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# Unifying Principles in Terrestrial Locomotion: Do Hopping Australian Marsupials Fit In?<sup>\*</sup>

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## ABSTRACT

Mammalian terrestrial locomotion has many unifying principles. However, the Macropodoidea are a particularly interesting group that exhibit a number of significant deviations from the principles that seem to apply to other mammals. While the properties of materials that comprise the musculoskeletal system of mammals are similar, evidence suggests that tendon properties in macropodoid marsupials may be size or function dependent, in contrast to the situation in placental mammals. Postural differences related to hopping versus running have a dramatic effect on the scaling of the pelvic limb musculoskeletal system. Ratios of muscle fibre to tendon cross-sectional areas for ankle extensors and digital flexors scale with positive allometry in all mammals, but exponents are significantly higher in macropods. Tendon safety factors decline with increasing body mass in mammals, with eutherians at risk of ankle extensor tendon rupture at a body mass of about 150 kg, whereas kangaroos encounter similar problems at a body mass of approximately 35 kg. Tendon strength appears to limit locomotor performance in these animals. Elastic strain energy storage in tendons is mass dependent in all mammals, but exponents are significantly larger in macropodid. Tibial stresses may scale with positive allometry in kangaroos, which result in lower bone safety factors in macropods compared to eutherian mammals.

## Introduction

Hopping and bounding are the major gaits used by a large number of Australian marsupial species. An in-phase bipedal

hopping is characteristic of the majority of the Macropodoidea—the kangaroos and wallabies (Macropodidae) and rat kangaroos (Potoroidae; Windsor and Dagg 1971). Many of the smaller species, together with other marsupials (e.g., tree kangaroos and members of the Peramelidae, Dasyuridae) employ quadrupedal bounding gaits either exclusively or as part of a broader locomotor repertoire.

Hopping is obviously not restricted to macropodids, and there are many examples of hopping birds and mammals (e.g., Thompson et al. 1980; Hayes and Alexander 1983). Most of these hopping non-Macropodoidea have an adult body mass of less than 1 kg, the exception being the 4-kg springhare (*Pedetes capensis*). Modern hopping marsupials have adult body masses ranging from about 1 kg to about 70 kg, although the extinct giant kangaroos from the Pleistocene period are estimated to have reached about 150 kg (Murray 1991).

It is unclear what evolutionary pressures or constraints led to macropodoid marsupials using a hopping gait in contrast to the quadrupedal gaits commonly used by most eutherian terrestrial mammals. Hopping may have evolved from the bounding or half-bounding gaits that are commonly used by many of the smaller marsupials, such as bandicoots, dasyurids, potoroos, and some of the smaller macropods. The reasons why macropodids are the only large animals to use a hopping gait are not the primary focus of this article. However, some insight into the benefits and the limitations provided by adopting this gait may be obtained by examining the anatomical and physiological traits of macropodids in relation to locomotion.

A significant difference in the energetic cost between quadrupedal eutherian locomotion and bipedal kangaroo locomotion has been shown to exist (see Taylor et al. 1970; Baudinette 1989, 1994). This observation provides a starting point to explore hopping and quadrupedal forms of locomotion, emphasising unifying principles but also highlighting differences (or nonunifying principles) between gaits and the animals that use them. Although this article is primarily a study of whether kangaroos and their kin conform to typical placental mammal models, it should be noted that the observed differences may be the result of phylogeny or the mode of locomotion (hopping) used by macropodids.

## Material and Methods

Much of the data used in this article are from the published literature. New information on the musculoskeletal systems of macropodid marsupials and the northern brown bandicoot,

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*Isoodon macrourus*, is presented. The following macropod species were collected under Department of Environment and Heritage scientific purposes permit H0/000006/95SAA: *Aepyprymnus rufescens*, *Hypsiprymnodon moschatus*, *Macropus rufus*, *Macropus giganteus*, *Macropus eugenii*, *Macropus robustus*, *Macropus agilis*, *Onychogalea unguifera*, *Potorous tridactylus*, *Thylogale thetis*, *Thylogale stigmatica*, and *Wallabia bicolor*. Pelvic limbs were dissected fresh or after being stored frozen at  $-18^{\circ}\text{C}$ . Muscle mass, muscle fibre length, pinnation angle, sarcomere spacing, tendon length, and cross-sectional area data were collected for all muscles in the crural and pedal regions using the methods of Ker et al. (1988) and Bennett (1995). Moment arms of gastrocnemius, plantaris (flexor digitorum superficialis), and flexor digitorum profundus muscles about the ankle (hock) joint were measured (Bennett and Taylor 1995).

A number of tendons were tested to failure using an Instron 8031 servo-hydraulic materials-testing machine. Tendons dissected from the limbs of macropodids were wrapped in saline-soaked tissues, sealed in polythene bags, and stored frozen ( $-18^{\circ}\text{C}$ ) until testing. Each tendon was thawed and tested at room temperature ( $28^{\circ}\text{C}$ ). All tendons were loaded in tension at a strain rate of about  $1.10^{-2} \text{ s}^{-1}$ . The x-y plots of force  $v$  extension were used to determine failure stress, failure strain, and the tangent Young's modulus,  $E$ , for the linear portion of the curve.

Transverse plane computed tomography (Toshiba TCT-80A) was used to take 5-mm virtual slices of the tibial mid-shaft of macropods and bandicoots. National Institutes of Health image software and a digitising tablet linked to a PC were used to calculate the second moment of areas,  $I$ , after determination of the centroid for each bone (NIH image analysis performed on a Macintosh computer using the public domain NIH Image program, version 162, developed at the U.S. National Institutes of Health and available on the Internet at <http://rsb.info.nih.gov/nih-image>). All values of  $I$  were calculated about a medial-lateral axis on the assumption that the tibia bends in the anterior-posterior plane. Strain data verifying that this is the bending axis are not currently available for any of the Macropodoidea or Peramelidae. Additional second moment of area data for other mammals and birds were obtained from the literature.

## Results and Discussion

### Energetics

Taylor et al. (1970) were the first to study the locomotor energetics of terrestrial vertebrates, with many other studies occurring since that time (see Baudinette 1994). The majority have employed motor-driven treadmills and have measured oxygen uptake for individual animals travelling at constant speed. The rate of oxygen consumption ( $\dot{V}\text{O}_2$ ) under aerobic, steady-state conditions is indicative of the metabolic energy

cost, and these empirical studies have shown that  $\dot{V}\text{O}_2$  increases linearly with speed for the majority of vertebrates. The equation

$$\dot{V}\text{O}_2/M = 0.533M^{-0.316} \times v + 0.300M^{-0.303}$$

(where  $M$  = body mass [kg], and  $v$  = speed [ $\text{m s}^{-1}$ ]; Taylor et al. 1982) describes the mass-specific rate of oxygen consumption. It is widely used to estimate the aerobic cost of locomotion of terrestrial vertebrates irrespective of whether bipedal or quadrupedal gaits are used (Fedak and Seeherman 1979). This linear relationship between speed and energy cost is a strong unifying principle in terrestrial locomotion. Ninety percent of avian and mammalian species were reported to have  $\dot{V}\text{O}_2/M$  values that fall within 25% of the observed values provided by this regression at the middle of the speed range where measurements were made (Taylor et al. 1982).

However, there are exceptions to the rule. The red kangaroo (*Megaleia rufa* = *Macropus rufus*) data (Dawson and Taylor 1973) did not conform to this standard vertebrate model. *Macropus rufus* exhibited linear increases in oxygen consumption with increasing speed while using a pentapedal gait (involving the tail as a fifth supporting limb [Windsor and Dagg 1971]), but oxygen consumption became independent of speed once the animal started hopping bipedally. This uncoupling of locomotor speed from oxygen consumption has since been shown to occur in the tammar wallaby (*Macropus eugenii*; Baudinette et al. 1987). It is commonly assumed that all kangaroos and the larger wallabies conform to this pattern, but this has yet to be tested.

There are data available for other members of the Macropodoidea. The long-nosed potoroo (*Potorous tridactylus*; Baudinette et al. 1993) and brush-tailed bettong (*Bettongia penicillata*; Thompson et al. 1980), both of which are members of the family Potoroidae, appear unable to uncouple  $\dot{V}\text{O}_2$  from the speed of locomotion. The equation of Taylor et al. (1982) is reasonably effective in describing the linear increases in  $\dot{V}\text{O}_2$  with speed for these two species. The maximum speed reached by the quokka (*Setonix brachyurus*) was insufficient to determine whether an uncoupling occurs when the animal adopts a bipedal hopping gait (Baudinette 1977). The red-bellied pademelon (*Thylogale billardieri*) showed a low rate of increase of oxygen consumption with increasing speed when hopping (Warren 1979), a pattern not dissimilar to that seen in a much larger *M. rufus* (Kram and Dawson 1998).

New data on the locomotor energetics of *M. rufus* (Kram and Dawson 1998) reinforces Dawson and Taylor's (1973) original observations of uncoupling energy costs from speed. However, in the first study, the  $\dot{V}\text{O}_2$  plateau was about  $3.6 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for an 18-kg individual and about  $4.7 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for a 20.4-kg specimen in the latter study (Fig. 1). This relatively large difference in locomotor energetic performance from two animals of similar mass illustrates the need for a more thorough

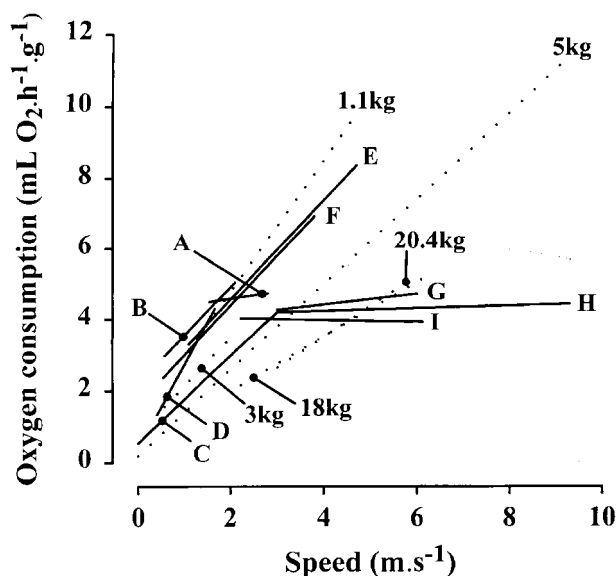


Figure 1. Rate of oxygen consumption as a function of speed for members of the Macropodoidea. Solid lines indicate the measured  $\dot{V}O_2$ . Dotted lines are the predicted rates of oxygen consumption for individuals of the masses indicated based on 62 mammal and bird species (Taylor et al. 1982). Macropodoidea data: A = pademelon, ca. 4 kg, hopping (Warren 1979); B = quokka, 3 kg, half bound (Baudinette 1977); C = tammar wallaby, 5 kg, half bound (Baudinette et al. 1992); D = red kangaroo, 18 kg, pentapedal gait (Dawson and Taylor 1973); E = bettong, 1.1 kg, hopping (Thompson et al. 1980); F = potoroo, 1.1 kg, half bound (Baudinette et al. 1993); G = red kangaroo, 20.4 kg, hopping (Kram and Dawson 1998); H = tammar wallaby, 5 kg, hopping (Baudinette et al. 1992); I = red kangaroo, 18 kg, hopping (Dawson and Taylor 1973).

study of the Macropodoidea using a wide range of species and body sizes.

With respect to locomotor energetics, the smaller bipedal hoppers have more in common with their eutherian counterparts than do larger ones. Current data suggest that the energetic benefits of bipedal hopping, relative to the locomotor costs of placental mammals of the same size, may be limited to animals of about 3 kg or more. It is yet to be seen whether these larger macropods are bound by their own unifying principle with respect to locomotor energetics. The following sections examine aspects of the musculoskeletal systems of eutherian and marsupial mammals identifying similarities and differences in structure and function.

#### Muscle

The fundamental mechanical properties of skeletal muscle in hopping, bipedal marsupial mammals are the same as in eutherian mammals. Muscle efficiency in *M. rufus* was estimated by measuring the additional metabolic cost of uphill hopping

(compared to level-ground hopping), where muscles must perform mechanical work against gravity. The efficiency of 28.8% calculated for hopping up an 11.7°-inclined treadmill (Kram and Dawson 1998) was similar to the 30.7% efficiency calculated for dogs running on an 11.5°-inclined treadmill (Raab et al. 1976). The ability of large kangaroos to uncouple metabolic costs from their speed of locomotion does not appear to be due to unusually efficient muscles. Nor does it derive from the elastic properties of short-range movement of muscle fibres, with muscles acting more as tension generators while their attached tendons act as springs. Tendon elongation was found to be about eight times that of muscle fibre elongation in a gastrocnemius muscle preparation from a pademelon, *T. billardieri* (body mass ca. 5–7 kg; Morgan et al. 1978). Larger species are predicted to have relatively smaller muscle extensions as a result of the scaling relationships of muscle and tendon as is examined below in a consideration of muscle-tendon interactions.

In kangaroos, the muscles of the crus and pes that provide the power for hopping through ankle extension and/or digital flexion are plantaris (flexor digitorum superficialis), gastrocnemius, and flexor digitorum profundus. Dennington and Baldwin (1988) considered that these muscles might show biochemical specialisations linked to energy production that would complement the studies on whole animal oxygen consumption. Their study of plantaris, the medial and lateral heads of gastrocnemius, and soleus muscle from *Macropus parma* (2.8–4.2 kg) and *Macropus fuliginosus* (35 and 68 kg) showed that muscle-fibre-type distributions were broadly similar for both species. In both species, the plantaris and gastrocnemii contained predominantly type 2A fibres (43%–67%) with type 2B (20%–37%) and type 1 (10%–25%) also present. Both species had a small soleus (vestigial or absent in kangaroos) that was composed entirely of type 1 slow-twitch fibres. These fibres are generally considered to be concerned with slow movements and postural control.

The small lateral head of gastrocnemius was shown to contain a significantly higher proportion of type 1 fibres than the medial head (25.2% : 14.1%) in *M. parma* and may, therefore, have a greater involvement in slower forms of locomotion. This functional distinction is less marked in *M. fuliginosus*, as the population of type 1 fibres in the lateral head was 19.2% with a commensurate increase in type 2A fibres. In general, the proportions of fibre types in each muscle fell within the ranges reported for eutherian limb muscles (Dennington and Baldwin 1988), which indicates that macropod marsupials have no functional specialisation at this level of organisation. It should be noted that fibre-type proportions range widely in mammals, and although indicative of functional demands, they may be influenced by phylogeny. Without a more complete data set, it is difficult to interpret whether the macropod results are indicative of a general marsupial pattern or a specialisation for hopping. Certainly, the nonhopping marsupial opossum, *Di-*

*delphis virginiana*, has a significantly higher proportion of type 1 fibres (53%) in the medial gastrocnemius than either of the two macropods (Peters et al. 1984).

Ratios of enzyme activities in ankle extensors provided the only notable metabolic differences in biochemical profiles between muscles of macropods and eutherians. The activity ratios of several key enzymes suggested an association with high levels of aerobic work, which is consistent with observations of high metabolic scope in kangaroos (Dennington and Baldwin 1988; Kram and Dawson 1998).

Eutherian and therian skeletal muscles have been assumed to be able to produce peak stresses of about 300 kPa (Pollock and Shadwick 1994a; Bennett and Taylor 1995). This value (see Wells 1965; Wilson and Stephenson 1990) compares favourably with an *in vivo* muscle stress of 262 kPa determined for *M. eugenii* when hopping at  $6.3 \text{ m s}^{-1}$ , well below its maximum speed (Baudinette et al. 1992; Biewener and Baudinette 1995). The isometric muscle stress is important for calculating upper limits for strain energy storage (see “Elastic Strain Energy” below), where muscle fibre area ( $\text{CSA}_m$ ) is given by

$$\text{CSA}_m = \text{muscle mass}/(\text{muscle density} \times \text{fibre length}),$$

assuming a muscle density of  $1,060 \text{ kg m}^{-3}$  (Ker et al. 1988), and predicted force production is given by

$$\text{force} = \text{CSA}_m \times \text{isometric muscle stress}.$$

### Tendon

Ontogenetic changes in tendon properties occur, with juvenile animals generally having more compliant tendons of lower strength (Haut 1983). However, mammalian tendons from adult animals are reported to have remarkably similar mechanical properties (Bennett et al. 1986; Pollock and Shadwick 1994b). All tendons exhibit a J-shaped curve when loaded in tension. Limb tendons, when tested dynamically in tension, exhibit between 6% and 10% of hysteresis, have a linear elastic modulus of 1–1.5 GPa and an ultimate strength of about 100 MPa at 10% strain (Ker 1981; Bennett et al. 1986; Ker et al. 1986; Pollock and Shadwick 1994b). Somewhat higher values of  $E$  and failure stress have been reported for wallaby tail tendons (Wang and Ker 1995). Our understanding of the mechanical properties of tendons is based on material from a broad range of mammals and birds but includes only one macropod species—Bennett’s wallaby, *Macropus rufogriseus*.

There are no reported variations in the biomechanical properties of tendons in relation to body mass based on simple tensile test results for tendons from ground squirrels (0.47 kg) to camels (545 kg; Bennett et al. 1986; Pollock and Shadwick 1994b).

The possibility that differences in material properties may

exist between tendons that have different functional roles has been raised (Woo et al. 1980, 1981; Pollock and Shadwick 1994b). Tendons attaching to muscles that are load bearing during locomotion (e.g., ankle extensors and digital flexors) are more likely to be subjected to high stresses than those that are not (e.g., digital extensors). Studies on pigs suggest that the former tendons may have a higher modulus and lower hysteresis (Woo et al. 1980, 1981), although in active wild animals, tendon properties are reported to be similar irrespective of their loading environment (Pollock and Shadwick 1994b). (Interestingly, there are recent data to show that the properties of tendons do exhibit marked site [i.e., functional] dependence when subjected to tensile fatigue loading [Ker et al. 2000]. There does not seem to be any difference between marsupial and placental mammals with respect to these fatigue properties.)

As a unifying principle, current data suggest uniform tendon properties occur in adult mammals regardless of whether they walk, trot, gallop, bound, or hop. However, tendons from the Macropodoidea may prove to be the exception to the rule. Tensile tests were conducted on tendons from the crural region of 25 individuals representing 10 species. All test specimens were from free-living, healthy animals (roadkills and animals culled by professional hunters). Only one specimen was sub-adult. Body mass-related differences were found, with modulus and possibly failure stress increasing with body size (Fig. 2). The results indicate that there may be site-specific or function-specific differences in material properties. For example, extensor digitorum longus tendons exhibit higher moduli and failure stresses than primary ankle extensors and digital flexor tendons. If tendon modulus does scale positively with body mass (Fig. 2, top), smaller hoppers may be able to utilise strain energy storage to a greater extent than predicted (Bennett and Taylor 1995). Lower ultimate strength of tendons in smaller individuals would not place the tendons at risk of failure, as they would still operate with a safety factor of 4 or 5.

### Elastic Strain Energy

Tendons, and to a lesser extent ligaments, in the limbs and back are important sites for elastic strain energy storage during locomotion in many animals (Alexander 1988). The principle by which animals can temporarily convert kinetic energy and gravitational potential energy to elastic strain energy (in stretched collagenous structures) is widely accepted. Stored strain energy may be usefully employed to reduce the metabolic costs of locomotion but only if the elastic recoil of stretched tendons and/or ligaments occurs at the appropriate phase of the stride (Alexander 1988).

Each tendon in the limbs of mammals is in series with its muscle belly. We have seen that physiological cross-sectional area determines muscle force, with mammalian muscle generating an isometric stress of 250–300 kPa (see “Muscle”). What effectively determines the amount of energy that can be stored

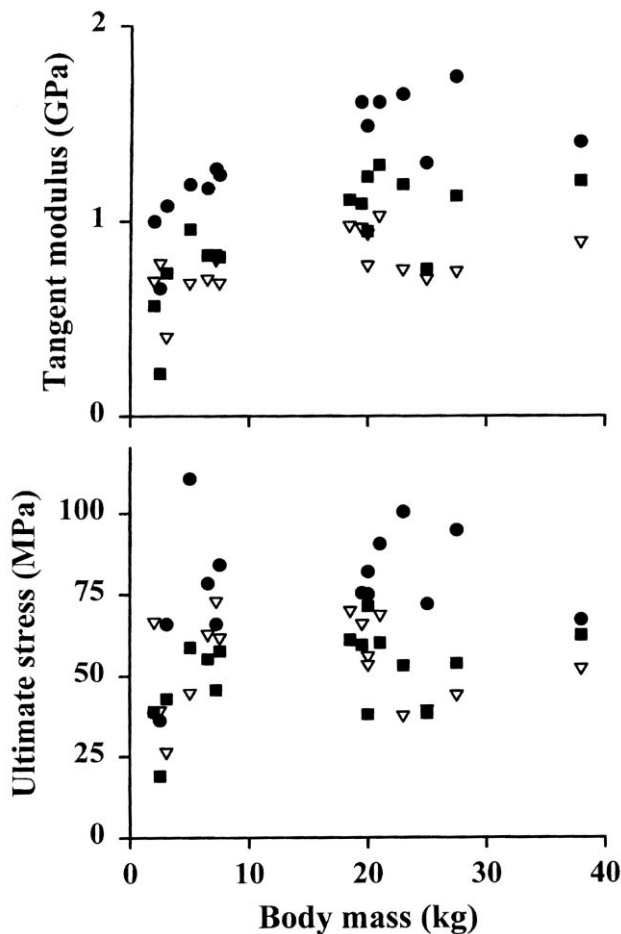


Figure 2. Mechanical properties of crural tendons from macropodid and potoroid marsupials as a function of body mass. Tangent Young's modulus (*top*) and failure stress (*bottom*) for extensor digitorum longus (*filled circles*), plantaris (*open triangles*), and flexor digitorum profundus (*filled squares*).

in a stretched tendon is the amount of force to which it is exposed and the stretch that it undergoes. As tendon is a quasi-Hookean material,

$$U \approx (\text{force} \times \text{tendon extension})/2,$$

where  $U$  = strain energy.

As mammalian skeletal muscle contractile properties are relatively invariant (particularly in analogous muscles), the ratio of muscle physiological cross-sectional area to tendon cross-sectional area provides a direct measure of the stress to which a tendon can be loaded by its muscle (Ker et al. 1988). As tendon stress-strain graphs are also uniform (if tensile properties are species and site independent—but see the section “Tendon” above), it follows that the peak tendon strain can be

estimated, and  $U$  can be calculated if the length of tendon is known.

This approach has been used widely and demonstrates that nonspecialised muscle-tendon units in mammals have a mean ratio of 34. This equates to a peak tendon stress of about 10 MPa—a level of stress that will not result in useful storage of elastic strain energy. Digital extensor muscle-tendon units, whether from quadrupeds or bipeds, conform to this principle. In contrast, ankle extensor and digital flexor muscle-tendon cross-sectional area ratios are usually much greater, reaching about 300 in some animals. A ratio of 300 infers that the tendon could be exposed to a peak stress of 100 MPa, close to its ultimate strength. At this stress, assuming the tendon is of reasonable length, the quantity of strain energy stored could be of potential significance in the overall locomotor efficiency of the individual.

This type of approach, sometimes coupled with *in vivo* measurement of muscle force (e.g., Biewener and Blickhan 1988), has shown that utilisation of elastic strain energy to offset the costs of locomotion is restricted to larger animals (Biewener and Blickhan 1988; Pollock and Shadwick 1994a; Bennett and Taylor 1995). As a unifying principle, smaller mammals (quadrupeds and bipeds) appear to derive some benefit—for example, rapid acceleration to avoid predators (Biewener and Blickhan 1988)—from having relatively stiff tendons. Larger mammals (as we will see in “Scaling”) are more likely to use their relatively compliant load-bearing limb tendons to store strain energy during locomotion.

### Scaling

**Skeletal Stress.** It has long been recognised that if animals are geometrically similar, then the capacity of the limb bones to support load decreases relative to the increase in body mass ( $M$ ). Under the conditions of geometric similarity, linear dimensions  $\propto M^{0.33}$ , areas  $\propto M^{0.67}$ , and volume ( $\approx$ mass)  $\propto M^{1.00}$ , resulting in limb bone stresses being  $\propto M^{0.33}$ . However, measurements using strain gauges bonded to bone surfaces and calculations based on force platform and kinematic analyses show that bone strains and stresses are effectively independent of body mass. This applies over a large size range of eutherian mammals from mice to elephant (see Biewener 1990). Calculations of tibial stresses in macropods showed that *M. rufogriseus* (10.5 kg) conforms to the eutherian pattern, but *M. rufus* (42 kg) with a compressive stress of 150 MPa does not (Alexander and Vernon 1975).

It has been argued that animals avoid this scale-dependent increase in mechanical stress by adopting more erect limb postures as they increase in size (Biewener 1990). Having a relatively straight limb posture during the midstance phase of a step results in a smaller moment arm of the ground reaction force ( $R$ ) about the ankle joint, which decreases external joint moments (Fig. 3). Additionally, the ankle extensor muscle mo-

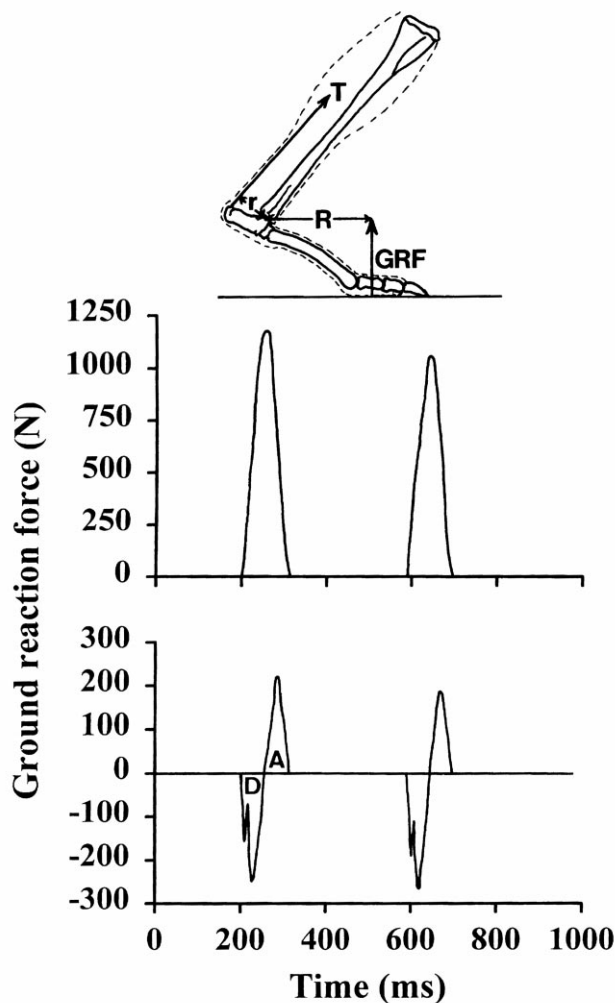


Figure 3. Diagrammatic representation of a macropodid hind limb at midstance where the ground reaction force (GRF) is vertical and acts at distance  $R$  from the ankle joint. The main tendons of the leg that balance the rotational moments at this joint have a moment arm of  $r$  (after Bennett and Taylor 1995). Vertical and anterior-posterior GRFs versus time for a kangaroo hopping at  $6.8 \text{ m s}^{-1}$  are shown in the middle and lower panels, respectively (after Cavagna et al. 1977). A decelerating impulse ( $D$ ) occurs in the first half of the ground contact phase, followed by an acceleration impulse ( $A$ ). At midstance, the vertical GRF is maximal, and there is zero force in the anterior-posterior direction.

ment arm ( $r$ ) increases as animal size increases, which decreases the magnitude of muscle force needed to support the animal while running. The combination of these two changes with body size is that the muscle effective mechanical advantage ( $\text{EMA} = r/R$ ) is proportional to  $M^{0.27}$  for eutherians. This scaling-induced postural sequence, from crouching postures in small animals to upright limb postures in large animals, is a broadly unifying feature of eutherians.

Once again, hopping marsupials prove to be a major exception to this principle. Analysis of skeletal material showed that both  $r$  and  $R$  increase with increasing body mass, such that  $\text{EMA} \propto M^{0.00}$  in the Macropodoidea (Bennett and Taylor 1995). This finding is not surprising, as hopping requires the use of crouched limb postures irrespective of body size. However, maintenance of these postures with increasing body mass has implications for bone stresses, the ankle extensor muscle forces required during hopping midstance, and strain energy storage. This may explain why the tibial stress calculated for *M. rufus* appeared large.

*Muscle, Tendon, and Elastic Strain Energy.* Scaling relationships of muscle mass, fibre lengths, and force production capacities have been determined for limb muscles of eutherian mammals (Pollock and Shadwick 1994a) and the Macropodoidea (Bennett and Taylor 1995). Plantaris, gastrocnemius, and deep digital flexor muscles of eutherians show isometric scaling with respect to mass, negative allometry for fibre length, and thus positive allometry for fibre area and force production (Pollock and Shadwick 1994a). Kangaroos differ from this pattern by showing strong positive allometry for muscle mass resulting in even larger exponents for fibre area and force (Table 1). This finding is consistent with predictions based on a lack of size dependence of EMA in macropodids.

The scaling of ankle extensor and digital flexor tendon CSA is approximately isometric in eutherians and kangaroos, whereas exponents for tendon length indicate isometry in eutherians and positive allometry for kangaroos (Pollock and Shadwick 1994a; Bennett and Taylor 1995; Table 1).

Two specific and unifying outcomes flow from these studies. First, in both groups, the ratio of muscle to tendon area increases with body mass. This implies that the tendons of larger animals can be subjected to larger stresses by their attached muscles (Ker et al. 1988; Bennett 1995; Fig. 4). Second, and related to the first observation, both groups demonstrate strong positive allometry for the potential for storing elastic strain energy,  $U$ , in their distal limb tendons (Table 1). This means that small mammals are incapable of utilising elastic strain energy storage to any useful extent. They tend to have relatively thick, and hence stiff, tendons. This may be of advantage to small individuals by allowing muscle shortening to be translated directly into movements about joints, which results in more precise limb movements and/or more rapid acceleration. In large animals, the tendons are relatively slender, which possibly leads to less precise limb control and reduced acceleration ability but also to enhanced strain energy storage.

Kangaroos, with their particular postural, muscle, and tendon scaling relationships, appear to use this elastic strain energy storage to make hopping an economical gait. However, this ability has been shown to be strongly mass dependent, with hopping more economical than quadrupedal locomotion in

Table 1: Allometric equations describing morphological and biomechanical characteristics of the Macropodoidea and eutherian mammals

Dependent Variable ( $y$ )	Gastrocnemius	Plantaris	Flexor Digitorum Profundus	Extensor Digitorum Longus
Muscle mass (g):				
Macropodoidea .....	$3.69M^{1.19}$	$2.46M^{1.30}$	$1.71M^{1.12}$	$.30M^{1.20}$
Eutherian mammals .....	$3.52M^{.97}$	$1.23M^{.97}$	$1.28M^{1.03}$	$.46M^{.93}$
Muscle CSA (mm <sup>2</sup> ):				
Macropodoidea .....	$214M^{1.06}$	$169M^{1.19}$	$145M^{.81}$	$22.0M^{.79}$
Eutherian mammals .....	$304M^{.77}$	$134M^{.91}$	$125M^{.85}$	$28.1M^{.69}$
Tendon length (mm):				
Macropodoidea .....	$76.8M^{.49}$	$138M^{.47}$	$132M^{.47}$	$57.3M^{.53}$
Eutherian mammals .....	$63.7M^{.56}$	$131M^{.35}$	$107M^{.38}$	$107M^{.35}$
Tendon CSA (mm <sup>2</sup> ):				
Macropodoidea .....	$3.52M^{.56}$	$2.34M^{.75}$	$3.85M^{.56}$	$1.69M^{.72}$
Eutherian mammals .....	$2.97M^{.68}$	$1.36M^{.68}$	$2.51M^{.64}$	$.74M^{.56}$
Area ratio:				
Macropodoidea .....	$61.8M^{.49}$	$72.1M^{.44}$	$37.5M^{.24}$	$35.0M^{.06}$
Eutherian mammals .....	$102M^{.08}$	$97.9M^{.24}$	$50.0M^{.21}$	$39.2M^{.13}$
Elastic strain energy (J):				
Macropodoidea .....	$.08M^{1.85}$	$.12M^{1.93}$	$.07M^{1.41}$	...
Eutherian mammals .....	$.14M^{1.14}$	$.14M^{1.38}$	$.07M^{1.32}$	$.01M^{1.08}$

Note.  $M$  = body mass (kg). Allometric equations were obtained by least squares regression of data from kangaroos and eutherian mammals following logarithmic transformation and are reported in the form  $y = ax^b$ .

animals of about 5 kg or more and then only when travelling at moderate to high speed ( $>5 \text{ m s}^{-1}$ ).

A further aspect of the scaling argument is that while tendon safety factors in small macropodids are about 10—in common with most tendons in most mammals (Ker et al. 1988)—those in the larger kangaroos approach values of about 1. At this safety factor, the tendon is likely to be broken by its attached muscle (but it is also capable of storing a maximum amount of strain energy). Tendons of gastrocnemius and plantaris muscles are predicted, by extrapolation of the available data set, to have safety factors of  $<1$  in macropods of about 35–40 kg or more. This is obviously an undesirable condition.

Similar problems may beset eutherian mammals but only at body masses of about 150 kg or more (see Pollock and Shadwick 1994a, Fig. 6). There is indirect evidence to support this hypothesis provided by Garland et al. (1988), who examined the locomotor performance of mammals. Their data show that maximum running speed reaches a plateau at a body mass of about 150 kg. Performance declines when animal mass exceeds about 1,000 kg. Current data for macropods are not sufficient to determine whether locomotor performance declines at masses over about 35–40 kg (Bennett 1987).

It seems that the mechanical tensile strength of tendon (ca. 100–150 MPa) may place an upper limit on certain aspects of the locomotor performance of placental and marsupial mam-

mals. Tendon properties certainly determine the elastic strain energy capacity of animals, which has a dramatic effect in reducing the metabolic energy requirements of fast locomotion in many large species. It is in these species, which operate their tendons with low factors of safety, that muscle-tendon area ratios are optimal for energy storage.

Following scaling arguments, macropods over 40 kg and placental mammals over 100 kg would still need to increase their muscle fibre areas with increasing mass if agility or maximum speed of locomotion were to be maintained. A disproportionate increase in tendon cross-sectional area would have to accompany this in order to avoid tendon breakage. Such a change in the muscle-tendon area ratios would result in a reduction in the mass-specific strain energy storage capacity and/or the locomotor performance of the individual compared to the strain-energy-optimised animal. Other arguments can be made to explain why large animals have a poorer locomotor performance than animals of intermediate size, such as reduced predation pressure on very large animals obviating the need to run fast. However, this does not alter the fact that tendon properties may be pivotal in affecting size-related locomotor performance.

As a footnote, digital extensor tendon CSAs in eutherian and marsupial mammals scale in accordance with the predictions of geometric similarity as do their muscle-tendon area ratios



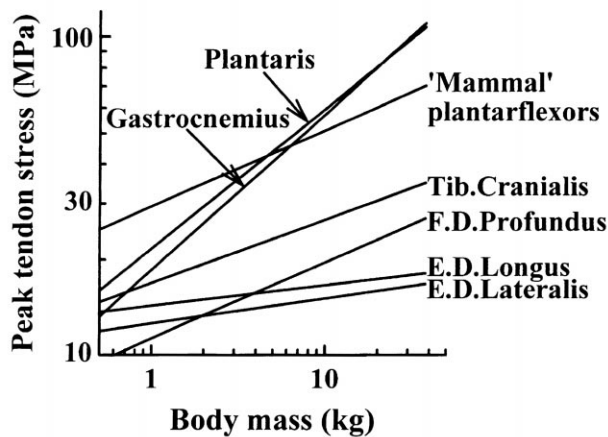


Figure 4. Graph on logarithmic axes of calculated tendon stress versus body mass for mammals. Least square regression lines are shown for six crural muscles from eight species of Macropodoidea and for ankle extensor muscles for eutherian mammals (after Pollock and Shadwick 1994a; Bennett and Taylor 1995).

and the associated values of  $U$  (Pollock and Shadwick 1994a; Bennett and Taylor 1995). In this respect, the interrelationship of muscle and tendon is both a unifying and conservative principle (Ker et al. 1988). Deviations from this norm only appear to occur where there are special functional roles, such as energy storage during fast locomotion (Fig. 4).

**Bone.** Ground reaction forces on individual pelvic limbs generally peak at about three times body weight for running and hopping mammals, with a peak of about twice body weight for galloping mammals (Cavagna et al. 1977; Bryant et al. 1987; Kram and Dawson 1998; Bennett 1999). In the section on "Skeletal Stress," it was noted that kangaroos, unlike placental mammals, do not have size-dependent postural changes (i.e., EMA increases in placental mammals  $\propto M^{0.27}$  but remains constant in macropodids). The implication is that macropodid ankle extensor forces required to balance joint torques during load bearing will increase proportionally faster than in eutherians. This is evidenced by the observation that gastrocnemius and plantaris muscle fibre area exponents differ by about 0.29 between the two groups (Pollock and Shadwick 1994a; Bennett and Taylor 1995). The result of using a bent limb posture at midstance is that the ground reaction force is angled at about  $30^\circ$  to the long axis of the leg (Alexander and Vernon 1975), which requires large muscle forces to balance joint torques.

Alexander and Vernon (1975) calculated the stresses that would act in the tibia, based on force platform and cine-film records of 6.6 and 42 kg *M. rufus* and measurements of hind-limb musculoskeletal structures on a 10.5-kg *M. rufogriseus*. Their calculations showed that stresses would be greatest in the midshaft region, and peak stresses would reach 60 MPa tensile

and 90 MPa compressive, and 110 MPa tensile and 150 MPa compressive in the small and large red kangaroos, respectively. The authors commented that the values for the large red kangaroo may be too high, as they assumed that section modulus,  $Z$ , of the tibia ( $Z = I/\text{distance from the centroid to the most distant point on the bone in the anterior-posterior direction and has the dimensions } [\text{length}]^3$ ) would be  $\propto M^{1.00}$ , whereas larger animals generally have relatively stouter limb bones than small animals.

Figure 5, based on preliminary data, shows tibial  $Z$  in macropodids to scale  $\propto M^{1.04}$  in line with the initial geometric similarity prediction of Alexander and Vernon (1975). This

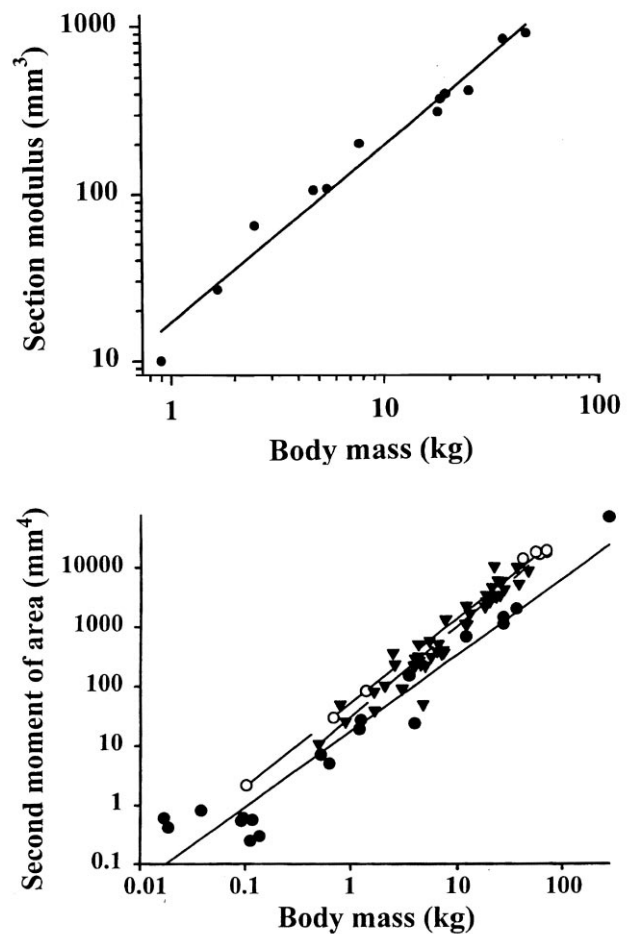


Figure 5. Graphs of section modulus of macropodid tibiae (top) and second moments of area of tibiae (bottom) from hopping marsupials (filled triangles) and bipedal (open circles) and quadrupedal (filled circles) placental mammals. Equations describing the least square regression lines follow and are reported in the form  $y = ax^b$ : section modulus ( $\text{mm}^3$ ) =  $16.9M^{1.04}$  (kangaroos); second moment of area ( $\text{mm}^4$ ) =  $30.7M^{1.52}$  (kangaroos),  $53.3M^{1.42}$  (bipeds), and  $17.8M^{1.28}$  (quadrupeds).  $M$  = body mass (kg).

suggests that macropodids, once again, are somewhat exceptional. During high-speed hopping, they would have considerably higher bone stresses than occur routinely in other mammals. They may operate with a safety factor of about 2 rather than the generally accepted value of about 4 for limb bones in other mammals (Biewener 1990).

Interestingly, the second moment of area (measured in  $\text{mm}^4$ ), which is a measure of bending rigidity, scales with positive allometry ( $\propto M^{1.52}$ ) at tibial midshaft. At a body mass of about 1 kg, tibial bending stiffness is the same for quadrupedal and bipedal mammals (Fig. 5, *bottom*), but as mass increases, the regression lines describing bipedal hoppers and runners diverge from the quadrupedal line. At a body mass of 40 kg, quadruped tibiae are only 20% as resistant to bending than those of bipeds. This presumably relates to differences in the magnitudes of the forces imposed on the tibia by muscles and interaction with the ground.

Unifying principles linking bone geometry, stresses, and strains in hopping and running mammals are presently lacking. The question of whether hoppers (particularly macropods) and runners operate using the same principles requires further study. In particular, data for tibial midshaft bone strains during macropod hopping are needed.

In summary, kangaroos appear to differ significantly from the normal mammalian situation with respect to aspects of their locomotor performance and musculoskeletal structure and function. Many of these differences have merited individual mention in earlier articles (e.g., Alexander and Vernon 1975; Cavagna et al. 1977; Pollock and Shadwick 1994a; Bennett and Taylor 1995), and new data presented here suggest that the differences may be more extensive than previously noted.

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