

Mechanics of generating friction during locomotion on rough and smooth arboreal trackways

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SUMMARY

Traveling on arboreal substrates is common among most small mammals living anywhere vegetation grows. Because arboreal supports vary considerably in surface texture, animals must be able to adjust their locomotor biomechanics to remain stable on such supports. I examined how gray short-tailed opossums (*Monodelphis domestica*), which are generalized marsupials living on or near the ground, adjust to travel on rough and smooth 2cm-diameter arboreal trackways. Limb contact position was determined *via* high-speed videography, and substrate reaction force was measured by an instrumented section of each branch trackway. Normal and shear forces were calculated from substrate reaction force and limb contact position around the branch trackways. Normal force is greater in forelimbs, probably because of the forelimb's greater weight support role. Shear force was identical between limb pairs, most likely because of interactions between vertical force, limb placement, mediolateral force, and torque. The opossums adjusted to the smooth trackway mainly by reducing speed, changing footfall patterns and increasing normal force. I predict that arboreal specialists will show less change in performance between rough and smooth arboreal trackways because of their greater ability to grasp or maintain contact with arboreal substrates.

Key words: arboreal locomotion, gray short-tailed opossum, *Monodelphis domestica*, normal force, shear force, substrate reaction force.

INTRODUCTION

Most small quadrupedal mammals are at least somewhat proficient at moving on or under tree trunks, branches, twigs and shrubs (Jenkins, 1974). Such substrates are commonly encountered by any animal that lives where vegetation grows. The texture of such arboreal substrates varies considerably. Some have rough bark, and animals moving on them can easily generate enough friction between the substrate and their hand or foot. The animal can also (or instead) use claws to generate or take advantage of surfaces that are relatively perpendicular to the direction of locomotion (Cartmill, 1985). On smooth arboreal surfaces, creating and maintaining a stable contact with the branch is probably more challenging. There may be fewer places for claws to engage with the surface, and generating adequate friction force may be difficult because the coefficient of static friction (μ_s , which is a dimensionless number expressing shear force divided by normal force) is lower.

When generating friction force (μ_s multiplied by normal force) is the method (or an important method) of maintaining contact with a substrate, there are three ways for the animal to generate enough friction force. First, it can increase the normal force, which is directed perpendicular to the substrate. On an arboreal substrate, which is roughly cylindrical, a normal force runs from the center of pressure of the hand or foot toward the centerline of the long axis of the branch (Fig. 1). Normal force can be increased by muscular effort; for example, contralateral limbs can adduct, squeezing the branch between them and generating greater normal force. If the contact is near the top of the branch (that is, near the dorsal-most part of a long, narrow, horizontal cylinder), then considerable normal force will be generated from vertical force. The vertical component of SRF is typically the largest component, and when the limbs contact the top of the branch, most or all of the vertical force is normal to the branch surface. The second way

to generate adequate friction force is to increase μ_s . It might be possible for an animal to increase the effective μ_s by changing the shape or moisture content of its hand or foot (Haffner, 1998). Finally, the animal can decrease the need to generate friction force by decreasing the shear forces. Vertical and mediolateral components of the substrate reaction force (SRF) typically have a shear component whose magnitude corresponds with the location of the center of pressure on the branch cylinder (Fig. 1). In addition, the entire craniocaudal (fore-aft or anteroposterior) force component is a shear force. Finally, the torque around the long axis of the branch, which is generated separately from SRFs (abbreviated as $\tau_{CC,musc}$, which stands for craniocaudal torque generated by muscular effort) (Lammers and Gauntner, 2008), also generates shear force (applied around a moment arm). Shear force can be decreased by moving more slowly (which should decrease braking and propulsive craniocaudal forces), by placing the limb on the top of the branch (which decreases the shear component of the vertical force) or by decreasing $\tau_{CC,musc}$. It is possible that an animal might use all three methods (increasing normal force, increasing μ_s and decreasing shear force) to ensure adequate friction force with a particular substrate.

In this paper, I explore the first and third methods of friction force generation. Two questions are addressed. First, how does the texture of an arboreal trackway affect the means by which a small, generalized quadrupedal mammal produces friction force between the substrate and the manus or pes? To answer this question, I compared normal and shear forces between trackways and between the hand and foot. In this way, I could determine whether the opossums tended to reduce shear forces, increase normal force or some combination of these strategies. Second, how does contact location of the hand or foot affect friction force generation? A limb contact on the top of the branch should generate relatively large

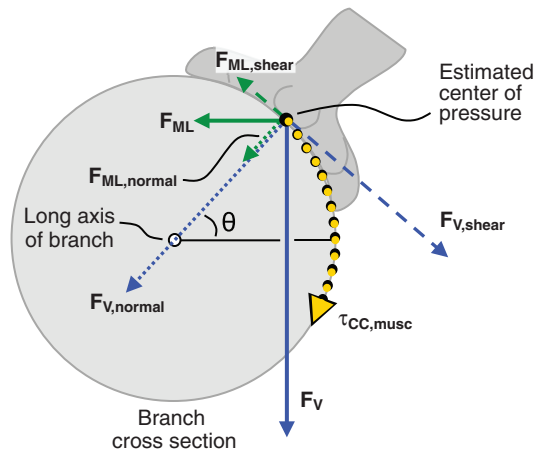


Fig. 1. Cross section of a cylindrical branch trackway with vertical force (F_V ; shown in blue) and mediolateral force (F_{ML} ; shown in green) represented by solid arrows. Normal components ($F_{V,normal}$ and $F_{ML,normal}$) are represented by arrows with dotted lines, and shear components ($F_{V,shear}$ and $F_{ML,shear}$) by arrows with dashed lines. Torque around the long axis of the branch trackway, generated by muscular exertion and not as a result of substrate reaction forces applied tangentially to the branch, is represented by the yellow dotted arrow ($\tau_{CC,musc}$) [see Lammers and Gauntner (Lammers and Gauntner, 2008) and the Materials and methods section for further explanation]. θ represents the angle formed by the normal force vector and a horizontal line passing through the long central axis of the branch trackway. Note that the arrows represent applied force, which is equal and opposite in direction from the substrate reaction force.

amounts of normal force because the large vertical force, supporting body weight, contributes more to normal force as the center of pressure moves to the top (dorsal surface) of the cylindrical arboreal trackway. Likewise, when a limb contacts the sides (or near the sides) of a branch trackway, the shear force (as measured by peak and median shear rate) should increase because the large vertical force is mostly tangential to the branch's surface. To answer this question, I examined the covariance between contact location and the required coefficient of friction (μ_{req} , which is the ratio of shear force to normal force), shear force and normal force.

MATERIALS AND METHODS

Five gray short-tailed opossums [*Monodelphis domestica* (Wagner, 1842)] were used for these experiments. All animal care and procedures conform to the Cleveland State University Institutional Animal Care and Usage Committee guidelines and NIH guidelines.

The opossums were encouraged to run across two cylindrical trackways constructed of wooden dowel rods, 2 cm in diameter and about 2 m long. The first (rough) trackway was covered with 60-grit sandpaper, which provided a large μ_s between the trackway and the hand or foot. The second (smooth) trackway was covered with thick paper (actually, sandpaper with the grit side facing inward). Thus, the trackways were identical except for the surface texture. It is unlikely that the animals could sink their claws into the substrates because the glue used to attach paper to the cylinders was very hard. The animals ran into an enclosure placed at the end of the trackway.

A 3.8-cm-long region of each trackway was instrumented to measure the vertical, craniocaudal (fore–aft or anteroposterior) and mediolateral components of the SRF (F_V , F_{CC} and F_{ML} , respectively). The force pole design is described more fully by Lammers and Gauntner (Lammers and Gauntner, 2008). Force data

(in the form of voltage changes) were collected at 2000 Hz with a National Instruments signal conditioning block (SC-2345 with SCC-SG04 and SCC-DO01 modules) and a LabView 7.1 virtual instrument (National Instruments, Austin, TX, USA). Each force trace consisted of a right forelimb contact followed by a right hindlimb contact; typically, there was little or no overlap between fore- and hindlimb. Voltages were then filtered using a moving average filter (average of points 1–33, then points 2–34, etc.) in Microsoft Excel (Redmont, WA, USA). This filter removed 60 Hz noise, but it had a negligible effect on the timing and magnitude of peaks and valleys in the voltage record. A second LabView virtual instrument was used to convert voltages into force [measured in Newtons (N)]. For the final analysis, the body weights of individual opossums were taken into account by converting Newtons into body weight units (BW units).

It was necessary to estimate the center of pressure in the hand and foot in order to calculate shear and normal forces. Thus, the opossums were filmed with three 60 Hz video cameras (JVC-DF550, JVC, Wayne, NJ, USA) focused on the force pole and the limb contacts. Videos were uploaded to a computer using U-Lead Videostudio 9.0 (Ulead Systems, Inc., Taipei, Taiwan), and the videos were synchronized by kinematic event (usually forelimb touchdown time) using the Trimmer module of APAS motion analysis system (Ariel Dynamics, San Diego, CA, USA). Using the Digitize module of APAS, the distal tip of all digits on the hand and foot were digitized, along with the lateral aspects of the wrist joint and fifth metatarsophalangeal joint of the right limbs. The coordinates from the three views were then combined into a single, three-dimensional set of coordinates using the Transform module of APAS. Preliminary data from a flat trackway indicate that the center of pressure is roughly in the middle of the hand and foot. Although the center of pressure moves anteriorly throughout the step, this was irrelevant for this study because I needed only the center of pressure around the circumference of the cylindrical trackways. The average of digits 1–5 was calculated for the hand and foot, and this value was used to calculate θ , the center of pressure measured in polar coordinates. The angle θ was then used to calculate the shear and normal force components (F_{shear} and F_{normal} , respectively) of each SRF component (Eqns 1 and 2 and Fig. 1). The torque around the long axis of the branch that did not result from shear components of F_V or F_{ML} ($\tau_{CC,musc}$) (Lammers and Gauntner, 2008) was included in the vector sum to calculate F_{shear} . [If the animal were moving on a branch that was free-floating in space instead of being attached to a planet, then the $\tau_{CC,musc}$ would produce a rotation around the long axis of the branch; no linear translation would take place. SRFs applied to the free-floating branch produce both translation *and* rotation. The shear, or tangential, components of SRFs produce only rotation of the free-floating branch, and normal components cause linear translation. Because the branch is anchored (somewhat indirectly) to the Earth, each SRF and torque results in linear translation and/or rotation of the opossum's center of mass].

$$F_{shear} = [F_{CC}^2 + (-F_{ML} \sin \theta + F_V \cos \theta + \tau_{CC,musc})^2]^{0.5}, \quad (1)$$

$$F_{normal} = F_{ML} \cos \theta + F_V \sin \theta. \quad (2)$$

Because $\tau_{CC,musc}$ has a distance factor in addition to force, F_{shear} is also a torque around the long axis of the branch. The distance from the manus/pes center of pressure to the long axis of the branch was 1 cm, and torque was measured in BW units cm^{-1} . Thus, the numbers are not affected by the distance component of torque, and I treated F_{shear} the same as F_{normal} . Slipping from the substrate is

Table 1. Summary of samples per substrate, limb pair and individual opossum

Individual	Rough trackway	Smooth trackway
1	4	4
4	4	6
7	5	2
8	2	1
9	1	2

most likely to occur during the peak F_{shear} ; therefore, peak F_{shear} (and F_{normal}) were calculated. The μ_{req} , which is the ratio of F_{shear} to F_{normal} , was calculated as a measure of how likely the animal was to slip from the substrate. A higher value of μ_{req} implies a higher F_{shear} and/or a lower F_{normal} . The animal is most likely to slip when μ_{req} is at its peak; therefore, I calculated the peak μ_{req} . Finally, to gain an overall measure of shear and normal forces and μ_{req} during each step, I calculated the median F_{shear} , F_{normal} and μ_{req} .

I measured speed with a high-speed video camera (120Hz, JVC DVL 9800). I digitized the tip of the nose each time a forelimb (right or left) touched down and then calculated the craniocaudal displacement that occurred during each step. Craniocaudal displacement was divided by time to acquire step speed, and step speeds were averaged to calculate the speed for the individual trial. If step speeds were always within 15% of trial speed, then I accepted the trial as steady speed. This process eliminated many trials, resulting in small sample sizes for some individuals (Table 1).

Systat version 11 (Richmond, CA, USA) was used for all analyses. Speed and limb phase were compared between substrates using a two-sample *t*-test. To determine if speed was a significant predictor of shear and normal forces and the μ_{req} , I calculated Pearson correlation coefficients for each limb on each substrate. Because speed was generally poorly correlated with peak and median forces and μ_{req} , speed was ignored in subsequent analyses. To determine the effects of substrate texture and limb pair (hand *versus* foot) on how friction force is generated, I used three analyses to compare the peak and median F_{shear} and F_{normal} , peak and median μ_{req} , and θ between limbs and between substrate textures. Duty factor was also compared between limbs and between substrates in the same way. First, for each measurement (e.g. peak shear force), the measurements were averaged within individual opossum. Thus, each individual was weighted equally, and a fixed-factor two-way analysis of variance (ANOVA) was used to determine significant differences between substrates and between limb pairs. (Because samples were very small for some individuals, a repeated-measures analysis could not be performed; Table 1.) In the second analysis,

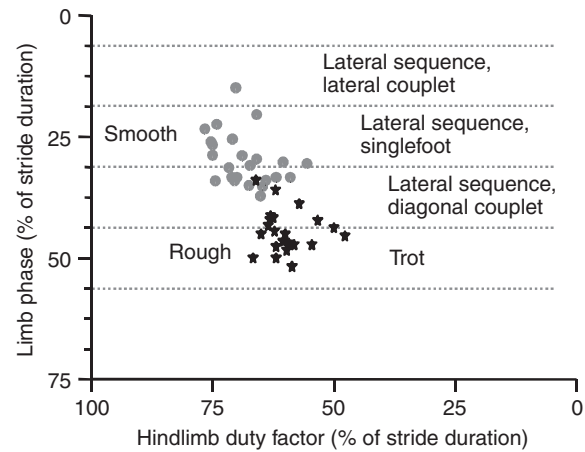


Fig. 2. Limb phase *versus* duty factor. Note that the axes are reversed, as per the convention of Hildebrand (Hildebrand, 1976). Only hindlimb trials are shown; the number of trials is somewhat greater than the sample sizes indicated in Tables 2 and 4 because trials with no force trace could be incorporated. Rough trackway is indicated by black stars; smooth trackway by filled gray circles.

I calculated the percentage contribution of fore- and hindlimbs to each force and μ_{req} measurement [$\text{forelimb}/(\text{forelimb}+\text{hindlimb}) \times 100\%$]. These percentages were compared between substrate textures using a two-sample *t*-test. In the third analysis, I used two-way analysis of covariance (ANCOVA), with the polar coordinate of the manus and pes contact locations in the transverse axis of the branch trackways (θ) as the covariate, to determine how forces and μ_{req} were affected by limb contact position among the substrate and limb groups. When slopes were homogeneous between groups, the least-squares means were compared. When slopes were not homogeneous, the slopes were calculated using least-squares regression.

RESULTS

Speed was significantly greater on the rough arboreal trackway ($43 \pm 3 \text{ cm s}^{-1}$; mean \pm s.e.m.) compared with the smooth trackway ($16 \pm 2 \text{ cm s}^{-1}$; $P < 0.0001$). Limb phase was also significantly greater on the rough trackway compared with the smooth trackway ($45 \pm 1\%$ *versus* $30 \pm 1\%$; $P < 0.0001$) (Fig. 2). Duty factor was higher in forelimbs than hindlimbs ($P = 0.0228$) and higher on the smooth trackway regardless of limb ($P = 0.0002$; interaction term, $P = 0.43$) (Table 2). Speed was usually poorly correlated with peak and median

Table 2. Results of two-way ANOVAs

	Least-squares means			Least-squares means		
	Forelimb (N=31)	Hindlimb (N=29)	P-value	Rough (N=32)	Smooth (N=28)	P-value
Peak F_{shear} (BW units)	1.13 \pm 0.10	1.40 \pm 0.10	0.3116	1.19 \pm 0.10	1.33 \pm 0.10	0.1891
Median F_{shear} (BW units)	0.81 \pm 0.06	0.70 \pm 0.06	0.2633	0.68 \pm 0.06	0.83 \pm 0.06	0.1350
Peak F_{normal} (BW units)	0.55 \pm 0.02	0.32 \pm 0.02	0.0001	0.47 \pm 0.02	0.40 \pm 0.02	0.4273
Median F_{normal} (BW units)	0.43 \pm 0.02	0.23 \pm 0.02	<0.0001	0.37 \pm 0.01	0.30 \pm 0.02	0.2769
Peak μ_{req}	4.8 \pm 0.7	9.1 \pm 0.8	0.0358	6.8 \pm 0.7	7.3 \pm 0.8	0.6651
Median μ_{req}	2.1 \pm 0.3	3.7 \pm 0.3	0.0999	2.6 \pm 0.3	3.2 \pm 0.3	0.3162
θ (deg.)	63 \pm 3	42 \pm 3	0.0393	55 \pm 3	50 \pm 3	0.5879
Duty factor (% of stride duration)	66 \pm 1	64 \pm 1	0.0002	61 \pm 1	69 \pm 1	0.4161

Means \pm s.e.m. are provided for each group. Interaction was never significant ($P \geq 0.081$). Abbreviations: F_{shear} , shear force; F_{normal} , normal force; μ_{req} , required coefficient of friction; θ , angle formed by normal force vector and a horizontal line passing through the long axis of the branch trackway (also see Fig. 1).

shear and normal forces, and peak and median μ_{req} . Pearson correlation coefficients were low; the maximum coefficient was 0.61, and minimum was -0.59 ; least-squares regression yielded only six significant regressions out of 24 possible relationships. Although relationships between speed and other variables were weak or non-existent, usually the coefficients were negative when comparing F_{shear} and μ_{req} with speed, and positive when comparing F_{normal} with speed.

Typical SRFs, μ_{req} , F_{shear} and F_{normal} are shown in Fig. 3. ANOVA revealed no significant differences in F_{shear} between limbs or between substrates ($P \geq 0.0910$) (Table 1; Fig. 4). Peak and median F_{normal} was significantly higher in forelimbs compared with hindlimbs ($P \leq 0.0001$). Peak and median F_{normal} were not significantly different between trackway surface textures ($P \geq 0.2769$). Peak μ_{req} was higher in hindlimbs, but there were no significant differences in μ_{req} between rough and smooth arboreal

trackways ($P \geq 0.3162$). Mean θ was significantly higher in forelimbs than hindlimbs ($P = 0.0393$), but there was no significant difference in θ between substrates ($P = 0.5879$). There were no significant differences between substrate textures with respect to the percentage contribution of the forelimb to the total fore- and hindlimb contribution of force or μ_{req} ($P \geq 0.1589$) (Table 3).

Two-way ANCOVA was used to determine if peak and median F_{shear} and F_{normal} , and peak and median μ_{req} , changed with limb contact position (θ) and if this variation differed between substrates and/or between fore- and hindlimbs (Table 4; Fig. 5). The first part of this test determined if the slopes (e.g. peak F_{shear} versus θ) were homogeneous among groups. In the case of peak and median F_{normal} , the slopes were significantly different between limb pairs (peak F_{normal} slopes were 0.0071 for forelimbs and 0.0034 for hindlimbs; median F_{normal} slopes were 0.0060 for forelimbs and 0.0025 for hindlimbs; $P \leq 0.0024$). The second part of the ANCOVA determined

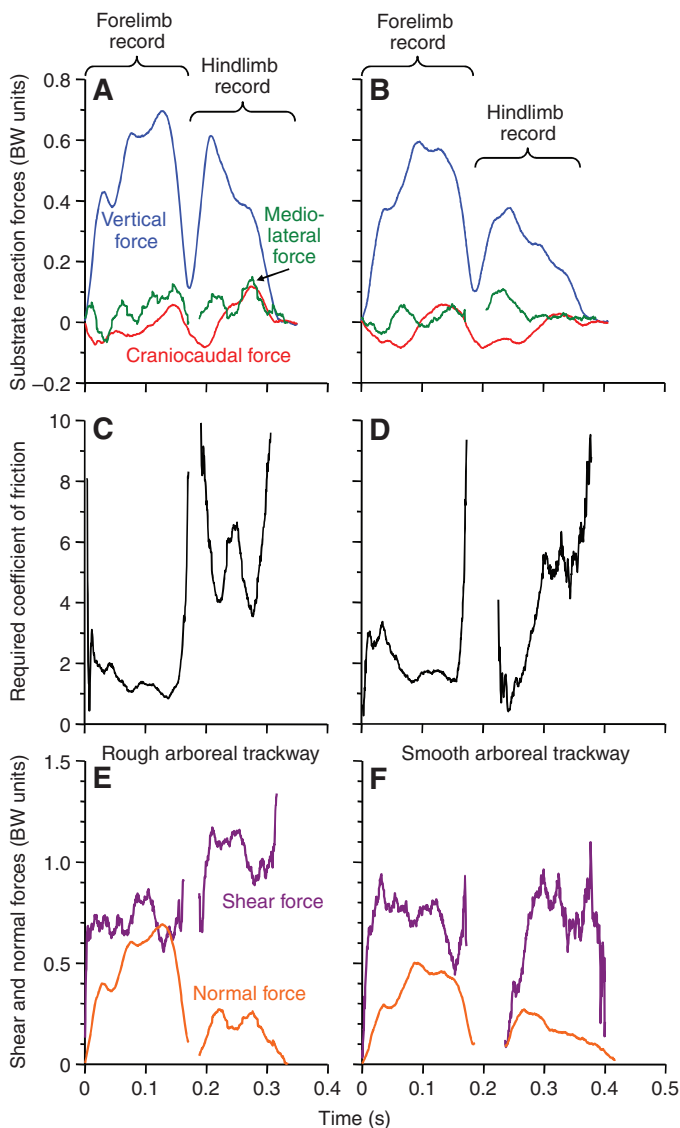


Fig. 3. Sample plots showing substrate reaction forces versus time (A,B), μ_{req} versus time (C,D) and F_{shear} and F_{normal} versus time (E,F). Within each trial, forelimb force traces were recorded first, followed by the ipsilateral hindlimb traces. These traces are shown on the left and right of each plot, respectively. A, C and E show traces from the rough trackway, and B, D and F illustrate results from the smooth trackway.

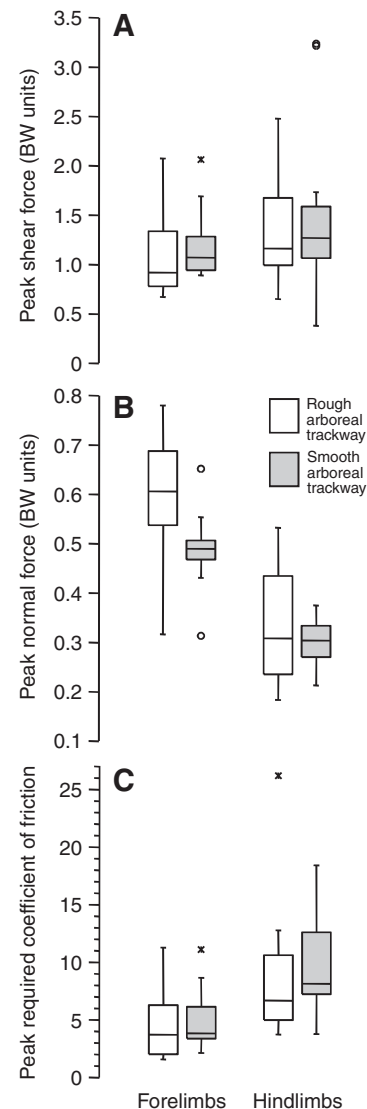


Fig. 4. Box and whisker plots indicating peak (A) F_{shear} , (B) peak F_{normal} and (C) peak μ_{req} between substrate textures (rough=60 grit, smooth=painted paper) and between limbs (forelimb, hindlimb). Each box represents 50% of the data, each whisker corresponds to 25% of the data, the asterisks indicate outliers, and circles designate extreme outliers.

Table 3. Percentage contribution of forelimb to total fore- and hindlimb contributions

	Rough trackway	Smooth trackway	P-value
Peak F_{shear} (BW units)	45.4±2.5	48.7±3.0	0.4125
Median F_{shear} (BW units)	51.9±4.0	59.5±3.6	0.1775
Peak F_{normal} (BW units)	65.0±1.7	62.2±1.2	0.1968
Median F_{normal} (BW units)	66.8±1.7	64.8±1.5	0.3970
Peak μ_{req}	36.7±4.7	36.4±4.5	0.9607
Median μ_{req}	35.0±3.7	43.2±4.3	0.1589

Abbreviations: F_{shear} , shear force; F_{normal} , normal force; μ_{req} , required coefficient of friction.

if slopes were significantly different from zero and if least-squares means were significantly different. Median F_{shear} was not correlated with θ . When θ was taken into account by ANCOVA, patterns were essentially identical to those revealed by the two ANOVA comparisons. The only difference was that peak and median F_{normal} were not significantly different between rough and smooth trackways ($P \geq 0.0651$).

DISCUSSION

During locomotion on any surface, the effective friction force must be equal to or greater than the sum of all shear forces. Effective friction force can be increased by escalating the normal force and by increasing the μ_s . Gray short-tailed opossums are considered terrestrial (Cartmill, 1972; Lee and Cockburn, 1985), and they are not particularly proficient at traveling on arboreal substrates [as measured by the significant decreases in speed, increases in duty factor, and changes in footfall sequence when switching from terrestrial to arboreal substrates (Lammers and Biknevicius, 2004)]. Nevertheless, it seems that they have features that enable them to negotiate arboreal substrates of various textures (Cartmill, 1974; Hamrick, 2001). Thus, Jenkins' supposition that most small mammals must be at least somewhat well-adapted to traveling on arboreal substrates (Jenkins, 1974) is supported.

Comparative data describing the effects of substrate texture on locomotion are few, and the kinetic adjustments that cows, dogs, geckos, humans and opossums use to remain stable on relatively slippery surfaces are probably rather different because of body size, bipedalism versus quadrupedalism, and having very different autopodial surfaces. A study by Phillips and Morris (Phillips and Morris, 2001) found that dairy cows walking on surfaces with low μ_s (0.33) walked slowly and with relatively upright limbs (higher stride frequency, but short step length). On medium μ_s floors ($\mu_s=0.42$ and 0.49), they walked fastest and with the greatest step length. On high μ_s floors (0.74), they slowed down again, presumably to limit the amount of wear on their hooves. The

relatively upright posture of the limbs should increase normal force and decrease shear force because body mass is being accelerated in a horizontal direction (or more force is redirected through the limbs in a horizontal direction). Thus, this posture (and decrease in speed) should also decrease shear force when the cows move on relatively slippery surfaces. By contrast, Kapatkin et al. found no differences in peak forces or impulses (vertical and craniocaudal components of the SRF) generated by dogs trotting on linoleum versus carpet-surfaced trackways (Kapatkin et al., 2007). Therefore, dogs make no change in shear force, at least when running on carpet versus linoleum. Finally, Tokay geckos may increase shear force (up to twice the adhesive force, depending on the direction of shear force relative to the setae) within arrays of thousands of setae to cause powerful friction and adhesion forces that can prevent a gecko from slipping from smooth, dry glass (Autumn et al., 2006). My comparison among these three groups is simplistic, mainly because the data collected and the taxa are so varied. Nevertheless, it demonstrates astonishing diversity among tetrapods in how they cope with traveling on relatively smooth surfaces.

When the μ_{req} that I calculated is compared with values of μ_{req} and μ_s from the literature, my values of μ_{req} appear surprisingly high. Cartmill reported a μ_s of ~0.3–0.4 for leather on clean wood (Cartmill, 1974). Redfern et al. reported μ_{req} data for humans walking down ramps; even at the steepest ramp angle (20 deg.), μ_{req} was less than 0.6 (Redfern et al., 2001). The μ_{req} represents $F_{\text{shear}}/F_{\text{normal}}$; F_{shear} was rather high in my experiments because the vertical force had a considerable shear component when the hands and feet contacted the sides of the branch. The values of θ might have also been underestimated (that is, they show center of pressure of the hand and foot as closer to the sides of the branch than they actually are); this underestimation would occur if the center of pressure was closer to the medial side of the hand and foot as opposed to the center. Furthermore, the $\tau_{\text{CC,musc}}$ contributed substantially to the F_{shear} . Finally, it seems likely that not all F_{normal} could be measured. When the opossums gripped the branch, the hand and foot most likely generate some internal squeezing force, some or all of which is normal to the cylindrical surface. My equipment could not measure this source of F_{normal} . It is possible that μ_{req} is higher in the hindlimbs because the opposable hallux of the foot allowed greater F_{normal} to be generated (but not measured). It seems that designing a force pole that can measure center of pressure in the transverse plane and the squeezing forces will be quite valuable.

Peak and median F_{normal} were higher in forelimbs compared with hindlimbs. This result is most likely caused by two important factors. First, vertical force is greater in the forelimbs than in the hindlimbs (measured by calculating peak vertical force and the vertical impulse) (Lammers and Biknevicius, 2004). This pattern is the result of the location of the body center of mass, which is closer to the

Table 4. Results of two-way ANCOVA, with θ as covariate

	Least-squares means			Least-squares means		
	Forelimb (N=31)	Hindlimb (N=29)	P-value	Rough (N=32)	Smooth (N=28)	P-value
Peak F_{shear} (BW units)	1.04±0.10	1.49±0.11	0.0072	1.17±0.10	1.36±0.10	0.1839
Median F_{shear} (BW units)	Regressions not significant					
Peak F_{normal} (BW units)	Slopes significantly different					
Median F_{normal} (BW units)	(i.e. slopes were not homogeneous)					
Peak μ_{req}	5.5±0.8	8.3±0.8	0.0256	6.7±0.7	7.1±0.8	0.7155
Median μ_{req}	2.5±0.3	3.2±0.3	0.2232	2.7±0.3	3.0±0.3	0.4191

Interactions between limb and substrate texture factors were never significant ($P \geq 0.389$). Regressions were significantly different from zero ($P \leq 0.0357$) unless otherwise indicated.

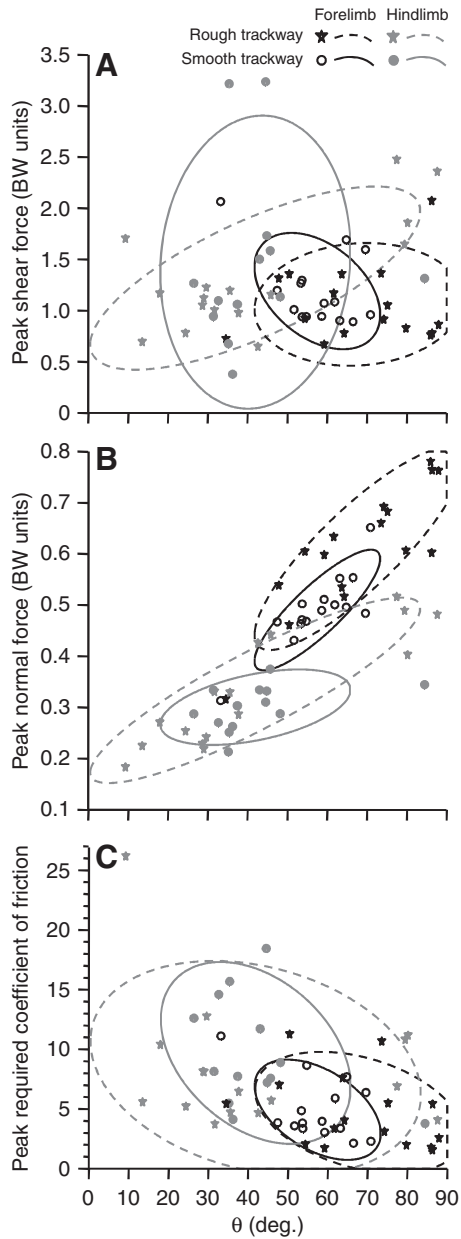


Fig. 5. Plots of (A) peak normal and (B) peak shear forces versus θ (contact position of the manus or pes around the pole). (C) Peak μ_{req} versus θ . To emphasize the overall direction of the relationships, 68% confidence ellipses were drawn for each group (black=forelimbs, gray=hindlimbs; dashed lines and stars=rough trackway, solid lines and circles=smooth trackway).

forelimbs than to the hindlimbs (Lammers et al., 2006). Friction force is the result of $F_{normal} \times \mu_s$; thus, the opossum's weight is acting to increase the friction force generated by both limbs, but more so in the forelimbs. The second factor is where the fore- and hindlimbs contact the cylindrical trackway around its circumference. Regardless of substrate texture, forelimbs typically contacted the branch trackways at about 63 deg., whereas hindlimbs contacted at about 42 deg. Because forelimbs contacted the branch at a point closer to the top of the branch, the very large vertical forces should contribute more to F_{normal} in the forelimbs than in the hindlimbs.

Peak and median F_{shear} were not significantly different between limb pairs. At least three important factors contributed to this pattern

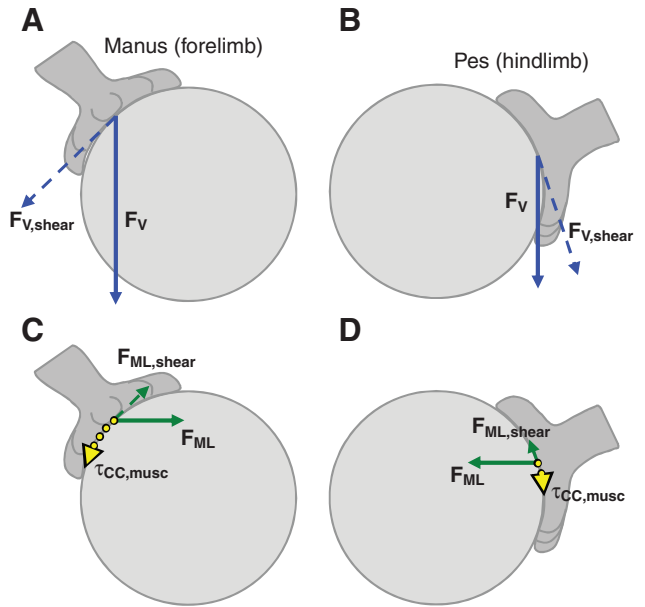


Fig. 6. Schematic of contributions to shear force (except for craniocaudal force) in forelimbs and hindlimbs. (A,B) Vertical force (F_V) and the shear component of vertical force ($F_{V,shear}$) for the forelimbs and hindlimbs, respectively. (C,D) Mediolateral force (F_{ML}), the shear component of mediolateral force ($F_{ML,shear}$), and the torque generated by rotational forces around the long axis of the branch trackway ($\tau_{CC,musc}$) for forelimbs and hindlimbs, respectively. Symbols and colors are as shown in Fig. 1.

(Fig. 6). The first major factor is the interaction between vertical force and the contact location. Because the hindlimb contacts the branch more laterally, a greater proportion of the vertical force generated by the animal's body weight is tangential to the branch surface (that is, shear force). But the forelimbs support more body weight (Lammers et al., 2006), and so vertical force is greater. Thus, the hindlimbs have a smaller vertical force contributing proportionally more to shear force, whereas the forelimbs have a larger vertical force contributing proportionally less to shear. The second major factor contributing to the lack of differences between fore- and hindlimbs with respect to shear force is the interaction between the shear component of mediolateral force and the $\tau_{CC,musc}$. Lammers and Biknevicus found that fore- and hindlimbs exerted net mediolateral impulse in a medial direction (Lammers and Biknevicus, 2004). Thus, contralateral limbs squeeze the branch between them. At the same time, the $\tau_{CC,musc}$ was found to be in the same direction in ipsilateral fore- and hindlimbs, but it was much smaller in magnitude in hindlimbs (Lammers and Gauntner, 2008). Therefore, in forelimbs, the shear component of mediolateral force contributes *more* to shear force than in the hindlimbs because of limb contact location (Fig. 6). The $\tau_{CC,musc}$ contributes only to shear force, and it is greater in the forelimbs. It appears that for the most part, the $\tau_{CC,musc}$ and shear component of mediolateral force within each limb pair cancel each other out. Third, the craniocaudal force, all of which contributes to shear force, apparently makes a minor contribution to the *total* shear force. Craniocaudal shear force differs from the other components of shear force because it presumably does not contribute to making the animal slip from the sides of the branch. Lammers and Biknevicus found that on a similar 2 cm arboreal trackway, *M. domestica* exerted significantly greater braking and propulsive impulses than the hindlimbs (Lammers and Biknevicus, 2004); recently collected (A.R.L., unpublished) data

confirm that pattern. It seems likely that craniocaudal force is not large enough to influence shear force so much that significant differences between fore- and hindlimbs are observed. Finally, it is also possible that there is some interaction between grip location and claw use or in the positioning of the digits. The opossums have claws on all digits except for the hallux, and the foot may more effectively grip the substrate and reduce shear force with claws or the somewhat opposable hallux.

The opossums did not change grip location on the 2 cm-diameter arboreal trackways to cope with the relatively smooth surface. Not only did θ not differ significantly between substrates, but F_{shear} was also not correlated with θ , or was very weakly correlated. [It is worth pointing out that $\tau_{\text{CC,musc}}$ contributes considerably to F_{shear} , and $\tau_{\text{CC,musc}}$ apparently has no relationship with θ (Lammers and Gauntner, 2008).] Correlations between peak and median F_{normal} and θ within each group (e.g. forelimb on the rough trackway) were usually weak or non-existent ($r^2 \leq 0.32$). Thus, it appears at first that grip location has little influence on how the opossums generate normal and shear forces. However, it is also possible that the within-group variation in θ is not great enough to produce strong correlations with normal and shear forces. The opossums may be biomechanically constrained to grip the 2 cm-diameter branch trackway such that the forelimb grips closer to the top of the branch and the hindlimb grips approximately midway between the top and the sides of the branch. If, on the smooth trackway, they place their hands or feet closer to the top of the branch, then normal force will greatly increase because a much greater proportion of the animal's weight is applied normal to the branch surface. But gripping the top of the branch provides very little bracing against mediolateral undulation or (in a natural environment) wind and branch movement because the opossum's hand has no opposable digits, and it seems likely that neither hand nor foot has a large enough span on the 2 cm branch to grip strongly. If the opossums grip the sides of the branch, then with sufficient mediolateral forces they could create a very stable grip with opposable limbs. But gripping the sides of the branch will increase the shear force because most of the vertical force will be tangential to the surface of the branch. Thus, it appears that the size of the branch and the sizes and morphologies of the hand and foot limit the ways that these opossums can adjust to a more slippery substrate.

The gray short-tailed opossums, with their morphology being relatively unspecialized for arboreal locomotion, seem constrained to grip the 2 cm branch in one particular way. When they attempt to move on a trackway with the same diameter but a smoother surface texture, the only way they can adapt is to move more slowly and increase the total substrate–limb contact time with as many limbs as possible. Many arboreal specialists have morphological differences that almost certainly allow greater flexibility in how they can move on rough or smooth branches. For example, many arboreal marsupials have significantly longer digits than closely related terrestrial marsupials (Lemelin, 1999). These longer digits probably allow the animals to grip branches more strongly than they can if their digits were shorter. Some arboreal rodents have pads with glands that secrete fluid so as to increase the friction between autopodia and substrate (Haffner, 1998). I predict that animals that are morphologically specialized to move in trees will have greater flexibility in terms of where and how they grip branches. An animal with long, opposable digits (or fluid-secreting glands, claws or microscopic setae that interact with the substrate at a molecular level) (Cartmill, 1985; Haffner, 1998; Autumn et al., 2006) should be able to grip the top of a branch, which means that much more of its body weight is applied normal to the branch. Thus, even when moving about on a relatively

smooth or slippery branch, such a specialized animal will be able to avoid slowing its speed and adjusting its footfall patterns (as measured by duty factor and limb phase) as much as *M. domestica*.

LIST OF ABBREVIATIONS

F_{CC}	craniocaudal (or anteroposterior) force
F_{ML}	mediolateral force
$F_{\text{ML,normal}}$	normal component of mediolateral force
$F_{\text{ML,shear}}$	shear component of mediolateral force
F_{normal}	normal force (perpendicular to the substrate at the center of pressure)
F_{shear}	shear force (tangential to the substrate at the center of pressure)
F_{V}	vertical force
$F_{\text{V,normal}}$	normal component of vertical force
$F_{\text{V,shear}}$	shear component of vertical force
SRF	substrate reaction force
θ	the angle between a horizontal line intersecting the long axis of the branch and a line passing through the center of pressure of the limb and the long axis of the branch
μ_{req}	required coefficient of friction (ratio of shear forces to normal forces)
μ_{s}	coefficient of static friction
$\tau_{\text{CC,musc}}$	torque around the long axis of the branch, not resulting from the shear component of substrate reaction forces

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