

The mechanics of jumping *versus* steady hopping in yellow-footed rock wallabies

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Summary

The goal of our study was to explore the mechanical power requirements associated with jumping in yellow-footed rock wallabies and to determine how these requirements are achieved relative to steady-speed hopping mechanics. Whole body power output and limb mechanics were measured in yellow-footed rock wallabies during steady-speed hopping and moving jumps up to a landing ledge 1.0 m high (~3 times the animals' hip height). High-speed video recordings and ground reaction force measurements from a runway-mounted force platform were used to calculate whole body power output and to construct a limb stiffness model to determine whole limb mechanics. The combined mass of the hind limb extensor muscles was used to estimate muscle mass-specific power output. Previous work suggested that a musculoskeletal design that favors elastic energy recovery, like that found in tammar wallabies and kangaroos, may impose constraints on mechanical power generation. Yet rock wallabies regularly make large jumps while maneuvering through their environment. As jumping often requires high power, we hypothesized that yellow-footed rock wallabies would be able to generate

substantial amounts of mechanical power. This was confirmed, as we found net extensor muscle power outputs averaged 155 W kg⁻¹ during steady hopping and 495 W kg⁻¹ during jumping. The highest net power measured reached nearly 640 W kg⁻¹. As these values exceed the maximum power-producing capability of vertebrate skeletal muscle, we suggest that back, trunk and tail musculature likely play a substantial role in contributing power during jumping. Inclusion of this musculature yields a maximum power output estimate of 452 W kg⁻¹ muscle.

Similar to human high-jumpers, rock wallabies use a moderate approach speed and relatively shallow leg angle of attack (45–55°) during jumps. Additionally, initial leg stiffness increases nearly twofold from steady hopping to jumping, facilitating the transfer of horizontal kinetic energy into vertical kinetic energy. Time of contact is maintained during jumping by a substantial extension of the leg, which keeps the foot in contact with the ground.

Key words: locomotion, jumping, hopping, muscle power, rock wallaby, *Petrogale xanthopus*.

Introduction

In an uneven and unpredictable world, many terrestrial animals that utilize energy-saving mechanisms while moving at steady speed are confronted with the need to generate substantial mechanical power to accelerate or jump in order to avoid an obstacle, negotiate uneven terrain, or evade a predator. During steady locomotion over level ground, animals employ various mechanisms to minimize the energy required to maintain a constant speed. At faster speeds this is often characterized by a bouncing gait, such as running, trotting or hopping, in which animals may use compliant structures to store and return elastic strain energy during the stance phase of a stride (Cavagna, 1977; Heglund, 1982). Excellent examples of this are large macropod marsupials (kangaroos and wallabies), which are able to store and recover as much as 35% of the mechanical energy of a single hop in their ankle

extensor tendons alone (Alexander and Vernon, 1975; Ker et al., 1986; Biewener and Baudinette, 1995).

However, a spring system can only return the energy that has been previously stored in it. Additional mechanical power needed to accelerate or decelerate during non-steady locomotion must be supplied by the contractile elements of the muscles. It has also been suggested that musculoskeletal designs favoring elastic energy storage may be constrained in their ability to generate large amounts of power (Biewener, 1998; Biewener and Roberts, 2000; Daley and Biewener, 2003), although there is evidence of distal muscle–tendon units that contribute substantial shortening work for incline running (Gabaldon et al., 2004; Roberts et al., 1997). While much work has contributed to understanding the mechanics of energy-saving mechanisms during steady-speed locomotion, only

recently have a few studies addressed the mechanics of generating power to meet the non-steady demands that animals often encounter moving in their environment (Dutto et al., 2004; McGowan et al., 2005; Roberts and Scales, 2002, 2004).

The aim of this study was to explore the differences in whole-body mechanics associated with steady-speed hopping vs moving jumps in yellow-footed rock wallabies *Petrogale xanthopus* L. by means of force plate and high-speed video analysis. Rock wallabies provide an excellent model for investigating these differences due to the diversity of habitats that they naturally utilize. Rock wallabies forage in open ground, presumably benefiting from elastic energy storage while hopping at steady speeds, but make their homes in steep cliff environments in which they are required to make jumps of up to several times their body length. Previous work on macropods has shown that the ability to store elastic energy in their ankle extensor tendons contributes greatly towards a unique locomotor economy (Alexander and Vernon, 1975; Biewener and Baudinette, 1995) and that this may be a general feature of this clade (Bennett and Taylor, 1995). Recent studies of tammar wallabies *Macropus eugenii* L. showed that their ability to store and recover elastic energy is not compromised when hopping on an incline (Biewener et al., 2004), and that they are capable of producing relatively high muscle power outputs during level accelerations (McGowan et al., 2005). However, unlike rock wallabies, tammar wallabies are not known habitually to make large jumps.

Because jumping involves high power output, it has often been used to explore the limits of mechanical power produced by muscles (Aerts, 1998; Bennet-Clark, 1977; Marsh and John-Alder, 1994; Peplowski and Marsh, 1997; Roberts and Marsh, 2003). In vertebrates, mean muscle power outputs as high as 1100 W kg^{-1} muscle have been estimated for jumping in galagoes (Aerts, 1998; Hall-Craggs, 1965) and 800 W kg^{-1} muscle for jumping in Cuban tree frogs (Peplowski and Marsh, 1997). As these values exceed the maximum power producing capability of vertebrate skeletal muscle ($\sim 250\text{--}400 \text{ W kg}^{-1}$; Weis-Fogh and Alexander, 1977; Lutz and Rome, 1994; Marsh and John-Alder, 1994), it is likely that these animals use energy storage mechanisms to amplify their power output. Roberts and Marsh (2003) have shown that this is likely to be the case for bullfrogs. The mechanisms presented in the above studies all likely rely on an animal's ability to store strain energy in elastic elements prior to moving, and then release this energy rapidly when the animal accelerates (Aerts, 1998; Marsh 1999; Roberts and Marsh, 2003). Further modeling studies have shown that the presence of an elastic element in series with a muscle and an inertial load can amplify power output by as much as twofold (Alexander, 2002; Galantis and Woledge, 2003).

To date, relatively few studies (Alexander, 1974; Depena and Chung, 1988; Seyfarth et al., 1999; Stefanyshyn and Nigg, 1998) have explored jumping from a moving start, and little is known about the power outputs achieved during such activity. Therefore, a goal of this study was to measure the whole body mechanical power output during moving jumps of yellow-

footed rock wallabies. From this, muscle power output was calculated based on the assumption that the majority of the whole body power was provided by the hind limb extensor muscles.

In addition to looking at whole body and muscle power generation, we sought to examine several kinematic and kinetic parameters associated with jumping compared with steady hopping. Differences in hopping speed, time of contact, leg extension, leg angle and initial leg stiffness were analyzed to evaluate how wallabies approached and executed a jump compared with steady-speed hopping. We expected that the wallabies would use similar approach speeds, as the condition of our study was a jump for height and not distance (Alexander, 1990). However, we anticipated that the rock wallabies would have a longer period of ground contact, increasing the time available to accelerate their body. We expected that net leg extension during stance would also be greater in jumping to achieve the vertical acceleration required to reach the platform height. Both leg contact angle and leg stiffness have been shown to play an important role in converting an individual's forward horizontal kinetic energy into vertical kinetic energy in human long-jumps and high-jumps (Alexander, 1990; Seyfarth et al., 1999). Thus, we predicted that the wallabies would contact the ground with a shallower leg angle and have a higher initial leg stiffness during jumping.

Materials and methods

Animals

Four adult yellow-footed rock wallabies *Petrogale xanthopus* L. (one male and three female, ranging from 5.10 to 5.50 kg body mass) were obtained from a captive breeding colony at the Adelaide Zoo in Adelaide, South Australia. The threatened status of these animals made them difficult to obtain and limited experimentation to non-invasive techniques only. All procedures, care and use of the animals for the study were approved by the University of Adelaide Animal Ethics Committee. Throughout the experiments, the animals were housed at the Waite Institute campus of Adelaide University in a system of large outdoor paddocks. Runways for conducting steady hopping and jumping experiments were constructed within the confines of one of these paddocks.

Runways and experimental protocol

To record steady-speed hopping, a $20 \text{ m} \times 0.75 \text{ m}$ runway was constructed from 1 m high light-gauge field fence strung from fence posts placed in the ground over a relatively level ($\sim 5\%$ grade) stretch of the grassy outdoor paddock. The fences had to be extended to 3 m high with shade cloth to keep the animals from jumping out of the runway, which was closed at both ends to contain the animals. A $0.60 \text{ m} \times 0.40 \text{ m}$ force plate was set flush with the ground at approximately the midpoint of the runway. The force plate was positioned on a 5 cm thick concrete slab buried in the ground and a wooden frame the same depth as the force plate was used to keep the surrounding soil from contacting the plate. The wallabies were placed in

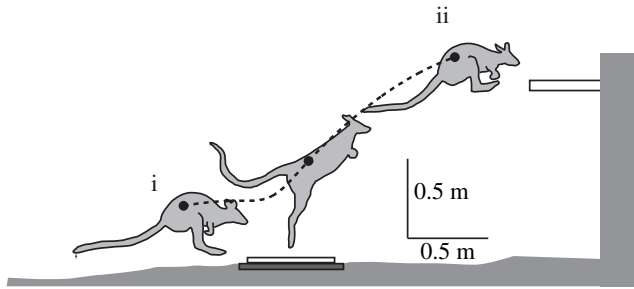


Fig. 1. A schematic of the runway used to collect jumping trials showing the position of the force plate, the height of the jump and rock wallaby's actual body size relative to the jump. The first outline (i) and the last outline (ii) are representative of the frames chosen to calculate initial velocity conditions (see text for details).

the runway area and encouraged to hop from end to end. Only trials in which the animals were moving up the slight grade were recorded. Approximately 15–20 trials were collected from each animal; however, only a small subset of these was considered suitable for analysis. For trials to be included, the wallaby had to hop at a relatively steady forward velocity (<10% change in velocity while the animal was in contact with the force plate, as determined by integration of the horizontal ground reaction force and the initial horizontal velocity), both feet had to strike the plate simultaneously, and all joint markers had to be visible for video analysis. A total of 18 trials, with a minimum of four trials from each animal, fit these criteria for analysis.

In order to collect data for moving jumps, a mound 3 m high was constructed of soil and stone with ledges made of wooden beams. This was integrated with a second 25 m × 0.75 m runway built of the same light-gauge field fence and shade-cloth walls. The runway was open at both ends and provided a 15 m approach to a ledge 1.10 m high (Fig. 1). The force plate was positioned in the middle of the runway on 5 cm thick concrete slab with the center of the plate 1.3 m from the ledge. Placement of the force plate was determined by hopping the animals through the runway and noting their preferred take-off position. The wallabies were chased into an opening at the approach end of the runway and allowed to make the jump at their preferred speed. Once in the runway, the animals readily moved through to a hiding area provided on the far side of the mound. Between 15 and 20 jumps were recorded for each animal. But again, only a small sample fit the study's analysis criteria. Trials were analyzed when both of the wallabies' feet contacted the force plate simultaneously with all joint markers visible and the animal's jump was dominantly in the sagittal plane (medio-lateral ground reaction force impulse <5% of vertical impulse). A total of 20 jumping trials, representing five moving jumps from each animal, were included in the final jumping analysis.

Video data

Jumping and level hopping trials were filmed in lateral view using a digital high-resolution high-speed video camera

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

Ground reaction forces and mechanical energy

Ground reaction forces (GRF) were recorded using a multi-component piezoelectric force-plate (Kistler type 9286AA, Kistler Instruments Corp., Amherst, NY, USA) equipped with an integrated charge amplifier (crosstalk between channels <1.0%). Forces were recorded in the vertical, horizontal and lateral directions. Lateral forces were small as a requirement for analysis of the trials, and for the purposes of this study were ignored. Force-plate recordings were sampled at 2500 Hz, transferred to computer, and stored by means of a BioWare™ type 2812A1-3 A/D system (DAS1602/16 A/D board) operated using BioWare v.3.0 software (Kistler Instruments Corp.).

Integration of the vertical and horizontal ground reaction forces, with simple assumptions about initial velocity and position conditions, provides an accurate means of determining changes in the velocity and position of an animal's center of mass (CoM) during the support period of a stride (Cavagna, 1975). However, this approach has traditionally been used in experiments where subjects move at a steady-speed on level ground, in which the subject's average forward velocity and zero net change in CoM height provide good estimates of initial conditions. In non-steady activities, such as the moving jumps studied here, neither of these conditions applies. Because of this, we developed and adopted a technique that minimizes dependence on kinematic information to determine the animal's initial velocities in the horizontal and vertical directions. With the actual position of the wallaby's CoM unknown in any given frame, its ilium was used as proxy of CoM position. Two widely spaced (not necessarily the first and last) video frames were chosen, in which the body was in a similar posture, with a similar CoM position relative to the proxy point (Fig. 1). Our method assumes that when all forces acting on the CoM between the initial and final position are known (ignoring aerodynamic drag), only one set of initial conditions produces a path that goes through both the initial and final CoM proxy. These initial conditions are determined mathematically following the equations provided in Appendix A. Even if an exact postural match was not possible, the large

interval between initial and final frames ensured that information derived from movements of the whole body overwhelmed the relatively small errors due to movements of the CoM within the body. At most, the actual CoM of the animal can shift an estimated 5 cm, relative to the proxy point, while during the span between the two selected video frames, the wallabies traveled approximately 1.1 m vertically and 1.5 m horizontally.

Using this approach to provide integration constants, GRF data were integrated to determine velocities of the CoM, which were used to calculate kinetic energy in both the horizontal and vertical directions. Vertical CoM velocity was integrated to determine CoM position, which was used to calculate gravitational potential energy (see Appendix A). These energies were summed to give the total mechanical energy of the wallaby's CoM.

Mechanical power was obtained by differentiating the animal's total energy with respect to time. It was assumed that the majority of power produced during steady hopping and jumping was produced by the extensor musculature in both hind legs, thus mechanical power was converted to muscle mass-specific power by dividing through by the total mass of the hind limb extensor muscles. In order to estimate the hind limb extensor muscle mass for the animals used in this study, dissections of five similarly sized cadavers (mass: 5.93 ± 1.78 kg, mean \pm S.D.) obtained from the Adelaide Zoo were conducted and total extensor muscle mass was calculated as a percentage of body mass.

Leg stiffness

To explore differences in initial leg stiffness between steady hopping and jumping trials, both legs were modeled as a single spring in series with a linear actuator and the body was considered to be a point mass located at the ilium point, which was a proxy for the position of the CoM. The presence of an actuator can have a significant influence on the apparent stiffness of the leg. Therefore, our model assumed that the actuator remained a fixed length until maximal compression and produced only positive work when the leg was extending in the later part of stance. All of the negative energy associated with leg compression was assumed to be stored in the spring element and recovered elastically. The length of the leg was measured as a line from the ilium point to the tip of the toe, spanning the hip, knee, ankle and metatarsalphalangeal joints. The ilium point was chosen instead of the hip point because the hip likely plays a large role in controlling CoM position, and thus affects limb stiffness. The initial length of the leg (L_0) was determined at foot touch-down. Changes in leg length ($\Delta L_{(t)}$) were measured throughout stance, and leg stiffness was determined at the time of maximum leg compression ($\Delta L_{(t)\max}$) by the ratio:

$$k_{\text{leg}} = \mathbf{F}_{R(t)} / \Delta L_{(t)\max}$$

where k_{leg} is leg stiffness and $\mathbf{F}_{R(t)}$ is the resultant GRF at the time of maximum leg compression. This differs from previous mass-spring models developed for steady locomotion (Farley

et al., 1993; McMahon and Cheng, 1990), which assume that the GRF curve and changes in leg length are relatively symmetrical during stance and calculate leg stiffness as the ratio of peak resultant GRF to maximum leg compression. In rock wallabies these events do not coincide and there is net extension of the limb in both steady speed and jumping. For the purpose of this study, we were interested in the leg's ability to resist compression and redirect the CoM, therefore we chose to calculate initial leg stiffness at the point of maximum leg compression as described above.

Kinematics

The leg model was also used to measure limb angles, relative to the horizontal, at foot touch-down and take-off. The horizontal velocity of the wallabies, as they approached the force plate, was determined by the same technique used to derive the integration constants (see above and Appendix A). The magnitude and orientation of the velocity vector of the CoM at take-off were also determined from the integrated vertical and fore-aft horizontal ground reaction forces. Time of contact was measured from the force plate when the vertical force was greater than 1.5 N (>3% body weight).

Statistics

A repeated-measures analysis of variance (ANOVA) was used to determine statistical significance between steady-speed and jumping trials. Mean variables were determined for each animal by averaging across the trials that each performed. These were in turn used to calculate mean values for steady speed and jumping. No significant effect of individual on the variables measured was determined by ANOVA. All variables comparing level hopping and jumping are reported as means \pm S.E.M. Body mass and percent hind limb muscle mass are reported as mean \pm S.D., as these address individual variation.

Results

The average forward velocity of the wallabies approaching the jump did not differ from the speed that they used when moving through the steady-speed course (4.14 ± 0.18 ms⁻¹ and 4.22 ± 0.12 ms⁻¹, respectively; mean \pm S.E.M.). The average change in horizontal velocity during stance was $4.3 \pm 0.7\%$ in steady trials and $-16.0 \pm 1.1\%$ during jumps, indicating large decelerations in jumping trials. The time of contact was consistent in all trials and was not significantly different between conditions, averaging 116 ± 4 ms in steady hopping and 120 ± 5 ms during jumps. The magnitude of the velocity vector of the CoM at take-off in steady hopping was 4.70 ± 0.16 m s⁻¹ and 5.23 ± 0.14 m s⁻¹ during jumping trials. While this difference was small, it was significant ($P=0.047$). The angle of the velocity vector at take-off was much steeper in jumping trials ($48.8 \pm 0.8^\circ$) than in steady trials ($20.7 \pm 1.3^\circ$, $P<0.0001$).

Ground reaction forces

The ground reaction forces (GRF) produced by the rock

wallabies during steady hopping and jumping differed significantly in magnitude and timing, leading to significant differences in the impulses produced in both the vertical and horizontal directions (Fig. 2). The mean GRF vector during stance is shown in Fig. 2A, overlaid on an outline of a wallaby showing the average limb angle during stance for steady-speed hopping and for jumping. In steady-speed trials, the mean GRF angle was $1.8 \pm 0.5^\circ$ relative to vertical, while during jumping trials the mean angle was $-6.4 \pm 1.3^\circ$. During steady-speed

trials, the vertical ground reaction force (V_{GRF}) peaked at $41.4 \pm 0.9\%$ of stance and, normalized to body weight (BW), the peak magnitude averaged 6.37 ± 0.31 BW. In jumping trials, the peak V_{GRF} was reached later, at $45.9 \pm 1.0\%$ of stance and the average peak magnitude was 8.35 ± 0.43 BW. Both values were significantly greater in the jumping trials ($P < 0.017$). Due to these differences in magnitude and timing, the vertical impulse produced during stance was also significantly greater in jumping trials than in steady-speed trials (0.53 ± 0.04 BW s and 0.40 ± 0.01 BW s, respectively, $P = 0.020$; Fig. 2C).

Not surprisingly, patterns of the fore–aft horizontal ground reaction force (H_{GRF}) also differed significantly for the two locomotor conditions (Fig. 2B). In steady-speed trials, a negative or decelerating force was produced for the first 40% of stance followed by positive or accelerating force for the remainder of stance. Peak negative and peak positive forces were similar in magnitude, averaging -0.99 ± 0.07 BW and 1.04 ± 0.08 BW, peaking at ~ 25 and 65% of stance, respectively. In contrast, during jumping H_{GRF} was almost entirely decelerating, being negative for the first 68% of stance with a peak negative H_{GRF} of -2.15 ± 0.18 BW occurring at $\sim 29\%$ of stance. The smaller positive peak H_{GRF} averaged 0.50 ± 0.08 BW and was reached at $\sim 80\%$ of stance. As for vertical ground reaction force, all horizontal ground reaction force timing and magnitude variables differed significantly between steady-speed and jumping trials ($P < 0.007$). As a requirement of the steady-speed trials, positive and negative horizontal impulses were similar (0.04 ± 0.01 BW s and -0.02 ± 0.01 BW s, respectively); however, on average, the trials were slight accelerations. The resulting net horizontal impulse was near zero (0.02 ± 0.01 BW s; Fig. 2C). Because of the temporal (and thus horizontal) force asymmetry during jumping trials, the wallabies produced a large negative impulse (-0.08 ± 0.01 BW s) and only a small positive impulse (0.01 ± 0.01 BW s). This resulted in a net negative impulse (-0.07 ± 0.01 BW s) that decelerated the animals by roughly 16% of their forward speed as they initiated their jumps.

Changes in CoM energy

During the stance phase of the jumps, the wallabies generated a substantial amount of net mechanical energy, which was primarily associated with large changes in CoM kinetic energy. Not surprisingly, net fluctuations in energy were relatively small during steady-speed trials (Fig. 3). The majority of CoM energy gained in jumping resulted from a large increase in the animal's vertical kinetic energy (KE_{vert}) that was generated between 30% and 80% of stance (Fig. 3B). This energy gain occurred simultaneously with a loss in the animal's horizontal kinetic energy (KE_{horiz} , Fig. 3C), resulting in a net change in total energy (E_{tot} , Fig. 3D) that was less than the net gain in KE_{vert} . An elevation of the CoM during stance also produced a net increase in gravitational potential energy (PE ; Fig. 3A); however, this contributed much less to the gain in E_{tot} . Net changes in energy during steady-speed trials were small relative to jumping trials. On average a small net increase in E_{tot} was observed, due to the fact that the steady-speed

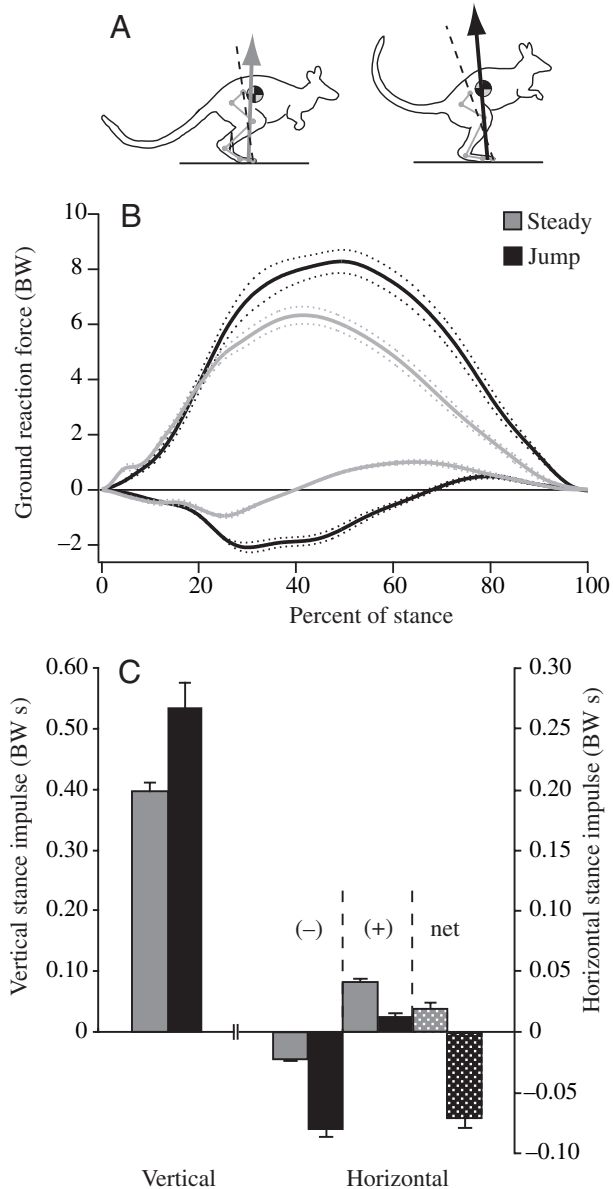


Fig. 2. Mean ground reaction force (GRF) data for steady-speed hopping (gray) and jumping (black). (A) The GRF vector is shown relative to the rock wallaby's average body position, leg angle (broken line) and estimated CoM position during stance. (B) Mean GRF recordings in body weights (BW) plotted against percent of stance. (C) Vertical and horizontal stance impulses. Horizontal impulses are divided into negative (-), positive (+) and net (patterned bars) impulses. Dotted lines (B) and error bars (C) indicate S.E.M.

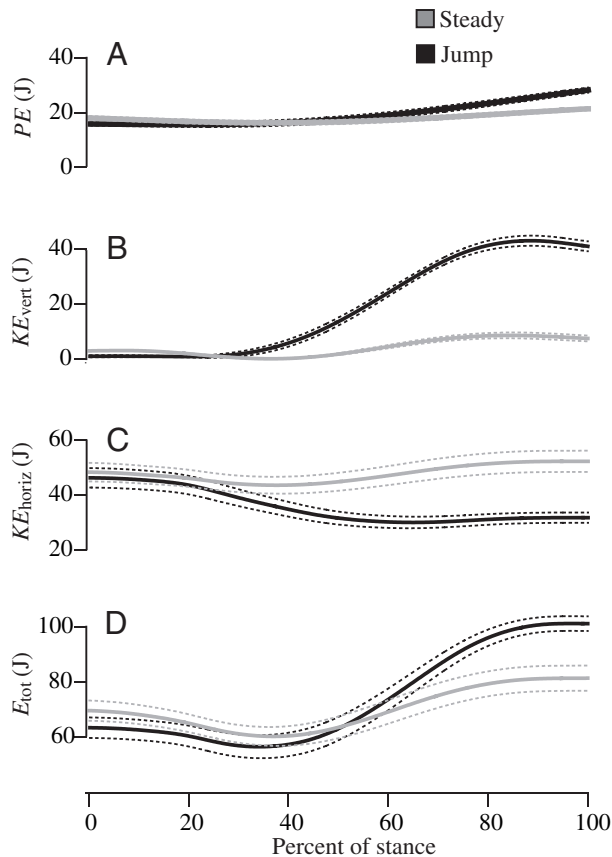


Fig. 3. Mean changes in (A) gravitational potential energy (PE), (B) vertical kinetic energy (KE_{vert}), (C) horizontal kinetic energy (KE_{horiz}) and (D) total energy (E_{tot}) during stance, plotted for steady-speed (gray) and jumping (black) trials. Dotted lines indicate S.E.M.

runway was on an approx. 5% gradient and the animals accelerated slightly when hopping on the force plate. Small net increases in PE , KE_{vert} and KE_{horiz} contributed equally to the small gain in E_{tot} (Fig. 3D).

Mechanical power and work

Rock wallabies generated the power required to make the jumps examined here by more than doubling the energy produced during the latter 62–65% of stance. In contrast, the energy and power absorbed (and potentially stored elastically) in the first 35–38% of stance was similar for jumping and steady-speed hopping (Fig. 4A). Peak positive CoM power outputs averaged $103.1 \pm 9.7 \text{ W kg}^{-1} M_b$ in steady-speed trials compared with $208.0 \pm 16.3 \text{ W kg}^{-1} M_b$ in jumping trials. The highest peak CoM power recorded during jumping was $\sim 280 \text{ W kg}^{-1} M_b$.

The animal's mean power was determined by averaging its CoM power output over the entire period of stance. This mean power output represents the minimum that the animal's limb and trunk muscles would have to produce; assuming that all of the negative power is recovered by elastic elements in the limbs, trunk and tail, and work from the muscles can only be contributed while the foot is in contact with the ground. Mean

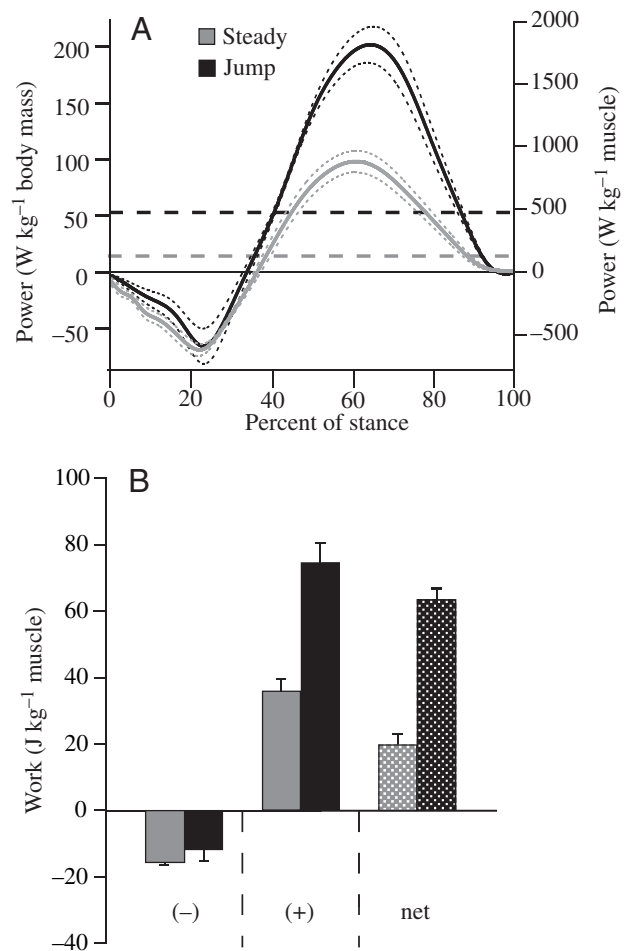


Fig. 4. Mean power and work produced during steady speed (gray) and jumping (black) trials. (A) Power output during stance normalized to body mass (left y axis) and hind limb extensor muscle mass (right y axis). Horizontal broken lines represent the mean power produced during stance. (B) Negative (-), positive (+) and net (patterned bars) muscle mass-specific work produced during stance. Dotted lines (A) and error bars (B) indicate S.E.M.

CoM power recorded for steady-speed hopping ($19.0 \pm 3.3 \text{ W kg}^{-1} M_b$) averaged one-third of that achieved during jumping ($60.9 \pm 1.9 \text{ W kg}^{-1} M_b$), which reached values as high as $79 \text{ W kg}^{-1} M_b$.

Assuming that the observed CoM power was produced by the combined action of the extensor musculature of the hind limbs ($12.31 \pm 0.55\% M_b$), peak muscle mass-specific power outputs ranged from $837.6 \pm 78.4 \text{ W kg}^{-1}$ during steady-speed hopping to $1689.7 \pm 132.1 \text{ W kg}^{-1}$ muscle during jumping. It is important to note that these values ignore any contribution by pelvic and trunk extensor muscles. Averaged over the entire stance phase, mean hind limb extensor muscle power output was $154.5 \pm 26.7 \text{ W kg}^{-1}$ during steady hopping and $495.0 \pm 15.0 \text{ W kg}^{-1}$ during jumping, reaching a value as high as 639 W kg^{-1} (Fig. 4A). The difference in mean power between steady-speed and jumping trials was due to the large increase in positive power output in the second half of stance.

Whereas mean muscle mass-specific power averaged over the positive portion of the power curve more than doubled from $488.2 \pm 50.3 \text{ W kg}^{-1}$ during steady hopping to $1030 \pm 83.5 \text{ W kg}^{-1}$ during jumping, average negative power did not differ significantly between conditions (steady hopping: $-218.9 \pm 9.0 \text{ W kg}^{-1}$ vs jumping $-169.3 \pm 47.9 \text{ W kg}^{-1}$; $P=0.348$).

Consistent with differences in power production, net work by the muscles was threefold less during steady-speed hopping ($19.6 \pm 3.1 \text{ J kg}^{-1}$) muscle compared with jumping ($62.7 \pm 3.1 \text{ J kg}^{-1}$; Fig. 4B). The net positive work done during steady-speed hopping again reflects minor accelerations and the runway being on a slight gradient. The close match between differences in muscle work and differences in average power reflects the fact that the time of limb contact on the ground did not differ between conditions. Consequently, differences in net muscle work were, again, predominately due to differences in positive work rather than negative work, which was nearly the same for both conditions ($P=0.282$).

Limb kinematics and stiffness

The mean angle of attack of the leg (α_{on} , Fig. 5A) at the beginning of stance during steady hopping was $49.7 \pm 1.9^\circ$, relative to the horizontal. In jumping trials, the angle of attack was significantly shallower, averaging $42.7 \pm 1.1^\circ$ ($P=0.018$). The limb angles at take-off (α_{off} , Fig. 5A) were also significantly different, with the mean angle during jumping being $80.3 \pm 0.7^\circ$ as compared to $61.6 \pm 0.4^\circ$ during steady hopping ($P < 0.0001$). The unloaded 'initial' length of the leg (L_0) determined at foot-down was $0.41 \pm 0.01 \text{ m}$ and did not differ significantly between steady hopping and jumping trials ($P=0.472$). The minimum leg length, or maximum compression of the limb (ΔL), was reached earlier in stance during jumping (41% of stance, Fig. 5C) than in steady-speed trials (47% of stance, Fig. 5B). Thus, in jumping trials a larger proportion of stance time was spent extending the limb. Leg compression, measured as a percentage of L_0 ($\Delta L_{\text{max}}/L_0$), averaged $27.7 \pm 2.2\%$ in steady-speed trials (Fig. 5B). While this was greater than the $20.0 \pm 3.3\%$ measured during jumping trials (Fig. 5C), the difference was not significant ($P=0.101$). In all trials, leg length was greater at take-off than at touch-down, resulting in net leg extension (L_{ext}) more than three times greater during jumping trials (Fig. 5B,C). Net leg extension averaged $7.0 \pm 1.7\%$ during steady hopping compared with $24.5 \pm 2.6\%$ during jumping.

Leg stiffness was determined for the initial landing phase of stance only, based on the point of maximum leg compression relative to initial contact leg length. Peak GRF at this time was significantly greater during jumping trials (jumping: $409.77 \pm 19.19 \text{ N}$ vs steady: $322.45 \pm 19.19 \text{ N}$; $P=0.021$). As a result, when coupled with having less leg compression (above), initial leg stiffness was nearly twice as high during jumping ($5.50 \pm 0.71 \text{ kN m}^{-1}$) compared with steady-speed hopping ($2.98 \pm 0.31 \text{ kN m}^{-1}$, $P=0.018$).

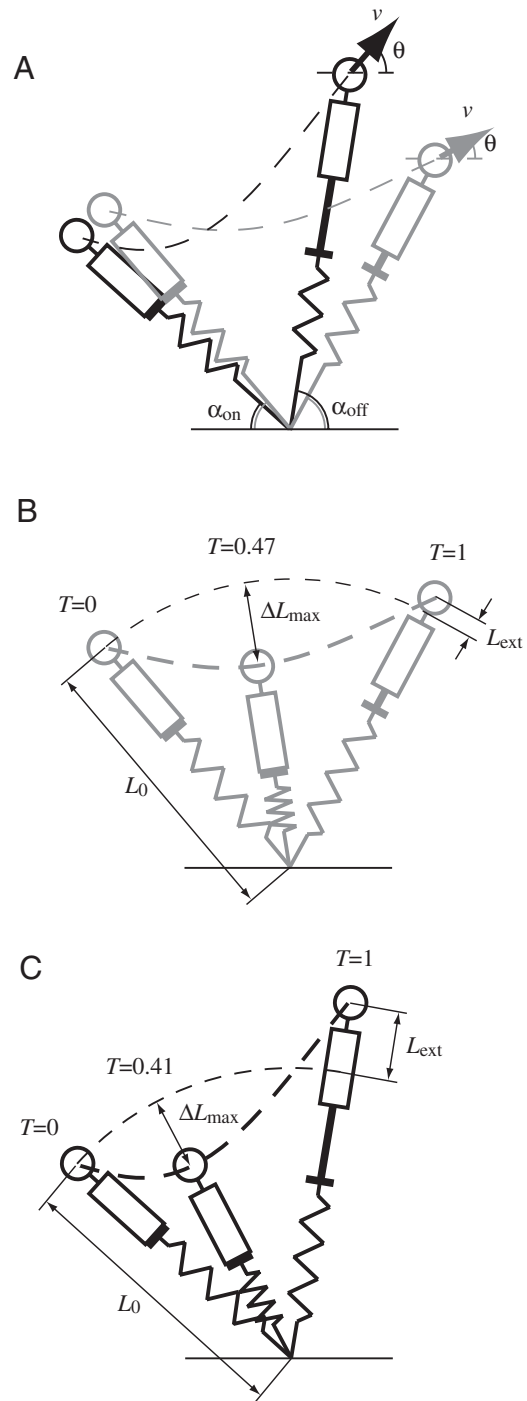


Fig. 5. A schematic of the virtual leg model representing the mean values for the variables measured during steady-speed (gray) and jumping (black) trials. (A) Leg angle of attack (α_{on}), leg angle at take-off (α_{off}), and the CoM velocity vector at take-off (v). The arrows represent the relative magnitude and angle (θ) of velocity vector. (B,C) Initial leg length (L_0), path of the CoM (thick broken line), path of the of the CoM if the leg did not compress (thin broken line) and the point of maximum leg compression (ΔL_{max}), as a function of normalized stance time (T) for steady-speed (B) and jumping (C) trials. The relative angles of the legs shown are representative of the mean leg angles observed, as is the relative amount of leg extension measured at take-off (L_{ext}).

Discussion

The goal of our study was to explore the mechanical power requirements associated with jumping in yellow-footed rock wallabies and to determine how these requirements are achieved relative to steady-speed hopping mechanics. Jumping can require extremely high muscle power output. Although a musculoskeletal design favoring elastic energy savings, like that found in wallabies and kangaroos, may limit an animal's ability to produce high power (Biewener and Bertram, 1991; Biewener, 1998; Biewener and Roberts, 2000; Daley and Biewener, 2003), rock wallabies regularly make large jumps while maneuvering in their natural environment. Our analysis of moving jumps, which appear well within their performance range, shows that rock wallabies achieve substantial whole body and muscle mass-specific power output, averaging 208 W kg^{-1} and 495 W kg^{-1} , respectively. Our analysis indicates that in addition to the legs, muscles of the back, pelvis and tail are likely important in contributing mechanical power for jumping. Additionally, it is possible that elastic elements in the legs may act to amplify the power output of the muscles (Alexander, 2002; Anderson and Pandey, 1993; Wilson et al., 2003; Galantis and Woledge, 2003; Roberts and Marsh, 2003; and see discussion below). However, this possibility is difficult to examine and could not be tested in the current study.

Whether or not the ability of rock wallabies to generate considerable mechanical power during relatively pedestrian jumps reflects a more limited capacity for elastic energy storage during steady hopping requires further study. Nevertheless, because steady movement is unlikely to be a frequent occurrence in their natural environment, it is reasonable to expect that selection for elastic savings may not be strong in these and other rock wallaby species. It is noteworthy that similarly sized tammar wallabies, which can store significant energy in their leg tendons (Biewener and Baudinette, 1995) and reduce their metabolic cost of steady hopping (Baudinette et al., 1992), were unwilling to make the 1 m high jumps in this study. Our casual observation is that tammar wallabies hop around rather than over barriers, which rock wallabies readily negotiate.

Mechanical power output during moving jumps

The height and distance of the jumps in this study were approximately equal ($\sim 1 \text{ m}$); however, the horizontal distance traveled during the jumps was only slightly greater than that traveled during the aerial phase of a steady-speed hop ($\sim 0.75 \text{ m}$). Therefore, we characterized this jump as one for height rather than distance. Consistent with our predictions for a jump to gain height, rock wallabies use similar approach speeds when jumping as they do during steady hopping. However, in contrast to our expectation, rock wallabies do not increase their time of contact to increase the ground impulse during moving jumps. Thus, the nearly threefold greater net work performed during jumping (Fig. 4B) has to be produced in the same period of time as in steady-speed hopping. This leads to extremely high power outputs in jumping.

The whole body and muscle mass-specific power outputs

measured during jumping are comparable to those found in previous studies of standing jumps in vertebrates. Net hind limb extensor muscle power averaged nearly 500 W kg^{-1} and reached values as high as 639 W kg^{-1} . While this is not as high as 1100 W kg^{-1} reported for galagoes *Galago senegalensis* (Aerts, 1998) or 800 W kg^{-1} measured in Cuban tree frogs *Osteopilus septentrionalis* (Peplowski and Marsh, 1997), the jumps made by the rock wallabies reported here almost certainly did not represent their maximal effort. Even so, these values likely exceed the maximum power producing capability of vertebrate skeletal muscle ($250\text{--}400 \text{ W kg}^{-1}$; Weis-Fogh and Alexander, 1977; Lutz and Rome, 1994; Marsh and John-Alder, 1994). In galagoes and frogs, it has been shown that these exceptionally high power outputs are achieved through a mechanical power amplifier.

In a jump from rest, animals are able to load elastic elements in the limbs prior to leg extension, allowing muscle work to be stored as elastic energy, which can be recovered rapidly just prior to take-off, amplifying the mechanical power produced by the muscles. Although the rock wallabies were moving prior to the jump, muscle power may still be amplified by the presence of elastic elements in series with their muscles. In addition to releasing energy much faster than muscles can do work, energy release from tendon recoil is nearly independent of speed (Ker, 1981). In contrast, the force and work that a muscle can produce declines at faster shortening velocities. Thus, even when an animal is moving its leg muscles may contract throughout most of stance, doing work to stretch the tendons. The tendons then recoil rapidly at the end of stance as their tension drops, returning the energy in a very brief period of time. Modeling studies have shown that the presence of an inertial load in series with a muscle tendon unit can result in power outputs of up to twice what muscles alone can produce (Alexander, 2002; Galantis and Woledge, 2003). Given the anatomy of the rock wallabies' hind limbs, we believe that some power amplification likely occurs; however, our current data do not allow us to test this hypothesis.

Another likely explanation for the exceptionally high muscle power outputs estimated during rock wallaby jumping is that the hind limb extensor muscles are not the only muscles recruited to produce power. A recent study measuring power generation in accelerating tammar wallabies (McGowan et al., 2005) showed that in the largest accelerations the legs only supply 60–65% of the work done on the animal's CoM, with the remainder likely produced by movements of the trunk and tail. Therefore, a more accurate estimate of muscle power output in the present study should include muscles of the back, trunk and tail, in addition to hind limb extensors. While these measurements were not made on all of the cadavers used in this study, masses of the major back and tail muscles were taken for a single specimen. Together, these muscles constituted 5.1% of the animal's total body mass. Assuming that this is consistent in all animals, and given the hind limb extensor muscle mass constitutes 12.3% M_b , it is likely that at least 17% of the animal's body mass comprises muscles that could play a role in producing power during a jump. This would indicate that the muscles achieved a mass-specific

power output of 452 W kg⁻¹ muscle. While this value is still high, it is more likely within the range that vertebrate skeletal muscle can produce. Even so, it is unlikely that all of these muscles are fully active throughout stance. Consequently, we believe 452 W kg⁻¹ represents a minimum estimate for the muscle mass-specific power output achieved by the rock wallabies for what we believe were fairly pedestrian jumps.

Leg stiffness

In studies of human long-jumping, it has been shown that leg stiffness plays an important role in jump performance. A stiff leg and relatively steep angle of attack allows the jumper to generate a high vertical impact (Seyfarth et al., 1999), accelerating the body upward while much of the horizontal kinetic energy is translated into horizontal distance for the jump. And, while the jump in our study was for height rather than distance, we predicted that increased leg stiffness would play a role in jumping. Consistent with this prediction, the legs are nearly twice as stiff during jumping as they are in steady-speed hopping (5.5 kN m⁻¹ vs 3.0 kN m⁻¹). This increase in stiffness allows the leg to act to some degree as a strut, to redirect a portion of the animal's horizontal kinetic energy (KE_{horiz}) into vertical kinetic energy (KE_{vert}).

The majority of the energy for the jumps comes from the substantial gain in KE_{vert} between 30% and 75% of stance (Fig. 3B). This gain in KE_{vert} occurs simultaneously with a decrease of KE_{horiz} (Fig. 3C). This KE transfer reduces the amount of energy that must be supplied by the muscles by ~25%. However, because the increase in KE_{vert} is greater than the decrease KE_{horiz} , the muscles must supply this difference in energy to accelerate the body upward. Because the time of limb contact is unchanged from steady-speed hopping, the majority of the increase in muscle power is achieved through extension of the limb (L_{ext}), which the leg model shows is increased threefold (Fig. 5B,C).

The angle of attack of the leg used by the wallabies during jumping is only slightly shallower, relative to the ground, than in steady hopping, and within the range shown to produce maximum height in human high-jumping (~45–55°; Alexander, 1990; Dapena and Chung, 1988). It has been suggested that a shallower leg angle allows the foot to be on the ground longer while the body travels a longer distance (Alexander, 1990). A shallow leg angle is also associated with a greater negative horizontal GRF. In rock wallabies it is clear that a greater negative horizontal GRF is present during jumping (Fig. 2B,C); however, as noted above, the time of contact is unaffected. In fact, due to a much steeper angle at take off during jumps (Fig. 2A), the excursion angle of the leg is smaller than during steady-speed trails. Time of contact is maintained during jumping by increasing extension of the leg, which keeps the foot in contact with the ground.

Conclusions

For the jumps recorded in this study, estimates of muscle mass-specific power output (450 W kg⁻¹ muscle) suggest that all of the musculature of the legs, back and tail are recruited to

produce jumps and that power output is near the maximum expected for vertebrate skeletal muscle. Even so, the moving jumps examined in this study appeared routine for the animals. In over 70 jumping trials recorded, the wallabies only failed to make the jump twice. This suggests that jumps of greater height (and distance), of which we believe the animals are capable, would be associated with longer contact times. Otherwise, the muscles and elastic tissues would have to deliver more power. However, this remains to be tested. Although moving jumps may not allow as much power amplification *via* preloading of elastic elements in the limb compared with standing jumps, it is likely that rapid energy release from the tendons and other elastic elements significantly contributes to increased power output of rock wallaby jumping. This study does not specifically address the sources of power during jumping and further work is required to determine which muscle groups play the greatest role. Approach speed and limb angles suggest that the mechanics of the jump being made in this study is similar to human high-jumping. However, like human long-jumping, initial leg stiffness also appears to play a significant role and likely facilitates transfer of the animal's horizontal kinetic energy into vertical kinetic energy. Additional research is also required to determine which joints and muscle–tendon units change stiffness and how changes in individual joint stiffness and actuation affect overall leg stiffness.

In conclusion, our study shows that rock wallabies are capable of achieving very high mechanical power outputs during moving jumps. Whether this comes at the expense of tendon and aponeurosis strain energy savings by rock wallabies during steady level hopping will require a more detailed kinetic analysis of their level hopping mechanics.

Appendix A

Classical calculation of CoM mechanics from force platform measurements

Measured instantaneous forces f provide both horizontal and vertical instantaneous accelerations a given the total body mass m :

$$a_{\text{horiz}} = \frac{f_{\text{horiz}}}{m}; \quad (\text{A1})$$

$$a_{\text{vert}} = g + \frac{f_{\text{vert}}}{m}, \quad (\text{A2})$$

where g is the vertical acceleration due to gravity (–9.81 m s⁻²) and subscripts _{horiz} and _{vert} indicate horizontal and vertical components, respectively, throughout. These expressions can be integrated once to provide instantaneous velocities v at time t :

$$v_{\text{horiz}} = V_{\text{init,horiz}} + \int_t a_{\text{horiz}} dt; \quad (\text{A3})$$

$$v_{\text{vert}} = V_{\text{init,vert}} + \int_t a_{\text{vert}} dt, \quad (\text{A4})$$

with initial velocity conditions V_{init} acting as integration constants. This can be integrated again to provide instantaneous horizontal and vertical positions s :

$$s_{\text{horiz}} = S_{\text{init,horiz}} + \int_t v_{\text{horiz}} dt ; \quad (\text{A5})$$

$$s_{\text{vert}} = S_{\text{init,vert}} + \int_t v_{\text{vert}} dt , \quad (\text{A6})$$

given initial positions for integration constants S_{init} . Instantaneous kinetic and potential energies ke and pe can thus be derived from Eq. A3, A4 and A6:

$$ke = \frac{1}{2}m(v_{\text{horiz}}^2 + v_{\text{vert}}^2) \quad (\text{A7})$$

$$pe = mgs_{\text{vert}} . \quad (\text{A8})$$

Initial velocity conditions

The horizontal and vertical initial velocity conditions ($V_{\text{init,horiz}}$ and $V_{\text{init,vert}}$) required are critical: a small error in V_{init} results in a progressive error of instantaneous position over time, and subsequently whole-body energies are highly sensitive to V_{init} . These initial velocity conditions must be derived from kinematic observations – force platform measurements alone are not sufficient. While, for steady locomotion, average velocities are often close enough to initial velocities that they may be used as initial velocities, allowing simple methods of determining the integration constants (such as triggering photocells), this is clearly not the case for unsteady locomotion.

Using the kinematic information from two video frames widely spaced in time and in which the animal's posture is similar (see Materials and methods), the following equations can be employed to determine the initial velocities of the CoM.

Initial (subscript init) and final (subscript end) positions separated by a time T relate, by a combination of Eq. A1–A6, by

$$S_{\text{horiz,end}} = S_{\text{horiz,init}} + V_{\text{horiz,init}} T + \int_T \int \left(\frac{f_{\text{horiz}}}{m} \right) dt \quad (\text{A9})$$

in the horizontal direction, and

$$S_{\text{vert,end}} = S_{\text{vert,init}} + V_{\text{vert,init}} T + \frac{gT^2}{2} + \int_T \int \left(\frac{f_{\text{vert}}}{m} \right) dt \quad (\text{A10})$$

in the vertical direction (and so including the gravitational acceleration term). This means that initial velocity conditions can be determined that require the calculated path to go through the initial and final positions:

$$V_{\text{horiz,init}} = \frac{1}{T} \left\{ S_{\text{horiz,end}} - \left[S_{\text{horiz,init}} + \int_T \int \left(\frac{f_{\text{horiz}}}{m} \right) dt \right] \right\} \quad (\text{A11})$$

for the horizontal direction, which is an explicit form of that described in a force platform study on dogs (Lee et al., 1999), and

$$V_{\text{vert,init}} = \frac{1}{T} \left\{ S_{\text{vert,end}} - \left[S_{\text{vert,init}} + \left(\frac{gT^2}{2} \right) + \int_T \int \left(\frac{f_{\text{vert}}}{m} \right) dt \right] \right\} \quad (\text{A12})$$

for the vertical direction.

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