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Diagonal gaits in the feathertail glider *Acrobates pygmaeus* (Acrobatidae, Diprotodontia): Insights for the evolution of primate quadrupedalism

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ABSTRACT

Research on primate origins has revolved around arboreality and, more specifically, the adaptations that are linked to safe navigation in the fine-branch niche. To this end, extant non-primate mammals have been used as models to assess the significance of these adaptations. However, the size of these models is larger than that estimated for early primates. In contrast, the feathertail marsupial glider *Acrobates pygmaeus*, with a body mass of 12 g, a clawless opposable hallux, and terminal branch feeding habits appears more suited to modeling behavioral adaptations to the small branch milieu. Analysis of video recordings of 18 feathertail gliders walking on poles of variable diameter and inclination revealed that they preferentially used diagonal sequence gaits, fast velocities and low duty factors. Diagonal gaits did not correlate to duty factor, but increased as substrate size decreased, and from descending to ascending locomotion. Furthermore, the duty factor index increased in more diagonal gaits and ascending locomotion. Finally, velocities were lower on smaller substrates, and were mainly regulated by stride frequency and, to a lesser degree, stride length. Feathertail glider gaits displayed noteworthy behavioral convergences with primate quadrupedalism, but some of these results need additional investigation. Despite any discrepancies, these features appear to be favorable for quadrupedal progression on small branches, providing a selective advantage for navigating within a fine branch niche and highlighting the importance of small body size in early primate evolution.

1. Introduction

Understanding the origin of primates has always been one of the major research goals of biological anthropology. The quest for these origins has focused on the ecological and behavioral correlates of the unique morphological package of the order, primarily concerning the grasping, nailed feet and hands, and orbital convergence (Cartmill, 1974a,b; 1992). Regarding the adaptive significance of these evolutionary novelties, research on primate origins has revolved around arboreality, and more especially the habitual use of the fine-branch niche, whether it be foraging for arthropods, fleshy fruit or both (Cartmill, 1974a,b; Szalay and Dagosto, 1980; Dagosto, 1988, 2007; Sussman, 1991; Rasmussen and Sussman, 2007). Whatever the case, negotiation of such small branches requires a small body size and, apart from Soligo and Martin's (2006) scenario, in which a larger body size was proposed as the basis for early primate adaptations, a small ancestral body size has been emphasized as part of a series of stages leading to primate evolution (Cartmill, 1974a; Larson et al., 2000; Gebo, 2004; Sargis et al., 2007). More particularly, these stages include (a) a scansorial, non-grasping, clawed small mammal, (b) an arboreal, clawed mammal with non-opposable, 'non-powerful' pedal grasping, (c) an arboreal clawed mammal with a clawless hallux, capable of opposable 'powerful' pedal grasping that facilitates the efficient use of terminal branches, and (d) a true arboreal primate with nails on all digits and grasping feet and hands (Gebo, 2004; Sargis et al., 2007). Stages b and c are of primary importance in the evolutionary history of primates as they attempt to reconstruct the acquisition of grasping, nailed extremities and primate-like quadrupedal gait mechanics, and recent investigations have used extant analogs, mainly marsupials, to model them (i.e. Rasmussen, 1990; Cartmill, 1992; Lemelin, 1999; Schmitt and Lemelin, 2002; Lemelin et al., 2003; Youlatos, 2008; Shapiro et al., 2014).

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In this context, woolly opossums (*Caluromys philander*) have been extensively used as models due to their primate-like gait, limb kinematics, morphological (long grasping digits, clawless hallux), as well as ecological and behavioral similarities to primates (Schmitt and Lemelin, 2002; Lemelin et al., 2003; Cartmill et al., 2007b; Youlatos, 2008, 2010). However, woolly opossums are comparably large, weighing between 200 and 400 g, contrasting with predictions of small body masses (at least < 100 g) in early primate ancestors. Another marsupial analogue is the sugar glider (*Petaurus breviceps*), which also bears ecological, morphological and behavioral similarities to the alleged early stages of primate evolution [see (Shapiro and Young, 2010) for a summary of morphological and eco-behavioral adaptations of sugar gliders], but, albeit smaller than *Caluromys,* they too are comparably large, ranging between 90 and 160 g. On the other hand, the use of juvenile subjects of *P. breviceps* and gray short-tailed opossums, *Monodelphis domestica*, for testing small body size effects on gait kinematics over narrow substrates (Shapiro et al., 2014), is hindered by the effect of ontogeny on locomotion, which has proven to be substantial across a great number of taxa (i.e. Altman and Sudarshan, 1975; Peters, 1983; Berkum et al., 1989; Carrier, 1996; Doran, 1997; Eilam, 1997; Irschick, 2000; Wells and Turnquist, 2001; Niemitz, 2002; Shapiro and Raichlen, 2006; Young, 2012), with its effects surpassing those predicted by body size (Vilensky et al., 1990). As small size appears to be of vital importance in inferring early primate behavioral and morphological adaptations, other small mammals, such as shrews (Gebo, 2004) and treeshrews (Jenkins, 1974; Sargis, 2001) have been also proposed as models for early primate evolutionary stages. However, shrews are far from typically arboreal, with only a few species classified as scansorial (Churchfield, 1990), and the Tupaiidae do not seem suitable candidates, due to their increased terrestriality and low maternal care (Emmons, 2000). Recently, Eurasian harvest mice *Micromys minutus*, with a body mass at 10 g, flexible locomotion, foot grasping skills, and extensive use of fine branches, were suggested as models for finer scaled evolutionary stages (Urbani and Youlatos, 2013), underscoring the significance of tiny size during early primate evolution.

Feathertail gliders *Acrobates pygmaeus* (Fig. 1) weigh between 10 and 15 g and are among the smallest extant marsupials (Nowak, 1999). They are primarily nocturnal arborealists, feeding and foraging mainly on arthropods, fruit, honeydew and pollen (Goldingay and Kavanagh, 1995). Feathertail gliders possess an opposable clawless hallux, capable of efficient grasping, and volar pads with extensive sweat gland complexes in all digits that enable increased adhesion on all types of surfaces, even glass panes (Rosenberg and Rose, 1999). These adaptations facilitate the use of both tree trunks and the finer branches of upper foliage and lower shrubs of subtropical, temperate and mature woodlands in their habitats in eastern Australia (Ward and Woodside, 2008). Furthermore, *A. pygmaeus* exhibits slow growth, and high maternal investment, which continues after weaning (Ward, 1990). All these morpho-behavioral features could fit well within suggested scenarios of early primate evolution (Cartmill, 1974a,b, 1992; Sussman, 1991; Gebo, 2004; Rasmussen and Sussman, 2007) and could render feathertail gliders a useful extant model to test some of the unique aspects of primate arboreal quadrupedalism (such as the frequent use of diagonal sequence [DS] gaits, ultimately related to fine branch exploitation).

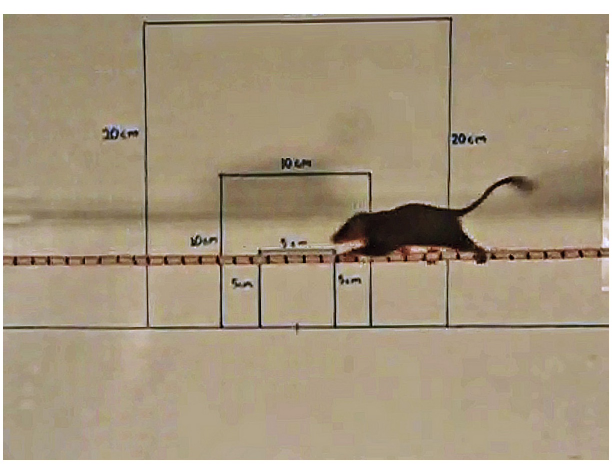

Figure 1. Feathertail glider *(Acrobates pygmaeus*) walking diagonally on a 2 mm pole (the pole is marked with vertical blue lines per 1 cm for a reliable estimation of absolute lengths; squares on the background represent different marked dimensions for video software calibration). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The frequent use of DS gaits is a general trait of primates, with only a few exceptions (Hildebrand, 1967; Cartmill et al., 2002; Shapiro and Raichlen, 2005; Cartmill et al., 2007b; Nyakatura and Heymann, 2010). Primates commonly use DS gaits, in which the forelimbs touch down soon after the contralateral hind limbs, while most other mammals commonly use lateral sequence (LS) gaits, in which the forelimbs land right after their ipsilateral hind limbs (Hildebrand, 1967). Diagonal sequence gaits have likely evolved to promote inspection of new, unknown and unstable substrates, while moving on terminal branches (Cartmill et al., 2007a). This is partially supported by the common use of DS gaits by some arboreal marsupials (White, 1990; Pridmore, 1994; Cartmill et al., 2002; Schmitt and Lemelin, 2002), and kinkajous (Lemelin and Cartmill, 2010). On the other hand, Vilensky and Larson (1989) proposed that gait selection is not related to locomotor stability, and the dominance of DS gaits in primates is a by-product of neurological reorganizations related to forelimb dexterity. The use of DS or LS gaits is, nevertheless, influenced by substrate properties, but if DS gaits were related to unstable substrate use, as Cartmill et al. (2007a) have proposed, they should be more frequent on narrower and upwards or downwards inclined substrates. However, findings are conflicting. Most strepsirrhines do not exhibit a higher rate of DS gaits on narrower substrates (Stevens, 2008), and *P. breviceps* does not increase frequencies of DS gaits with decreasing substrate size (Shapiro and Young, 2010). Furthermore, no correlation between substrate size and DS gait use was detected in free-ranging *Saguinus mystax*, and DS gaits were less common on smaller substrates in *Saguinus fuscicollis* (Nyakatura and Heymann, 2010). Regarding substrate inclination, past research on a number of arboreal mammals has shown that ascents are characterized by more frequent use of DS gaits than descents (Prost and Sussman, 1969; Lammers, 2007; Nyakatura et al., 2008; Nyakatura and Heymann, 2010; Shapiro and Young, 2010; Shapiro et al., 2014). It has thus been argued that DS gaits reduce the retarding effect of the forelimbs during ascents (Nyakatura et al., 2007), whereas LS gaits allow the forelimbs to provide retardation though a “stop-jolt” before the hind limbs contact the substrate (Rollinson and Martin, 1981). These findings indicate that there is a link between diagonality and the control of locomotion over substrate inclination and size.

Another feature unique to primate arboreal quadrupedalism is that primates control locomotion on fine arboreal substrates by relative stride length to a greater extent than stride frequency (Larson et al., 2000, 2001). Increased stride length, rather than stride frequency, is regularly employed by primates to reach higher velocities without increasing involuntary branch sway (Demes et al., 1990). In contrast, most other arboreal mammals, marsupials included, tend to increase their velocity by higher stride