

Review

Energetics and biomechanics of locomotion by red kangaroos (*Macropus rufus*)

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Abstract

As red kangaroos hop faster over level ground, their rate of oxygen consumption (indicating metabolic energy consumption) remains nearly the same. This phenomenon has been attributed to exceptional elastic energy storage and recovery via long compliant tendons in the legs. Alternatively, red kangaroos may have exceptionally efficient muscles. To estimate efficiency, we measured the metabolic cost of uphill hopping, where muscle fibers must perform mechanical work against gravity. We found that uphill hopping was much more expensive than level hopping. The maximal rate of oxygen consumption measured ($3 \text{ ml O}_2 \text{ kg}^{-1} \text{ s}^{-1}$) exceeds all but a few vertebrate species. However, efficiency values were normal, $\sim 30\%$. At faster level hopping speeds the effective mechanical advantage of the extensor muscles of the ankle joint remained the same. Thus, kangaroos generate the same muscular force at all speeds but do so more rapidly at faster hopping speeds. This contradicts a recent hypothesis for what sets the cost of locomotion. The cost of transport ($\text{J kg}^{-1} \text{ m}^{-1}$) decreases at faster hopping speeds, yet red kangaroos prefer to use relatively slow speeds that avoid high levels of tendon stress. © 1998 Elsevier Science Inc. All rights reserved.

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1. Introduction

Some 25 years ago, Dawson and CR Taylor reported that red kangaroos (*Macropus rufus*)¹ consume metabolic energy at nearly the same rate whether they hop slowly (2 m s^{-1}) or as fast as 6 m s^{-1} [17]. In the ensuing years, several species of wallabies have also been shown to have a nearly constant rate of energy consumption across hopping speed [5,48]. The biomechanics of the phenomenon have been investigated [4,5,7,9,24,30,35,37] but two questions still do not have

fully satisfactory answers. What mechanisms can account for the remarkable energetics? Why don't red kangaroos hop at very fast speeds on a regular basis, since it appears to be a cheaper way to travel a given distance? Although this paper does not fully resolve these questions, we present some unique data that adds new insight is presented.

In the original report, Dawson and Taylor [17] suggested that the remarkable energetics of hopping are "probably due to a greater storage and recovery of energy in the elastic elements... in the rear limbs". Several research groups have explored this possibility. Alexander and Vernon [4] estimated that at 6 m s^{-1} , elastic energy storage saves a red kangaroo up to 70% of the metabolic energy which would otherwise be required. However, subsequent measurements suggest

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¹ In 1973, this species was known as *Megaleia rufa*.

that some of their assumptions were in error and that this 70% value is probably too high [9]. Ker et al. [30] estimated that in the wallaby, *Macropus rufogriseus*, at least one third of the mechanical energy per hop is stored and recovered elastically. Griffiths [24] studied the wallaby, *Thylogale billardieri*, using a combination of kinematic and force sensing tendon buckles. He reported about 41% savings due to elastic energy reutilization but no increase in elastic savings at faster speeds. Most recently, Biewener and Baudinette [9] studied the Tammar wallaby, *Macropus eugenii*, over a range of hopping speeds and suggested that without the elastic energy storage in the ankle extensor tendons, the metabolic rate would be nearly twice as great as that observed.

Traditionally, there has been an assumed link between the metabolic cost and the mechanical work done in running [13]. However, muscle consumes metabolic energy when it generates force isometrically even though it does no work. The idea has emerged that tendons act largely as springs and that muscles act primarily as tension generators. If true, the metabolic cost of level running would be dominated by the cost of generating muscular force rather than reflecting the mechanical work done by muscle [31,44,45]. Recent direct measurements of muscle fiber length changes in running turkeys support this view of muscles as primarily acting as tension generators [39]. However, even if elastic storage and recovery of mechanical energy is such that no additional mechanical work output of muscle is needed at faster hopping speeds, an energetic puzzle still remains.

According to the cost of generating force approach [31], metabolic rate increases at faster speeds because muscle forces must be developed more quickly, requiring muscle fibers with faster intrinsic speeds. Muscle fibers with faster intrinsic speeds are less economical force generators. Thus, in most animals, metabolic cost increases with running or hopping speed. Kram and Taylor [31] proposed that the time of foot-ground contact reflects the time of muscle force development. In a variety of animals, across a wide speed range, they found that metabolic rate is inversely proportional to foot-ground contact time [31].

Macropodids maintain a nearly constant hop frequency over their normal speed range but the fraction of the stride period when the feet are on the ground (duty factor) decreases at faster speeds [7]. Therefore, contact time decreases at faster hopping speeds. Thus, red kangaroos appear to be an exception to the cost of generating force approach; at faster hopping speeds, contact time decreases but metabolic rate remains nearly constant. At present, the unusual energetics of red kangaroo locomotion are not explained by the traditional mechanical work based

approach or by the newer cost of generating force approach.

Regardless of the mechanism behind the energetics, the behavior of red kangaroos seems to violate another general 'rule' of animal locomotion. That 'rule' is that within each gait, animals prefer to use the speed that minimizes the amount of energy required to travel a unit distance (i.e. minimize the cost of transport). This idea was established for human walking more than 60 years ago [34]. Hoyt and Taylor [27] demonstrated that the idea applies to the three basic gaits of quadrupeds and there are many other examples in nature [3]. Because metabolic rate remains nearly constant at faster hopping speed in red kangaroos, the cost per unit distance monotonically decreases. If red kangaroos were to follow the rule of preferring to travel at the speed with the lowest cost of transport, they would prefer to hop at their maximum speed on a regular basis. Red kangaroos are reported to be capable of hopping as fast as 14 m s^{-1} yet they normally travel at much slower speeds [15]. All measurements of oxygen consumption for red kangaroo locomotion have been made during treadmill hopping where air resistance is zero. Baudinette et al. [5] suggested that at higher speeds, air resistance may play an increasingly important role such that a minimum cost of transport would be reached at about 12 m s^{-1} . However, there are no empirical metabolic data beyond 6 m s^{-1} . Moreover, red kangaroos rarely hop as fast as 12 m s^{-1} .

Biomechanical limitations may explain the behavioral preference of red kangaroos for moving at speeds below the energetically optimal speed. In some situations, quadrupeds appear to select their gait based on acceptable levels of musculoskeletal stress rather than minimizing metabolic cost [21]. Animals appear to choose speeds that allow for some safety factor in terms of avoiding dangerous levels of bone, muscle or tendon stress (stress = force/cross sectional area) [11,36]. While Biewener and Baudinette's [9] data for Tammar wallabies (<6 kg) indicate that muscle and tendon stresses do not approach critical levels even at speeds of 10 m s^{-1} , Bennett and GC Taylor's [7] insightful analysis suggests that large hopping macropodids might easily reach critical tendon stress levels. However, Bennett and Taylor's [7] allometric comparison did not examine a large speed range for any one species. Thus, better estimates of mechanical stresses in red kangaroos over a range of speeds are needed to consider if stress levels can explain their locomotor behavior.

Given these unresolved issues, three experiments were conducted that pertain to the energetics and biomechanics of red kangaroo locomotion.

1. During level hopping, muscle fibers may do little work because the tendons can store and recover en-

ergy from hop to hop. On the other hand, the muscles of red kangaroos may be exceptionally efficient. We wanted to understand the various functions of muscle during locomotion (perform work versus generate tension) and the associated metabolic cost. We hypothesized that red kangaroos have exceptionally efficient muscles compared to other similarly sized animals. To test this hypothesis, we measured the rate of oxygen consumption during uphill hopping and calculated the efficiency of performing mechanical work against gravity.

2. One way that the energetics of red kangaroo hopping could be explained within the cost of generating force approach would be if they need to generate less muscle force at faster hopping speeds. We hypothesized that at faster speeds, red kangaroos use a more upright limb posture (i.e. less flexed joints) that allows their muscles to operate with greater effective mechanical advantage. To test this hypothesis, we measured the limb posture of animals hopping over a wide speed range.

3. Because the preferred speeds of red kangaroos can not be easily explained on an energetic basis, we investigated if biomechanical stresses influence the selection of preferred speeds and/or limit locomotor performance. We hypothesized that high levels of tendon stress occur during level hopping at relatively modest speeds. Also, the ultimate tendon breaking stress of 100 MPa limits maximum hopping speed [6,43]. To test this hypothesis, we measured the biomechanics of red kangaroos hopping over a wide speed range to estimate the peak tendon stresses they experience.

2. Materials and methods

All data presented here are for red kangaroos (*Macropus rufus*). Studies took place at two locations, the Concord Field Station of the Museum of Comparative Zoology, Harvard University (USA) and the Fowler's Gap Field Station of the University of New South Wales (Australia). The oxygen consumption and force platform studies took place in the USA and the open field hopping experiments took place in Australia. Dissections were done at both locations.

2.1. Animals

Kangaroos in the US were obtained through USDA approved breeders and maintained in paddocks that allowed for ad libitum exercise. Kangaroos in Australia were captured in the wild using the techniques that minimize stress myopathy [41]. The animals were housed in a large (8 ha) outdoor paddock for several weeks with water ad libitum and plentiful forage material.

2.2. Oxygen consumption measurements

One female (body mass 20.4 kg) was cooperative and readily trained to hop on a motorized treadmill. We attempted to train a much larger male kangaroo to hop on the treadmill but we were unsuccessful. The treadmill was located in a temperature controlled room that was cooled to approximately 5°C to prevent the animal from overheating. A typical open flow system was used to measure oxygen consumption. The animal wore a custom-made, loose fitting polyethylene mask that covered the mouth and nose. Air was drawn from the mask at a metered flow rate. A sample of the air was drawn from the main flow through tubes of Drierite (to remove water vapor) and Ascarite (to remove carbon dioxide). The sample then was analyzed with a Beckman F-3 oxygen analyzer. The change in the gas composition during exercise was recorded on a chart recorder and then converted to a rate of oxygen consumption. The system was calibrated with known flow rates of nitrogen as per Fedak et al. [22]. Values were calculated to STPD. The treadmill speed was determined from knowing belt length and timing ten revolutions with a stopwatch.

2.3. Force platform measurements

We obtained simultaneous force platform and film recordings for one male kangaroo (body mass 46.1 kg). The animal hopped down a 30 m runway with fencing along both sides that directed it across a force platform. The force platform (Kistler Instruments, model 9261a) was mounted flush with the ground in the middle of the runway. The vertical and horizontal force signals were collected at 1 kHz using a microcomputer and A/D board. The animal's movements were filmed from a lateral view using a Photosonics IPL camera at 100 frames s⁻¹. The force signals and film frames were synchronized with a simple electrical circuit that flashed a small LED that was visible on the film and simultaneously sent a voltage pulse to the computer. To measure the animal's speed, the signals were collected from four photoelectric cells mounted 1 m apart from each other along the runway. The animals legs were palpated and marked with non-toxic white paint to highlight the joint centers. The tendinous insertions were also palpated to measure the extensor muscle moment arms about the joints externally. Subsequent dissection of the animal confirmed these measurements.

2.4. Overground hopping kinematics

A high speed cine camera was positioned inside the paddock so that it had a perpendicular view of the intended hopping path. The intended pathway was adjacent to the fence line of the enclosure. To calibrate

the field of view, two stakes were driven in the ground a known distance (10.0 m) apart along the intended pathway. Three mature female animals (body mass 16.4, 18.2 and 23.4 kg) were filmed as they hopped along the path. Trials were filmed when the animal freely chose to move through the field of view and when pursued on foot by an assistant. Varying the degree of active pursuit resulted in a range of hopping speed trials. Speed was calculated from the time that the animal took to traverse the 10 m distance. Time was calculated by analyzing the film frame by frame noting the number of frames and knowing the framing rate (100 s^{-1}). Only trials where the animal maintained a steady speed were selected for analysis.

For each hop selected, we established the time for a complete hop cycle (t_{stride}) and the time of ground contact (t_c) per stride from the film recordings. This allowed us to calculate duty factor (Df), which is equal to the fraction of a stride that a foot is in contact with the ground, t_c/t_{stride} .

We then returned to the film frame that corresponded to the middle of the ground contact time (i.e. mid-stance). Essentially digitigrade, only a short section of the foot of a kangaroos is in contact with the ground and we determined the horizontal midpoint of that section. The horizontal distance was measured from that point to the center of the ankle joint using a Vanguard Film Analyzer. This distance—the moment arm of the vertical ground reaction force (R)—was calibrated by knowing the true length of the limb segments as measured during the dissections. The muscle moment arm (r) for each animal was measured during dissection. The ratio of r/R is termed the effective mechanical advantage (EMA) [8]. Based on data in the literature [4], we assumed that the peak ground reaction force occurs at mid-stance and that at that time the ground reaction force vector is oriented vertically.

We estimated peak ground reaction force using the method proposed by Alexander [2]. According to this method, the peak vertical ground reaction force under both feet of a hopping biped can be estimated with the equation: $F_{\text{peak}} = (\pi mg)/(2 \text{ Df})$. In this equation, m is body mass, g is 9.81 m s^{-2} and Df is duty factor. This assumes that the force–time plot of the vertical ground reaction force approximates a half sine wave. The method is based on the fact that over a complete stride, the average vertical force is equal to body weight. Dividing this estimate of ground reaction force by the EMA yields the force in the extensor tendons.

2.5. Morphometry

Total animal mass was recorded with an appropriate scale. After removing the skin, the muscle moment arms about each of the joints were measured for the

major muscles. Individual muscles and tendons were then dissected out. The free tendon was cut off and its length and mass recorded. The mean free tendon cross sectional area was calculated by assuming a tendon density of 1.12 g cm^{-3} [28] and dividing volume by length. The individual muscles were weighed and then sliced to allow fiber length measurements. A density of 1.06 g cm^{-3} was used [1]. All measurements were made for both left and right limbs and then averaged.

The 46 kg male kangaroo died several months after the biomechanical measurements. Autopsy revealed a probable cerebral stroke. Prior to death, the animal was very active and appeared to be in excellent health. The kangaroos in Australia were wild caught and kept in a very large fenced paddock. The animals were active in the paddock, observed to have normal gait and maintained weight from capture date to euthanasia and dissection date. During dissection, no unusual parasite load or other infirmity was noted. Thus, we are confident that the measurements of muscle and tendon morphometry data reflect healthy animals.

3. Results

3.1. Treadmill energetics

We measured the animal's rate of oxygen consumption for speeds ranging from 2.94 to 6.42 m s^{-1} on the level. We found essentially the same pattern as reported by Dawson and Taylor [17] (Fig. 1). The regression equation for the rate of oxygen consumption in $\text{ml O}_2 \text{ kg}^{-1} \text{ s}^{-1}$ was $1.08 + 0.036v$, where v is hopping speed in m s^{-1} ($R^2 = 0.21$). The slope of this regression was not significantly different from zero

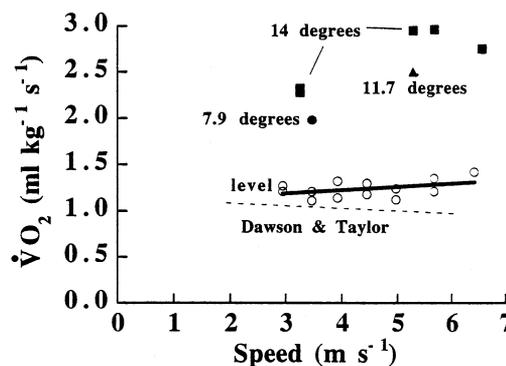


Fig. 1. During level hopping, the rate of oxygen consumption was essentially constant across speed. However, at steeper uphill inclines the rate of oxygen consumption increased substantially. Open circles indicate values for level hopping and the solid line is the corresponding linear least squares regression line. The equation for the rate of oxygen consumption in $\text{ml O}_2 \text{ kg}^{-1} \text{ s}^{-1}$ was $1.08 + 0.036v$, where v is hopping speed in m s^{-1} ($R^2 = 0.21$, $P = 1.0$). The dashed line indicates the regression from Dawson and Taylor [17].

($P = 0.10$). Hopping uphill dramatically increased their rates of oxygen consumption. In addition, unlike hopping on the level, for a given incline, the rate of oxygen consumption increased with an increase in speed. At the 14° incline, the animal reached essentially the same rate of oxygen consumption at 5.28 and 5.67 m s^{-1} . At 6.56 m s^{-1} , the animal could not sustain the speed and the rate of oxygen consumption measured did not reach a plateau during the measurement period. The highest rate of oxygen consumption recorded was $2.96 \text{ ml kg}^{-1} \text{ s}^{-1}$.

3.2. Overground hopping energetics-mechanics

A total of 22 satisfactory trials were obtained from three animals. The trials spanned slightly more than a 2-fold speed range (4.3 – 9.7 m s^{-1}). The data from the three animals was pooled because they were similar in mass. As expected, kangaroos had shorter ground contact periods when they hopped at faster speeds. Over a 2-fold increase in speed from 4.3 to 8.6 m s^{-1} , contact time decreased by 33% (see Fig. 2A). Because Kram and Taylor [31] proposed that metabolic rate is proportional to the rate of force development as indicated by $1/t_c$, that variable was calculated as well. The rate of force development, $1/t_c$, increased by 51% across the same 2-fold speed range.

The effective mechanical advantage (EMA) at the ankle joint was nearly invariant across this hopping speed range. A linear regression of the data indicates a slope not significantly different from zero ($P = 0.75$) (see Fig. 2B). For a 2-fold increase in speed, the effective mechanical advantage increased less than 1%.

3.3. Overground hopping mechanics

When directed to hop down the force platform runway, the large male strongly preferred a speed of 3.9 m s^{-1} . It hopped within 0.3 m s^{-1} of that mean for 85% of the trials. At 3.9 m s^{-1} , the peak ground reaction force was 2162 N (for both feet). At the ankle joint, the effective mechanical advantage (EMA) was 0.32 and so the sum of the forces in the tendons of the gastrocnemius and plantaris muscles was 3378 N per leg. Note that the names plantaris and flexor digitorum superficialis are synonymous [26]. The combined cross sectional area of the plantaris and gastrocnemius tendons was 0.75 cm^2 per leg. Assuming equal stress distribution between tendons, the peak tendon stress was 45.4 MPa which is about 45% of the commonly cited values for the ultimate strength of mammalian tendon (100 MPa) [6,43]. It appears that at the preferred speed, the kangaroo operated with a safety factor of just over two.

To gain insight into the mechanical stresses at faster speeds, the tendon stress of the animals studied during overground hopping in Australia was also estimated.

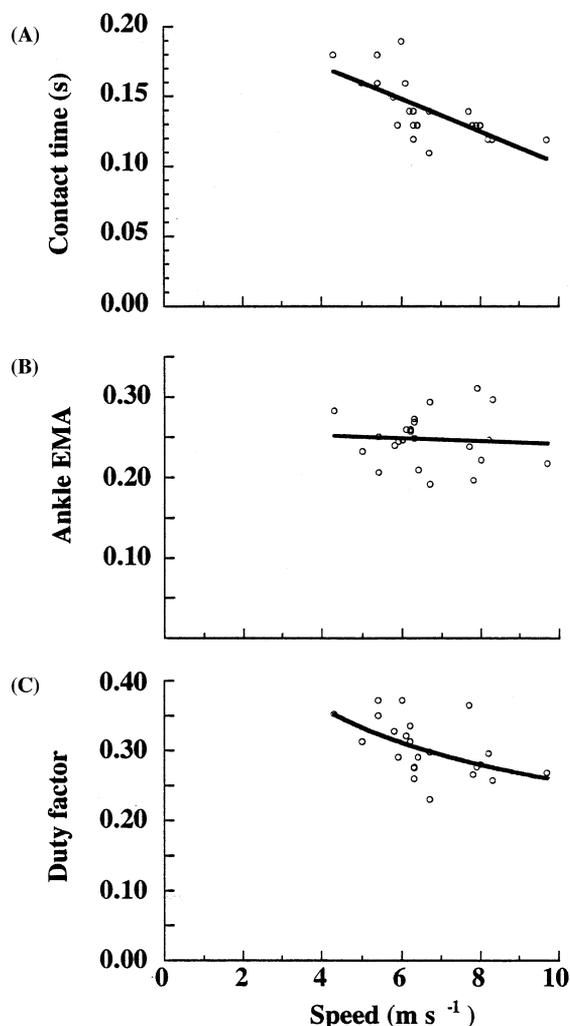


Fig. 2. A, Time of foot contact per stride versus hopping speed. At faster speeds, contact time decreased ($P = 0.004$). Linear least squared regression equation: $t_c = 0.218 - 0.012v$, ($R^2 = 0.45$) where v is hopping speed in m s^{-1} . Each open circle represents one trial for one animal. B, Mechanical advantage (r/R) of ankle extensor muscles at midstance plotted versus speed. R is the moment arm of the ground reaction force about the ankle joint and r is the moment arm of the gastrocnemius and plantaris tendons about the ankle joint. EMA did not change with hopping speed: $\text{EMA} = 0.260 - 0.002v$, ($R^2 = 0.005$, $P = 0.75$, slope not significantly different from zero). C, Duty factor versus hopping speed. At faster speeds, duty factor decreased ($P = 0.009$). Solid line indicates a regression equation $\text{Df} = 0.60v^{-0.37}$ ($R^2 = 0.28$).

According to the method of Alexander [2], the duty factor data was used (Fig. 2C) to estimate the peak ground force (for both legs combined). It ranged from about 4.5 times body weight at the slowest speed (4.3 m s^{-1}) to almost six times body weight at the fastest speed measured (9.7 m s^{-1}). Combining these estimates with the measurements of EMA and tendon cross sectional areas yielded surprisingly high peak tendon stress values (Fig. 3).

4. Discussion

At all level hopping speeds measured, the metabolic rate was about $1.25 \text{ ml kg}^{-1} \text{ s}^{-1}$. At rest, red kangaroos consume about $0.12 \text{ ml O}_2 \text{ kg}^{-1} \text{ s}^{-1}$ [16] and so level hopping consumes about ten times the resting metabolic rate. Hopping uphill dramatically increased the rates of oxygen consumption (Fig. 1). The highest rate of oxygen consumption recorded was nearly $3.0 \text{ ml O}_2 \text{ kg}^{-1} \text{ s}^{-1}$ or about 25 times the resting rate. These are substantially greater than the metabolic rates and aerobic scopes observed for all but the most athletic animals [33]. For example, dogs of similar mass as these kangaroos have maximal rates of oxygen consumption between 2.29 and $2.64 \text{ ml kg}^{-1} \text{ s}^{-1}$ [40,42,46] or a metabolic scope of 15 times their resting metabolic rate. A red kangaroo hopping at speeds of at least 6 m s^{-1} on the level is operating at only 43% of $\text{O}_{2\text{max}}$ and thus appears to be nowhere near a fatiguing intensity.

How did we assess, if during level hopping a true steady state condition was achieved in terms of the rate of oxygen consumption? Just from observation, it was noted that all the level speeds could be sustained without fatigue. The inability to obtain data for faster speed comes from the animals unwillingness to hop faster on the treadmill for any duration. Secondly, the rates of oxygen consumption reached a plateau during the measurement period. In fact, a brief 'spike' in the rate of oxygen consumption traces was often observed at the very beginning of the trial before the animal settled into the speed. Thirdly, at greater exercise intensities, (i.e. uphill hopping), higher rates of oxygen consumption occurred. No example is known of a mammal preferentially sustaining use of anaerobic pathways for supplying energy without utilizing its full aerobic capacity. Finally, the rate of the increase in the rate of oxygen

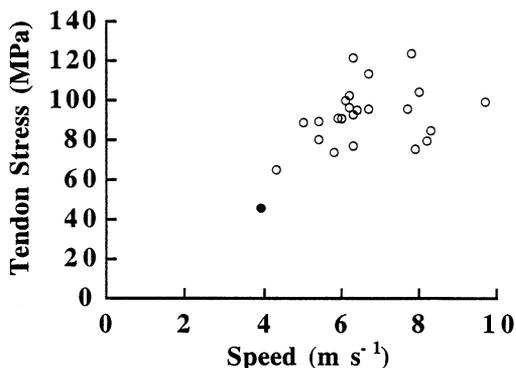


Fig. 3. The peak stress in the ankle extensor tendons plotted versus speed. The filled circle indicates value for 46 kg kangaroo based on combined force platform, cine film analysis and morphological measurements. Open circles are estimates for the 16, 18 and 24 kg animals. Estimates calculated using the duty factor method of Alexander [2]. Numerous data points are above the 100 MPa value reported for the ultimate strength of tendon in vitro [6,43].

consumption (a.k.a. the 'oxygen kinetics') during uphill hopping are much faster than during level hopping. Thus, during level hopping at speeds up to 6 m s^{-1} there is no limitation in activating the delivery of oxygen or the oxidative machinery.

Could the remarkable energetics of level locomotion by red kangaroos be explained by unusually efficient muscles? To calculate efficiency, measures of both the mechanical work done and the metabolic cost of doing that work were needed. During level hopping it is problematic to estimate the mechanical work done [14,47]. However, during uphill locomotion the increased mechanical work can be measured less ambiguously. The external work rate or mechanical power needed to lift the body mass vertically is equal to the product of the animal's weight ($mg = \text{product of mass and gravitational acceleration, } 9.81 \text{ m s}^{-2}$) and the vertical velocity. Knowing the angle of the hopping surface, ϕ and the treadmill speed, v , the mechanical power is simply equal to $mgv \sin(\phi)$. If a normal energetic equivalent for oxygen consumption ($20.1 \text{ J ml}^{-1} \text{ O}_2$ consumed) is assumed, then it is possible to calculate a value of efficiency for the additional mechanical work done against gravity. This type of an efficiency calculation might best be described as a 'vertical efficiency'. Efficiency was nearly the same, 30.0, 28.8 and 30.7% at each of the three inclines, 7.9, 11.7 and 14° , respectively. How do these value compare to those of other animals? Raab et al. [38] measured the energetic cost of dogs running on a treadmill inclined to 11.5° . When we calculated the vertical efficiency from their dog data in the same way we have done for kangaroos, we found a value of 30.7%. Thus, it appears that the remarkable locomotor energetics of red kangaroos during level hopping are probably not due to unusually efficient muscles. As an aside, the efficiency value calculated for red kangaroos lends credence to the 25% value assumed by Biewener and Baudinette for Tammar wallabies [9]. Moreover, the fact that the kangaroo's rate of energy consumption increased directly with the extra mechanical work done against gravity strongly suggests that during level hopping, their muscles are not performing more work at faster speeds.

Our second hypothesis was that red kangaroos adopt a more upright limb posture at faster hopping speeds and thereby reduce the muscular forces that need to be developed. As shown in Fig. 2B, this was clearly not the case at the ankle joint. Biewener [8] has previously shown that in quadrupedal mammals there is also no systematic change in EMA with speed. To support body weight, the average ground reaction force over a complete stride must always equal body weight. Because EMA does not change with speed, at slow and fast hopping speeds, the ankle extensor muscles of red kangaroos must exert the same average force (about two times body weight in the ankle extensors of each

leg). The value for ankle EMA of 0.26 which was nearly constant across speed is essentially the same as that reported by Bennett and Taylor (0.24) for an interspecific comparison of macropodids that span a large range of body masses [7]. The EMA at the ankle of macropodids appears to be the same across both speed and size.

At faster speeds, the kangaroos hopped with shorter contact times (t_c), Fig. 2A. This indicates that muscular force was developed more quickly, at faster speeds. According to the cost of generating force hypothesis, generating force more quickly is metabolically more expensive, yet the metabolic rate remained nearly the same across speed. Thus, the data for red kangaroos can not yet be reconciled with the basic cost of generating force approach [31]. Although it remains tempting to explore further the elastic storage and recovery of mechanical energy in tendons, Dimery et al. [18,19] have argued that, in fact, quadrupeds have even more specialized tendons and appear to store and recover elastic energy more effectively than kangaroos. Despite this, these quadrupedal trotting and galloping animals do not have remarkable locomotor energetics.

The relationship between body size and effective mechanical advantage (EMA) has important energetic implications in macropodids. In quadrupedal mammals, EMA changes systematically with body mass, $EMA \propto M_b^{0.26}$ [8]. Large animals like horses have more upright limb posture than small crouched rodents. In these quadrupedal mammals, both EMA and muscle fiber length increase with body size. As a result, the volume of muscle required to exert a unit force on the ground is nearly the same in small and large quadrupeds. Bennett and Taylor [7] reported that the muscle fibers of the gastrocnemius and plantaris muscles are longer in larger macropodids, though fiber length scales less than would be expected from geometric similarity. More notably, Bennett and Taylor [7] found that in macropodids, EMA is independent of animal size. Thus, the combined result is that larger macropodids must activate a greater muscle volume to exert a unit force on the ground.

It has been proposed that the metabolic cost of locomotion depends on two factors: (1) the volume of muscle that must be activated to support body weight; and (2) the rate of developing that force [31]. Given the constant EMA, we would predict that the metabolic cost of locomotion in large macropodids would be the same or even relatively more expensive than smaller macropodids. This is in contrast to the case of quadrupedal mammals, where at a given speed, a larger animal consumes metabolic energy at a lower mass specific rate [31]. More data are needed to determine if the metabolic cost of locomotion in macropodids scales differently with body mass than it does in quadrupedal mammals. For now, it is intriguing to note that at a

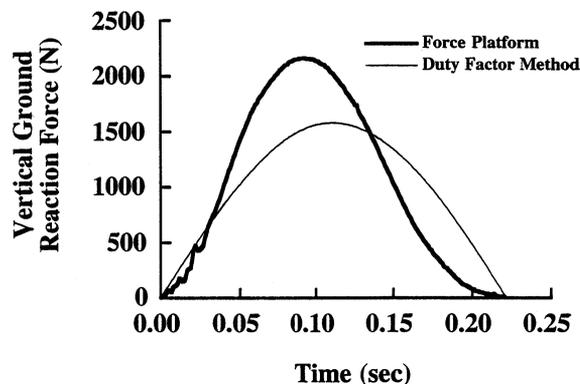


Fig. 4. Comparison of vertical ground reaction force data collected with a force platform to the duty factor method of Alexander [2] for a 46 kg male red kangaroo hopping at 3.9 m s^{-1} . In this case, the model under-predicts the peak force; actual force was 36% greater than the predicted value. If this relationship holds at all hopping speeds, actual tendon stresses are substantially greater than those indicated in Fig. 3.

given hopping speed, 5 kg Tammar wallabies consume energy at nearly the same mass specific rate as 20 kg red kangaroos ([5,17] and present data). This may be the result of red kangaroos having longer muscle fibers combined with slower rates of force development (as evidenced by longer ground contact times).

Our biomechanical data suggest that red kangaroos experience unusually high tendon stress at speeds well below their maximum speed (Fig. 3). Because we were skeptical of these high values, we reconsidered the method of estimating ground reaction force from duty factor. We compared the force platform measurements for the 46 kg kangaroo experiments to an estimate based on that animal's duty factor. At 3.9 m s^{-1} , the duty factor was 0.45. That duty factor predicts a peak vertical ground reaction force of 1593 N. The actual measured ground reaction force was 2162 N or 36% greater than that predicted by the duty factor method [2]. The under-prediction of the duty factor method is due to the shape of the vertical ground reaction force pattern versus time not being a perfect half sine wave (Fig. 4). If one were to adjust the ground reaction force estimates based on this, even higher levels of tendon stress would be calculated.

High tendon stress values could also be the result of an under-estimate of the tendon area involved. Our estimates of tendon stress considered only the gastrocnemius and plantaris tendons. We did not include the flexor digitorum profundus (FDP) muscle or tendon in the calculations for several reasons. The primary action of this muscle is to flex the digits and its moment arm about the ankle joint is less than one third that of the gastrocnemius and plantaris. It also has a much smaller cross sectional fiber area (about 1/7 of the gastrocnemius + plantaris) [7]. We believe that if the FDP was not included it would lead to at most a 5% reduction in

tendon stress. Alexander and Vernon apparently drew the same conclusion as they did not consider the FDP in their analysis [4]. Biewener and Baudinette [9] report that appropriate adjustments to Alexander and Vernon's data [4] for red kangaroos yields estimates of tendon stress of 79 MPa in the gastrocnemius tendon for hopping at 6.2 m s^{-1} . Based on the data at hand, it appears that red kangaroos locomote with very small margins of safety for avoiding tendon rupture or the ultimate strength of tendon in vitro differs from that measured in vitro.

In most locomotor muscle–tendon combinations, the muscle is weaker than the tendon. That is, maximal stimulation of the muscle does not produce enough stress to rupture the tendon [29]. In the 46 kg kangaroo, the gastrocnemius and plantaris tendons of one leg had a combined cross sectional area of 0.75 cm^2 . Given an ultimate breaking stress of 100 MPa for tendon [6,43], a force of 7500 N would be required to rupture the ankle extensor tendons. The combined physiological cross sectional area of gastrocnemius and plantaris muscle was 208 cm^2 per leg. If the muscle can exert an isometric stress of 250 kPa, then the maximal isometric muscle force would be 5200 N. Stretch enhancement of muscle force could increase the muscle force considerably beyond the tendon limits. Experiments performed in vitro indicate that force could be enhanced to as much as 1.7 times the isometric levels [12,23,25] and kangaroo rats have been shown to have similar enhancement in vivo [10]. It seems that a red kangaroo traveling at high speeds could easily rupture its tendons on uneven natural terrain.

It is intriguing to note that animals of similar morphology but smaller in size (e.g. Tammar wallabies, $\sim 5 \text{ kg}$) are not in nearly as great of danger of tendon rupture [9]. Over their normal hopping speed range, Tammar wallabies have tendon stresses less than 40 MPa, while their muscles are exerting nearly their maximal stress (250 kPa). Bennett and Taylor [7] were the first to recognize these allometric trends and they speculated that large macropodids ($\sim 150 \text{ kg}$, now extinct) likely faced severe biomechanical constraints on their locomotion.

Previously published data indicate some kinematic aspects of red kangaroo locomotion may prevent tendon stresses from increasing more dramatically at faster hopping speeds. The hop frequency is nearly constant over the range of common hopping speeds. However, stride frequency appears to increase sharply at speeds faster than 10 m s^{-1} [15]. For a given contact time, a higher stride frequency would increase duty factor, reducing the peak ground reaction force and tendon stress. The forward velocity of an animal is equal to the distance moved during the contact phase (L_c) divided by the contact time (t_c). Farley et al. [20] reported that kangaroos differ from quadrupedal animals in that at

faster velocities they land and take off with much shallower angles relative to the ground. In other words, they substantially increase the distance (L_c) traveled during the contact time. Kangaroos can thus hop faster with more modest decreases in t_c . Since t_c has been linked to the metabolic cost of locomotion, this aspect of kangaroo kinematics may afford energetic as well as biomechanical benefits.

The energetics and biomechanics of red kangaroo locomotion are clearly not yet resolved. This research has concentrated almost exclusively on the ankle joints of these animals but the answers may lie at the knee or hip joint musculature and tendons. The present metabolic and biomechanical data do not extend over the entire speed range that kangaroos are capable of using. Direct measurements of: (a) kinematics; (b) ground reaction forces; (c) individual tendon forces; and (d) energetics at the fastest speeds used by animals in the wild are needed to obtain satisfactory answers to the paradoxes of red kangaroo locomotion. Comparative physiologists have often followed the Krogh Principle of studying the species most appropriate for answering a particular question [32]. It appears that 25 years ago, Dawson and Taylor [17] unintentionally invoked the 'inverse Krogh principle' by choosing to study a species that has been most appropriate for stimulating new questions rather than providing definitive answers.

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