

REVIEW

Why do mammals hop? Understanding the ecology, biomechanics and evolution of bipedal hopping

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ABSTRACT

Bipedal hopping is a specialized mode of locomotion that has arisen independently in at least five groups of mammals. We review the evolutionary origins of these groups, examine three of the most prominent hypotheses for why bipedal hopping may have arisen, and discuss how this unique mode of locomotion influences the behavior and ecology of modern species. While all bipedal hoppers share generally similar body plans, differences in underlying musculoskeletal anatomy influence what performance benefits each group may derive from this mode of locomotion. Based on a review of the literature, we conclude that the most likely reason that bipedal hopping evolved is associated with predator avoidance by relatively small species in forested environments. Yet, the morphological specializations associated with this mode of locomotion have facilitated the secondary acquisition of performance characteristics that enable these species to be highly successful in ecologically demanding environments such as deserts. We refute many long-held misunderstandings about the origins of bipedal hopping and identify potential areas of research that would advance the understanding of this mode of locomotion.

KEY WORDS: Heteromyid, Saltation, Macropod, Locomotion

Introduction

Bipedal hopping is a specialized mode of terrestrial locomotion characterized by sustained saltatory motion in which the hindlimbs contact the ground simultaneously with no involvement of the forelimbs (Bartholomew and Caswell, 1951; Howell, 1932). Within extant animals, bipedal hopping is most prevalent in mammals, having arisen once in marsupials and five times independently in rodents (Table 1, Fig. 1). One independently derived bipedal hopping clade that includes jerboas utilizes asymmetrical gaits more than 50% of the time and its members are not considered obligate hoppers (Moore et al., 2017a; Schröpfer et al., 1985). However, hopping is the fastest mode of steady-state locomotion in the lesser Egyptian jerboa, *Jaculus jaculus* and therefore is an important component to their ecology and evolution (Moore et al., 2017a); thus, we include them in this Review. Hopping may also have been used by some extinct marsupials and early reptile-like mammals (Chen and Wilson, 2015; D'Orazi Porchetti et al., 2017; Mares, 1975). In addition to its use by mammals, bipedal hopping is utilized by some small birds and was possibly used by some dinosaurs (Benton, 1999; Hayes and Alexander, 1983). Australian hopping mice *Notomys* occupy fundamentally different dietary

niches (Morton, 1985; Morton et al., 1994) and their foraging behavior, movement patterns and locomotor mechanics may be dissimilar from those of the Heteromyids, which are comparatively over-represented in the available literature. More work to understand hopping mice is urgent given the rapid extinction rates of Australian vertebrates. In this Review, we will focus on mammals and only those species that utilize bipedal hopping for sustained locomotion (not just for a quick escape).

The most salient morphological aspects of bipedal hoppers are elongated hindlimbs, reduced forelimbs, specializations of the hindfeet and relatively long tails. Forelimb length to hindlimb length ratios of 0.5 or less generally distinguish bipedal hoppers from their quadrupedal counterparts and all extant bipedal rodents that have been measured have a ratio of 0.43 or less (Fig. 2). However, tree kangaroos (*Dendrolagus matschiei*) have regained relatively long forelimbs in response to re-establishing an arboreal lifestyle. Hindlimb elongation is primarily accomplished via distal elements (e.g. metatarsals and toes), although the tibia is also substantially elongated in macropods (Bennett, 2000; Berman, 1980; McGowan et al., 2008a; Moore et al., 2015). In addition to elongation of the segments, foot specialization is characterized by digital reduction and fusion of the metatarsals. Finally, bipedal hoppers have a relatively long and/or heavy tail that performs functions ranging from balance in steady hopping to providing propulsion in slow locomotion of larger kangaroos (Alexander and Vernon, 1975; Biewener et al., 1981; Moore et al., 2013; O'Connor et al., 2014; Webster and Dawson, 2004). The tail also likely plays an important role in body control during escape jumps by smaller species (Bartholomew and Caswell, 1951; Whitford et al., 2017).

Ecological functionality of these morphological traits appears to be clade specific and may be related to body size. Within large macropods (i.e. kangaroos and wallabies >3 kg), hopping is associated with exceptional locomotor efficiency; in rodents, debate oscillates around enhanced sprint speed, metabolic efficiency and endurance, unpredictability, and extreme acceleration and jumping. It is also clear from an analysis of convergent evolution that beyond the base similarities associated with bipedal hopping, there are significant differences in morphology across radiations of hopping rodents that indicate different origins and may reflect different selective pressures (Berman, 1980). Bipedal hopping has captured the imagination of scientists for over a century (Howell, 1932; Muybridge, 1887) and numerous hypotheses have been posited for why this unique mode of locomotion has arisen. In this paper, we review some of these hypotheses and examine whether and how morphological or behavioral adaptations drive the ecology and evolution of mammalian bipedal hopping. In other words, we ask: why do mammals hop?

When and where did bipedal hopping arise?

One of the most poorly understood aspects of bipedal hopping is the evolutionary origin. Although many bipedal hoppers presently inhabit arid or semi-arid habitats, fossil evidence indicates several

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Table 1. Known extant bipedal hoppers

Family	No. of genera	No. of species
Pedetidae	1	2
Dipodidae	11	25
Heteromyidae	2	22
Muridae	1	10
Macropodidae	11	65

lineages likely arose in humid, structurally complex forests. Macropodoidea (the clade containing kangaroos, wallabies and potoroos) originated around 40 million years ago from a small, arboreal, possum-like ancestor (Burk and Springer, 2000; Burk et al., 1998; Meredith et al., 2009; Szalay, 1994). Bipedal hopping appears to have evolved once within this clade to the exclusion of one genus, *Hypsiprymnodon*, which utilizes quadrupedal bounding and may represent an intermediate in the evolution of bipedal hopping (Burk et al., 1998; Meredith et al., 2009; Szalay, 1994; Westerman et al., 2002). All macropodid species share at least some morphological features associated with bipedal hopping, including elongated feet and tarsal modifications that stabilize the ankle joint and limit motion to flexion–extension (Marshall, 1973; Warburton and Dawson, 2015; Warburton and Prideaux, 2009; Szalay, 1994). The ancestral habitat for this group was likely dense forest; however, in the last 5–10 million years, macropodines underwent a rapid

radiation (Meredith et al., 2009) and extant species now inhabit a diverse range of habitats. While the majority still live in forested environments, species have evolved to live in almost every niche available, including deserts, grasslands, rocky cliff faces and even trees (Van Dyck and Strahan, 2008). Macropods also encompass a wide size range, from 1 to 90 kg, although extinct species likely reached as much as 250 kg (Helgen et al., 2006). Much of this increase in body size appears to have coincided with Australia becoming cooler and drier, with rainforests giving way to grasslands and now deserts (Burk et al., 1998; Martin, 2006; Prideaux and Warburton, 2010).

Rodent bipedal hopping is often referred to as an adaptation to desert environments (Bartholomew and Caswell, 1951; Berman, 1980; Ford, 2006; Howell, 1932; Mares, 1975; Moore et al., 2017a; Webster and Dawson, 2004); however, a large body of literature indicates bipedal ancestors of Heteromyids and Dipodidae first appeared in mesic to wet, structurally complex forests, grasslands and riparian environments (e.g. Voorhies, 1975; Wu et al., 2014). Ancestral and/or extinct bipedally hopping Heteromyidae include *Prodipodomys*, found extensively in the moist lowland savannahs of eastern Nebraska during the late Tertiary. This genus and *Eodipodomys* populated habitats in or near wetlands before North American deserts evolved, but already exhibited inflated auditory bullae and locomotor morphological traits similar to those of modern *Dipodomys* (Voorhies, 1975). Recent work suggests that ancestral jerboas were hopping before 14 million years ago in humid, forested environments and that dental morphology evolved to meet the demands of changing food resources in arid environments (Wu et al., 2014). Extant Pedetidae includes two species, *Pedetes capensis* from Southern Africa and *Pedetes surdaster*, which appears in Eastern Africa. The earliest known Pedetidae representatives, known as genus *Megapedetes*, appeared around 20 million years ago (Senut, 2016). As the name suggests, these rodents were more robust in body size as well as morphological features related to locomotion. Species in this genus exhibit five rather than four toes, shorter femoral shafts, tibias and calcaneums, and various skeletal features that suggest members of this genus were less agile than extant *Pedetes* (Senut, 2016). *Megapedetes* occupying warm, wooded Namibia during the middle Miocene were smaller and relatively more gracile compared with members of this genus living in forests of Kenya (Senut, 2016). In Australia, species of the hopping mice genus *Notomys* diverged in locomotor morphology from quadrupedal ancestors well before the recent appearance of true deserts; however, the prevalent misconception that bipedal hopping evolved in arid environments often leads to a confounding timeline (Ford, 2006). The fossil record and paleoecological reconstruction suggest conflicting environments for the extinct, putatively bipedal hopping marsupial *Microtragulus* during the Pliocene. Hydrochoeridae and crocodile remains suggest warm, humid environments, but contemporaneous small rodents are more likely indicative of xeric environments (Ortiz et al., 2012).

Quadrupedal bounding species in the genera *Zapus* and *Napeozapus* are sister taxa to bipedal Dipododinae and are thought to represent intermediate morphological forms between bipedal hoppers and strictly quadrupedal rodents (Hamilton, 1935; Berman, 1980; Lebedev et al., 2013). Species in these genera exhibit long hindlimbs relative to forelimbs (but do not fall below the 0.43 forelimb length:hindlimb length ratio; Fig. 2) and have been reported to leap up to 4 m away from potential predators (Hamilton, 1935). However, species in this clade lack secondarily simplified distal hindlimb skeletal elements (Berman, 1980; Lebedev et al., 2013), inhabit cluttered, forested environments (Hamilton, 1935) and only use bipedalism during rapid escape

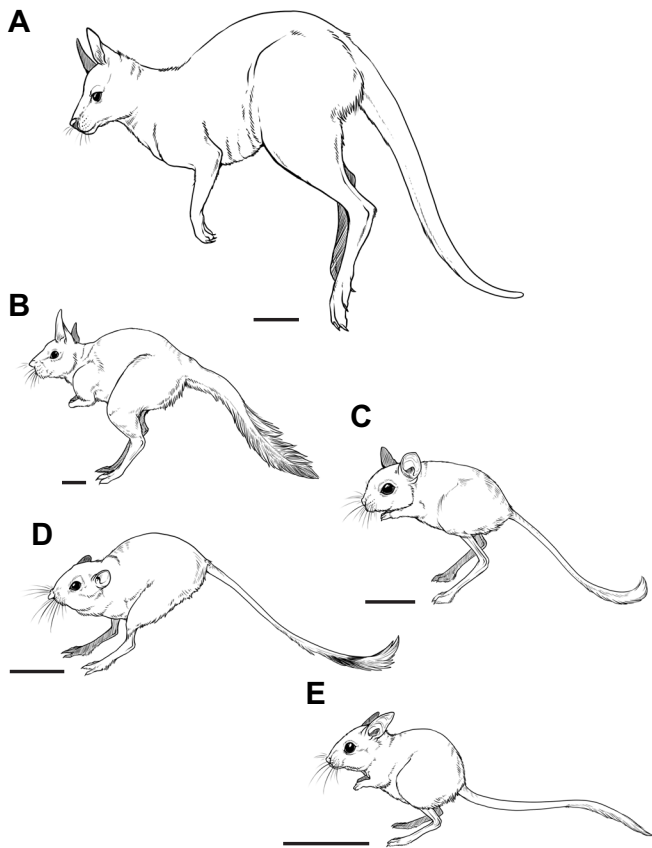


Fig. 1. Representative drawings of each extant bipedal hopping lineage. (A) Tammar wallaby (*Macropus eugenii*, mass=5 kg). (B) South African springhare (*Pedetes capensis*, mass=2.5 kg). (C) Desert kangaroo rat (*Dipodomys deserti*, mass=100 g). (D) Lesser Egyptian jerboa (*Jaculus jaculus*, mass=120 g). (E) Spinifex hopping mouse (*Notomys alexis*, mass=32 g).

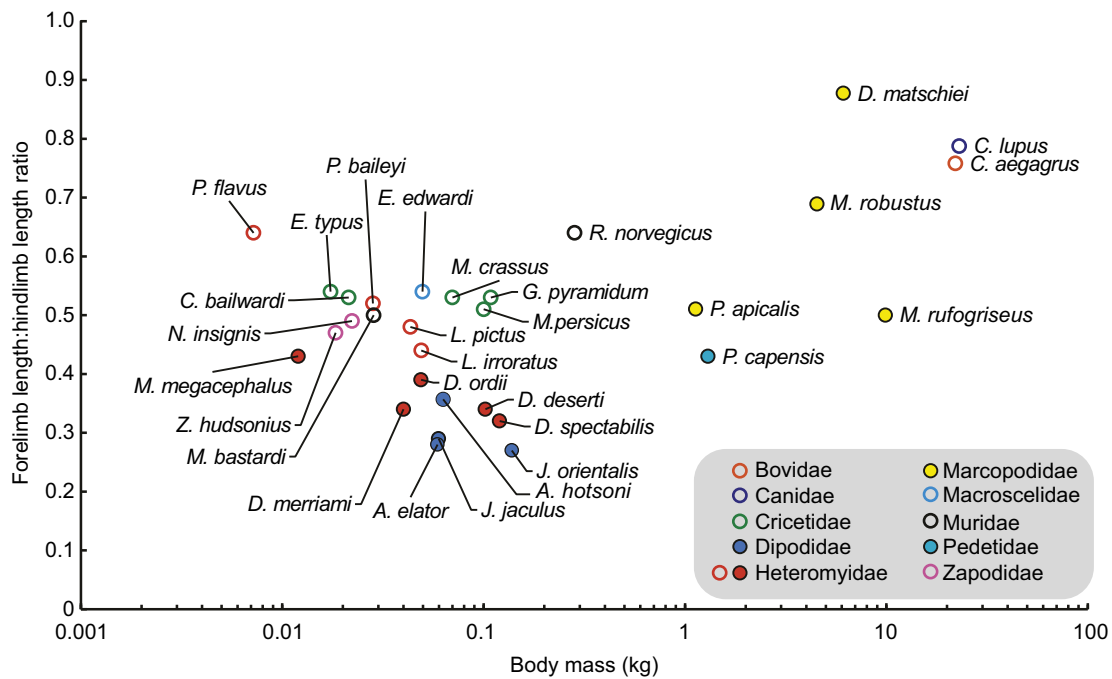


Fig. 2. Forelimb/hindlimb length ratios of data as a function of body mass of bipedally hopping rodents, bipedal macropods and quadrupedal animals of similar sizes. Bipedal species are represented by open circles, quadrupedal species are represented by filled circles. Note: tree kangaroos (*D. matschiei*) have reacquired characteristics for an arboreal lifestyle, including longer forelimbs relative to other macropod species. Data derived from Berman (1980); Bowers and Brown (1982); Grand (1990); Pontzer (2007); Samuels and van Valkenburgh (2008).

maneuvers (Harty, 2010). The intermediate forelimb:hindlimb ratio, bipedal escape behavior and use of forest or shrub environments suggest tradeoffs between bipedal hopping and effectively moving through dense, cluttered habitats.

Given the overwhelming paleoecological evidence, we conclude that mammalian bipedal hoppers likely first appeared in humid, structurally complex forests. At the very least, no evidence suggests bipedal hopping evolved in deserts (Burk and Springer, 2000; Ford, 2006; Meredith et al., 2009; Ortiz et al., 2012; Senut, 2016; Voorhies, 1975; Wu et al., 2014). Jaw, tooth and gut morphology evolved after bipedal hopping to meet the challenges of increasingly arid environments (Alhajeri et al., 2016; Burk et al., 1998; Hume, 1989; Wu et al., 2014). Specific adaptations are beyond the scope of this Review; however, they are likely fundamental drivers of extant rodent and macropodid diversity.

Although bipedal hoppers did not arise in deserts, this mode of locomotion is clearly effective in this environment. For example, although bipedal hoppers are less species rich relative to quadrupedal fauna in North America, *Dipodomys merriami* is the most commonly encountered species in any North American desert (Kelt et al., 1999). Furthermore, bipedal hoppers are the most dominant mammals in the Gobi and Turan Desert regions (Kelt et al., 1999). In Australia, several species of macropods inhabit desert regions (Morton, 1979) where locomotor efficiency may enable them to access scarce water resources (Webster and Dawson, 2004). Given the conundrum that bipedal hopping did not evolve in deserts, but almost all extant bipedal hoppers are found in arid or semi-arid environments, we review the literature that corresponds to selective pressures inhibiting, maintaining and promoting diversification of bipedal hopping mammals.

Why did bipedal hopping arise?

The specific selective pressures that drove the evolution of bipedal hopping, and the related morphological adaptations, remain elusive.

Since the early-mid 20th century, a number of hypotheses have been proposed for why this mode of locomotion may have arisen. Here, we will examine three of the most prevalent hypotheses which have been the subject of numerous studies.

Hypothesis 1: bipedal hopping evolved to enhance locomotor efficiency

Likely the most notable physiological feature associated with bipedal hopping locomotion is the remarkable ability of larger species to decouple oxygen consumption, a proxy for metabolic energy use, from steady-state hopping speed. For animals using all other gaits, the rate of oxygen consumption increases linearly with increasing speed (Taylor et al., 1982), but for some hopping species, the rate of oxygen consumption remains constant or even decreases with speed (Baudinette et al., 1987, 1992; Dawson and Taylor, 1973; Kram and Dawson, 1998; Webster and Dawson, 2003). This phenomenon was first described over 40 years ago in red kangaroos by Dawson and Taylor (1973) and provided an early hypothesis for why bipedal hopping may have arisen. Subsequent studies of macropods also found this decoupling of metabolic cost from speed; however, there appears to be a lower limit on body size of approximately 3 kg for species that enjoy this unique benefit (Baudinette et al., 1987; Thompson et al., 1980). Some debate still remains on the possibility of an energetic advantage for smaller marsupials. One study of bettongs (*Bettongia penicillata*, ~1 kg) reported that at hopping speeds, oxygen consumption increased linearly, but at a significantly slower rate than for a similarly sized quadruped (Webster and Dawson, 2004), whereas another study of the same species showed no difference between oxygen consumption by bettongs and values expected for quadrupeds of the same size (Thompson et al., 1980). Studies of bipedal hopping rodents up to 3 kg (e.g. *Pedetes*) also showed no energetic advantage relative to quadrupeds of similar size (Bennett and Taylor, 1995; Heglund and Taylor, 1988; Kram and Taylor, 1990;

Taylor et al., 1982; Thompson et al., 1980). While the exact mechanism for decoupling oxygen consumption from speed still cannot be fully explained (see below for discussion), it appears that body size is likely a greater factor than phylogeny.

The ability to decouple oxygen consumption from speed by large macropods has largely been attributed to their ability to store and return elastic strain energy from their relatively specialized ankle extensor muscle–tendon units (i.e. Achilles tendons) (Alexander and Vernon, 1975; Bennett and Taylor, 1995; Cavagna et al., 1977; Griffiths, 1989). *In vivo* measurements reveal that the amount of elastic energy stored and returned from these tendons increases with increasing hopping speed, while the mechanical work done by the associated muscles remains low and relatively constant (Biewener, 2004; Biewener and Baudinette, 1995; Biewener et al., 1998). The amount of energy returned from the tendons may account for up to 50% of the energy required for steady-speed hopping (Alexander and Vernon, 1975; Biewener et al., 1998). However, it should be noted that substantial elastic energy storage and return from distal leg tendons is not unique to macropods, and several large mammals, including humans, are estimated to store and return as much or more energy during running (Alexander et al., 1982; Dimery et al., 1986; Gregersen et al., 1998; Ker et al., 1987; Rubenson et al., 2011; Stearne et al., 2016). Muscle–tendon units that are best suited for efficient elastic energy storage and return, such as those found in large macropods, are typically composed of short, pennate muscle fibers connected to relatively long, thin tendons (Biewener and Roberts, 2000). Short, pennate muscles are capable of generating the high forces necessary to produce significant tendon stress, while doing so with a relatively small muscle volume, which reduces metabolic cost (Roberts et al., 1998). During hopping, these muscles contract nearly isometrically, doing little mechanical work, which further reduces the cost of generating force (Biewener, 2004; Biewener et al., 1998). In order for tendons to store a substantial amount of elastic energy, they must be thin so that they experience high stresses, and therefore strains, under the loads generated during hopping. And the tendon must be long, because the amount of elastic energy stored in a tendon is proportional to its volume (volume=length×area). The capacity to store and return elastic strain energy is also a function of body size. Across species, the ratio of muscle cross-sectional area to tendon cross-sectional area scales with strong positive allometry (Fig. 3), meaning that larger species can generate higher tendon stresses. However, the decrease in tendon safety factor (failure stress/operating stress) associated with increasing body size also likely placed a limit on how large species could be and still hop (Bennett and Taylor, 1995; McGowan et al., 2008a). Therefore, while small bipedal hoppers share a similar general body plan with larger species, the underlying muscle–tendon architecture is substantially different. Smaller species have relatively thicker ankle extensor tendons that do not experience high stresses during steady-speed hopping (Biewener et al., 1981, 1988; C.P.M., unpublished). For example, for one species of kangaroo rat (*Dipodomys spectabilis*) moving at a moderate speed (3.1 m s^{-1}), elastic energy recovery accounts for only 14% of the cost of hopping.

Alternative mechanisms have been proposed for why bipedal hopping may be more efficient than other gaits. Two examples of these are locomotor–respiratory coupling and stride frequency independence versus speed. Locomotor–respiratory coupling is a phase lock between stride frequency and respiratory frequency (Alexander, 1989; Baudinette, 1989; Bramble and Carrier, 1983) that results in the inertia of the animal's viscera contributing to the work of respiration and therefore reduces the metabolic cost. As the

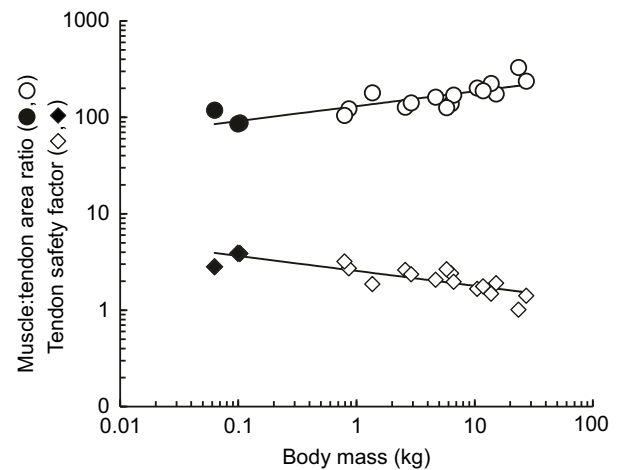


Fig. 3. Scaling of muscle cross-sectional area to tendon cross-sectional area and tendon safety factors for the combined ankle extensor of macropods and bipedal hopping rodents. Macropods are represented by open symbols, bipedal hopping rodents by filled symbols. As animals get larger, the capacity to store and return elastic strain energy increase, while the tendon safety factor decreases. Safety factors below 1 indicate that the muscles can generate enough force to rupture the attached tendon. Data adapted from Biewener et al. (1981); McGowan et al. (2008a); Moore et al. (2017b); C.P.M., unpublished.

viscera move back and forth in response to contacting and leaving the ground, they create pressure fluctuations that induce respiratory gas flow. Although this mechanism is not unique to bipedal hoppers (Bramble and Carrier, 1983; Daley et al., 2013; Giuliodori et al., 2009), it may be particularly effective in species that use this gait. Macropods have a tight 1:1 coupling between gait frequency and breathing frequency and the diaphragm has an enlarged central tendon that likely facilitates a ‘visceral piston’ (Baudinette et al., 1987). Locomotor–respiratory coupling has not yet been explored in hopping rodents; however, we predict there would be a similar 1:1 ratio. Bipedal hoppers also differ from animals that use other gaits in how they increase locomotor speed. To increase speed, animals must increase stride frequency, stride length or some combination of both. At slow to moderate speeds, quadrupeds and striding bipeds (i.e. birds and humans) tend to increase speed by increasing both stride frequency and stride length (Gatesy and Biewener, 1991; Heglund and Taylor, 1988), whereas bipedal hoppers increase speed by increasing stride length and holding stride frequency relatively constant (Baudinette et al., 1987; Dawson and Taylor, 1973). A comparison of stride frequency for similarly sized quadrupeds, running birds and bipedal hoppers (Fig. 4) shows that while stride frequency decreases with size across all groups, the slope of the relationship between stride frequency and speed is at least two times greater for quadrupeds and birds compared with bipedal hoppers. The only exception is the large galloping quadruped, which has a similar slope to the large hopper, and is consistent with the fact that large mammals tend to increase speed during galloping primarily by increasing stride length (Biewener, 2003). These differences are important for locomotor economy because mass-specific cost of transport is proportional to stride frequency (Heglund and Taylor, 1988), and therefore holding stride frequency constant across speeds may contribute to the decoupling of oxygen consumption from speed. Yet, this does not explain why small bipedal hoppers do not also benefit from reduced metabolic cost of transport.

Based on the body of research to date, we conclude that, although locomotor efficiency is undoubtedly a factor contributing to the

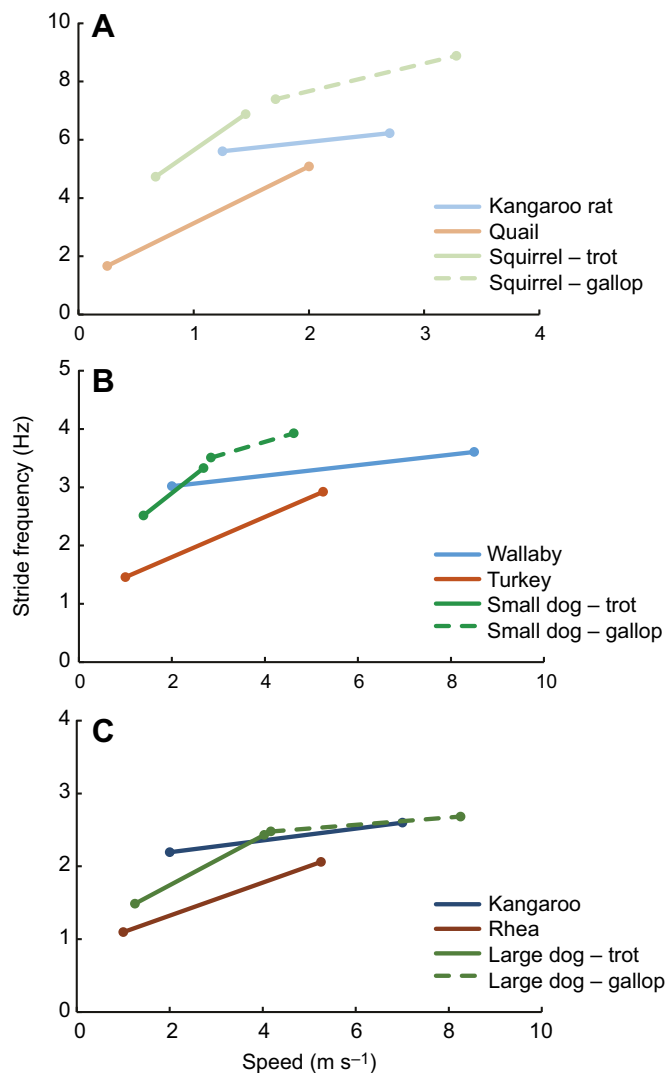


Fig. 4. Stride frequency versus speed for small, medium and large bipedal hoppers, bipedal striders and quadrupeds. (A) Small (0.1–0.2 kg), (B) medium (3.9–5.7 kg) and (C) large (18–25 kg). Stride frequency decreases with body size for all groups; however, stride frequency increases with speed to a much greater extent in striders and quadrupeds. Data derived from Baudinette et al. (1987); Dawson and Taylor (1973); Gatesy and Biewener (1991); Heglund and Taylor (1988); C.P.M., unpublished.

evolution of all terrestrial species, it is unlikely that it was a primary selective pressure leading to the evolution of bipedal hopping. As discussed above, energetic benefits are only present in larger species, yet all bipedal hopping radiations arose from relatively small quadrupedal ancestors. The energetic benefit of hopping likely arose as a consequence of scaling as macropods grew larger in response to their changing environment. And although hopping does allow species to increase speed without increasing stride frequency, the lack of an energetic benefit for small extant species further suggests that locomotor efficiency did not drive the evolution of bipedal hopping.

Hypothesis 2: bipedal hopping evolved to permit greater forelimb specialization for food handling and digging

Members of the rodent family Heteromyidae possess external, fur-lined cheek pouches that are used to receive, store and transport seeds. Forelimbs are used to harvest and insert seeds from the environment

into the cheek pouches, a behavior termed ‘pouching’. Therefore, if forelimb morphology is decoupled from constraints related to locomotion, then bipedal hoppers would enjoy greater degrees of freedom to evolve specializations for digging and harvesting food. Experiments using high-speed cinematography revealed limb cycling frequency and pouching rates are not increased in bipedal rodents relative to similarly sized, sympatric quadrupedal species, suggesting feeding–locomotion decoupling is neither a driver nor a consequence of hopping (Nikolai and Bramble, 1983; Price, 1993; Price and Brown, 1983). Also, many quadrupedal rodents use fur-lined cheek pouches and many quadrupedal rodents use their forelimbs to process food and show no tendencies towards bipedal behavior (Berman, 1980). Further, multiple species of the bipedally hopping jerboas and macropods are herbivorous and no known forelimb specializations for grazing are related to this energy acquisition mode.

Careful anatomical dissections revealed that shape variation in forelimb lever arms distinguished between desert-dwelling heteromyids and forest-dwelling *Heteromys* and *Liomys*, but not between bipedal and quadrupedal species (Price, 1993). In fact, similarity in forelimb shape is concordant with environmental similarity, topography and soil characteristics, but not locomotor mode. However, Price (1993) cautioned that limiting analysis to Heteromyidae restricts statistical power to reject the hypothesis of forelimb specialization. Indeed, Price (1993) indicates ‘non-statistical’ differences between bipedal *Dipodomys* and non-bipedal Heteromyids in anterior scapula area, acromion, humerus, ulna and deltoid process sizes. Thus, we conclude that bipedalism in mammals did not arise to facilitate food handling, but more analysis is needed to understand tradeoffs between digging and locomotion in bipedal and quadrupedal rodents.

Hypothesis 3: bipedal hopping evolved to enhance predator avoidance and escape

This is the most debated and exciting hypothesis regarding rodent bipedal locomotion. While predation is a fact of life for small mammals, bipedally hopping rodents are preyed upon at lower rates than sympatric quadrupedal rodents (Kotler et al., 1988; Longland and Price, 1991; Pavey et al., 2008). Three mechanisms fundamental to this hypothesis are that (1) bipedal hopping increases speed relative to quadrupedal running (Djawdan and Garland, 1988), (2) bipedal hopping, often called ricochet movement, decreases a predator’s ability to predict the trajectory of bipedal rodents in open environments (Bartholomew and Caswell, 1951; Howell, 1932; Moore et al., 2017a) and (3) bipedality enables rapid, ballistic jumps during predator–prey interactions (Freymler et al., 2017; Higham et al., 2017; Longland and Price, 1991). While predation was almost certainly a selective pressure acting on all the earliest hopping radiations, relatively little is known about these interactions. However, bipedal hopper skeletal remains are found in fossil owl pellets, suggesting owls exerted predation pressure historically and continue to do so now (Kotler et al., 1988; Ortiz et al., 2012).

Bipedal heteromyids are generally faster than quadrupedal species of similar size, as measured using treadmills and by timing escape-like runs in field settings (Djawdan, 1993; Djawdan and Garland, 1988). In fact, desert kangaroo rats (*Dipodomys deserti*) have been recorded running at 18.3 m s⁻¹ in the field. However, bipedal kangaroo mice (*Microdipodops*) are not faster than quadrupedal species of similar size. Furthermore, no studies have experimentally tested the hypothesis that sprint speed predicts survivorship or is heritable in bipedal rodents. This is complicated by the fact that kangaroo rats do not exert maximal effort in laboratory settings (Djawdan and Garland, 1988). Because

kangaroo rats readily tame in the lab (C.P.M., personal observation), ecological and evolutionary interpretation of laboratory data from these species should be approached cautiously.

In addition to possible differences in speed, bipedal rodent locomotor trajectories are less predictable than trajectories of sympatric quadrupedal rodents, possibly conferring advantages to prey species in some contexts. Interest in the ecological and evolutionary consequences of the tendency of rodent bipedal hoppers to move unpredictably has carried on at least since Howell (1932) and continues to excite researchers today (Moore and Biewener, 2015; Moore et al., 2017a). Most recently Moore et al. (2017a) found that bipedal jerboas, *Dipus sagitta* and *Allactaga elater*, are less likely to respond to human-simulated predation risk by seeking shelter in open environments relative to a sympatric, quadrupedal jird (*Meriones* sp.). Gaits of bipedal *A. elater* and *D. sagitta* oscillate between hopping, skipping and running in open environments, and hopping is associated with the greatest acceleration and deceleration. The ecological and evolutionary consequences of gait choice are unclear, but these gait transitions may decrease a potential predator's ability to generate a pursuit strategy. In other words, altering gait, path trajectory and length, and vertical oscillations during locomotion likely enhances a bipedal hopper's chances of avoiding predation. Interestingly, the predictability of locomotor trajectory only 'trended toward significance' between bipedal *D. sagitta* and quadrupedal *Meriones* sp. and the two bipedal rodents in this study differed in their axis (lateral versus vertical) of ricochet motion. *Allactaga elater* tended to turn more than *D. sagitta* and the gait of both bipedal species exhibited a more vertical vector than that of the quadrupedal species. Quadrupedal rodents also exhibit ricochet and 'unpredictable' behaviors when exploring environments where risk is high or unknown (Rogovin et al., 1985), suggesting that being unpredictable inhibits potential predation but is not necessarily restricted to bipedal rodents. It remains unknown why bipedal rodents employ ricochet locomotor trajectories under various ecological contexts, including predation risk, substrates and movement speed, whether this is an artefact of human observation, and whether the extent or magnitude of this feature of bipedal rodents varies with ecological context. Future studies should manipulate predation pressure, or use populations that naturally differ in predation pressure, to test this hypothesis. An additional, but important, observation is that the erratic nature of bipedal hopping may actually attract visually oriented predators, especially owls (Djawdan and Garland, 1988; Longland and Price, 1991).

A rapid vertical or lateral leap, followed by aerial reorientation, to evade the ballistic strike of a predator is likely under strong selective pressure in many small bipedal hoppers. The morphological adaptations of the hindlimbs are well suited for generating the rapid accelerations and high mechanical power output needed to produce the extreme jumping performance seen in many species, with jumps often reaching as high as 10 times the animal's hip height (Bartholomew and Caswell, 1951; Biewener and Blickhan, 1988; Moore et al., 2017b; Schwaner et al., 2017). The elongated hindlimbs of bipedal hoppers enable them to accelerate the body over longer periods of time (Alexander, 1995), and hoppers tend to have substantially more hindlimb muscle mass relative to similarly sized quadrupeds (Berman, 1980; Grand, 1990). Also, as discussed above, small bipedal hoppers have relatively thicker ankle extensor tendons than large hoppers, that store less elastic energy during steady-speed hopping but are capable of transmitting the high forces necessary for jumping. For example, during steady-speed hopping, 0.1 kg kangaroo rats operate with relatively high tendon safety

factors of ~10 (Biewener and Blickhan, 1988), whereas kangaroos and wallabies operate with safety factors of 3 or less (Alexander and Vernon, 1975; Biewener, 1998; McGowan et al., 2008b). However, during vertical jumping, the stresses placed on the tendons are significantly higher, and tendon safety factors may drop to as low as 2 in jerboas and kangaroo rats (Biewener et al., 1988; Moore et al., 2017b; Schwaner et al., 2017). And although tendon stress may limit the acceleration capacity of kangaroos (Biewener and Bertram, 1991), relatively large yellow-footed rock wallabies (*Petrogale xanthopus*, ~5 kg) are capable of extremely high-powered jumps (McGowan et al., 2005a). Rock wallabies have secondarily evolved to live in steep rocky cliffs and have anatomical adaptations that reduce tendon stress relative to that of similarly sized plains-dwelling species (McGowan et al., 2008b). This exception highlights the need to be cautious when interpreting scaling data, where large size ranges can mask variation at a given body size.

Another interesting feature of the hindlimb musculoskeletal anatomy of bipedal hoppers is that all the primary ankle extensor muscles (i.e. gastrocnemii, plantaris) are biarticular, and the uniarticular soleus muscle is vestigial (Alexander and Vernon, 1975; Berman, 1980; Biewener and Blickhan, 1988; Moore et al., 2017b; Rankin et al., 2018). This biarticularity creates a direct linkage between the powerful proximal muscles and the distal limb joints where external mechanical work is typically done. In a recent study of desert kangaroo rats, we showed that while the majority of mechanical work for vertical jumping is delivered at the ankle, approximately 40% of this energy is transferred from proximal muscles (Schwaner et al., 2017), and in a previous study we showed that proximal to distal energy transfer also likely plays an important role in horizontal accelerations by tammar wallabies (McGowan et al., 2005b). The ratio of the moment arms of the ankle extensors at the ankle and knee is approximately 2:1 and is remarkably similar in macropods and bipedal rodents (Alexander and Vernon, 1975; Moore et al., 2017b; Rankin et al., 2018). If the ankle extensor muscle-tendon unit were to act exclusively as a strut, a 4-bar linkage would be created and any torque generated at the knee would be doubled at the ankle. At least in smaller species, this anatomical arrangement may be an adaptation for powerful jumping movements (Rankin et al., in review), although further studies are needed to examine the functional roles of these muscles *in vivo* and in larger species.

We conclude that bipedal hopping, at least in rodents, likely evolved first as an adaptation to jumping and predator avoidance in structurally complex forested environments and now acts to enable predation avoidance or to enhance escape from the ballistic attacks of owls and snakes. More research is needed to understand tradeoffs between long-distance locomotion and rapid escape, how behaviors such as gait and unpredictability vary under changing risk environments, and the mechanics of locomotion on substrates that vary in their mechanical properties.

Desert life, foraging and risk management

Kangaroos and wallabies today occupy nearly every habitat on the continent of Australia and surrounding islands (Kaufmann, 1974; Raven and Gregory, 1946; Van Dyck and Strahan, 2008). One fundamental aspect of macropod ecology is body size. The evolution of macropods is characterized by enlargement and enhanced complexity of the gut, and changes in dental morphology (Burk and Springer, 2000; Burk et al., 1998). Increased body size corresponds with increased gut size and the ability to use foregut fermentation to extract energy from nutrient-poor food sources (Hume, 1989). Critical to desert life in macropods

is the ability to dissipate heat, efficient water metabolism and access to critical freshwater resources (Webster and Dawson, 2004). Therefore, large kangaroos and wallabies likely derive benefits via decoupling energy consumption from locomotor speed. In other words, moving to a water resource or refuge from insolation is relatively less costly for larger macropods.

Life in deserts for hopping rodents is best understood by studying competition between bipedal and quadrupedal species, thereby revealing morphological underpinnings in the context of microhabitat use, risk management and resource scarcity (Bowers and Brown, 1982; Brown and Lieberman, 1973; Kotler and Brown, 1988; Perri and Randall, 1999; Price et al., 2000; Schroder, 1987). Bipedally hopping rodents in North America, Northern Africa and Asia purportedly exhibit an affinity to arid, open and often sandy substrata (Brown, et al., 1994a; Shenbrot, 1992). Rodent communities among deserts exhibit evolutionary convergence in body size, habitat use and community structure (Bowers and Brown, 1982; Brown, 1989). Bipedal jerboas (e.g. *Jaculus jaculus*), like desert kangaroo rats (*D. deserti*), prefer unstabilized, open dunes (Brown et al., 1994a). *Jaculus jaculus* exhibits poor foraging efficiency, moving widely to 'skim the cream' and may be largely herbivorous. Thus, long-distance travel over soft sand may be an important factor in determining movement, range and selection in Dipodidae. Members of the bipedal genus *Dipodomys* preferentially forage in the open as opposed to bush microhabitats in the wild (Bouskila, 1995) (but see the discussion, below, of seasonal flexibility in this behavior). D'Orazi Porchetti et al. (2017) suggest the extinct synapsid *Brasilichnium elusivum* shifted from half-bounding to bipedal skipping when running up sandy slopes, attributing this shift to greater vertical displacement. These authors argue that because bipedal hopping first appeared in humid, forested habitats, the vertical force vector associated with a hop, or at least bipedality, may be an exaptation in extant bipedal rodents to move more effectively in terrain that varies in incline and compliance.

How does ecology maintain or promote selection for the bipedal hopping of rodents? Within communities, bipedal hopping rodents are generally larger than sympatric quadrupedal rodents (Kotler et al., 1988). Therefore, distinguishing between bipedal hopping and body size in rodents is difficult. However, natural and semi-natural experiments disentangling body size, locomotor mode and habitat use reveal ecological and evolutionary differentiation between bipeds and sympatric quadrupedal species. Giving-up density (GUD) experiments, the final density of seeds left in a food tray after rodents have completed foraging, are useful to determine foraging efficiency under varying environmental and predation pressures. Evidence from these types of experiment suggests that for a given size, bipedal species predominate in open, riskier microhabitats and quadrupedal rodents forage under shrubs (Kotler, 1984; Price and Brown, 1983). Bipedally hopping rodents may interfere with foraging by sympatric quadrupeds, dominating 'open' microhabitats where energy-rich seeds are deposited by the wind (Ben-Nathan et al., 2004; Ziv et al., 1993). These microhabitat affiliations are seasonally flexible – when owls are more abundant than snakes in the autumn and winter, bipedal rodents use bush microhabitats. Responding to increased risk from snakes in warmer months, they shift to open spaces between shrubs (Brown et al., 1994a,b). However, what ultimately explains the association between bipedal rodents and open habitats remains unclear. Longland and Price (1991) found that bipedal rodents are attacked more often in the open relative to quadrupeds, but that their likelihood of escape given an attack was higher. These authors suggest, along with others (Djawdan, 1993; Djawdan and Garland,

1988), that the erratic and rapid movements of bipeds lure owl attacks while simultaneously enhancing escape.

When attacked by owls, kangaroo rats leap perpendicular to the trajectory of the attack but jump vertically or backwards away from snakes, supporting the hypothesis that snakes can adjust the mediolateral trajectory but not the length or pitch of a strike and that owls can extend the length of a strike from the air but cannot alter the mediolateral trajectory of a strike (Freymiller et al., 2017; Higham et al., 2017; Longland and Price, 1991). Unsuccessful Mojave rattlesnake (*Crotalus scutulatus*) strikes were shown to be preceded by a rapid response and acceleration by Merriam's kangaroo rats (*D. merriami*), suggesting rapid force production in the hindlimb couples with augmented hearing capacity and extremely low reaction times to successfully evade high-speed strikes (Freymiller et al., 2017; Webster and Webster, 1975). Recent work by Freymiller et al. (2017) indicates that desert kangaroo rats (*D. deserti*) exposed to a live rattlesnake outperform individuals not exposed to a rattlesnake in both take-off velocity and reaction. Although the most obvious difference between bipeds and quadrupeds is in limb morphology, auditory adaptations play a significant role in influencing foraging behavior (Price, 1986; Webster, 1962; Webster and Webster, 1975). While it is true that bipedal rodents are more likely to escape a given owl attack, the probability of escape increases with auditory bullae size, which are largest in bipedal species (Longland and Price, 1991; Webster and Webster, 1975). In fact, experimental reduction of hearing performance correlated with increased predation rates in a wild population of *D. merriami* (Webster, 1962). Thus, predator evasion cannot be attributed to bipedal hopping or jumping alone. We conclude that enhanced hearing capacity coupled with the ability to rapidly accelerate out of the trajectory of a ballistic predatory strike facilitates foraging in open, risky environments.

While microhabitat partitioning (i.e. shrub versus open) is a fundamental mechanism of quadruped and biped co-existence, a spectrum of other factors facilitate sympatry between multiple bipedal hopping rodents. Risk, competition and the temporal variability (i.e. pulses and depletions) of resources produce multiple, interacting effects on the timing of activity in bipedally hopping Heteromyids (Brown and Lieberman, 1973; Kotler, 1984; Price and Waser, 1985). By experimentally manipulating light levels and seed placement, Kotler (1984) revealed that four or more bipedally hopping *Dipodomys* and *Microdipodops* co-exist by varying their behavioral flexibility in response to spatial changes in seed abundance and to perceived risk posed by light. In other words, risk facilitates species diversity when some species respond more strongly than others.

Risk management is a predominant task for all nocturnal desert rodents, including bipedal hoppers. For gerbils, Kotler et al. (1992) demonstrated that 'the fangs of snakes are driving gerbils into the talons of hawks'. In other words, the presence of one predator facilitates foraging of a second predator. This may also be the case for kangaroo rats, which are depredated by both snakes and owls. Yet, while owls consume multiple bipedal species, they do so at lower rates compared with sympatric quadrupedal species (Kotler, 1985). Furthermore, how bipedal hoppers avoid being preyed upon by snakes, and whether or not they even need to, is unclear. Whitford et al. (2017) demonstrated that desert kangaroo rats are adept at antagonizing rattlesnakes to the extent that many snakes leave the area after discovery. Antagonistic behaviors include sand kicking, foot drumming and rolling, and jump backs (Randall, 1993; Whitford et al., 2017). In fact, snakes struck at *D. deserti* zero times after displays. Furthermore, *D. deserti* often survive verified strikes. More research into the ecology of envenomation and the

physiology of recovery is needed to determine how kangaroo rats survive snake bites. Close encounters with Mojave rattlesnakes leads *D. merriami* to increase head temperature, snout temperature and hindleg temperature, which could signal to the snake that the prey is aware of its presence, or indicate that temperature strongly affects escape maneuvering, displaying or bite recovery (Schraft and Clark, 2017). Thus, we conclude that behavioral and physiological mechanisms may be just as important as locomotor capacity in preventing predation.

Conclusions

We have reviewed the most pertinent, though often under-cited, literature demonstrating the evolution, ecology and biomechanics of mammalian hopping. We have identified several performance advantages of individual radiations, but none of these advantages generalize to all hopping species. All bipedal hoppers share a common morphology, suggesting convergent selective pressures for this specialized mode of locomotion. However, specific differences in muscle–tendon architecture between groups or across sizes indicate that the performance advantages (e.g. highly efficient locomotion versus extreme jump performance) reviewed here are not available to all bipedal hopping species. Based on the hypotheses discussed, we conclude that the most likely reason that bipedal hopping evolved is to enhance predator avoidance by relatively small species in forested environments. Morphological specializations associated with this mode of locomotion subsequently facilitated the secondary acquisition of performance characteristics enabling success in deserts. Future research aimed at understanding the functional trade-offs associated with bipedal hopping and comparative studies between hopping radiations, and within radiations containing both quadrupedal and bipedal species, are needed to better understand what specific selective pressures enabled and maintain multiple, independent lineages of this unique mode of locomotion. By refuting long-held misconceptions about the origins of bipedal hopping, this Review enables a renewed focus on identifying selective pressures that drive its evolution. Innovatively integrating disciplines including biomechanics, behavioral ecology and evolutionary biology will be key to transforming our understanding this unique mode of locomotion going forward.

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Competing interests

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