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Received: 1 February 2020 | Revised: 20 March 2020 | Accepted: 20 April 2020

DOI: 10.1111/joa.13214

ORIGINAL PAPER

ANATOMICAL SOCIETY Journal of Anatomy WILEY

Functional morphology of the ankle extensor muscle-tendon units in the springhare *Pedetes capensis* shows convergent evolution with macropods for bipedal hopping locomotion

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Funding information
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Abstract

This study assesses the functional morphology of the ankle extensor muscle-tendon units of the springhare *Pedetes capensis*, an African bipedal hopping rodent, to test for convergent evolution with the Australian bipedal hopping macropods. We dissect and measure the gastrocnemius, soleus, plantaris, and flexor digitorum longus in 10 adult springhares and compare them against similar-sized macropods using phylogenetically informed scaling analyses. We show that springhares align reasonably well with macropod predictions, being statistically indistinguishable with respect to the ankle extensor mean weighted muscle moment arm (1.63 vs. 1.65 cm, respectively), total muscle mass (41.1 vs. 29.2 g), total muscle physiological cross-sectional area (22.9 vs. 19.3 cm^2), mean peak tendon stress (26.2 vs. 35.2 MPa), mean tendon safety factor (4.7 vs. 3.6), and total tendon strain energy return capacity (1.81 vs. 1.82 J). However, total tendon cross-sectional area is significantly larger in springhares than predicted for a similar-sized macropod (0.26 vs. 0.17 cm^2, respectively), primarily due to a greater plantaris tendon thickness (0.084 vs. 0.048 cm^2), and secondarily because the soleus muscle-tendon unit is present in springhares but is vestigial in macropods. The overall similarities between springhares and macropods indicate that evolution has favored comparable lower hindlimb body plans for bipedal hopping locomotion in the two groups of mammals that last shared a common ancestor ~160 million years ago. The springhare's relatively thick plantaris tendon may facilitate rapid transfer of force from muscle to skeleton, enabling fast and accelerative hopping, which could help to outpace and outmaneuver predators.

KEYWORDS
energy, muscle, predation, strain, stress, tendon

1 | INTRODUCTION

Bipedal hopping is a specialized form of terrestrial locomotion characterized by the sustained saltatory motion of well-developed elongate hindlimbs that cycle in-phase to propel the animal forward. It has evolved independently in at least five groups of mammals—springhares (rodents, family Pedetidae), three other rodent lineages (families Dipodidae, Heteromyidae, and Muridae), and the marsupial macropods (superfamily Macropodoidea, e.g. Australian rat-kangaroos, wallabies, and kangaroos). In the early 1970s, by training two

red kangaroos *Macropus rufus* (18 and 28 kg body mass) to undertake sustained hopping on a treadmill, Dawson and Taylor (1973) revealed an uncoupling of metabolic rate from travel speed, a pattern later also observed by Baudinette et al. (1992) in 13 tammar wallabies *Macropus eugenii* (4.9 kg mean body mass). Both studies defied expectations of a markedly more expensive and linear relationship between the rate of energy use and travel speed, based on earlier measurements of running quadrupeds (Taylor *et al*., 1970). Subsequent studies on smaller hopping rodents and macropods (0.03–3.0 kg body mass) showed that the uncoupling of metabolic rate with travel speed either does not occur (Thompson *et al*., 1980) or is less pronounced compared with the larger hopping animals (Dawson, 1976; Webster and Dawson, 2003). Indeed, a linear relationship between metabolic rate and travel speed was observed for two hopping springhares (3.0 kg mean body mass), exhibiting a pattern similar to that predicted for a similar-sized running quadrupedal mammal (Figure 1, reproduced from Thompson *et al*., 1980). It has been noted, although never quantified, that the bipedal hopping pattern of springhares is characterized by hindlimbs that appear more extended when they first make contact with the ground compared with those of larger macropods (Offermans and De Vree, 1987).

Why the energy savings of hopping locomotion become evident, or more pronounced, with increasing body mass remains an open question. During locomotion, muscle-tendon forces must balance the rotational moments generated at limb joints by opposing ground reaction and inertial forces of the swinging limbs, which will increase with travel speed (Alexander, 2003; Biewener and Patek, 2018). In quadrupeds, peak muscle force requirements are attenuated in larger individuals due to changes in limb posture that improve effective mechanical advantage (muscle-to-external moment arm ratio) of the extensor muscles (Biewener, 1989, 2000, 2005), and decreased peak gravitational body weight-normalized forces experienced during fast running (Biewener, 2000; Alexander, 2003; Dick and Clemente, 2017). In macropods, there is little mechanical assistance provided by changes in locomotor limb posture afforded to larger individuals, and in fact the effective mechanical advantage of the ankle extensor muscles may scale independently of body mass, meaning that macropods remain relatively crouched across their body mass range (Bennett and Taylor, 1995; McGowan *et al*., 2008). Accordingly, the peak force requirements of the ankle extensor muscles increase largely in direct proportion to body mass among the macropods. The increase in peak force requirements is met by a steep (positively allometric) increase in the physiological cross-sectional area (PCSA) of the ankle extensor muscles, but not by a concomitant steep increase in the cross-sectional area (CSA) of the adjoining tendons. Consequently, peak tendon stress is predicted to approach breaking point in the largest macropods for movement at high speeds (Bennett and Taylor, 1995; McGowan *et al*., 2008; Snelling *et al*., 2017). Thus, the ankle extensor tendons of smaller macropods, similar to those of small kangaroo rats (Biewener *et al*., 1981; Biewener and Blickhan, 1988), are relatively thick and likely designed for rapid force transmission to facilitate fast and accelerative hopping, whereas those of larger macropods are relatively thin and so designed to experience high stresses that facilitate the storage and recovery of strain energy during locomotion. Such body size-related change in functional morphology of the ankle extensor muscle-tendon units of macropods may help to explain the improved hopping efficiency, and decoupling of metabolic rate versus speed, at larger body size (Biewener and Bertram 1991). In larger kangaroos and wallabies, hopping efficiency might also improve with increasing travel speeds up to a point, because faster speeds are achieved primarily by increasing stride length, rather than stride frequency, which should reduce the energetic cost of limb cycling (Webster and Dawson, 2003; Dawson and Webster, 2010; Dawson, 2012).

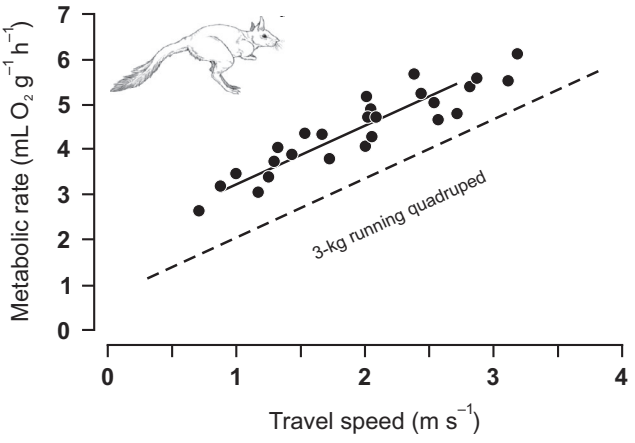


FIGURE 1 Metabolic rate increases linearly with travel speed during bipedal hopping in the springhare *Pedetes surdaster* (solid line), a pattern similar to that predicted for a running quadrupedal mammal (dashed line) of equivalent body mass (reproduced from Thompson *et al*., 1980). Originally published as *P. capensis*, prior to taxonomic revision that now separates Africa's southern species (*P. capensis*) from its eastern species (*P. surdaster*). Note arithmetic data plotted on arithmetic axes

The ability to engage in fast and accelerative hopping among smaller members of certain rodent and macropod lineages is believed to be an example of convergent evolution driven by predation pressure (McGowan and Collins, 2018). For example, despite considerable phylogenetic distance, the large contribution of muscle work over tendon strain energy to the leaping performance of the North African-Middle Eastern jerboas *Jaculus jaculus* (ca. 65 g body mass; Moore *et al*., 2017) is comparable to that observed during hopping and leaping in similar-sized North American kangaroo rats *Dipodomys spectabilis* and *Dipodomys deserti* (ca. 100 g body mass; Biewener *et al*., 1981; Biewener and Blickhan, 1988; Schwaner *et al*., 2018). Presumably, the fitness benefit of outmaneuvering predators outweighed that of energy-efficient locomotion during evolution in both groups of bipedal hopping rodents. It is at present unclear whether convergent evolution might also be evident between bipedal hopping springhares and similar-sized macropods, two groups of mammals that last shared a common ancestor ~160 million years ago (Luo *et al*., 2011). The springhare represents a unique evolution

into a bipedal hopping state, given there are no living hopping or non-hopping close relatives. The ancestral *Megapedetes* occupied grassy woodlands of Namibia and forests of Kenya approximately 20 million years ago before giving rise to the modern species associated more with semi-arid habitats (Senut, 2016). Today, springhares occur patchily across southern and eastern Africa (Skinner and Chimimba, 2005). They are herbivorous animals (Peinke and Brown, 2006) that selectively forage above-ground at night (Butynski, 1984) and shelter in burrow systems during the day (Butynski and Mattingly, 1979; Peinke and Brown, 2005). Their metabolic rate increases approximately 15-fold from resting to hopping at 2.8 m s^{-1}, a speed reportedly achieved without incurring a significant increase in lactate (Müller *et al*., 1979; Thompson *et al*., 1980; Peinke and Brown, 2003). On the one hand, the springhare is of significantly larger body size (ca. 3 kg body mass) than the jerboas and kangaroo rats, and so selection for energy-efficient hopping locomotion may have taken greater priority during its evolution. On the other hand, the springhare is often under intense predation pressure, and so selection may instead have favored fast and accelerative hopping. In support of the latter scenario, behavioral observations report that springhares can 'bolt suddenly' to avoid predators (Butynski and Mattingly, 1979) and change 'speed and direction of movement and this will reduce the success of predators' (Peinke and Brown, 2005).

We therefore assessed the functional morphology of the four ankle extensor muscle-tendon units that balance rotational moments at the ankle joint during bipedal hopping in the springhare, to test for convergent evolution with similar-sized bipedal hopping macropods. This unique mode of locomotion that is shared between the springhare (a placental) and macropods (marsupials) offers an opportunity to assess the degree to which evolution has selected for similar morphological solutions to corresponding functional tasks in two phylogenetically unrelated groups of mammals. We measured springhare moment arms, muscle volumes, muscle PCSAs and tendon CSAs, and calculated peak tendon stresses, tendon safety factors, and tendon strain energy return capacities in the gastrocnemius, soleus, plantaris, and flexor digitorum longus muscle-tendon units. We extend the analysis by comparing the mean value of selected traits in the springhare against a series phylogenetically informed scaling analyses using published data of 16 species of bipedal hopping macropods. We show that, for most traits, springhares align well with macropod predictions, except they have a plantaris tendon CSA significantly greater than predicted in an equivalent-sized macropod, and a soleus muscle-tendon unit that is vestigial in macropods. The springhare's ability to engage in fast and accelerative hopping is considered with particular reference to the plantaris tendon thickness, life history, and body size.

2 | METHODS

2.1 | Animal collection

The carcasses of 10 adult springhares *Pedetes capensis* (Forster 1778), comprising four males and six females weighing 2.73 ± 0.24 kg body mass (mean ± SD), were collected opportunistically during management culls in the Kalahari, Northern Cape, South Africa, under the approval of the University of the Witwatersrand Animal Research Ethics Committee (2018/01/02/O). All carcasses were placed into plastic bags, tied shut, frozen within 4 hr of death, and kept frozen for 4–8 weeks. On the day of dissection, each carcass was thawed at room temperature, weighed to 0.05 kg on a calibrated strain gauge scale (PCE-CS 300; PCE Instruments), and the hindlimbs then removed and wrapped in damp cloth to prevent water loss.

2.2 | Moment arms

The lower hindlimbs contain four ankle extensor muscle-tendon units (MTUs) that balance rotational moments at the ankle joint. The muscle bellies are located in the posterior compartment, caudal to the partly fused tibia and fibula, and comprise the medial and lateral heads of the gastrocnemius (GAS), the soleus (SOL), plantaris (PL), and flexor digitorum longus (FDL). The GAS and SOL tendons both insert directly on the calcaneus (ankle extensors), whereas the PL tendon passes behind the calcaneus and inserts on the intermediate phalanges of the toes (ankle extensor and digital flexor), and the FDL tendon passes around the ankle and inserts on the distal phalanges of the toes (digital flexor).

The GAS, SOL, and PL muscle moment arms ($r_{gas,sol,pl}$; cm), and the FDL muscle moment arm (r_{fdl}; cm) were estimated as the perpendicular distance between the tendon's line of action and the center of rotation of the ankle joint. The GAS, SOL, and PL muscle moment arms were treated as one because their respective tendons follow very similar paths toward the calcaneus and thus their moment arms at the ankle are virtually identical. The external (ground reaction force) moment arm (R_{ext}; cm) was estimated as the perpendicular distance between the estimated ground reaction force and the center of rotation of the ankle joint (Biewener, 1989; Bennett and Taylor, 1995; McGowan *et al*., 2005; 2008; Snelling *et al*., 2017). The ground reaction force was assumed to act in a vertical direction halfway along the proximal phalanx of the longest toe, digit III (Bennett and Taylor, 1995; Bennett, 2000; Snelling *et al*., 2017). We standardized our measurements by holding the ankle joint at approximately 90° (McGowan *et al*., 2008; Snelling *et al*., 2017), which we assume corresponds to the in vivo mid-stance hopping position when peak ground forces acting in a vertical direction are expected. Our measurements of muscle and external moment arms are estimates only, informed by published traces of a single springhare hopping on a treadmill recorded at 100 fps by high-speed cinematography (Offermans and De Vree 1987). We used a set of 15-cm digital vernier calipers to measure the muscle moment arms to 0.01 cm, and we used a 30-cm ruler to measure the external moment arm to 0.1 cm.

To evaluate the combined action of the four muscles at the ankle joint, a mean weighted muscle moment arm ($\bar{r}$; cm) was calculated as $\bar{r} = (r_1 A_{m,1} + r_2 A_{m,2} + r_n A_{m,n}) / \sum A_m$, where $r_n A_{m,n}$ is the product of the muscle moment arm and the PCSA (see calculation below) for each individual muscle, and $\sum A_m$ is the total summed PCSA of

all four muscles (Biewener, 1989; McGowan *et al*., 2008), implying equal stresses across the four muscle agonists. The effective mechanical advantage of the GAS, SOL, and PL ($ema_{gas,sol,pl}$), and of the FDL (ema_{fdl}), was calculated as the quotient of the relevant muscle moment arm ($r_{gas,sol,pl}$ or r_{fdl}) and the estimated external moment arm (R_{ext}; cm). A mean weighted effective mechanical advantage ($\overline{ema}$) was then calculated as the quotient of the mean weighted muscle moment arm ($\bar{r}$) and the external moment arm (R_{ext}).

2.3 | Muscle-tendon unit morphology

Each MTU was dissected free from the bone, its total length (l_{mtu}; cm) measured to 0.01 cm with the calipers, and its total mass (m_{mtu}; g) measured to 0.01 g on a calibrated digital balance (BJ-1000C; Precisa). The muscle belly was isolated from each MTU, and its length (l_m; cm) and mass (m_m; *g*) recorded to the same precisions. Muscle volume (V_m; cm^3) was calculated as $V_m = m_m/\rho_m$, where ρ_m is the mass-density of mammalian muscle (= 1.06 g cm^{-3}; Méndez and Keys, 1960). An incision was then made along the length of the muscle, so that it could be parted along its central axis, photographed with a scale, and three to five measurements made of fascicle length (l_f; cm), and three to five measurements of pennation angle (θ), using computer graphics software (CorelDRAW 15; Corel Corporation) (Figure 2). The PCSA of each muscle (A_m; cm^2) could then be obtained given as $A_m = V_m \cos\theta / l_f$, where l_f and θ are the average values from each muscle (Sacks and Roy, 1982). The PCSA calculation adjusts for the askew alignment, and thus direction of force, of the fascicles in a pennate muscle.

The extra-muscular fraction of the tendon of each MTU was laid straight and its length ($l_{t,ext}$; cm) measured to 0.01 cm and its mass ($m_{t,ext}$; g) recorded to 0.01 g, using the same calipers and balance. The small part of the PL and FDL tendons that pass behind the calcaneus and ankle, respectively, have low elastic moduli relative to other parts of the tendon (Ker *et al*., 1986) and thus were removed prior to measurement (McGowan *et al*., 2008; Snelling *et al*., 2017). The intra-muscular fraction of the tendon could not be measured directly, but its length ($l_{t,int}$; cm) was determined given $l_{t,int} = l_{mtu} - l_{t,ext} - l_f \cos\theta$. Thus, total tendon length ($l_{t,int+ext}$) was obtained from the sum of $l_{t,int}$ and $l_{t,ext}$. The CSA of each tendon (A_t; cm^2) was calculated as $A_t = m_{t,ext}/(\rho_t l_{t,ext})$, where ρ_t is the mass-density of tendon (=1.12 g cm^{-3}; Ker, 1981). The total volume of each tendon (V_t; cm^3) was then calculated by $V_t = A_t\, l_{t,int+ext}$.

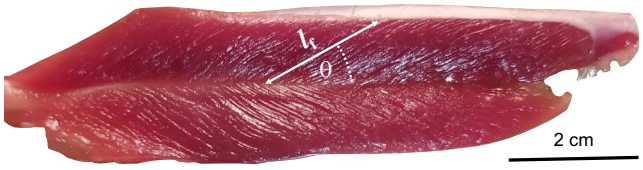


FIGURE 2 Fascicle length (l_f) and pennation angle (θ) were measured from bisected muscle bellies of the ankle extensor muscle-tendon units (SOL shown here) in 10 adult springhares *Pedetes capensis*

2.4 | Tendon stress loading, safety factor, and strain energy return capacity

The muscle and tendon are connected in series, meaning that total muscle PCSA force is distributed across the adjoining tendon CSA, thus allowing peak tendon stress ($\sigma_{t,max}$; MPa) to be estimated as $\sigma_{t,max} = \sigma_{m,max}(A_m/A_t)$ (Ker *et al*., 1988; Pollock and Shadwick, 1994a), where $\sigma_{m,max}$ is maximum isometric stress of mammalian muscle (=0.3 MPa; Biewener, 2003). We assume that A_m corresponds approximately to the optimal sarcomere length for producing maximum force. The tendon safety factor (S_t) was calculated as $S_t = \sigma_{t,fail}/\sigma_{t,max}$, where $\sigma_{t,fail}$ is the stress under which tendons are typically expected to rupture (=100 MPa; Bennett *et al*., 1986). Lastly, the strain energy return capacity of the tendon (U_t; J) was estimated according to the equation, $U_t = V_t\left(\frac{\sigma^2_{t,max}}{2E}\right)0.93$ (Biewener and Baudinette, 1995; McGowan *et al*., 2008; Snelling *et al*., 2017), where *E* is the elastic modulus of tendon calculated for tammar wallaby (=1,000 MPa; Biewener and Baudinette, 1995) and 0.93 accounts for tendon's 7% energy loss due to mechanical hysteresis (Bennett *et al*., 1986; Biewener, 2008). Although *E* can vary with species, location, and pathology (LaCroix *et al*., 2013), our assumed value of 1,000 MPa is functionally applicable to the present investigation, having been derived for the ankle extensor tendons in the tammar wallaby (4.8 kg mean body mass) operating over their normal stress range during hopping locomotion.

2.5 | Phylogenetically informed comparisons with bipedal hopping macropods

To provide an interspecific backdrop against which to assess the springhare, we used published morphological and phylogenetic information to undertake scaling analyses of selected traits as a function of body mass, across 16 species of bipedal hopping macropods (species inventory in Supporting Information Table S1; data taken from McGowan *et al*., 2008; Snelling *et al*., 2017). The comparison of the springhare against the macropods is validated, in part, by consistent methodology among the studies. Macropod trait and body mass data were $\log_{10}$-transformed and analyzed using a phylogenetic generalized least squares (PGLS) regression model (Grafen, 1989; Martins and Hansen, 1997; Garland and Ives, 2000) in the caper v1.0.1 package (Orme, 2018) within the R v3.6.1 software environment (R Core Team, 2013). The phylogenetic tree used for the analysis was constructed from a published supertree of 5,020 extant mammals (Fritz *et al*., 2009). A measure of phylogenetic correlation, λ (Pagel, 1999), was estimated by fitting PGLS regression models with different values of λ and finding the value that maximizes the log likelihood.

2.6 | Statistical analyses

All mean values are reported with 95% confidence intervals (CI) unless stated otherwise. Measurements were taken from both the left

and right lower hindlimbs and averaged for each individual (except for two specimens where measurements could be obtained only from a single intact leg). Mean values thus represent an average corresponding to a single leg only. Statistical differences among mean values ($p<.05$) were tested with either a paired t test or a repeated-measures ANOVA followed by Tukey's post hoc test, as appropriate, within R v3.6.1 (R Core Team, 2013). We also wished to test whether springhares are significantly different from a typical bipedal hopping macropod of the same body mass. To this end, we superimposed the mean value of selected traits of springhares onto the PGLS regression models derived for the macropods. A statistical difference was identified when the springhare's mean value fell outside the macropods' 95% prediction belt, containing the area in which 95% of all data points are expected to fall (as recommended in Cooper and Withers, 2006). This analysis was performed within R v3.6.1 and with commercial statistical software (PRISM 8; GraphPad Software).

3 | RESULTS

3.1 | Moment arms

The springhares were all adults of similar size (2.40–3.25 kg body mass) and so we present absolute mean values, with statistical comparisons across the MTUs, in Tables 1–3. The ankle extensor estimated mean weighted muscle moment arm ($\bar{r}$), which characterizes the combined action of the GAS, SOL, PL, and FDL at the ankle joint, was 1.63 ± 0.09 cm, whereas the estimated mean external (ground reaction force) moment arm (R_{ext}) was 7.91 ± 0.23 cm (Table 1). Thus, the mean weighted effective mechanical advantage of these four MTUs ($\overline{ema}$) was 0.21 ± 0.01. The effective mechanical advantage of the GAS, SOL, and PL ($ema_{gas,sol,pl} = 0.23 \pm 0.01$) was approximately threefold greater than that of the FDL ($ema_{fdl} = 0.08 \pm 0.01$).

3.2 | Muscle-tendon unit morphology

Mean muscle mass was greatest in the GAS (18.9 ± 1.3 g) and PL (12.4 ± 0.6 g), but less than half in the FDL (6.0 ± 0.4 g) and SOL (3.8 ± 0.3 g). Mean fascicle length varied from 1.3 to 1.9 cm and mean pennation angle from 24.4 to 31.9° among the different muscles (Table 2). Mean muscle PCSA was greatest in the GAS (9.4 ± 1.2 cm^2) and PL (8.0 ± 0.9 cm^2), and again less than half in the FDL (3.8 ± 0.4 cm^2) and SOL (1.8 ± 0.3 cm^2). Mean tendon CSA was greatest in the PL (0.084 ± 0.008 cm^2), statistically indistinguishable in the GAS and FDL (pooled mean of 0.070 ± 0.004 cm^2), and smallest in the SOL (0.032 ± 0.007 cm^2). The ratio of muscle PCSA-to-tendon CSA was greatest in the GAS (141 ± 16), followed by the PL (95 ± 7), and then by the SOL and FDL, with statistically indistinguishable ratios (pooled mean of 57 ± 8).

3.3 | Tendon stress loading, safety factor, and strain energy return capacity

Mean estimated peak tendon stress was greatest in the GAS (42.3 ± 4.9 MPa), followed by the PL (28.6 ± 2.2 MPa), and then by the SOL and FDL, with statistically indistinguishable stresses (pooled mean of 17.0 ± 2.5 MPa) (Table 3). Thus the estimated tendon safety factor was lowest in the GAS and PL (pooled mean of 3.0 ± 0.3) and greatest in the SOL and FDL (pooled mean of 6.4 ± 0.8). The estimated tendon strain energy return capacity was greatest in the GAS and PL (pooled mean of 0.77 ± 0.12 J), followed by the FDL (0.22 ± 0.04 J), and then by the SOL (0.06 ± 0.02 J). Accordingly, the GAS and PL contribute approximately 42.5% each, the FDL only 12.0%, and the SOL only 3.0% to the total energy return capacity of the ankle extensor tendons.

3.4 | Phylogenetically informed comparisons with bipedal hopping macropods

Scaling analyses of selected traits as a function of body mass across 16 species of bipedal hopping macropod indicate a consistent absence of phylogenetic signal among the residuals, with an estimated maximum log likelihood of $\lambda = 0$, rendering the PGLS equivalent to an OLS regression model. For simplicity, we either summed or averaged trait values across the multiple MTUs before regressing the overall value against body mass (Figures 3–5) (regressions of individual MTUs in Supporting Information).

In the macropods, mean weighted muscle moment arm ($\bar{r}$) scales against body mass with an exponent of 0.43 ± 0.03 (hyperallometry); the springhare's value of 1.63 ± 0.09 cm is almost exactly as predicted (1.65 cm) for a macropod of the same body mass (Figure 3). Total

TABLE 1 Mean ± 95% CI values of the moment arms and effective mechanical advantages of the ankle extensor muscle-tendon units in the springhare *Pedetes capensis* (n = 10 individuals)

	GAS, SOL, and PL	FDL	t test
Muscle moment arm, r (cm)	1.84 ± 0.10	0.61 ± 0.07	$t_{1,9}$ = 25.8, p < .0001
Effective mechanical advantage, ema (r/R_{ext})	0.23 ± 0.01	0.08 ± 0.01	$t_{1,9}$ = 25.3, p < .0001

The mean weighted muscle moment arm is $\bar{r}$ = 1.63 ± 0.09 cm, mean external (ground reaction force) moment arm is R_{ext} = 7.91 ± 0.23 cm, and mean weighted effective mechanical advantage is $\overline{ema}$ = 0.21 ± 0.01. Values correspond to a single leg only. GAS, SOL and PL were treated as one because their moment arms at the ankle are virtually identical. GAS, gastrocnemius; SOL, soleus; PL, plantaris; FDL, flexor digitorum longus.

TABLE 2 Mean ± 95% CI values of the morphology of the ankle extensor muscle-tendon units in the springhare (n = 10)

	GAS	SOL	PL	FDL	ANOVA
Muscle-tendon unit					
Mass, m_{mtu} (g)	19.4 ± 1.3[a]	4.0 ± 0.3[b]	14.1 ± 0.7[c]	7.5 ± 0.5[d]	$F_{3,27}$ = 580, p < .0001
Length, l_{mtu} (cm)	14.0 ± 0.3[a]	13.2 ± 0.4[b]	24.3 ± 0.5[c]	24.0 ± 0.3[c]	$F_{3,27}$ = 1,432, p < .0001
Muscle belly					
Mass, m_m (g)	18.9 ± 1.3[a]	3.8 ± 0.3[b]	12.4 ± 0.6[c]	6.0 ± 0.4[d]	$F_{3,27}$ = 592, p < .0001
Volume, V_m (cm^3)	17.8 ± 1.2[a]	3.6 ± 0.3[b]	11.7 ± 0.5[c]	5.6 ± 0.3[d]	$F_{3,27}$ = 592, p < .0001
Muscle length, l_m (cm)	7.1 ± 0.3[a]	9.4 ± 0.4[b]	8.5 ± 0.3[c]	8.8 ± 0.3[c]	$F_{3,27}$ = 62.6, p < .0001
Fascicle length, l_f (cm)	1.6 ± 0.2[a]	1.9 ± 0.2[b]	1.3 ± 0.2[c]	1.3 ± 0.2[c]	$F_{3,27}$ = 23.7, p < .0001
Pennation angle θ (deg)	31.9 ± 2.7[a]	24.4 ± 2.2[b]	28.8 ± 2.7[a]	31.5 ± 3.0[a]	$F_{3,27}$ = 11.5, p < 0.0001
PCSA, A_m (cm^2)	9.4 ± 1.2[a]	1.8 ± 0.3[b]	8.0 ± 0.9[c]	3.8 ± 0.4[d]	$F_{3,27}$ = 134, p < .0001
Tendon					
Volume, V_t (cm^3)	0.85 ± 0.08[a]	0.36 ± 0.07[b]	2.09 ± 0.18[c]	1.90 ± 0.11[d]	$F_{3,27}$ = 368, p < .0001
Length, $l_{t,int+ext}$ (cm)	12.6 ± 0.4[a]	11.4 ± 0.4[b]	23.1 ± 0.5[c]	22.9 ± 0.4[c]	$F_{3,27}$ = 1871, p < .0001
CSA, A_t (cm^2)	0.067 ± 0.005[a]	0.032 ± 0.007 [b]	0.084 ± 0.008[c]	0.073 ± 0.005 [a]	$F_{3,27}$ = 91.0, p < .0001
PCSA-to-CSA ratio, A_m/A_t	141 ± 16[a]	62 ± 16[b]	95 ± 7[c]	52 ± 4[b]	$F_{3,27}$ = 57.6, p < .0001

Values correspond to a single leg only.

[a,b,c,d]Tukey's post hoc test for significant differences among means (p < .05). PCSA, muscle physiological cross-sectional area; CSA, tendon cross-sectional area. See Table 1 for muscle abbreviations.

TABLE 3 Mean ± 95% CI estimates of the peak tendon stress, tendon safety factor, and tendon strain energy return capacity of the ankle extensor muscle-tendon units in the springhare (n = 10)

	GAS	SOL	PL	FDL	ANOVA
Peak tendon stress, $\sigma_{t,max}$ (MPa)	42.3 ± 4.9[a]	18.5 ± 4.8[b]	28.6 ± 2.2[c]	15.5 ± 1.3[b]	$F_{3,27}$ = 57.6, p < .0001
Tendon safety factor, S_t	2.4 ± 0.3[a]	6.3 ± 1.6[b]	3.5 ± 0.3[a]	6.6 ± 0.5[b]	$F_{3,27}$ = 24.1, p < .0001
Strain energy return capacity, U_t (J) *	0.73 ± 0.20[a]	0.06 ± 0.02[b]	0.81 ± 0.14[a]	0.22 ± 0.04[c]	$F_{3,27}$ = 156, p < .0001

Values correspond to a single leg only.

See Table 1 for muscle abbreviations.

[a,b,c,d]Tukey's post hoc test for significant differences among means (p < .05).

*Data $\log_{10}$-transformed to attain normality prior to ANOVA.

muscle mass ($\sum m_m$) in the macropods scales with an exponent of 1.18 ± 0.08 (hyperallometry); the springhare's value of 41.1 ± 2.3 g is approximately 40% higher than predicted (29.2 g) but nonetheless falls within the 95% prediction bands (Figure 4a). Total muscle PCSA ($\sum A_m$) in the macropods scales with an exponent of 0.87 ± 0.09 (hyperallometry), and the springhare's value of 22.9 ± 2.3 cm^2 is approximately 20% higher than predicted (19.3 cm^2), once again falling within the 95% prediction bands (Figure 4b). Total tendon CSA ($\sum A_t$) in the macropods scales with an exponent of 0.64 ± 0.06 (isometry); the springhare's value of 0.26 ± 0.02 cm^2 is approximately 50% greater than predicted (0.17 cm^2), representing a significant difference by falling outside the 95% prediction bands (Figure 4c). Closer examination shows that the springhare's large total tendon CSA results primarily from having a disproportionately thick PL tendon relative to its body mass (mean ± SD of 0.084 ± 0.012 cm^2) (Figure 4c inset).

We also ran scaling analyses on the estimated tendon stress loading, safety factor, and strain energy return capacity in the bipedal hopping macropods. Mean peak tendon stress ($\bar{\sigma}_{t,max}$) increases with body mass in the macropods scaling with an exponent 0.21 ± 0.08; the springhare's value of 26.2 ± 2.5 MPa is approximately 30% lower than predicted (35.2 MPa) for a macropod of the same body mass, falling within the 95% prediction bands (Figure 5a). Mean tendon

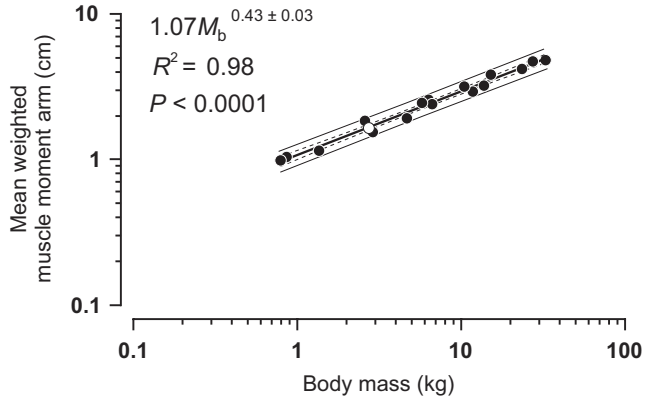


FIGURE 3 Mean weighted muscle moment arm at the ankle joint ($\bar{r}$) in the springhare (empty circle), superimposed onto a scaling analysis of $\bar{r}$ against body mass (M_b) in 16 species of bipedal hopping macropods (filled circles) plotted on logarithmic axes. Solid inner line is the regression mean, dashed outer lines represent the 95% confidence band, and solid outer lines represent the 95% prediction band. Note that $\bar{r}$ in the springhare includes the small contribution of the SOL, which is vestigial in the macropods. The small contribution of the FDL to $\bar{r}$ is unavailable in one macropod species (*Macropus eugenii*). The springhare (2.73 kg body mass) is straddled to the immediate left by the Pearson Island rock-wallaby *Petrogale lateralis pearsoni* (2.59 kg) and to the immediate right by the quokka *Setonix brachyurus* (2.89 kg). Macropod data were taken from the literature (species inventory in Table S1; McGowan *et al*., 2008; Snelling *et al*., 2017)

safety factor ($\bar{S}_t$) decreases with body mass in the macropods, scaling with an exponent of −0.22 ± 0.11; the springhare's value of 4.7 ± 0.5 is approximately 30% higher than predicted (3.6), once again within the 95% prediction bands (Figure 5b). These differences in tendon stress and safety factor reflect the springhare's greater total tendon CSA. Lastly, total tendon strain energy return capacity ($\sum U_t$) increases with body mass in the macropods, scaling with a very steep exponent of 1.56 ± 0.19, and the springhare's value of 1.81 ± 0.34 J is almost exactly as expected (1.82 J) for a macropod of the same body mass (Figure 5c).

4 | DISCUSSION

This study is the first to assess the functional morphology of the ankle extensor MTUs in the bipedal hopping springhare. The reason for studying the ankle extensor MTUs is because of their important role in locomotion, particularly during bipedal hopping, with variation in their position, arrangement, and architecture apparently facilitating profound variation in function, from the accelerative (but less energy-efficient) movement typical of smaller hoppers, to the energy-efficient (but less accelerative) movement characteristic of larger hoppers. To place our results into context, we superimposed the mean value of selected traits in the springhare onto a series of PGLS regression models using published data derived from 16 species of bipedal hopping macropods weighing 0.79–32.7 kg body mass. By taking a comparative approach, we make a number of

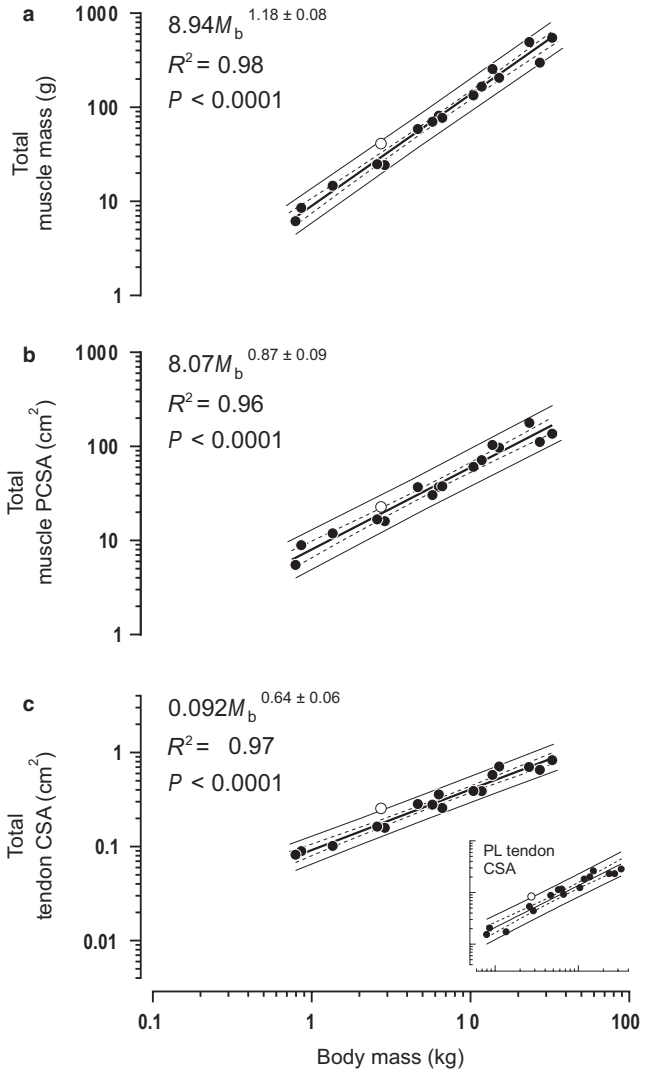


FIGURE 4 Total muscle mass (a; $\sum m_m$), total muscle PCSA (b; $\sum A_m$), and total tendon CSA (c; $\sum A_t$ with PL tendon CSA inset) of the ankle extensor muscle-tendon units in the springhare (empty circles), superimposed onto scaling analyses of $\sum m_m$, $\sum A_m$, and $\sum A_t$ against body mass (M_b) in 16 species of bipedal hopping macropods (filled circles) plotted on logarithmic axes. Solid inner line is the regression mean, dashed outer lines represent the 95% confidence band, and solid outer lines represent the 95% prediction band. Note that $\sum m_m$, $\sum A_m$, and $\sum A_t$ in the springhare include the small contribution of the SOL, which is vestigial in the macropods. PCSA is muscle physiological cross-sectional area and CSA is tendon cross-sectional area

findings that inform on the biomechanics and physiology of hopping locomotion in the springhare (a placental) compared with that of macropods (marsupials). We find the mean weighted muscle moment arm, total muscle mass, and total muscle PCSA of the springhare are not significantly different to those predicted for an equivalent-sized macropod. However, total tendon CSA in the springhare is significantly greater than predicted, driven primarily by the springhare's disproportionately thick PL tendon, and secondarily by the springhare's soleus muscle-tendon unit, which is vestigial in macropods. As such, the springhare's mean peak tendon stress and mean tendon

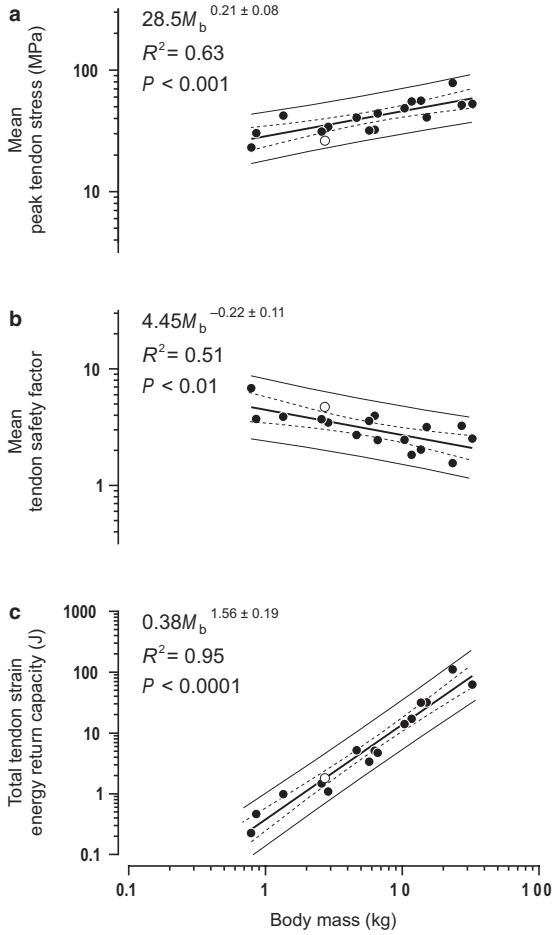


FIGURE 5 Estimated mean peak tendon stress (a; $\overline{\sigma}_{t,max}$), mean tendon safety factor (b; $\overline{S}_t$), and total tendon strain energy return capacity (c; $\sum U_t$) of the ankle extensor muscle-tendon units in the springhare (empty circles), superimposed onto scaling analyses of $\overline{\sigma}_{t,max}$ and $\overline{S}_t$ against body mass (M_b) in 16 species of bipedal hopping macropods, and $\sum U_t$ against M_b in 15 species of macropods (filled circles), plotted on logarithmic axes. Solid inner line is the regression mean, dashed outer lines represent the 95% confidence band, and solid outer lines represent the 95% prediction band. Note that $\overline{\sigma}_{t,max}$, $\overline{S}_t$ and $\sum U_t$ in the springhare includes the contribution of the SOL, which is vestigial in the macropods. The small contribution of the FDL to $\sum U_t$ is unavailable in two macropod species (*Macropus eugenii* and *Petrogale xanthopus*) and $\sum U_t$ is entirely unavailable in another (*Macropus rufus*)

safety factor tend to be somewhat lower and higher than predicted, respectively, for an equivalent-sized macropod, but the total tendon strain energy return capacity is almost exactly as predicted. We discuss these findings and their implications for fast and accelerative hopping in the springhare.

The ankle extensor mean weighted muscle moment arm scales with body mass with a hyperallometric exponent of 0.43 among the macropods, which may partly assist with opposing larger gravitational forces and joint moments experienced by larger individuals (McGowan *et al*., 2008). The springhare's mean weighted muscle moment arm of 1.63 cm is almost exactly as predicted for a macropod of the same body mass (1.65 cm) and falls well within the macropods' 95% prediction bands (Figure3). Indeed the springhare's individual muscle moment arms are all quite comparable to those of a macropod of the same body mass (Supporting Information Figure S1). Furthermore, the springhare's GAS, SOL, and PL muscle moment arm of 1.84 cm, the springhare's external (ground reaction force) moment arm of 7.91 cm, and the springhare's GAS, SOL, and PL effective mechanical advantage of 0.23, each agree within ~10% with that predicted in a similar-sized macropod (1.70 cm, 7.09 cm, and 0.24, respectively) (Bennett and Taylor, 1995). The similarity of the various moment arms is significant because it indicates that, despite the independent evolution of hopping bipedalism in springhares and macropods, the two groups have converged towards a very similar mechanical posture and body plan, particularly with respect to the lower hindlimbs and their position at mid-stance, to achieve the same mode of locomotion.

The ankle extensor total muscle mass scales with body mass with a hyperallometric exponent of 1.18 among the macropods, primarily to accommodate the increasing total muscle PCSA, which also scales with a hyperallometric exponent of 0.87. The hyperallometry of total muscle PCSA presumably translates to hyperallometry of peak muscle force, which may act in partnership with the hyperallometry of the mean weighted muscle moment arm, to oppose the larger gravitational forces experienced by larger individuals (McGowan *et al*., 2008). The springhare's total muscle mass of 41.1 g is 40% larger than predicted for a macropod of the same body mass (Figure 4a) due to the contribution of a SOL muscle, as well as the GAS and PL muscle masses being somewhat larger than predicted, but nonetheless falling within the macropods' 95% prediction bands (Supporting Information Figure S2). The springhare's total muscle PCSA of 22.9 cm^2 is only 20% greater than predicted for a macropod of the same body mass (Figure 4b), despite the contribution of the SOL, because the other muscles have PCSAs quite similar to that predicted for a macropod of similar body size (Supporting Information Figure S3). The springhare's total muscle mass is 40% larger than predicted, whereas its total muscle PCSA is only 20% greater than predicted, reflecting modest differences in the springhare's fascicle length and pennation angle compared with macropod predictions. Our measure of total muscle PCSA is informative because it largely determines the muscle's capacity to generate force. Hence, the similarity of total muscle PCSA indicates that springhares can produce peak muscle forces that are comparable to those predicted by a macropod of similar body mass. The way these forces are transmitted from the muscle to the skeleton, however, depends in large part on the morphology of their adjoining tendons.

The ankle extensor total tendon CSA scales with body mass with a near-isometric exponent of 0.64 among the macropods. Because the specific mechanical properties of tendons are fairly uniform among mammals (Bennett *et al*., 1986; Pollock and Shadwick, 1994b), adaptations of tendon CSA (i.e. tendon thickness) and variation in tendon length largely determine the amount of strain energy stored and released by elastic recoil under a given muscle load during locomotion. Due to their geometric scaling, the ankle extensor tendons of larger macropods are relatively thin

compared with the PCSA of the adjoining muscles. Muscle forces therefore are concentrated over a relatively smaller tendon area, increasing stress and augmenting the tendon's capacity to store and release strain energy. Indeed, this likely helps to explain the uncoupling of metabolic rate from travel speed in large wallabies and kangaroos (Biewener and Baudinette, 1995). By comparison, the ankle extensor tendons of smaller macropods are relatively thick compared with muscle PCSA, resulting in lower stress and reduced capacity for strain energy recovery. As has been shown for yellow-footed rock wallabies (McGowan *et al*., 2005), relatively thicker tendons are less compliant and, by stretching less under a given force, facilitate the rapid and accelerative movements of rat kangaroos and other small hoppers, similar to North American kangaroo rats (Biewener *et al*., 1981).

The 3-kg springhare is within the intermediate body mass range of bipedal hoppers where it is hypothesized that a transition may occur from relatively thick tendons that assist with acceleration, to relatively thin tendons that facilitate energy savings (Baudinette, 1994). We found that the springhare's total tendon CSA of 0.26 cm^2 is approximately 50% greater than predicted for a macropod of the same body mass and falls outside the macropods' 95% prediction bands (Figure 4c). This is primarily because the PL tendon is disproportionately thick compared with that of a similar-sized macropod (Figure 4c inset). In fact, the springhare PL tendon CSA of 0.084 cm^2 is approximately 80% greater than predicted (Supporting Information Figure S4). In theory, the thick PL tendon should transmit forces more rapidly from the muscle to the tendon's skeletal attachment points, favoring speed and acceleration performance. The ability to engage in rapid locomotion may assist the springhare to outpace and outmaneuver predators (e.g. birds of prey, canine and feline predators), particularly at night, when it is foraging aboveground. For instance, springhares in the southern Kalahari are frequently targeted by cheetahs. However, a successful hunt rate of only ~20% was the lowest from a total of 15 recorded prey species and 989 hunting interactions, and has been attributed to the springhare's ricochetal hopping enabling sudden and sharp turns, as well as the proximity of burrows for escape (Mills and Mills, 2017). The disproportionately thick PL tendon of springhares may also be an adaptation to assist with burrow excavation in these semi-fossorial animals. Although the long-clawed forelimbs are used for digging, the hindlimbs are also used for kicking clear the excavated soil (Butynski and Mattingly, 1979). Conceivably, this task might require reasonably high forces transmitted along relatively stiff tendons.

The mismatch in the scaling of the ankle extensor total muscle PCSA (exponent of 0.87) and total tendon CSA (exponent of 0.64) among macropods indicates that peak tendon stresses are expected to increase with body mass, scaling with an exponent of 0.21, such that mean tendon safety factors decrease with body mass, scaling with an exponent of −0.22. It is inevitable, therefore, that larger macropods are at greater risk of tendon rupture due to reduced safety margins, especially as forces increase during fast hopping locomotion (Biewener and Bertram, 1991). Indeed, the increased likelihood of ankle extensor tendon rupture has been argued to impose an upper body mass limit of approximately 140–160 kg among hopping macropods (McGowan *et al*., 2008; Snelling *et al*., 2017). The tradeoff benefit for operating tendons closer to failure during locomotion is that the high stresses provide increased strain energy storage and recovery, reducing the metabolic cost of locomotion. Thus, the ankle extensor total strain energy return capacity increases with body mass among macropods with a steep exponent of 1.56, affording energy savings of approximately 50% (vs. muscle work) during hopping locomotion in larger wallabies and kangaroos (Biewener *et al*., 1998).

Our findings indicate that the springhare's mean peak tendon stress estimate of 26.2 MPa and mean tendon safety factor of 4.7 are approximately 30% lower and 30% higher, respectively, than predicted for a macropod of the same body mass, yet within the macropods' 95% prediction bands (Figure 5a,b). Once again, it is primarily the springhare's disproportionately thick PL tendon, with estimates of a relatively low peak stress and a high safety factor, that influence these relationships (Supporting Information Figures S5 and S6). The springhare's total tendon strain energy return capacity of 1.81 J is almost exactly as expected for a macropod of equivalent body mass (Figure 5c), and indeed the springhare's individual tendon strain energy return capacities are all very similar to predictions (Supporting Information Figure S7). Apparently, even the springhare PL tendon retains a reasonable capacity to store and return elastic strain energy, because although its relatively large CSA reduces stress, tendon CSA and length increase tendon volume, providing more material to store strain energy. Thus, the springhare's total tendon strain energy return capacity is as predicted for a macropod of similar body mass, but is nonetheless modest when compared with that of larger macropods. Consistent with prior metabolic measurements of springhares showing no evidence of the energy–speed uncoupling observed in larger wallabies and kangaroos (Thompson *et al*., 1980), our results here further indicate that energy savings during hopping locomotion is likely not a strong selective pressure in this species. This view is further reinforced by the observation that springhares normally do not travel far while foraging (Peinke and Brown, 2005), whereas larger macropods can cover vast distances, economically, across the Australian Outback in search of sparsely distributed food and water sources (Dawson, 2012).

In summary, our analysis of the functional morphology of the ankle extensor MTUs in the springhare reveals generally remarkable agreement with that of similar-sized macropods, despite the two groups independently evolving bipedal hopping locomotion. We observed close agreement with regard to the ankle extensor muscle moment arms, estimated ground reaction force external moment arm, and effective mechanical advantage at the ankle joint, indicating that the springhare shares similar mid-stance hopping mechanics with an equivalent-sized macropod. Likewise, the springhare's GAS and FDL muscle-tendon units have very similar muscle PCSAs, tendon CSAs, peak tendon stresses, safety factors, and strain energy return capacities compared with an equivalent-sized macropod. However, we found that although the

springhare's PL muscle PCSA is reasonably similar to macropod predictions, its PL tendon CSA greatly exceeds that predicted for a macropod of similar body size. We posit that the relatively overbuilt PL tendon may have evolved to assist in translating forces more rapidly from the muscle to the skeletal attachment points, facilitating fast and accelerative hopping, likely to be advantageous in predator-dense habitats.

ACKNOWLEDGEMENTS

The authors acknowledge the humane method of the management culls and we thank the marksman for allowing access to carcasses. We thank Craig White from Monash University for his assistance with the phylogenetically informed analyses, Channen Long from the University of Pretoria for her advice on R, Amy Cheu of basiliskos.com for the springhare illustration in Figure 1, and Roger Seymour at Adelaide University for his comments on an earlier draft of the manuscript. This research was supported by a South African Claude Leon Foundation Postdoctoral Fellowship to E.P.S. and a University of the Witwatersrand FRC Individual Grant to E.P.S. and A.F.

CONFLICT OF INTEREST

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

All authors contributed significantly to the study.

DATA AVAILABILITY STATEMENT

Data available at ResearchGate (www.researchgate.net/profile/Edward_Snelling).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Veiga GN, Biewener AA, Fuller A, et al. Functional morphology of the ankle extensor muscle-tendon units in the springhare *Pedetes capensis* shows convergent evolution with macropods for bipedal hopping locomotion. *J. Anat.* 2020;237:568–578. https://doi.org/10.1111/joa.13214