

The biodynamics of arboreal locomotion: the effects of substrate diameter on locomotor kinetics in the gray short-tailed opossum (*Monodelphis domestica*)

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Summary

Effects of substrate diameter on locomotor biodynamics were studied in the gray short-tailed opossum (*Monodelphis domestica*). Two horizontal substrates were used: a flat 'terrestrial' trackway with a force platform integrated into the surface and a cylindrical 'arboreal' trackway (20.3 mm diameter) with a force-transducer instrumented region. On both terrestrial and arboreal substrates, fore limbs exhibited higher vertical impulse and peak vertical force than hind limbs. Although vertical limb impulses were lower on the terrestrial substrate than on the arboreal support, this was probably due to speed effects because the opossums refused to move as quickly on the arboreal trackway. Vertical impulse decreased significantly faster with speed on the arboreal substrate because most of these trials were relatively slow, and stance duration decreased with speed more rapidly at these lower speeds. While braking and propulsive roles were more

segregated between limbs on the terrestrial trackway, fore limbs were dominant both in braking and in propulsion on the arboreal trackway. Both fore and hind limbs exerted equivalently strong, medially directed limb forces on the arboreal trackway and laterally directed limb forces on the terrestrial trackway. We propose that the modifications in substrate reaction force on the arboreal trackway are due to the differential placement of the limbs about the dorsolateral aspect of the branch. Specifically, the pes typically made contact with the branch lower and more laterally than the manus, which may explain the significantly lower required coefficient of friction in the fore limbs relative to the hind limbs.

Key words: locomotion, arboreal, terrestrial, substrate reaction force, required coefficient of friction, gray short-tailed opossum, *Monodelphis domestica*.

Introduction

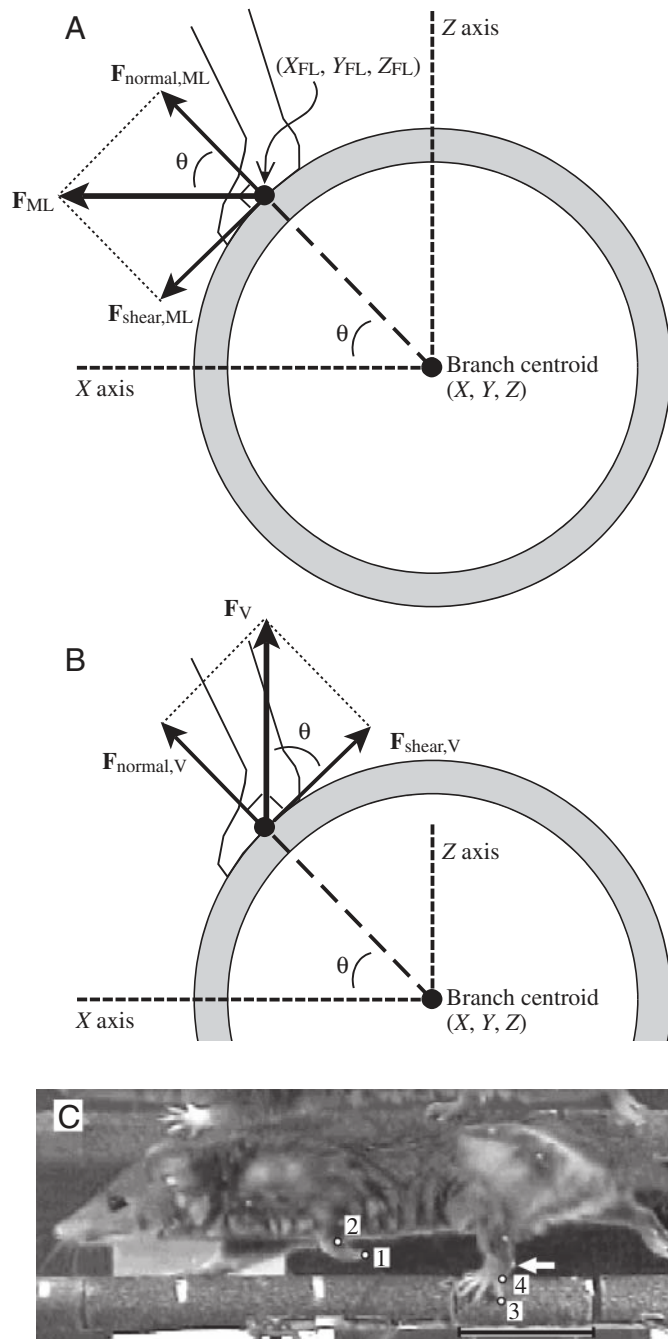
Substrate reaction forces (SRFs) are often used to summarize limb function during terrestrial locomotion, and a single pattern characterizes most quadrupeds (summarized in Demes et al., 1994). Body-weight support is reflected by the vertical component of the SRF, and, because the center of mass of most mammals is cranially displaced, the vertical SRF is most commonly greater in the fore limbs than in the hind limbs. The craniocaudal force has two active parts: a braking component followed by a propulsive component. During terrestrial locomotion, braking impulse (area under the force-time curve) is typically greater than propulsive impulse in the fore limb; by contrast, the hind limb tends to be net propulsive. Mediolateral force and impulse are considered negligible for cursorial animals moving along a straight path (Biewener, 1990). However, sprawling tetrapods commonly generate a more substantial medially directed SRF (laterally directed limb force) so that their mediolateral impulse is comparable in magnitude to craniocaudal impulse (Christian, 1995; Willey et al., 2004).

Quadrupeds adapted to arboreal locomotion display an altered pattern of SRF (Kimura, 1985; Ishida et al., 1990;

Demes et al., 1994; Schmitt, 1994, 1999; Schmitt and Lemelin, 2002): peak vertical forces tend to be reduced, hind limbs commonly take on a greater role in body-weight support, and the limbs exert strong laterally directed SRFs (medially directed limb forces). Differences between the terrestrial and arboreal SRF patterns have been related to differences in substrates. For example, lowered peak vertical forces observed in primates moving on horizontal, narrow supports may help reduce branch oscillations (Demes et al., 1990; Schmitt, 1999).

To date, studies on arboreal locomotor kinetics have concentrated almost exclusively on primates. Yet, virtually any small mammal must negotiate heterogeneous terrain that includes some non-terrestrial substrates. For example, many species of rodents (Montgomery, 1980) and the didelphid marsupial *Didelphis virginiana* (Ladine and Kissell, 1994) utilize fallen logs and branches on the forest floor as arboreal runways. Terrestrial mammals navigating an arboreal substrate are likely to adapt their locomotor behavior in an attempt to enhance stability on this curved substrate, and some of these strategies may result in observable differences in limb function

and, thus, SRFs. Such strategies might include adjustments in speed, limb placement and gait. Terrestrial mammals may choose to move more slowly on arboreal supports; decreased speed is generally associated with lower peak vertical forces (Demes et al., 1994; Schmitt and Lemelin, 2002). Limb placement about a curved substrate will affect the potential for slipping off of the sides of a branch. When limb contacts occur on the top of the branch (or anywhere on a flat substrate), then the shear force is the vector sum of the mediolateral and craniocaudal forces, while the normal force is equivalent to the vertical force. But vertical and mediolateral forces will each contribute shear and normal components when contact occurs on any other part of the branch (Fig. 1A,B). Therefore, the



relative proportions of the three-dimensional SRFs may be altered to avoid excessive shear forces. It is also possible that the limb force could be reoriented towards the centroid of the branch, which would increase the normal reaction force. Finally, it is possible that gait (defined by Hildebrand, 1976, as timing and duration of foot contacts relative to stride duration) shifts may occur between terrestrial and arboreal locomotor bouts. A gait that is dynamically stable (where stability is provided by motions through conditions that are statically unstable) on a terrestrial substrate may be inadequate on arboreal substrates, particularly if speeds are reduced. Animals may switch to more statically stable gait (e.g. towards a single-foot gait) (Hildebrand, 1976).

The aim of this study was to determine whether and how limb function, as reflected by SRFs, differ in terrestrial and arboreal locomotion in a non-arboreal specialist. We used *Monodelphis domestica* (Wagner, 1842), the gray short-tailed opossum, as our model. *M. domestica* is a small terrestrial marsupial (Cartmill, 1972; Nowak, 1999) that is readily capable of moving on narrow substrates (Lammers, 2001). Although specialization for arboreal locomotion evolved several times within the family Didelphidae, terrestrial habitation is probably primitive (Fig. 2). Furthermore, *Monodelphis* is considered the most terrestrial genus within the family (Nowak, 1999). In this paper, we address the mechanics of arboreal locomotion through two primary questions. Firstly, do terrestrial mammals necessarily adopt SRF patterns observed in arboreal specialists? Arboreal specialists, such as *Caluromys philander* have morphological as well as behavioral adaptations for arboreal habitation and locomotion (Schmitt and Lemelin, 2002), whereas the terrestrial *M. domestica* presumably must rely much more on behavioral modifications to move on arboreal substrates. Thus, it is likely that *M. domestica* will move along a branch differently than would an arboreal specialist. Secondly, how does limb placement about a curved substrate affect stability on a branch?

Materials and methods

Animals

We used six adult male *Monodelphis domestica* (Wagner, 1842; gray short-tailed opossums) for all experiments (body

Fig. 1. Arboreal locomotion in *Monodelphis domestica*. (A) Resolution of substrate reaction forces (SRFs) into normal and shear components ($F_{\text{normal,ML}}$ and $F_{\text{shear,ML}}$, respectively) as illustrated for a fore limb and its mediolateral SRF (F_{ML}). X_{FL} , Y_{FL} and Z_{FL} are coordinates of the estimated center of fore limb pressure. (B) Resolution of vertical SRFs into shear and normal components ($F_{\text{normal,V}}$ and $F_{\text{shear,V}}$, respectively). (C) Cropped representative image of *M. domestica* on the arboreal trackway illustrating the limb landmarks: (1) distal tip of the third manual digit; (2) lateral aspect of the wrist joint; (3) distal tip of the fifth pedal digit; (4) lateral aspect of the metatarsophalangeal joint. Note that the heel (see arrow pointing to the ankle marker) was typically not in contact with the substrate during arboreal and terrestrial trials. Scale bar (4 cm) denotes the length and location of the arboreal force transducer.

mass: 0.105–0.149 kg), and all procedures were approved by the Ohio University Animal Care and Use Committee. Animals were anaesthetized prior to each experiment by placing them and approximately 0.3–0.4 ml of isoflurane (Abbott Laboratories, North Chicago, IL, USA) into a plastic container (~2 min). The fur covering the lateral aspect of the left fore and hind limb was shaved and white 1.3×1.7 mm beads were glued to the skin overlying bony landmarks. Landmarks used in this study include: distal tip of the third manual digit, the lateral aspect of the wrist, distal tip of the fifth pedal digit and fifth metatarsophalangeal joint (Fig. 1C). The animals typically awoke within 2 min and appeared to suffer no ill effects.

Kinetic data

Force transducers for recording SRFs were constructed based on the spring-blade design described in Biewener and Full (1992) and Bertram et al. (1997). The terrestrial trackway was 160 cm long, with a 48×11 cm force platform integrated in the middle and was covered with 60-grit sandpaper for traction. This force platform was initially developed to evaluate whole-body mechanics, so its length necessitated capturing individual fore and hind limb SRFs in separate trials. Fore limb data were obtained as the first footfall on the platform whereas hind limb data represent the last limb off the platform. The arboreal trackway was constructed from 2.03 cm diameter aluminum tubing (including 60-grit sandpaper covering); the trackway, therefore, corresponded to approximately one-half body width. This trackway was 151 cm long, with a 4 cm force-transducer instrumented section. Because the force transducer was short in the arboreal trackway, sequential fore and hind limb SRFs were obtained in each trial. Animals were encouraged to run towards a wooden box placed at the end of each trackway. Force transducer calibration protocol followed Bertram et al. (1997). Briefly, the vertical transducers were calibrated by placing known weights on the platform or hanging weights from the

pole; craniocaudal and mediolateral directions were calibrated by hanging weights through a pulley apparatus.

SRF data were collected at 1200 Hz for 3–6 s. Analog outputs from the force transducers were amplified (SCXI-1000 and 1121; National Instruments, Austin, TX, USA), converted to a digital format (National Instruments; NB-M10-16L), and recorded as voltage changes with a LabVIEW 5.1 (National Instruments) virtual instrument data-acquisition program. Voltage changes were then converted into forces (in N) using calibration scaling factors. All force traces were filtered with Butterworth notch filters at 60 Hz, 48–58 Hz and 82–92 Hz for the terrestrial trials, and at 60 Hz, 115–125 Hz and 295–305 Hz for the arboreal trials.

Only trials that approximated steady speed over the force transducers were analyzed. This was determined in the arboreal trials by comparing the total braking impulse of both fore and hind limbs to the total craniocaudal impulses [(braking impulse)/(craniocaudal impulse)×100%]; see below for description of impulse calculations. If this percentage fell between 45–55%, then the trial was considered to be steady speed. A different criterion for steady speed was developed for the terrestrial trials. Whole-body SRFs were obtained as the animals crossed the force platform. The craniocaudal SRFs were divided by mass and then integrated to obtain craniocaudal velocity profiles; the integration constant was set as mean speed determined videographically over three 12 cm intervals. Terrestrial trials were accepted as steady speed when braking and propulsive components of the whole body velocity were balanced. We made every effort to obtain steady-speed trials at a large range of speeds on each substrate, but despite our persistence only one slow terrestrial trial (0.724 m s⁻¹) was acceptable.

Kinetic data include peak vertical force, time to peak vertical force, vertical impulse, braking impulse, propulsive impulse and net mediolateral impulse for fore and hind limbs. A fourth LabVIEW virtual instrument was used to calculate impulse

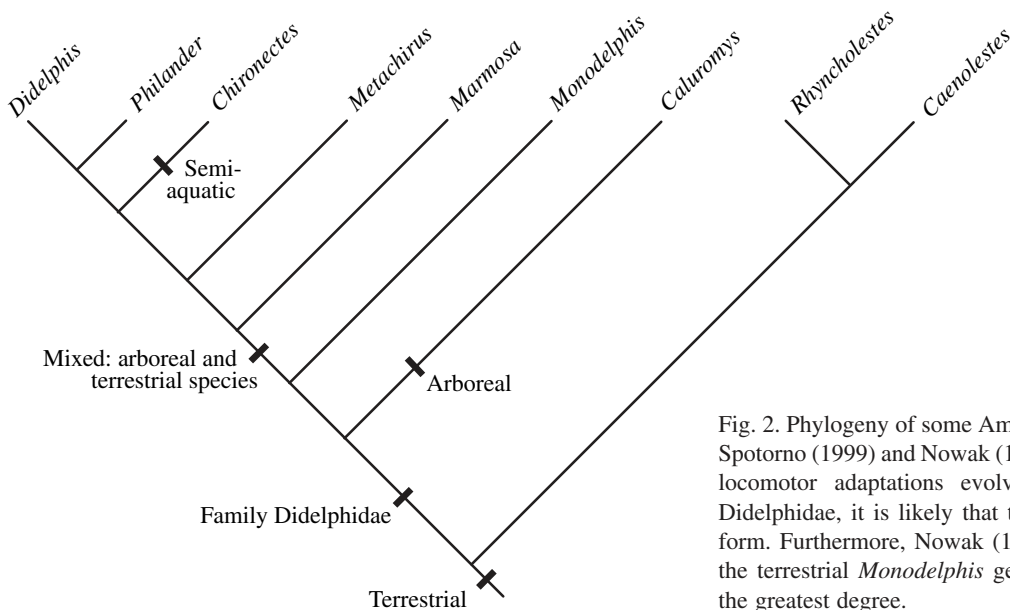


Fig. 2. Phylogeny of some American marsupials, based on Palma and Spotorno (1999) and Nowak (1999). Although scansorial and arboreal locomotor adaptations evolved more than once in the family Didelphidae, it is likely that the common ancestor was a terrestrial form. Furthermore, Nowak (1999) and Cartmill (1972) suggest that the terrestrial *Monodelphis* genus retains the primitive condition to the greatest degree.

by integrating the force/time curve separately for each limb and each orthogonal direction (vertical, craniocaudal, mediolateral). In this study, ‘impulse’ refers to the impulse generated by individual limbs (contact impulse) rather than the change in momentum of the whole body (Bertram et al., 1997). Substrate reaction forces were divided by the animal’s body weight to account for the 0.105–0.149 kg range in mass; forces and impulses were therefore analyzed in units of body weight (BW) and BW·s, respectively.

Kinematic data

The trackways were illuminated with three 233.3 Hz strobe lights (Monarch-Nova, Amherst, NH, USA) as two high-speed 120 Hz digital cameras with a 1/250 s shutter speed (JVC GR DVL 9800; Yokohama, Japan) captured footfall patterns and limb movement. The first camera obtained a lateral view of the left side of the animal and the second obtained a dorsolateral view. These videos were uploaded to a computer using U-lead Video Studio 4.0 (Ulead, Taipei, Taiwan), and then the APAS motion analysis system (Ariel Dynamics, San Diego, CA, USA) was used to synchronize the kinematic events from the two camera views, digitize the landmarks and convert each two-dimensional set of digitized data into three-dimensional coordinates for each landmark.

The center of pressure for each foot was estimated using the landmarks. Because the fore limb assumed a fully plantigrade posture on both arboreal and terrestrial substrates, the center of pressure of the manus (‘hand’, composed of the structures distal to the wrist joint) was estimated as the geometric midpoint between the wrist and third manual digit landmarks. Because the heel did not contact either substrate, the center of pressure of the pes (‘foot’, composed of the structure distal to the angle joint) was set as the geometric midpoint between the metatarsophalangeal and fifth pedal digit landmarks. Given that the distance between manual and pedal landmarks was short (15.7 and 6.8 mm, respectively), placing the center of pressure at the midpoint between proximal and distal contacts was not unreasonable. This estimate also assumes that the manus and pes contact the substrate without gripping, which is reasonable for the fore limb because the manus in *M. domestica* is short and lacks opposable digits. Although the pes is longer than the manus and has an opposable hallux, the diameter of the substrate is considerably greater than the span of the grip of the pes and the grit of the sandpaper did not offer much claw penetration. Furthermore, because the heel did not touch the substrate, only a small part of the pes was used to connect with the branch.

Timing variables (speed, stance duration, stride frequency, stride length) were also measured from the videos. Gaits were identified by footfall patterns using limb phase, which is the proportion of stride duration that the left fore limb contacted the substrate after the left hind limb contact (Hildebrand, 1976). Hildebrand (1976) divided limb phase into octiles of equal size. A limb phase close to 50% (between 43.75 and 56.25%) indicates a trot; limb phases greater than 56.25% are different lateral sequence gaits (for further details see Reilly and Biknevicius, 2003). [We acknowledge that ‘trot’ has been

applied differently in kinematic (Hildebrand, 1976) and whole-body mechanics (Cavagna et al., 1977) studies, the former as a footfall pattern, the latter as bouncing mechanics or in-phase fluctuations of kinetic and gravitational potential energies. In the present study, ‘trot’ is used in its traditional, kinematic sense, namely, diagonal couplet footfalls (Newcastle, 1657). Whole-body mechanics was not assessed in the arboreal trials.] Duty factor of the hind limb (ratio of stance duration to stride duration) was also calculated. Differences between arboreal and terrestrial duty factor and limb phase were determined by Student’s *t*-test.

Calculating required coefficient of friction

The required coefficient of friction (μ_{req}), the ratio of shear force to normal force, is one way of estimating the ability of an animal to generate friction with its limbs. If the limb does not slip when it makes contact with the substrate, then the true coefficient of friction is greater than the required coefficient of friction. On the flat terrestrial substrate, shear force is the vector sum of craniocaudal and mediolateral forces, and normal force is the vertical force. On the arboreal substrate, the animal’s limbs contacted the pole between its lateral aspect to its dorsal-most surface. Thus, while craniocaudal forces continue to contribute exclusively to shear force in the arboreal trackway, vertical and mediolateral forces each contribute to shear and normal forces (Fig. 1A,B).

To calculate μ_{req} on the arboreal substrate, the components of the vertical, craniocaudal and mediolateral SRFs contributing to shear, and normal, forces were computed as:

$$\text{Shear force component} = [(\mathbf{F}_{\text{ML}} \sin \theta - \mathbf{F}_{\text{V}} \cos \theta)^2 + (\mathbf{F}_{\text{CC}})^2]^{0.5}$$

$$\text{Normal force component} = (\mathbf{F}_{\text{ML}} \cos \theta) + (\mathbf{F}_{\text{V}} \sin \theta),$$

where \mathbf{F}_{V} , \mathbf{F}_{CC} and \mathbf{F}_{ML} are vertical, craniocaudal and mediolateral force, respectively, and θ is the angle formed by the coordinates of the limb contact, the center of the pole, and the horizontal (Fig. 1A,B). \mathbf{F}_{V} was always in the same direction, but when \mathbf{F}_{ML} was occasionally medially directed, this component of the SRF was given a negative sign so that the same calculations could be used throughout.

Statistical analyses

Data from all individuals were pooled, and Systat 9.0 (Point Richmond, CA, USA) was used for all analyses. Least squares regression was used to determine the correlation of forces and impulses with speed for each substrate and limb-pair grouping. Because most of the regressions of vertical impulse *versus* speed were significant, a two-way analysis of covariance (ANCOVA) with speed as the covariate was used to determine differences among groups with respect to vertical impulse. However, because peak vertical force and remaining impulses were typically not significantly correlated with speed, a two-way analysis of variance (ANOVA) was used to determine significant differences between substrates and limbs. We considered $P \leq 0.05$ to be the cut-off for statistical significance, and data are reported as means \pm standard error of the mean (S.E.M.) unless otherwise indicated.

Results

Gait characteristics

Locomotor speed was significantly lower on the arboreal trackway (arboreal, $1.00 \pm 0.03 \text{ m s}^{-1}$; terrestrial, $1.51 \pm 0.05 \text{ m s}^{-1}$; $P < 0.00001$, $N = 76$; Table 1). Because we used similar methods to encourage the animals to move quickly across the trackway, it is likely that the speeds we obtained on the arboreal trackway approached the animals' maximal efforts. Attempts to obtain slower trials on the terrestrial trackway yielded unacceptable acceleration or deceleration within trials.

The animals predominantly used trotting (diagonal couplet) gaits on terrestrial and arboreal substrates (limb phase range: 34.7–57.1%; Fig. 3A). However, arboreal trials had a significantly lower limb phase than terrestrial trials (t -test, $N = 38$, $P = 0.0003$), where 22.7% of the arboreal trials were classified as a lateral-sequence diagonal-couplet gait (a trot-like gait with limb phase between 31.25–43.75%).

Duty factor was significantly larger in arboreal trials (arboreal $42.4 \pm 0.8\%$; terrestrial $30.2 \pm 1.0\%$; t -test, $N = 38$, $P < 0.00001$; Fig. 3A). Stance duration decreased with speed in a concave-up manner (Fig. 3B). The slope of stance duration *versus* speed was significantly steeper in the arboreal trials than in terrestrial trials (one-way analysis of covariance, ANCOVA, $N = 76$, $P = 0.00621$). Stride frequency increased linearly with speed, and there was no significant difference in slope with respect to limb pair or substrate (two-way ANCOVA, $N = 76$, $P = 0.8$). However, the arboreal trials had a significantly higher stride frequency than the terrestrial trials (least squares means: arboreal, $6.92 \pm 1.01 \text{ Hz}$; terrestrial, $6.02 \pm 1.26 \text{ Hz}$; $N = 76$, $P = 0.00012$).

Substrate reaction forces

Sample force traces from the arboreal and terrestrial trackways are shown in Fig. 4. Two patterns were observed in the terrestrial trials. Vertical force profiles for both fore and hind limbs on the arboreal trackway always yielded single peaks (Fig. 4A,B) as did most terrestrial trials (Fig. 4C,D). However, at the slowest speeds on the terrestrial substrate (below 1.5 m s^{-1} for the fore limbs and below 1.25 m s^{-1} for the hind limbs; Fig. 4E,F) vertical force profiles displayed a double-peak.

Peak vertical force was not correlated with speed for any substrate–limb pair except for terrestrial hind limbs. Fore limbs had significantly higher peak vertical force than hind limbs on each substrate (two-way ANCOVA, $N = 75$, $P < 0.00001$;

Fig. 5A; Table 2). Peak vertical forces of fore and hind limbs were higher in the terrestrial trials than in arboreal trials ($N = 75$, $P < 0.00001$). Interaction was also significant ($N = 75$, $P = 0.01006$), so that the substrate effect on peak vertical force was significantly more pronounced in the fore limbs than in hind limbs. Relative to percent stance duration, peak vertical force occurred significantly earlier in hind limbs than in fore limbs, regardless of substrate (two-way analysis of variance, ANOVA, $N = 75$, $P < 0.00001$). Furthermore, this peak occurred significantly earlier in arboreal trials than in terrestrial trials ($N = 75$, $P = 0.00753$; Fig. 4E,F). The ratio of fore limb to hind

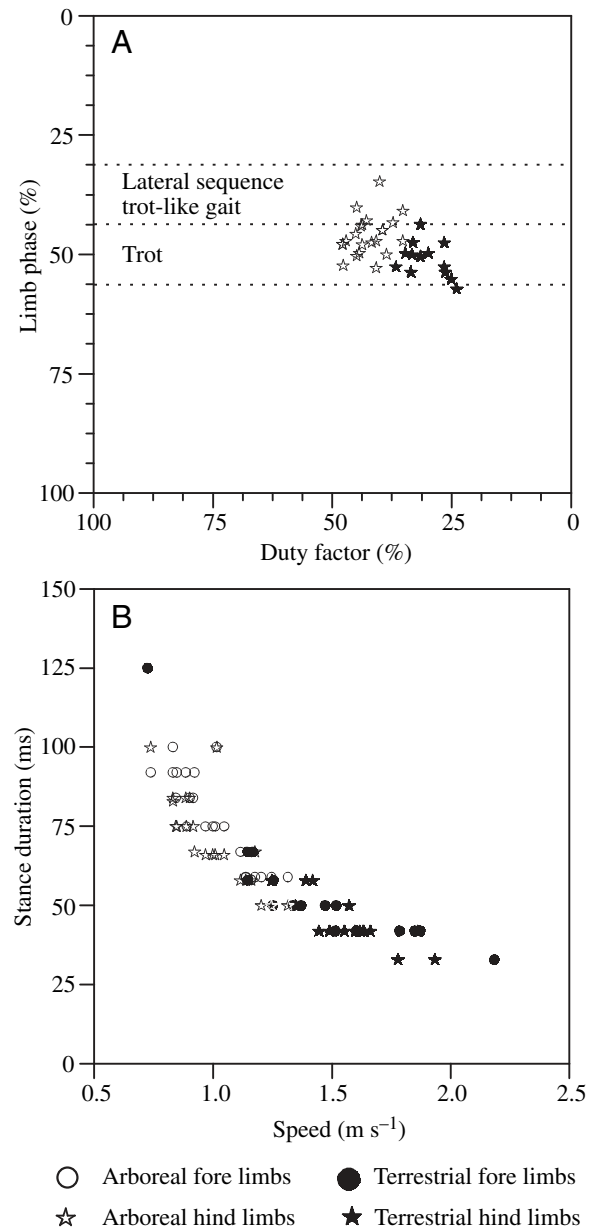


Fig. 3. (A) Symmetrical gait plot for *M. domestica* during terrestrial and arboreal locomotion following Hildebrand (1976). Terrestrial and arboreal trials lie mostly within trots, although arboreal trials extend into smaller limb phases (lateral-sequence diagonal-couplet gait). (B) Relationship between stance duration and speed.

Table 1. *General kinematics*

	<i>N</i>	Arboreal	Terrestrial
Speed (m s^{-1})	76	1.00 ± 0.02 (0.74, 1.31)*	1.51 ± 0.05 (0.72, 2.18)
Limb phase (%)	38	46.0 ± 0.6 (34.7, 52.8)*	50.1 ± 0.7 (41.3, 57.1)
Duty factor (%)	38	44.6 ± 0.8 (35.2, 58.2)*	33.9 ± 1.0 (24.0, 51.7)

*Significant difference between substrates ($P \leq 0.0003$). Values are means \pm S.E.M. (minimum, maximum).

limb peak vertical forces was higher for the terrestrial substrate (1.702) than the arboreal substrate (1.617; ratios were calculated using mean peak vertical forces for each limb and substrate).

Vertical impulse decreased significantly with speed in all

substrate–limb groups except for the terrestrial hind limb group (Fig. 5B; Table 3). Slopes were significantly different from each other (two-way ANCOVA, $N=75$, $P=0.00003$), and in both fore and hind limbs the slope of vertical impulse *versus* speed was

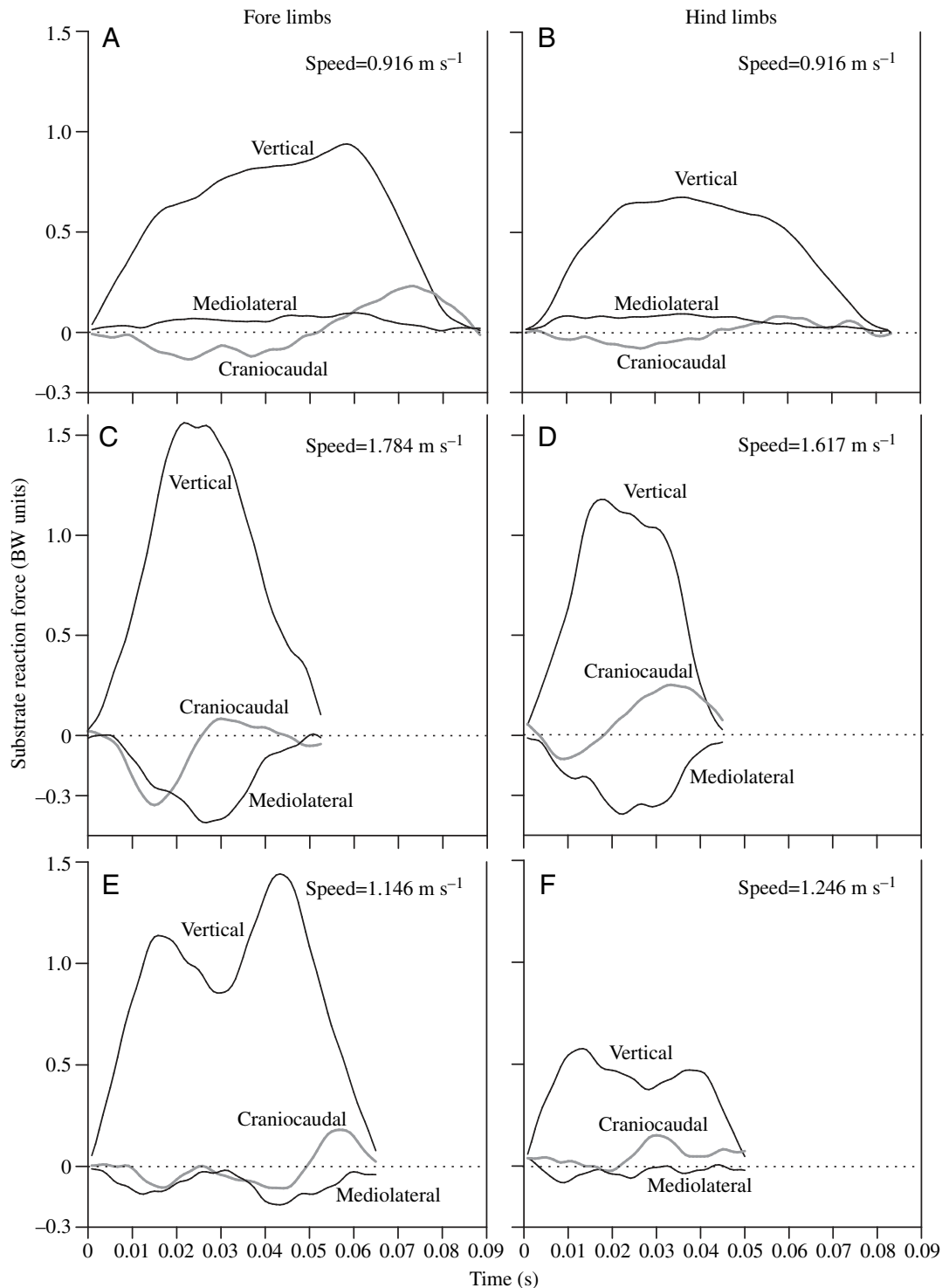


Fig. 4. Representative substrate reaction force (SRF) profiles from the terrestrial and arboreal trackways (speed indicated on each plot). (A,B) Fore limb and hind limb arboreal trials. (C,D) Typical terrestrial trials for the fore limb and hind limb. (E,F) Slow terrestrial fore limb and hind limb trials with double-peaked vertical force traces. Negative craniocaudal forces indicate a braking effort and positive indicates propulsion. Negative mediolateral force designates a medially directed SRF (laterally directed limb force) and positive designates a medially directed limb force. For clarity, craniocaudal force is shown in gray.

Table 2. Peak vertical force (BW units), and vertical, fore–aft and mediolateral impulses (BW·s)

	Arboreal		Terrestrial	
	Fore limb	Hind limb	Fore limb	Hind limb
Peak vertical force	1.010±0.0285 (0.821, 1.309)	0.625±0.0290 (0.383, 0.897)	1.528±0.0724 (0.901, 2.075)	0.898±0.0565 (0.577, 1.241)
Vertical impulse	0.0423±0.00186 (0.0378, 0.0663)	0.0239±0.00186 (0.0180, 0.0420)	0.0519±0.00157 (0.0333, 0.0645)	0.0216±0.00292 (0.0126, 0.0321)
Braking impulse	0.00362±0.00031 (0.0014, 0.0065)	0.00163±0.00029 (0.0003, 0.0053)	0.00322±0.00040 (0.0008, 0.0069)	0.00092±0.00017 (0.0002, 0.0029)
Propulsive impulse	0.00368±0.00041 (0.0003, 0.0080)	0.00164±0.00028 (0.00000, 0.0042)	0.00245±0.00028 (0.0005, 0.0043)	0.00312±0.00058 (0.0008, 0.0079)
Net fore–aft impulse	0.00006±0.00058 (–0.0047, 0.0066)	0.00000±0.00052 (–0.0053, 0.0039)	–0.00077±0.00054 (–0.0064, 0.0017)	0.00221±0.00066 (–0.0007, 0.0074)
Net mediolateral impulse	0.00444±0.00053 (–0.0021, 0.0096)	0.00450±0.00044 (0.0008, 0.0107)	–0.00496±0.00159 (–0.0158, 0.0085)	–0.00310±0.00107 (–0.0121, 0.0050)

Values are means ± S.E.M. (minimum, maximum), *N*=75.

steeper on the arboreal substrate than on the terrestrial. On each substrate, the vertical impulse of fore limbs had significantly higher *y*-intercept means than that of hind limbs (least squares linear regression, 95% confidence intervals to determine slope and *y*-intercept differences, *N*=38, *P*<0.00001). Arboreal fore limb and hind limb slopes were not significantly different. On the terrestrial substrate, fore limb vertical impulse was negatively correlated with speed (*N*=16, *P*<0.00001), while terrestrial hind limb vertical impulse was not correlated with speed. The ratio of fore limb to hind limb vertical impulse was 2.047 on the terrestrial substrate and 1.727 on the arboreal.

Regardless of substrate, craniocaudal force traces were characterized by a braking phase followed by a propulsive phase (Fig. 4). On the terrestrial substrate, the fore limbs usually exerted a net braking impulse and the hind limbs a net propulsive impulse. However, when propulsive impulse was considered alone, there was no significant difference between fore limb and hind limbs on the terrestrial substrate. On the arboreal substrate, fore limbs exerted braking and propulsive impulses that were both strong and not significantly different from each other (Fig. 5C,D). Hind limbs similarly generated braking and propulsive impulses that were equal, but these impulse magnitudes were significantly lower than those produced by the fore limbs (*N*=75, *P*=0.00017). The net fore–aft impulse of fore and hind limbs on the arboreal substrate was nearly zero.

Within each substrate, there were no significant differences between limb pairs with respect to net mediolateral impulse (Fig. 6). On the terrestrial substrate, both limb pairs produced strong medially directed SRFs. Among the arboreal trials, the limbs generated strong medially directed limb force (laterally directed SRFs). Differences between substrates were highly significant (*N*=75, *P*<0.00001).

Limb placement and required coefficient of friction

On the arboreal trackway, the pes was usually placed

considerably lower on the branch than manus (Fig. 7A). The required coefficient of friction (μ_{req}) at foot touchdown for all trials on both substrates was initially high, but quickly dropped for most of the stance phase, only to rise again at the end of the step (Fig. 7B). The highest values were typically found at touchdown. Because we used the filtered data for these calculations, it is unlikely that these high values were the result of impact noise. The median μ_{req} was significantly higher in the arboreal trials than in terrestrial trials (*N*=74, *P*<0.00001; Fig. 7C). In arboreal trials hind limbs had significantly higher median μ_{req} than fore limbs (*N*=74, *P*=0.0008). No significant difference in μ_{req} was found between limb pairs in the terrestrial trials (*t*-test, *N*=32, *P*=0.172).

Discussion

In this study *Monodelphis domestica* predominantly trotted on terrestrial and arboreal substrates, with occasional lateral-sequence diagonal couplet trials observed on the arboreal trackway. This largely conforms to gaits (footfall patterns) reported previously for this species (Pridmore, 1992; Lemelin et al., 2003; Parchman et al., 2003) although the present study analyzed fewer lateral-sequence walks on the terrestrial trackway simply because slower trials often failed to meet the steady speed criterion. While more arboreally adapted opossums (brush-tailed opossum, *Trichosurus vulpecula*; monito del monti, *Dromecops australis*; woolly opossum, *Caluromys philander*) also trot, they shift to diagonal sequence gaits at slower locomotor speeds (White, 1990; Pridmore, 1994; Lemelin et al., 2003). This observation led Pridmore (1994) to conjecture that diagonal sequence gaits are an arboreal adaptation in marsupials, a suggestion that parallels the arboreal, ‘fine-branch’ explanation for diagonal sequence gaits in primates (e.g. Cartmill, 1972). That *M. domestica* did not resort to a diagonal sequence gait when moving along arboreal substrates

(Lemelin et al., 2003; present study) supports the contention that terrestrial animals may not have the same locomotor response to curved and more narrow substrates as have arboreal specialists.

Substrate diameter does appear to have some effect on locomotor behavior in *M. domestica*. Narrow substrates (<12.5 mm) clearly challenge the species' stability, as individuals were frequently observed to falter and fall (Pridmore, 1994). Once habituated to the 20 mm arboreal trackway, *M.*

domestica in the present study appeared quite capable of freely traversing the 1.5 m trackway, but we were unable to entice animals to travel at steady speeds higher than 1.32 m s⁻¹. Thus, it appears that speed is an important behavioral adaptation to moving on a more treacherous substrate.

M. domestica relies more heavily on the fore limbs than on the hind limbs to support its body weight on both terrestrial and arboreal trackways. The vertical component of the SRF reflects

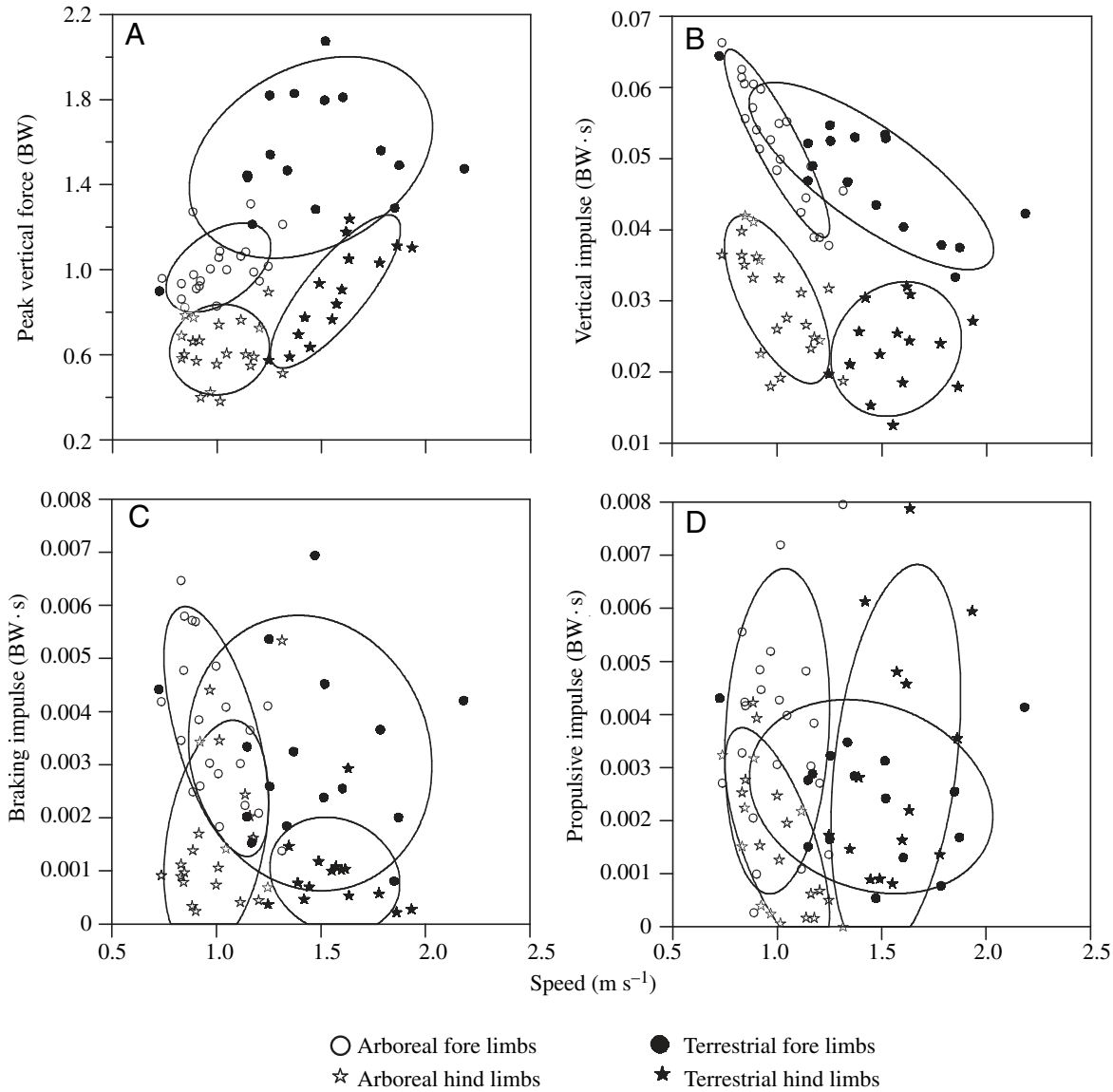


Fig. 5. Relationship of kinetic variables *versus* speed. (A) Peak vertical force. (B) Vertical impulse. (C) Braking impulse. (D) Propulsive impulse. The sample ellipses emphasize substrate and limb groups. The dimensions of the ellipses were determined from the standard deviations of the *y* and *x* variables; sample covariance between *y* and *x* determines the orientation of the ellipse.

Table 3. Least squares regression results for vertical impulse (BW·s) versus speed (m s⁻¹)

	Slope	95% confidence intervals	R ²	N	P-value
Arboreal fore limbs	-0.0472	-0.0581, -0.0362	0.791	22	<0.00001
Arboreal hind limbs	-0.0303	-0.0471, -0.0134	0.383	22	0.00126
Terrestrial fore limbs	-0.0179	-0.0258, -0.0010	0.599	16	0.00026
Terrestrial hind limbs	-	-	-	16	0.60063

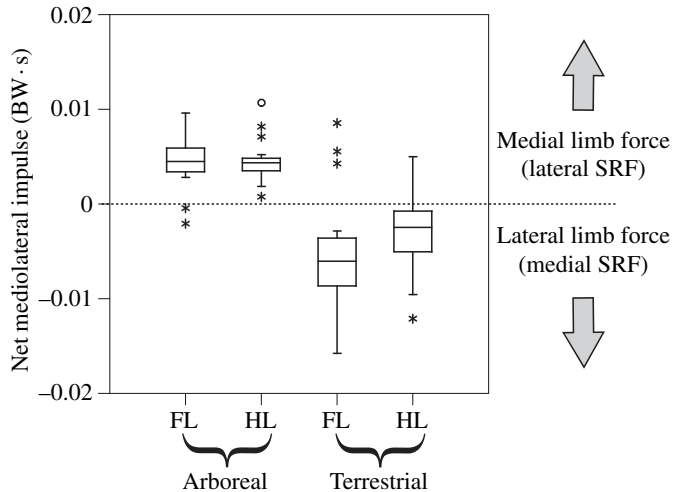


Fig. 6. Box-and-whisker plots of net mediolateral impulse for each substrate and extremity group. The line in the middle of each box plot represents the median; each box and each whisker corresponds to a fourth of the data; asterisks designate outliers; circle denotes extreme outliers. Positive values indicate a medially directed limb force [laterally directed substrate reaction force (SRF)], and negative values indicate a laterally directed limb force. Substrates were significantly different ($N=75$, $P<0.00001$), but there were no differences between limbs within substrate groups.

limb function in body-weight support. Peak vertical forces in terrestrial trials of *M. domestica* conform to the pattern of typical terrestrial mammals, namely, fore limb values exceed hind limb values (Demes et al., 1994; Schmitt and Lemelin, 2002; present study). The most likely explanation for this finding is that the center of mass in *M. domestica* lies closer to the fore limbs than to the hind limbs (about 40% of the distance between the shoulder and hip joints; A.R.L., unpublished data). Fore limbs continue to dominate in body mass support when *M. domestica* moved along the arboreal trackway, but the ratio of fore limb to hind limb peak vertical force drops. This occurs largely because hind limbs display somewhat higher than expected peak vertical forces relative to speed (as displayed by an extrapolation of the terrestrial hind limb slope into the arboreal speed range; Fig. 5A). This shift in body-weight support between fore and hind limbs is relatively small in comparison to the pattern exhibited by the arboreal *C. philander* (Schmitt and Lemelin, 2002): whereas peak vertical force on arboreal substrates for the hind limbs are comparable in the two species (0.5–0.9 BW units in *M. domestica*; 0.6–1.0 in *C. philander*), *C. philander*'s fore limb forces (0.5–0.8 BW units) fall below the range observed in *M. domestica* (0.8–1.3 BW units).

Comparisons of peak vertical force beyond the marsupials fail to uphold a strict terrestrial–arboreal dichotomy. Although most primates are hind limb dominant in body-weight support (Demes et al., 1994), the highly arboreal slow loris (*Nycticebus coucang*) and common marmoset (*Callithrix jacchus*) display higher fore limb peak vertical forces when moving pronograde (over the branch) on an arboreal trackway (Ishida et al., 1990; Schmitt, 2003a). Furthermore, the more terrestrial chipmunk and the more arboreal squirrel are both fore limb dominant in body-mass

support when moving over a terrestrial trackway (Biewener, 1983).

The effect of substrate curvature on peak vertical force does, however, appear to be consistent across arboreal specialist and more terrestrial species. Primates and marsupials alike typically apply lower peak vertical forces when switching from a terrestrial trackway to an arboreal one (Schmitt, 1994, 1999, 2003b; Schmitt and Lemelin, 2002; this study). Furthermore, there is a significant reduction in peak vertical force as primates move on progressively smaller arboreal substrates (Schmitt, 2003b). A benefit for reducing vertical forces on arboreal substrates might be a concomitant reduction in branch oscillation (Demes et al., 1994; Schmitt, 1999). Therefore, while hind limb dominance in body-weight support is not a prerequisite for moving along an arboreal support, reduction in vertical force application relative to terrestrial values does appear to be an inescapable consequence of arboreal locomotion, especially if arboreal speeds are slow. To support body weight, however, these lower forces must then be distributed over a longer interval. This could be accomplished with greater stance duration and/or stride frequency on the arboreal substrate (as was the case in this study).

Our data do suggest, however, that a small degree of posterior weight shift occurred on the arboreal substrate. First, the fore limb to hind limb ratio of peak vertical force (BW) and vertical impulse (BW s) was higher on the terrestrial substrate than on the arboreal substrate. Also, the time (relative to stance duration) that the peak vertical force occurred was significantly delayed in both limb pairs on the arboreal substrate. Because the time at which peak vertical force occurs is closely associated with the time that a limb is supporting the greatest amount of body weight, if the center of mass is effectively moved posteriorly relative to the base of support, then both fore and hind limbs will support the greatest weight at a later portion of the stance phase. Posterior weight shift has been found for most primate species, whether on arboreal or terrestrial substrates (Schmitt and Lemelin, 2002); furthermore, this posterior weight shift tends to be exaggerated when arboreal specialists move on arboreal substrates.

Limb differences in vertical impulse largely parallel those of peak vertical force in *M. domestica*, except that vertical impulse tends to decrease with speed as is common in mammals moving with symmetrical gaits. The decrease in vertical impulse with speed is driven primarily by a speed-dependent reduction in stance duration, more so than any increase in peak vertical force. A concave-up negative relationship between support duration versus speed is typical for terrestrial locomotion (e.g. Demes et al., 1990; Abourachid, 2001), a pattern that may reflect the need to move more cautiously to remain stable at slower speeds. The particularly long stance durations in the slower arboreal trials in *M. domestica* may indicate an increased perception of hazard by the animals when moving on an arboreal substrate. Because vertical impulse, which is responsible for body-weight support, decreases with speed faster on the arboreal trackway, the higher stride frequency on the arboreal trackway may be a way of compensating so that body-weight support is adequately maintained.

Our final note on vertical forces concerns force profile shape in the terrestrial trials: double-peaked at lower speeds and single-peaked at higher speeds. The same pattern has been reported in humans (Enoka, 2002), sheep and dogs (Jayes and Alexander,

1978), and horses (Biewener et al., 1983). A double-peaked vertical force is normally indicative of a vaulting mechanic ('mechanical walk'), that is, the animal is exchanging kinetic and gravitational potential energy *via* an inverted pendulum mechanism (Cavagna et al., 1977). Because our terrestrial trials were obtained with a force platform system that also captures whole body forces, we evaluated the fluctuations of external mechanical energies of the center of mass in the slowest trials. In spite of the double-peaked configuration of the trials, the whole-body mechanics indicated in-phase fluctuations in the kinetic and gravitational potential energies (phase shift $<45^\circ$) and low recovery of mechanical energy *via* pendulum-like mechanisms ($<20\%$). This is consistent with the findings of Parchman et al. (2003), which reported only trot and trot-like gaits, and only bouncing mechanics in *M. domestica*. Parchman et al. (2003) suggested that some of the slower trials may represent a high compliance locomotor behavior ('Groucho' running).

Craniocaudal forces control forward impulsion, and all mammals moving at steady speed on a terrestrial substrate rely on the hind limbs to provide most of the propulsive force (Demes et al., 1994). Although craniocaudal forces fluctuate from an initial braking action to a final propulsive action in both fore and hind limbs, hind limbs generate greater propulsive impulses than do fore limbs. Previous studies on arboreal specialists report similar functions for locomotion on arboreal trackways (Ishida et al., 1990; Schmitt, 1994). Shifting between terrestrial and arboreal substrates resulted in either no significant changes in craniocaudal force (Schmitt, 1994) or smaller propulsive forces on arboreal substrates (fore limbs only were evaluated; Schmitt, 1999). By contrast, results reported here suggest that terrestrial mammals may shift a greater role in forward propulsion to the fore limbs when moving on an arboreal support.

Most terrestrial mammals generate small and erratic mediolateral forces (e.g. Hodson et al., 2001), yet mediolateral forces in *M. domestica* are often substantial, with magnitudes that rival the craniocaudal forces (Fig. 4). The net direction of the mediolateral SRF is medial (reflective of a laterally directed limb force). This is consistent with SRF data on terrestrial animals that use a more sprawled and semi-erect posture, such as lizards and alligators (Christian, 1995; Willey et al., 2004). A similar orientation (but lesser magnitude) was also reported for higher primates (Schmitt, 2003c). The polarity of mediolateral forces switches to reflect medially directed limb forces when *M. domestica* moved along the arboreal trackway. Not surprisingly,

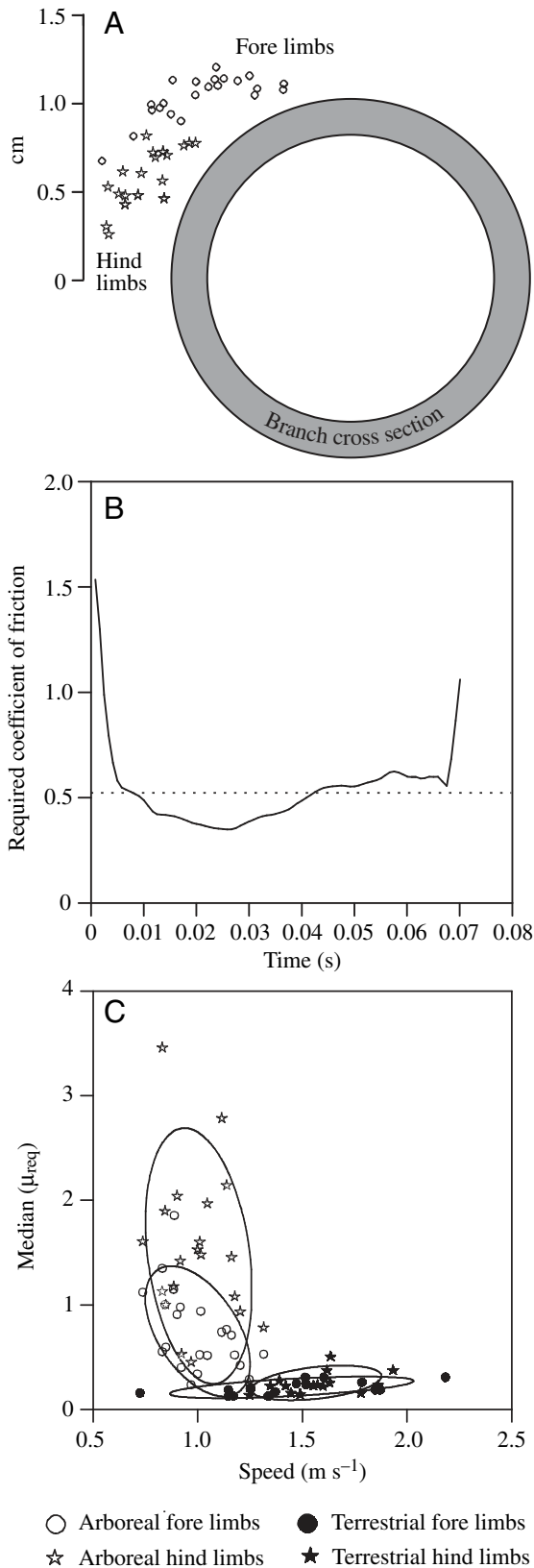


Fig. 7. (A) Manus and pes placement about the arboreal trackway. Location of the center of pressure of each foot is drawn to scale relative to branch cross-sectional shape. (B) Representative required coefficient of friction data from *M. domestica* on the arboreal trackway ($1.10\ m\ s^{-1}$). High values occur at the foot touchdown and again at the end of the step. The broken line indicates the median value for this record (0.528). (C) Median required coefficient of friction for fore limbs and hind limbs on horizontal terrestrial and arboreal substrates. Ellipses are used to make each group more visible, and are calculated as in Fig. 5.

this is also the primary orientation for most other mammals when moving on arboreal substrates (Schmitt, 2003c). Thus, on the terrestrial substrate, the mediolateral SRFs are ‘tipping’ (i.e. oriented in such a way to provide stability against rolling), whereas on the arboreal substrate they are ‘gripping.’

Thus, compared with more arboreally adapted mammals, *M. domestica* appears to retain fore limb dominance in body-weight support and to shift a greater role in forward impulsion to the fore limbs when moving on an arboreal substrate. We believe that the explanation of the dominance of the fore limb during arboreal locomotion lies in the differences in limb placement about the curved substrate. This is best illustrated by a consideration of friction. Kinoshita et al. (1997) estimated that the coefficient of static friction (μ_s) between 220-grit sandpaper and human skin is 1.67 ± 0.24 (index finger) and 1.54 ± 0.27 (thumb); Cartmill (1979) estimated values of μ_s in excess of five between the volar skin of primates and a plastic surface. It is likely that the true μ_s in our study was higher than the values reported by Kinoshita et al. (1997) because: (1) we used 60-grit sandpaper, which is rougher than 220-grit, and (2) the claws and the palmar tubercles on the manus and pes of the opossums may improve the degree of interlocking between foot and substrate (as per Cartmill, 1974), and (3) the limbs did not demonstrably slip (implying that the true coefficient of static friction is higher than the mean μ_{req}).

The values for the median μ_{req} , and thus the potential for slipping, was significantly higher in both fore and hind limbs in the arboreal trials than in terrestrial trials, which verifies the more precarious nature of arboreal locomotion. The reason for this may be twofold. First, vertical force was significantly lower on the arboreal substrate than on the terrestrial (in both limbs), so that there simply was less vertical force to contribute to the generation of normal force (although see the section above). The normal force is the stabilizing force for maintaining the position of the manus and pes on the substrate. Second, some proportion of vertical force results in a shear force across the surface of arboreal substrates because of the placement of the manus and pes laterally off the top of the branch. Consequently, a smaller proportion of vertical force is available to contribute to the normal force during arboreal locomotion.

Similarly, the positioning of manus and pes can explain the significantly greater μ_{req} of hind limbs on the arboreal trackway. Hind limbs were nearly always placed lower and more laterally on the branch than fore limbs, and they supported significantly less body weight than the fore limbs. The difference in μ_{req} and foot placement between fore and hind limbs on the arboreal trackway may also serve to explain why the fore limbs were apparently so dominant in body-weight support, braking and propulsion. By placing the manus closer to the top of the branch, the fore limbs were more stable than the hind limbs and so they were recruited to assume a greater role in propulsion than is normally found during terrestrial locomotion. The hind limbs, with their more lateral placement on the branch and their smaller role in body-weight support, were perhaps less able to exert significantly higher propulsive forces without slipping.

Behavioral adaptations for arboreal locomotion

The results of this paper suggest that there are three important factors that animals may regulate in order to maintain stability during locomotion: speed, gait and limb placement. We propose that all three of these factors should be analyzed when conducting locomotor analyses, especially if different substrates are used.

This study examines arboreal locomotion in a terrestrial mammal with a primitive, generalized morphology and behavior (Lee and Cockburn, 1985), in the context of comparing terrestrial generalists and arboreal specialists. Although some animals move within arboreal habitats with impressive skill and speed (e.g. squirrel and many primates), many arboreal specialists apparently use speed reduction to maintain stability on branches and to reduce detection by predators (e.g. slow loris, woolly opossum, chameleon). Thus, speed reduction may serve as a common behavioral adjustment to arboreal locomotion.

On the terrestrial and arboreal substrates, *M. domestica* almost always kinematically trotted, although this species tended somewhat to dissociate the diagonal couplets and list towards the lateral sequence trot-like gait on arboreal trackways (Hildebrand, 1976). That this gait shift may be reflective of a need to increase stability is supported by data from Lammers (2001) that indicate that opossums use lateral sequence trot-like and single-foot gaits at slow speeds and/or on narrow (a quarter body diameter) supports. By contrast, most primates and the woolly opossum (Lemelin et al., 2003) use a diagonal sequence trot-like gait on both arboreal and terrestrial substrates. It appears that divergent gait (footfall) patterns exist between arboreal specialists and terrestrial generalists.

When arboreal specialists move on branches that are narrower than their body diameter, but too wide to grasp with opposable digits, do they place manus and pes on branches in different locations than terrestrial generalists? Data and/or tracings of images indicate that like *M. domestica*, the lesser mouse lemur (*Microcebus murinus*), fat-tailed dwarf lemur (*Cheirogaleus medius*), slow loris (*Nycticebus caucang*), and the brown lemur (*Eulemur fulvus*) may place their manus relatively dorsally on the branch and the pes more laterally (Cartmill, 1974; Jouffroy and Petter, 1990; Larson et al., 2001). However, illustrations of chameleon (*Chameleo* spp.) locomotion suggest that the manus and pes contact the branch in approximately the same location around a large arboreal support (manus: Peterson, 1984; pes: Higham and Jayne, 2004). The common opossum (*Didelphis marsupialis*) places its manus slightly laterally to the pes on narrow supports (Cartmill, 1974). Finally, the aye-aye (*Daubentonia madagascariensis*) contacts branches in a wide variety of locations (Krakauer et al., 2002). It is not yet possible to determine whether the kinetic and kinematic patterns observed in the present study represent a general behavioral adaptation to the challenges of arboreal locomotion by terrestrial mammals or simply a solution specific for this species.

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