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RESEARCH ARTICLE

Elastic energy storage across speeds during steady-state hopping of desert kangaroo rats (*Dipodomys deserti*)

Brooke A. Christensen[1,2,*], David C. Lin[3,4,5], M. Janneke Schwaner[1,2] and Craig P. McGowan[1,5,6]

ABSTRACT

Small bipedal hoppers, including kangaroo rats, are not thought to benefit from substantial elastic energy storage and return during hopping. However, recent species-specific material properties research suggests that, despite relative thickness, the ankle extensor tendons of these small hoppers are considerably more compliant than had been assumed. With faster locomotor speeds demanding higher forces, a lower tendon stiffness suggests greater tendon deformation and thus a greater potential for elastic energy storage and return with increasing speed. Using the elastic modulus values specific to kangaroo rat tendons, we sought to determine how much elastic energy is stored and returned during hopping across a range of speeds. *In vivo* techniques were used to record tendon force in the ankle extensors during steady-speed hopping. Our data support the hypothesis that the ankle extensor tendons of kangaroo rats store and return elastic energy in relation to hopping speed, storing more at faster speeds. Despite storing comparatively less elastic energy than larger hoppers, this relationship between speed and energy storage offers novel evidence of a functionally similar energy storage mechanism, operating irrespective of body size or tendon thickness, across the distal muscle–tendon units of both small and large bipedal hoppers.

KEY WORDS: Strain energy, Bipedal hopping, Ankle extensor tendons, Elastic modulus

INTRODUCTION

Locomotion, while critical to the survival of terrestrial mammals, comes at an unavoidable, and often significant, energetic cost. To satisfy the demands of movement, animals must perform work to replace the energy lost to the environment. While positive work is contributed through active muscle contraction, overall work requirements can be reduced via energy storage and return mechanisms found in the spring-like elements of an animal's musculoskeletal system (Alexander, 1984). Elastic structures, such as tendons and ligaments, convert kinetic and potential energy during stance into recoverable strain energy (Cavagna et al., 1977). This capacity for elastic energy storage and recovery has been broadly investigated, with highly effective 'biological springs' present across a range of terrestrial mammals including horses (Biewener, 1998a,b), kangaroos (Alexander and Vernon, 1975) and humans (Ker et al., 1987). Despite body plan variation across the aforementioned taxa, there is support for a connection between morphology and energy storage capacity, with long, thin tendons being better suited for elastic energy storage for a given force when compared with shorter, thicker tendons (Biewener, 1997; Biewener and Roberts, 2000). Accordingly, the magnitude of strain energy stored in a tendon results from the tendon's stiffness and subsequent deformation as an external force is applied. Thus, while the specific mechanical demands of a locomotor task dictate the force that a tendon will experience during movement, the magnitude of elastic energy stored and returned is ultimately a reflection of the tendon's material properties and overall geometry as these determine deformation (Ilton et al., 2018).

Several species of large bipedal hoppers boast incredibly efficient locomotion, in part due to specialized ankle extensor muscle–tendon units (MTUs), which have a large capacity to store and return elastic energy (Alexander and Vernon, 1975; Cavagna et al., 1977; Griffiths, 1989; Bennett and Taylor, 1995; Kram and Dawson, 1998). Furthermore, oxygen consumption in both red kangaroos (*Osphranter rufus*) and tammar wallabies (*Macropus eugenii*) during steady-state hopping is independent of speed unlike all other terrestrial mammals, which increase oxygen consumption with increasing speed (Dawson and Taylor, 1973; Baudinette et al., 1992; Kram and Dawson, 1998). These two observations provided indirect support for the functional role of elastic structures for determining the cost of transport for these animals (Alexander and Vernon, 1975; Biewener and Baudinette, 1995; Biewener et al., 1998; Baudinette and Biewener, 1998). In contrast to large bipedal hoppers, smaller bipedal hoppers, such as kangaroo rats, are not thought to benefit from comparable elastic energy storage and return (Thompson et al., 1980; Biewener et al., 1981; Biewener and Blickhan, 1988; Moore et al., 2017a). They are also not thought to store elastic energy in the same speed-dependent manner as kangaroos and wallabies (Biewener et al., 1981). Specifically, while these animals regularly perform complex locomotor behaviors, such as jumping vertically over 10-times standing hip height (Biewener and Blickhan, 1988), their comparatively thick tendons have been credited with the inability to exploit energetic benefits analogous to larger hoppers (Biewener et al., 1981; Biewener and Blickhan, 1988). Under the rationale of a greater area eliciting reduced stress for a given force, Biewener and Bertram (1991) supported this supposition by delineating a connection between the large hindlimbs of kangaroo rats and the requirement of an elevated safety factor to tolerate the large forces generated for rapid acceleration during predator evasion.

Although erratic, high-powered jumps undoubtedly remain key to survival for small hoppers such as kangaroo rats (Moore et al., 2017b; McGowan and Collins, 2018), recent material properties

[1]Department of Biological Sciences, University of Idaho, Moscow, ID 83844, USA. [2]Department of Ecology and Evolutionary Biology, University of California, Irvine, Irvine, CA 92697, USA. [3]Voiland School of Chemical Engineering and Bioengineering, Washington State University, Pullman, WA 99164, USA. [4]Department of Integrative Physiology and Neuroscience, Washington State University, Pullman, WA 99164, USA. [5]Washington Center for Muscle Biology, Washington State University, Pullman, WA 99164, USA. [6]Keck School of Medicine of the University of Southern California, Los Angeles, CA 90033, USA.

*Author for correspondence (brookec1@uci.edu)

B.A.C., 0000-0003-1347-6115; M.J.S., 0000-0002-1666-3111

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Received 28 May 2021; Accepted 30 December 2021

Journal of Experimental Biology (2022) 225, jeb242954. doi:10.1242/jeb.242954

research has raised questions regarding the interpretation of previous data underlying the rationale for why kangaroo rats cannot significantly store and utilize elastic energy. Previously, to calculate strain energy storage, studies have relied on a generic elastic modulus value of 1 GPa (Alexander and Vernon, 1975; Biewener et al., 1981; Schwaner et al., 2018), an assumed constant across mammalian tendons (Ker, 1981; Bennett et al., 1986; Shadwick, 1990; Pollock and Shadwick, 1994). However, recently, Javidi et al. (2019a) revealed the ankle extensor tendons of desert kangaroo rats (*Dipodomys deserti*) to be considerably less stiff than originally thought, with elastic moduli values falling close to half the original 1 GPa assumption. In fact, several studies have shown elastic moduli values across other rodent species to be consistently and considerably lower than 1 GPa (Huang et al., 2003; Lavagnino et al., 2005; Legerlotz et al., 2007; LaCroix et al., 2013; Javidi et al., 2019a). Thus, while kangaroo rats do have relatively thicker tendons than larger bipedal hoppers (Biewener et al., 1981; Biewener and Blickhan, 1988), their tendons are considerably more compliant than had been assumed. Under the assumption of uniform loading, a decreased elastic modulus for these animals implies greater tendon deformation and thus increased potential for elastic energy storage and recovery via tendon recoil (Alexander, 1984). For instance, for a single jumping task, a recalculation of elastic energy return based on these species-specific values for elastic modulus resulted in almost 2.5 times more energy recovery than originally calculated (Schwaner et al., 2021). Moreover, because the force experienced by a tendon during locomotion is a result of force generation by the muscle (Roberts, 2016), the higher forces demanded by faster locomotor speeds elicit greater tendon deformation (Roberts and Azizi, 2011; Farris and Sawicki, 2012; Lai et al., 2014) and, consequently, a greater capacity for strain energy storage and return.

Our objective was to determine how much elastic energy is stored during hopping from estimates using direct force measurements and elastic modulus values specific to kangaroo rat tendons. Further, we hypothesize that elastic energy storage and return by the ankle extensor tendons of kangaroo rats will increase with hopping speed. To test this hypothesis, we recorded direct *in vivo* measurements of tendon force in the main distal MTUs of kangaroo rats – the plantaris longus (PL) and the gastrocnemii (GAS) – as animals hopped at a steady state across a range of speeds.

MATERIALS AND METHODS

Animals and training

Five adult desert kangaroo rats (*Dipodomys deserti* Stephens 1887; mean±s.e.m. body mass=111±9.4 g) were used in these experiments. Animals were wild caught in the Mojave Desert of southeast Nevada (USA) under permits from the Nevada Department of Wildlife and the Bureau of Land Management. Animals were trained over several weeks to hop on an enclosed, motorized treadmill at speeds of 1.3, 1.5, 1.7 and 1.9 m s^{-1}; selected speeds represent the full range of speeds at which these animals will hop steadily on a treadmill in a laboratory environment. The presence of a researcher's hand at the rear of the treadmill exploited the animals' natural escape behavior to encourage forward, steady-state hopping during training sessions. All experimental and animal husbandry protocols were approved by the University of Idaho Institutional Animal Care and Use Committee prior to the study.

Experimental design

In vivo equipment

For *in vivo* force recordings, a small strain gauge (Micro-Measurements Inc., Raleigh, NC, USA) was bonded to a custom-made E-shaped stainless-steel tendon buckle and surgically implanted on the animals' ankle extensor tendons (Fig. 1). Tendon buckle force transducer design and methodology used in this study were modeled after previously established techniques (Walmsley et al., 1978; Loeb et al., 1985), a detailed description of which can be found in Biewener (1992). In desert kangaroo rats, the ankle extensor tendons consist of two distinct MTUs. The GAS tendon attaches to the lateral gastrocnemius (LG) and medial gastrocnemius (MG) muscles; the PL tendon attaches to the PL muscle. Although the two are anatomically separate tendons enclosed in a common sheath, both the GAS and PL tendons share an attachment point on the calcaneus and possess uniform anatomical actions (Rankin et al., 2018; Javidi et al., 2019b). Owing to size limitations, the sheath was left intact, the two tendons were treated as one structure, and a single buckle was implanted onto both.

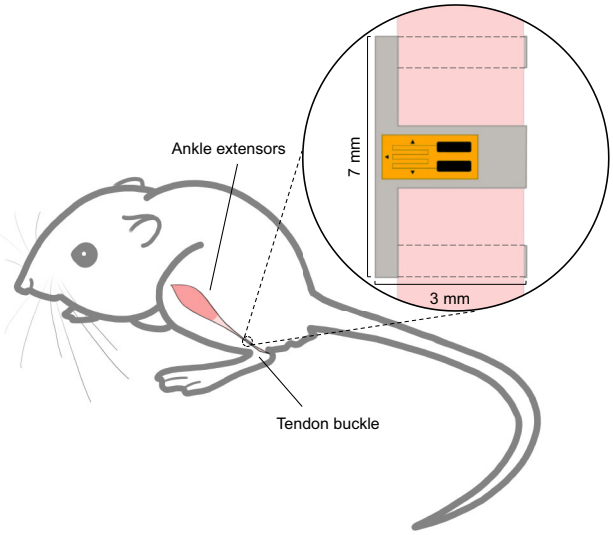

Fig. 1. Schematic drawing of *Dipodomys deserti* showing tendon buckle force transducer design and *in vivo* placement on the ankle extensor tendons [gastrocnemius (GAS)+plantaris (PL)].

Surgical procedures

Animals were placed into an induction chamber connected to an isoflurane vaporizer and anesthetized at 3%. After induction, animals were fitted with a respiratory mask and maintained at 1–2% isoflurane for the duration of the procedure. Electric clippers were used to shave the surgical field (top of head and left hindlimb). Shaved areas were sanitized with alcohol and an antiseptic solution; aseptic techniques were used for the entirety of the procedure. Incision locations were determined by morphological indicators and manual palpation. An initial incision was made parallel to the ankle extensor tendons. A second incision was made at the rear base of the animal's skull. The tendon buckle, previously soldered to a custom-made micro-connector plug, was inserted into the incision at the base of skull and subcutaneously guided to the lower incision. The buckle was carefully slid onto the tendons, appropriate positioning and signal output of the buckle was confirmed, and the incision was closed with 3-0 suture. The micro-connector plug was attached to the top of the animal's head with cyanoacrylate adhesive and 3-0 suture. Animals were administered an analgesic (meloxicam SR; 4 mg kg^{-1} body mass) and allowed a 24-h recovery period with unrestricted food access.

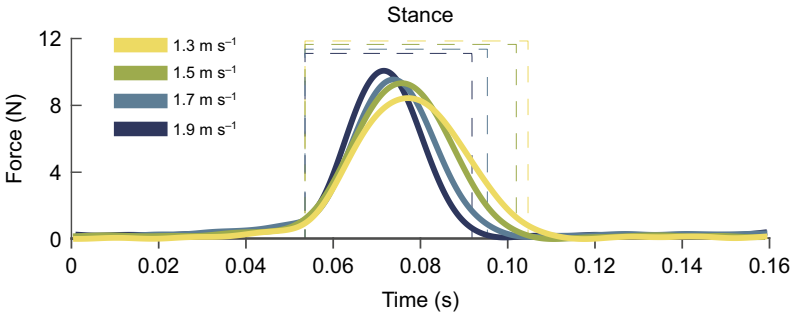

Fig. 2. Average force recordings from the ankle extensor tendons (GAS+PL) across individuals (*N*=5) of *D. deserti*. Data represents mean force for a single stride across four hopping speeds. Stance phase per speed condition is indicated with dashed lines. Standard deviations are omitted for visual clarity.

Data collection

Following recovery, non-toxic white paint and black permanent marker were used to draw high-contrast markers on the animal's skin over the following joint centers of rotation: metatarsophalangeal (MTP), ankle, knee and hip. For *in vivo* data acquisition, a lightweight shielded cable was attached from the micro-connector plug on the animal's head to recording equipment located adjacent to the experimental set-up. Animals were placed onto a plexiglass-enclosed, motorized treadmill and baseline *in vivo* data were collected while animals sat still and inactive on the treadmill. Using the presence of a researcher's hand towards the rear of the treadmill, animals were encouraged to hop at a steady-state while the treadmill was set to run at each of the four predetermined speeds. A high-speed video camera (Xcitex Inc., Woburn, MA, USA) collected video data at 500 Hz from a sagittal view. Buckle data were processed through a bridge amplifier (Micro-Measurements, Raleigh, NC, USA); data were sampled at 4000 Hz and collected with a PowerLab A/D board and LabChart software (ADInstruments Inc., Colorado Springs, CO, USA). An external pulse trigger was manually operated by a researcher throughout data collection for *post hoc* synchronization of video and analog data. Representative data are shown in Fig. 2. Following *in vivo* data collection, appropriate tendon buckle placement was confirmed via dissection and the transducer was calibrated using established methods (Biewener, 1992). *In vivo* equipment was removed, and a variety of morphological measurements were recorded. Length measurements (LG, MG, PL: muscle length, fascicle length; GAS tendon length; PL tendon length; femur length; tibia length; metatarsal length; toe length; knee moment arm, ankle moment arm) were collected via digital calipers to a resolution of 0.01 mm. Mass measurements (LG, MG, PL: muscle mass; GAS tendon mass; PL tendon mass) were collected via an electronic balance to a resolution of 0.001 g.

Data analysis

Kinematics

Trials, containing five hops each, were selected for analysis based on *in vivo* signal quality, as well as locomotor performance in the form of consecutive, fully bipedal hops. For each individual animal, two trials were analyzed at each of the four speeds, resulting in eight total trials per animal. Trials were processed on an individual basis to calculate the mean values for an individual animal at each speed. For each trial, foot-on and foot-off times were manually collected from the video data using ProAnalyst software (Xcitex). These times were used to determine gait parameters including stride frequency (Hz), ground contact time (s) and duty factor (fraction of hop cycle on the ground). For joint kinematic analysis, high-contrast joint markers in the video data were digitized via DeepLabCut open-source software (Mathis et al., 2018) to obtain 2D coordinate data for the MTP, ankle, knee and hip joints. Coordinate data were filtered with a fourth-order low-pass Butterworth filter with a cut-off frequency of 30 Hz and used to calculate joint angle changes for the ankle and knee. To allow comparison across speeds and individual animals, kinematics time scales were normalized to cycle time. Data analysis was performed in MATLAB using a custom-written analysis script (2018b, MathWorks, Natick, MA, USA).

Tendon stress, tendon elastic strain energy and percent energy recovery

Tendon cross-sectional area (CSA_t) and tendon volume (V_t) were calculated independently for the GAS and PL tendons (see Table 1). CSA_t was calculated from tendon length, tendon mass, and an assumed tendon density of 0.00112 g mm^{-3} (Ker, 1981). V_t was calculated via CSA_t and effective tendon length (L_{eff}) (V_t=CSA_t×L_{eff}) (Alexander and Vernon, 1975; Biewener and and Baudinette, 1995). Effective tendon length, representing the length of tendon that undergoes strain, was determined by subtracting muscle fiber length (L_{fiber}) from the product of MTU length (L_{MTU}) multiplied by the cosine of the mean fiber pennation angle (L_{eff}=L_{MTU}–L_{fiber}×cosθ). Tendon stress (σ_t) was also determined independently for the two tendons using CSA_t and force (F) recordings from the buckle transducer (σ_t=F/CSA_t). Because the transducer recorded total force acting across both tendons, we partitioned force for the GAS and PL tendons by their relative muscle physiological cross-sectional areas (PCSAs) (lateral and medial gastrocnemius for the GAS tendon; plantaris longus for the PL tendon); see Discussion for further details. Individual muscle PCSA was calculated as:

$$\mathrm{PCSA} = (m \times \cos\theta)/(\rho_m \times L_{fiber}), \quad (1)$$

Table 1. Morphological data used to partition force and calculate tendon stress and tendon elastic energy storage

	Gastrocnemius (GAS)			Plantaris (PL)		
Animal	Tendon CSA (mm^2)	Tendon volume (mm^3)	Muscle PCSA (mm^2)	Tendon CSA (mm^2)	Tendon volume (mm^3)	Muscle PCSA (mm^2)
1	0.98	37.31	151.84	0.37	12.00	66.49
2	1.33	50.01	131.80	0.37	14.31	81.91
3	1.55	53.62	189.68	0.54	17.94	63.52
4	1.19	44.38	120.08	0.49	15.37	39.26
5	1.22	48.01	152.71	0.70	25.30	58.16

CSA, cross-sectional area; PCSA, physiological cross-sectional area.

Journal of Experimental Biology (2022) 225, jeb242954. doi:10.1242/jeb.242954

where m is muscle mass, L_{fiber} is muscle fiber length, θ is muscle fiber pennation angle, and skeletal muscle density (ρ_m) is assumed to be 0.001056 g mm^{-3} (Mendez and Keys, 1960).

After determining muscle PCSA-weighted force contributions, we calculated peak tendon stresses for each tendon. We continued to treat the GAS and PL tendons as independent units for the subsequent strain energy return calculations. Elastic strain energy return was estimated according to the following equation:

$$U = 0.5\left(\frac{\sigma_t^2}{E}\right)V_t \times 0.93, \quad (2)$$

where U represents the strain energy returned for a single tendon, σ_t represents tendon stress, E represents tendon elastic modulus and V_t represents tendon volume. Tendon hysteresis, which assumes a 7% energy recovery loss, is represented by the 0.93 constant (Bennett et al., 1986; Shadwick, 1990; Biewener et al., 1998). Based on the results of our recent study, the GAS and PL tendons of *D. deserti* had elastic modulus values of 330 and 528 MPa, respectively (Javidi et al., 2019a). These unique elastic moduli were used to calculate strain energy return independently for the two ankle extensor tendons. Resulting energy return values were then summed to represent total strain energy return (mJ) for the combined MTU for one leg.

To determine the contribution of elastic energy return to overall cost of locomotion for these animals, we calculated relative energy recovery as a percentage. Percent recovery, after normalizing for body mass and cycle time, was calculated as strain energy returned per hop divided by total energy cost per hop, multiplied by 100 [% recovery=100×($E_{returned}/E_{cost}$)]. Energy cost per hop was estimated via mechanical power requirements for kangaroo rats previously published by our laboratory in Gutmann et al. (2013):

$$P = 0.656v + 0.649, \quad (3)$$

where P represents mechanical power (W kg^{-1}) and v represents forward velocity (m s^{-1}).

Statistics

Statistical tests were performed using R statistical software 3.3.2 (R Core Team, The R Foundation for Statistical Computing, Vienna, Austria). To test for differences in our dependent variables across hopping speeds, we used linear mixed-effects modeling (via the R package lme4; Bates et al., 2015) with hopping speed assigned to fixed effect and individual to random effect. Dependent variables included in the model were tendon strain energy return, peak tendon force, peak tendon stress, stride frequency, ground contact time, duty factor, peak ankle flexion, peak ankle extension and peak knee flexion (Table 2). *Post hoc* pairwise comparisons between speed conditions were then performed with a Holm–Bonferroni P-value correction. For all tests, statistical significance was assessed based on a P-value of ≤0.05. To use as a representation of pooled data, measurements were averaged per animal to obtain a single value for each variable at each of the four speeds. All values are reported as means±s.d., unless otherwise indicated.

RESULTS

Gait parameters and joint kinematics

Gait parameters per condition are shown in Table 2. Stride frequency was independent of speed (P=0.2578). Duty factor decreased as hopping speed increased (P=0.0022). There was a significant relationship between ground contact time and hopping speed, with stance phase decreasing as speed increased (P=0.0001). Angle changes for both the ankle and knee displayed statistically uniform patterns across speed conditions (Fig. 3). During stance phase, the ankle joint flexed then extended (Fig. 3, top). Average peak flexion and average peak extension at the ankle joint were consistent across conditions (P=0.1124, P=0.1374). During stance phase, the knee joint primarily underwent flexion followed by a brief period of extension directly prior to take-off (Fig. 3, bottom). Average peak flexion at the knee joint during hopping was independent of speed (P=0.5916).

Tendon force, stress, elastic strain energy, and percent recovery

As hopping speed increased, peak forces recorded from the ankle extensor tendons also increased, on average, from 8.16±1.67 N at 1.3 m s^{-1} to 10.19±2.20 N at 1.9 m s^{-1} (N=5; Table 2). The relationship between peak forces and hopping speed was significant (P=0.0002). Data illustrating this pattern are shown in Fig. 2. Also shown in Fig. 2 is the relationship between hopping speed, ground contact time and tendon force. As hopping speed increased, ground contact time decreased and peak force increased. Consequently, peak tendon stress, shown in Table 2 as an average for the GAS and PL tendons across all animals in the study, significantly increased with hopping speed (P=0.0002). Across all animals, elastic strain energy return from the ankle extensor

Table 2. Tendon, kinematic and gait parameters during level hopping

	Speed (m s^{-1})					
	1.3	1.5	1.7	1.9	*N*	*P*
GAS+PL tendon						
Peak force (N)	8.16±1.67	9.35±1.55	9.59±1.72	10.19±2.20	5	*
Peak stress (MPa)	4.91±1.13	5.65±1.28	5.84±1.62	6.50±1.79	5	*
Energy return (mJ)	3.79±1.57	4.91±1.56	5.28±2.17	6.40±2.71	5	*
Energy recovery (%)	15.68±7.50	18.67±6.65	19.20±8.56	20.74±8.65	5	*
Joint kinematics						
Peak ankle flexion	98.28±1.69	97.92±3.14	97.53±2.44	100.76±1.82	5	
Peak ankle extension	112.75±4.13	111.08±3.38	112.64±3.21	115.02±3.74	5	
Peak knee flexion	71.09±3.74	72.80±4.15	70.58±3.83	72.02±4.33	5	
Gait parameters						
Stride frequency (Hz)	6.69±0.470	6.78±0.480	6.92±0.423	6.93±0.374	5	
Ground contact time (s)	0.062±0.009	0.058±0.006	0.054±0.004	0.051±0.007	5	*
Duty factor (fraction of hop cycle on the ground)	0.41±0.046	0.39±0.038	0.37±0.041	0.35±0.061	5	*

Values are means±s.d. *P≤0.05.

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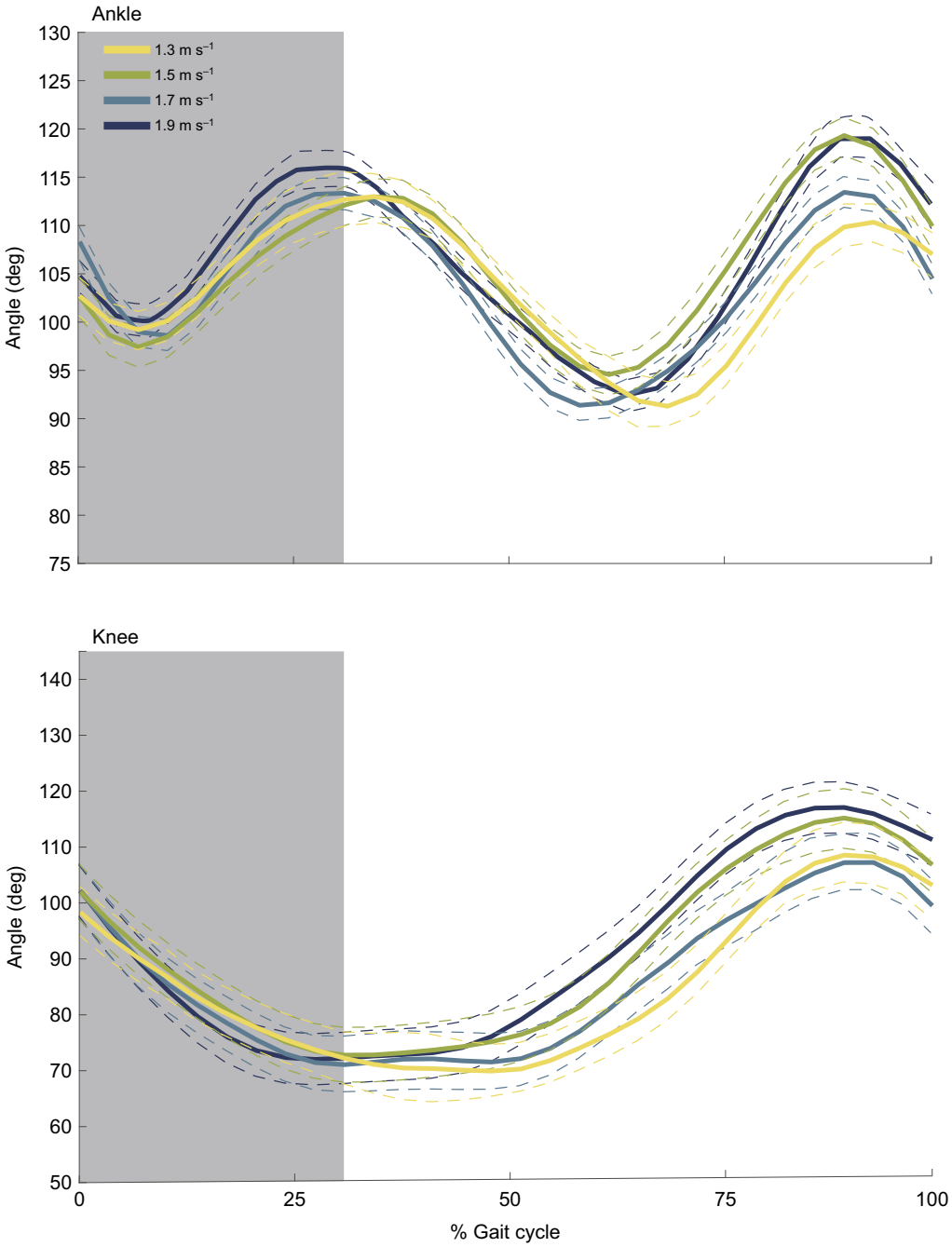

Fig. 3. Average ankle (top) and knee (bottom) joint angle changes versus time (shown as percentage of gait cycle) for a single stride across hopping speeds in *D. deserti*. Data represents means across individuals (*N*=5). Standard deviations are indicated via dashed lines. Grey area indicates average stance phase duration.

tendons increased significantly with hopping speed (P=0.0003; Table 2, Fig. 4). Under the assumption of hindlimb symmetry, strain energy values reported in Table 2 and Fig. 4 represent summed energy return for the ankle extensor tendons of both legs (N=5). Percent energy recovery increased with hopping speed, ranging from approximately 16% at 1.3 m s^{-1} to 21% at 1.9 m s^{-1} (P=0.0166; Fig. 4).

DISCUSSION

Our data support the hypothesis that the ankle extensor tendons of kangaroo rats store and return greater levels of elastic energy at faster hopping speeds. With a 50% increase in hopping speed (1.3 to 1.9 m s^{-1}), strain energy return increased almost 70% (3.79 to 6.4 mJ). Our energy storage estimates indicate that the relationship between speed and elastic energy storage in these small hoppers aligns well with that of larger bipedal hoppers, though to a lesser magnitude (as detailed below).

Kinematics

Joint angle changes over the stance phase remained consistent across conditions for both the ankle and knee joints, with patterns of knee flexion during hopping mirroring those of ankle flexion. Ground contact time decreased with increased hopping speed (Table 2). When comparing between the slowest (1.3 m s^{-1}) and fastest (1.9 m s^{-1}) speed trials shown in representative data (Fig. 2), a 46% increase in hopping speed elicited an approximately 20 ms decrease in ground contact time, while force increased by almost 40%. The consistency of stride frequency across hopping speeds aligns with what has been shown previously for both large and small bipedal hoppers (McGowan and Collins, 2018).

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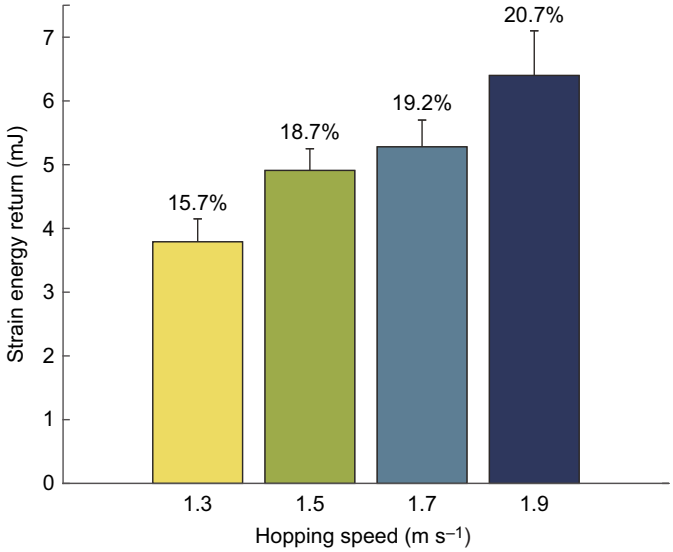

Fig. 4. Histogram of strain energy return via the ankle extensor tendons (GAS+PL) of *D. deserti* (*N*=5) as a function of hopping speed, with average estimated percent energy recovery listed above each condition. Values (means±s.e.m.) represent summed energy return for the ankle extensor tendons of both legs.

Elastic energy storage

We found that elastic energy recovery increases with hopping speed, likely playing a larger role during steady-state hopping of kangaroo rats than previously indicated. Based on published data (Gutmann et al., 2013), and after normalizing for body mass and cycle time, we calculated average percentage recovery during hopping to range from 16% at 1.3 m s^{-1} to 21% at 1.9 m s^{-1}. With increased hopping speed, tendon stress, strain energy storage and percentage energy recovery all correspondingly increased. In a comparable study of kangaroo rats, no relationship was found between hopping speed and percentage energy recovery (Biewener et al., 1981). In that study, under the assumption of equal force contributions by the PL and GAS muscles, the authors estimated that an average 14% energy is recovered via the ankle extensor tendons during hopping across a speed range of 0.9 to 3.1 m s^{-1}. These calculations relied on an assumed elastic modulus of 1.2 GN m^{-2} and did not account for tendon hysteresis. At our slowest hopping speed, our data suggest that strain energy storage in the ankle extensor tendons accounts for similar percentage energy recovery as that indicated by Biewener and colleagues. In contrast, we found a significant relationship between hopping speed and percentage energy recovery (Fig. 4). If we were to linearly extrapolate out the correlation seen in our data to the substantially higher speeds of 3.1 m s^{-1} tested by Biewener et al. (1981), we would predict these animals return almost twice the amount of elastic energy previously reported, recovering around 30% energy during hopping. Further, kangaroo rats have been observed hopping much faster in the wild, with recorded speeds up to 8.3 m s^{-1} (Djawdan and Garland, 1988). Faster hopping speeds, while currently unable to be replicated in a controlled, laboratory environment, would suggest greater peak tendon stresses and thus greater elastic energy return than described here.

A challenge of conducting a study on an animal of this size is the constraint of a single tendon buckle on both ankle extensor tendons. Because we were unable to determine exact fractional forces exerted by the GAS and PL tendon, we relied on muscle PCSA weighting to partition the force and subsequently calculate strain per individual tendon based on its specific elastic modulus value reported by Javidi et al. (2019a). Though commonly used, this method allows for potential inaccuracy as equal activation of the muscles must be assumed (Maas et al., 2004; Herzog, 2017). The LG, MG and PL muscles are short-fibered, pennate, ankle extensors (Rankin et al., 2018) composed primarily of fast-twitch muscle fiber types (Ross and Meyers, 2021). The muscles' similarities in anatomical action and fiber type composition may suggest further parallels in terms of force contribution during hopping. However, recent research has indicated PCSA alone may be inadequate for accurately partitioning force contribution of individual muscles across a functional group under some conditions (Javidi et al., 2020). That study, looking specifically at the ankle extensor muscles of kangaroo rats, showed that individual muscle force contribution is more strongly influenced by muscle state, such as fiber length, fiber pennation angle, and thus fiber shortening velocity, than solely muscle PCSA. Furthermore, the findings of Javidi et al. (2020) found that force contribution from the PL muscle could be smaller than that of the LG or MG despite larger PCSA depending on joint velocity. To accommodate for potential inaccuracies due to force partitioning techniques used in the current study, we conducted a local sensitivity analysis in which assumed GAS to PL ratios of force contribution spanned a range from total force contribution via the GAS tendon, to total force contribution via the PL tendon. Even at the extremes of GAS-only and PL-only force contribution ratios, both of which produced variation in average percent energy recovery across conditions (GAS only: 5–15% increase; PL only: 5–10% increase), results of the analysis broadly support the robustness of our primary conclusion that elastic energy return increases linearly with hopping speed (GAS only: P=0.0026; PL only: P=0.0018).

The connection between hopping faster and storing more strain energy is well evidenced for larger bipedal hoppers, such as kangaroos and wallabies, with the bulk of strain energy storage occurring in their hindlimb tendons (Alexander and Vernon, 1975; Biewener and Baudinette, 1995; Biewener et al., 1998). Although our data suggest that the distal MTUs of kangaroo rats function in a similar fashion to that of larger hoppers, the magnitude of elastic energy returned by their ankle extensor tendons is comparatively less. Tammar wallabies (*Macropus eugenii*) are capable of substantial elastic energy recovery, experiencing close to 45% metabolic savings owing to this energy storage during steady-state hopping at 6 m s^{-1} (Biewener and Baudinette, 1995; Biewener et al., 1998). Because of body size and speed differences, we used published data (Gutmann et al., 2013) to normalize by leg length and determine equivalent hopping speeds for *D. deserti* and *M. eugenii*. At a Froude number of 2.0, kangaroo rats hopping at 1.56 m s^{-1} move in a dynamically similar fashion to wallabies traveling at 3.50 m s^{-1}. When normalized for body mass, this equates to an approximate energy return of 0.04 J kg^{-1} for kangaroo rats compared with 0.30 J kg^{-1} for wallabies (Biewener et al., 1998), indicating that kangaroo rats return less elastic energy than wallabies when hopping at equal Froude numbers.

Effective elastic energy recovery in large macropodids, which has historically been credited, at least in part, with the unique decoupling of hopping speed and oxygen consumption, is not exclusive to these animals. Kangaroo rats do not store equivalent magnitudes of elastic energy, recovering around 21% of the cost of transport during hopping, whereas wallabies recover close to 45%. Although kangaroo rats do not exhibit the energetic decoupling mechanism mentioned above (Thompson et al., 1980), comparable magnitudes of elastic energy storage have been evidenced across a range of terrestrial species, including horses with 40% recovery

(Biewener, 1998b), humans with 35% recovery (Ker et al., 1987), camels with 45% recovery (Alexander et al., 1982) and turkeys with 60% recovery (Roberts et al., 1997). While more efficient strain energy storage is undoubtedly a contributing factor, the rivaling energy storing capabilities possessed by these species, paired with their lack of this uniquely specific metabolic benefit, suggest that tendon recoil cannot fully explain the decoupling of hopping speed and oxygen consumption in kangaroos and wallabies (Biewener et al., 1998). This discrepancy, while not a novel idea, does indicate that future research is needed to explore alternative explanations for why a wallaby with 45% energy recovery during hopping benefits from this mechanism, while a horse recovering up to 40% does not (Biewener, 1998b). One caveat of this interpretation is the multitude of ways in which one can estimate percent energy recovery. Depending on the assumptions implicit in the calculations, direct comparison of these values across studies should be approached with caution.

The disconnect between strain energy storage and apparent metabolic benefit implies that tendon compliance may be more linked to locomotor function, playing a role during hopping that is unrelated to a prioritization of strain energy storage via elastic recoil. Tendon compliance has additionally been shown to allow a decoupling mechanism in which muscle fascicles may shorten at a different velocity than that of the whole MTU (Roberts, 2002; Lichtwark and Wilson, 2005; Wakeling et al., 2011). This mechanism was recently shown to allow optimal muscle power output during jumping by kangaroo rats, permitting fascicles to contract at shortening velocities for optimal power generation with a longer duration (Schwaner et al., 2021). While playing a functional role during both hopping and jumping, evidence seems to suggest that the relatively compliant tendons of desert kangaroo rats may be more important in jumping than in hopping. When considering the selective pressures acting on these animals in their natural habitat, an ability to successfully evade predators, which is a direct reflection of jumping ability, has an arguably stronger influence on their musculoskeletal evolution than the pressure to increase foraging efficiency. Despite not typically traveling long distances, and thus lacking the underlying influence to prioritize anatomy suited for economy, it is important to consider what locomotor efficiency realistically means for small mammals such as these kangaroo rats. Energetically efficient locomotion may initially appear to be a priority for small mammals owing to their relatively elevated mass-specific cost of transport when compared with larger mammals (Taylor et al., 1970; Taylor, 1977). But, owing to the metabolic impacts of possessing a substantially higher surface area to body mass ratio than their larger counterparts, the resting energy requirements of a small mammal far surpass those of a large one. In this context, locomotor efficiency, and particularly locomotor efficiency as a result of elastic energy storage and return, may simply be less impactful for smaller mammals as the relative discrepancy between their cost to move and their cost of simply existing may fall short of that incurred by larger mammals.

Tendon material properties

A secondary motivation of the study was to examine the impact of using commonly assumed generic elastic modulus data for mammalian tendon (Ker, 1981; Bennett et al., 1986; Shadwick, 1990; Pollock and Shadwick, 1994) versus recent species-specific measurements of material properties for kangaroo rat ankle extensor tendons (Javidi et al., 2019a). Based on these new tendon modulus values, our data support the advantageous role of increased tendon compliance for elastic energy recovery, at least in our desert kangaroo rat model. Owing to variation in the tendon stiffnesses reported by Javidi et al. (2019a), we performed a sensitivity analysis to explore how using a range of tendon stiffnesses, rather than single mean values, would influence our energy storage results. When calculated across a range of elastic modulus values, derived from the standard deviations reported across individuals in Javidi et al. (2019a) (approximately ±100 MPa for the PL, ±50 MPa for the LG), strain energy return followed a similar pattern of increased energy return at faster hopping speeds. Likewise, energy return values calculated from the experimentally measured range of stiffnesses remained consistent with those determined in original calculations (P=0.0041). While statistically uniform, energy return did vary across tendon stiffnesses. For instance, the lowest (GAS: 280 MPa; PL: 428 MPa) moduli values elicited an average 1 to 2 mJ increase in energy return, while the highest stiffness values (GAS: 380 MPa; PL: 628 MPa) elicited an average decrease in energy return of 0.5 mJ across speed conditions.

While following this general pattern, the actual magnitude of strain energy being stored and recovered by these animals in their hindlimb tendons does not come close to that of the dynamically similar kangaroos and wallabies. Despite an initial assumption that the lower tendon modulus revealed by Javidi et al. (2019a) would primarily function to offset energy storage limitations inherent to possessing thick tendons in relation to body size, a morphological attribute that has been shown to decrease the capacity for energy storage and recovery during hopping (Biewener, 1997; Lichtwark and Wilson, 2006), our results suggest that an ideal tendon property has a stiffness that balances energy storage during hopping with optimal power generation during jumping. Additionally, owing to a lack of understanding of the mechanical role of elastin in tendons, a growing body of literature hints at large variations in tendon structure and material properties, especially in tendons with high functional demands such as the ankle extensors (Eekhoff et al., 2017, 2021). Going forward, to truly understand the species-level specificities generated by different tendon properties, our results broadly highlight the need to consider the diversity of mammalian tendon properties in future studies.

Conclusions

The ankle extensor tendons of kangaroo rats store and return elastic energy in relation to hopping speed, storing more at faster speeds. In spite of differences in body size and tendon thickness, our results support a common functional trend of similar elastic energy storage mechanisms across small and larger bipedal hoppers. Subsequently, we emphasize the influence of not only species-level variation in tendon material properties, but also the biological relevance of, and mechanical demands dictated by, specific locomotor tasks on strain energy storage capacity.

Acknowledgements

The authors would like to thank members of the McGowan and Lin laboratories for assistance with data collection, as well as the reviewers for their insightful and comprehensive comments.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: B.A.C., D.C.L., C.P.M.; Methodology: B.A.C., D.C.L., C.P.M.; Formal analysis: B.A.C., D.C.L., M.S., C.P.M.; Investigation: B.A.C., D.C.L., M.S., C.P.M.; Writing - original draft: B.A.C.; Writing - review & editing: B.A.C., D.C.L., M.S., C.P.M.; Visualization: B.A.C.; Supervision: C.P.M.; Funding acquisition: D.C.L., C.P.M.

Funding

This work was supported by National Science Foundation [NSF 1553550 to C.P.M.] and Army Research Office [ARO 66554-EG to D.C.L. and C.P.M.]. Open access funding provided by University of California, Irvine. Deposited in PMC for immediate release.

References

Alexander, R. M. (1984). Elastic energy stores in running vertebrates. *Amer. Zool.* **24.1**, 85-94. doi:10.1093/icb/24.1.85

Alexander, R. M. and Vernon, A. (1975). The mechanics of hopping by kangaroos (Macropodidae). *J. Zool. Lond.* **177**, 265-303. doi:10.1111/j.1469-7998.1975.tb05983.x

Alexander, R. M., Maloiy, G. M., Ker, R. F., Jayes, A. S. and Warui, C. N. (1982). The role of tendon elasticity in the locomotion of the camel (*Camelus dromedarius*). *J. Zool. Lond.* **198**, 293-331. doi:10.1111/j.1469-7998.1982.tb02077.x

Bates, D., Machler, M., Bolker, B. M. and Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Software.* **67**, 1. doi:10.18637/jss.v067.i01

Baudinette, R. V. and Biewener, A. A. (1998). Young wallabies get a free ride. *Nature* **395**, 653-654. doi:10.1038/27111

Baudinette, R. V., Snyder, G. K. and Frappell, P. B. (1992). Energetic cost of locomotion in the tammar wallaby. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **262**, R771-R778. doi:10.1152/ajpregu.1992.262.5.R771

Bennett, M. B. and Taylor, G. C. (1995). Scaling elastic strain energy in kangaroos and the benefits of being big. *Nature.* **378**, 56-59. doi:10.1038/378056a0

Bennett, M. B., Ker, R. F., Dimery, N. J. and Alexander, R. M. (1986). Mechanical properties of various mammalian tendons. *J. Zool.* **209**, 537-548. doi:10.1111/j.1469-7998.1986.tb03609.x

Biewener, A. A. (1992). *Biomechanics Structures and Systems: A Practical Approach*. Oxford: Oxford University Press.

Biewener, A. A. (1997). Effects of elastic energy storage on muscle work and efficiency. *J. Appl. Biomechanics.* **13**, 422-426. doi:10.1123/jab.13.4.422

Biewener, A. A. (1998a). Muscle function *in vivo*: a comparison of muscles used for elastic energy savings versus muscles used to generate mechanical power. *Am. Zool.* **38**, 703-717. doi:10.1093/icb/38.4.703

Biewener, A. A. (1998b). Muscle tendon stresses and elastic energy storage during locomotion in the horse. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* **120**, 73-87. doi:10.1016/S0305-0491(98)00024-8

Biewener, A. A. and Baudinette, R. V. (1995). *In vivo* muscle force and elastic energy storage during steady-speed hopping of tammar wallabies (*Macropus eugenii*). *J. Exp. Biol.* **198**, 1829-1841. doi:10.1242/jeb.198.9.1829

Biewener, A. A. and Bertram, J. E. A. (1991). Efficiency and optimization in the design of skeletal support systems. In *Efficiency and Economy in Animal Physiology* (ed. R.W. Blake), pp. 65-82. Cambridge: Cambridge University Press.

Biewener, A. A. and Blickhan, R. (1988). Kangaroo rat locomotion: design for elastic energy storage or acceleration? *J. Exp. Biol.* **140**, 243-255. doi:10.1242/jeb.140.1.243

Biewener, A. A. and Roberts, T. J. (2000). Muscle and tendon contributions to force, work, and elastic energy savings: a comparative perspective. *Exerc. Sport Sci. Rev.* **28**, 99-107.

Biewener, A. A., Alexander, R. M. and Heglund, N. C. (1981). Elastic energy storage in the hopping of kangaroo rats (*Dipodomys spectabilis*). *J. Zool. Lond.* **195**, 369-383. doi:10.1111/j.1469-7998.1981.tb03471.x

Biewener, A. A., Konieczynski, D. D. and Baudinette, R. V. (1998). *In vivo* muscle force–length behavior during steady-speed hopping in tammar wallabies. *J. Exp. Biol.* **201**, 1681-1694. doi:10.1242/jeb.201.11.1681

Cavagna, G. A., Heglund, N. C. and Taylor, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditures. *Am. J. Physiol.* **233**, R243-R261.

Dawson, T. J. and Taylor, R. C. (1973). Energetic cost of locomotion in kangaroos. *Nature* **246**, 313-314. doi:10.1038/246313a0

Djawdan, M. and Garland, T. J. (1988). Maximal running speeds of bipedal and quadrupedal rodents. *J. Mammal.* **69**, 765-772. doi:10.2307/1381631

Eekhoff, J. D., Fang, F., Kahan, L. G., Espinosa, G., Cocciolone, A. J., Wagenseil, J. E., Mecham, R. P. and Lake, S. P. (2017). Functionally distinct tendons from elastin haploinsufficient mice exhibit mild stiffening and tendon-specific structural alternation. *J. Biomech. Engin.* **139**, 111003. doi:10.1115/1.4037932

Eekhoff, J. D., Steenbock, H., Berke, I. M., Brinckmann, J., Yanagisawa, H., Wagenseil, J. E. and Lake, S. P. (2021). Dysregulated assembly of elastic fibers in fibulin-5 knockout mice results in a tendon-specific increase in elastic modulus. *J. Mech. Behav. Biomed. Materials.* **113**, 104134. doi:10.1016/j.jmbbm.2020.104134

Farris, D. J. and Sawicki, G. S. (2012). Human medial gastrocnemius force-velocity behavior shifts with locomotion speed and gait. *Proc. Natl. Acad. Sci. USA* **109**, 977-982. doi:10.1073/pnas.1107972109

Gutmann, A. K., Lee, D. V. and McGowan, C. P. (2013). Collision-based mechanics of bipedal hopping. *Biol. Letters.* **9**, 20130418. doi:10.1098/rsbl.2013.0418

Griffiths, R. I. (1989). The mechanics of the medial gastrocnemius muscle in the freely hopping wallaby (*Thylogale billardierii*). *J. Exp. Biol.* **147**, 439-456. doi:10.1242/jeb.147.1.439

Herzog, W. (2017). Skeletal muscle mechanics: questions, problems, and possible solutions. *J. Neuroeng. Rehabil.* **14**, 1-17. doi:10.1186/s12984-017-0310-6

Huang, T. F., Perry, S. M. and Soslowsky, L. J. (2003). The effect of overuse activity on Achilles tendon in an animal model: a biomechanical study. *Ann. Biomed. Eng.* **32**, 336-341. doi:10.1023/B:ABME.0000017537.26426.76

Ilton, M., Bhamla, M. S., Ma, X., Cox, S. M., Fitchett, L. L., Kim, Y., Koh, J., Krishnamurthy, D., Kuo, C.-Y. and Temel, F. Z. (2018). The principles of cascading power limits in small, fast biological and engineered systems. *Science.* **360**, eaao1082. doi:10.1126/science.aao1082

Javidi, M., McGowan, C. P., Shiele, N. R. and Lin, D. C. (2019a). Tendons from kangaroo rats are exceptionally strong and tough. *Sci. Rep.* **9**, 1-9. doi:10.1038/s41598-019-44671-9

Javidi, M., McGowan, C. P. and Lin, D. C. (2019b). The contributions of individual muscle-tendon units to the plantarflexor group force-length properties. *Ann. Biomed. Eng.* **47**, 2168-2177. doi:10.1007/s10439-019-02288-z

Javidi, M., McGowan, C. P. and Lin, D. C. (2020). Estimation of the force-velocity properties of individual muscles from measurement of the combined plantarflexor properties. *J. Exp. Biol.* **223**, jeb219980. doi:10.1242/jeb.219980

Ker, R. F. (1981). Dynamic tensile properties for the plantaris tendon of sheep (*Ovis aries*). *J. Exp. Biol.* **93**, 283-302. doi:10.1242/jeb.93.1.283

Ker, R. F., Bennett, M. B., Bibby, S. R., Kester, R. C. and Alexander, R. M. (1987). The spring in the arch of the human foot. *Nature* **325**, 147-149. doi:10.1038/325147a0

Kram, R. and Dawson, T. (1998). Energetics and biomechanics of locomotion by red kangaroos (*Macropus rufus*). *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* **120**, 41-49. doi:10.1016/S0305-0491(98)00022-4

LaCroix, A. S., Duenwald-Kuehl, S. E., Lakes, R. S. and Vanderby, R. J. (2013). Relationship between tendon stiffness and failure: a metanalysis. *J. Appl. Physiol.* **115**, 43-51. doi:10.1152/japplphysiol.01449.2012

Lai, A., Schache, A. G., Lin, Y. C. and Pandy, M. G. (2014). Tendon elastic strain energy in the human ankle plantar-flexors and its role with increased running speed. *J. Exp. Biol.* **217**, 3159-3168.

Lavagnino, M., Arnoczky, S. P., Frank, K. and Tian, T. (2005). Collagen fibril diameter distribution does not reflect changes in the mechanical properties of *in vitro* stress-deprived tendons. *J. Biomech.* **38**, 69-75. doi:10.1016/j.jbiomech.2004.03.035

Legerlotz, K., Schjerling, P., Langberg, H., Bruggemann, G. and Niehoff, A. (2007). The effect of running, strength, and vibration strength training on the mechanical, morphological, and biochemical properties of the Achilles tendon in rats. *J. Appl. Physiol.* **102**, 564-572. doi:10.1152/japplphysiol.00767.2006

Lichtwark, G. A. and Wilson, A. M. (2005). Effects of series elasticity and activation conditions on muscle power output and efficiency. *J. Exp. Biol.* **208**, 2845-2853. doi:10.1242/jeb.01710

Lichtwark, G. A. and Wilson, A. M. (2006). Interactions between the human gastrocnemius muscle and Achilles tendon during incline, level and decline locomotion. *J. Exp. Biol.* **209**, 4379-4388. doi:10.1242/jeb.02434

Loeb, G. E., Hoffer, J. A. and Pratt, C. A. (1985). Activity of spindle afferents from cat anterior thigh muscles. I: identification and patterns during normal locomotion. *J. Neurophysiol.* **54**, 549-564. doi:10.1152/jn.1985.54.3.549

Maas, H., Baan, G. C. and Huijing, P. A. (2004). Muscle force is determined also by muscle relative position: Isolated effects. *J. Biomech.* **37**, 99-110. doi:10.1016/S0021-9290(03)00235-5

Mathis, A., Mamidanna, P., Cury, K. M., Abe, T., Murthy, V. N., Mathis, M. W. and Bethge, M. (2018). DeepLabCut: markerless pose estimation of user-defined body parts with deep learning. *Nat. Neurosci.* **21**, 1281-1289. doi:10.1038/s41593-018-0209-y

McGowan, C. P. and Collins, C. E. (2018). Why do mammals hop? Understanding the ecology, biomechanics, and evolution of bipedal hopping. *J. Exp. Biol.* **221**, 12. doi:10.1242/jeb.161661

Mendez, J. and Keys, A. (1960). Density and composition of mammalian muscle. *Metabolism.* **9**, 184-188.

Moore, T. Y., Rivera, A. M. and Biewener, A. A. (2017a). Vertical leaping mechanics of the Lesser Egyptian Jerboa reveal specialization for maneuverability rather than elastic energy storage. *Front. Zool.* **14**, 32. doi:10.1186/s12983-017-0215-z

Moore, T. Y., Cooper, K. L., Biewener, A. A. and Vaudevan, R. (2017b). Unpredictability of escape trajectory explains predator evasion ability and microhabitat preference of desert rodents. *Nat. Commun.* **8**, 440. doi:10.1038/s41467-017-00373-2

Pollock, C. M. and Shadwick, R. E. (1994). Relationship between body mass and biomechanical properties of limb tendons in adult mammals. *Am. J. Physiol.* **266**, R1016-R1021.

Rankin, J. W., Doney, K. M. and McGowan, C. P. (2018). Functional capacity of kangaroo rat hindlimbs: adaptations for locomotor performance. *J. R. Soc. Interface.* **15**, 20180303. doi:10.1098/rsif.2018.0303

Roberts, T. J. (2002). The integrated function of muscles and tendons during locomotion. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **133**, 1087-1099. doi:10.1016/S1095-6433(02)00244-1

Roberts, T. J. (2016). Contribution of elastic tissues to the mechanics and energetics of muscle function during movement. *J. Exp. Biol.* **219**, 266-275. doi:10.1242/jeb.124446

Roberts, T. J. and Azizi, E. (2011). Flexible mechanisms: the diverse roles of biological springs in vertebrate movement. *J. Exp. Biol.* **214**, 353-361. doi:10.1242/jeb.038588

Roberts, T. J., Marsh, R. L., Weyand, P. G. and Taylor, C. R. (1997). Muscular force in running turkeys: the economy of minimizing work. *Science* **275**, 1113-1115. doi:10.1126/science.275.5303.1113

Ross, C. D. and Meyers, R. A. (2021). Immunohistochemistry of kangaroo rat hindlimb muscles. *Anat. Rec.* doi:10.1002/ar.24791

Schwaner, M. J., Lin, D. C. and McGowan, C. P. (2018). Jumping mechanics of desert kangaroo rats. *J. Exp. Biol.* **221**, 22. doi:10.1242/jeb.186700

Schwaner, M. J., Lin, D. C. and McGowan, C. P. (2021). Plantar flexor muscles of kangaroo rats (*D. deserti*) shorten at a velocity to produce optimal power during jumping. *J. Exp. Biol.* **224**, jeb24263. doi:10.1242/jeb.242630

Shadwick, R. E. (1990). Elastic energy storage in tendons: mechanical differences related to function and age. *J. Appl. Physiol.* **68**, 1033-1040. doi:10.1152/jappl.1990.68.3.1033

Taylor, C. R. (1977). The energetics of terrestrial locomotion and body size in vertebrates. In *Scale Effects in Animal Locomotion* (ed. T.J. Pedley), pp. 17–19. London: Academic Press.

Taylor, C. R., Schmidt-Nielsen, K. and Raab, J. L. (1970). Scaling of energetic cost of running to body size in mammals. *Am. J. Physiol.* **219**, 1104-1107. doi:10.1152/ajplegacy.1970.219.4.1104

Thompson, S. D., MacMillen, R. E., Burke, E. M. and Taylor, C. R. (1980). The energetic cost of bipedal hopping in small mammals. *Nature* **287**, 223-224. doi:10.1038/287223a0

Wakeling, J. M., Blake, O. M., Wong, I., Rana, M. and Lee, S. S. M. (2011). Movement mechanics as a determinate of muscle structure, recruitment, and coordination. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **366**, 1554-1564. doi:10.1098/rstb.2010.0294

Walmsley, B., Hodgson, J. A. and Burke, R. E. (1978). Forces produced by medial gastrocnemius and soleus muscles during locomotion in freely moving cats. *J. Neurophysiol.* **41**, 1203-1216. doi:10.1152/jn.1978.41.5.1203