Differential design for hopping in two species of wallabies[☆]

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Abstract

Hindlimb musculoskeletal anatomy and steady speed over ground hopping mechanics were compared in two species of macropod marsupials, tammar wallabies and yellow-footed rock wallabies (YFRW). These two species are relatively closely related and are of similar size and general body plan, yet they inhabit different environments with presumably different musculoskeletal demands. Tammar wallabies live in relatively flat, open habitat whereas yellow-footed rock wallabies inhabit steep cliff faces. The goal of this study was to explore musculoskeletal differences between tammar wallabies and yellow-footed rock wallabies and determine how these differences influence each species' hopping mechanics. We found the cross-sectional area of the combined ankle extensor tendons of yellow-footed rock wallabies was 13% greater than that of tammar wallabies. Both species experienced similar ankle joint moments during steady-speed hopping, however due to a lower mechanical advantage at this joint, tammar wallabies produced 26% more muscle force. Thus, during moderate speed hopping, yellow-footed rock wallabies operated with 38% higher tendon safety factors, while tammar wallabies were able to store 73% more elastic strain energy (2.18 J per leg vs. 1.26 J in YFRW). This likely reflects the differing demands of the environments inhabited by these two species, where selection for non-steady locomotor performance in rocky terrain likely requires trade-offs in locomotor economy.
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1. Introduction

Bipedal hopping is the primary mode of fast locomotion in all members of the family Macropodoidea, the group containing wallabies and kangaroos (Windsor and Dagg, 1971). In several species within this group, bipedal hopping has been found to be a remarkably efficient mode of locomotion, with larger macropods (above ~ 5 kg) being able to decouple speed and metabolic cost (Dawson and Taylor, 1973; Baudinette et al., 1992). Unlike all other animals studied, red kangaroos and tammar wallabies are able to increase steady-state speed without increasing their rate of metabolic energy use. Macropods are a diverse group, however, and rock wallabies (Petrogale xanthopus) are one species that has seemingly abandoned the need for locomotor economy, having

adapted a hopping bipedal gait for moving adeptly over steep and uneven cliff faces. The physical demands of such a life-style are quite different from those placed on their plains-dwelling relatives (e.g. tammar wallabies, Macropus eugenii), yet their body forms are outwardly very similar.

The uncoupling of metabolic cost and hopping speed in macropods has been attributed to the storage and recovery of elastic energy in the ankle extensor tendons (Alexander and Vernon, 1975; Ker et al., 1986; Biewener and Baudinette, 1995). For a tendon to store significant amounts of elastic strain energy, it must be relatively thin so that it undergoes high stresses (force per unit cross-sectional area) and high strains during steady-speed hopping (Alexander, 1988; Biewener, 1998). This likely limits these animals' ability to withstand higher forces associated with acceleration and jumping (Biewener and Bertram, 1991). In addition to being able to withstand higher absolute forces, thicker tendons also increase the fidelity of force transmission between the muscles and the bone, and ultimately the environment. This suggests that having

relatively thicker tendons may enhance an animal's control (Alexander, 1988; Ker et al., 1988; Rack and Ross, 1984).

This study explores musculoskeletal differences between tammar wallabies and yellow-footed rock wallabies with the goal of determining how these differences influence each species' steady-speed hopping mechanics. Specifically, we seek to evaluate how this relates to each species' capacity for elastic energy storage and locomotor economy versus their potential to accelerate.

Based on their choice of habitat use and presumably the demands on their musculoskeletal system, we predict that yellow-footed rock wallabies have relatively thicker ankle extensor tendons, as compared to tammar wallabies, enabling them to produce and withstand the higher forces experienced in their daily lives. In a recent study, McGowan et al. (2005b) showed that peak vertical ground reaction forces were ∼ 30% higher during moderate height jumping than during level hopping. Further, given both species are of similar body mass and limb proportions, we predict that peak ankle joint moments are similar when hopping at the same speed. Based on these predictions, we examine the following set of related hypotheses regarding their steady-speed hopping mechanics. We hypothesize that rock wallabies experience relatively lower peak stresses in their ankle extensor tendons, and thus operate with higher safety factors but store less elastic energy than tammar wallabies, assuming that the material properties of their tendons are the same.

2. Materials and methods

Data included in this study were collected in conjunction with separate studies that were conducted at different times over a 3 year period.

2.1. Animals

Five adult tammar wallabies, *M. eugenii* (three male and two female, ranging from 5.77 to 7.15 kg body mass) and five adult yellow-footed rock wallabies, *P. xanthopus* (two males and three females, ranging from 5.10 to 7.00 kg body mass) were obtained from captive breeding colonies maintained at the Waite Institute campus of the University of Adelaide and the Adelaide Zoo, respectively. In addition to the live animals used in this study, 4 yellow-foot rock wallaby cadavers (average body mass: 5.16± 0.52 kg, ±S.D.) were obtained for dissection purposes. As a threatened species, we relied on the cadaver measurements obtained for our morphometric analysis of the yellow-foot rock wallabies. All procedures, care, and use of the animals were approved by the University of Adelaide Animal Ethics Committee. Through the course of the each experiment, animals were housed at the Waite Institute campus of the University of Adelaide in a system of large outdoor paddocks. Runways for conducting steady hopping experiments were constructed within the confines of one of these paddocks.

2.2. Morphological measurements

In both groups, segments lengths, joint centers of rotation and muscle moment arms were palpated and measured with

digital calipers. For tammar wallabies, these measurements were later confirmed and additional measurements were made via dissection of the animals, which had been euthanized following a subsequent experiment designed to record in vivo muscle strain patterns during hopping. Additional measurements obtained from these animals included individual muscle masses and moment arms, muscle fiber lengths, fiber pennation angle, tendon masses and tendon lengths. These measurements were used to calculate muscle and tendon cross-sectional areas in order to determine muscle and tendon stresses (force/cross-sectional area). The measurement techniques and calculations used have been described elsewhere in detail (Alexander and Vernon, 1975; Biewener and Baudinette, 1995; Roberts et al., 1998). Data for plantaris (PL), lateral gastrocnemius (LG) and medial gastrocnemius (MG) are shown in Table 1.

Because of their threatened status, confirmation of external measurements and measurements of tendon cross-sectional area of the yellow-footed rock wallabies were obtained via CT scan

Table 1
Morphological variables for tammar and yellow-footed rock wallabies (YFRW)

	Tammar wallabies $n=5$	YFRW cadavers $n=4$	P values*	YFRW live $n=5$
Body mass (kg)	6.64±0.52	5.16±0.26	–	5.66±0.34
Gastrocnemius				
Lateral				
L (mm)	21.2±1.5	22.4±3.1	0.325	
A_m (cm^2)	5.50±0.79	5.66±0.52	0.122	
Medial				
L (mm)	16.2±1.3	21.7±2.78	0.018	
A_m (cm^2)	9.57±0.58	6.72±0.59	0.129	
Tendon				
L (mm)	153.3±4.6	168.9±4.1	0.003	
A_t (mm^2)	7.48±1.62	8.37±0.24	0.005	
Plantaris				
L (mm)	16.2±0.9	19.7±2.0	0.001	
A_m (cm^2)	14.57±1.29	10.70±0.64	0.080	
Tendon				
L (mm)	284.0±5.6	308.9±4.5	0.001	
A_t (mm^2)	8.43±1.92	9.90±0.76	0.017	
Total muscle area	29.64±1.10	23.08±0.75	0.212	24.92±0.12**
Total tendon area	15.85±0.35	18.27±0.76	0.004	17.95±1.17
Percent of total area				
Gastrocnemius				
Lateral A_m	0.19±0.01	0.25±0.03	0.082	
Medial A_m	0.32±0.01	0.29±0.02	0.126	
A_t	0.47±0.01	0.46±0.02		
Plantaris				
A_m	0.49±0.01	0.46±0.02	0.700	
A_t	0.53±0.01	0.54±0.02	0.135	
Fiber length factor				
Gastrocnemius	2.15±0.16	2.97±0.29	0.047	3.26±0.20**
Plantaris	1.03±0.09	2.02±0.29	0.013	1.60±0.10**
Muscle/tendon area ratio				
Gastrocnemius	203.6±11.4	148.1±4.1	0.005	
Plantaris	174.4±11.1	109.3±7.4	0.003	
Total	187.7±10.2	126.9±5.8	0.002	140.7±7.3**

* *P* values for ANOVA performed on mass normalized variables assuming geometric similarity. Live values were used for YFRW where available.
** Scaled from cadaver data assuming geometric similarity.

and/or ultrasound (St. Andrews Hospital, Adelaide, Australia). In cases where direct measurements could not be reliably made on the animal in the study, values were estimated from cadaver measurements assuming geometric similarity (Table 1).

The dimensionless 'fiber length factor' (FLF) is a measure that has been introduced to assess a muscle–tendon unit's potential to actively control joint position (Ker et al., 1988, Pollock and Shadwick, 1994a). FLF represents the ratio of muscle fiber length to the tendon strain that would occur if the muscle produced maximal stress (0.3 MPa). Muscles favorable for elastic energy storage have FLF<2, while muscles that likely play an intermediate role range from 2 to 4. Muscles with FLF>4 likely play a major role in controlling joint displacement.

2.3. Runway and experimental protocol

A 22 by 0.75 m runway was constructed from light-gauge field fence strung from fence posts placed in the ground over a level stretch of the grassy outdoor paddock. The runway was closed at both ends to completely contain the animals. A 0.60×0.40 m force-plate (Kistler type 9286AA) was set flush with the ground at approximately the midpoint of the runway. The force plate was positioned on a 5 cm thick concrete slab buried in the ground and a wooden frame the same depth as the force-plate was used to keep the surrounding soil from contacting the plate. The wallabies were placed in the runway area and encouraged to hop from end to end. Approximately 15–20 trials were collected from each animal but only a small subset could be analyzed for this study. For trials to be included, the wallaby had to hop at a relatively steady forward velocity (<10% change in velocity while the animal was in contact with the force plate, as determined by integration of the horizontal ground reaction force and the animal's initial horizontal velocity), both feet had to strike the plate simultaneously, and all joint markers had to be visible for video analysis. Twenty-six trials from the tammar wallabies and 17 trials from the yellow-foot rock wallabies fit these criteria. There was no significant effect of individual on the variables measured as determined by an analysis of variance (ANOVA).

2.4. Kinematics

All trials were filmed in lateral view using a digital high-speed video camera (Redlake Motionscope PCI-500 or Photron Fastcam-X 1280 PCI; Photron USA Inc., San Diego, CA, USA) recording at 250 Hz. Video and force-plate data were synchronized via a trigger that simultaneously stopped video recording and had its voltage pulse recorded in conjunction with the force-plate outputs. The camera was positioned approximately 7 m from the runway to minimize parallax effects. The hind limbs of the animals were shaved using small animal clippers so they could be marked with white paint. Points marked included the tip of the longest phalanx (IV), ankle, knee, hip and a trunk point identified by the anterior tip of the ilium. Joint markers, as well as the location of the force-plate and in-field scale bars were digitized using a customized MATLAB (v.6.5, The MathWorks, Natick, MA, USA) routine (coded by Tyson Hedrick, University of Washington) and filtered using a quintic spline fit to known RMS data, using the generalized cross-validatory/spline (GCVSPL) program (Woltring, 1986).

2.5. Ground reaction forces and ankle joint moments

Ground reaction forces (GRF) were recorded with a multi-component piezoelectric force-plate (Kistler type 9286AA, Kistler Instruments Corp., Amherst, N.Y.) with an integrated charge amplifier (crosstalk between channels<1.0%). Forces were recorded in the vertical, horizontal and lateral directions. Lateral forces were always quite small and for the purposes of this study were ignored. Force-plate recordings were sampled at 1000 Hz and transferred to computer and stored by means of a BioWare™ type 2812A1-3 A/D system (DAS1602/16 A/D board) operated using BioWare v.3.0 software (Kistler Instruments Corp., Amherst, NY).

Inverse dynamics analysis was used to calculate the total net moment at the ankle joint. Briefly, the analysis consisted of combining GRF, kinematics and morphometric data to create a linked segment model of the limb and solving the equations of motion for each segment (Winter, 1990; McGowan et al., 2005a,b). The center of pressure (CoP) of the GRF acting on the toe was supplied by the force-plate. Muscle–tendon unit forces for the combined ankle extensors were calculated by dividing the ankle joint moment by the calcaneus length, the common lever arm for these muscles. GRF and muscle force impulses were determined by integrating the resultant GRF and muscle force over the period of stance.

2.6. Muscle stress, tendon stress and elastic energy storage

Peak stresses were calculated for the combined major ankle extensor muscles and tendons of the plantaris and gastrocnemius. Peak muscle stresses were calculated by dividing measurements of peak muscle force by the combined muscle physiological cross-sectional area (PCSA) estimated by scaling from cadaver measurements. Muscle forces were determined for individual trials based on the calcaneal moment arm obtained for each individual animal. Peak tendon stress was calculated by dividing peak muscle force by the combined tendon cross-sectional area measured directly from the animals used in the study. Following Biewener and Baudinette (1995), in order to calculate elastic strain energy recovery in the tendons we assumed an elastic modulus 1.0 GPa. Although this is slightly lower than values which have been reported for wallaby and other mammalian tendons (1.2–1.7 GPa; Ker et al., 1986; Bennett et al., 1986; Pollock and Shadwick, 1994a), this value corresponds to the elastic modulus of the tendon determined for the functional stress range observed *in vivo* for tammar wallabies (Biewener and Baudinette, 1995). Elastic strain energy recovery was calculated using the following equation:

$$U_{\text{tot}} = 0.5(\sigma^2/E)V_t \times 0.93 \qquad (1)$$

where σ is the peak stress in the tendons in MPa, E is the elastic modulus (1.0 GPa) and V_t is the total volume of the tendons in m^3 (determined from the tendon's sampled weight and assuming a
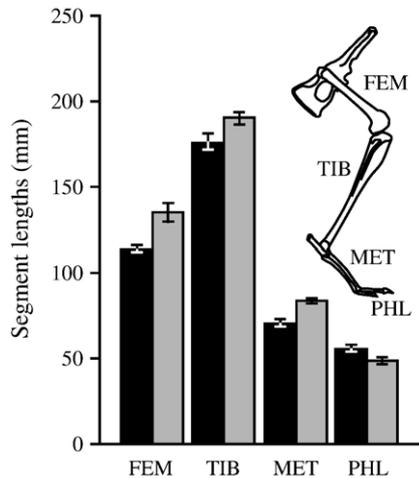
Fig. 1. All hindlimb segment lengths of tammar wallabies (black) are significantly different from yellow-footed rock wallabies (gray). The femur (FEM), tibia (TIB) and metatarsals (MET) are longer in yellow-footed rock wallabies, and the longest phalanx (PHL) is shorter. FEM: $P=0.009$, TIB: $P=0.041$, MET: $P<0.001$, PHL: $P=0.010$. $n=5$ for both species. Error bars represent ± 1 standard error. Inset: schematic diagram of a wallaby hindlimb and pelvis.

density of 1120 kg m^{-3}; Alexander and Vernon, 1975; Biewener and Baudinette, 1995; Biewener et al., 2004). The constant 0.93, accounts for a 7% loss in energy recovery due to hysteresis (Bennett et al., 1986; Shadwick, 1990).

2.7. Normalization and statistics

Due to small but significant differences between the mean masses of the populations used, variables were normalized to body mass, assuming geometric similarity, prior to performing statistical analyses. Significant differences between species were determined for all normalized variables using a general linear model ANOVA. All values are reported as absolute means $\pm$ standard error (unless otherwise noted) and reflect values from or scaled to the experimental animals.

3. Results

3.1. Morphology

The average mass of the tammar wallabies used in this study was slightly, but significantly ($P=0.045$) higher than the yellow-foot rock wallabies (YFRW) used for the experimental portion of this study. Despite having similar body mass, all limb segment lengths were found to be significantly different (Fig. 1). Whereas the femur, tibia and metatarsals are significantly longer in YFRW, the longest phalanx is significantly longer than in tammar wallabies. Additionally, the YFRW calcaneus is significantly longer than the calcaneus of tammar wallabies (29.2$\pm$0.9 mm vs. 25.7$\pm$0.6 mm; $P=0.010$).

Fig. 2 and Table 1 report morphological variables determined through dissections and CT scans. Although the average combined physiological cross-sectional area (PCSA) of the major ankle extensors, the plantaris and both heads of the gastrocnemius, is absolutely higher in tammar wallabies than YFRW,

this difference is not significant when normalized to body size (Fig. 2A, Table 1; $P=0.212$) Muscle fiber lengths of the plantaris and medial head of the gastrocnemius were significantly longer in YFRW (Table 1; $P<0.020$), whereas the fiber lengths of the lateral head of the gastrocnemius were very similar. As predicted, combined Achilles tendon cross-sectional area was significantly greater in YFRW (Fig. 2B; Table 1; $P=0.004$). Therefore, the ratio of muscle to tendon cross-sectional area, a measure that is has been used to characterize a muscle–tendon unit's potential to store and return elastic energy (Ker et al., 1988), is significantly greater in tammar wallabies (Fig. 2C; 187.7$\pm$10.2 vs. 140.8$\pm$7.3; $P=0.002$; average values for the gastrocnemius and plantaris combined). Consistent with our predictions, this suggests that the ankle extensor muscle–tendon units of tammar wallabies are better suited for storing and recovering elastic strain energy than those of YFRW. Fiber
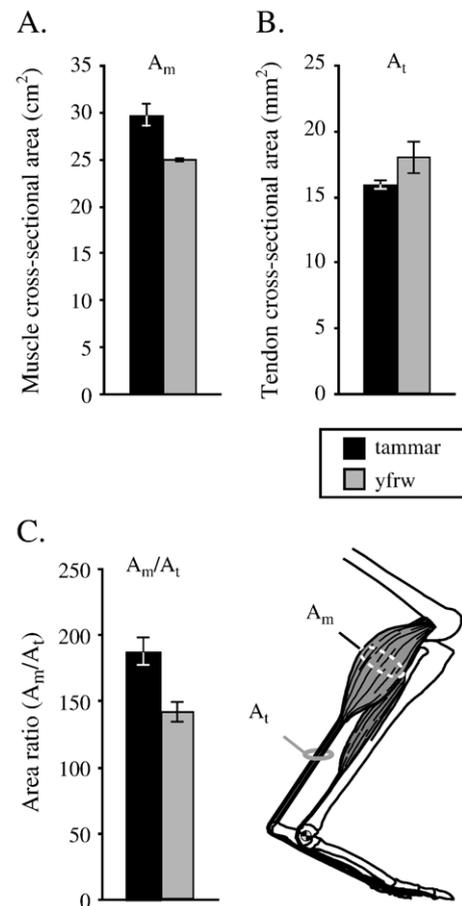

Fig. 2. Morphological data for tammar wallabies (black) and yellow-footed rock wallabies (yfrw; gray) obtained from cadavers and CT scans. For yellow-footed rock wallabies, muscle dimensions were scaled from cadavers to match the experimental animals size (see text for more details), assuming geometric similarity. A) The combined muscle physiological cross-sectional area for the ankle extensors (medial and lateral gastrocnemius and plantaris; A_m, inset) tended to be greater in tammar wallabies, however when normalized to body mass, the difference was not significant ($P=0.211$). B) Combined Achilles tendon cross-sectional area (A_t, inset) is significantly greater in yellow-footed rock wallabies ($P=0.004$). C) The ratio of muscle to tendon cross-sectional area is significantly greater in tammar wallabies ($P=0.002$), suggesting a greater potential to store and return elastic strain energy. Error bars represent ± 1 standard error. Inset: schematic diagram of a wallaby distal hindlimb and ankle extensors.
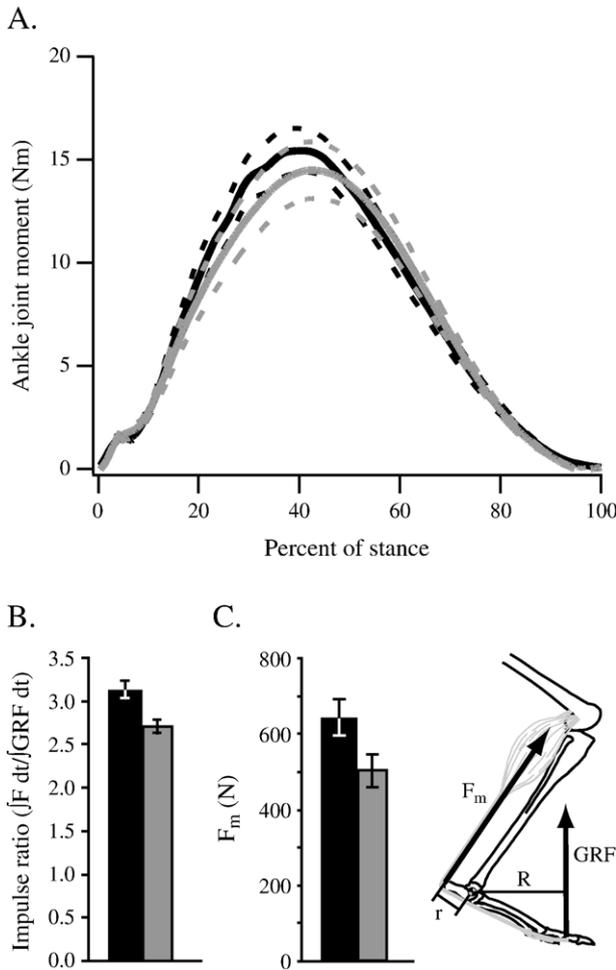
Fig. 3. A) Mean ankle joint moment patterns for a single leg during stance for tammar wallabies (black) and yellow-footed rock wallabies (gray). B) A histogram of muscle force (F_m) to ground reaction force (GRF) impulse ratio, which effectively gives the amount of muscle force required to produce a unit of ground reaction force. Muscle force is calculated by dividing joint moment by the muscle moment arm (r). This ratio is significantly greater for tammar wallabies ($P=0.011$). C) A histogram of peak muscle force for the experimental wallabies. Peak force tended to be higher in tammar wallabies but due to high individual variation, the difference is not significant ($P=0.075$). Inset: a schematic diagram of the relationship between forces and moment arms. Error bars and dashed lines represent ±1 standard error.

length factors (ratio of muscle fiber length to tendon length change under maximal muscle stress) were significantly smaller for both muscles of the tammar wallabies as compared to YFRW, and in both species, the fiber length factors were significantly smaller in the plantaris as compared to the gastrocnemius (Table 1). These differences, again suggest greater elastic energy savings capacity in tammar wallabies.

3.2. Ankle joint moments and muscle force

Both species were encouraged to hop at their preferred speed across the force plate. Tammar wallaby speeds ranged from 2.5 m s^{-1} to 6.2 m s^{-1} and averaged 4.1±0.2 m s^{-1}. YFRW speeds spanned a slightly narrower range from 3.4 m s^{-1} to 5.6 m s^{-1}; however the average, 4.4±0.1 m s^{-1}, did not differ

significantly from the average for tammar wallabies ($P=0.198$). Ankle joint moments, calculated using an inverse dynamics model, were similar for the two species over the measured range of speeds (Fig. 3A). Peak ankle moments for tammar wallabies averaged 16.19±1.05 N m per leg while YFRW were slightly lower, averaging 14.64±1.35 N m ($P=0.334$). The ratio of muscle force impulse (calculated by dividing the ankle moment by calcaneus length) to ground reaction force impulse was determined as a measure of muscle force required to produce a unit of ground reaction force. This value, which reflects an inverse measure of muscle mechanical advantage (R/r) over the time period of support (Roberts et al., 1998; Biewener et al., 2004), was significantly higher for tammar wallabies (Fig. 3B; 3.11±0.10) than for YFRW (2.71±0.08; $P=0.011$). Peak muscle forces tended to be higher for tammar wallabies (Fig. 3C; 633.1±48.3 N) than for YFRW (502.1±42.1 N); however due to relatively high variation among individuals, this difference was not significant ($P=0.075$).

3.3. Peak muscle and tendon stress

Peak muscle stress did not differ between species (Fig. 4A; tammar: 214.2±16.0 kPa vs. YFRW: 201.2±16.2 kPa; $P=0.567$); however, due to a significantly smaller Achilles tendon cross-sectional area, tammar wallabies experienced significantly higher
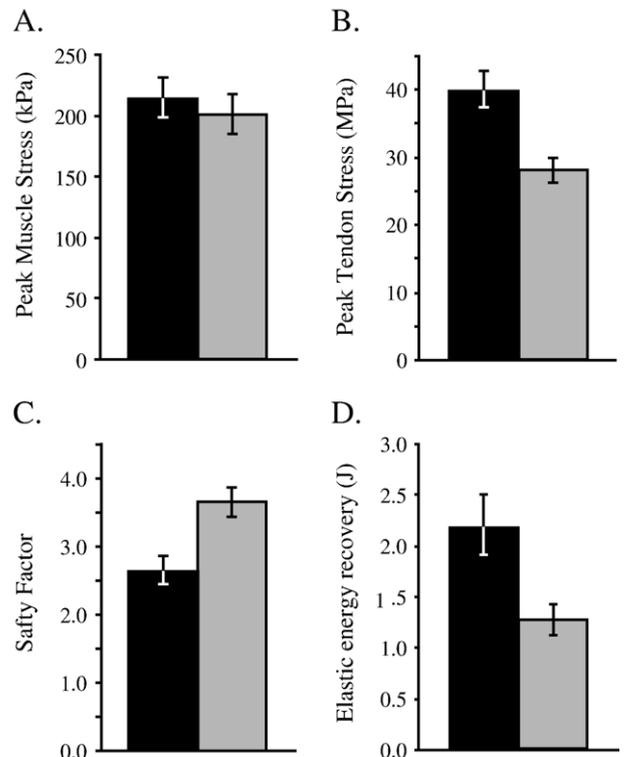

Fig. 4. Histograms of peak muscle (A) and tendon (B) stress, safety factor (C) and elastic energy recovery (D) during steady speed hopping. Peak muscle stress was not significantly different between tammar wallabies and rock wallabies ($P=0.567$); however, due to relatively thinner tendons, peak tendon stress was significantly greater for tammar wallabies ($P=0.006$). Higher peak stress yields significantly lower safety factors ($P=0.007$) but significantly higher elastic energy recovery ($P=0.024$) in tammar wallabies as compared to yellow-footed rock wallabies. Error bars represent ±1 standard error.
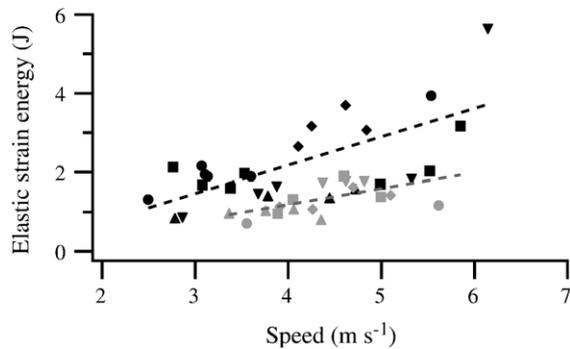
Fig. 5. Elastic energy recovery for the combined ankle extensor tendon per leg increases with speed in tammar (black) and yellow-footed rock wallabies (gray). Different symbols represent different individuals. Regression equations; tammar: $y = 0.66x - 0.49$, $R^2 = 0.43$, $P < 0.001$; YFRW: $y = 0.34x - 0.20$, $R^2 = 0.29$, $P = 0.025$.

tendon stresses (Fig. 4B; 39.9 ± 2.7 MPa) compared with YFRW (28.0 ± 1.7 MPa; $P = 0.006$).

3.4. Safety factor and elastic energy recovery

Safety factor for the ankle extensor tendons, given a failure strength of 100 MPa, was significantly higher in YFRW, averaging 3.65 ± 0.21 during preferred speed level hopping compared with 2.63 ± 0.19 in tammar wallabies (Fig. 4C; $P = 0.007$). However, due to their higher tendon stresses, and corresponding tendon strains, tammar wallabies are able to recover significantly more elastic strain energy than YFRW hopping at the same speed. In both species, elastic strain energy increased with increasing speed (Fig. 5). Over the observed speed ranges, the average energy recovered from the ankle extensor tendons of tammar wallabies was 2.18 ± 0.29 J per leg, as compared to 1.26 ± 0.15 J in YFRW ($P = 0.024$).

4. Discussion

Tammar wallabies and yellow-footed rock wallabies are two relatively closely related species of similar size and general body plan, yet they live in very different environments. The goal of this study was to explore musculoskeletal differences between the two species to determine how these differences influence each species' hopping mechanics. We chose to examine steady-speed hopping as a biologically relevant behavior, which both species do regularly. (In contrast, we found it very difficult to induce tammar wallabies to jump under our field experimental conditions.) As anticipated, we found that yellow-footed rock wallabies have relatively thicker ankle extensor tendons, which experience less stress than those of tammar wallabies hopping at the same speed. Thus, yellow-footed rock wallabies operate with a higher tendon safety factor, but do not store and recover as much elastic strain energy.

4.1. In vivo mechanics: linking morphology to functional loading patterns

Our results show that when hopping at similar preferred speeds, both wallaby species develop similar ankle joint moments

(Fig. 3A). However, because of their lower mechanical advantage (requiring a greater muscle to ground force impulse ratio, Fig. 3B) tammar wallabies exert significantly greater muscle forces at the ankle. These averaged 26% more than ankle extensor forces of YFRW during moderate steady-speed hopping (Fig. 3C). Despite this, the relatively higher PCSA of the tammar wallaby ankle extensors resulted in similar muscle stresses (200–215 kPa) acting within the two species (Fig. 4A). These stresses are consistent with direct *in vivo* muscle–tendon measurements made in tammar wallabies hopping on a treadmill at similar speeds (Biewener and Baudinette, 1995) and are below the maximum isometric muscle stress (300 kPa) derived from literature values used in morphological analyses of energy savings capacity (Bennett and Taylor, 1995; Close, 1971; Ker et al., 1988; Pollock and Shadwick, 1994b; Wells, 1965). However, our current study only examined steady speed hopping and it is likely these animals generate higher muscle stresses when accelerating or jumping.

A lower mechanical advantage at the ankle joint in tammar wallabies is consistent with a biomechanical design that facilitates elastic energy storage and recovery. By requiring greater muscle force per unit ground reaction force, this design couples high muscle forces with the lower tendon cross-sectional areas of tammar wallabies, resulting in peak tendon stresses that are more than 40% higher than in YFRW (Fig. 4B). Given an elastic modulus for tendon of 1.0 GPa, the average peak tendon stress of 40 MPa suggests that tammars operate with tendon strains of 4.0% during preferred steady speed hopping, compared with an average peak stress in YFRW of 28 MPa and an operating strain of only 2.8%. Despite a lower tendon volume (length × area, Table 1), tammar wallabies recover 73% more strain energy than YFRW during steady hopping (Fig. 4D). In both species, elastic energy recovery increases with increasing speed (Fig. 5); however, the rate of increase for yellow-footed rock wallabies is less than for tammars.

4.2. Why have thicker tendons?

Although there are obvious advantages to being able to increase locomotor speed without increasing energetic cost, a necessary trade-off exists between safety factor and elastic energy storage. At the moderate hopping speeds observed in this study, tammar wallabies operated with safety factors ranging from 1.5 to 3.9 (mean: 2.6; Fig. 4C). With a safety factor as low as 1.5, there is little margin for increased force, suggesting that tammars have a limited ability to accelerate and jump. In a comparison of red kangaroos (*Macropus rufus*) and kangaroo rats (*Dipodoyis spectabilis*), Biewener and Bertram (1991) showed that red kangaroos, another open plains dwelling macropod, would be incapable of the high accelerations achieved by kangaroo rats during jumping because the large forces required would rupture their tendons. This largely results from the scale effect of a relative decrease of tendon area at larger size (which we return to below). It also suggests that, by living in relatively open and predictable environments with few natural predators, tammar wallabies and red kangaroos may not require high safety factors. A recent study (McGowan et al., 2005a) showed that tammars adjust their limb posture to reduce joint moments when they accelerate. As a result,

they do not significantly increase tendon stresses even when they produce higher ground forces. Therefore, it is possible that a similar change in posture occurs during jumping that would enable tammar wallabies to mediate the limitations posed by low tendon safety factors. However, the forces experienced during jumping are significantly higher than during level accelerations (McGowan et al., 2005a,b) and it is not likely that changes in limb posture could enable tammar wallabies to maintain a relatively constant peak ankle joint moment during jumping as is the case in level accelerations.

Conversely, yellow-foot rock wallabies live in steep, unpredictable environments that routinely require them to make vertical jumps of over a meter ($\sim 3\times$ their hip height). In this habitat, elastic energy storage for locomotor economy might be less beneficial to their overall locomotor performance requirements. Instead, their thicker tendons and greater ankle extensor mechanical advantage means that YFRW operate with a larger safety factor, allowing them to produce much higher forces required for jumping and negotiating steep, uneven terrain. In a recent study of moderate height (1.0 m) jumping in YFRW, McGowan et al. (2005b) found that peak vertical ground reaction forces were 30% greater than those observed during level hopping. Assuming a similar increase in muscle force, their tendon safety factor during these jumps would be reduced to ~ 2.8. If a tammar wallaby were to undertake a jump of this height (a behavior that we were unable to elicit in studying this species), its safety factor would be reduced to below two. The values of tendon safety factor measured during steady speed hopping and moderate jumping in YFRW can be used to estimate the maximum jump heights of these two species. From these values, we would predict that tammar wallabies could jump to nearly 2 m height, whereas YFRW could attain heights of nearly 3 m.

In addition to being able to withstand higher operating forces, thicker tendons also likely improve control by increasing the fidelity of force transmission between the muscle, skeleton, and the ground (Alexander, 1988; Ker et al., 1988; Rack and Ross, 1984). Muscles with short fibers and long thin tendons may not be able to shorten enough to overcome the strain in their tendons. Muscles favorable for elastic energy storage have FLF<2, while muscles that likely play an intermediate role range from 2 to 4. Muscles with FLF>4 likely play a major role in controlling joint displacement. Not surprising, both the plantaris and gastrocnemius of the tammar wallabies have a FLF near or below 2, with values of 1.03 and 2.15, respectively, indicating that both of these muscles play a predominant role in elastic energy storage, rather than controlling joint displacement. Values for the YFRW are significantly higher, averaging 2.02 and 2.97 for the plantaris and gastrocnemius, respectively. This suggests that the YFRW gastrocnemius is better designed to actively control joint and foot position compared with the plantaris, which acts predominately as a biological spring. However, an FLF of 2.97 suggests that the gastrocnemius is still likely to store significant elastic strain energy.

4.3. Comparisons among other macropods

How do these two species of wallabies compare with other macropods? Anatomical analyses of this group have shown that,

like other mammals, muscle fiber/tendon area ratios of the ankle extensor tendons scale with positive allometry, but with a steeper slope than eutherian mammals (Pollock and Shadwick, 1994b; Bennett and Taylor, 1995; Bennett, 2000). Thus, larger macropods have lower safety factors and a greater capacity to store and return elastic strain energy. Coupled with measurements of oxygen consumption from macropods of varying size (Dawson and Taylor, 1973; Thompson et al., 1980; Baudinette et al., 1992, 1993; Kram and Dawson, 1998), this scaling relationship has led to the suggestion (Bennett and Taylor, 1995; Bennett, 2000) that all large macropods ($>\sim 5$ kg) exhibit a plateau in oxygen consumption with speed. Using the scaling equations of Bennett and Taylor (1995) and averaging the values for the plantaris and gastrocnemius, a similarly sized (6 kg) macropod would be predicted to have a muscle/tendon area ratio of 155. Consistent with this, our study of tammar and yellow-foot rock wallabies suggests that, even for macropods, the yellow-foot rock wallaby does not have a muscle/tendon design that is particularly well-suited to elastic energy savings. Therefore, this relatively large macropod may not exhibit the distinctively flat rate of energy use versus speed relationship often associated with this group. Whether or not this is also the case for other large macropods inhabiting steep, uneven terrain remains to be examined.

In conclusion, while tammar and yellow-foot rock wallabies are two macropod species of similar body size and appear to be of similar proportions, significant differences in their hindlimb anatomy exist that relate directly to their locomotor mechanics, and these appear to reflect adaptations to differing habitats and locomotor requirements. A trade-off exists between a design that favors elastic energy storage at moderate speeds versus a design that is capable of withstanding the higher force demands of moving in a steep and unpredictable environment. Although our study is a simple comparison of two species (ignores possible effects to due to phylogeny, Felsenstein, 1985; Garland and Adolph, 1994), our results for these species suggest that macropods are a promising group in which to explore evolutionary relationships between body form, locomotor function, and habitat use. Although previous energetic and biomechanical studies have suggested that macropods greater than ~ 5 kg body mass should generally benefit from elastic energy storage and potentially show a leveling-off in oxygen consumption with speed, our study of yellow-foot rock wallabies suggests this is not necessarily the case. Selection for non-steady locomotor performance in rocky terrain, and for climbing (e.g. tree kangaroos, Szalay, 1994), likely requires trade-offs in locomotor economy. Additional metabolic and biomechanical studies of rock wallabies and other macropodoid species are needed to establish how ubiquitous the unique locomotor energetics are within this group, and may help to shed light on the musculoskeletal adaptations that underlie the remarkable energy savings of at least certain of these species.

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