

# IS THE ENERGETICS OF MAMMALIAN HOPPING LOCOMOTION ADVANTAGEOUS IN ARID ENVIRONMENTS?

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Although hopping is a relatively rare mammalian gait, hopping mammals are common in arid environments. Arid environments are open, with patchy resources, and the widespread use of hopping by arid zone mammals appears to be related to the benefits of fast locomotion. In several species, fast hopping is economical in comparison to fast quadrupedal running. These hopping species can reach greater maximum aerobic speeds than similarly sized runners. Faster locomotion can reduce predation risk and increase opportunities to exploit open microhabitats. More economical locomotion may improve a hopping mammal's ability to adopt alternative foraging strategies. The disadvantages of hopping include an increased cost of slow locomotion, reduced manoeuvrability at slow speeds and reduced ability to exploit densely vegetated patches.

Key words: Arid-zone, bettong, energetics, hopping, kangaroo, locomotion, potoroo, rodent, wallaby.

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CONTINUOUS locomotion using the bipedal hop, also known as saltatory locomotion, is an unusual mammalian gait. It is found in just four families of rodents and a single super-family of marsupials, the kangaroos, wallabies and rat-kangaroos (super-family Macropodoidea). The Macropodoidea occupy a broad range of habitats, with many species inhabiting arid and semi-arid regions (Frith and Calaby 1969). Hopping rodents also appear common in the drier areas of the continents in which they occur. In the Americas, kangaroo rats (family Heteromyidae) are found most commonly in arid or semi-arid habitats in the western parts of both continents (Vaughan *et al.* 2000). The hopping mice of Australia (family Muridae, genus *Notomys*) largely inhabit the deserts of the interior (Strahan 1995). In Africa, the spring hare (*Pedetes capensis*; family Pedetidae) is found through sandy soils of the eastern and southern regions of the continent (Vaughan *et al.* 2000). The strongly saltatorial jerboas (family Dipodidae) are widespread throughout the arid and semi-arid regions of northern Africa, the Middle East through to Mongolia and north-eastern China. There are some breaks in this pattern of favouring arid habitats; in this same family also occur some moderately saltatorial jumping mice from Arctic regions of North America and Europe (Vaughan *et al.* 2000).

Why is hopping locomotion favoured in arid environments? Arid environments are often lacking in vegetation for adequate concealment from predators, and food and water resources are usually limited and patchily spread. Hopping may improve acceleration or agility, thereby improving predator avoidance. Hopping also may allow an animal to forage over wide areas. The first scenario would be strongly influenced by biomechanical and anatomical features of hopping mammals, while the latter assumes energetic trade-offs during foraging. This review examines what is known about the physiology and biomechanics of hopping mammals, and how this may impact on a life in the arid zone.

## Large hopping mammals

Of hopping mammals, only the Macropodoidea contains large species, with the extant kangaroos and wallabies (family Macropodidae) ranging in adult body mass from 3 kg up to 85 kg (Strahan 1995). The hopping rodent *P. capensis* reaches 3 – 4 kg, but other species are small, with body mass typically being below 200 g (Vaughan *et al.* 2000). In the literature there has tended to be a distinction between large (above 5 kg) and small hopping mammals (e.g., Baudinette 1989). The reason for this distinction was purportedly a difference in the energetics of the two

size classes (Thompson *et al.* 1980). However, we have doubts about the validity of this distinction.

The studies by Dawson and Taylor (1973) on the red kangaroo (*Macropus rufus*) focused interest on the locomotion energetics and gait characteristics of hopping mammals. In this relatively large species hopping has unusual energetic characteristics: during treadmill locomotion *M. rufus* does not significantly increase its energy expenditure over a large range of hopping speeds. This pattern is unlike that of quadrupedal running mammals, in which energetic costs tend to increase with increasing speed under the same conditions (Taylor *et al.* 1982). Notably, at fast speeds the metabolic cost of hopping by *M. rufus* is less than that of running quadrupeds of the same mass. However, slow hopping and slow progression (or 'pentapedal') locomotion are more costly than running. *M. rufus* begins to hop between 2 and 3 ms<sup>-1</sup> but does not travel inexpensively until reaching speeds above 4 ms<sup>-1</sup> (Dawson and Taylor 1973). The tammar wallaby (*Macropus eugenii*) exhibits similar energetic characteristics of locomotion but it uses less energy than a running mammal at almost all hopping speeds (above 3 ms<sup>-1</sup>; Baudinette *et al.* 1992). Do larger hoppers have to go faster before hopping becomes energetically economical?

A feature of the hopping of kangaroos and wallabies is a relatively constant stride frequency (Dawson and Taylor 1973; Dawson 1977; Baudinette *et al.* 1987). Does this play a role in the low cost of fast locomotion? Quadrupeds increase their locomotory speed by increasing both the frequency and length of their strides, with the rate of increase in stride frequency being highest when walking and lowest when galloping (Heglund and Taylor 1988). There is a reduction in the rate of increase in metabolic rate in quadrupedal runners when they switch to a gallop (Hoyt and Taylor 1981; Heglund and Taylor 1988), leading to the proposal that the cost of locomotion is determined by stride frequency; kangaroos and wallabies may fit this model. In *Macropus rufus*, hopping frequency and the rate of oxygen consumption are strongly linked over the speed range of 2 - 7 ms<sup>-1</sup>. At speeds greater than 10 ms<sup>-1</sup>, stride frequency of hopping *M. rufus* begins to increase and Dawson (1977) suggested that costs rise, but until metabolic measurements are made at higher speeds, we will not know if the stride frequency model is appropriate.

At low speeds, however, 'walking' kangaroos increase speed by increasing both stride length and frequency, with frequency predominating; this is associated with a large increase in energetic costs (Dawson and Taylor 1973). Although in their walking gait kangaroos actually move pentapedally with the tail acting like a fifth limb, these gait and

energetics patterns are similar to those of quadrupedal walking. In terms of gait characteristics, it appears that macropodid gaits can be thought of as exaggerated forms of quadrupedal gaits: pentapedal locomotion is analogous to walking, while hopping is analogous to galloping.

Another model relating biomechanical parameters to the metabolic cost of locomotion is that of Kram and Taylor (1990). In several species the metabolic rate was inversely proportional to the foot contact time ( $t_c$ ) over a large speed range (Kram and Taylor 1990). They suggest that at fast speeds the decrease in  $t_c$  necessitates rapid development of muscle forces, requiring the recruitment of faster and less energy efficient muscle fibres. However, this model does not explain locomotory costs in *M. rufus*; at faster hopping speeds,  $t_c$  decreases, but metabolic rate remains nearly constant (Kram and Dawson 1998). The same is the case for a small hopping marsupial, the brush-tail bettong (*Bettongia penicillata*) (Webster and Dawson 2003) and stride frequency appears to be a much better index of metabolic cost in both these hopping species.

The spring-like nature of saltatory motion has focused interest on elastic energy storage during movement. Both hopping and galloping animals store energy in the tendons and muscles during the first part of a stride, and recover it during the subsequent phase (Alexander and Vernon 1975; Cavagna *et al.* 1977; Ker *et al.* 1986; Bennett and Taylor 1995). This energy recovery may reduce the energetic costs of movement, and is substantial in cursorial quadrupeds such as the ungulates (Dimery and Alexander 1985; Dimery *et al.* 1986; Ker *et al.* 1988; Biewener 1998). Ker *et al.* (1986) indicate that for optimal storage and recovery of elastic energy, the muscle fibres must be exceedingly short and the tendons very long; these are anatomical features of the ungulates but not of the kangaroos in general. However, Bennett and Taylor (1995) showed that the larger kangaroos have proportionally longer ankle extensor tendons and proportionally shorter fibres in lower leg muscles than smaller species (wallabies and rat-kangaroos). Thus while elastic energy effects may explain differences between large and small hopping kangaroos, they do not fully explain the low metabolic costs of hopping locomotion in comparison to animals such as galloping ungulates.

Overall, models that attempt to explain the differences in locomotion costs between hopping and running mammals should be regarded with circumspection. However, they do have some implications for our understanding of the importance of size to hopping locomotion. Small quadrupedal animals have higher stride frequencies and higher mass-specific costs of locomotion than larger animals

running at the same speed (Taylor *et al.* 1982; Heglund and Taylor 1988) and the same applies for hoppers (Webster and Dawson 2003). Also, if small hopping mammals show stable stride frequencies over a large speed range then their energy use over these speeds may be reduced in comparison to running mammals. However, the potential for reductions in energy use by small hopping mammals may be restricted by size effects on elastic energy storage, as seen in the hopping marsupials (Bennett and Taylor 1995).

### Small hopping marsupials

It is often assumed that apparent differences in locomotion energetics or gait parameters between kangaroos and smaller hopping mammals are a function of body size. However, there is a valid argument for possible phylogenetic effects: since most small hopping mammals are rodents, they may have evolved different physiological features from the marsupial kangaroos. Conversely, those small hopping mammals that are marsupials might be expected to be similar to their larger relatives. What then do we know of the locomotion of small hopping marsupials?

There has been general uncertainty about the energetic features of hopping in small marsupials. The smallest macropodoid marsupial, the musky rat-kangaroo (*Hypsiprymmodon moschatus*) (~ 500 g), apparently uses only a quadrupedal bounding gait (Johnson and Strahan 1982), but there is conjecture because its locomotion energetics or gait characteristics at high speed are inadequately studied. An early study of a small (3 kg) hopping macropodid, the quokka (*Setonix brachyurus*), was inconclusive since energetics were not measured at hopping speeds (Baudinette 1977). *S. brachyurus* exhibited a quadrupedal-like linear increase in oxygen consumption at speeds from 0.6 to 2.2 ms<sup>-1</sup>; stride frequency increased over this speed range but stabilized at higher speeds for which oxygen consumption rates were not measured.

Among the rat-kangaroos (family Potoroidae) propensity to hop varies, with the arid inhabiting bettongs seeming to be the more obligatory hoppers than the more mesic potoroos. The long-nosed potaroo (*Potorous tridactylus*) is primarily quadrupedal but can hop at fast speeds (Buchmann and Guiler 1974). However, bipedal hopping was rare during a treadmill study by Baudinette *et al.* (1993). Like *S. brachyurus*, *P. tridactylus* exhibited a quadrupedal locomotion energetics pattern when moving quadrupedally. Although the stride frequency of *P. tridactylus* did not stabilize during quadrupedal bounding, the rate of increase in stride frequency declined at higher speeds (Baudinette *et al.* 1993). In

our laboratory, (M McCloskey and TJ Dawson, unpubl. data) we also found *P. tridactylus* to be quadrupedal when moving on a treadmill, with equivalent locomotory energetics. By contrast, *B. penicillata* was a consistent hopper, with low locomotory costs at high speeds and a relatively stable stride frequency during hopping.

We have recently followed up the work of McCloskey and Dawson with a detailed examination of locomotion energetics and gait characteristics of *B. penicillata* (Webster and Dawson 2003). We showed that this small marsupial has significantly lower energetic costs than a quadruped of the same size when hopping at speeds above 2 ms<sup>-1</sup> (Fig. 1a). Unlike the larger hopping species, *B. penicillata* does generally exhibit an increasing cost of locomotion with increasing speed, but the rate of increase is significantly lower than that of quadrupeds. This differed from the results of Thompson *et al.* (1980), who found no significant difference from quadrupedal running energetics for this species. The divergence between the two *B. penicillata* data sets appears to be due to both differences in measurements at quadrupedal speeds and generally higher energetics measurements by Thompson *et al.* (1980) at all speeds. We also found that like kangaroos and wallabies, *B. penicillata* increases its hopping speed by lengthening its stride. There is effectively no increase in stride frequency over a nearly six-fold increase in hopping speed (Fig. 1b).

### Evolution of hopping in marsupials

Among the rodents the evolution of hopping is usually associated with arid environments. What do we know about the origin of hopping in the super-family Macropodoidea? It appears to be a phylogenetically old trait that arose in pre-arid Australia. Given the gaits used by the extant species of super-family Macropodoidea (i.e., that *H. moschatus* does not hop), it is likely that bipedal hopping arose after the divergence of the common ancestor of the families Macropodidae and Potoroidae from the Hypsiprymodontidae, but before the macropodids and potorooids diverged. All three families are represented in late Oligocene fossil deposits (between 23 and 26 million years old), and so must have diverged earlier (Archer *et al.* 1999). Unfortunately, Australia's fossil record for terrestrial mammals is virtually non-existent between middle Eocene and middle Oligocene times, from around 55 – 26 million years before present (mybp). Using molecular techniques, Burk *et al.* (1998) estimated that the divergence of family Hypsiprymodontidae from the common ancestor of families Potoroidae and Macropodidae occurred around 45 mybp, and a divergence of potorooids from macropodids around 30 mybp, during the middle to late Oligocene. If

Fig. 1. **a**) Rate of oxygen consumption ( $\text{VO}_2$ ) versus speed for *B. penicillata* (means  $\pm$  SE;  $n = 5$ ), connected by a cubic curve of best fit (from Webster and Dawson 2003). The heavy dashed line indicates the expected  $\text{VO}_2$  for a 1 kg running mammal (equation derived from Taylor *et al.* 1982) and the light dashed line denotes the gait transition speed. The dotted 'VO<sub>2</sub>max line' indicates the expected VO<sub>2</sub>max of a 1 kg mammal ( $1.94 \text{ ml s}^{-1} \text{ kg}^{-1}$ ; from Taylor *et al.* 1981); *B. penicillata* reaches this level at  $6.2 \text{ ms}^{-1}$  while a running mammal would reach it at only  $3 \text{ ms}^{-1}$ . **b**) Stride frequency versus speed for *B. penicillata* (means  $\pm$  SE;  $n = 5$ ) (from Webster and Dawson 2003).

these divergence dates are used, it appears hopping locomotion developed during the middle to late Oligocene (Fig. 2), when Australia was largely covered by temperate forest. From post-cranial macropodid fossils Kear (1998) has suggested a later transition from quadrupedal to bipedal gaits, possibly during the late Oligocene to early Miocene. This infers that hopping evolved twice among the Macropodoidea; we feel that this is unlikely because by the middle to late Miocene (15–25 mybp), macropodids had an obvious bipedal morphology (Kear 1998; Archer *et al.* 1999).

With the drying out of the continent and the spread of grasslands during the Miocene, the Macropodoidea underwent a major radiation (Archer

*et al.* 1999). The dominance of this group of hopping herbivores continued until European times, with both families Potoroidae and Macropodidae having many arid-adapted species. Of the potoroids, bettongs in the arid zone tended to be the more specialized hoppers. The recently extinct desert rat-kangaroo (*Caloprymnus campestris*), was probably the most accomplished potoroid hopper. Despite weighing less than a kilogram, it could outrun horses over a distance of up to about 20 km (Finlayson 1932; Finlayson 1943: p.102).

Our study of *B. penicillata* provides insights into how hopping bettongs may have been advantaged in arid conditions. In arid environments food resources are patchily and widely distributed and predation risk is generally high due to the openness of the habitat. Fig. 1a indicates that hopping *B. penicillata* can reach higher speeds than quadrupedal mammals, due to the locomotory economy at speeds where hopping is well established. Because of the limitation on aerobic capacity in both groups, *B. penicillata* has a maximum speed more than twice that predicted for a similar sized quadruped (Fig. 1a). Predation risk would presumably be reduced by the ability to reach relatively high speeds. Conversely, if not hopping at maximum speed, *B. penicillata* can move with lower costs than a quadruped. This would facilitate foraging over a wide area. There are trade-offs associated with hopping; at lower speeds locomotory costs are actually higher than those for quadrupedal movement, presumably because of the anatomical specializations associated with bipedality.

### Hopping rodents

Hopping has evolved in at least four rodent families and is associated with arid or semi-arid environments in all groups. Unlike in the hopping marsupials, the influence of phylogeny on rodent hopping is unclear. The phylogenetic position of family Pedetidae is uncertain, and although the families Heteromyidae, Dipodidae and Muridae probably share a common ancestor, not all species in these families are hoppers (Vaughan *et al.* 2000). The evolution of hopping in all four families appears to have been strongly affected by the world-wide increase in aridity in the late Miocene and the appearance of deserts during the Pliocene (Vaughan *et al.* 2000).

There has been debate about the energetics and mechanics of hopping locomotion in rodents. Thompson *et al.* (1980) examined three species of hopping rodents; 2 *Pe. capensis* 3 kg, 8 desert kangaroo rats (*Dipodomys deserti*) 100 g, and 1 Merriam's kangaroo rat (*Dipodomys merriami*) 30 g. They reported that for all species oxygen consumption rates ( $\text{VO}_2$ ) increased linearly with increasing speed, with no statistical difference from the predicted line for quadrupeds of equivalent mass.

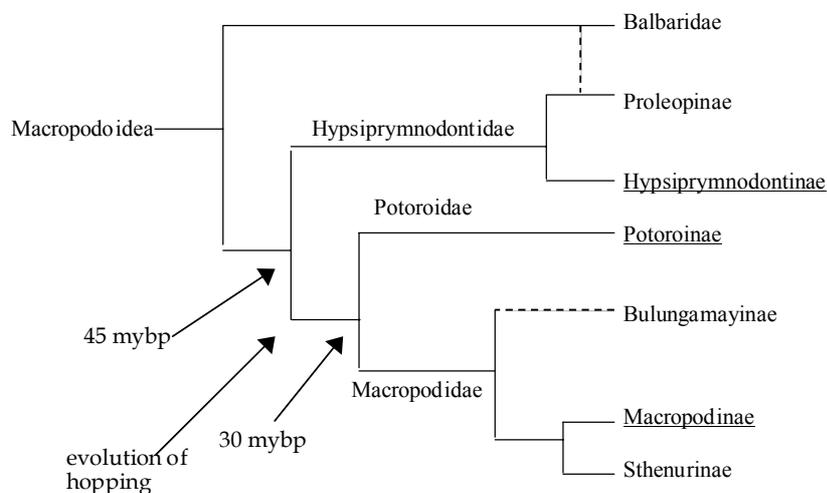


Fig. 2. Cladogram of probable relationships within the super-family Macropodoidea (after Archer *et al.* 1999). Dotted lines indicate uncertain relationships and the extant subfamilies are underlined. Some likely divergence dates and the probable point at which bipedal hopping locomotion evolved are shown (based on the gaits of the extant groups and the molecular data of Burk *et al.* 1998).

These results must be treated with circumspection, as measurements were not made over the full range of hopping speeds of these species. The mean maximum hopping speeds of *D. merriami* and *D. deserti* measured on a laboratory race-track were  $3.2 \text{ ms}^{-1}$  and  $4.2 \text{ ms}^{-1}$ , respectively (Djawdan and Garland 1988); in the field both species have been recorded hopping at speeds as fast as  $7-9 \text{ ms}^{-1}$  (Djawdan and Garland 1988; Kenagy 1973). However, Thompson and his colleagues made measurements of the locomotory energetics of these species only up to speeds of about  $2 \text{ ms}^{-1}$ . Similarly, measurements of *Pe. capensis* energetics were obtained at speeds of less than  $3.5 \text{ ms}^{-1}$ , although this species can move at higher speeds in the wild (B Lovegrove, pers. comm.).

The results of Thompson *et al.* (1980) differ substantially from measurements made by Dawson (1976) on a small hopping rodent, the fawn hopping mouse (*Notomys cervinus*). This species is similar to hopping marsupials in both its locomotory energetics and gait parameters. On a treadmill, *N. cervinus* moves using a trot or a gallop up to about  $0.8 \text{ ms}^{-1}$ , after which it intersperses hopping with galloping, reaching complete bipedal hopping by about  $1.7 \text{ ms}^{-1}$  (Fig. 3). All locomotion at speeds greater than about  $0.5 \text{ ms}^{-1}$  use less energy than predicted for a quadruped, and stride frequency is constant at speeds above  $0.7 \text{ ms}^{-1}$  (Fig. 3). A congener, the spinifex hopping mouse (*Notomys alexis*), exhibits a relatively constant stride frequency at speeds above  $0.8 \text{ ms}^{-1}$  – the speed at which its gait changes from a walk to a quadrupedal bound – up to at least  $1.2 \text{ ms}^{-1}$  (Baudinette *et al.* 1976). The hopping energetics of

this species are unknown, as it changes gaits to a bipedal hop at about  $3 \text{ ms}^{-1}$  (Baudinette *et al.* 1976) and no measurements have been made at these speeds.

The economical fast hopping of *N. cervinus* enables this species to travel faster than a running quadruped of similar size. A mammal running at just  $1.8 \text{ ms}^{-1}$  has reached its  $\text{VO}_2\text{max}$ , while the speed at which *N. cervinus* reaches  $\text{VO}_2\text{max}$  is well above  $2 \text{ ms}^{-1}$  (Fig. 3a). In fact the maximum aerobic speed of *N. cervinus* could well be close to its maximum measured hopping speed of  $4.4 \text{ ms}^{-1}$  (Garland *et al.* 1988). Generally, hopping rodents can move quickly, with heteromyids (*Dipodomys* species) being able to reach the greatest maximum speeds of almost all rodents (Djawdan and Garland 1988). The maintenance of fast hopping speeds requires either a large aerobic capacity or economical fast locomotion. There are fundamental limits on aerobic capacity for all mammals (Hoppeler and Weibel 1998; Dawson *et al.* 2004), so economical fast hopping is likely to be a feature of hopping rodents in general.

In arid environments the risk of predation by large and fast predators, such as raptors and canids, results in selection pressure for fast movement. Hopping rodents have an advantage if they are able to move more quickly than runners for the same energetic output. In addition, the specialization of the hind limbs for bipedal locomotion allows the fore limbs to be specialized for foraging. Species of *Dipodomys* are particularly well adapted for a speedy transition from foraging to rapid locomotion. These species store gathered food in cheek pouches for later

*Fig. 3. a)* Rate of oxygen consumption ( $\text{VO}_2$ ) versus speed for *N. cervinus* (means;  $n = 3$ ), connected by a cubic spline curve of best fit (from Dawson 1976). The heavy dashed line indicates the expected  $\text{VO}_2$  for a 37 g running mammal (equation derived from Taylor *et al.* 1982) and the light dashed lines denote the gait transition speeds. The dotted 'VO<sub>2</sub>max line' indicates the expected  $\text{VO}_{2\text{max}}$  of a 36 g mammal ( $3.6 \text{ ml s}^{-1} \text{ g}^{-1}$ ; from Taylor *et al.* 1981); a running mammal reaches this level at about  $1.8 \text{ m s}^{-1}$ . *b)* Mean stride frequency ( $n=3$ ) versus speed for *N. cervinus* (from Dawson 1976).

consumption, and their eyes and ears are not directly involved in foraging, making them available for sensing potential danger (Bartholomew and Caswell 1951). Avoiding predation may also be dependent on agility. Again, hopping rodents may be advantaged as they can execute rapid changes in direction, such as the seemingly erratic escape leaps of *Dipodomys* species (Bartholomew and Caswell 1951).

Other selection pressures in arid environments include the scarcity and patchiness of water and food resources. Hoppers that can move economically at moderate speeds (e.g., *N. cervinus*, Fig. 3a) are able to cover more ground than runners for the same expenditure. They can access more resource patches in a given time. In addition, the increased maximal

speeds of hopping rodents compared to their running counterparts enables them to move quickly between dispersed resource patches. The most efficient foraging strategy for a hopping rodent is probably to forage over long distances, at fast speeds, for rich patches of food. Conversely, small quadrupeds in arid environments may be better suited to slow speed foraging over short distances. This dichotomy of foraging strategies is seen in the family Heteromyidae, where *Dipodomys* species forage for large dispersed clumps of seeds but their quadrupedal relatives specialize on small clumps or individual seeds encountered when foraging over short distances (Reichman 1981).

Are there trade-offs involved in the development of bipedal hopping? It is likely that the extreme anatomical adaptations required for bipedal movement result in relatively high energetic costs at slow speeds (Figs 1a, 3a). There are also additional consequences. Slow bipedal movement may reduce manoeuvrability and therefore reduce the potential of hoppers to exploit patches of dense vegetation (Schröpfer *et al.* 1985; Kotler *et al.* 1994). In arid environments dense patches of vegetation may be rare, but they are not non-existent. Therefore the exclusion of hoppers from these microhabitats must be offset by the benefits they obtain from fast bipedal locomotion. If open microhabitats are riskier than vegetation patches, the riskiest microhabitats are the richest in resources and distances between resources are large, bipedal hopping will be favoured (Kotler *et al.* 1994).

### Conclusions

In several species of hopping mammal it has been clearly demonstrated that fast hopping is economical in comparison to fast quadrupedal running (Dawson and Taylor 1973; Dawson 1976; Baudinette *et al.* 1992; Webster and Dawson 2003). These hopping species can reach greater maximum aerobic speeds than similarly sized runners. We feel that the widespread use of hopping by arid zone mammals is related to the benefits of fast locomotion, which include increased opportunities to exploit open microhabitats, reduced predation risk, and ability to adopt alternative foraging strategies. While such ecological factors are reasonably well understood for the hopping rodents (e.g., Kotler *et al.* 1994; Reichman 1981), hopping marsupials may require further ecological research. Conversely, the locomotion energetics and gait characteristics of hopping marsupials are quite well documented, but further studies of hopping rodents are required. Further work is also required to measure aerobic limits and the potential role of anaerobic metabolism in both groups.

The patchiness of resources and the openness of the habitat in arid environments probably provided a stimulus for the evolution of hopping among the rodents. By contrast, hopping marsupials evolved in temperate forest habitats, the first macropodoid marsupials probably being small ground-dwelling frugivores, not unlike the extant *H. moschatus*. Such rainforest mammals might benefit from hopping locomotion because rainforests are also patchy environments; resources such as fruiting trees tend to be widely dispersed. The later macropodoids were perhaps 'pre-adapted' for exploiting arid environments with patchy resource distributions and this presumably enabled them to expand into new areas as the Australian continent dried out during the Pliocene. Today kangaroos are the dominant herbivores in Australia and these specialised hoppers provide a fine example of the advantages of moving on two feet rather than four.

#### REFERENCES

- ALEXANDER RM AND VERNON A, 1975. The mechanics of hopping by kangaroos (Macropodidae). *Journal of Zoology, London* **177**: 265–303.
- ARCHER M, ARENA R, BASSAROVA M, BLACK K, BRAMMALL J, COOKE B, CREASER P, CROSBY K, GILLESPIE A, GODTHELP H, GOTT M, HAND S, KEAR B, KRIKMANN A, MACKNESS B, MUIRHEAD J, MUSSER A, MYERS T, PLEDGE N, WANG Y AND WROE A, 1999. The evolutionary history and diversity of Australian mammals. *Australian Mammalogy* **21**: 1–45.
- BARTHOLOMEW GA AND CASWELL HH, 1951. Locomotion in kangaroo rats and its adaptive significance. *Journal of Mammalogy* **32**: 155–167.
- BAUDINETTE RV, 1977. Locomotion energetics in a marsupial, *Setonix brachyurus*. *Australian Journal of Zoology* **25**: 423–428.
- BAUDINETTE RV, 1989. The biomechanics and energetics of locomotion in Macropodoidea. Pp. 245–253 in *Kangaroos, wallabies and rat-kangaroos* ed by G Grigg, P Jarman and I Hume. Surrey Beatty and Sons: Sydney.
- BAUDINETTE RV, GANNON BJ, RUNCIMAN WB AND WELLS S, 1987. Do cardiorespiratory frequencies show entrainment with hopping in the tammar wallaby? *Journal of Experimental Biology* **129**: 251–263.
- BAUDINETTE RV, HALPERN EA AND HINDS DS, 1993. Energetic cost of locomotion as a function of ambient temperature and during growth in the marsupial *Potorous tridactylus*. *Journal of Experimental Biology* **174**: 81–95.
- BAUDINETTE RV, NAGLE KA AND SCOTT RAD, 1976. Locomotory energetics in a marsupial (*Antechinomys spenceri*) and a rodent (*Notomys alexis*). *Experientia* **32**: 583–585.
- BAUDINETTE RV, SNYDER GK AND FRAPPELL PB, 1992. Energetic cost of locomotion in the tammar wallaby. *American Journal of Physiology* **262**: R771–R778.
- BENNETT MB AND TAYLOR GB, 1995. Sclaing of elastic strain energy in kangaroos and the benefits of being big. *Nature* **378**: 56–59.
- BIEWENER AA, 1998. Muscle-tendon stresses and elastic energy storage during locomotion in the horse. *Comparative Biochemistry and Physiology* **120B**: 73–87.
- BUCHMANN OLK AND GUILER ER, 1974. Locomotion in the potoroo. *Journal of Mammalogy* **55**: 203–206.
- BURK A, WESTERMAN M AND SPRINGER MS, 1998. The phylogenetic position of the musky rat-kangaroo and the evolution of bipedal hopping in kangaroos (Macropodidae: Diprotodontia). *Systematic Biology* **47**: 437–474.
- CAVAGNA GC, HEGLUND NC AND TAYLOR CR, 1977. Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *American Journal of Physiology* **233**: R243–R261.
- DAWSON TJ, 1976. Energetic cost of locomotion in Australian hopping mice. *Nature* **259**: 305–307.
- DAWSON TJ, 1977. Kangaroos. *Scientific American* **237**: 78–89.
- DAWSON TJ, MIFSUD B, RAAD MC AND WEBSTER KN, 2004. Aerobic characteristics of red kangaroo skeletal muscles: Is a high aerobic capacity matched by muscle mitochondrial and capillary morphology as in eutherian mammals? *Journal of Experimental Biology* **207**: 2811–2821.
- DAWSON TJ AND TAYLOR CR, 1973. Energetic cost of locomotion in kangaroos. *Nature* **246**: 313–314.
- DIMERY NJ AND ALEXANDER RM, 1985. Elastic properties of the hind foot of the donkey, *Equus asinus*. *Journal of Zoology, London* **207**: 9–20.
- DIMERY NJ, KER RF AND ALEXANDER RM, 1986. Elastic properties of the feet of deer (Cervidae). *Journal of Zoology, London* **208**: 161–169.

- DJAWDAN M AND GARLAND T, 1988. Maximal running speeds of bipedal and quadrupedal rodents. *Journal of Mammalogy* **69**: 765–772.
- FINLAYSON HH, 1932. *Caloprymnus campestris*, its recurrence and characters. *Transactions of the Royal Society of South Australia* **56**: 148–1676.
- FINLAYSON HH, 1943. *The red centre: man and beast in the heart of Australia*. Halstead Press: Sydney.
- FRITH HJ AND CALABY JH, 1969. *Kangaroos*. F.W. Cheshire: Melbourne, Canberra, Sydney.
- GARLAND T, GEISER F AND BAUDINETTE RV, 1988. Comparative locomotor performance of marsupial and placental mammals. *Journal of Zoology, London* **215**: 505–522.
- HEGLUND NC AND TAYLOR CR, 1988. Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *Journal of Experimental Biology* **138**: 301–318.
- HOPPELER H AND WEIBEL ER, 1998. Limits for oxygen and substrate transport in mammals. *Journal of Experimental Biology* **201**: 1051–1064.
- HOYT DF AND TAYLOR CR, 1981. Gait and the energetics of locomotion in horses. *Nature* **292**: 289–290.
- JOHNSON PM AND STRAHAN R, 1982. A further description of the musky rat-kangaroo, *Hypsiprymnodon moschatus* Ramsay, 1876 (Marsupialia, Potoroidae), with notes on its biology. *Australian Zoologist* **21**: 27–46.
- KEAR BP, 1998. Postcranial morphology and phylogenetics of Oligo-Miocene kangaroos (Marsupialia: Macropodoidea) from Riversleigh, Northwestern Queensland. Honours thesis, University of New South Wales, Sydney.
- KENAGY GJ, 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. *Ecology* **54**: 1201–1219.
- KER RF, ALEXANDER RM AND BENNETT MB, 1988. Why are mammalian tendons so thick? *Journal of Zoology, London* **216**: 309–324.
- KER RF, DIMERY NJ AND ALEXANDER RM, 1986. The role of tendon elasticity in hopping in a wallaby (*Macropus rufogriseus*). *Journal of Zoology, London* **208**: 417–428.
- KÖTLER BP, BROWN JS AND MITCHELL WA, 1994. The role of predation in shaping the behaviour, morphology and community organisation of desert rodents. *Australian Journal of Zoology* **42**: 449–466.
- KRAM R AND DAWSON TJ, 1998. Energetics and biomechanics of locomotion by red kangaroos (*Macropus rufus*). *Comparative Biochemistry and Physiology* **120B**: 41–49.
- KRAM R AND TAYLOR CR, 1990. Energetics of running: a new perspective. *Nature* **346**: 265–267.
- REICHMAN OJ, 1981. Factors influencing foraging in desert rodents. Pp. 195–213 in *Foraging behaviour: Ecological, ethological and psychological approaches* ed by AC Kamil and TD Sargent. Garland STPM Press: New York and London.
- SCHRÖPFER R, KLENNER-FRINGS B AND NAUMER E, 1985. Locomotion pattern and habitat utilisation of the two jerboas *Jaculus jaculus* and *Jaculus orientalis* (Rodentia, Dipodidae). *Mammalia* **49**: 445–454.
- STRAHAN R (ED), 1995. *The mammals of Australia*. Australian Museum/Reed Books: Sydney.
- TAYLOR CR, HEGLUND NC AND MALOIJ GMO, 1982. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *Journal of Experimental Biology* **97**: 1–21.
- TAYLOR CR, MALOIJ GMO, WEIBEL ER, LANGMAN VR, KAMAU JMZ, SEEHERMAN HJ AND HEGLUND NC, 1981. Design of the mammalian respiratory system. III. Scaling maximum aerobic capacity to body mass: wild and domestic mammals. *Respiration Physiology* **44**: 25–37.
- THOMPSON SD, MACMILLEN RE, BURKE EM AND TAYLOR CR, 1980. The energetic cost of bipedal hopping in small mammals. *Nature* **287**: 223–224.
- VAUGHAN TA, RYAN JM AND CZAPLEWSKI NJ, 2000. *Mammalogy (4th edition)*. Saunders College Publishing: Fort Worth.
- WEBSTER KN AND DAWSON TJ, 2003. Locomotion energetics and gait characteristics of a rat-kangaroo, *Bettongia penicillata*, have some kangaroo-like features. *Journal of Comparative Physiology B* **173**: 549–557.