demonstrated for Fe/Ge, Fe/GaAs, Fe/ZnSe, and Co/GaAs. Many of the applications discussed here might be suitable for nonepitaxial magnetic films as well, which opens the way for a host of new possibilities, including alloys of both rare-earth and transition metal ferromagnets, as well as ferromagnetic and ferrimagnetic insulators. Work on these possibilities is under way at a number of laboratories, and it can be anticipated that new hybrid magnetic-semiconducting materials will provide not only technological opportunities but also opportunities for scientifically probing condensed matter behavior.

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Biomechanics of Mammalian Terrestrial Locomotion

ANDREW A. BIEWENER

Mammalian skeletons experience peak locomotor stresses (force per area) that are 25 to 50% of their failure strength, indicating a safety factor of between two and four. The mechanism by which animals achieve a constant safety factor varies depending on the size of the animal. Over much of their size range (0.1 to 300 kilograms), larger mammals maintain uniform skeletal stress primarily by having a more upright posture, which decreases mass-specific muscle force by increasing muscle mechanical advantage. At greater sizes, increased skeletal allometry and decreased locomotor performance likely maintain stresses constant. At smaller sizes, skeletal stiffness may be more critical than strength. The decrease in mass-specific muscle force in mammals weighing 0.1 to 300 kilogram indicates that peak muscle stresses are also constant and correlates with a decrease in mass-specific energy cost of locomotion. The consistent pattern of locomotor stresses developed in long bones at different speeds and gaits within a species may have important implications for how bones adaptively remodel to changes in stress.

THE INVASION AND EXPLOITATION OF THE EARTH'S TERRESTRIAL environment has yielded a diverse range of animals that share the common problem of movement and support against gravity. This diversity is manifest in size (terrestrial mammals alone span six orders of magnitude in body mass), morphology (shape and number of supporting limbs), locomotor performance, and skeletal materials used. Such diversity raises two important questions: (i) how do animals that differ greatly in size cope with the problem of mechanical support and (ii) do similar mechanical constraints apply to all terrestrial species? Engineering theory can be applied to biological systems to help answer these questions, revealing basic principles that govern locomotor function and the design of skeletal support in living organisms (*1*).

The most important and obvious mechanical requirement for most structures is to avoid breaking. Selection therefore may be expected to favor changes in the form, material organization, or mass of biological structures that decrease the probability of their failure during a lifetime of use. Forces acting on structures, such as those acting on an animal's skeleton during locomotion, are supported as stresses (force per area) developed within the structure. The ratio of failure stress (mechanical strength) to functional stress defines a structure's safety factor (*2*). Failure in a biological sense however need not involve actual rupture of the structure, as excessive deformation (yielding) may render the structure nonfunctional without being ruptured. Although the principle that functional stresses not cause mechanical failure may seem trivial, the question of precisely what safety factor a particular structural element, such as a bone or a tendon, should have (that is, is favored by natural selection) is far less clear, yet critical to an organism's success.

Human-engineered structures commonly are designed to have safety factors ranging from four to ten, depending on the materials of which the structure is built, the cost of the materials, and the accuracy with which the range of forces that the structure is likely to experience can be predicted (*2*). To determine the safety factor of biological structures and whether one safety factor is appropriate for a broad range of species and for different skeletal tissue components, the material properties of skeletal tissues from various species must

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be compared to the stresses developed in them during activities such as locomotion. Although other criteria may be important in evaluating the quality of design and functional role of skeletal structures (*2–4*), mechanical stress and strain (percentage deformation of a material when loaded) are most easily determined empirically and are those for which reasonable data exist in a range of living mammals.

Before considering experimental data on the magnitude of locomoter stress and the safety factor of the mammalian skeleton, it should be noted that, as for safety factors of human engineered structures (*2*), both the biological cost of failure (ultimately measured in terms of fitness) and the energy cost to build, maintain and transport a structure probably affect the safety factor favored by natural selection (*5*). For instance, if the cost of failure to the organism is low (in that the structure can be repaired or does not critically compromise the overall functional integrity of the system), a lower safety factor is likely to be favored, reducing the costs of construction and transport. If, on the other hand, the cost of failure is high, the additional mass required to achieve a greater safety factor will be tolerated. However, in that these costs are difficult to quantify, virtually no data exist to test how they affect the safety factors of biological structures. Developmental processes underlying the differentiation, growth and regulation of skeletal form and mass also likely affect a structure's safety factor in terms of the variability of strength in adult elements. The symmetry of form and the control of material strength of contralateral avian limb bones (mean strength varies by less than 0.24%) (*6*) indicate that biological control of skeletal growth and maintenance is precise and thus unlikely to be an important factor compared to the variation associated with activity-related loading in determining the safety factor favored for bone.

In this article, then, I address the evolution and biomechanics of musculoskeletal design by focusing on the selection of biological safety factors in relation to the stresses developed during strenuous locomotion in mammals. As these stresses are unlikely to be the maximum stresses that the skeletons of these species experience over a lifetime of use, the safety factors obtained are defined in the context of an allowable stress range (*2*). Principles that emerge for mammals likely apply to other groups of terrestrial organisms constructed of similar tissue components. I also examine how mechanical constraints may influence the energetic cost of locomotion, change of gait, and preferred speed within a gait, as well as the adaptive response of bone to changes in stress.

Tissue Properties

Phylogenetically, bone is a conservative tissue; the earliest vertebrates exhibited histological tissue types similar to those found in living species (*7*). Among terrestrial mammals, then, it is not surprising that the organization and composition of bone in the limb skeleton is quite similar, possessing fairly uniform material properties in a diverse range of species (*4*). Percentage mineralization of compact cortical bone typically ranges from 63 to 69%, compressive failure strength ranges from 180 to 220 megapascals, and stiffness (elastic modulus) ranges from 14 to 22 GPa. Given that bone mineralization levels and attendant mechanical properties can vary considerably when the range of functions subserved are distinct (*8*), the consistency of bone tissue properties in the limb skeletons of terrestrial mammals suggests a compromise between selection for energy absorbing capacity (impact loading) versus strength and stiffness (effective force transmission) (*4, 8, 9*).

Vertebrate striated muscle and tendon are also highly conservative tissues, possessing similar force-generating or force-resisting properties in a variety of species. Although the speed of shortening and oxidative capacity of muscle fibers can vary considerably in different muscles and among different species (*10, 11*), maximum isometric myofibrillar stress is fairly uniform, ranging from 160 to 300 kPa in a variety of vertebrate skeletal muscles (*10, 12, 13*). (Much of the variation is due to differing volume fractions of non-contractile components—mitochondria and capillaries—in aerobic versus more glycolytic muscle fibers (*14*). The strength of a variety of mammalian tendons similarly ranges very little, from 80 to 100 MPa, rupturing at a strain of 0.08 to 0.10, and having an elastic modulus of about 1.0 GPa (*15*).

Given the generally similar mechanical properties of these tissues, it seems likely that, regardless of an animal's size, the shape and mass of its skeleton or its locomotor ability, selection favors similar peak functional stresses in each type of skeletal support element (muscle, tendon or bone), ensuring a uniform safety factor to failure in all mammalian species (*16–18*). This hypothesis has been tested by experimentally determining the stresses developed in limb bones of mammals ranging 3000-fold in size, and in animals of similar size, but differing locomotor ability.

Body Size and Skeletal Stress

As with the mass-specific transport capacity of many physiological processes (*19*), the capacity of a bone, muscle or tendon to support or generate force also decreases relative to the increase in mass or weight of the animal. Under geometric similarity [in which shape remains constant and all linear dimensions scale proportional to ($\propto$) body mass $(M)^{1/3}$] the expected increase in skeletal or muscle stress, assuming force increases proportional to increases in body mass, would be (force/area, F/A) $\propto$ $(M^{1.0}/M^{2/3})$ $\propto$ $M^{1/3}$. First recognized by Galileo (*20*), this problem has been reexamined during the past century (*21*) with the assumption that selection strongly favors

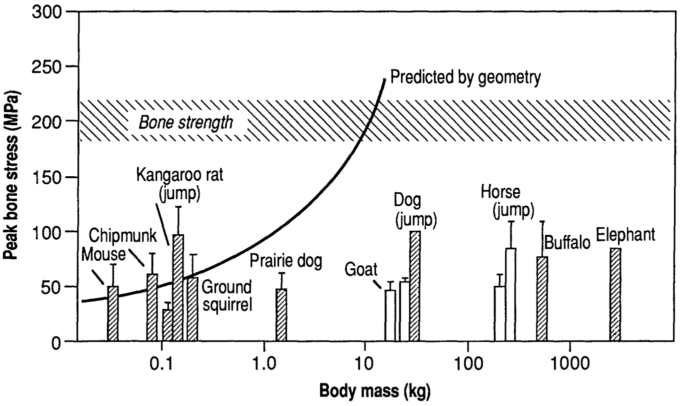

Fig. 1. Mean peak compressive stresses calculated for the major long bones of each species when galloping or when jumping, plotted as a function of body mass on semilogarithmic coordinates. Hatched bars are stress data obtained from force platform and kinematic analyses. Open bars are stresses calculated from in vivo principal strain recordings at the bone's midshaft. Error bars are 1 SD of the mean for the different limb bones measured within each species. The solid line shows the change in peak bone stress predicted based on the scaling of the limb bone dimensions (*22, 23*), assuming a peak stress of 50 MPa at 0.1 kg body mass. Safety factor is calculated based on compressive failure strength [180 to 220 MPa (*4*)], rather than yield strength, as the latter is difficult to define accurately. Yield strength represents a more realistic failure limit for most bones, however, so that the safety factor of bone based on yield strength is somewhat lower than the values derived based on compressive strength. Data for the mouse (n = 3) and prairie dog (n = 3) are from (*60*); for ground squirrel (n = 3) and chipmunk (n = 3) from (*29*); for kangaroo rat (n = 4) (*30*); for goat (n = 3) (*16*); for dog galloping (n = 2) (*24*); for dog jumping (n = 1) (*59*); for horse (n = 5) (*17, 25*); and for buffalo (n = 1) and elephant (n = 1) (*28*).

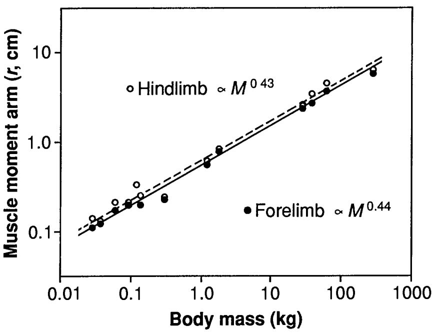

Fig. 2. The scaling of muscle moment arm (r) for the forelimb (solid line) and hindlimb (dashed line) plotted as a function body mass on logarithmic coordinates. The data represent the species mean moment arm for anti-gravity (support phase) muscle groups of the forelimb and the hindlimb based on measurements from radiographs or dissection of 13 mammalian species. Moment arms were determined corresponding to the angular displacement of each joint during the middle third of the support phase. Least squares regression slopes for the forelimb (slope, 0.443 ± 0.026 95% CI) and the hindlimb (slope, 0.434 ± 0.042 95% CI) show the same allometric increase in muscle moment arm *versus* body mass, which increases the moment produced at a joint for a given mass-specific muscle force.

changes in skeletal form or function to avoid a significant size-dependent increase in stress.

Changes in bone shape (skeletal allometry) were initially hypothesized as the means by which animals avoid a scale-dependent increase in mechanical stress. Though present, changes in bone shape are far less drastic than would be required to maintain similar peak stress and a uniform safety factor in the skeleton of different sized mammals. When considered over most of their size range (0.005 to 2000 kg), terrestrial mammals are nearly geometrically similar (isometric) (*22*). On the basis of the scaling of limb bone dimensions, peak skeletal stress is predicted to increase $\propto M^{0.28}$ (*23*).

Measurements of in vivo bone strain (*16–18, 24–26*) and calculation of bone stress from force platform recordings and high-speed light and x-ray cine films (*27–30*) in different sized terrestrial species during strenuous locomotion and jumping, however, demonstrate a safety factor of between two and four for the limb skeletons of these animals (Fig. 1). Rather than increasing sharply with size [as predicted by the scaling of bone geometry (Fig. 1, solid line)], peak locomotor stresses range from 50 to 100 MPa. (Much of the variation in this value is due to differences in technique for determining skeletal stress and to nonequivalence of exercise conditions for the different sized animals.) A safety factor of between two and four matches fairly well the estimates of safety factor (range, 1.3 to 8) for other biological tissues (*5*).

Muscle Mechanical Advantage and Musculoskeletal Stress

Given that only minor changes occur in bone shape, mass-specific forces acting on the skeleton must decrease to maintain a uniform safety factor in larger animals. Rather than alter shape or material strength, selection appears to have favored an allometric change in muscle mechanical advantage (or moment arm, r) and the configuration of limb elements (*31*) as the primary means to lower mass-specific bone and muscle force as animals increase in size. The mechanical advantage of forelimb and hindlimb agonist muscle groups scales allometrically with increased size, proportional to $M^{0.43 \pm 0.03}$ (Fig. 2) (isometry predicts $r \propto M^{0.33}$). Consequently, with a greater mechanical advantage the muscles of larger animals produce greater joint moments for a given mass-specific force.

In addition, large mammals run on less bent limbs than small mammals, which aligns their limb joints more closely with the resultant ground reaction force vector ($\mathbf{F}_g$, Fig. 3). This shift in posture diminishes external joint moments by decreasing the moment arm of the ground reaction force (R) acting about the joints of the limb. As a result, the "effective mechanical advantage" ($EMA = r/R$) of limb muscles (*32*) is increased, which further decreases the magnitude of muscle force needed to support the animal while running.

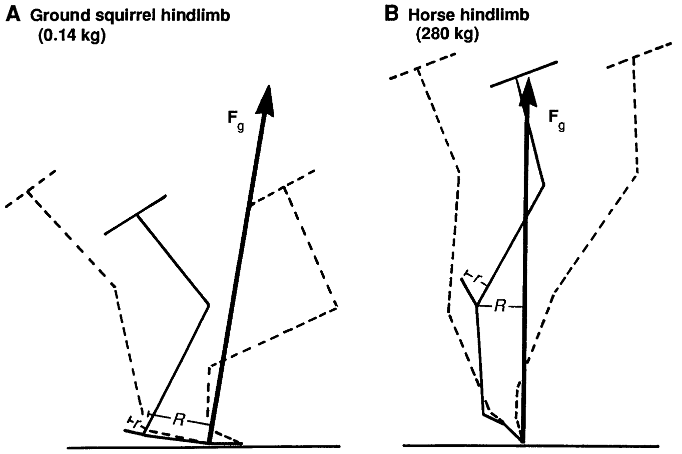

Fig. 3. Diagram of the hindlimb posture of (**A**) a ground squirrel and (**B**) a horse during the support phase of a gallop drawn to equivalent scale. Dashed lines indicate limb position at the beginning and the end of the support phase. Solid lines show the position of the limb at midsupport, relative to the orientation of the ground reaction force vector ($\mathbf{F}_g$) acting up from the foot at this time. Effective mechanical advantage (*EMA*) is defined as the ratio of the agonist muscle moment arm (r) to the moment arm (R) of $\mathbf{F}_g$. These distances are shown for the ankle joint of each animal. The more crouched posture of the ground squirrel results in a greater value of R for its size, compared to the horse, which increases the magnitude of mass-specific force required to balance external joint moments. Muscle *EMA*, therefore, is greater in larger species (Fig. 4) due to both an allometric increase in muscle moment arm (r, Fig. 2) and a size-dependent change in posture that reduces the moment arm (R) of the ground reaction force ($\mathbf{F}_g$).

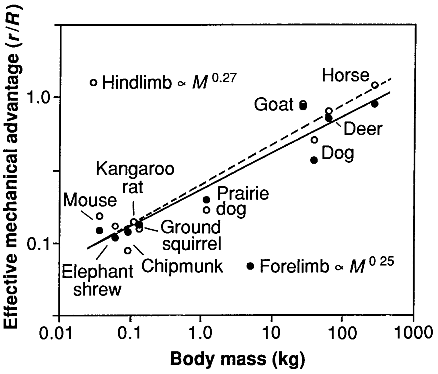

Fig. 4. Muscle effective mechanical advantage (*EMA*) as a function of body mass on logarithmic coordinates. Data represent the mean for the joints of each limb. All data, except for the prairie dog and deer (*60*) are from (*31*). The least-squares regression slopes for the forelimb (solid line: slope, 0.251 ± 0.065 95% CI) and hindlimb (dashed line: slope, 0.273 ± 0.072 95% CI) do not differ significantly ($P > 0.5$). The overall scaling for both limbs is $EMA \propto M^{0.258} \pm 0.043$. Though less robust, the scaling of *EMA* for individual joints is also significant (*31*).

Measurements of limb kinematics and ground reaction forces for ten mammalian species, ranging from 0.045 to 280 kg body mass, shows that the effective mechanical advantage of agonist muscle groups in the forelimb and hindlimb of these species increases $\propto M^{0.26}$ (with a 95% confidence interval of ±0.04) (Fig. 4). As the force exerted by muscles constitutes the major fraction (50 to 90%) of force that must be resisted by limb bones during locomotion (*29, 33*), the observed increase in muscle mechanical advantage accounts for 85% (*31*) of the decrease in force required to maintain similar skeletal stresses in large and small animals. Due to differences in *EMA*, peak muscle force ranges from 10 times the magnitude of $\mathbf{F}_g$

Table 1. Mechanical constraints on mammalian skeletal design.

Body mass (kg)	Criterion of bone dimensions	Determinant	Mechanism
0.001–0.1	Stiffness	Muscle force-length properties	Geometric similarity
0.1–300	Safety factor	Failure stress	Muscle mechanical advantage and limb posture; bone allometry slight
300–2500	Safety factor	Failure stress	Reduced locomotor performance; bone allometry strong

in the mouse (*EMA* = 0.1) to one $\mathbf{F}_g$ in the horse (*EMA* = 1.0).

Animals generally exert ground reaction forces that are a constant multiple of body weight (two to three times body weight for each limb) (*29, 33, 34*). Consequently, because of the scaling of muscle mechanical advantage, muscle force increases proportional to $M^{0.74}$ (M/EMA). Given that muscle fiber area, calculated from measurements of muscle mass and fiber length in a diverse sample of terrestrial mammals (*35*), scales proportional to $M^{0.80}$, peak muscle stress is also nearly independent of body size, scaling proportional to $M^{-0.06}$ ($F/A \propto M^{0.74} \times M^{-0.80}$). Normalized to changes in muscle mass (rather than body mass), the magnitude of force exerted per unit volume of muscle decreases with increasing size, proportional to $M^{-0.29}$ ($\propto M^{0.74} \times M^{-1.03}$, assuming constant muscle density).

Differential Allometry

Changes in limb posture and muscle mechanical advantage provide an explanation for stress similarity in terrestrial mammals ranging from 0.1 to 300 kg body mass, but can such changes account for similar stresses in species outside this size range? The limb skeletons of the largest land mammals, the ceratomorphs (rhinos, tapirs, and their fossil relatives), in fact scale with extreme allometry (*36*), close to that predicted by a model of static stress similarity ($1 \propto d^{1/2}$) (*37*). Mass increase in these animals results mainly from increases in diameter (and hence, area), rather than length, leading to very robust skeletons in the largest species. For mammals greater than 300 kg, then, further adjustments in limb posture may be of limited utility; extreme changes in bone shape are required to maintain an acceptable safety factor (Table 1). Very large, robust species also exhibit an apparent decline in locomotor performance (speed and mobility) (*31, 38, 39*), which may represent an additional requirement to keep locomotor stresses within a safe range.

Variation in the scaling of limb bone dimensions in mammalian taxa of differing ranges of size, when examined at lower taxonomic levels, reinforces the view of differential skeletal allometry (*40, 41*). Within the order Carnivora, families exhibit progressive (intrafamilial) skeletal allometry with increased mean family body mass (*41*). At a higher taxonomic level, comparison among orders reveals that bovids (artiodactyl ungulates spanning the largest size range of any mammalian family) scale similarly to the largest carnivoran species (*37, 41*), and thus, are intermediate between the extremely large ceratomorphs (static stress similarity) and much smaller rodents (geometric similarity, $1 \propto d$) (*40, 42*). Evolutionary reduction in distal limb skeletal element number, increased bone length, and restricted joint mobility, features long recognized as adaptations for speed and increased body size in ungulates (*9, 38*), presumably have also evolved to maintain peak stress levels within a biologically acceptable range.

Traditionally, studies of scale effects in biology have focused on functional constraints associated with increased size within a lineage (*19, 43*), with strength assumed to be the limiting constraint: an isometric increase in size promotes increased stress and decreased safety factor (Table 1). In contrast, however, an evolutionary decrease in body size, in which geometric similarity is preserved, should favor increased safety factors (*44*). Although this trend is countered by the increase in mass-specific force resulting from decreased limb mechanical advantage as smaller species become more crouched (*31*), isometric reduction in body size diminishes the importance of peak stress as a limiting constraint on skeletal form. Stiffness, rather than strength, may be the more important factor underlying skeletal form in small terrestrial species (<0.1 to 0.3 kg body mass) (Table 1). Theoretical work (*45*) and experimental work (*46*) show that tendon stiffness is critical to the functional shortening range of a muscle (dependent on the force-length properties of the muscle fibers and the extent of tendon stretch, or "series elasticity"). Most tendons are considerably thicker and have a greater safety factor than would be expected solely on the basis of strength (*45*), apparently to ensure sufficient stiffness for control of length and more rapid force development by the muscle.

If strength were the sole mechanical constraint, decreases in body size would favor decreases in bone diameter $\propto M^{0.4}$ (*37*). Under these conditions, overall bone deflection would constitute a progressively greater fraction of muscle fiber length. Isometric decreases in body size, although producing excess tissue structure in terms of strength, therefore, may be required for sufficient skeletal stiffness to ensure effective muscle function in very small species. Once again, this is in contrast to evolutionary increases in body size in which larger species must maintain an adequate safety factor by one of several possible mechanisms, such as changes in limb posture or bone allometry (Table 1).

Muscle Force Generation and the Energy Cost of Locomotion

As the basic function of muscle is to convert chemical energy into mechanical work, it is likely that mechanical requirements for force generation greatly affect the overall energy cost of animal locomotion. In studies of 66 mammalian species, Taylor and co-workers (*47*) find that the minimum mass-specific energy cost of locomotion (cost of transport) decreases regularly with increasing size, $\propto M^{-0.30}$. The decrease in mass-specific cost cannot be explained, however, by the mechanical work performed by muscles to move the body's center of mass and swing the limbs. Small and large animals perform the same work to move each kilogram of their mass a given distance (*48*). Although limb muscles perform net positive work (shortening contraction) to move an animal over the ground, certain muscles may act as springs (undergoing brief phases of active lengthening and subsequent shortening) to store and recover elastic strain energy in concert with their tendons (*49, 50*), other muscles may only be actively lengthened, performing negative work to decelerate motions of the animal's mass, and still others may contract isometrically (performing zero work) to stabilize joints (*51*). Therefore, though all muscle contractions entail adenosine triphosphate (ATP) use associated with the cycling of cross-bridges, all contractile events do not correspond to a given amount of work performed. The lack of correlation between net mechanical work and energy cost of locomotion (*48*) reflects the multiple functional roles of skeletal muscle.

Other factors related to the cost of muscle force production, then, must determine the cost of animal locomotion. Two factors related to both muscle force generation and ATP use are (i) the magnitude of force generated per unit time, or the "tension-time integral" of force ($\int Fdt$) and (ii) the rate of force development (related to a muscle's intrinsic shortening velocity) and frequency of muscle activation (*10, 11, 52*). Although it is likely that the mechanical nature of the contractile event affects ATP use, the magnitude of muscle force exerted per unit time dominates the energy cost of locomotion. In support of this interpretation, when animals carry weights during locomotion their energy expenditure (oxygen consumption) at a given speed increases in direct proportion to the percentage increase in mass (*53*). In these experiments, stride frequency and limb contact time did not change, indicating that increases in energy cost likely involved increases in the time-integrated force generated by the muscles. Consequently, the observed decrease in volume-specific muscle force per unit time (or distance travelled) which keeps stress uniform in larger animals (*31*) could also explain, at least in part, a lower cost of transport. The agreement between the scaling of volume-specific muscle force ($\propto M^{-0.29}$) and whole animal cost of transport ($\propto M^{-0.30}$) strongly indicates that energy expenditure is coupled to the mechanical constraint of maintaining uniform muscle stress in animals ranging from 0.1 to 300 kg (Table 1).

In addition to the magnitude and duration of force generation, differences in the rate of muscle activation and force development also appear to underlie changes in energy cost. When compared at equivalent speeds, larger animals have lower stride frequencies ($\propto M^{-0.15}$ at the trot-gallop transition) than small animals (*54*). Associated with this lower stride frequency, the skeletal muscles of larger animals develop force and shorten more slowly than the muscles of small animals (*10, 11*). Lower rates of force development and shortening, in turn correspond to reduced energy expenditure in skeletal muscle (*11, 49*). As originally suggested by Gold (*55*), if energy cost is normalized for differences in stride frequency, terrestrial mammals expend the same amount of energy per unit mass during a stride at equivalent gaits (for example, 5.3 ± 0.3 J kg^{-1} per stride at the trot-gallop transition) (*54*). Consequently, it must be the case that changes in both force-dependent and time-dependent properties of muscle activation underlie changes in mass-specific cost of locomotion. The relative importance of these two factors on the cost of muscle force production during locomotion remains unclear, however, because muscle specific force and shortening speed both decrease with increased size in the species that have been studied.

Determinants of Speed and Gait

Terrestrial mammals use a variety of gaits to move. Although changes of gait clearly enable animals to run faster or achieve greater stability at lower speeds (*38*), it is less clear why animals consistently change gait at particular speeds and prefer a narrow range of speed within a gait (*12, 56, 57*). Preliminary data suggest that both mechanical and energetic factors underlie the choice of speeds preferred by animals and the speeds at which gait changes occur.

In nearly all mammalian species studied, rates of aerobic energy expenditure generally increase linearly with running speed and change of gait (*47*). When examined more closely in horses (*56*), however, energy use increases as a nonlinear (power greater than one) function of speed *within* a gait and actually decreases when the animals change gait. The curvilinear increase in energy cost *versus* speed within a gait indicates that horses, and possibly other species, have a minimal cost of transport at some intermediate speed within each gait. If allowed to freely select their speed within a gait, horses prefer speeds close to that at which cost of transport is minimal (*56*). In another study comparing the mechanics of quadrupedal white rats *versus* bipedal kangaroo rats (*12*), similar stresses (30 to 35% of maximal isometric) acted in the ankle extensors of each species when it moved at its preferred speed, suggesting that selection may favor a similar scope for the recruitment of muscle force from preferred to maximal speed in different species.

When compared at equivalent points in a gait, maximal principal strains recorded *in vivo* at the midshafts of the radius and tibia of goats (*17*) and dogs (*25*) are also similar, despite large differences in the absolute speed of each species. For example, at the fastest galloping speed measured (dog, 8.5 ms^{-1} versus goat, 4.5 ms^{-1}), maximal (compressive) bone strains differed little between the two species (dog, $-0.213 \pm 0.009\%$ versus goat, $-0.191 \pm 0.031\%$). Dogs achieve strain levels similar to those in goats by having thicker bones (greater cortical area and second moment of area) to withstand the greater ground reaction forces exerted at the higher speed. Skeletal modifications which maintain a uniform safety factor in these two similarly sized animals, therefore, are achieved by altering bone shape and mass in relation to locomotor performance, rather than by changes in locomotor limb posture.

Implications for Adaptive Skeletal Remodeling

Bone, like muscle and other connective tissues, is generally perceived to be capable of adaptively responding to changes in its loading during use. A causal relation between biological form and function in fact was first argued quantitatively in the late 1800s on the basis of trabecular bone organization (*61*). Studies of the relation between skeletal form and mechanical function during the past century have led to the general belief that adaptive changes in skeletal form are mediated by skeletal tissue strain (*4, 62–64*). Though it is clear that physical activity affects remodeling processes of the skeleton, and that cyclic, rather than static, loading is more effective as an osteogenic stimulus (*63, 65, 66*), the algorithm by which physical stimuli are transduced and invoke a cellular and ultimately, an organ level, response is largely unknown. In addition, it is unclear whether local cell populations in differing regions of a bone respond similarly to a given physical strain stimulus or are site-specific, varying from one site to the next.

Although strain magnitude is likely to be important in the regulation of bone remodeling (*67*), other features of the mechanical stimulus, such as strain rate, number of loading cycles, and strain distribution, are also probably involved (*4, 26, 63–66*). Recently, finite element models of developing endochondral bone primordia, in which strain energy density was used to distinguish between regions of hydrostatic stress (hypothesized to maintain·cartilage) as opposed to regions of shear stress (hypothesized to initiate subsequent ossification) (*68*), describe well the timing and pattern of ossification in developing fetal anlaga. However, experimental verification of strain energy density as the stimulus or controlling variable of mechanically induced bone remodeling is lacking.

One feature of a bone's loading history to emerge from comparative studies of locomotor mechanics that is relevant to tissue remodeling, is the consistent distribution of cortical strain maintained in a limb bone over an animal's normal range of gait and speed (*16, 17, 26, 27, 63, 69*). Although the magnitude of skeletal strain increases as an animal runs faster, the distribution of strain across the bone's cortex and along its length remains remarkably similar. The distribution of functional strain in a bone also changes little during post-natal growth (*26*). By simplifying the design requirements for the range of forces that a bone must support, a uniform functional strain distribution is likely advantageous and thus, relevant to the process of adaptive remodeling.

Experimental studies of skeletal remodeling in fact show the greatest response (change in bone mass or cortical area) when the bone's normal functional strain distribution is disrupted (*66*). These findings support the hypothesis that selection has favored a regulatory signal capable of distinguishing unusual loading circumstances from those more commonly experienced by the skeleton. Given the uniform strain patterns recorded in terrestrial locomotion, this would imply that, for most animals, adaptive skeletal remodeling is a fairly limited and infrequent event under natural conditions.

On the other hand, if maintenance of a bone's normal strain distribution is central to the process of tissue remodeling during growth and in response to exercise, cellular communication among differing regions within the bone may be a key requirement of this process, facilitating an integrated, organ-level response to changes in physical activity. Ultrastructural evidence for cellular communication among osteocytes and bone lining cells (*70*) and the correlation of translational activation of osteocytes immediately following a brief bout of physical loading (*71*) support this possibility.

In summary, comparative studies of the biomechanics of organisms provide an important approach for identifying and understanding general principles underlying the design and function of biological materials and structures, as well as mechanical constraints imposed on their evolution. Changes in the composition and properties of biomaterials are far less common than changes in shape or higher (system) level function to maintain a similar safety factor, in response to evolutionary change in an organism's physical requirements. Knowledge of the general relation between mechanical design and function, in turn, can provide important insight into clinically relevant questions concerning the adaptive response of skeletal tissues to physical activity. Still important to understand are (i) which aspects of the skeleton's loading history are most critical to determining its safety factor and likely influence adaptive tissue remodeling responses, (ii) whether similar design criteria hold for more diverse taxa, and (iii) how mechanical requirements for muscle force generation affect locomotor energy cost.

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