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Stride lengths and frequencies of arboreal walking in seven species of didelphid marsupials

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Didelphid marsupials differ in their use of the forest strata, with corresponding differences in morphology and arboreal walking performances. Similar performances may be reached by different combinations of stride length and frequency, but it has been suggested that arboreal walkers increase velocity by longer strides. Our objective was to determine how stride length and frequency contribute to the velocity in the arboreal walking of seven species of didelphid marsupials of the Atlantic Forest of Brazil. Animals were stimulated to cross five 3-m long horizontal supports of different diameters. The cycle of maximum velocity was chosen to measure relative stride length, frequency, and relative velocity. Except for *Caluromys philander*, the more arboreal species were faster than the terrestrial species, but maximum velocity of arboreal species was reached by two strategies, increasing stride frequency (*Gracilinanus microtarsus*, *Micoureus demerarae*, and *Didelphis aurita*), or reducing frequency and increasing stride length *(Marmosops incanus* and *C. philander*). Increasing velocity in arboreal walking by more frequent strides may reduce oscillations of the body, whereas longer strides may reduce branch swaying. Among the terrestrial species, *Philander frenatus* performed similarly to more arboreal species, suggesting a potential ability to use the canopy, undetected in field observations.

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Introduction

The locomotion of didelphid marsupials on the ground or along tree branches is basically quadrupedal (Jenkins and McClearn 1984). Along tree branches, in arboreal walking, didelphids move slowly and carefully, crossing discontinuities between branches with the help of their grasping ability and prehensile tail (Enders 1935, McManus 1970, Charles-Dominique *et al.* 1981, Charles-Dominique 1983, Rasmussen 1990, Schmitt and Lemelin 2002). For an arboreal quadruped, keeping balance on an unstable support during walking would be a critical aspect of performance (Cartmill 1974).

The balancing ability of a cursorial animal walking on a branch would clearly differ from a specialized arboreal dweller, but individual differences in balancing ability among different species of arboreal animals are not so clear-cut, and are difficult to quantify. An alternative is to use velocity in arboreal walking as a measure of performance (Arnold 1983, Bennett 1989, Ricklefs and Miles 1994). Animals reaching high velocities in arboreal walking without falling are capable of moving, escaping from predators, and feeding in the upper strata of the forest (Cant 1992).

Velocity results from a combination of stride length and frequency. It has been argued that clawless primates increase contact time to enhance stability and security when traveling in a small-branch habitat (Larson *et al.* 2001), hence increasing velocity by relatively longer rather than more frequent strides. High frequency gaits would be potentially disruptive in a terminal branch because they cause greater branch sway, which is both dangerous and energetically costly (Demes *et al.* 1990). Weather all arboreal walkers increase velocity by longer strides remains an open question until other groups of arboreal walkers are studied. Another factor potentially important for stride length and frequency is body size. Because of the instability of arboreal supports, the effect of body size on arboreal locomotion should be even stronger than in terrestrial locomotion.

Didelphid marsupials are basically arboreal walkers, hence provide a suitable group to determine if the pattern of primates also applies to other arboreal walkers. Besides, body size of didelphid marsupials varies from 100 to 2000 g, also providing an opportunity to determine the allometry of stride length and frequency, and their contribution to velocity. Genera of didelphid marsupials such as *Micoureus*, *Marmosops*, and *Caluromys* are all considered arboreal but differ in their phylogenetic history (Kirsch *et al.* 1997, Astúa de Moraes 2004), morphology of the post-cranial skeleton (Works 1950, Hildebrand 1961, Grand 1983, Creighton 1984, Vieira 1997, Lemelin 1999, Argot 2001, 2002, 2003), body size (Emmons 1990), and use of the vertical strata of the forest (Charles-Dominique *et al.* 1981, Passamani 1995, Cunha and Vieira 2002, Grelle 2003, Vieira and Monteiro-Filho 2003). Also, stride length and frequency of didelphid marsupials are significantly associated with the evolutionary history of the group (Delciellos and Vieira 2006*)*, with genera and tribes (but not subfamilies) differing in the relationship between support diameter and stride length, after accounting for body size (Delciellos and Vieira 2006). However, the relative contribution of stride length and frequency to velocity was not yet examined in didelphid marsupials.

In this study, we compare the stride length and frequency in arboreal walking of didelphid marsupials. The species studied differ in their use of the vertical strata of the forest, and cover most of the body size range of the group. The more specific objectives were to determine how velocity changes with the support diameter, and if velocity of more arboreal didelphids increases by longer strides as in primates, after accounting for differences in body size between species.

Material and methods

Specimens of study

Marsupials of seven species (Table 1) were captured in remnants of Atlantic Forest near or in the mountain range of Serra dos Órgãos (22°22'S, 42°45'W), on the border of the Serra dos Órgãos National Park, State of Rio de Janeiro, Brazil, in the municipalities of Guapimirim, Teresópolis, Cachoeiras de Macacu, and Sumidouro, from January 1999 to December 2001. Only individuals with four functional molars were considered adults and tested (Tyndale-Biscoe and Mackenzie 1976, D'Andrea *et al.* 1994). Individuals physically debilitated, and females with pouch young were not tested. This study was approved by the environmental protection agency of the Brazilian government, IBAMA/MMA (Proc. n° 02001, 004671/98-51).

Performance tests

After capture, individuals were transported to the laboratory and their locomotor performance was tested during arboreal walking, using tests developed previously with didelphid marsupials (Vieira 1995, 1997, Delciellos and Vieira 2006). Tests consisted of making the animal cross

Table 1. Measurements and use of the vertical strata of the species of didelphid marsupials studied. Measurements were based on the individuals studied. Relative tail length is tail length divided by body length. Sample size (*n*) is the total number of individuals tested, but not all individuals were tested in all supports. ([1]Charles-Dominique 1983, [2]Emmons 1990, [3]Szalay 1994, [4]Cunha and Vieira 2002, [5]Schmitt and Lemelin 2002).

Species	*n*	Head-body length (cm ± SD)	Tail length (cm ± SD)	Relative tail length	Body mass (g ± SD)	Use of the vertical strata
Gracilinanus microtarsus	3	9.8 ± 1.2	15.0 ± 5.5	1.53	31.2 ± 13.9	Arboreal of the canopy and understorey(1, 2)
Marmosops incanus	9	13.2 ± 1.5	19.6 ± 2.2	1.48	58.1 ± 18.2	Arboreal of the understorey(4)
Micoureus demerarae	18	16.9 ± 1.1	25.2 ± 1.5	1.49	152.1 ± 50.7	Arboreal of the canopy and understorey(1, 2)
Caluromys philander	5	20.2 ± 1.5	28.3 ± 1.9	1.40	212.3 ± 65.6	Arboreal of the canopy(1, 2, 5)
Metachirus nudicaudatus	11	24.5 ± 4.4	29.8 ± 5.1	1.22	332.8 ± 129.8	Specialized terrestrial(2, 3, 4)
Philander frenatus	11	24.9 ± 3.1	29.0 ± 3.0	1.16	422.0 ± 141.8	Semi-terrestrial, using the understorey(4)
Didelphis aurita	15	34.7 ± 3.1	34.0 ± 3.1	0.98	1033.6 ± 273.3	Semi-terrestrial, using the canopy or the understorey(4)

the top of 3 m long horizontal supports 1 m above the ground. Five supports were used, four supports made of PVC cylinders of 2.54, 5.08, 7.62, and 10.16 cm diameter, simulating branches of trees, and a 15 cm wide flat wooden board to determine the effect of the round surface of the cylinders on the locomotory performance. The supports were covered with commercially available masking tape to increase their frictional properties. The floor was covered with 5 cm thick foam to prevent any injury to the animal in case it fell.

In valid trials, the animal was taken out of its cage, placed onto one end of the support, and encouraged to cross the support by an observer approaching from the posterior direction, touching the tail of the animal or shaking a key ring. These stimuli were sufficient to make most individuals quickly cross the support, apparently at their maximum velocity. Animals that did not respond to these stimuli, or did not run, were excluded. The locomotion on the supports was recorded with a camcorder (NTSC standard, 30 complete frames s^{-1}, shutter speed = 0.01 s) fixed approximately 2 m away perpendicularly to the plane of movement of the individual. Animals were tested during the afternoon in normal daylight conditions because no difference was observed between diurnal and nocturnal tests (Vieira 1995). Each test was repeated 3 times for each individual. Each repetition of the test recorded a single stride cycle in *Didelphis aurita*, the largest species, and up to 3 cycles in the small didelphid species. In the 3 tests of each individual, the cycle of maximum constant velocity was chosen to measure stride length and frequency. The number of individuals tested for each species varied depending on their availability in the field (Table 1). Some individuals could not be tested in all supports because they stopped responding the stimuli or showed signs of stress or physical discomfort. These individuals were not tested further to avoid the possibility of injuries.

Image analyses

Stride length was the distance covered by the right posterior limb between the first and last frames of the chosen stride cycle. It was measured by digitizing the first and last frames using ATI All-in-Wonder 128 video card and software (ATI Technologies Inc.), overlapping the two using fixed reference marks in each picture, and measuring the distance between the two points where the right posterior limb touched the support. Stride frequency was the inverse of stride duration, which was the number of frames for the whole sequence multiplied by duration of a single frame (30^{-1} s). Velocity was stride length multiplied by its frequency (Hildebrand 1988). Because relative stride length and velocity are more directly related to fitness than absolute measurements (Van Damme and Van Dooren 1999), we calculated relative velocity and stride length by dividing the original measurements of each individual by its head-body length, to emphasize differences between species independent of body size. Relative velocity and stride length are in units of body length covered by unit of time (seconds $bl \cdot s^{-1}$).

Relative velocity, relative stride length, and stride frequency also were compared among species using supports of diameters equivalent to their body sizes. Standardizing body size in terrestrial locomotion can be achieved by analysis of covariance, ratios or dimensionless numbers. In arboreal locomotion, the relative width of the support also changes with body size, hence also needs to be standardized. Standardization of relative width of the support can be achieved by comparing species on supports of equivalent body size diameter. Supports for comparison were chosen based on the mean trunk diameter for each species, estimated by modeling the trunk as a cylinder of length equal to body length, and volume in cm^3 proportional to body mass. Estimated trunk diameters were 2.8 cm for *Gracilinanus microtarsus*, 3.4 cm for *Marmosops incanus*, 4.2 cm for *Micoureus demerarae*, 5.4 cm for *Caluromys philander*, 5.9 cm for *Philander frenatus*, 6.8 cm for *Metachirus nudicaudatus*, and 9.6 cm for *D. aurita.* Accordingly, diameters of support equivalent to body size were 2.54 cm for *G.*

microtarsus and *M. incanus*, 5.08 cm for *C. philander*, *M. nudicaudatus*, *M. demerarae* and *P. frenatus*, and 10.14 cm for *D. aurita*.

In terrestrial locomotion, body size is standardized using the dimensionless Froude number (Alexander and Jayes 1983), which standardizes the effects of gravity on the pendulum action of the limbs and their free fall (Alexander and Jayes 1983). At a given Froude number, species should have the same gait, even if body size and velocity differ between species. In arboreal locomotion, however, gait also would be determined by the instability of the support generated by the stride length and frequency, and not simply by the pendulum action of the limbs.

Statistical analyses

Differences between species were tested with parametric analyses of variance, ANOVAs, one for each support, using log-transformed relative measures. The significance of pairwise comparisons was tested with Bonferroni *a posteriori* tests, but all significant differences between species in Bonferroni tests corresponded to pairs without overlap in their 95% confidence intervals. Therefore, we presented only confidence intervals of species means. Significant differences between species can be evaluated by visual inspection of confidence intervals. Means and confidence intervals were back-transformed to linear scale for visual inspection.

The stability of mean values for each species in each support diameter was evaluated by jackknifing the mean frequency, relative stride length and relative velocity (Sokal and Rohlf 1981). A more appropriate test of the effect of support diameter on performance would be an analysis of variance with repeated measures (Sokal and Rohlf 1981). However, this design requires repeated measures of all individuals in the five supports tested, which was not possible for all individuals. Occasionally they stopped responding to the stimuli to walk or, more rarely, suffered a light injury such as a damaged claw, preventing tests on the five supports. The jackknife procedure allowed us to (1) determine the sensitivity of the results to the addition or removal of individuals, and (2) compare the performance of the same species in different supports. For each species and support diameter, an individual was removed from the sample, and the sample mean calculated. The individual was returned, a new individual removed, and the mean recalculated. The process was repeated for all the individuals of the sample (n), resulting in a total of n means. The grand mean $\bar{x}$, and its standard deviation were the estimate and standard error, SE, of the jackknife. According to the central limit theorem, a distribution of means should approach a normal distribution (Sokal and Rohlf 1981), hence confidence intervals were calculated as $\bar{x} \pm 1.96$ SE.

Results

Significant differences between species in relative stride length, stride frequency, and relative velocity were detected in all supports (Fig. 1 and ANOVA statistics there in). The relative performance of each species changed slightly from the thinnest support (2.54 cm) to the flat board, hence in Fig. 1 we show only the performance on these extremes. Comparisons between supports of equivalent body size diameters followed exactly the same pattern, hence will not be presented to avoid redundancy.

In pairwise comparisons of relative stride length, significant differences were detected mainly between two groups, one formed by *D. aurita* and *M. nudicaudatus*, and the other formed by *G. microtarsus*, *M. incanus*, *M. demerarae*, and *P. frenatus* (see confidence intervals in Fig. 1). In stride frequency and relative velocity, three groups can be identified, one formed by *D. aurita* and *M. nudicaudatus* as before, one formed by *G. microtarsus* and *M. incanus*, and a third formed by *M. demerarae* and *P. frenatus* (Fig. 1). The performance of *C. philander* was always intermediate between the *D. aurita–M. nudicaudatus* group, and *P. frenatus* (Fig 1), with a wide confidence interval.

The arboreal *C. philander* tended to be faster on the large supports, reaching a relative velocity of 3.84 bl · s^{-1} in the 10.16 cm support (Fig. 2). However, the small sample size (Table 1) and large confidence intervals in each support make these differences non-significant. The high velocities in the larger supports resulted mostly from relatively longer strides (Fig. 3). *Caluromys philander* was slower than the other arboreal species, *M. incanus*, *M. demerarae*, and *G. microtarsus*.

In the large semi-terrestrial *D. aurita*, significant differences in velocity appeared when support diameter changed from 5.08 to 7.62 cm (Fig. 2). The highest velocity occurred in the three largest supports (reaching around 2.5 bl · s^{-1}), which did not differ significantly between each other in relative velocity. However, relative stride length and frequency differed significantly between these three largest supports, where relative stride length decreased and stride frequency increased with the diameter of the support (Fig. 3).

In the small arboreal *G. microtarsus*, relative velocity differed significantly only between the round surface supports and the flat board (Fig.

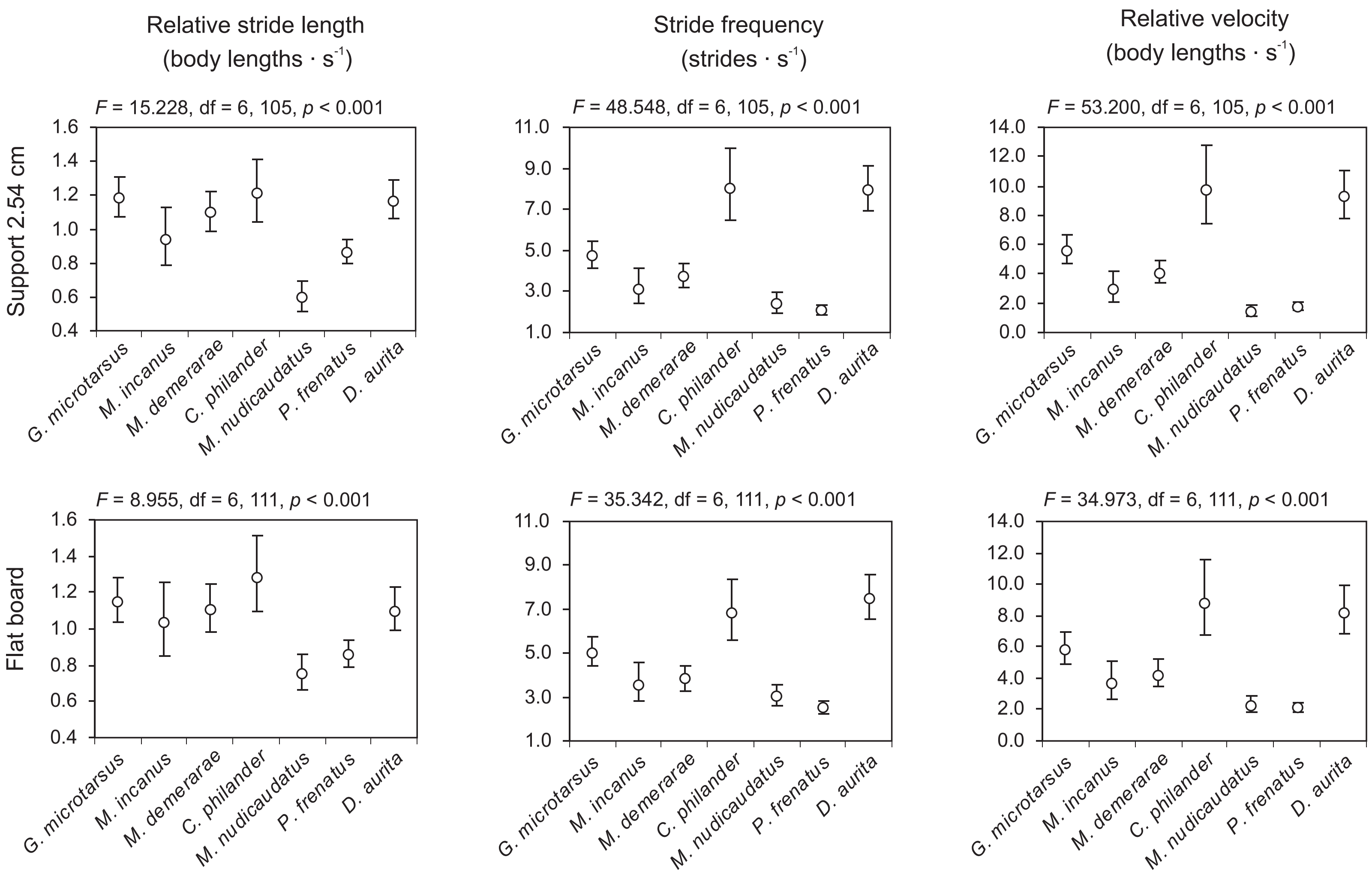

Fig. 1. Performance in arboreal walking (means and confidence intervals) of the seven species of didelphid marsupials on the thinnest support (2.54 cm) and on the 15 cm wide flat board, with statistics of one-way ANOVAs (0.05 significance level). Species are in order of body mass.

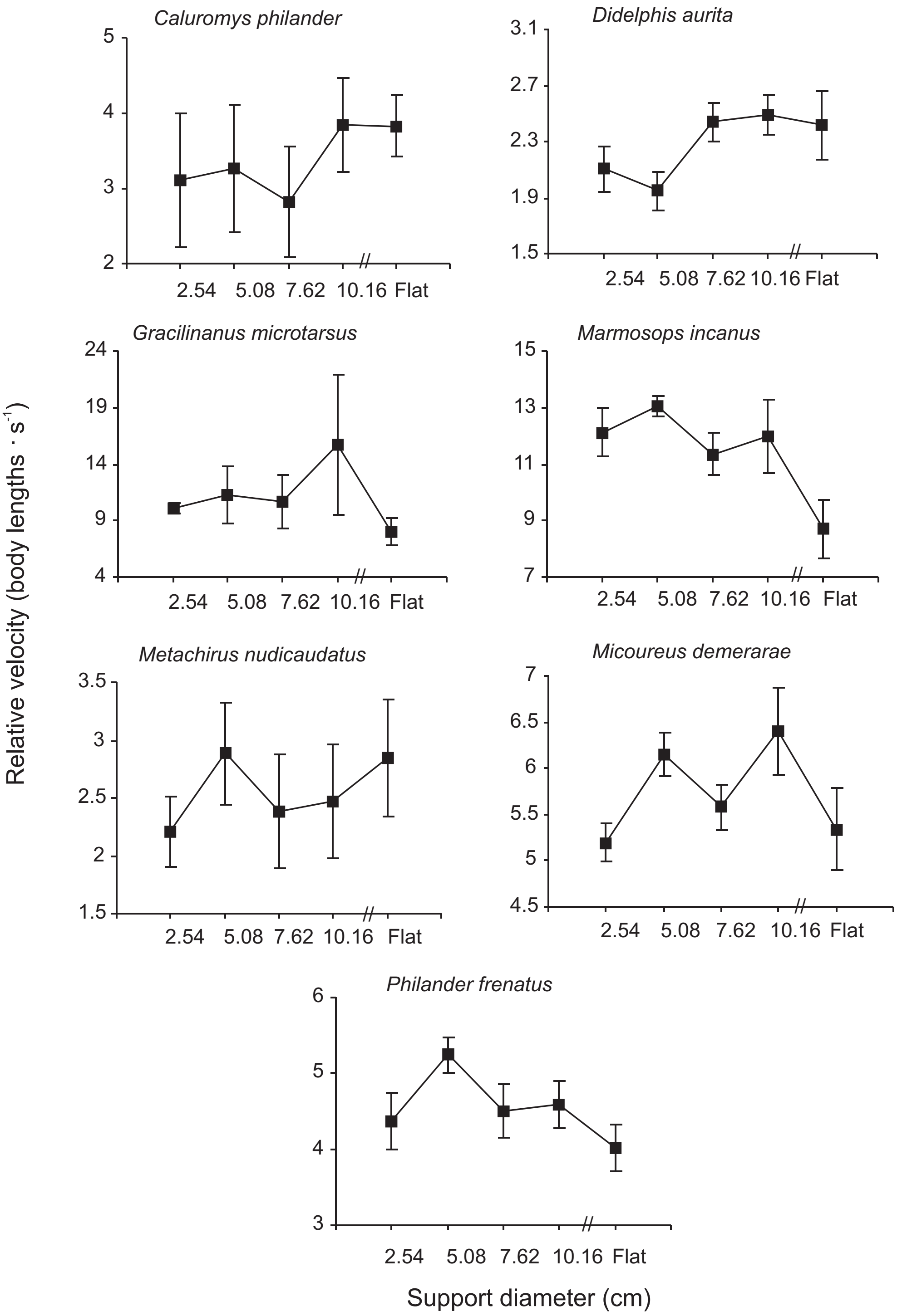

Fig. 2. Relative velocity of the seven species of didelphid marsupials on supports of five diameters, including a 15 cm wide flat board (“Flat”). Error bars are the jackknife confidence intervals.

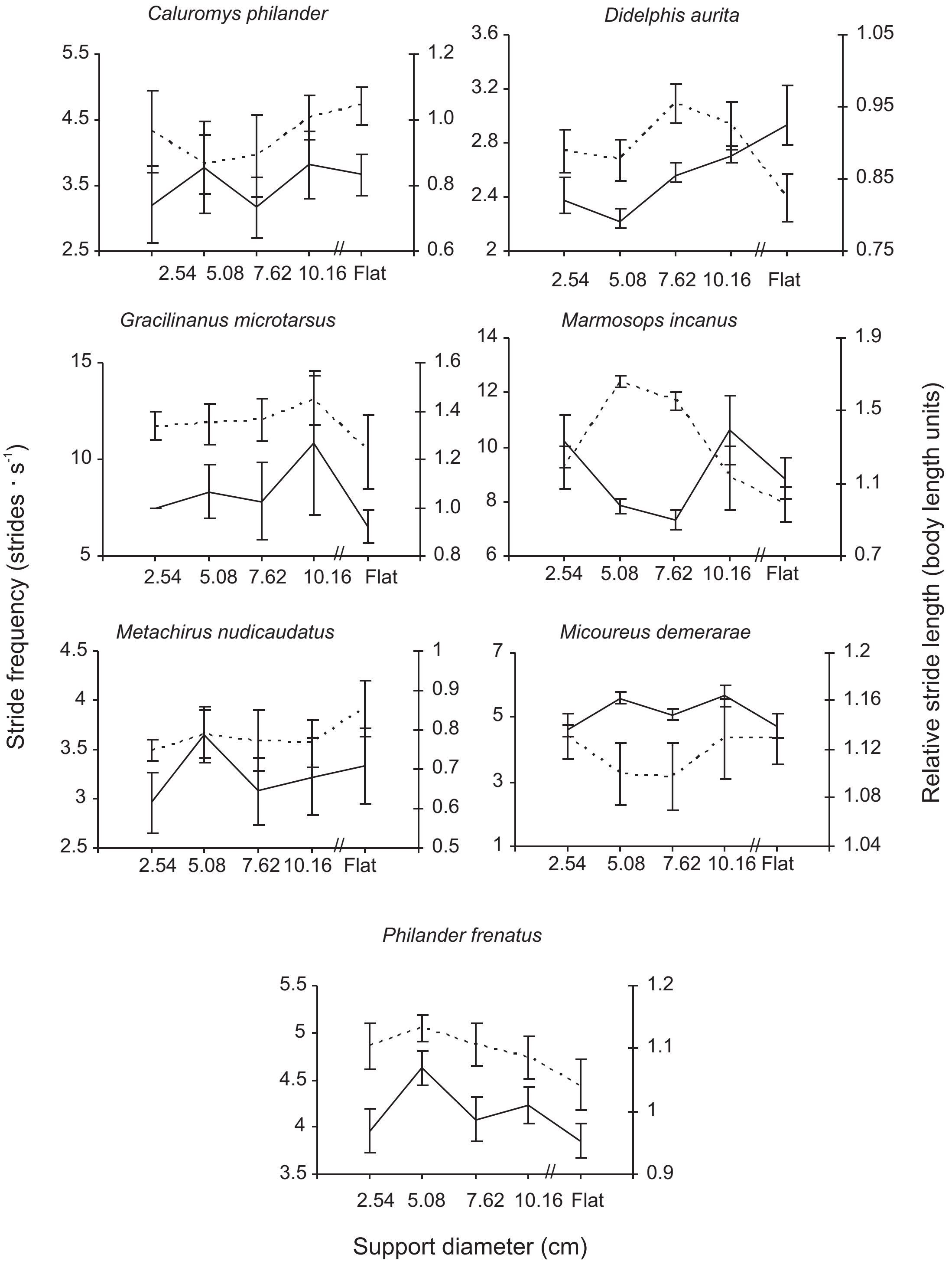

Fig. 3. Stride frequency (continuous lines) and relative length (discontinuous lines) of the seven species of didelphid marsupials on supports of five diameters, including a 15 cm wide flat board (“Flat”). Error bars are the jackknife confidence intervals.

2). The highest relative velocity of 15.7 bl · s^{-1} was reached in the 10.16 cm support, but it was highly variable and did not differ significantly from other supports. The reduced velocity in the flat board resulted from a reduction in both relative stride length and frequency (Fig. 3).

In the small arboreal *M. incanus*, relative velocity was significantly higher in the thinnest supports, reaching 13.0 bl · s^{-1} in the 5.08 cm support (Fig. 2). In the two thinnest supports relative velocity did not differ significantly, but relative stride length and frequency differed clearly (Fig. 3). Relative stride lengths were significantly longer and stride frequencies lower in the 5.08 and 7.62 cm supports (Fig. 3). *Gracilinanus microtarsus* and *M. incanus* had the highest stride frequencies regardless of support diameter.

In the terrestrial *M. nudicaudatus*, relative velocity was similar and did not differ significantly between the supports, although there was a trend to increase velocity in the larger supports (Fig. 2). The highest relative velocity of 2.8 bl · s^{-1} was reached on the flat board. Relative stride length and frequency did not differ significantly between supports either, but the same trend of increasing stride length and frequency with support diameter was observed (Fig. 3).

Relative velocity of the arboreal *M. demerarae* alternated significantly high and low values between supports, with relative velocity significantly higher in two supports of intermediate diameter, 5.08 and 10.16 cm, reaching around 6.0 bl • s^{-1} (Fig. 2). Variation of stride frequency along the supports followed the same pattern of velocity, also with significant differences between two supports of intermediate diameter, 5.08 and 10.16 cm, and the other supports (Fig. 3).

In the semi-terrestrial *P. frenatus*, relative velocity was higher on the round supports compared to the flat board (Fig. 2). Among round supports, relative velocity was significantly higher in the 5.08 cm support, reaching 4.7 bl•s^{-1} (Fig. 2). Relative stride length and frequency followed a similar pattern, with highest values in the 5.08 cm support (Fig. 3). However, only the increase in stride frequency in this support differed significantly from the other supports (Fig. 3).

In summary, the small arboreal species *M. incanus* and *G. microtarsus* were relatively faster than all other species, terrestrial and arboreal (Fig. 2), using relatively longer and more frequent strides (Fig. 3). The relatively slowest species were the large and terrestrial *D. aurita* and *M. nudicaudatus*. However, the velocity of another terrestrial species, *P. frenatus*, was similar to the arboreal *M. demerarae*, and higher than the arboreal *C. philander* (Fig. 2). Maximum and minimum performances for each species occurred in supports of different diameters, but most small arboreal species (*M. incanus*, *G. microtarsus*, and *M. demerarae*) and the terrestrial *P. frenatus* reached the highest velocities in the round supports. The other terrestrial species and the arboreal *C. philander* reached their highest velocities on the flat board (Fig. 2). The highest velocity of each species – regardless of the support diameter where it occurred – was reached by increasing both stride length and frequency (*M. nudicaudatus*, and *P. frenatus*), increasing stride frequency more than stride length (*G. microtarsus*, *D. aurita*, and *M. demerarae*), or increasing stride length more than stride frequency (*C. philander*, and *M. incanus*) (Fig. 3).

Discussion

The velocity of the fastest species, *M. incanus* and *G. microtarsus*, compared to other species of didelphid marsupials resulted both from their high stride length and frequencies, which is different than the pattern observed in primates (Alexander and Maloiy 1984). The highest velocities of the smallest and largest didelphids, *G. microtarsus* and *D. aurita*, respectively, and of *M. demerarae* were reached mostly by increasing stride frequencies. Increasing velocity by higher stride frequencies may be energetically costly (Strang and Steudel 1990), but the assumption that it is potentially disruptive in a terminal branch (Demes *et al.* 1990) may not apply to all didelphid marsupials. For a small species such as *G. microtarsus*, more frequent strides may not cause much branch sway, and could be safer than longer strides to increase velocity. In an arboreal environment longer strides increase contact time, but also increase oscillations of the body (Macrini and Irschick 1998), hence reducing stability for a swift small animal such as *G. microtarsus*.

Oscillations of the body would be even worse for large animals (Cartmill 1985, Pridemore 1992, Shapiro *et al.* 2001), hence, long strides would not necessarily be safer than more frequent strides. Increasing velocity would always involve potential risks, whether by increasing stride length (increasing body oscillations) or frequency (increasing branch sway). The present study suggests that reduction of oscillations of the body is the strategy used by *G. microtarsus*, *M. demerarae* (ca. 150 g), and the largest *D. aurita* (ca. 2 kg), whereas reduction of branch sway was the strategy of *M. incanus* (ca. 55 g) and *C. philander* (ca. 200 g).

The largest arboreal species of the group, *C. philander*, differed from other arboreal didelphids by its relatively slow velocity, and maximum velocity on the flat board, being more similar to the largest terrestrial *D. aurita.* In the field, *C. philander* was described as moving slowly and carefully on fine branches (Charles-Dominique 1983, Schmitt and Lemelin 2002). Minimizing branch sway by reducing stride frequencies is in agreement with such slow and careful motion.

The velocity of the more terrestrial species of similar body size, *M. nudicaudatus* and *P. frenatus*, was determined by an increase in both stride length and frequency, supporting the conclusions of Heglund *et al.* (1974) for terrestrial mammals moving on the ground. However, these terrestrial didelphids reached a similar result by different means, using different combinations of stride length and frequency. No common pattern of change in stride length and frequency with support diameter was observed in terrestrial species, except that they were slower than more arboreal species.

Among the terrestrial species, the velocity of the large *D. aurita* and the only specialized cursorial species of the group, *M. nudicaudatus*, tended to increase in the supports of large diameter. The exception to this trend was *P. frenatus*, a semi-terrestrial species, whose relative velocity tended to reduce on large supports similarly to more arboreal species. Indeed, the overall performance in arboreal walking of *P. frenatus* is intermediate between arboreal and terrestrial species, regardless of phylogenetic effects (Delciellos and Vieira 2006). This suggests that *P. frenatus* has an intrinsic potential arboreal capacity, at least in their arboreal walking performance. Climbing performance and behavior of *P. frenatus* also are more similar to arboreal species (Antunes 2003). Extrinsic factors could be restricting its use of the arboreal strata, such as the presence of competitors or vulnerability to predation.

The weak effect of body size on maximum observed velocities contradicts the results in the literature, which detected significant effects of body size on maximum velocities and performance variables in comparisons across species (Alexander and Maloiy 1984, Van Damme and Vanhooydonck 2001). Also, velocity and stride frequency in mammals vary regularly and predictably with body size, with small mammals being slower but possessing high stride frequencies (Heglund and Taylor 1988). The reason for the apparently weak effect of body size could be the relatively small range of body size variation of didelphid marsupials, which weigh less than 1 kg, with the exception of *Didelphis.*

The tail is an important balancing organ, for arboreal and terrestrial mammals (eg Walker *et al.* 1998). In arboreal marsupials, the tail also has a prehensile function, which may be its more important use considering that marsupials cross discontinuities by grasping (Cartmill 1974). In the marsupials we studied, there is a negative association between relative tail length and body size, regardless of being arboreal or terrestrial. The only truly cursorial of group, *M. nudicaudatus*, whose tail is not prehensile, also has a long tail (longer than body length). Thus, tail length may help balance in arboreal walking, but it is associated with body mass regardless of the species being arboreal or terrestrial.

Arboreal walking by didelphid marsupials is not uniform across species, even if only arboreal species are considered. At least two opposing strategies to increase velocity were observed in didelphid marsupials, more frequent and short strides, or longer and less frequent strides. These strategies seem to be associated with reduction of different risks in arboreal walking, oscillations of the body and branch swaying, respectively. Increasing velocity by more frequent strides, reducing oscillations of the body, may be the safest strategy for marsupials of the size of *G. microtarus* (< 35 g), but also for the larger didelphids such as *D. aurita*.

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