

RESEARCH ARTICLE

Jumping mechanics of desert kangaroo rats

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ABSTRACT

Kangaroo rats are small bipedal desert rodents that use erratic vertical jumps to escape predator strikes. In this study we examined how individual hind limb joints of desert kangaroo rats (*Dipodomys deserti*) power vertical jumps across a range of heights. We hypothesized that increases in net work would be equally divided across hind limb joints with increases in jump height. To test this hypothesis, we used an inverse dynamics analysis to quantify the mechanical output from the hind limb joints of kangaroo rats jumping vertically over a wide range of heights. The kangaroo rats in this study reached maximal jump heights up to ~9-times hip height. Net joint work increased significantly with jump height at the hip, knee and ankle, and decreased significantly at the metatarsal–phalangeal joint. The increase in net work generated by each joint was not proportional across joints but was dominated by the ankle, which ranged from contributing 56% of the work done on the center of mass at low jumps to 70% during the highest jumps. Therefore, the results of this study did not support our hypothesis. However, using an anatomical model, we estimated that a substantial proportion of the work delivered at the ankle (48%) was transferred from proximal muscles via the biarticular ankle extensors.

KEY WORDS: *Dipodomys*, Inverse dynamics, Biarticularity, Joint work

INTRODUCTION

Bipedal hopping is a highly specialized mode of terrestrial locomotion that has arisen independently in six lineages of mammals (McGowan and Collins, 2018). It has been hypothesized that bipedal hopping evolved as an adaptation for erratic behavior (e.g. Moore and Biewener, 2015) and extreme jump performance to evade predators (Bartholomew and Caswell, 1951; Webster and Webster, 1980). For example, small hopping species, such as kangaroo rats and jerboas are capable of jumping over 10-times their standing hip height (Biewener and Blickhan, 1988; Moore et al., 2017). Kangaroo rats are also capable of very rapid jump take-off times in response to snake strikes (Freymler et al., 2017). Alternatively, larger bipedal hopping species (>3 kg) benefit from a decoupling of metabolic cost from steady-speed hopping enabling remarkably efficient locomotion (Dawson and Taylor, 1973; Biewener and Baudinette, 1995).

The morphological specializations associated with bipedal hopping include greatly elongated hind limbs in which the muscle mass is concentrated proximally. These proximal muscles tend to have relatively long fibers and large cross-sectional areas that are well suited for generating muscle power, whereas distal muscles tend to have short, pennate fibers with long tendons that are better suited for developing high force (Biewener and Roberts, 2000). Within larger bipedal hoppers, these long distal tendons are relatively thin, enabling the elastic energy storage and return that contributes to locomotor efficiency in these animals (Biewener et al., 1998), but may also limit acceleration capacity during rapid movements due to low tendon safety factors (Biewener and Bertram, 1991). Studies of tammar wallabies hopping on level and inclined surfaces have shown that a division of labor exists between proximal and distal muscle groups, with proximal muscles providing the work to raise the animals' center of mass and specialized distal muscle–tendon groups retaining spring-like function (Biewener, 2004; McGowan et al., 2007). While relatively long, the distal tendons of small bipedal hoppers tend to be comparatively thick and probably do not store and return significant elastic energy during hopping (Biewener et al., 1981, 1988; Moore et al., 2017). Rather, these muscle–tendon units (MTUs) are better suited for direct transmission of mechanical work by the muscle to the environment. Therefore, it is not clear if a division of labor exists between proximal and distal muscles in these smaller hopping species when doing work against the environment.

Small bipedal hoppers rely on their ability to jump in order to escape predation, yet relatively little is known about the mechanics of how they achieve these high-power maneuvers. Previous studies of *in vivo* muscle performance by kangaroo rats (*Dipodomys spectabilis*) suggest that the ankle plantarflexor MTUs generate extremely high forces (up to 175% of the maximal isometric force) during their highest jumps (Biewener et al., 1988). And an analysis of jumping by jerboas (*Jaculus jaculus*) indicates that the ankle delivers the majority of the mechanical work done at the joint level (Moore et al., 2017); however, this study did not examine how the distribution of work changed across jump heights. Despite proximal muscles being morphologically better suited for developing power, most jumping animals deliver the highest power outputs at the distal joints (Van Soest et al., 1985; Aerts, 1998; Moore et al., 2017). This distal delivery of power can be facilitated by the return of energy from elastic elements and/or energy transfer from proximal to distal joints, often through biarticular muscles (Gregoire et al., 1984; Bobbert et al., 1986), although power can also be transferred between leg segments through inertial coupling (Zajac et al., 2002). The previous studies of jumping by kangaroo rats and jerboas both concluded that elastic energy storage did not contribute significantly to the power required to achieve the measured jump heights, but neither considered the role of energy transfer.

The aim of this study was to determine how desert kangaroo rats (*Dipodomys deserti* Stephens 1887) modulate the mechanical output at each joint to power jumps over a range of heights. To achieve our aim, we used an inverse dynamics approach to

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investigate the hind limb net joint power and work by examining which joints increased power output in response to increasing jump heights. Furthermore, we used a geometric model based on the animals' anatomy to estimate energy transfer from proximal to distal joints. Because these animals lack the distal MTU specialization for elastic energy storage, we hypothesized that increases in net work would be equally divided across leg joints with increases in jump height.

MATERIALS AND METHODS

Animals and training

Eight adult, wild-caught desert kangaroo rats were used for this study (body mass of 72–120 g). Animals were caught in the Mojave Desert in southeast Nevada under permits issued by the Nevada Department of Wildlife and the Bureau of Land Management. At least 24 h prior to experiments, the animals were trained to familiarize them with the experimental environment and task. During training sessions, the animals were exposed to jumping obstacles of different heights and they were motivated to jump by hand movements close to the animal. All experimental procedures and the husbandry of the animals were approved by the University of Idaho Institutional Animal Care and Use Committee (IACUC).

Experimental design

Between 10 and 20 jumping trials with different obstacle heights were performed by each animal. High-speed video data were recorded at 200 frames s^{-1} using a camera (Xcitex, Woburn, MA, USA), which was positioned with a sagittal view of the animal. The jump arena had plexi-glass walls and included a built-in force plate (AMTI HE6x6, Watertown, MA, USA). Animals were encouraged to jump over an obstacle of a given height (ranging from 0.12 to 0.45 m) after taking off from a force plate that was sampled at 600 Hz. Animals landed on a foam pad on the opposite side of the barrier.

Because animals frequently used their front limbs to grab the barrier, the jump height that would have been achieved without a barrier was calculated (Eqn 1). Jump height was calculated based on conservation of energy, assuming no effect of drag on the animal, with the following equation:

$$\Delta h = \frac{v_{\text{foot-off}}^2}{2g}, \quad (1)$$

where Δh is the change in the height of the center of mass (COM), $v_{\text{foot-off}}$ is the take-off velocity and g is the gravitational constant. $v_{\text{foot-off}}$ was calculated from the integral of the vertical ground reaction force (GRF) and body mass since:

$$v_{\text{foot-off}} = \frac{\int_{t_0}^{t_{\text{foot-off}}} (F - mg) dt}{m}. \quad (2)$$

With the numerator being the integral of F , which represents the vertical GRF during take-off; m is body mass and mg is body weight.

Data analysis

Trials were selected for analysis based on completeness (complete set of video and force plate data) and on jump performance (total $n=62$; 4–15 trials per animal). Jump performance requirements were that the animal was oriented sagittal to the camera and took off from both legs simultaneously. Trial length was determined based on the GRF pattern. Start time of the trial was designated as the time at which the force exceeded body weight (BW). Countermovements,

visible in the force trace as a drop below BW, occurred in a few trials, but the amount of change in force in these trials was minimal ($<6.5\%$ BW). If countermovements occurred, then the starting point of the trial was defined as prior to the countermovement when the force trace was still equal to BW. The end of the jump was defined as the first point in time at which the vertical GRF was zero.

Prior to the experiment, markers were placed on the animals' hind leg joint centers of rotation [toe, metatarsophalangeal (MTP), ankle, knee, hip]. An additional marker was placed on the ischium. Following the experiment, these markers and the position of the eye were digitized using ProAnalyst software (Xcitex) and a low-pass fourth-order Butterworth filter was applied with a cut-off frequency of 30 Hz. The coordinate data were used to calculate joint angles and joint angular velocities. GRFs were filtered with a low-pass second-order Butterworth filter with a cut-off frequency of 55 Hz. Owing to skin movement, the knee joint position was calculated based on the position of ankle and hip joint and segment lengths of the tibia and femur (McGowan et al., 2005a). Net joint moments about the MTP, ankle, knee and hip were obtained from the kinematic and force plate data with custom inverse dynamics analysis software (McGowan et al., 2005a) written in MATLAB 2015a. Joint power was calculated by multiplying joint moment by joint angular velocity. Net joint work was calculated by integrating joint power with respect to time.

In some trials, the feet were not aligned with respect to the sagittal plane. In these cases, the center of pressure (COP) from the force plate was not in the appropriate horizontal location for the leg of interest and we therefore corrected the COP for the difference in x coordinates between the left and right longest toes. We checked the new position of the COP by plotting the GRF vector relative to left hind leg joint positions and examined the behavior of the COP during the jumping trial. Since the position of the COP changed during the trials, only trials where the COP stayed between the MTP joint and the tip of the toes were used for further analysis.

To examine how mechanical variables changed with jump height, we performed linear regression analysis on joint excursions, peak extensor moments, joint power and joint work using R version 3.1.1 (2008, R Core Team, Vienna, Austria). We considered linear correlation statistically significant where $P < 0.05$. In cases of $P < 0.05$, values of R^2 , and $F_{1,59}$ statistics are provided. In addition, we used a general linear model (GLM) in JMP 14.0.1 (2018, SAS Institute) to test for any individual effects, which were not found.

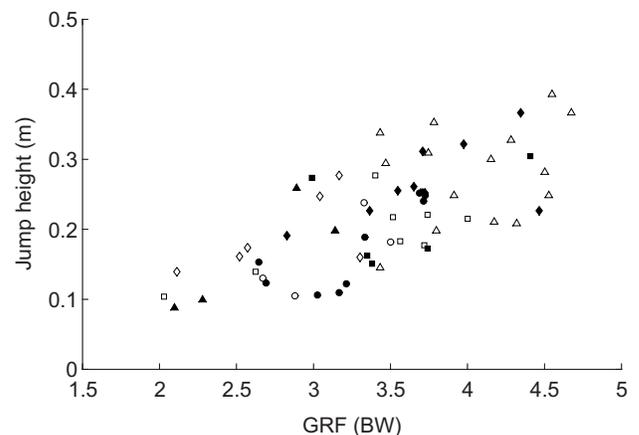


Fig. 1. Peak ground reaction force versus jump height. Peak GRFs in body weights, for a single leg, were plotted against jump height. Each symbol represents a jump from an individual animal. Jumps from each animal were equally distributed over jump height.

Energy transfer

We used a geometric model based on the animals' anatomy to investigate how much of the work measured at the ankle joint originated from proximal muscles and was transferred over the biarticular ankle extensors during jumping. Work done by the MTUs was calculated from the length change of the combined distal MTUs (L_{MTU}) and the force produced by these MTUs (F_{MTU}). For calculation of the change in length of MTUs we used the following equation:

$$\Delta L_{MTU} = r_a \Delta \theta_a - r_k \Delta \theta_k, \quad (3)$$

for which r is the distance between the joint and the insertion point of the MTU of the ankle (a) or knee (k), θ_a is the angle between metatarsophalangeal joint and an axis line drawn through the knee

and ankle joint center of rotation, and θ_k is the angle between the femur and an axis line drawn through the knee and ankle joint center of rotation. For these calculations we used fixed values for r since a recent study showed that the moment arms of the ankle extensor muscles are relatively constant across a wide range of ankle angles in desert kangaroo rats (Rankin et al., 2018). Both of these angles are expressed in radians. The force of the MTU was calculated according to the following equation:

$$F_{MTU} = \frac{M_a}{r_a}, \quad (4)$$

for which F_{MTU} is the force in the MTUs, M_a is the moment around the ankle joint center of rotation, and r_a the distance between the joint and the insertion point of the MTU of the ankle (a), the length

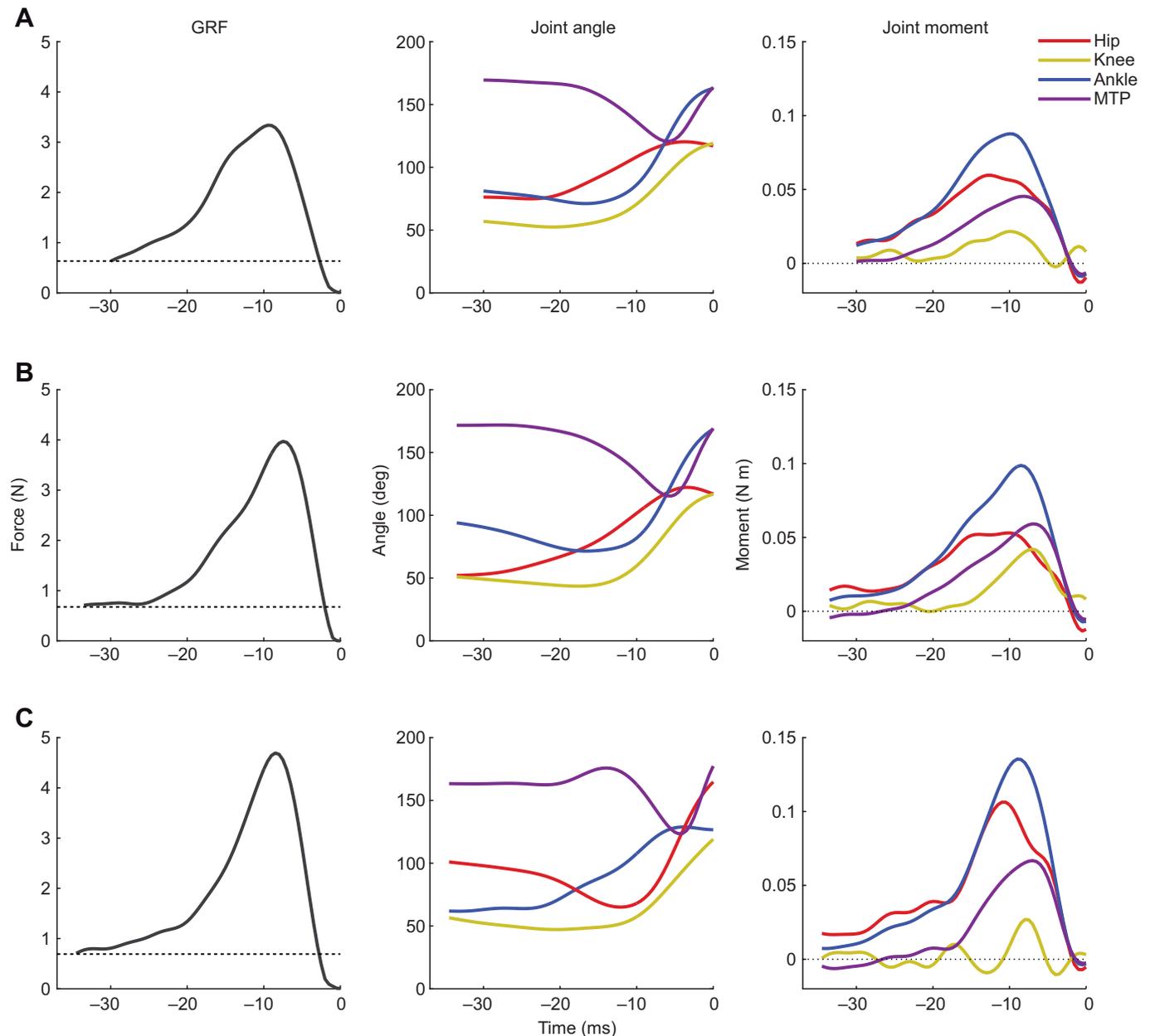


Fig. 2. Ground reaction force, joint angles and joint moments for three representative trials at three different jump heights in one animal. GRF, joint angles and joint moments for three representative trials of (A) 0.15 m, (B) 0.25 m and (C) 0.35 m jumps. GRFs are for one single leg for 40 ms prior to the animal leaving the ground. Dashed lines in the GRF plots indicate the body weight in Newtons.

between ankle center of rotation and end of the calcaneus. Power values over a full jumping trial were calculated by multiplying the rate of ΔL_{MTU} (Eqn 3) by F_{MTU} (Eqn 4). By taking the integral of these power values with respect to time, we obtained the work done by the MTU. The work transferred from proximal muscles was calculated by subtracting work done by the MTU from the work delivered by the ankle joint.

RESULTS

Jump patterns

The jumps recorded ranged from 0.08 to 0.40 m. The highest jump was equal to 8.8-times standing hip height (average hip height at the start of the jumping motion was 45.7 mm). The total power required to produce these jumps ranged from 10.2 to 43.2 W kg⁻¹ BM, which corresponds to an estimated 365.44 W kg⁻¹ muscle in the highest jump. The average peak GRF for one leg was 3.48 BW, with a minimum of 2.03 BW and a maximum of 4.68 BW for the highest jump recorded (Fig. 1). There is a positive association between jump height and peak vertical GRF ($P<0.001$, $R^2=0.48$, $F=58.39$). MTP and ankle joints flexed before they extended but the ankle flexion was minimal. The MTP joint flexed gradually followed by a relatively rapid extension of similar magnitude; the hip and knee joints only extended in all trials. MTP and ankle joint moments were predominately positive for all trials, whereas there was more variation in the knee and hip joint moments (Fig. 2).

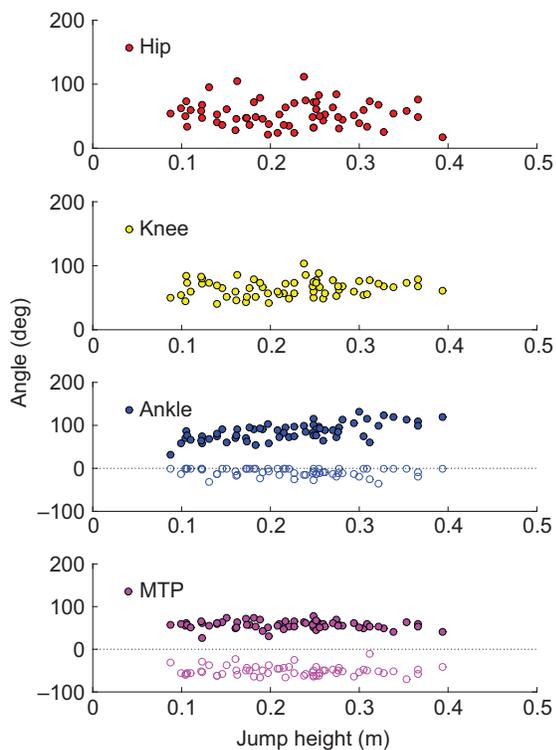


Fig. 3. Joint excursions versus jump height for all trials. Joint excursions for hip, knee, ankle and MTP are plotted against jump height. MTP and ankle joints showed a period of flexion before extension took place, which are represented in negative excursion values. In the MTP, this flexion was of similar magnitude to the extension, whereas the ankle only showed a flexion in 33 trials, and in these cases, the flexion was minimal. MTP flexion and extension showed no significant relationship with jump height ($P=0.713$ and $P=0.293$). The ankle joint extension did have a positive relationship with jump height ($P<0.001$, $R^2=0.419$, $F=44.97$), whereas ankle flexion showed no significant relationship with jump height ($P=0.111$). Hip and knee extension did not increase with jump height ($P=0.569$ and $P=0.231$).

Joint excursion

Changes in joint angles were generally independent of jump height, except for those in the ankle (Fig. 2B and Fig. 3). The MTP joint underwent a flexion (negative values)–extension (positive values) pattern that did not change with jump height (flexion $P=0.71$, extension $P=0.29$). In the 33 trials with a countermovement, the ankle underwent an initial flexion, which was inconsistent and independent of jump height. Ankle extension increased significantly with jump height ($P<0.001$, $R^2=0.42$, $F=44.97$), ranging from approximately 60 deg at low jumps to 110 deg at the high jumps. Knee and hip excursion did not increase significantly with increasing jump height ($P=0.231$ and $P=0.569$, respectively).

Joint moments

Peak joint moments increase significantly with jump height at all joints except the knee (Fig. 4) (MTP, $P<0.003$, $R^2=0.12$, $F=9.66$; ankle, $P<0.001$, $R^2=0.35$, $F=33.74$; hip, $P<0.001$, $R^2=0.23$, $F=23.2$). Peak extensor moments at the knee varied widely and were independent of jump height ($P=0.584$).

Joint power

As jump height increased, peak joint power increased at the hip and ankle (Fig. 5). Energy was absorbed, indicated by negative power, at the MTP joint during dorsiflexion because the joint was flexing with an extensor moment. During the fast extension of the MTP joint at the end of the take-off, power output became positive. The ankle produced the highest peak power, which increased significantly with jump height ($P<0.001$, $R^2=0.49$, $F=59.41$). Peaks of knee powers arose around the same time as peaks in ankle power occurred

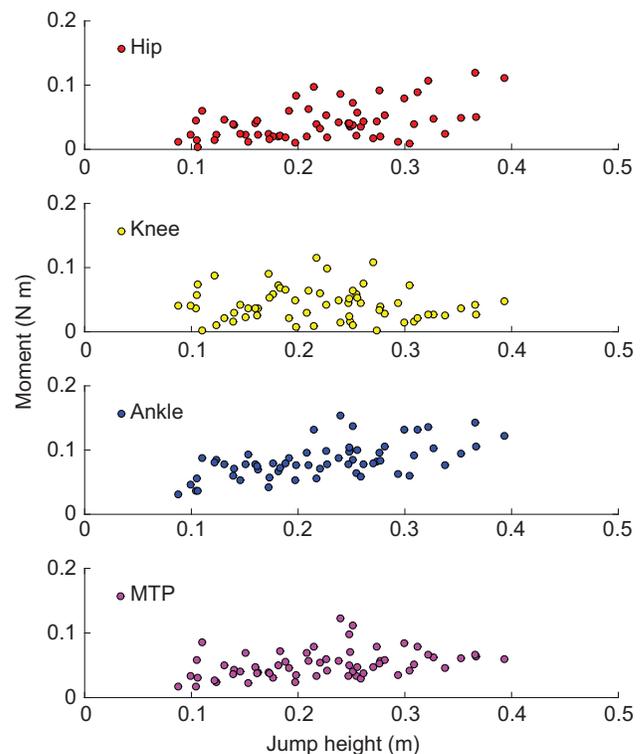


Fig. 4. Peak extensor joint moments versus jump height for all trials. Peak extensor moments for hip, knee, ankle and MTP for all trials are plotted against jump height. MTP, ankle and hip joint peak extensor moments showed an increase with increasing jump height (MTP: $P=0.003$, $R^2=0.1244$, $F=9.663$; ankle: $P<0.001$, $R^2=0.349$, $F=33.74$; hip: $P<0.001$, $R^2=0.267$, $F=23.2$). Knee peak extensor moments show more variety with jump height ($P=0.584$).

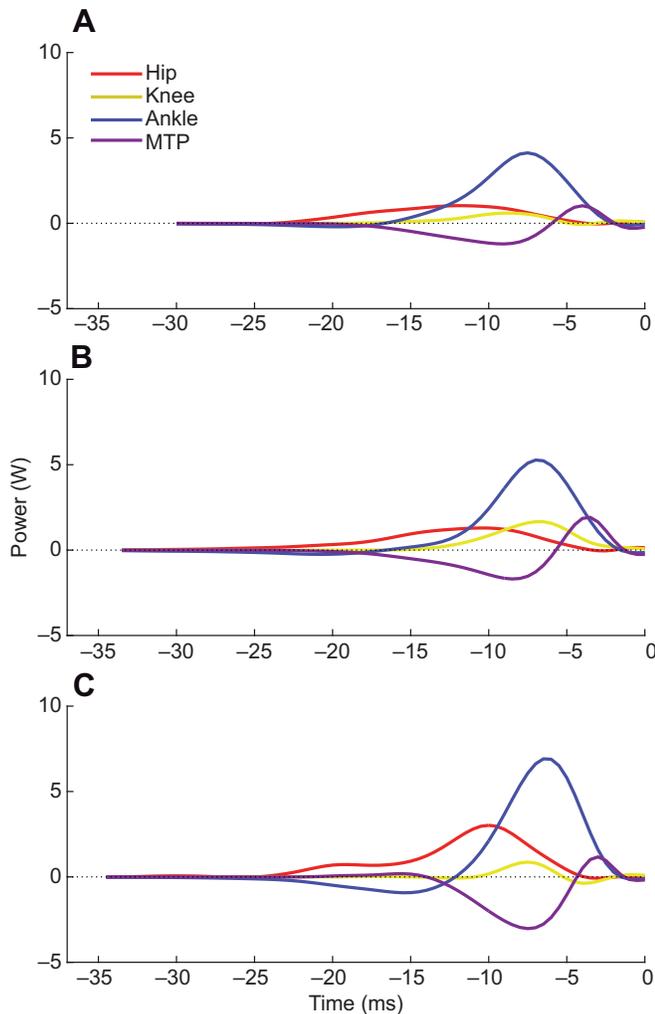


Fig. 5. Joint power for three representative trials of three different jump heights in a single animal. Joint powers are presented for the MTP, ankle, knee and hip joints in (A) 0.15 m, (B) 0.25 m and (C) 0.35 m jumps for the 40 ms before the animal loses contact with the ground. Hip powers peak first, followed by ankle and the knee. The MTP showed a large negative power first during the period of joint flexion (energy absorption), followed by a positive power during joint extension.

but were independent of jump height ($P=0.329$). Hip power peaked first, before peak power in other joints, and increased significantly with jump height ($P<0.001$, $R^2=0.16$, $F=12.58$).

Net joint work

To determine that the work done by the limbs accounted for the majority of the work done on the COM, we plotted work done on the COM against the sum of all work done by the hind limbs (Fig. 6). The slope of the best fit line, solid line, was 0.92. Potential work that was not accounted for in the sum of work done by the hind legs probably originates from the work done by trunk extension.

The mechanical role of individual joints during jumping was examined by calculating net joint work for individual jumps across jump heights (Fig. 7). Net MTP work was near zero (-0.434 to 0.159 J kg⁻¹ BW) and decreased with increasing jump height ($P<0.001$, $R^2=0.18$, $F=14.66$). Net joint work by the ankle ($P<0.001$, $R^2=0.73$, $F=165.5$), knee ($P=0.018$, $R^2=0.08$, $F=5.97$) and hip ($P=0.002$, $R^2=0.14$, $F=10.48$) all correlated positively with jump height. The relative contribution to the total positive joint

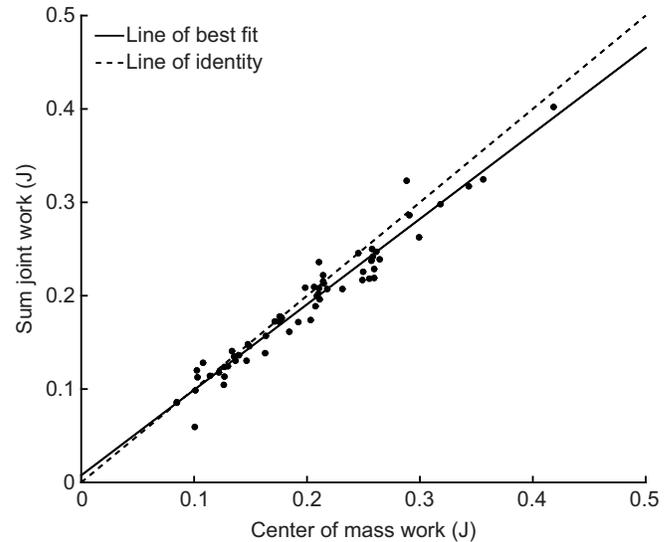


Fig. 6. Center of mass (COM) work versus the sum of joint work in joules. The work done at the center of mass (x -axis) is plotted against the sum of all work done by the hind limbs (y -axis). The solid line represents the line of best fit through the data, whereas the dashed line is a line of identity, which is a line through the origin and with a slope of one. The slope of the best fit line was 0.92.

work done by the hind limb was greatest at the ankle and ranged between 56% at low jumps to 70% at high jumps (Fig. 8). The relative contributions to total positive work by the knee and hip both decreased with jump height, from 24% and 20%, respectively, at low jumps to ~15% for both joints during high jumps.

Energy transfer

The net work delivered at the ankle is the sum of the work done by the ankle extensor muscles and the work transferred from proximal muscles via the bi-articular MTU. During jumping, there was an increase with increasing jump height in both the work done by the ankle extensors ($P<0.01$, $R^2=0.50$, $F=61.2$) and the work that was transferred ($P<0.01$, $R^2=0.43$, $F=47.02$) (Fig. 9). Although there was a high level of variation, on average, the amount of transferred work was 48% and equal over all jump heights ($P=0.801$) (Fig. 10).

DISCUSSION

Vertical jumps by the kangaroo rats in this study ranged from 0.08 m to 0.40 m, with the highest jump reaching almost 9-times resting hip height. The average power required for the highest jump was 2.78 W, which is equivalent to 365 W kg⁻¹ of muscle, assuming all leg extensor muscles contribute to the jump. Across the range of jump heights examined in this study, the ankle joint provided the greatest contribution to the power and work of vertical jumping. These results do not support our hypothesis that increases in net joint work would be equally divided across hind leg joints with increasing jump height.

Several species of vertebrates have been shown to produce power outputs during jumping that far exceed the capacity of vertebrate skeletal muscles (reported averages for maximum power range from 250 to 433 W kg⁻¹ muscle: Weis-Fogh and Alexander, 1977; Lutz and Rome, 1994; Marsh and John-Adler, 1994; Askew et al., 2001). For galagos and Cuban tree frogs, peak muscle power values were reported to be 1700 W kg⁻¹ muscle and 1650 W kg⁻¹ muscle, respectively (Aerts, 1998; Peplowski and Marsh, 1997). For wallabies, an average muscle power value of 495 W kg⁻¹ muscle

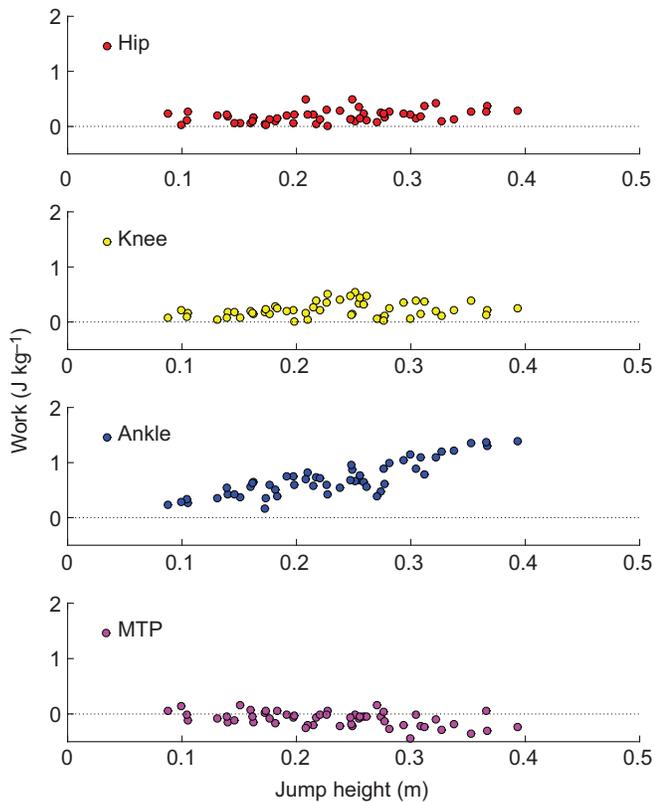


Fig. 7. Joint work versus jump height for all trials. Hip, knee and ankle joint did show a significant increase in contributed work (in J kg^{-1} body mass) with increasing jump height (hip: $P=0.002$, $R^2=0.135$, $F=10.48$; knee: $P=0.018$, $R^2=0.075$, $F=5.968$; ankle: $P<0.001$, $R^2=0.729$, $F=165.5$). The MTP joint power showed a negative relationship with jump height ($P<0.001$, $R^2=0.183$, $F=14.66$), which indicates that more energy is absorbed with increasing jump height.

was reported (McGowan et al., 2005b). Animals exceeding maximal power outputs of skeletal muscles must use a mechanism, in the form of a countermovement, elastic energy storage and return, and/or inertial catch mechanism, to enhance their

power output. Power values reported here, for jumping kangaroo rats (365 W kg^{-1} muscle) did not exceed the maximum power capacity of skeletal muscles, suggesting that these animals do not require a power enhancement mechanism to produce these jumps.

The increase in mechanical work required to achieve higher jump heights was produced by increases in positive net work from the hip, knee, and ankle; whereas the MTP tended to absorb more energy as jump height increased (Fig. 7). The increases in positive net work were greatest at the ankle, leading to an increase in the relative contribution of this joint compared with the knee and hip across jump heights. During the highest jumps, the ankle produced over 4-times more work than the knee or hip. This is consistent with previous studies that showed the ankle plays a primary role in powering jumps (e.g. Aerts, 1998). In a recent study of jumping by jerboas, which are hopping bipeds similarly sized to the kangaroo rat, Moore et al. (2017) showed that the ankle also contributes the most net joint work, but its relative contribution to total work was less than that found for kangaroo rats. For example, in a comparable jump of 0.37 m, the ankle joint of kangaroo rats produced a net work of 1.19 J kg^{-1} , while the knees produced 0.29 J kg^{-1} and the hip 0.29 J kg^{-1} , whereas for jerboas, these values were 0.23 J kg^{-1} , 0.18 J kg^{-1} and 0.13 J kg^{-1} , respectively (Moore et al., 2017). Although both species produce the most work at the ankle, kangaroo rats produce substantially more work per unit body mass compared with jerboas. Both species have net energy absorption at the MTP joint during jumping; although kangaroo rats have a flexion-extension pattern at the MTP which produces some positive power just before take-off whereas jerboas do not. This difference may be due to the fact that jerboas have relatively short toes compared with kangaroo rats.

While most net mechanical work done during jumping was delivered at the ankle, caution is needed when inferring contributions from individual muscles. Inverse dynamics analyses have limitations and cannot account for the effects of co-contraction, biarticular muscles or elastic energy storage and return. The role of biarticular muscles is particularly important during high acceleration tasks, where energy from proximal muscles is delivered at the ankle via multi-joint muscles (Jacobs et al., 1996;

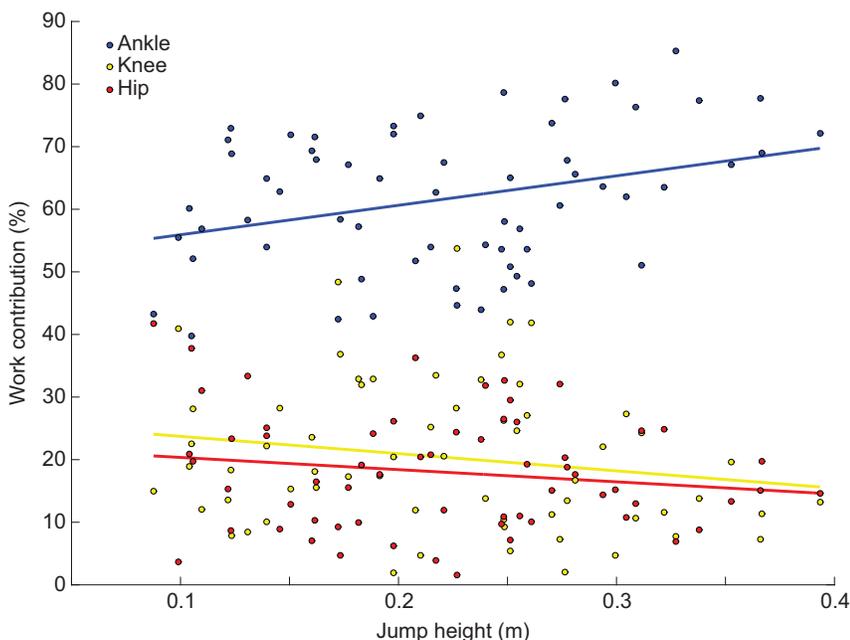


Fig. 8. Contribution of each hind leg joint towards the positive joint work. Percentage contribution of ankle, knee and hip, towards the positive joint work plotted against jump height (m). The contribution of the ankle joint to the positive joint work increased with increasing jump height ($P=0.012$, $R^2=0.089$, $F=6.939$). The knee and hip joint contribution showed no significant relationship with jump height ($P=0.165$ and $P=0.214$, respectively).

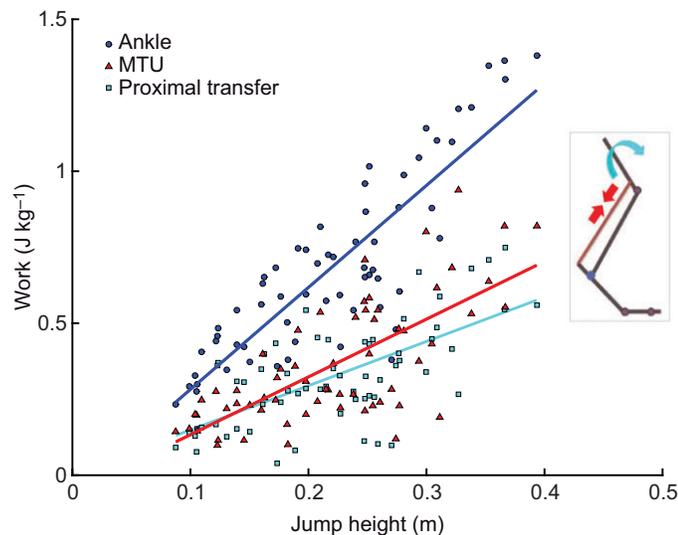


Fig. 9. Muscle–tendon unit (MTU) work versus jump height. Work measured at the ankle, calculated work values for the MTU (triangles) and work that was transferred over the MTU (squares) were plotted against jump height. The origin of the data points is represented in the stick figure on the right. The curved arrow represents the transferred work from proximal musculature to the ankle and the two arrows pointing toward each other represent muscle contraction within the MTU. The blue dot represents the work that is measured at the ankle joint. Work due to proximal transfer and work produced by the MTU both showed a positive correlation with jump height (proximal transfer: $P < 0.001$, $R^2 = 0.43$, $F = 47.02$; MTU: $P < 0.001$, $R^2 = 0.497$, $F = 61.21$).

Aerts, 1998; Dutto et al., 2004). This is clearly the case during jumping by desert kangaroo rats as well. In this species, all major ankle extensor muscles (gastrocnemii and plantaris) are biarticular, with origins on the femur and insertions on the calcaneus. The uniaxial ankle extensors are vestigial (e.g. soleus). This anatomical arrangement enables the ankle extensors to act as both a motor, producing mechanical work by shortening, and a strut,

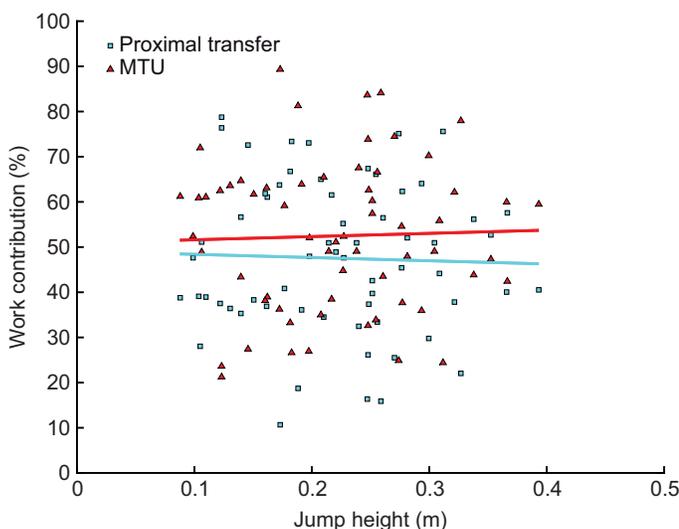


Fig. 10. Relative work contributions of ankle extensor muscles and proximal transfer at the ankle joint versus jump height. Relative joint work contributions of the ankle extensor muscle (triangle) and percentage of work transferred over the bi-articular ankle extensor showed no significant relationship with jump height ($P = 0.8014$).

transferring energy from proximal muscles. Consistent with the MTU operating like a strut, the ankle and knee joints undergo a coordinated extension pattern (Fig. 2). Based on muscle moment arms and joint angle changes during jumping, we estimated that, on average, 48% of the work done at the ankle is transferred from proximal muscles, with the remaining work being done by the muscle shortening (Figs 8 and 9). This substantial amount of energy transfer is greater than the 25% that had been calculated for human jumping (Gregoire et al., 1984; Bobbert et al., 1986), but less than the 65% estimated for galagos (Aerts, 1998).

Elastic energy storage and return also play an important role in achieving high peak power outputs for many jumping species (e.g. Aerts, 1998; Peplowski and Marsh, 1997; McGowan et al., 2005b). However, previous studies have shown that small bipedal hoppers such as kangaroo rats and jerboas probably do not benefit substantially from energy storage in tendons (Biewener and Blickhan, 1988; Moore et al., 2017). Based on estimates of peak MTU force, tendon cross-sectional area and an elastic modulus for tendons of 1 GPa (Ker, 1981; Bennett et al., 1986), this is also the case for the desert kangaroo rats in this study. For the highest jumps recorded, elastic energy returned from the ankle extensor tendons likely contributed no more than 3.75% of the energy required for the jump, according to the calculation of the elastic strain energy return:

$$U = 0.5 \left(\frac{\sigma_t^2}{E} \right) V_t 0.93, \quad (5)$$

where U is the elastic strain energy of one leg, σ_t is strain, E is elastic modulus and V_t is the volume of the tendon. The value is multiplied by 0.93 to account for the 7% loss due to hysteresis (Biewener et al., 1998). However, it should be noted that the material properties of kangaroo rat tendons have not been measured and this value would change with a different elastic modulus. Still, these results are consistent with the hypothesis that kangaroo rats are adapted for predator escape behavior (acceleration) rather than elastic energy storage (Biewener and Blickhan, 1988).

The experimental design of this study provides insights into the general mechanics of vertical jumping by desert kangaroo rats; however, it must be noted that these jumps do not represent true escape responses. In contrast to their ballistic escape maneuvers in the wild, the staging gave the animals in our study time to ‘plan’ their jumps, resulting somewhat variable jump strategies. Starting from a range of initial postures, animals in 33 of 62 trials had a small countermovement at the ankle prior to extension for the jump. However, these minimal countermovements were not reflected in the GRF patterns and likely contributed little to the jumping mechanics. During a predator attack in the wild, the time it takes to produce a countermovement could be detrimental to the animals’ ability to escape, since a quicker response increases escape success (Freymiller et al., 2017). This may explain why we did not observe substantial countermovements in our study. This is consistent with what has been observed for jerboas under similar experimental conditions (Moore et al., 2017).

Kangaroo rats are capable of extreme jumping behaviors, typically associated with predator avoidance. The highest jumps recorded in this study required average power outputs of over 360 W kg^{-1} of muscle and did not involve countermovements or other significant elastic energy storage and return. This suggests that kangaroo rats power jumping via high power muscle output, although this remains to be tested directly. The animals in this study increased their jump height by increasing joint power and work across all joints, with the ankle joint contributing the largest

percentage. However, a substantial portion of work delivered at the ankle joint (on average 48%) was transferred from proximal muscles via the biarticular ankle extensor MTU. Future studies, using sonomicrometry techniques, could give direct measures of the contributions of the ankle and knee extensors.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: M.J.S., D.C.L., C.P.M.; Methodology: M.J.S., D.C.L., C.P.M.; Investigation: M.J.S., D.C.L.; Writing - original draft: M.J.S., C.P.M.; Writing - review & editing: M.J.S., D.C.L., C.P.M.; Supervision: C.P.M.; Funding acquisition: D.C.L., C.P.M.

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References

- Aerts, P. (1998). Vertical jumping in *Galago senegalensis*: the quest for an obligate mechanical power amplifier. *Philos. Trans. R. Soc. Lond. B* **353**, 1607-1620.
- Askew, G., Marsh, R. L. and Ellington, C. (2001). Mechanical power output of the flight muscles of Blue-breasted Quail (*Coturnix chinensis*) during take-off. *J. Exp. Biol.* **204**, 3601-3619.
- Bartholomew, G. A. and Caswell, H. H. (1951). Locomotion in kangaroo rats and its adaptive significance. *J. Mammal.* **32**, 155-169.
- Bennet, M. B., Ker, R. F., Dimery, N. J. and Alexander, R. M. N. (1986). Mechanical properties of various mammalian tendons. *J. Zool.* **209**, 537-548.
- Biewener, A. A. (2004). *Animal Locomotion*. Oxford, UK: Oxford University Press.
- Biewener, A. A. and Baudinette, R. (1995). In vivo muscle force and elastic energy storage during steady-speed hopping of tammar wallabies (*Macropus Eugenii*). *J. Exp. Biol.* **198**, 1829-1841.
- 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.
- 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**, 99-108.
- Biewener, A., Alexander, R. M. N. and Heglund, N. C. (1981). Elastic energy storage in the hopping of kangaroo rats *Dipodomys spectabilis*. *J. Zool.* **195**, 369-383.
- Biewener, A. A., Blickhan, R., Perry, A. K., Heglund, N. C. and Taylor, C. R. (1988). Muscle forces during locomotion in kangaroo rats: force platform and tendon buckle measurements compared. *J. Exp. Biol.* **137**, 191-205.
- 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.
- Bobbert, M. F., Huijling, P. A. and Van Ingen Schenau, G. J. (1986). An estimation of power output and work done by the human triceps surae muscle-tendon complex in jumping. *J. Biomech.* **19**, 899-906.
- Dawson, T. J. and Taylor, C. R. (1973). Energetic cost of locomotion in kangaroos. *Nature* **246**, 313-314.
- Dutto, D. J., Hoyt, D. F., Clayton, H. M., Cogger, E. A. and Wickler, S. J. (2004). Moments and power generated by the horse (*Equus Caballus*) hind limb during jumping. *J. Exp. Biol.* **207**, 667-674.
- Freymler, G. A., Whitford, M. D., Higham, T. E. and Clark, R. W. (2017). Recent interactions with snakes enhance escape performance of desert kangaroo rats (Rodentia: Heteromyidae) during simulated attacks. *Biol. J. Linn. Soc.* **XX**, 1-10.
- Gregoire, L., Veeger, H. E., Huijling, P. A. and Van Ingen Schenau, G. J. (1984). Role of mono- and biarticular muscles in explosive movements. *Int. J. Sports Med.* **5**, 301-305.
- Jacobs, R., Bobbert, M. F. and Van Ingen Schenau, G. J. (1996). Mechanical output from individual muscles during explosive leg extensions: the role of biarticular muscles. *J. Biomech.* **29**, 513-523.
- Ker, R. F. (1981). Dynamic tensile properties of the plantaris tendon of sheep (*Ovis aries*). *J. Exp. Biol.* **93**, 283-302.
- Lutz, G. J. and Rome, L. C. (1994). Built for jumping: the design of the frog muscular system. *Science* **263**, 370-372.
- Marsh, R. L. and John-Adler, H. B. (1994). Jumping performance of hylid frogs measured with high-speed cine film. *J. Exp. Biol.* **188**, 131-141.
- 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**, jeb161661.
- McGowan, C. P., Baudinette, R. V., Usherwood, J. R. and Biewener, A. A. (2005a). The mechanics of jumping versus steady hopping in yellow-footed rock wallabies. *J. Exp. Biol.* **208**, 2741-2751.
- McGowan, C. P., Baudinette, R. V. and Biewener, A. A. (2005b). Joint work and power associated with acceleration and deceleration in tammar wallabies (*Macropus eugenii*). *J. Exp. Biol.* **208**, 41-53.
- McGowan, C. P., Baudinette, R. V. and Biewener, A. A. (2007). Modulation of proximal muscle function during level versus incline hopping in tammar wallabies (*Macropus eugenii*). *J. Exp. Biol.* **210**, 1255-1265.
- Moore, T. Y. and Biewener, A. A. (2015). Outrun or outmaneuver: predator-prey interactions as a model system for integrating biomechanical studies in a broader ecological and evolutionary context. *Integr. Comp. Biol.* **55**, 1188-1197.
- Moore, T. Y., Rivera, A. M. and Biewener, A. A. (2017). Vertical leaping mechanics of the Lesser Egyptian Jerboa reveal specialization for maneuverability rather than elastic energy storage. *Frontier. Zool.* **14**, 32.
- Peplowski, M. M. and Marsh, R. L. (1997). Work and power output in the hindlimb muscles of Cuban tree frogs *Osteopilus septentrionalis* during jumping. *J. Exp. Biol.* **200**, 2861-2870.
- 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.
- Van Soest, A. J., Roebroek, M. E., Bobbert, M. F., Huijling, P. A. and Van Ingen Schenau, G. J. (1985). A comparison of one-legged and two-legged countermovement jumps. *Med. Sci. Sport Exerc.* **17**, 635-639.
- Webster, D. B. and Webster, M. (1980). Morphological adaptations of the ear in the rodent family Heteromyidae. *Am. Zool.* **20**, 247-254.
- Weis-Fogh, T. and Alexander, R. M. (1977). *The Sustained Power Output from Striated Muscle. Scale Effects in Animal Locomotion*. London: Academic Press.
- Zajac, F. E., Neptune, R. R. and Kautz, S. A. (2002). Biomechanics and muscle coordination of human walking. Part I: Introduction to concepts, power transfer, dynamics and simulations. *Gait Posture* **16**, 215-232.