL SCALECONSTRAINTS WITHIN A TREE

As with the scaling of the mammalian musculoskeletal system, differential constraints on mechanical design also appear to apply to the scaling of branch architecture within trees. By sampling the branching architecture of a single tree, Bertram [5] has shown that two distinct size classes and scale patterns exist within a silver maple (*Acer saccharinum*). Nonperipheral branches (trunk and main supporting branches) scaled with strong positive allometry, closely matching McMahon’s [19] elastic similarity model (Figure 4). Reduced major axis (RMA) and least-squares (L-S) regression give exponents that bracket the predicted $2/3$ value for elastically similar deflections that McMahon and Kronauer [22] previously have found for white oak (*Quercus alba*). On the other hand, the peripheral (leaf bearing) branches scaled with substantial negative allometry: $L \propto D^{1.39}$ (RMA regression), such that these smaller branches become relatively more slender as they grow. The divergence in scale pattern is clearly seen when the slenderness ratio (L/D) of different size classes of the tree’s peripheral and nonperipheral branches is plotted versus branch diameter (Figure 4(c)).

These distinct scaling patterns suggest that, whereas strength and stiffness are important to the design of the nonperipheral weight-support branches, in which elastic similarity applies, flexibility is key to the function of the peripheral branches. Being flexible enables the tree’s peripheral branches and leaves to reorient in the wind to reduce drag. The small diameter of these branches also means that they are difficult to break by bending: the smaller a beam’s diameter, the less strain can be developed for a given bending curvature (an analogous but more extreme example of this is glass optical fibers, which have considerable flexibility and rarely break, despite the high stiffness and brittleness of glass as a material). An advantage of studying scaling patterns within a single individual, such as the sugar maple, is the absence of

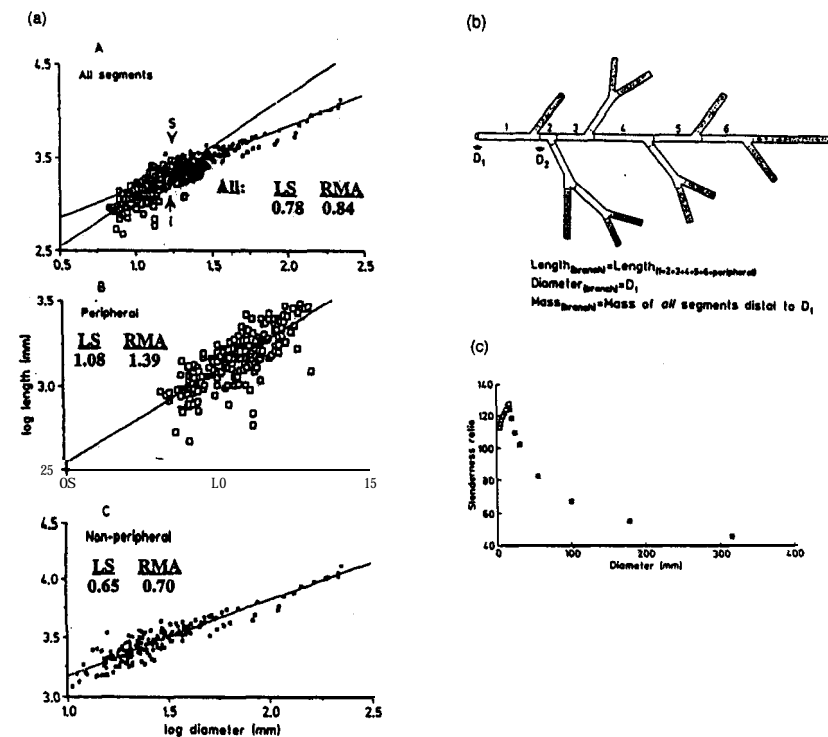
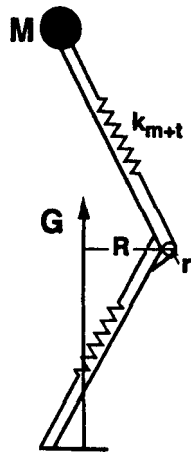


FIGURE 4 (a) Differential scaling of branch dimensions (length versus diameter) within a silver maple (*Acer saccharinum*). Branches were divided into two size classes: nonperipheral supporting branches (small solid squares) and peripheral leaf-bearing branches (larger open squares); branch length and diameter being determined as shown in (b). Nonperipheral and peripheral branches separated statistically into two size classes (large and small) and showed significantly different scale relations. Whereas nonperipheral branches scaled with strong positive allometry (slope < 1), close to McMahon’s [19] elastic similarity model and similar to the branching scaling observed for a white oak [22], the peripheral branches scaled with strong negative allometry (slope > 1), making them increasingly more slender as they grew in length. The change in scale pattern between the two branch size classes is clearly observed in (c), which shows the slenderness ratio (L/D) plotted against diameter (smaller peripheral branches, open squares; large nonperipheral branches solid squares).

SPRING STIFFNESS $O = F / \Delta x$



Leg Stiffness depends on 2 Factors:

- 1) muscle mechanical advantage (r/R)
 r/R a Stiffness
- 2) structural stiffness of elements (k_{m+t} , k_{bone})
 E & A , I

FIGURE 5 Whole limb spring stiffness (elastic deformation of the limb during ground support) depends on two factors: (1) muscle mechanical advantage (r/R) and (2) the structural stiffness of muscle tendon (k_{m+t}) and bone (k_b) support elements (depicted here for the “knee” joint). The latter depend on the elastic modulus of the tissues and their shape (cross-sectional area, A , and second moment of area, I , for bending).

genetic variation; however, the disadvantage is that generalizations to other individuals within the species and across species is more limited. Additional studies of other trees are needed to test the generality of these intriguing results.

6 SCALING OF LIMB MECHANICAL ADVANTAGE AND LEG STIFFNESS

Changes in limb mechanical advantage that allow terrestrial mammals of vastly differing size to maintain similar levels of peak bone and muscle stress were discussed above. In addition to affecting the magnitude of muscle force required to support an animal’s weight, changes in limb posture also likely affect the scaling of limb stiffness during running (Figure 5). Whole leg stiffness (k_{leg} , after McMahon and Cheng [21] and Farley et al. [12]) can be defined as the ratio of the displacement (AL) of the leg during the stance phase of a step to the peak ground reaction force (G): $k_{leg} = AL/G$ (Figure 6). In

running, trotting, galloping, and hopping gaits, when an animal lands on a limb, its CM falls during the first half of stance, compressing its leg spring. During the second half of stance its leg spring recoils, as its CM rises, until the limb leaves the ground. Displacements of the leg spring (AL) are a function of the cumulative angular excursions of the limb’s joints ($\Delta\theta$) during its contact with the ground (Figure 6). The notion that the leg functions like a spring derives from the fact that these “bouncing” gaits all utilize a similar energy conserving mechanism [10], in which the potential and kinetic energy that is lost as the body’s CM falls (Ay) and decelerates during the first half of stance is converted into and stored as elastic strain energy in the tendons, ligaments, and muscles of the limb. This elastic energy is subsequently recovered during the second half of stance, allowing the animal to regain its lost potential and kinetic energy as it leaves the ground. Consequently, compression of the “leg spring” actually reflects the stretching of muscle-tendon and ligamentous spring elements in the limb. (Displacements due to compression of articular cartilage and bone flexure, in comparison, are likely to be quite small: i.e., $k_b \gg k_{m+t}$.)

k_{leg} depends on two general factors (Figure 5): (1) the structural stiffness of limb support elements: the muscle-tendon units and bones (k_{m+t} and k_b), and (2) the limb’s muscle mechanical advantage (r/R , defined in Figure 1). The former depends on the material moduli (E) of the elements and, as noted above, their shape (length relative to cross-sectional area and second moment of area). The latter reflects the relative magnitude of force that the muscle-tendon (and bone) elements must generate (or support) for a given magnitude of ground reaction force at the foot. In a recent study of seven bipedal and quadrupedal mammals, Farley et al. [12] found that k_{leg} scaled proportionally to $M^{0.67}$, with larger animals having stiffer leg springs. This resulted from the fact that peak ground reaction forces scaled directly with the animal’s body weight ($G \propto M^{0.97}$) and displacements of their leg spring, AL , scaled proportional to $M^{0.30}$ (all exponents being close to simple fractional values predicted by geometric similarity: $M^{2/3}$, M^1 , and $M^{1/3}$).

This pattern of leg spring stiffness matches the predicted changes in whole limb displacement associated with postural adjustments in muscle mechanical advantage. As discussed above, these changes in muscle mechanical advantage are required to maintain bone and muscle stress constant in different-sized mammals (0.03 and 300 kg) [8], by matching muscle force to the scaling of bone area and muscle area (Table 1). The stiffness of the muscle-tendon spring ($k_{m+t} = F/\Delta x$) reflects the ratio of force transmission relative to its stretch, which can be related to the joint moment arm (r) and joint angular displacement ($\Delta\theta$) according to

$$\Delta x = r \Delta\theta. \quad (1)$$

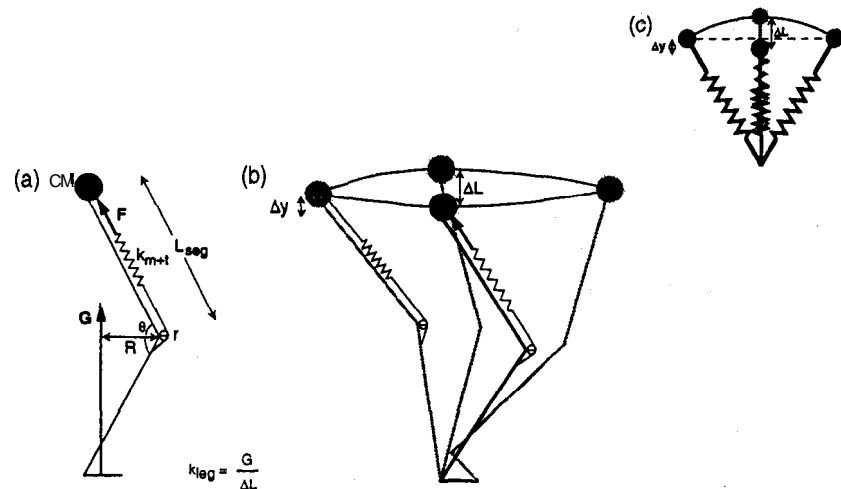


FIGURE 6 (a) Following McMahon and Cheng [21] and Farley et al. [12] the stiffness of the whole limb (k_{leg}) can be defined as the maximum displacement of the limb (ΔL) divided by the ground reaction force (G) acting on the limb. ΔL represents the displacement of the limb, which occurs due to flexion of limb joints, as the limb contacts the ground (initially ground force and muscle-tendon force are zero), becoming compressed at mid-support when maximum G and muscle force (F) are developed (dark lines in (b)). Subsequently, the limb rebounds as the “leg spring” is unloaded, causing the CM to rise during the second half of stance. The muscle-tendon model of leg spring stiffness depicted in (a) and (b), for the purpose of analyzing how limb mechanical advantage affects leg spring stiffness, is analogous to the simple mass-spring model. (c) used by McMahon and Cheng [21] and Farley et al. [12]. Reprinted with permission from Elsevier Science.

Correspondingly, the vertical displacement of the whole leg (ΔL) will be a function of leg segment lengths and joint angular displacements. Given

$$L = 2L_{seg} \sin \theta \quad (2)$$

we can write

$$\Delta L = 2L_{seg} \cos \theta \Delta \theta. \quad (3)$$

Following a similar analysis by McMahon et al. [23], we can assess how much changes in limb posture (reduced mechanical advantage, r/R) versus muscle-tendon stiffness (k_{m+t}) contribute to L_{leg} . Given

$$k_{leg} = \frac{G}{\Delta L} \quad (4)$$

and

$$G = \frac{Fr}{R} \quad (5)$$

it follows that

$$k_{leg} = \frac{Fr}{\Delta LR}. \quad (6)$$

Substituting for F in terms of k_{m+t} and Δx , gives

$$k_{leg} = k_{m+t} \frac{\Delta x r}{\Delta LR}. \quad (7)$$

Using Eqs. (1) and (3), we can rewrite Eq. (7) as

$$k_{leg} = k_{m+t} \frac{r^2}{2L_{seg} \cos \theta R} \quad (8)$$

and recognizing that $R = L_{seg} \cos \theta$, Eq. (8) simplifies to

$$k_{leg} = k_{m+t} \frac{r^2}{2R^2}. \quad (9)$$

Hence, the ratio of k_{leg} to k_{m+t} scales as

$$\frac{k_{leg}}{k_{m+t}} \propto \frac{r^2}{R^2} \propto M^{0.54} \quad (10)$$

suggesting that k_{m+t} scales $\alpha M^{0.13}$ ($M^{0.67}/M^{0.54}$). A theoretical basis for why the muscle-tendon stiffness scales in this manner ($\alpha M^{2/3}$) is unclear because it reflects a geometric change in leg stiffness ($\alpha M^{2/3}$) divided by an allometric change in limb mechanical advantage squared (approximately $\alpha M^{1/2}$). This result may also depend on modeling k_{leg} based on the displacement of a single joint. When other joints are taken into account, the scaling of leg stiffness relative to limb mechanical advantage, and hence, muscle-tendon stiffness, may differ from the analysis shown above. It will also be important to explore the function of muscles and muscle-tendon components in different-sized animals in order to determine whether their active force-length properties match the overall scaling predicted by whole leg stiffness and postural shifts in mechanical advantage.

The scaling of k_{m+t} suggested by the forgoing analysis indicates, therefore, that other size-related changes in muscle-tendon architecture are likely to contribute to the enhanced stiffness of larger animal limbs. Given that muscle stiffness is less than tendon stiffness, it seems likely that the relatively shorter muscle fibers ($\alpha M^{0.28}$) [1] of larger mammals and their relatively longer tendons may both contribute to the suggested overall increase in muscle-tendon stiffness. At present, these observations, and the predictions derived from them, require further study.

7 CONCLUSIONS

The observed scaling patterns of musculoskeletal design within terrestrial mammals suggests that differential mechanical constraints operate over different ranges of size and taxa. No one pattern, or general scaling model, explains the range of observed solutions. Whereas peak stress and safety factors are probably limiting constraints over much of the terrestrial size range, stiffness may be the key design constraint at smaller size. Further, differing mechanisms for maintaining uniform safety factors also appear to operate. Over much of their size range (0.1 to 300 kg), posture-related changes in limb mechanical advantage occur that enable terrestrial mammals to match locomotor forces to the scaling of bone and muscle areas. Intriguingly, within this size range there appears to be a link between the scaling of transport processes for energy supply and use, which obey a $3/4$ power law, and the scaling of muscle force requirements for terrestrial locomotion. However, at larger sizes (> 300 kg), more extreme positive allometry (robust scaling) and/or reductions in locomotor performance appear to be required in order to keep peak stresses within a safe range. How these adjustments in locomotor support affect muscle-force generating requirements in relation to the metabolic supply of energy as yet remains unknown. Posture-related changes in limb-muscle mechanical advantage are also shown to be consistent with recently observed changes in the stiffness of animal limbs (k_{leg}) [12], in which the shift to a more upright posture to reduce musculoskeletal loading for constant safety factor also results in an increased limb stiffness, counter to the decrease in stiffness predicted by geometric or elastic similarity scaling at larger size (Figure 3). Consequently, changes in limb stiffness that would be predicted by the structural scaling of limb support elements (Figure 3) must also take into account size-related changes in limb mechanical advantage. Finally, as for the limbs of terrestrial mammals, differential scaling patterns and design constraints are also to be found within the branching architecture of a single tree: larger structural support branches scale with positive allometry to avoid excessive deflection, whereas small leaf-bearing branches scale with negative allometry precisely in order to achieve flexibility, reduce drag, and avoid bending failure.

Although common design principles and a single scaling model may help to explain general features of vascular and respiratory supply networks within biology, no one scaling model appears sufficient for explaining how mammals and trees have evolved to meet the mechanical demands of life on land. Nevertheless, it is the case that certain features, largely those that reflect the strength of the materials of which even distantly related organisms are constructed, are scale invariant. As a result, regular size-related changes in other features are required either to maintain a constant mechanical safety factor or to achieve an appropriate limb (or branch) stiffness.

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