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Source: Australian Journal of Zoology, 69(4) : 136-157

Published By: CSIRO Publishing

URL: https://doi.org/10.1071/ZO21048

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REVIEW
https://doi.org/10.1071/ZO21048

Australian Journal of Zoology

Understanding Australia's unique hopping species: a comparative review of the musculoskeletal system and locomotor biomechanics in Macropodoidea

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Handling Editor:
Paul Cooper

Received: 8 November 2021
Accepted: 5 April 2022
Published: 13 May 2022

Cite this:
Thornton LH *et al.* (2021)
Australian Journal of Zoology, **69**(4), 136–157.
doi:10.1071/ZO21048

ABSTRACT

Kangaroos and other macropodoids stand out among mammals for their unusual hopping locomotion and body shape. This review examines the scaling of hind- and forelimb bones, and the primary ankle extensor muscles and tendons. We find that the scaling of the musculoskeletal system is sensitive to the phylogenetic context. Tibia length increases with positive allometry among most macropodoids, but negative allometry in eastern grey kangaroos and isometry in red kangaroos. Femur length decreases with stronger negative allometry in eastern grey and red kangaroos than among other macropodoids. Muscle masses scale with negative allometry in western grey kangaroos and with isometry in red kangaroos, compared to positive allometry in other macropodoids. We further summarise the work on the hopping gait, energetics in macropodoids, and stresses in the musculoskeletal system in an evolutionary context, to determine what trade-offs may limit locomotor performance in macropodoids. When large kangaroos hop, they do not increase oxygen consumption with speed, unlike most mammals, including small hopping species. We conclude that there is not enough information to isolate the biomechanical factors that make large kangaroos so energy efficient. We identify key areas for further research to fill these gaps.

Keywords: bone, efficiency, gait, locomotion, macropod, muscle, saltation, tendon.

Introduction

Kangaroos are instantly recognisable by their body form and hopping gait, but these distinct features are also some of the most baffling. Kangaroo locomotion defies mammalian trends. In particular, among placentals there is a general increase in mass-specific metabolic rate with movement speed, related to the increased cost of propelling the body forward (Taylor *et al.* 1970); however, kangaroo energy use when hopping is independent of their speed of locomotion (Dawson and Taylor 1973). This ability is a result of the complex function of limb segment ratios, body mass, and muscle–tendon structure, which has not yet been fully explored and interpreted. Further, we have little information on how this unique body form and style of locomotion influences the absolute body size that can be reached in this group.

Body size influences most aspects of organismal biology, including the evolution of body shape (Calder 1996). The body mass (M) of an animal is proportional to the gravitational force that it experiences; as an animal increases in mass under dynamically similar conditions, the amount of force that its skeleton needs to support or resist must also increase (Biewener 2005). If animals were to increase in size but keep the same shape, i.e. scale geometrically (or isometrically), their linear dimensions would increase proportional to ($\propto$) $M^{0.33}$ and the load-bearing area would increase $\propto M^{0.67}$. Geometric scaling predicts that stresses placed on the musculoskeletal system will increase $\propto M^{0.33}$ since mechanical stress (force per unit area) increases $\propto M^{1.00}$ as area increases $\propto M^{0.67}$. Thus, if animals increase in size geometrically, the strength of the limb bones would not keep up with the increased mechanical demands of support and locomotion (Biewener 2005).

To deal with this problem of size, many mammals deviate from geometric similarity in various ways. Previous studies have shown non-geometric (allometric) scaling in bone length, muscle and tendon architecture, and changes to how the musculoskeletal system is loaded due to changes in posture (Biewener 1990, 2005; Pollock and Shadwick 1994). However, the ability to alter specific parameters appears to be strongly linked with phylogenetic history (Dick and Clemente 2017). Kangaroos and potoroos (part of the superfamily Macropodoidea, hereafter macropodoids) are a particularly interesting group in which to explore size-related changes in musculoskeletal properties and locomotion, given their phylogenetically independent history and their unusual body form and style of locomotion.

This review aims to explore how morphology and locomotion change with body mass among macropodoids to understand the evolutionary drivers among this unique group of mammals. We review the existing literature on limb bones, muscles and tendons, and how these structures vary with body size among extant macropodoids. We summarise the energetics of macropodoids in comparison to quadrupedal mammals. Finally, we review the hopping gait and the associated forces that are transmitted through the mechanical structures of the body, the stresses of which likely determine the limits on size and performance.

Bones

Macropodoids are characterised by a unique skeletal system, which evolved at least partially in response to the demands of hopping locomotion. Both macropodoids and hopping rodents are distinguished by hindlimbs that are at least twice as long as their forelimbs, with specialisations in the hindfeet. The hindlimb is elongated principally by the tibia in macropods and by the distal metatarsal and phalangeal elements in hopping rodents (McGowan and Collins 2018).

We performed a meta-analysis on bone length data from 12 studies, covering 67 species of macropodoids (Fig. 1, see Supplementary documents). The combined dataset included the following length measurements for bones of the hind and forelimb: femur (n = 328), tibia (n = 323), calcaneus (n = 60), metatarsal IV (n = 235), phalanx IV (n = 87), humerus (n = 137), radius (n = 137), ulna (n = 85), and metacarpal III (n = 9). Length measurements for which a corresponding body mass was not recorded were excluded from regressions of individuals (see Supplementary Table S1 for n-values) but were included in species-mean lengths. However, for species-mean data, we determined mean body mass for these species from the published literature (41 sources, 436 records).

We used generalised least squares regression analysis to explore the size-related changes in skeletal morphology. To highlight the scaling relationships, we report the slope and 95% confidence intervals (CIs) at the individual (where each data point represents a single specimen), species-means, and phylogenetically corrected species-means levels (Fig. 2*b*, *d*, Table S1). Traits are deemed to scale with isometry if the CIs overlap with the geometric exponent (e.g. 0.333 for lengths) and are considered to scale with positive or negative allometry if the CI is greater or lower than geometric similarity, respectively. We compared Akaike information criterion (AIC) values and determined that the most suitable model for phylogenetic correction was the Brownian model of evolution. We also used this analysis to determine the relationship of muscle mass and tendon parameters with body mass in later sections.

Our meta-analysis results show that femur length scales with negative allometry in individuals ($\propto M^{0.316\pm0.015}$), and phylogenetic correction decreases the species-means slopes further (species-means: $\propto M^{0.322\pm0.022}$, corrected species-means: $\propto M^{0.310\pm0.035}$). Tibia length scales with strong positive allometry among all individuals ($\propto M^{0.427\pm0.028}$), and phylogenetic correction slightly reduces the slope towards isometry (species-means: $\propto M^{0.400\pm0.058}$; corrected species-means: $\propto M^{0.397\pm0.067}$).

The difference between species-means and phylogenetically corrected species-means indicates that there is variation between species, but this is more apparent when examining the intraspecific scaling of separate species. Within the *Macropus* species complex [see Celik *et al.* (2019)], there are sufficient data and a range of body masses to determine intraspecific scaling in the eastern grey kangaroo (*Macropus giganteus*) (M = 0.79–60 kg, n = 18) and the red kangaroo (*Macropus rufus*) (M = 13.4–72.5 kg, n = 18) (Fig. 2*d*). The results show strong negative allometry with femur length $\propto M^{0.287\pm0.010}$ and tibia length $\propto M^{0.291\pm0.012}$ in the eastern grey kangaroo, and femur length $\propto M^{0.263\pm0.033}$ in the red kangaroo. Tibia length in the red kangaroo is not significantly different from isometry ($\propto M^{0.313\pm0.037}$). The scaling of the tibia is most interesting; it is a reversal of the strong positive allometry seen in the broader scaling in Macropodoidea. The trend within both kangaroo species appears primarily driven by the small individuals having proportionally longer legs than other species.

There are no reports that have both body mass and calcaneus length for individuals; however, species-mean length shows strong positive allometry (species-means: $\propto M^{0.406\pm0.041}$, corrected species-means: $\propto M^{0.392\pm0.058}$). Calcaneus length is approximately equal to the moment arm, r, the distance from the gastrocnemius and plantaris muscle line of action to the ankle joint centre of rotation. Both the moment arm (r) and the out lever (moment arm of the ground reaction force, R) increase with body size in macropods, resulting in a near-constant effective mechanical advantage (EMA = r/R) with increasing body size (Bennett 2000).

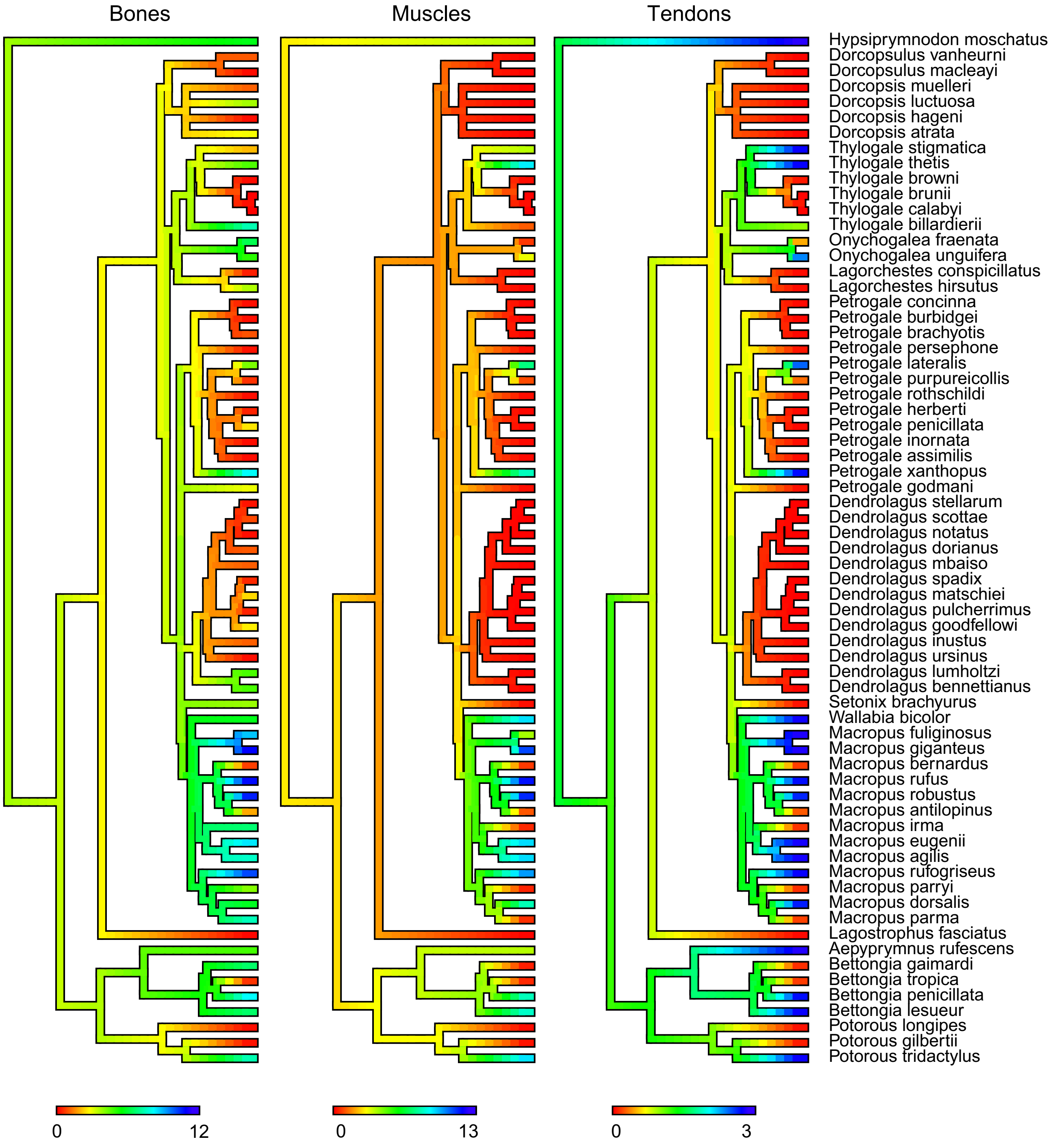

Fig. 1. Phylogeny of extant macropodoids indicating the number of limb bones, hindlimb muscles and tendons that have been quantitatively measured for each species. Red colours indicate little sampling whereas blue colours indicate extensive sampling. In some studies, *Macropus* has been subdivided into separate genera or subgenera: *Macropus*, *Osphranter*, and *Notamacropus* (Meredith *et al.* 2009; Celik *et al.* 2019).

Metatarsal IV length scales with isometry in all cases, although phylogenetic-correction does tend to increase the scaling factor (individuals: $\propto M^{0.333\pm0.038}$, species-means: $\propto M^{0.335\pm0.089}$, corrected species-means: $\propto M^{0.375\pm0.098}$). Previous research found sexual dimorphism in metatarsal length allometry: larger males have relatively shorter pes length, although there appears to be no dimorphism in femur or tibia length (Richards *et al.* 2015).

Phalanx IV (three phalanges minus keratin claw) length scales with isometry in individuals ($\propto M^{0.300\pm0.046}$); however,

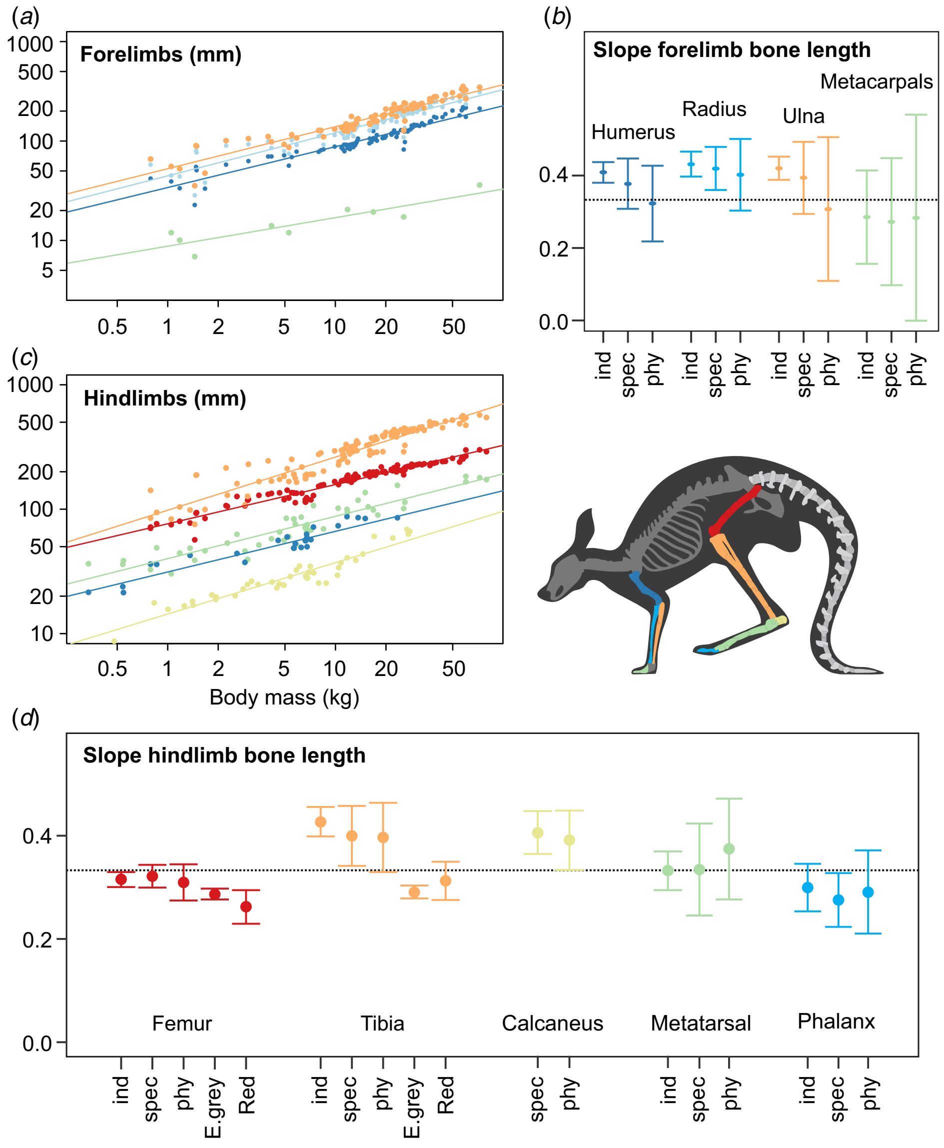

Fig. 2. (*a*) Plot of bone length against body mass for forelimb bones (humerus, radius, ulna, metacarpal III); (*b*) slope and 95% confidence intervals of forelimb bone length; (*c*) plot of bonelength against body mass for hindlimb bones (femur, tibia, calcaneus, metatarsal IV, phalanx IV); and (*d*) slope and 95% confidence intervals of hindlimb bone lengths. Intraspecific scaling for the eastern grey kangaroo (E.grey, *Macropus giganteus*) and red kangaroo (Red, *Macropus rufus*) are included for the femur and tibia. Ind, individual; spec, species-means; phy, phylogenetically corrected species-means.

only nine species are represented in this length measurement, and the species examined could have a significant impact on the output. The species-mean slope samples 38 species and is more representative of Macropodoidea. The species-mean phalanx length scales with negative allometry ($\propto M^{0.276\pm0.052}$) and returns to isometry with phylogenetic correction ($\propto M^{0.291\pm0.080}$).

The results in bone scaling studies are consistent: the positive allometry of the tibia accounts for the overall allometry of the hindlimb, while the length of the femur, metatarsal and phalanges scales with isometry (Kear *et al.* 2008; McGowan *et al.* 2008*b*; Doube *et al.* 2018).

Humerus length scales with positive allometry in individuals ($\propto M^{0.411\pm0.029}$), although the decrease from species-means ($\propto M^{0.379\pm0.069}$) with phylogenetic correction ($\propto M^{0.325\pm0.105}$) indicates allometry may be an artefact of the non-independence between species (which are represented mostly by *Macropus*), and that among-species humerus scaling is not distinguishable from isometry.

Radius length scales with strong positive allometry in individuals ($\propto M^{0.433\pm0.034}$) and species-means ($\propto M^{0.421\pm0.059}$); however, it decreases with phylogenetic correction ($\propto M^{0.404\pm0.099}$) and may not be significantly different from isometry. Similarly, ulna length increases with positive allometry in individuals ($\propto M^{0.422\pm0.032}$) but is not significantly different from isometry for both species-means ($\propto M^{0.396\pm0.100}$) and phylogenetically corrected species-means ($\propto M^{0.309\pm0.198}$). When the radius and ulna data are restricted to measurements from the same individuals, the bones scale with the same exponent, as expected. The large difference between the species-means slopes of the radius and ulna with unrestricted data is likely an artefact of sampling – the ulna is measured in fewer species (16) than the radius (26). This indicates the large effect sampling can have on scaling factors.

Metacarpal III length scales with isometry in all cases and phylogenetic correction does not affect the result (individuals: $\propto M^{0.287\pm0.129}$; species-means: $\propto M^{0.274\pm0.175}$; corrected species-means: $\propto M^{0.285\pm0.284}$).

The scaling factors at the individual and species-means levels are noticeably different for most of the limb bones. This indicates that there are factors in the data that can skew the result, depending on grouping or over-representation. In addition to the difference between species (indicated by the difference in intra- and interspecific scaling), we suspect that sex and age will influence scaling factors (see muscle section for further discussion); however, we cannot evaluate these influences because most sources do not report sex or age.

Bone stress

If animals scale isometrically, limb bone stresses would be expected to increase $\propto M^{0.33}$, as the bone cross-sectional area increases $\propto M^{0.67}$, whereas volume (=mass) increases with an exponent of 1. The outcome would be a progressive reduction in the ability to support body mass as animals become larger. However, mammals employ various strategies to manage bone stress, and mammals of all sizes usually maintain peak compressive bone stresses between 50 and 100 MPa. This allows a safety factor (=failure stress/maximum functional stress) of 2–4 for the compressive strength of cortical bone, which is consistently 180–220 MPa in terrestrial mammals as diverse as mice and elephants (Biewener 1990, 2005), and there is no evidence to suggest that the compressive strength of macropodoid bone is an exception.

To our knowledge, *in vivo* bone stresses have not been measured in large macropods. However, in a red-necked wallaby (*Macropus rufogriseus*, 10.5 kg) hopping at high speed, a calculated maximum midshaft compressive stress of 90 MPa occurred in the tibia, which is within the normal range experienced by other mammals (Alexander and Vernon 1975). Alexander and Vernon (1975) also estimated tibia stress in a large red kangaroo (42 kg) to be 150 MPa, assuming geometric similarity with the red-necked wallaby. The compressive stress would result in a safety factor of 1.2–1.5 at high speeds, which is considerably lower than the usual minimum of 2–4 seen in other mammals (Biewener 1990). Bennett (2000) explored the scaling of tibial section modulus in large kangaroos and calculated a safety factor of close to 2, in support of the previous findings. Allometry of bone dimensions suggests that bone stress increases with body size and that large macropods may experience higher stresses than the usual range for mammals (Bennett 2000; McGowan *et al.* 2008*b*; Doube *et al.* 2018), but *in vivo* bone strain measurements are needed to determine this experimentally.

Placental quadrupedal mammals up to 300 kg typically counter the greater demands of loading at larger body sizes by adopting a more upright supporting limb posture. However, there is a functional limit to how straight the limbs can become, and above 300 kg positive allometry of bone geometry becomes more influential for maintaining safety factors (Biewener 1990, 2005). Hopping constrains the hind limbs to a crouched bent limb posture, which limits or precludes postural adaptation as a biomechanical solution for the maintenance of suitable skeletal stresses as body mass increases. It is therefore expected that allometry of bone geometry will be significantly adjusted in macropodoids less than 300 kg.

Bone robusticity can be improved by increasing the bone diameter relative to the length, although this does not appear to be the case in macropodoids. The external diameter of all hindlimb bones scales with isometry against bone length in macropodoids (McGowan *et al.* 2008*b*); however, bone stiffness could be increased through cortical thickening, which would increase the load-bearing cross-sectional area. The second moment of area, $I_{\max}$ (area of the cross-section multiplied by the distance from the axis squared) scales with positive allometry against length in the femur midshaft (isometry $I_{\max} \propto L^4$), reducing the bending tendency, while scaling with isometry in the metatarsal and metacarpal and negative allometry in the humerus, radius, ulna and tibia (tibia $I_{\max} \propto L^{3.352}$), increasing the bending tendency with greater bone length (Doube *et al.* 2018). The strong negative allometry of the tibia $I_{\max}$ against length is particularly surprising, as it indicates that the tibia gets relatively thinner, and consequently less resistant to bending forces, with increasing bone length and body size (Doube *et al.* 2018). However, $I_{\max}$ scales with positive allometry against body mass in the tibia midshaft (tibia $I_{\max} \propto M^{1.499}$, isometry $I_{\max} \propto M^{1.33}$) (Bennett 2000; Doube *et al.* 2018). These effects combine such that the tibia section modulus (Z, fracture strength under bending) scales nearly isometrically in macropodoids ($\propto M^{1.04}$) (Bennett 2000).

Scaling of the hindlimb, particularly the tibia, suggests that larger macropodoids become more gracile (Doube *et al.* 2018). However, the result may not be generalisable across all macropodoid taxa. Measurements of midshaft diameter of the femur and tibia suggest that large extant species of *Macropus* display a gracile specialisation, which is distinct from the 'normal' condition in large extinct macropodoids (Janis *et al.* 2014), in which case, measuring only extant species will skew the scaling factor to appear less robust than the general case in Macropodoidea. Future studies should examine the phylogenetic effects of $I_{\max}$ scaling in the hindlimb bones.

Muscles

The muscles of hopping macropodoids appear to be adapted to their active lifestyle. Kangaroos and wallabies have a higher proportion of skeletal muscle than tree kangaroos and possums [50% of total body mass in red kangaroos (*Macropus rufus*), 44% in brush-tailed bettongs (*Bettongia penicillata*), 34% in the tree kangaroo (*Dendrolagus matschiei*), 32% in the ring-tailed possum (*Pseudocheirus peregrinus*) (Grand 1990)]. The majority of the skeletal muscle (80%) is located around the pelvis, particularly in the proximal hindlimb (44%) (Dawson *et al.* 2004). As a consequence of this distribution of muscle, the centre of mass is posteriorly located (Alexander and Vernon 1975) and shifts further toward the hip in larger kangaroos (Grand 1990; Webster and Dawson 2012). This location of the centre of mass is functionally important, as it reduces the tendency for the body to pitch forward during hopping (Grand 1990).

The majority of research to date has focused on muscles of the distal hindlimb, as it is the primary source of elastic strain energy (Alexander and Vernon 1975). The distal hindlimb contains the primary ankle extensor muscles: the gastrocnemius (GAS), plantaris (PL), and flexor digitorum longus (FDL). The GAS muscle consists of a medial and lateral head. The medial head is approximately 50% more massive than the lateral head, but they scale with similar exponents (medial: $0.575M^{1.021}$; lateral: $0.295M^{1.093}$).

These ankle extensors are specialised for storing elastic strain energy with short, pennate muscle fibres attached to a long tendon (Alexander and Bennet-Clark 1977). The muscles contract nearly isometrically while the elastic tendons undergo the majority of the muscle–tendon unit length changes, and, consequently, the mechanical work from muscle shortening is much less than the work from elastic energy storage and recovery in the tendons (Biewener *et al.* 1998). The ankle extensor muscles contract to generate force, but do little mechanical work, even when more mechanical work is required at higher locomotor speeds (Biewener *et al.* 1998) or while traversing inclines (Biewener *et al.* 2004), although the distal leg muscles are capable of producing more work and do so when accelerating from rest on the take-off hop (Griffiths 1989). Rather, in steady hopping, additional work is supplied by the proximal hindlimb. A primary hip extensor (biceps femoris) and knee extensor (vastus lateralis) have been shown to do more work when hopping uphill than on level surfaces (McGowan *et al.* 2007). Most of the power required for hopping and acceleration comes from the proximal hindlimb, particularly the knee and hip extensors, and is applied at the ankle joint *via* biarticular muscles (McGowan *et al.* 2005*a*). In contrast to the distal extensors designed for economical locomotion, the proximal hindlimb muscles have longer, parallel fibres that undergo greater changes in length to both generate and absorb mechanical energy during hopping. Similar regional specialisation is seen in other groups of animals and does not necessarily restrict the muscles to only one role (Roberts *et al.* 1997). However, a division of labour between proximal muscles that produce work and distal muscles that generate tension in tendons for strain energy return does seem to be apparent in tammar wallabies (*Macropus eugenii*) (Biewener *et al.* 2004). At the cellular level, the mitochondrial and capillary morphology of the skeletal muscle reflects the specialised use of the distal and proximal hindlimb and, additionally, the back and tail in locomotion (Dawson *et al.* 2004).

The force the muscle generates is proportional to the physiological cross-sectional area. Based on geometric similarity, muscle PCSA increases with body size $\propto M^{0.67}$, yet to meet the demands of gravitational loading, muscle force is required to scale $\propto M^{1.00}$. Muscles will be underpowered as animals increase in size, unless they compensate with either positive allometric scaling of muscle mass and PCSA to increase the amount of muscle force available, or positive allometric scaling of skeletal moment arms to reduce the relative force required from the muscle to produce joint torque (by positive allometry of EMA). The scaling of EMA in most mammals adjusts the lever system of the limb to reduce the muscle force required to balance external joint moments (Biewener 1989, 1990). In most mammals, PCSA scales with positive allometry due to a relative reduction in fascicle length rather than due to increased muscle volume (Pollock and Shadwick 1994). However, in macropodoids, EMA scales with isometry and thus is not able to accommodate the size-related increases in locomotor force requirements (Bennett and Taylor 1995). Instead, macropodoids meet increased force demands with high positive allometry of PCSA from a combination of greater muscle mass and shorter fascicle lengths (average PCSA of hindlimb primary extensor muscles $\propto M^{0.95}$) (McGowan *et al.* 2008*b*).

Macropodoids have larger, more forceful muscles compared with similarly sized placental mammals. The predominant hip, knee and ankle extensor muscle masses all scale with positive allometry in macropodoids (mean $\propto M^{1.22}$) (McGowan *et al.* 2008*b*). Macropodoids also increase joint torque, to a lesser extent, with positive allometry of muscle moment arms (hip, ankle $\propto M^{0.42}$, knee $\propto M^{0.40}$) (McGowan *et al.* 2008*b*). The required muscle force scales with a higher exponent than the observed muscle PCSA across macropodoid species ($\propto M^{1.00}$ vs $\propto M^{0.92}$), meaning that larger species will generate proportionally less force from their muscles than smaller macropods, particularly if we consider that muscle efficiency decreases as muscle mass increases (Ross and Wakeling 2021). However, when the scaling of the muscle moment arms is taken into account, the resulting joint moment capacity remains proportionate in larger macropodoids (McGowan *et al.* 2008*b*).

The ankle extensor muscles are the most widely researched. We performed a meta-analysis on the muscle mass data that are reported for 14 species from 11 sources, containing 117 measurements of GAS mass, 116 measurements of PL mass, and 101 measurements of FDL mass.

Our meta-analysis shows that muscle mass of the GAS, PL and FDL all scale with positive allometry in individuals and species-means (see Table S3). The PL has the highest exponent (individuals: $\propto M^{1.187\pm0.042}$; species-means: $\propto M^{1.310\pm0.088}$; corrected species-means: $\propto M^{1.220\pm0.169}$), followed by the GAS (individuals: $\propto M^{1.101\pm0.038}$; species-means: $\propto M^{1.162\pm0.113}$; corrected species-means: $\propto M^{1.179\pm0.179}$) and the FDL (individuals: $\propto M^{1.101\pm0.043}$; species-means: $\propto M^{1.184\pm0.111}$; corrected species-means: $\propto M^{1.214\pm0.214}$). The large scaling factors for macropodoids, particularly the PL, are apparent in comparison to a wide range of placental mammals, ~0.05–550 kg, in which the ankle extensor muscles scale with isometry [GAS $\propto M^{1.009\pm0.067}$, PL $\propto M^{0.968\pm0.062}$ and FDL $\propto M^{1.032\pm0.053}$, calculated from Pollock and Shadwick (1994)]. The difference between macropodoids and placental quadrupeds increases with body size; however, in macropodoids of all sizes these three muscles are larger than in placental quadrupeds of the same body mass (Fig. 3*a*–*c*). This does not necessarily mean that macropods produce more absolute muscle force, as quadrupeds use other methods in addition to muscle mass and PCSA to increase joint torques, such as changing the mechanical advantage of the limb.

Interspecies relationships differ from the intraspecific relationship in Macropodoidea. Scaling across the full size range for the western grey kangaroo (*Macropus fuliginosus*) (5.8–70.5 kg) shows that fascicle length and muscle volume both scale with negative allometry, resulting in isometric scaling of PCSA in the ankle extensor muscles, and, consequently, larger kangaroos generate proportionally less muscle force in the ankle extensors than smaller individuals of the same species (mean muscle mass $\propto M^{0.86}$) (Snelling *et al.* 2017). We analysed the scaling relationship within 45 eastern grey kangaroos (*Macropus giganteus*), 19 western grey kangaroos and 18 red kangaroos (*Macropus rufus*), and, similar to Snelling *et al.* (2017), the scaling exponents differ from Macropodoidea (Fig. 3*d*, Table S4). Muscle mass in the western grey kangaroo scales with negative allometry (GAS $\propto M^{0.845\pm0.050}$, PL $\propto M^{0.880\pm0.060}$ and FDL $\propto M^{0.876\pm0.053}$). The mass of the GAS, PL and FDL in red kangaroos is not significantly different from isometry (GAS $\propto M^{0.928\pm0.169}$, PL $\propto M^{0.972\pm0.136}$ and FDL $\propto M^{0.944\pm0.153}$). Unlike either species, muscle mass in the eastern grey kangaroo scales with positive allometry (GAS $\propto M^{1.048\pm0.034}$, PL $\propto M^{1.093\pm0.042}$ and FDL $\propto M^{1.060\pm0.030}$).

The difference between intra- and interspecies exponents complicates the process of estimating scaling across Macropodoidea. Scaling of the Macropodoidea slope will be sensitive to species sampling and to the distribution within each species. In species with negative allometry of muscle mass, oversampling small individuals of each species will increase the apparent allometry, and an abundance of large individuals in the species average will skew the slope in the negative direction. This may explain why our estimates for muscle mass scaling in individuals are lower than for species-means and corrected species-means. Sampling can greatly affect the scaling exponent (Labonte *et al.* 2016). For example, we processed 1000 random samples of 15 eastern grey kangaroos out of a pool of 45 individuals and the scaling estimates for GAS mass on these subsets were between $\propto M^{0.898\pm0.054}$ and $\propto M^{1.125\pm0.049}$, showing a full range from strong negative allometry to strong positive allometry. Larger species of macropodoids (>10 kg) have a greater range of adult sizes and more pronounced sexual dimorphism of size than smaller species (Weckerly 1998; Richards *et al.* 2015), and as such, error could correlate and compound with body size in Macropodoidea, if care is not taken to use a normal distribution of body mass within each species, or an average representative if using a single individual. As such, we suggest caution for research that examines trait scaling relationships across Macropodoidea.

Despite negative allometry of muscle mass in some species, the ankle extensor muscles of the extant kangaroos are still able to generate unusually high forces for mammals. Muscle stress has been measured in the tammar wallaby (Baudinette *et al.* 1992; Biewener and Baudinette 1995; McGowan *et al.* 2007, 2008*a*), and yellow-footed rock wallaby (*Petrogale xanthopus*) (McGowan *et al.* 2008*a*). In these small species (~6 kg), maximum isometric muscle stress is frequently above 215 kPa, which is higher than usual for mammalian skeletal muscle (Biewener and Baudinette 1995). The maximum recorded value is 262 kPa in the PL and 227 kPa in the GAS in the tammar wallaby hopping at 5.5 m s^{-1}, suggesting that the muscles may reach stresses of up to 350 kPa at their maximum speed, 12 m s^{-1} (Biewener and Baudinette 1995). To our knowledge, muscle stress has not been directly measured in larger macropods; however, muscle force is known to increase with both body size and speed in small macropods (Griffiths 1989). If the ankle extensor muscles in larger kangaroos (>50 kg) can produce similar stresses as those of small macropodoids, they may be capable of producing enough force to rupture the GAS or PL tendon at high speeds, which might explain why kangaroos rarely travel at their maximum speed (Kram and Dawson 1998). More research on *in vivo* muscle stress in large kangaroos, as well as the relationship of maximum speed with body size, would provide insights into whether performance

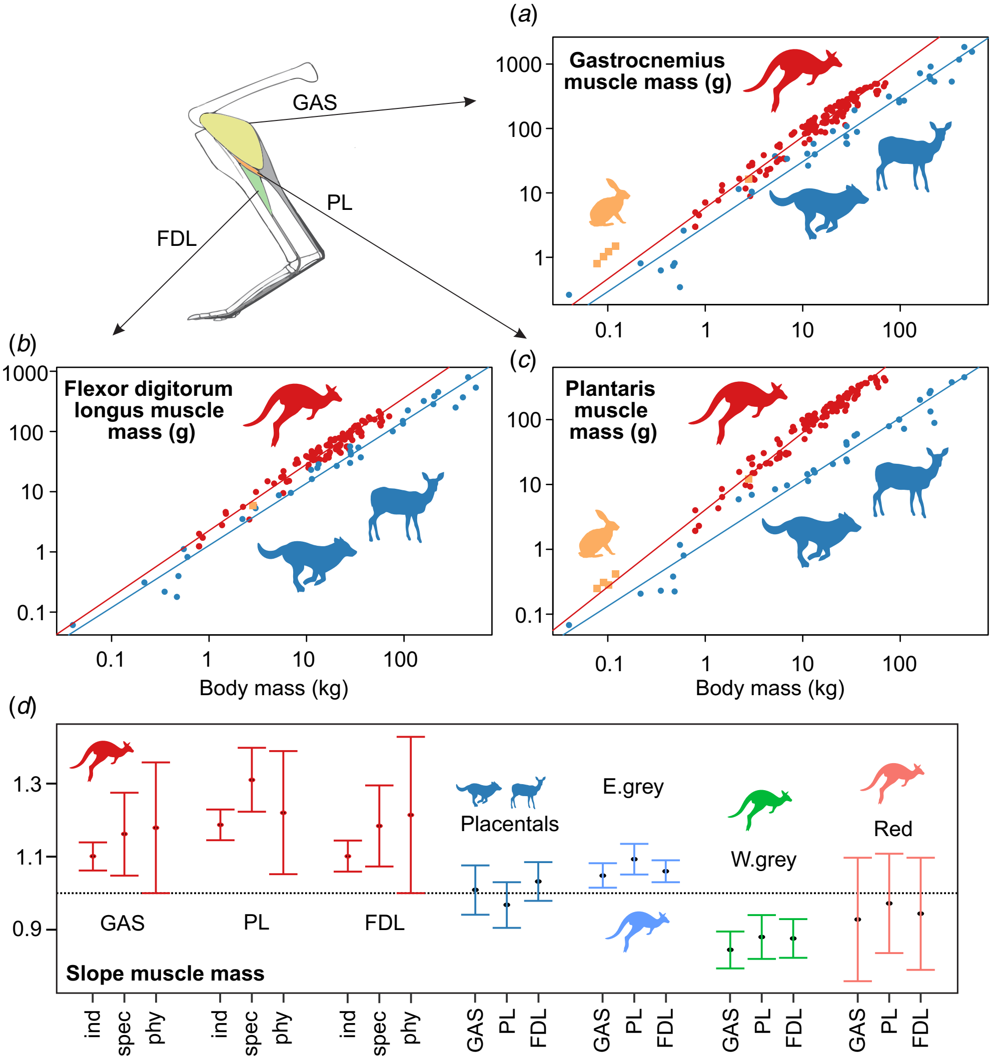

Fig. 3. Scaling relationships for (*a*) gastrocnemius (GAS) mass ($n = 117$), (*b*) flexor digitorum longus (FDL) mass ($n = 101$), and (*c*) plantaris (PL) mass ($n = 116$) against body mass for individual macropodoids (red) and placentals ($n = 30$, blue). Hopping placentals were excluded from slope analysis. Intraspecific scaling for the eastern grey kangaroo (*Macropus giganteus*), western grey kangaroo (*Macropus fuliginosus*) and red kangaroo (*Macropus rufus*) are included. The values for the slopes with 95% confidence intervals are presented in (*d*) for the three muscles and the subgroups. Ind, individual; spec, species-means; phy, phylogenetically corrected species-means.

declines in large macropods as a mechanism to limit peak muscle and tendon stress.

The hindlimbs have been the focus of locomotion research to date; however, macropods can use four or five points of contact with the ground during locomotion. All macropodoids use their forelimbs during locomotion; small species use a quadrupedal bounding gait in slow progression, large species use a pentapedal gait in which the forelimbs and tail provide support while the hindlimbs swing forward for the next stride, and tree kangaroos (*Dendrolagus*) climb (Dawson *et al.* 2015).

The total musculature of the forelimbs is substantially less than that of the hindlimbs, and the dichotomy is greater in larger (10 and 26 kg) *Macropus* species (1:10 fore- to hindlimb weight) than in smaller species, such as the long-nosed potoroo (*Potorous tridactylus apicalis*, ~1 kg body mass, 1:5 fore- to hindlimb weight) (Grand 1990). Among the larger macropodoids, forelimb muscle mass varies with species, size and sex; the forelimb muscles of some species are significantly larger in males than females and there is greater sexual dimorphism of size in larger species (Warburton *et al.* 2013; Richards *et al.* 2015). Forelimb muscle mass is more similar to hindlimb muscle mass in the tree kangaroo (*Dendrolagus matschiei*, 1:1.3 fore- to hindlimb muscle mass), likely due to the greater involvement of the upper body in climbing locomotion (Grand 1990). Forelimb use varies wildly in Macropodoidea, for instance, the use of the forelimbs in tree kangaroos is distinctly different from that in red kangaroos, in which the forelimbs predominantly provide braking force in pentapedal locomotion, while the tail provides most of the propulsive force (Warburton *et al.* 2011; O'Connor *et al.* 2014). However, the *in vivo* action of forelimb and tail muscles during locomotion has not been studied.

Kangaroos have large, heavy tails. Of those measured, tail mass is greatest in the red kangaroo (9% of total body mass in a 22 kg individual) and decreases with body size across macropodoid species (*Macropus rufogriseus*: 4.5% at 10 kg body mass; *Potorous tridactylus*: 3% at 1 kg body mass) (Hopwood 1976; Grand 1990). Large kangaroos use their tail as a supporting limb when fighting and to generate significant forces in the forward direction for propulsion during pentapedal locomotion, whereas smaller macropodoids do not (O'Connor *et al.* 2014; Dawson *et al.* 2015). In steady hopping, the tail swings in phase with the hindlimbs and torso, but in the opposite direction, effectively reducing the body pitch caused by the simultaneous movement of the hindlimbs (Alexander and Vernon 1975) and movement of the torso (Moore *et al.* 2019). Additionally, there is indirect evidence in tammar wallabies and yellow-footed rock wallabies that the tail, back or trunk muscle–tendon units are used to store elastic strain energy and produce power for hopping (McGowan *et al.* 2005*a*, 2007). This is supported by the observation that rock wallaby jumping exceeds the power output capacity of all the relevant hindlimb muscles (McGowan *et al.* 2005*b*).

Tendons

Tendons are elastic elements that store and return elastic strain energy *via* stretch and recoil. During the first half of the ground contact phase in hopping, kinetic and gravitational potential energy are transferred from the body and stored as elastic strain energy in hindlimb tendons (Dawson and Taylor 1973; Alexander and Vernon 1975). The tendon recoil in the later part of the contact phase returns the energy to the body, contributing to the mass-dependent energetic savings at high speeds (Bennett and Taylor 1995).

The amount of energy stored in a tendon depends on the tendon stress, tendon volume, Young's Modulus and the percentage of energy lost during recoil (hysteresis). Given constant material properties (Young's Modulus and hysteresis), differences between tendons emerge from morphology. The total energy storage capacity is determined by tendon volume (cross-sectional area (CSA) multiplied by length). Strain energy is generated by stretching the tendon – thick tendons require more force to produce a unit change in length. Tendons that are specialised for storing strain energy tend to be thin, for greater strains, and long, for greater volume.

The primary elastic strain energy stores in macropodoids are the tendinous structures at the ankle, principally the gastrocnemius (GAS), plantaris (PL) and flexor digitorum longus (FDL). The ankle extensor tendons have been studied for a wide range of body sizes, up to 70 kg (Snelling *et al.* 2017). The properties of other tendons in the body are relatively poorly studied, although there are anatomical descriptions of tendon attachment points in the whole hindlimb (Bauschulte 1972; Hopwood and Butterfield 1990) and tail (Dawson *et al.* 2014). Tail tendons were measured to fatigue failure, and the material properties do not stand out from those of other mammals (Bennett *et al.* 1986; Wang *et al.* 1995) but tail tendons are otherwise unstudied.

The primary ankle extensor tendons have been almost exclusively investigated in *Macropus*; other genera are under-represented (Fig. 1). Very few species (primarily in *Macropus*) have been measured for tendon length and CSA in the GAS and PL, while length and CSA of the FDL, as well as stress in all three tendons, have been measured only in *Macropus*. Consequently, phylogenetic correction in these traits is more of an indication of the correlation within *Macropus*, rather than Macropodoidea as a whole. For this reason, we expect phylogenetically corrected species-means to show much less divergence from species-means in tendon traits than with muscle masses or bone lengths, but this does not necessarily indicate that tendons are more similar than muscles or bones. On the contrary, tendon traits are known to diverge in specific cases. For example, the ankle extensor tendons in yellow-footed rock wallabies (*Petrogale xanthopus*) have a significantly larger CSA than those in tammar wallabies (*Macropus eugenii*), which corresponds to higher safety factors and lower strain energy storage (McGowan *et al.* 2008*a*). Tendons in the rock wallaby show specialisations for fast acceleration and vertical jumping, reflecting the demands of living on cliffs, while the thin tendons in the tammar wallaby show specialisations for energy efficient hopping (McGowan *et al.* 2008*a*). Research is needed to more broadly sample *Petrogale*, and Macropodoidea in general, to determine the effects of phylogeny on differences in tendon morphology. Sampling other groups, such as the tree kangaroos (*Dendrolagus*), will enable a broader understanding of how tendon morphology changes with ecology in macropodoids.

The results of our scaling analysis show that tendon length increases with positive allometry in the GAS ($\propto M^{0.499\pm0.074}$) and PL ($\propto M^{0.416\pm0.062}$), and with isometry in the FDL ($\propto M^{0.360\pm0.086}$) in individuals (Fig. S1). There is high uncertainty (Table S5) in species-means and phylogenetically corrected species-means due to the small species sample, and, perhaps as a consequence, all are indistinguishable from isometry (GAS: species-means $\propto M^{0.464\pm0.331}$, corrected species-means $\propto M^{0.446\pm0.343}$; PL: species-means $\propto M^{0.372\pm0.373}$, corrected species-means $\propto M^{0.374\pm0.378}$; FDL: species-means $\propto M^{0.518\pm1.618}$, corrected species-means $\propto M^{0.519\pm1.561}$).

Muscle–tendon unit length is correlated with bone length. The GAS muscle–tendon unit is approximately the length of the tibia, and the PL and FDL are the length of the tibia and metatarsal IV. Given that tibia length scales with strong positive allometry, the metatarsal with isometry, and muscle length with isometry [in western grey kangaroos, *Macropus fuliginosus*: Snelling *et al.* (2017)], tendon length would be expected to increase with positive allometry, and this has been observed in some studies (Bennett and Taylor 1995; Bennett 2000). Increasing the tendon length increases the tendon volume and the capacity to store elastic strain energy. At the individual level, GAS and PL tendon length scale with positive allometry, indicating that larger individuals also have greater tendon volume and capacity for energy storage. More species will need to be sampled to determine if this is true of Macropodoidea in general or if this is limited to *Macropus*, from which most of the species are sampled (Fig. 1).

Reports of tendon CSA scaling vary in the literature, between isometry [GAS $\propto M^{0.56}$, PL $\propto M^{0.75}$, FDL $\propto M^{0.56}$ (Bennett 2000)], negative allometry [GAS $\propto M^{0.57}$, FDL $\propto M^{0.58}$ (McGowan *et al.* 2008*b*)], and positive allometry [PL $\propto M^{0.83}$ (McGowan *et al.* 2008*b*)]. Regardless, tendon CSA increases at a slower rate than muscle PCSA, and, consequently, the ratio of muscle area to tendon area increases such that larger macropods have higher tendon loads, particularly in the GAS and PL (A_m/A_t: GAS $\propto M^{0.49}$, PL $\propto M^{0.44}$, FDL $\propto M^{0.24}$) (Bennett 2000). At the intraspecific level in the western grey kangaroo, the muscle to tendon ratio scales with positive allometry in the GAS only ($\propto M^{0.15}$), due to negative allometry of tendon CSA and isometric scaling of muscle PCSA (Snelling *et al.* 2017).

Our meta-analysis results suggest that the scaling of tendon CSA is not significantly different from isometry in any tendon, in any condition (GAS: individuals $\propto M^{0.609\pm0.075}$, species-means $\propto M^{0.285\pm1.082}$, corrected species-means $\propto M^{0.276\pm1.118}$; PL: individuals $\propto M^{0.638\pm0.064}$, species-means $\propto M^{0.426\pm0.725}$, corrected species-means $\propto M^{0.426\pm0.743}$; FDL: individual $\propto M^{0.655\pm0.062}$, species-means $\propto M^{0.685\pm3.207}$, corrected species-means $\propto M^{0.684\pm3.095}$). However, the ratio of muscle area (PCSA) to tendon area (CSA), which is an indication of the stress the muscle can load on the tendon, increases with positive allometry ($>M^0$) in the GAS (individuals $\propto M^{0.239\pm0.037}$, species-means $\propto M^{0.221\pm0.078}$, corrected species-means $\propto M^{0.273\pm0.165}$) and PL (individuals $\propto M^{0.165\pm0.059}$, species-means $\propto M^{0.187\pm0.131}$, corrected species-means $\propto M^{0.287\pm0.285}$). There is apparent positive allometry in the FDL at the individual and species-mean level ($\propto M^{0.215\pm0.085}$, $\propto M^{0.247\pm0.198}$); however, phylogenetic-correction reduces the scaling to isometry ($\propto M^{0.126\pm0.381}$).

We expect *in vivo* peak tendon stress to show a similar pattern as the muscle to tendon area ratio, although our analysis does not control for speed, which will impact stress (Biewener *et al.* 1998). Our meta-analysis shows that, at the individual level, tendon stress scales with isometry in the GAS ($\propto M^{0.303\pm0.139}$) and negative allometry in the PL and FDL (PL $\propto M^{0.208\pm0.112}$, FDL $\propto M^{0.040\pm0.116}$). Tendon stress has been measured in very few species, and, consequently, the species-means and corrected species-means scaling exponents are not robust (n = 3 or 4, see Table S5). Additionally, due to solely sampling from *Macropus*, the results could be skewed towards more negative allometry if intraspecific scaling of *Macropus* species is lower than in other macropodoids. This has some precedence; tendon stress and strain scale significantly lower in western grey kangaroos than in Macropodoidea in general (Snelling *et al.* 2017).

Elastic strain energy capacity and tendon safety factor are intrinsically linked to tendon stress; an increase in stress directly increases the strain energy ($\propto$stress^2). Elastic strain energy scales with strong positive allometry ($>M^1$) in the GAS and PL tendons (GAS: individuals $\propto M^{1.499\pm0.151}$, species-means $\propto M^{1.446\pm0.194}$, corrected species-means $\propto M^{1.618\pm0.337}$; PL: individuals $\propto M^{1.541\pm0.168}$, species-means $\propto M^{1.608\pm0.242}$, corrected species-means $\propto M^{1.760\pm0.612}$). Elastic energy in the FDL scales with positive allometry in individuals and species-means ($\propto M^{1.416\pm0.180}$, $\propto M^{1.603\pm0.340}$), but decreases to isometry when phylogenetic-correction is applied ($\propto M^{1.287\pm0.756}$). The exponent of the PL tendon is greater than that of the GAS tendon, indicating that energy storage in the PL is increasingly important in larger individuals and species, although this is the opposite in western grey kangaroos (Snelling *et al.* 2017). Elastic energy storage scales at a lower rate in placentals in the GAS ($\propto M^{1.185\pm0.100}$, Fig. 4*a*) but similarly in the PL ($\propto M^{1.382\pm0.133}$) and FDL ($\propto M^{1.312\pm0.102}$) to macropodoids. Due to this, macropodoids tend to store more strain energy than placental mammals of a given size.

In small macropods such as the tammar wallaby, most of the energy recovered in each hop is stored in the GAS tendon, despite the PL being longer, because tendon stresses are significantly higher in the GAS due to its smaller CSA (Biewener and Baudinette 1995). The PL is also significantly involved in energy storage (Biewener and Baudinette 1995); however, the FDL and digital extensors are not (Bennett 2000). The FDL is morphologically distinct from the GAS and PL tendon; it is thicker and undergoes much less stress and correspondingly less elastic energy storage (Biewener and Baudinette 1995). This morphological distinction likely reflects a functional difference; the stiffer FDL may play a greater role in foot control during locomotion (Biewener and Baudinette 1995; McGowan *et al.* 2008*b*).

Increasing stress necessarily decreases safety factor. In our analysis, safety factor scales with negative allometry ($<M^0$) in the GAS, PL and FDL for individuals and species means (GAS: individuals $\propto M^{-0.241\pm0.044}$, species-means $\propto M^{-0.203\pm0.087}$; PL: individuals $\propto M^{-0.170\pm0.059}$, species-means $\propto M^{-0.169\pm0.135}$; FDL: individuals $\propto M^{-0.219\pm0.080}$, species-means $\propto M^{-0.243\pm0.192}$). Phylogenetic-correction does

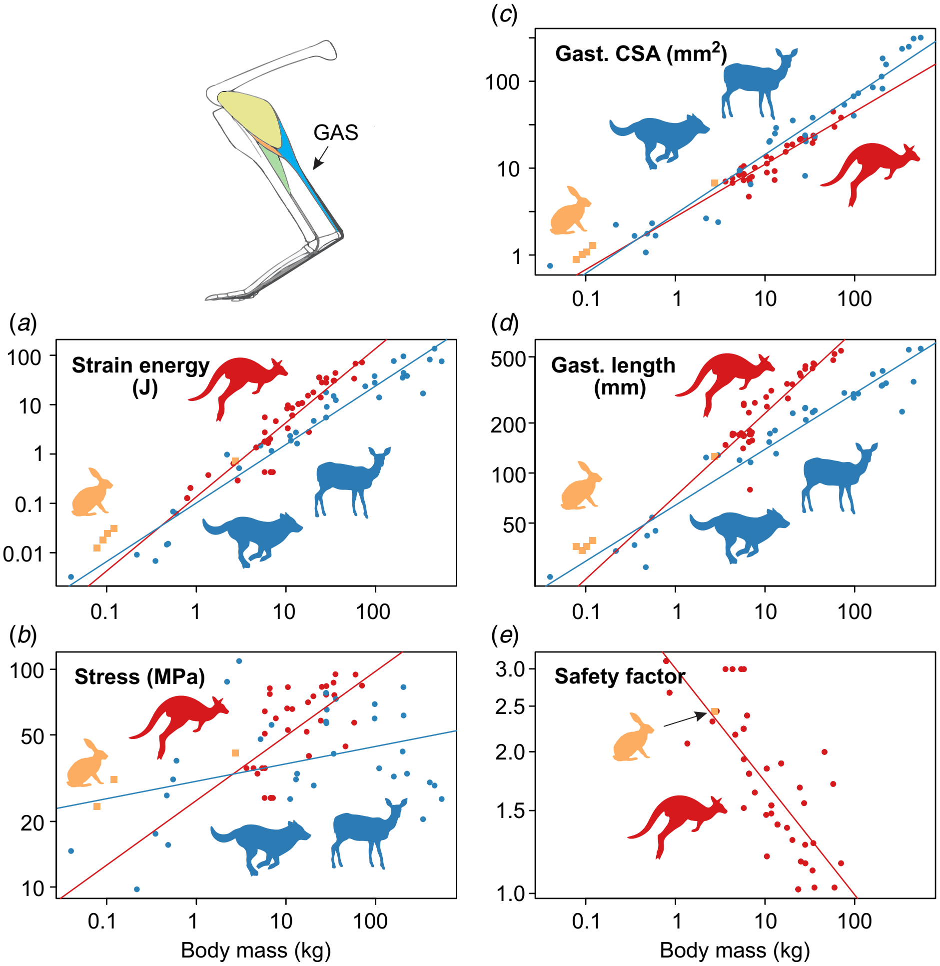

Fig. 4. Macropodoids (red) are plotted with quadrupedal placental mammals (blue) and hopping placental mammals (yellow) for comparison. Hopping placentals were excluded from slope analysis. Scaling relationships for the gastrocnemius (GAS) (*a*) tendon elastic strain energy (n = 61 macropodoids, n = 34 quadrupeds), (*b*) tendon stress (n = 33 macropodoids, n = 33 quadrupeds), (*c*) tendon cross-sectional area (n = 42 macropodoids, n = 34 quadrupeds), (*d*) tendon length (n = 46 macropodoids, n = 35 quadrupeds), and (e) safety factor of GAS against body mass (n = 62 macropodoids).

not change the scaling of the GAS safety factor ($\propto M^{-0.264\pm0.176}$); however, for both the PL and FDL, corrected safety factors are not significantly different from isometry (PL $\propto M^{-0.284\pm0.313}$, FDL $\propto M^{-0.164\pm0.371}$). Large macropods operate at much lower safety factors than small macropods over their normal speed range (Fig. 4*e*), and so large kangaroos moving at high speeds are likely operating dangerously close to failure points in the GAS or PL tendons (Kram and Dawson 1998).

Gait

There is a diverse range of gaits among macropodoid species. Some use quadrupedal bounding [generally for slow progression in small <10 kg macropodoids (Dawson *et al.* 2015)], whereas others use pentapedal locomotion [the alternative to bounding for large macropods, with additional support and thrust from the tail (O'Connor *et al.* 2014)]. Quadrupedal and bipedal walking appears limited to tree kangaroos (*Dendrolagus* spp.) in extant species, although a pacing gait has been reported during swimming in red kangaroos (*Macropus rufus*) (Wilson 1974), and it has been suggested that extinct sthenurines used bipedal striding (Janis *et al.* 2014). The most ubiquitous gait is bipedal hopping. Hopping is used in varying degrees by almost all macropodoids for fast movement, with larger species of macropods able to hop continuously over long distances – a unique feature among large animals, extinct or extant.

Hopping speed

Hopping is the fastest macropodoid gait; however, relatively little is known about the maximum speed for each species (Fig. 5). Maximum speed has been measured in the long-nosed potoroo (*Potorous tridactylus apicalis*, ~0.8 kg), Tasmanian bettong (*Bettongia gaimardi*, ~1.8 kg), Tasmanian pademelon (*Thylogale billardierii*, ~5 kg) and eastern grey kangaroo (*Macropus giganteus*, ~20–60 kg) (Bennett 1987). Top speed on treadmills, which is usually lower than top speed over ground, was reached in the brush-tailed bettong (*Bettongia penicillata*) (Webster and Dawson 2003) and tammar wallaby (*Macropus eugenii*) (Baudinette *et al.* 1992).

Bennett (1987) reported that maximum hopping speed scales ∝ $M^{0.36}$ in macropods, and given the tight correlation between body mass and leg length in macropods, maximum hopping speed is also proportional to hip height. All the species for which maximum speed has been recorded are small (<6 kg), except eastern grey kangaroos, which were measured to ~60 kg although they reach greater body masses (~80 kg). A more complete range of species and sizes should be sampled to determine if maximum speed peaks in moderately sized macropods, as it does in other animals (Dick and Clemente 2017).

Stride length and frequency relationship

Stride length and stride frequency have been more widely measured across species, including the Tasmanian bettong (Bennett 1987), brush-tailed bettong (Webster and Dawson 2003), tammar wallaby (Baudinette *et al.* 1987; Biewener and Baudinette 1995; Biewener *et al.* 2004; McGowan *et al.* 2007), eastern grey kangaroo (Bennett 1987), red-necked wallaby (*Macropus rufogriseus*) (Alexander and Vernon 1975), red kangaroo (Dawson and Taylor 1973; Alexander and Vernon 1975; Dawson 1977), long-nosed potoroo (Bennett 1987; Baudinette *et al.* 1993), quokka (*Setonix brachyurus*) (Baudinette 1977) and Tasmanian pademelon (Bennett 1987). Stride length and frequency have been determined across a wide range of speeds (up to 13.5 m s^{-1}), and body sizes. Although most species are small (<7 kg), there is still representation from moderate and large species [red-necked wallaby 10.5 kg (Alexander and Vernon 1975), red kangaroos 18 and 28 kg (Dawson and Taylor 1973), and eastern grey kangaroos ~20–60 kg (Bennett 1987)]. However, the relationship between stride length and frequency with speed has not been measured in large individuals over 28 kg moving at high speeds (over 7 m s^{-1}) (Dawson and Taylor 1973).

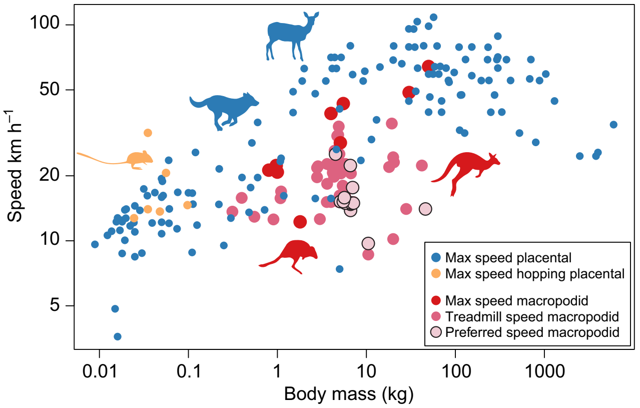

Fig. 5. Relationship between maximum speed and body mass for placental quadrupeds [*n* = 141, blue (Garland 1983)], placental hopping rodents (*n* = 5, yellow), and macropodoids (*n* = 8, red). Most measurements of macropodoid speeds were recorded on treadmills (*n* = 48) or in a captive environment where the animal was moving at its preferred speed (*n* = 16).

At low speeds, most macropodoids use quadrupedal bounding or pentapedal locomotion, and the increase in speed is achieved primarily by increasing stride frequency, with a comparatively minor increase in stride length (Dawson and Taylor 1973). After the transition to hopping, this pattern changes; hopping frequency is nearly constant and instead stride length increases linearly with speed (Dawson and Taylor 1973). This pattern appears to be similar regardless of size and is observed in the brush-tailed bettong (1 kg) (Webster and Dawson 2003), tammar wallaby (4–7 kg) (Biewener and Baudinette 1995; Biewener *et al.* 2004), red kangaroo (18 and 28 kg) (Dawson and Taylor 1973) and western grey kangaroo (*Macropus fuliginosus*) (Stewart and Setchell 1974). In the tammar wallaby, the increase in hopping speed from 2 to 7 m s^{-1} corresponds to an 89% increase in stride length and an 11% increase in stride frequency (Biewener *et al.* 1998).

The increase in stride length may reach a limit in red kangaroos at very high speeds, approximately 10 m s^{-1}, beyond which speed increases are due to an increase in stride frequency (Dawson 1977); however, this has not been confirmed in other species. Red kangaroos hop at such speeds for only short distances, and likely do so only when escaping danger (Dawson 1977). The preferred hopping speed of large kangaroos is well below their maximum capability, possibly to reduce tendon stress (Kram and Dawson 1998). At preferred hopping speeds, stride frequency is near-constant in the species that have been sampled thus far, but further data are required to test the general applicability of this observation.

It is interesting to note that the near-constant stride frequency is not entirely limited to the hopping gait in macropods, and that the relationship between stride frequency and speed is non-linear in the quokka hopping intermittently (Baudinette 1977) and in bounding long-nosed potoroos (0.1–1 kg) (Baudinette *et al.* 1993). In quadrupedal mammals, constant stride frequency with increasing speed is unusual, and, except for some large mammals which have a near-constant stride frequency when galloping, quadrupedal and bipedal mammals increase speed by increasing both stride length and frequency (Heglund and Taylor 1988).

The stride frequency in macropodoids is related to body mass ($\propto M^{-0.23}$) and leg length ($\propto$hip height$^{-0.54}$); larger macropodoids have lower stride frequency and longer stride lengths ($\propto M^{0.54}$) (Bennett 1987). Stride frequency scales at a lower rate in macropodoids than in quadrupedal mammals [$\propto M^{-0.15}$ (Heglund and Taylor 1988)], such that macropodoids have lower stride frequencies than similarly sized quadrupeds (Webster and Dawson 2003).

Ground contact time and forces

Duty factor is the proportion of the stride that the foot is in contact with the ground. Duty factor or contact time has been measured for many genera including *Bettongia, Potorous, Thylogale, Macropus, Aepyprymnus, Hypsiprymnodon* and *Wallabia* (Bennett 1987; Bennett and Taylor 1995; Biewener and Baudinette 1995; Baudinette and Biewener 1998; Biewener *et al.* 1998, 2004; Kram and Dawson 1998; McGowan *et al.* 2007). The ground applies an upward-directed ground reaction force (GRF) throughout the contact phase. Hopping GRF has been measured in the Tasmanian pademelon (Griffiths 1989), red-necked wallaby (Alexander and Vernon 1975), tammar wallaby (McGowan *et al.* 2005*a*, 2005*b*) and red kangaroo (Alexander and Vernon 1975; Cavagna *et al.* 1977; Kram and Dawson 1998), and estimated from individuals' foot–ground contact areas under known, applied pressures across Macropodidae (Bennett 1999). For a given impulse (integral of force acting over a period of time), a decrease in ground contact time is associated with an increase in peak GRF, as the same force is developed more quickly when contact times are shorter. Higher peak GRF forces in turn develop greater stresses in the body.

Higher locomotor speed is associated with lower ground contact times. Both duty factor and contact time decrease with increasing speed in tammar wallabies (Biewener *et al.* 1998, 2004) and red kangaroos (Cavagna *et al.* 1977; Kram and Dawson 1998). This seems to be true of macropodoids in general: duty factor decreases with speed ($\propto$speed$^{-0.39}$) in Macropodoidea (Bennett and Taylor 1995), which is difficult to distinguish from the increase in speed with size ($\propto M^{0.36}$) and the decrease in duty factor with size ($\propto M^{-0.10}$) (Bennett 1987). This contrasts with quadrupedal mammals, in which larger mammals tend to have higher duty factors, although, like macropodoids, duty factor decreases with speed (Alexander 1977; Biewener 1983). Given that higher speed (lower contact time) and body mass both increase forces, it is not surprising that GRF increases with body size (Bennett 1999) and speed ($\propto$speed$^{0.39}$) across Macropodoidea (Cavagna *et al.* 1977; Bennett and Taylor 1995).

Quadrupeds mitigate the increase in stress and peak force at large sizes by altering their limb posture to become more upright, which increases the effective mechanical advantage (EMA). EMA at the ankle scales $\propto M^{0.25}$ in quadrupeds (Biewener 2005), and, in comparison, macropodoids of different sizes retain a crouched posture for effective hopping, with constant ankle and knee EMA [ankle $\propto M^{0.00}$ (Bennett and Taylor 1995); knee $\propto M^{-0.04}$ (McGowan *et al.* 2008*b*)], whereas the hip EMA increases ($\propto M^{0.22}$) (McGowan *et al.* 2008*b*). The same is true within species: ankle EMA is independent of body size within the western grey kangaroo (Snelling *et al.* 2017); however, there may still be variation between species that live in markedly different habitats. Ankle EMA is higher in the yellow-footed rock wallaby (*Petrogale xanthopus*) than the tammar wallaby at mid-stance during steady speed hopping, which may impact the relative energetic capabilities of both species (see the Energetics section) (McGowan *et al.* 2008*a*). Partly due to this constant EMA, skeletal and muscle–tendon stresses may be higher in large macropodoids than in equivalently sized quadrupeds (see the bone stress section). In addition to size-related increases in stress, macropodoids and quadrupeds do not appear to use changes in posture to mitigate speed-related increases in stress. The EMA of the ankle joint is constant for speeds up to at least 9.7 m s^{-1} in red kangaroos, which suggests that stresses increase with increasing speed (Kram and Dawson 1998).

To our knowledge, ground contact time has not been measured in large individuals at high speeds [>46.1 kg at 4 m s^{-1} (Kram and Dawson 1998)]. Given that forces in these conditions are expected to put the ankle extensor tendons under such stress that they are near their breaking point (Bennett and Taylor 1995; McGowan *et al.* 2008*b*), it would be interesting to determine if large individuals show the same decrease in contact time as smaller individuals, or if there is a limit to how short contact time can become, and thereby a limit on maximum speed. Contact time limits top running speed in humans due to the time available to apply forces, rather than the peak force that the limbs can either withstand or produce (Weyand *et al.* 2000). However, this may not be a universal feature – for instance, top speed in dogs may not be limited by contact time (Usherwood and Wilson 2005). Measuring contact time in addition to GRFs in large macropods could help determine whether they reduce performance to maintain safe stress levels.

Energetics

Summary of research on energetics

Oxygen consumption is an indicator of metabolic energy use. Oxygen consumption in quadrupeds increases linearly with speed and the rate of increase is determined by body size (Taylor *et al.* 1970). The changes in oxygen consumption with speed have been measured in six macropodoid species: the brush-tailed bettong (*Bettongia penicillata*) (Thompson *et al.* 1980; Webster and Dawson 2003), tammar wallaby (*Macropus eugenii*) (Baudinette *et al.* 1992), red kangaroo (*Macropus rufus*) (Dawson and Taylor 1973; Kram and Dawson 1998), long-nosed potoroo (*Potorous tridactylus*) (Baudinette *et al.* 1993), quokka (*Setonix brachyurus*) (Baudinette 1977) and Tasmanian pademelon (*Thylogale billardierii*) (Warren 1979) (Fig. 6). Of these, the red kangaroo and tammar wallaby stand out as highly unusual: in contrast to the linear relationship in quadrupeds, oxygen consumption is uncoupled from speed (Dawson and Taylor 1973; Baudinette *et al.* 1992; Baudinette 1994; Kram and Dawson 1998). The phenomenon was first observed in treadmill hopping for red kangaroos, where oxygen consumption was highest at slow hopping speeds and decreased as speeds reached 6.1 m s^{-1} for a 18 kg individual and 3.9 m s^{-1} for a 28 kg individual (Dawson and Taylor 1973). In a separate study, oxygen consumption remained constant with increasing speed while hopping up to 6.6 m s^{-1} for a 20.4 kg individual (Kram and Dawson 1998). The mass-specific lower metabolic costs indicate that kangaroos are more efficient than similarly sized quadrupeds at speeds greater than ~4.2 m s^{-1} (Dawson and Taylor 1973). However, oxygen consumption in macropodoids has, thus far, been limited to measurements on treadmills. Research should focus on measuring oxygen consumption in free-ranging macropodoids to gain insight into energetics in more natural conditions.

Kangaroo oxygen consumption is predicted to increase at higher speeds than have yet been measured (Dawson 1977), particularly if air resistance is taken into consideration, since air resistance has a greater impact at higher movement speeds. Baudinette *et al.* (1992) calculated air resistance for a 20 kg red kangaroo and the energy cost per unit distance (cost of transport) is minimised at 12 m s^{-1}. Red kangaroos typically hop between 5.5 and 7 m s^{-1} and only travel at high speeds in short bursts (Dawson 1977). If kangaroos follow the minimum cost of transport hypothesis, as established in humans and horses, they are expected to hop at the speed that minimises the metabolic energy cost per unit distance (Hoyt and Taylor 1981); however, large kangaroos

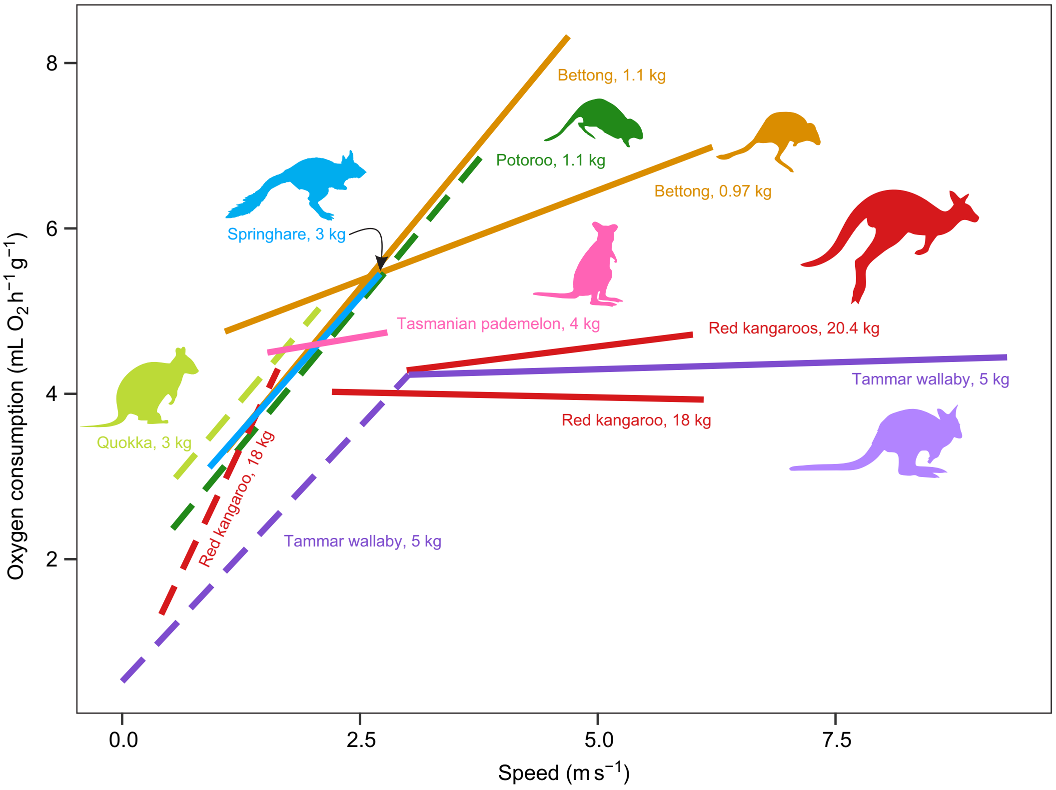

Fig. 6. The relationship between oxygen consumption and speed in hopping (solid lines) and bounding or pentapedal locomotion (dashed lines). Macropodoids include the Tasmanian pademelon (*Thylogale billardierii*) (Warren 1979), quokka (*Setonix brachyurus*) (Baudinette 1977), tammar wallaby (*Macropus eugenii*) (Baudinette *et al.* 1992), red kangaroo (*Macropus rufus*) 18 kg (Dawson and Taylor 1973) and 20.4 kg (Kram and Dawson 1998), brush-tailed bettong (*Bettongia penicillata*) 1.1 kg (Thompson *et al.* 1980) and 0.97 kg (Webster and Dawson 2003), and long-nosed potoroo (*Potorous tridactylus*) (Baudinette *et al.* 1993). Rodents include the springhare (*Pedetes capensis*) (blue) (Thompson *et al.* 1980). Data in all cases were collected on treadmills and does not include corrections for air resistance.

may travel slower than this optimum to operate at higher tendon safety factors (Kram and Dawson 1998). Experimental evidence is needed to confirm the oxygen consumption of kangaroos for a wider range of animal sizes and movement speeds. Red kangaroos can hop up to ~14 m s^{-1} (Dawson 1977) and males can reach up to 90 kg. These locomotor extremes place more stress on their musculoskeletal systems and will provide information into the biomechanical limits of high-speed hopping, which in turn may provide insight into the biomechanics of larger extinct macropods. However, new methods may need to be developed due to the experimental challenges associated with large kangaroos and hopping at high speeds on treadmills (Kram and Dawson 1998).

The tammar wallaby (3–7 kg) is perhaps even more remarkable than the red kangaroo. These wallabies use quadrupedal bounding at slow speeds and increase energy expenditure at a comparable rate to similarly sized quadrupeds. However, after the transition to hopping at 3 m s^{-1}, oxygen consumption does not increase, even at the maximum speed wallabies could sustain for 3–5 min (9.5 m s^{-1} in some individuals) (Baudinette *et al.* 1992). If air resistance is factored into the energetics of treadmill locomotion, the metabolic cost increases with speed, but the increase in cost is not high enough to outweigh the mass-specific savings at high speeds; thus the cost of transport decreases for the full range of speeds in wallabies, resulting in two-fold savings compared with an equivalent quadruped (Baudinette *et al.* 1992).

Some macropods do not completely uncouple oxygen consumption and speed, and yet they are still distinctly different from quadrupeds. Oxygen consumption in the quokka (3 kg) increases linearly with speed, at the same rate as a 3 kg quadruped, but oxygen consumption is higher by seven-fold, indicating higher energetic cost. The quokka was measured for bounding and intermittent hopping speeds only, and the increase in oxygen consumption is suspected to decline at higher speeds, but this has not been verified (Baudinette 1977). Additionally, the Tasmanian pademelon (4 kg, 1.5–2.7 m s^{-1}) had a lower increase in oxygen consumption than quadrupeds, but it is not completely uncoupled from speed (Warren 1979). Oxygen consumption increases linearly with speed in the brush-tailed bettong (0.97 kg), although at a significantly slower rate than a similarly sized quadruped (Webster and Dawson 2003). The bettong hops at speeds above 1 m s^{-1}, and it is more efficient than an equivalent quadruped from 2 m s^{-1} to the maximum sustainable speed, 6.2 m s^{-1} (Webster and Dawson 2003).

A separate study that measured the brush-tailed bettong (1.1 kg, 0.8–5 m s^{-1}) found no significant deviation in metabolic cost from the expected quadruped projection (Thompson *et al.* 1980). Likewise, the long-nosed potoroo (0.3–0.9 kg) (Baudinette *et al.* 1993), and several hopping rodents [the springhare (*Pedetes capensis*) (3 kg, 0.8–3.3 m s^{-1}), *Dipodomys deserti* (0.1 kg, 0.6–2 m s^{-1}), *Dipodomys merriami* (0.03 kg, 0.4–2 m s^{-1})] did not differ in oxygen consumption from quadrupeds (Thompson *et al.* 1980). Non-linear oxygen–speed relationships in hopping rodents *Notomys alexis* (Baudinette *et al.* 1976) and *Notomys cervinus* (Dawson 1976) may be due to treadmill training effects (Thompson *et al.* 1980; Griffiths 1989). The general consensus is that hopping animals under ~3 kg are not energetically distinct from quadrupeds (Thompson *et al.* 1980; Biewener *et al.* 1981).

The differences in oxygen consumption between macropods, hopping mammals and quadrupedal mammals begs the question: what characteristics enable some macropods, such as the red kangaroo and tammar wallaby, but not other macropods or hopping rodents, to increase speed without increasing the metabolic cost? Several possible energy-saving mechanisms have been proposed, including metabolism, tissue material properties, gait parameters and tendon elastic energy return.

Influence of muscle and tendon properties

Several studies considered that the efficiency of large macropods may be facilitated by unique aspects of their muscle–tendon physiology. Tendon material properties in adult mammals may vary with species and size (LaCroix *et al.* 2013). For instance, elastic modulus may scale with positive allometry in macropodoids, and, consequently, small species may be able to store more strain energy than expected (Bennett and Taylor 1995; Bennett 2000). This may contribute to the relatively (compared with placentals) lower slope of oxygen consumption with speed observed in the brush-tailed bettong, the long-nosed potoroo and the Tasmanian pademelon. The quokka, on the contrary, is less efficient than predicted for a mammal with standard tendons, although it is similar to the springhare (Thompson *et al.* 1980). Regardless, while macropodoid tendon material properties may increase absolute strain energy capacity, absolute capacity cannot explain the uncoupling of hopping speed and oxygen consumption.

Metabolic energy is required to generate positive (shortening) or negative (lengthening) muscle work. If large macropods have more efficient muscles, they will use less energy, but there is no indication that macropodoid muscles are more energy efficient (Baudinette 1994; Kram and Dawson 1998; Bennett 2000). The aerobic capacity, muscle morphometry, and muscle mitochondrial and capillary characteristics of skeletal muscle in red kangaroos (Dawson *et al.* 2004) and brush-tailed bettongs (Webster and Dawson 2012) are similar to those of athletic placental mammals. The biochemical profile and muscle fibre type distribution in the lower leg of parma wallabies (*Macropus parma*) and western grey kangaroos (*Macropus fuliginosus*) are consistent with other mammal limb muscles, although enzyme levels in macropod ankle extensors indicate that they may have a greater capacity for aerobic work than those of placentals (Dennington and Baldwin 1988).

The metabolic cost of the muscle could be reduced if the amount of muscle work decreases at higher speeds. Kangaroos do not adopt a more upright limb posture at high speeds, which would increase the mechanical advantage of the muscles and reduce the required muscle force (Kram and Dawson 1998). Alternatively, tendon elastic energy storage can reduce the work required of its attached muscle. If the elastic energy stored in the tendons is returned at the right point in the stride, the recoil will contribute to the propulsion of the animal, reducing the energy required to be supplied by muscles (Alexander and Vernon 1975). Tendon recoil in the ankle extensor tendons could contribute to the uncoupling of oxygen consumption from speed, provided the proportion of energy that is stored in the tendons increases with speed without requiring the muscles to perform more work, meaning the energy from the muscles can remain constant (Alexander and Vernon 1975).

Increasing tendon stress and strain with speed will result in more stored elastic strain energy, provided that there is minimal increase in the stretch of muscle fibres. Griffiths (1989) measured the medial GAS muscle of the Tasmanian pademelon *in situ* and concluded that the muscle was not stiff enough to allow the amount of stored energy to increase with speed. However, Biewener *et al.* (1998) used sonomicrometry to measure muscle fibres in the tammar wallaby *in vivo* and found that muscle fibres remained stiff and near isometric, undergoing very little length change compared with the tendon. Crucially, muscle fibre length did not increase with speed, despite a large increase in force (Biewener *et al.* 1998). Consequently, the mechanical work from muscle shortening is much less than the work from elastic energy recovered in the tendons, and the amount of stored strain energy increases with speed (Biewener *et al.* 1998). Griffiths (1989) may have underestimated muscle stiffness (Biewener and Baudinette 1995), or perhaps the Tasmanian pademelon's muscle physiology is not as specialised for strain recovery as that of the tammar wallaby, and this explains their lower energetic performance in Warren (1979).

Increasing tendon stress does result in an increase in elastic energy recovery and metabolic savings in some species. Baudinette and Biewener (1998) measured oxygen consumption in female tammar wallabies at 3.5 and 4.5 m s^{-1} and added weight to the pouch (equivalent to 15% of the female body weight). The metabolic rate did not increase with speed or added mass, although both muscle stress and tendon stress did increase. Duty factor also increased with added mass, but not speed, which could contribute to metabolic savings by enabling the recruitment of more efficient muscle fibres (Kram and Taylor 1990; Baudinette and Biewener 1998). These results indicate that elastic energy return can significantly reduce metabolic cost.

For some macropods, elastic energy return is high and significantly reduces the cost of each stride. Tendon recoil could reduce cost by an estimated 45% in the tammar wallaby at 6 m s^{-1} (Biewener *et al.* 1998). Macropods that save energy in this way require tendons capable of developing very high stresses. From our analysis and the literature, recall that larger macropodoids may have relatively longer tendons (Fig. 4*d*), resulting in a greater volume of material and thus higher strain energy capacity. The strong positive allometry of the ankle extensor muscle masses and PCSA, coupled with isometric or negative allometry of tendon CSA results in greater muscle to tendon area ratios with body size. The GAS, PL and FDL tendons are subject to increasingly larger muscle forces, which results in greater tendon stress, greater elastic strain energy and lower safety factors, particularly in the GAS and PL (Bennett and Taylor 1995; Bennett 2000; McGowan *et al.* 2008*b*; Snelling *et al.* 2017).

Small hopping animals, such as potoroos, bettongs and rodents, have proportionally thicker tendons. Biewener *et al.* (1981) noted that the ankle extensor tendons in the rodent *Dipodomys spectabilis* (~0.1 kg) are too thick for effective strain return and that the percentage of energy recovered does not increase with speed [but see Javidi *et al.* (2019)]. Scaling analysis implies that there is a lower limit to effective strain return, which presumably coincides with the observed trend that hopping animals smaller than 3 kg are not energetically distinct from quadrupeds (Thompson *et al.* 1980). However, 3 kg is not a hard limit, as small tammar wallabies of ~3 kg can completely uncouple oxygen consumption from hopping speed (Baudinette *et al.* 1992), whereas a 3 kg bounding quokka (Baudinette 1977) and a 3 kg hopping springhare rodent have similar rates of increase in oxygen consumption with speed compared with an equivalent placental quadruped (although their absolute use of oxygen is higher) (Thompson *et al.* 1980), and a 1 kg brush-tailed bettong is either indistinguishable from (Thompson *et al.* 1980), or somewhat more efficient than, a quadruped (Webster and Dawson 2003) (Fig. 6).

The variation in tendon morphology in Macropodoidea provides insight into the role of tendons in energy savings. While the research presents compelling reasons and implicates tendon elastic energy return, research has not, as yet, made the final link between differences in levels of tendon strain energy and corresponding differences in energetics. Presumably due to the requirements of vertical leaping and rapid acceleration ability, the yellow-footed rock wallaby (*Petrogale xanthopus*) has thicker tendons and a higher mechanical advantage at the ankle than the similarly sized tammar wallaby and, as a result, the rock wallaby stores less elastic strain energy (McGowan *et al.* 2008*a*). Oxygen consumption has not been measured in any *Petrogale* species. A comparison of the oxygen consumption of the tammar wallaby and the rock wallaby could shed light on the proposed role of stored elastic energy in reducing the metabolic cost of hopping.

Why are large macropods unique?

There is compelling evidence that tendon elastic energy return contributes to the energetic efficiency in some large macropods; however, it is unlikely to be the only contributing mechanism. Tendon energy return does not explain why macropodoids should receive metabolic savings while quadrupeds do not (Dawson and Webster 2010). Tendons in macropodoids are morphologically distinct from those of quadrupeds (Fig. 4); however, high strain return is not unique to macropodoids – some large quadrupedal mammals, such as deer, show similar muscle–tendon specialisations, and their tendons effectively store and return elastic energy at comparable levels to large macropodoids (Fig. 4*a*) (Dimery *et al.* 1986; Ker *et al.* 1986). Some quadrupeds may have greater elastic energy capacity, due to leg and tendon length being longer and less constrained than in macropodoids (Dawson and Webster 2010). However, deer and other large mammals (except the lion and macropods) display a linear increase in energy consumption with speed (Taylor *et al.* 1970, 1982). Why, then, do large macropods increase the percentage of strain return with speed, but quadrupeds do not? Perhaps this is where gait comes into play.

Influence of the hopping gait

Several elements of the hopping gait may reduce energy use and contribute to the uncoupling of oxygen consumption from speed. The first to note is the coupling of stride frequency and respiration (Baudinette *et al.* 1987). The inertia of the viscera can act as a piston to passively drive ventilation of the lungs, reducing the metabolic cost of respiration during locomotion. This is not unique to macropods; it is observed in quadrupeds (McGowan and Collins 2018).

Another contributing factor may be the regulation of ground contact time. Metabolic energy cost is inversely proportional to ground contact time in most mammals (Kram and Taylor 1990). The increase in energy is thought to be due to the shorter contact times requiring more rapid force development in muscles, recruiting less efficient muscle fibres (Kram and Taylor 1990). Increasing the mass of tammar wallabies by adding weight to the pouch did not change stride frequency but did increase duty factor, which may allow recruitment of slow, more efficient muscle fibres to contribute to the observed energy savings (Baudinette and Biewener 1998), but duty factor scales negatively with increasing body mass in Macropodoidea (Bennett 1987), so this is not the principal method by which macropods manage energetics or stress with size. Additionally, red kangaroos appear to be an exception to the trend in Kram and Taylor (1990), due to the decrease in contact time at greater speeds (Kram and Dawson 1998). Kram and Dawson (1998) inferred that red kangaroos generate the same muscle force at all speeds, but do so more rapidly at higher speeds; however, *in vivo* muscle measurements in the tammar wallaby suggest that muscle force and stress in the ankle extensor muscles increase with speed (Biewener and Baudinette 1995; Biewener *et al.* 1998) although muscle work does not (Biewener *et al.* 1998). Additional work when accelerating is produced from the proximal hindlimb (McGowan *et al.* 2005*a*).

A more promising explanation is the uncoupling of stride frequency and speed in hopping. Stride frequency is proportional to the mass-specific cost of transport in mammals. The metabolic energy cost per stride to move 1 kg of mass is the same for mammals regardless of body size, but increases with speed, suggesting that part of the cost of locomotion is due to limb cycling (Heglund and Taylor 1988). Hopping, unlike most gaits, increases speed by increasing stride length, while stride frequency is held almost constant. By maintaining a constant stride frequency, the costs associated with accelerating and decelerating the limb per stride should not increase with speed (Dawson and Webster 2010). While this may indeed contribute to energy savings in macropods, it does not explain why small hopping or large galloping mammals do not uncouple speed and oxygen consumption.

Small hopping animals, including the brush-tailed bettong, the springhare and other hopping rodents, maintain a constant or near-constant stride frequency with increasing speed, like large macropods, but see little or no energetic benefit compared with quadrupeds (Thompson *et al.* 1980; Webster and Dawson 2003; Gutmann *et al.* 2013). We are not aware of any differences in gait between small and large hopping mammals besides the factors such as stride frequency and contact time that scale with body size (see Gait section).

Furthermore, constant stride frequency is not limited to hopping. Some macropodoids, when predominantly bounding, have a non-linear relationship between stride frequency and speed, but a linear increase in oxygen consumption with speed (Baudinette 1977; Baudinette *et al.* 1993). Large galloping mammals, too, maintain a constant stride frequency with increasing speed but do not uncouple oxygen consumption from speed (Taylor *et al.* 1970, 1982; Heglund and Taylor 1988).

Conversely, the Tasmanian pademelon increases stride frequency with speed and, based on the cost of limb cycling, should increase oxygen consumption, but metabolic cost in this species is near-constant (Warren 1979; Baudinette 1994).

From the research thus far, it seems that the dominant factor in small hopping mammals is tendon stress and strain, which is low in steady speed hopping and prevents effective energy storage (Biewener *et al.* 1981; Biewener and Blickhan 1988). However, no single mechanism can currently explain the energetic differences between small and large hopping mammals, and quadrupeds. Perhaps there is some combination of stride frequency, ground contact time, or other gait factors that loads the ankle tendons in a way that is unique to large macropods. Or perhaps some mechanisms are yet to be discovered. This remains an open question.

Evolution

Macropodoidea originated from an arboreal, possum-like ancestor approximately 40 million years ago. Within the Macropodoidea, *Hypsiprymnodon* is the sister clade to Macropodidae (kangaroos and wallabies) and Potoroidae (potoroos and bettongs). All species use a bipedal hopping gait when moving at relatively fast speeds, except for the musky rat-kangaroo (*Hypsiprymnodon moschatus*), which uses a quadrupedal bounding gait. Hopping may have evolved only once in the Macropodoidea, possibly in forests, from small bounding mammals similar to the musky rat-kangaroo (Burk *et al.* 1998; Meredith *et al.* 2009; Prideaux and Warburton 2010). Subsequent rapid phylogenetic and size radiation occurred 5–15 million years ago, coinciding with major environmental changes and the spread of grasslands and deserts (Webster and Dawson 2004; Meredith *et al.* 2009). Bipedal hopping likely evolved in small rodents and macropodoids to facilitate rapid acceleration, jumping and erratic changes of direction to escape from predators, with energetic performance a secondary benefit once species grew larger than 3 kg (see McGowan and Collins (2018) for an in-depth review). The musculoskeletal physiology of hopping rodents and macropodoids reflects the convergent evolution of hopping. Springhares align more closely with macropodoids than with quadrupedal mammals in traits such as EMA, muscle mass, muscle PCSA and tendon stress (Veiga *et al.* 2020), and gait (Cavagna *et al.* 1977).

Constraints

Tendons are required to be exposed to high tensile stresses in order to store substantial amounts of elastic strain energy; however, increases in stress necessarily decrease safety factor. Tendon safety factors scale with negative allometry with body size in Macropodoidea, and are already unusually low in large kangaroos moving at moderate speeds (Kram and Dawson 1998), which has led researchers to question how kangaroos deal with the greater forces that come with increases in speed, acceleration and body size.

Research on the scaling of safety factors in Macropodidae determined that safety factors in the GAS and PL reach the safe limit at 35–40 kg, which is a size commonly exceeded by male red and grey kangaroos (*Macropus rufus*, *Macropus giganteus* and *Macropus fuliginosus*) (Bennett and Taylor 1995; Bennett 2000). A separate, similar study on tendon safety factors calculated the upper limit of body size to be 140 kg (McGowan *et al.* 2008*b*). Intraspecific scaling in western grey kangaroos puts the upper limit slightly higher, at 160 kg (Snelling *et al.* 2017), which is consistent with estimates of the closely related eastern grey kangaroo reaching at least 140 kg in the Pleistocene (Helgen *et al.* 2006). But many extinct kangaroos grew even larger – all extrapolations of maximum size from extant macropodoids fall well short of the largest extinct kangaroo we know of (*Procoptodon goliah*), which is estimated to weigh at least 240 kg (Helgen *et al.* 2006). This discrepancy implies that either extinct macropodoids scale unlike extant macropodoids for muscle and tendon dimensions, or locomotion in large extinct species was modified to reduce peak forces, such as by reducing performance.

Different scaling of muscle–tendon dimensions

To maintain the same level of performance with a constant EMA, macropodoids must disproportionately increase muscle mass, which exacerbates the problem of stress due to body weight in large kangaroos (McGowan *et al.* 2008*b*; Snelling *et al.* 2017). The low predictions of maximum size indicate that this is unsustainable: at some point, the allometry of muscle mass or tendon stress must decrease. Tendon CSA in the western grey kangaroo scales with slight negative allometry (combined GAS, PL and FDL is $\propto M^{0.63}$), which increases tendon stress rather than mitigates it (Snelling *et al.* 2017). Ankle extensor muscle mass scales with positive allometry in Macropodoidea overall; however, at the intraspecific level, muscle mass in some of the largest species scales at lower rates [the red and the western grey kangaroo (Snelling *et al.* 2017), Fig. 3*d*], indicating either that smaller individuals have proportionally larger muscles (possibly an ontogenetic effect) or that larger individuals have proportionally smaller muscles. Small red and grey kangaroos appear to have longer bones and larger muscles than other macropodoid species at similar sizes, but it is also possible that muscle mass scaling decreases in larger macropodoids, and the decline begins within the species body range (up to 90 kg). This has implications for performance, because muscle force demands may outpace the rate of muscle mass scaling, and thereby performance will decrease.

Reduced performance

The macropodoid megafauna, at 240 kg (Helgen *et al.* 2006), are well into the range where size-predicted increases in musculoskeletal stresses affect the shape of other mammals (Biewener 1990; Dick and Clemente 2017). Other species with crouched postures, such as felids and varanids, show a decline in maximum locomotor speed after a certain body mass is exceeded, as their methods to compensate with muscle and bone architecture reach their limits (Dick and Clemente 2017). If macropodoids mitigate tendon stress, the tendons will be less effective for storing strain energy and will be less energy efficient when hopping. If tendon stress continues to increase, maximum speed or acceleration ability may be reduced. Hopping performance is believed to have declined severely in the largest macropodoids. In some cases, they may not have hopped; it has been suggested that sthenurine kangaroos used bipedal striding locomotion instead (Janis *et al.* 2014).

Maximum speed

In large animals in general, when other stress mitigation strategies reach their limit, the only way to deal with the size-related increase in stress is to decrease maximum speed (Dick and Clemente 2017). At slower speeds, forces are distributed over longer ground contact times, reducing peak forces and thereby stress (Alexander 1977; Biewener 1983). It is unknown at what point, or to what extent, hopping performance declines in large macropods. Maximum speed and ground reaction force data are challenging to collect under natural conditions and the range of macropod body sizes is not fully represented in the existing literature (see Gait section). Maximum speed seems to be lower in macropodoids than in placental mammals; however, there is limited data to ascertain the speed-size relationship (Fig. 5). There is insufficient data on maximum speeds in macropodoids to determine at what size the highest hopping speeds occur, however, tendon stresses at moderate speeds in large kangaroos indicate that their maximum speed is likely limited. Tendon stress increases at higher speeds due to the decrease in ground contact time (Kram and Dawson 1998). The shorter contact time means there is an inverse relationship between speed and safety factor, which may explain why the preferred hopping speed of large kangaroos is much slower than their maximum or even their most efficient speed (Kram and Dawson 1998). Maximum speed must decrease in large macropodoids, if not in extant kangaroos, then certainly in the larger extinct species (Bennett and Taylor 1995; Bennett 2000; McGowan *et al.* 2008*b*).

Acceleration

Tendon stress varies between species to balance the demands of their habitat and locomotion, because there is a trade-off between traits that make tendons suitable for efficient locomotion and for acceleration. Thick tendons (e.g. high safety factors) quickly transmit forces from the muscles, enabling precise joint control and faster acceleration (Ker *et al.* 1988), but such tendons would not experience the high stresses during steady hopping that are required for substantial elastic energy return (Biewener *et al.* 1981; Biewener and Blickhan 1988). Most mammals have tendons that are thicker than the minimum necessary to avoid rupture; the highly stressed tendons in macropodoids are unusual, even among large quadrupedal mammals that have high strain energy return (Biewener 1990).

In macropodoids, where there is a marked difference in habitat, there is corresponding variation in tendon morphology, gait and energetics (see the relevant sections). For instance, the lower tendon CSA and higher muscle force in tammar wallabies (*Macropus eugenii*) develops 73% more strain energy, while the yellow-footed rock wallaby (*Petrogale xanthopus*) has 38% higher safety factors (McGowan *et al.* 2008*a*). Rock wallabies live in uneven terrain that requires large, irregular jumps, and presumably requires the finer joint control and acceleration that the tendons impart (McGowan *et al.* 2008*a*). It is interesting, though, that tammar wallabies are not necessarily limited in their ability to accelerate on level ground. Tammar wallabies maintain constant peak stresses by shifting the limb orientation to match the change in direction of the GRF, which maintains a constant peak load and, thereby, a constant safety factor of ~4.3 for accelerations between −6 and 8 m s^{-2} (McGowan *et al.* 2005*a*). It has not been verified if larger macropods use the same mechanism to maintain constant safety factors during acceleration.

Jumping

The tendons in small hopping mammals are relatively thick and have high safety factors in steady hopping; however, the considerably higher forces in vertical jumping reduce the safety factor [from 10 to 2.8 in the rodent *Dipodomys spectabilis* (Biewener and Blickhan 1988)]. Hopping rodents can execute a rapid vertical leap to a height that is several times their body length, and do so to escape strikes from predators such as snakes and owls (McGowan and Collins 2018). Large macropods have low safety factors to start with, and as a consequence, are presumably less capable of such jumps. This raises an interesting question about whether the crural muscle–tendon unit morphology observed in large macropodoids is related to relaxed pressure from ambush predators, or due to strong selection for tendons with a low safety factor and high capacity for strain energy storage to aid in economical hopping.

Conclusion

It has been nearly 50 years since the unusual energetics of red kangaroos was identified and interest in macropodoids spiked. The subsequent research increased our understanding of macropodoids and was invaluable for understanding animal locomotion more generally, by challenging what were assumed to be universal truths. We now have a broad foundation of research to stand on, with comprehensive work on macropodoid musculoskeletal anatomy, gait and energy consumption. The crucial gaps in our knowledge stand out against the background of information, and we have identified them throughout this review. We also highlighted the vulnerabilities; we found that the scaling of the musculoskeletal system is sensitive to the phylogenetic context, and that intraspecific scaling can differ from interspecific scaling, which means that sampling could influence the interpretation of scaling across Macropodoidea. We summarised the research on the hopping gait and unusual macropodoid energetics, which gains more nuance and variety with every species that is measured, but the core mystery remains: how do kangaroos increase speed seemingly for free? We conclude that none of the hypotheses fully explain the differences between large and small hoppers, and other mammals. There is not yet enough information to isolate the biomechanical factors that make large kangaroos so energy efficient. Answering these questions will open further doors to understanding the limits of scaling and performance in extinct and extant macropodoids.

Supplementary material

Supplementary material is available online.

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Data availability. We have made all data used to calculate scaling factors available on figshare https://doi.org/10.6084/m9.figshare.19195286.v1.

Conflicts of interest. The authors declare no conflicts of interest.

Declaration of funding. Not applicable.

Acknowledgements. We thank Robert Shadwick from the University of British Columbia, Benjamin Kear from Uppsala University and Tim Flannery from text publishing for making data available. We also thank the two reviewers for their helpful and detailed feedback that greatly improved this work.

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