

Locomotor kinetics and kinematics on inclines and declines in the gray short-tailed opossum *Monodelphis domestica*

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Summary

Small terrestrial animals continually encounter sloped substrates when moving about their habitat; therefore, it is important to understand the mechanics and kinematics of locomotion on non-horizontal substrates as well as on level terrain. To this end, we trained gray short-tailed opossums (*Monodelphis domestica*) to move along level, 30° inclined, and 30° declined trackways instrumented with a force platform. Vertical, craniocaudal and mediolateral impulses, peak vertical forces, and required coefficient of friction (μ_{req}) of individual limbs were calculated. Two high speed video cameras were used to simultaneously capture whole limb craniocaudal and mediolateral angles at limb touchdown, midstance and lift-off. Patterns on the level terrain were typical for non-primate quadrupeds: the forelimbs supported the majority of the body weight, forelimbs were net braking and hindlimbs net propulsive, and both limb pairs exerted small laterally directed impulses. *M. domestica* moved more slowly on sloped substrates in comparison to level locomotion, and

exhibited a greater μ_{req} . On inclines, both limb pairs were more protracted at touchdown and more retracted at lift-off, fore- and hindlimbs had equal roles in body weight support, forelimbs exerted greater propulsive impulse than hindlimbs, and μ_{req} was greater in the forelimbs than in hindlimbs. On declines, only the forelimbs were more protracted at touchdown; forelimbs supported the great majority of body weight while they generated nearly all of the braking impulse and, despite the disparity in fore- vs hindlimb function on the decline, μ_{req} was not significantly different between limbs. These differences on the inclined and declined surfaces most likely result from (1) the location of the opossums' center of mass, which is closer to the forelimbs than to the hindlimbs, and (2) the greater functional range of the forelimbs versus the hindlimbs.

Key words: locomotion, quadruped, substrate reaction force, limb excursion, required coefficient of friction.

Introduction

The natural habitats of most small mammals are replete with heterogeneous substrates, including sloped terrain, rocks, and fallen and growing vegetation, so that small mammals must frequently move over or around sloped substrates. In order to fully understand how small mammals utilize their habitats and the mechanics of movement in these habitats, it is necessary to examine locomotor biomechanics on a variety of substrates. Yet, until recently, data on the biomechanics of animal locomotion were usually gathered from the rarest of natural substrates: flat, horizontal, straight trackways. Such data are valuable as they provide a baseline condition to which locomotion along a graded or irregular substrate may be compared. Although differences among clades of mammals have been reported (e.g. Jayes and Alexander, 1978; Demes et al., 1994; Schmitt and Lemelin, 2002), the substrate reaction forces (SRFs, a measure of overall limb function) of most quadrupedal mammals moving linearly along a flat and level

trackway using a symmetrical gait follow a common pattern. The vertical component of the SRF is by far the largest in magnitude because of its role in body weight support. Forelimb vertical SRFs tend to exceed those of hindlimbs because the center of mass of most mammals is located closer to the forelimbs than to the hindlimbs. The craniocaudal (longitudinal or fore-aft) SRF is characterized by an initial braking component followed by a propulsive component; the braking component is typically larger than the propulsive component in the forelimbs whereas the hindlimbs are usually net propulsive. Mediolateral (transverse) forces tend to be relatively small and, at least for cursorial mammals, they show no strong pattern of direction.

Support of body weight, forward propulsion and stability are maintained during terrestrial locomotion (both level and graded substrates) in large part by adjusting limb function and locomotor posture, including the degree of limb excursion. The inescapable effects of gravity necessitate shifts in limb function

(as reflected by SRFs) when moving on graded substrates. The few studies that have reported SRFs on graded surfaces focused either on bipeds (Dial, 2003; Dick and Cavanagh, 1987; Gottschall and Kram, 2005) or highly derived tetrapods such as horses (Dutto et al., 2004). Based on these studies and on general principles of mechanics, we formulate several predictions for how a generalized mammal might adjust limb function when moving along a grade.

(1) Uphill locomotion is expected to unload the forelimb somewhat while downhill locomotion should increase the forelimb's load. If this prediction is borne out, then on the incline the vertical impulse and peak vertical force will decrease in the forelimb (relative to the vertical impulse and peak vertical force generated by the forelimb on the level trackway). Vertical impulse and peak force should increase in the hindlimb, relative to the level trackway trials. On the decline, this pattern should be reversed.

(2) Both limb pairs must generate additional propulsive effort to raise the center of mass uphill, whereas a greater braking effort is required when moving downhill to counter the acceleration due to gravity. It is obvious that more propulsive effort will be required on the incline (and more braking effort on the decline). But what is not known is the degree to which braking impulse will be reduced in the incline, and propulsive force on the decline. Kinetic studies of horses walking up 10% inclines show that braking forces are reduced, but not eliminated, when moving up-slope. Propulsive forces are increased (Dutto et al., 2004). In this study, the animals moved on 30° slopes. Relative to Dutto et al. we expect a greater reduction in braking forces on the incline (Dutto et al., 2004), and a similar reduction in propulsive forces on the decline.

(3) The required coefficient of friction [μ_{req} , the ratio of shear force to normal force (Redfern et al., 2001)] will be greater on sloped trackways than on the level trackway because shear forces should increase as a result of the gravitational force, while the normal force component of the animal's weight will decrease. In order to avoid slipping on a substrate, an animal must generate sufficient friction force by either increasing the normal force (perpendicular to the substrate) and/or decreasing the shear force (parallel to the substrate). Either or both of these adjustments effectively reduce the μ_{req} and thereby decrease the likelihood of slipping. Although we expect that the vertical force will vary between limb pairs on the inclines and declines, we do not expect that the body weight support roles of the forelimbs and hindlimbs to affect the μ_{req} . The reason for this is that normal and shear force components of the vertical force will naturally increase (or decrease) in proportion to the vertical force. However, if the braking and propulsive roles of a limb pair change substantially, then the corresponding increase or decrease in shear forces will cause an increase or decrease in μ_{req} .

(4) The mediolateral SRFs will not differ significantly among slopes because there is no change in the gravitational force in the mediolateral direction in these experiments. Furthermore, it seems unlikely that a 30° slope will sufficiently

destabilize the animal in a mediolateral axis to cause the mediolateral forces to differ among substrates.

(5) The limbs will adopt a more crouched posture on the sloped trackways, bringing the shoulder and hip joints closer to the substrate. This kinematic adjustment will make the animal more stable because the line of gravity passing through the animal's center of mass (**G**) will remain closer to the center of the base of support generated by the supporting limbs. Furthermore, animals climbing slopes and/or arboreal substrates might also be predicted to shorten their effective limb lengths in order to decrease the likelihood that the body will topple backward (in the case of uphill locomotion) or forward (in the case of downhill locomotion). This prediction is borne out in cats moving on inclined trackways (Carlson-Kuhta et al., 1998).

(6) On the inclined substrates, both limb pairs will adopt a more retracted limb excursion throughout the stance phase, and especially at lift-off. On the decline, the limbs will be more protracted throughout the stride, and especially so at touchdown. This kinematic adjustment, like prediction (5), should keep **G** closer to the center of the base of support. This prediction is consistent with kinematic data gathered from primates moving on inclined and declined branches (Vilensky et al., 1994; Stevens and Larson, 1999; Stevens, 2003), cats (Carlson-Kuhta et al., 1998; Smith et al., 1998), lizards *Dipsosaurus dorsalis* (Jayne and Irschick, 1999) and running humans (Iversen and McMahon, 1992).

To test these predictions of how SRFs and general limb kinematics change on sloped *versus* horizontal trackways in a generalized mammal, we ran gray short-tailed opossums *Monodelphis domestica* Wagner 1842 on level, 30° inclined, and 30° declined trackways. *M. domestica* is a small, terrestrial marsupial that retains many primitive morphological traits (Lee and Cockburn, 1985; Novacek, 1992), and so it is likely that these findings may yield insight into how primitive mammals might have been constrained to move on inclines and declines. When these data are compared to records of mammals which have evolved novel features, hypotheses about the evolution of locomotor mechanics among mammals can be generated.

Materials and methods

Animals

All animal care and experimental procedures followed Ohio University Institutional Animal Care and Use Committee approved guidelines. Locomotor biodynamics were assessed on a level trackway in six gray short-tailed opossums *Monodelphis domestica* Wagner 1842, 89–150 g) and on angled trackways with a separate set of five opossums (80–103 g). Prior to data collection, the opossums were trained to run on the trackways so that they would be accustomed to the apparatus and run steadily in a straight line. The carcasses of three additional *M. domestica* of comparable size (77–93 g) were used to calculate the craniocaudal location of the center of mass (COM) using the reaction board method (Özkaya and Nordin, 1999). Briefly, the animal was positioned on a platform with a knife-edge at

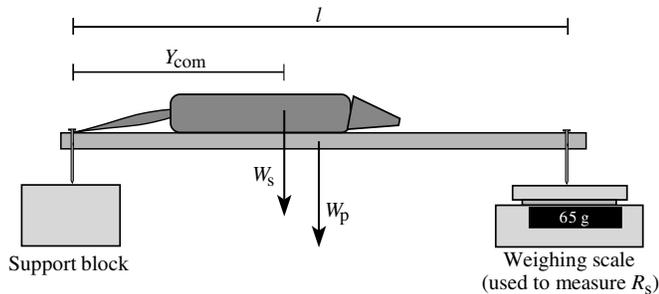


Fig. 1. Measurement of the craniocaudal center of mass. The dead animal was placed on its side, with the limbs arranged in a manner that resembled a standing position. The tail was positioned at about a 45° angle in the sagittal plane relative to the long axis of the body; this is approximately the same tail posture that is adopted during normal movement. l , length of platform between knife points; Y_{com} , distance between knife point and center of mass; W_s , weight of opossum; W_p , weight of knife point platform. See text for formula.

each end (Fig. 1); we constructed this platform by driving three nails through a piece of foamcore 40 cm long. One edge of the platform was placed on a digital scale, and the other end was placed upon a block so that the platform was level. The distance between the knife edges (l) was measured, and the weight of the platform (W_p) was obtained. The specimen was placed upon the platform so that its caudal end reached the knife edge of the platform opposite of the scale, and the digital scale measured the amount of weight supported by the knife edge over the scale (R_s). Using the actual weight of the specimen (W_s), the following equation was used to calculate the craniocaudal location of the center of mass:

$$Y_{\text{com}} = l / W_s(R_s - W_p/2),$$

where Y_{com} is the distance between the knife edge over the support block and the animal's center of mass.

Force data acquisition

Two terrestrial trackways were constructed, a level trackway (160 cm long, 11 cm wide) and a 30° sloped trackway (180 cm long, 11 cm wide). The sloped trackway was stabilized through the use of extensive buttressing and base weighting so that mechanical vibrations from the base were not introduced to the force transducers. A force platform (48 cm long, 11 cm wide for the level trackway, and 36 cm long, 11 cm wide for the sloped trackway) was installed flush and parallel to the surface of each trackway (Fig. 2A). The force platform was equivalent to the strain gage-based, spring-blade design described elsewhere (Parchman et al., 2003). Analog outputs from the force platforms captured at 1200 Hz (level trials) and 500 Hz (sloped trials) for 3–6 s were amplified (SCXI 1000 and 1121, National Instruments, Austin, TX, USA), converted from analog to digital (NB-M10-16L, National Instruments), and recorded using LabVIEW (National Instruments) virtual instruments. The raw voltages were then converted into three-dimensional substrate reaction forces (SRFs) oriented relative

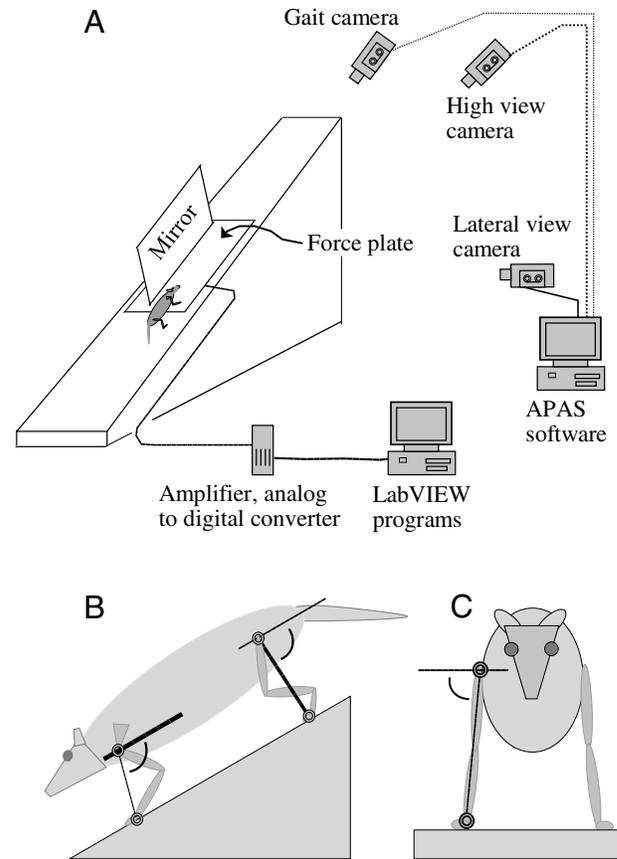


Fig. 2. (A) Data collection setup, illustrating how forelimb force data were collected (first contact with force platform). In this diagram, the opossum is moving up the incline, and a single forelimb has stepped onto the force plate. (B,C) Digitized landmarks and the calculation of overall limb excursion angles. Protraction angle was measured at touchdown, retraction angle was measured at lift-off, and mediolateral angles were measured at both events.

to the surface of the platform (and the opossum's body): dorsoventral (F_{DV}), craniocaudal (F_{CC}) and mediolateral (F_{ML}). These forces were filtered using a Butterworth notch filter (between 51–61 Hz for F_{DV} and F_{CC} ; between 93–103 Hz for F_{ML}) prior to analysis. Individual limb SRFs were obtained as the first footfall (forelimb) and last footfall (hindlimb) on the platform surface. Trials used to obtain fore- and hindlimb data did not differ significantly in speed.

Only trials in which the opossum moved at a near steady speed were evaluated further. This was determined either by calculating forward speed at four intervals from the overhead videos or (for the level trackway only) by integrating the whole body craniocaudal acceleration over the entire force plate to estimate forward speed (Parchman et al., 2003). If the speed over any part of the trial was 15% above or below step speed, the trial was discarded. In spite of great effort to obtain equivalent forward speeds on the level and sloped runways, the opossums moved significantly faster on the level trackway ($1.51 \pm 0.05 \text{ m s}^{-1}$) than on the sloped trackways (incline, $0.87 \pm 0.03 \text{ m s}^{-1}$; decline, $0.84 \pm 0.03 \text{ m s}^{-1}$; $P < 0.0001$; no

significant difference in speed between incline and decline trials). Previous studies in other species also found that preferred speed decreases on non-level substrates (Wickler et al., 2000).

The role of limbs in body weight support was assessed using vertical force (F_V , computed as the vector sum of the vertical components of F_{DV} and F_{CC}) and vertical impulse (calculated by integrating F_V through time). The function of limbs in controlling forward motion was determined by the magnitude of braking (negative) and propulsive (positive) components of the craniocaudal impulse. The net mediolateral impulse (sum of medial and lateral impulses) reflected overall limb function in maintaining lateral stability. In addition, time to peak F_V and time to $F_{CC}=0$ (when the F_{CC} profile switches from braking to propulsive) were measured relative to support duration. The required coefficient of friction (μ_{req}) was calculated as the ratio of shear force (vector sum of F_{CC} and F_{ML}) to normal force (F_{DV}) (Redfern et al., 2001). Although μ_{req} was determined over the entire stance phase, only median values were evaluated; the median was used rather than the mean because the median would be influenced less by the relatively large μ_{req} at touchdown and lift-off.

High-speed videography

Prior to each experiment, the opossums' limbs were shaved and white 1.3 mm \times 1.7 mm beads were applied onto darkened skin overlying major limb joints (wrist, glenohumeral joint, lateral metatarsophalangeal joint, and greater trochanter of the hip). Simultaneous high-speed video recordings (GR-DVL 9800, JVC, Yokohama, Japan), recording at 120 Hz with a shutter speed of 1/250 s, were obtained for all trials (Fig. 2A). Two cameras provided detailed images of either fore- or hindlimb strikes on the force platform; one additional camera supplied a broad view for evaluating forward speed. A single angled mirror was placed behind the trackway so that contralateral footfall timing could be measured. Three strobe lights (Monarch-Nova, Amherst, NH, USA) provided lighting (233.3 Hz).

Images from the cameras were uploaded using VideoStudio 4.0 (U-lead, Taipei, Taiwan) and three-dimensional coordinates for all landmarks were determined using APAS (Ariel Dynamics, San Diego, CA, USA). The timing of forelimb and hindlimb touchdown and lift-off was determined from the videos. The footfall timing data were used to calculate stride duration (time between two footfalls of the same hindlimb), duty factor (percentage of stride duration where the reference hindlimb was in contact with the substrate), and limb phase [percentage of the stride when the ipsilateral forelimb contacted the substrate after the reference hindlimb (Hildebrand, 1976)]. The three-dimensional coordinates were used to calculate angular data for the fore- and hindlimb (Fig. 2B,C). The craniocaudal angle of the whole limb was measured for each limb pair at touchdown, midstance and lift-off. For the forelimb, these angles were calculated from the coordinates of the shoulder, tip of the third manual digit, and a point projected directly posterior to the shoulder joint (parallel to the substrate

surface). In the hindlimb, these craniocaudal angles were calculated from the hip, metatarsophalangeal joint, and a point projected directly posterior to the hip joint (parallel to the substrate surface). Mediolateral angles at touchdown, midstance and lift-off were calculated for fore- and hindlimbs; the purpose of this measurement is to help explain differences in mediolateral impulses (if any) among substrates and between limb pairs. Mediolateral angles were calculated by projecting a point lateral to the shoulder or hip markers (parallel to the trackway surface), respectively. Shoulder and hip heights perpendicular to the trackway surface were measured at touchdown, midstance and lift-off. These were calculated by measuring the perpendicular distance between the shoulder and substrate and between the hip and substrate, respectively.

Statistics

Force data were adjusted for body weight to account for difference in body size across the sample. Data from all individuals were pooled, and the Systat 9.0 (Point Richmond, CA, USA) statistical package was used for all analyses. We used least-squares linear regression to determine if a relationship existed between speed and each kinematic and kinetic variable (shoulder and hip heights at touchdown, midstance and lift-off; craniocaudal and mediolateral angles at touchdown, midstance and lift-off; peak vertical force; vertical, braking, and propulsive impulses; and net mediolateral impulse). When significant correlations existed, we used two-way analysis of covariance (ANCOVA) to make comparisons among slopes (level, incline and decline) and between limb pairs (forelimb, hindlimb). There was no speed effect among most variables, however, and in these situations two-way fixed-factor ANOVA was used. Because different animals were used for level and non-level trials, we did not use repeated-measures ANOVA. When significant interaction between slope and limb groups was detected, we tested each factor (slope, limb) separately. The sequential Bonferroni technique (Rice, 1989) was used to determine significance level ($\alpha=0.05$). When significant differences among substrates were found, a Bonferroni *post-hoc* test was used to determine which substrates were significantly different from each other.

Results

The center of mass of *M. domestica* was determined to lie $37.0 \pm 1.8\%$ ($N=3$, mean \pm s.e.m.) of the distance between the glenohumeral and hip joints (i.e. closer to the glenohumeral joint).

Kinematics

The animals moved significantly faster on the level trackway (1.511 ± 0.051 m s⁻¹) than on the sloped trackways (incline, 0.874 ± 0.027 m s⁻¹; decline, 0.835 ± 0.029 m s⁻¹; $P < 0.0001$). There was no significant difference in speed between incline and decline trials. Furthermore, trials used to obtain fore- and hindlimb data on each trackway type did not differ significantly

in speed. Incline trials had the highest duty factor ($39.9 \pm 1.3\%$), followed by declines ($34.4 \pm 1.0\%$) and then level ($30.2 \pm 0.9\%$; $P \leq 0.012$; Fig. 2); duty factor never exceeded 50% on any slope. Gait, determined by limb phase, was also affected by substrate slope ($P \leq 0.001$): limb phase was significantly lower on decline trials ($38.7 \pm 1.2\%$) than on the incline ($46.8 \pm 1.6\%$) or level trials ($51.1 \pm 1.1\%$; $P \leq 0.001$; no significant difference between incline and level). Therefore, the opossums kinematically trotted during the level and incline trials whereas the decline trials are primarily lateral-sequence diagonal-couplets, a four-beat, trot-like gait (Fig. 3).

Shoulder and hip height data are summarized in Table 1. Hip height was always greater than shoulder height ($P < 0.0001$) on all substrates. During stance phase, shoulder height was lower at touchdown and midstance on the incline in comparison to the level and decline ($P = 0.0196$; no significant difference in shoulder height between decline and level substrates). By comparison, hip height was always significantly lower on the decline substrates than on incline or level substrates ($P = 0.0195$; no significant differences in hip height between incline and level substrates). Shoulder and hip heights (relative to the trackway surface) changed cyclically on all trackway orientations, so that shoulders and hips reached their lowest position at midstance.

Angular data are summarized in Table 1 and significant differences between slope groups are illustrated in Fig. 4. Fore- and hindlimbs were significantly more protracted at touchdown on all sloped trials than they were on the horizontal trackway ($P = 0.0001$); there was no significant difference in degree of protraction at touchdown between incline and decline trials. At

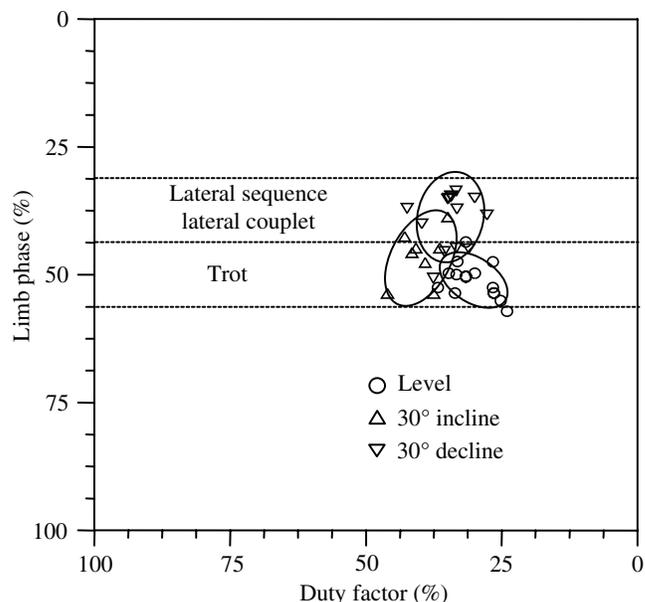


Fig. 3. Gait plot of limb phase against hindlimb duty factor. Trot and lateral-sequence trot-like (i.e. diagonal couplet) gait boundaries are denoted by broken lines. Following the convention of Hildebrand (Hildebrand, 1976), the axes are reversed. 67% confidence ellipses are drawn around each slope group (decline, incline and level).

midstance, both fore- and hindlimbs were retracted, regardless of substrate, but the amount of retraction decreased from level → incline → decline ($P \leq 0.0041$). Both limb pairs were

Table 1. Limb kinematic parameters during stance phase

Kinematic parameter	Limb	Level	Incline	Decline	Substrate differences
Height (cm)					
Shoulder, TD	FL	2.59±0.09*	2.28±0.08*	2.40±0.09*	L>U, L=D, U=D
Hip, TD	HL	3.76±0.10	3.81±0.13	3.21±0.10	L=U, L>D, U>D
Shoulder, MS	FL	2.17±0.09*	2.02±0.07*	2.14±0.08*	L=U, L=D, U=D
Hip, MS	HL	3.44±0.09	3.30±0.11	2.82±0.09	L=U, L>D, U>D
Shoulder, LO	FL	2.49±0.09*	2.18±0.08*	2.38±0.08*	L>U, L=D, U=D
Hip, LO	HL	3.62±0.09	3.66±0.12	3.12±0.10	L=U, L>D, U>D
Angle (degrees)					
Craniocaudal, TD	FL	101.4±2.0*	107.5±1.7	114.8±1.8	L<U, L<D, U=D
Craniocaudal, TD	HL	105.9±1.7	111.7±2.7	113.7±2.2	L<U, L<D, U=D
Craniocaudal, MS	FL	61.9±2.1	68.8±1.2	73.0±2.0	L<U, L<D, U<D
Craniocaudal, MS	HL	60.2±1.8	67.6±3.1	77.1±2.2	L<U, L<D, U<D
Craniocaudal, LO	FL	27.0±1.2*	29.6±0.8*	33.5±1.8*	L=U, L<D, U<D
Craniocaudal, LO	HL	41.0±1.3	40.7±1.7	50.2±1.4	L=U, L<D, U<D
Mediolateral, TD	FL	84.3±1.8*	78.9±1.7*	81.9±1.2*	L=U, L=D, U=D
Mediolateral, TD	HL	75.6±2.0	74.9±2.7	68.9±1.9	L=U, L=D, U=D
Mediolateral, MS	FL	83.3±1.8	83.0±1.2	82.0±1.0	L=U, L=D, U=D
Mediolateral, MS	HL	83.5±1.5	82.5±1.9	77.5±1.6	L=U, L=D, U=D
Mediolateral, LO	FL	84.5±1.7	85.4±0.9	85.6±1.0	L=U, L=D, U=D
Mediolateral, LO	HL	81.1±2.0	84.4±0.8	83.6±1.5	L=U, L=D, U=D

Values are means ± s.e.m. (N=97).

TD, touchdown; MS, midstance; LO, lift-off; FL, forelimb; HL, hindlimb; L, level; U, incline; D, decline.

*Significant difference between limb pairs on that substrate. >, significantly greater than; =, not significantly different; <, significantly less than, using the sequential Bonferroni correction (Rice, 1989).

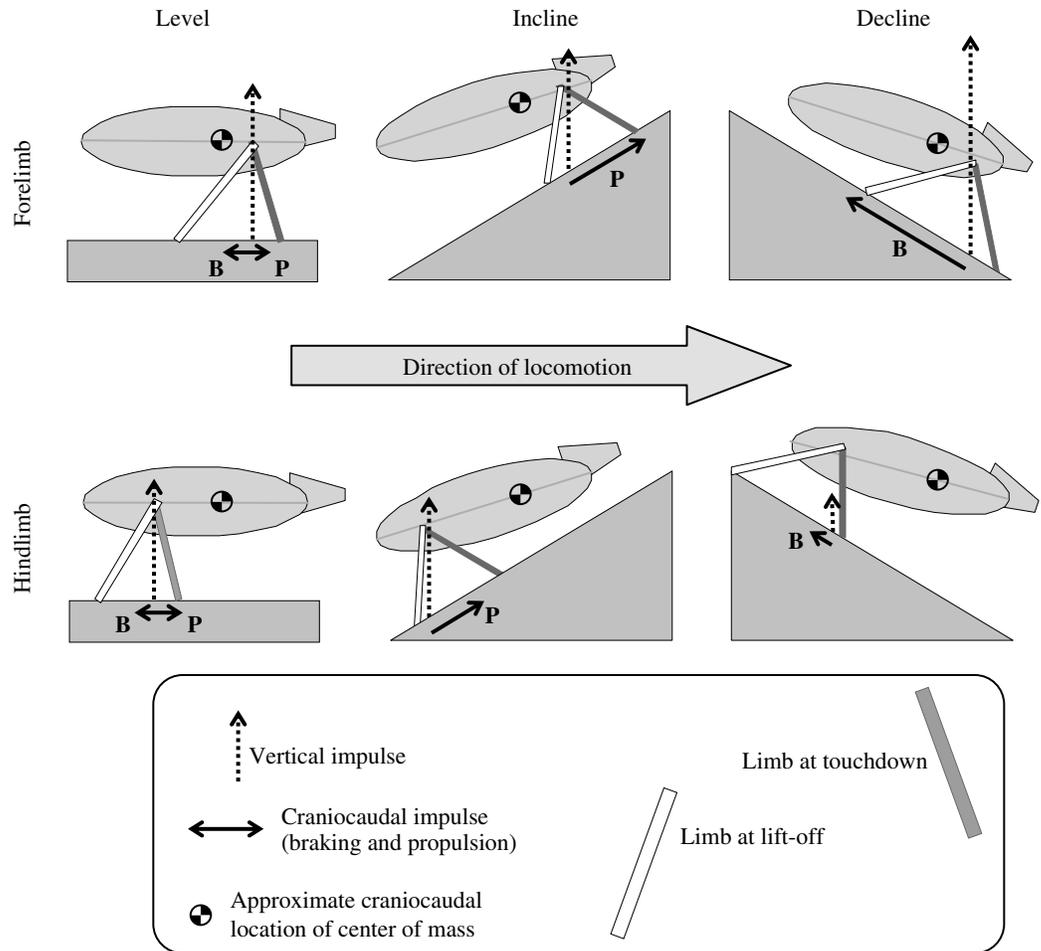


Fig. 4. Schematic of sagittal plane parameters for the forelimbs (above) and hindlimbs (below) of *M. domestica* on level, incline and decline trackways (left to right). Fore- and hindlimb touchdown (solid gray bar) and lift-off (open bar) angles are exaggerated to make differences between limbs and substrates more visible. Vertical impulse is represented by broken arrows, and braking and propulsive impulses by solid arrows; the magnitudes of these impulse vectors are also not shown to scale with each other for illustrative effect (see Table 1 for exact values). **B**, braking impulse; **P**, propulsive impulse.

significantly less retracted at lift-off on the declined trackway than on the level and inclined trackways ($P=0.0001$). Craniocaudal angles at touchdown, midstance and lift-off were not correlated with speed, with the exception of the hindlimb retraction angle at lift-off on the downslope (least-squares regression, $P=0.0035$, $r^2=0.483$, i.e. a weak tendency to undergo greater retraction at higher speeds). Mediolateral angle of each limb at touchdown, midstance and lift-off did not vary across substrates. However, mediolateral angle at touchdown was significantly lower in hindlimbs compared to forelimbs ($P<0.0001$).

Kinetics

Sample force profiles are shown in Fig. 5. Few speed-dependent relationships were found among the kinetic parameters. While significant correlations were determined for peak vertical force in forelimbs on declines and hindlimbs on all substrates (Table 2), only a single significant difference in regression slope was found (hindlimb peak vertical force on level versus on decline; $P=0.0080$).

Locomotor kinetic results are summarized in Table 3 and Figs 4 and 6, and differences in impulse magnitudes between limbs are illustrated in Fig. 7. Vertical impulse and peak vertical force of forelimbs exceed those of hindlimbs during

Table 2. Least squares regression analyses of peak vertical force ($BW s$) vs speed ($m s^{-1}$)

Substrate	Limb	Slope	95% confidence interval	R^2	P -value
Level	FL	–	–	–	0.25
Level	HL	0.935	0.529, 1.341	0.629	0.0003
Incline	FL	–	–	–	0.44
Incline	HL	1.263	0.234, 2.291	0.481	0.0229
Decline	FL	0.940	0.241, 1.639	0.269	0.0112
Decline	HL	0.293	0.094, 0.492	0.416	0.0076

Abbreviations as in Table 1.

level and decline trials ($P<0.0001$). Consequently, forelimbs support over 65% of the body weight when the opossums ran on the horizontal trackway and about 82% of body weight when they ran downhill. By contrast, fore- and hindlimbs take on nearly equal roles in body weight support during the incline trials. Vertical forces of forelimbs are greatest on downhill trials, intermediate on level trials, and least on uphill trials ($P<0.0001$). Hindlimbs largely follow an inverse relationship: the greatest mean values were obtained during level and uphill running and smaller vertical forces were recorded during

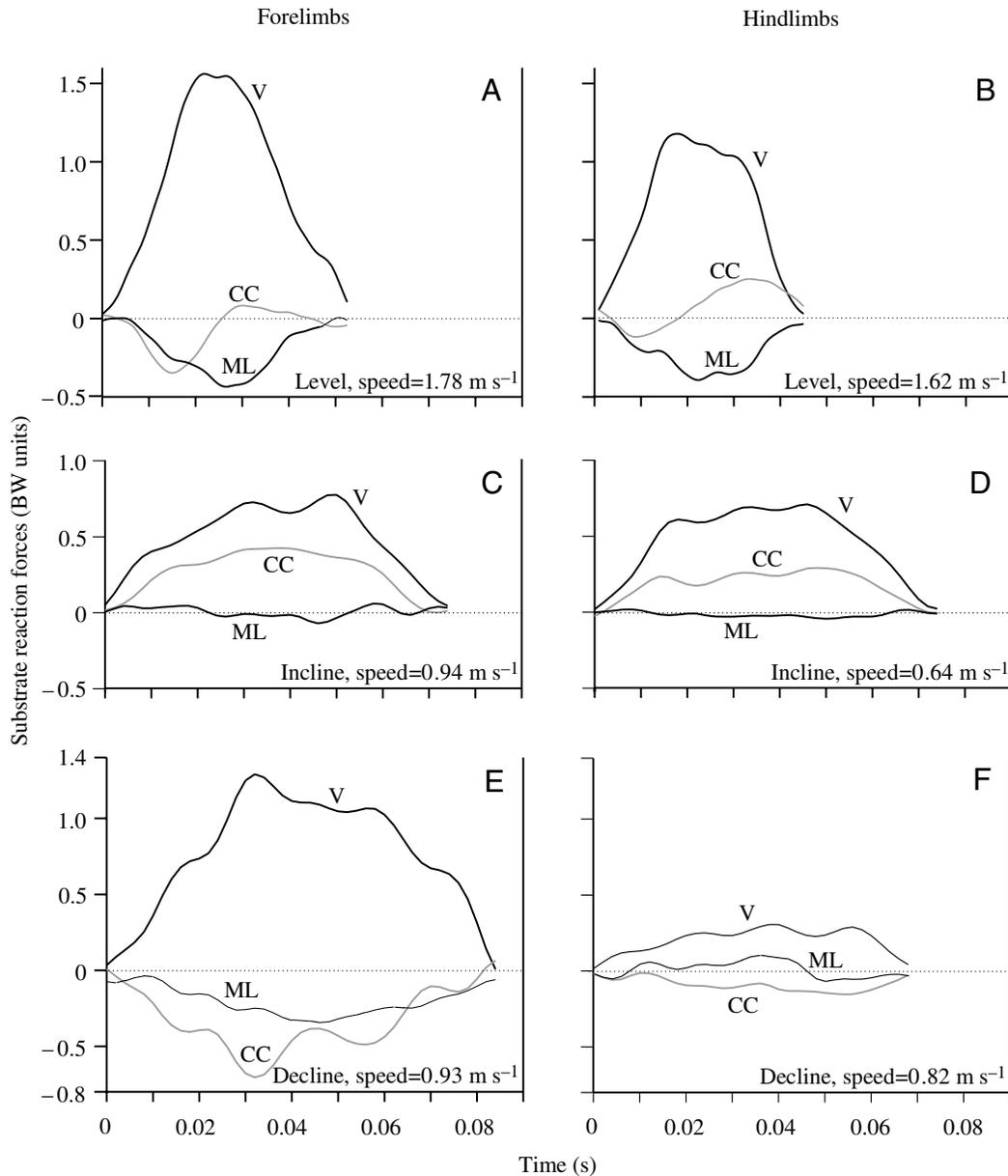
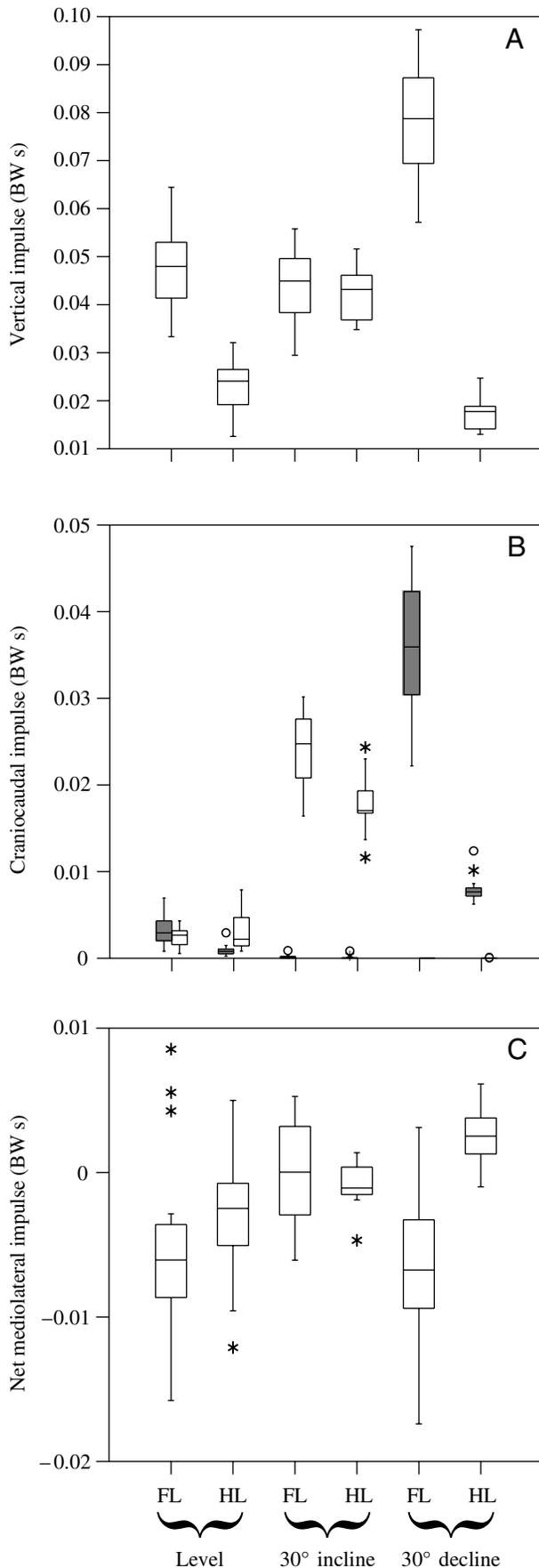


Fig. 5. Representative force traces for each limb (A,C,E, forelimb; B,D,F, hindlimb) and substrate type (A and B, level; C and D, incline; E and F, decline). Craniocaudal (CC) force profiles are shown in gray for clarity (negative, braking; positive propulsive). Mediolateral (ML) reaction forces are primarily medially directed (negative) except for hindlimbs on declined trackways. All axes are shown to the same scale. V, vertical force; BW, body weight.

downhill trials ($P < 0.0001$; level and uphill trials did not differ significantly). On the level trackway, peak vertical force occurred earlier in the stance phase of hindlimbs ($43.4 \pm 3.2\%$) than in forelimbs ($58.3 \pm 3.1\%$; $P = 0.0180$). There were no significant differences in the timing of peak vertical force between limb pairs on the sloped trackways, where peak occurred at $54.5 \pm 2.2\%$ of stance.

Craniocaudal impulses on the horizontal trackway were typical for terrestrial quadrupeds, in that an initial braking impulse was followed by a propulsive impulse. Braking impulse was significantly greater in the forelimbs than in the hindlimbs ($P = 0.0003$), such that the forelimbs generated nearly 78% of the total braking impulse during level locomotion. Although the hindlimb propulsive impulses tended to be greater than those of the forelimb, there was no significant difference

between limb pairs ($P = 0.31$). The transition between braking and propulsive phases occurred significantly later in the forelimbs ($62.0 \pm 2.1\%$ of stance duration) than in the hindlimbs ($33.3 \pm 3.7\%$; $P < 0.0001$). On inclines, the braking impulses were trivially small so that time of braking-to-propulsion transition was effectively at touchdown in both limb pairs. Both fore- and hindlimbs produced substantial propulsive impulse, approximately an order of magnitude greater than that exerted on the level, although forelimbs provided approximately 57.7% of the total propulsive impulse ($P = 0.001$). On declines, braking impulse was substantial for both limb pairs, with forelimbs generating on average 81.8% of the total braking impulse ($P = 0.0001$). The braking impulse generated by the forelimb on the decline trackway was the greatest of any craniocaudal impulse recorded in this study. Fore- and hindlimbs produced



virtually no propulsive impulse on the decline, so that in almost all decline trials there existed no effective braking-propulsion transition.

Mediolateral impulses of fore- and hindlimbs for level and inclined trials were equivalent in magnitude and orientation, and they consistently indicated a net medial substrate reaction impulse (i.e. laterally directed limb force) for each limb. Mediolateral impulses for level trials were fairly substantial, on the order of the craniocaudal impulses, whereas those for incline trials were substantially smaller than the craniocaudal impulses. While medially directed impulses were obtained for the forelimbs during downhill running, the hindlimbs indicated net lateral impulses, so that limb pairs on the decline exerted oppositely directed and significantly different net mediolateral impulses ($P=0.0001$). Across substrates, forelimbs consistently yielded net medial impulses that were smallest during uphill running ($P=0.0135$) and approximately equal on level and downhill trials. Hindlimbs during level and incline trials exerted equivalent net medial impulses whereas decline trials had net lateral impulses ($P<0.05$ for level *versus* decline means).

Required coefficient of friction

The overall shape of the required coefficient of friction (μ_{req}) curve was largely the same across substrates or between limb pairs (Fig. 8A): μ_{req} was typically highest at the beginning of the stance phase and then fell and remained at lower values until just before lift-off when the values rose again. Within most substrate/limb groupings, median μ_{req} was uncorrelated with speed. On the level, median μ_{req} of fore- and hindlimbs were statistically indistinguishable (0.211 ± 0.021 and 0.254 ± 0.022 , respectively) and their values were lower than either of the two sloped substrates ($P=0.0001$; Fig. 8B). Although median μ_{req} was not significantly different between inclined and declined substrates, a significant substrate-limb interaction term was found in the two-way ANOVA ($P=0.0001$). When limb pairs were evaluated separately using *t*-tests it was found that forelimbs had a significantly greater median μ_{req} than hindlimbs on inclines (forelimb, 0.694 ± 0.018 ; hindlimb, 0.478 ± 0.028 ; $P=0.0002$), whereas the reverse pattern existed on the declined trackway (forelimb, 0.540 ± 0.019 ; hindlimb, 0.651 ± 0.023 ; $P=0.0067$).

Discussion

Body weight support

Limb function during terrestrial locomotion, as reflected by SRF patterns and limb kinematics, has best been characterized on level substrates (Demes et al., 1994; Schmitt and Lemelin,

Fig. 6. Box and whisker plots of (A) vertical, (B) braking, propulsive and (C) mediolateral impulses. Each box represents 50% of the data, and the line within the box represents the median. Each whisker corresponds to 25% of the data. Asterisks represent outliers, and circles denote extreme outliers. Note that the scale of the y axis in each plot is different. BW, body weight; FL, forelimb; HL, hindlimb.

Table 3. Peak vertical force (BW units) and impulse (BW s)

Impulses and forces	Limb	Level	Incline	Decline	Substrate differences
Peak vertical force	FL	1.528±0.043*	0.843±0.038	1.342±0.040*	L>U, L>D, U<D
	HL	0.898±0.045	0.935±0.060	0.401±0.048	L=U, L>D, U>D
Vertical impulse	FL	0.04756±0.00190*	0.04386±0.00162	0.07878±0.00170*	L=U, L<D, U<D
	HL	0.02323±0.00196	0.04245±0.00253	0.01720±0.00203	L<U, L>D, U>D
Braking impulse	FL	0.00322±0.00083*	0.00015±0.00071	0.03581±0.00074*	L=U, L<D, U<D
	HL	0.00092±0.00086	0.00014±0.00111	0.00796±0.00089	L=U, L<D, U<D
Propulsive impulse	FL	0.00245±0.00063	0.02430±0.00053*	0±0.00056	L<U, L>D, U>D
	HL	0.00312±0.00065	0.01784±0.00083	0.00001±0.00067	L<U, L>D, U>D
Net mediolateral impulse	FL	-0.00496±0.00109	-0.00025±0.00093	-0.00687±0.00100	L>U, L=D, U<D
	HL	-0.00310±0.00112	-0.00085±0.00145	0.00240±0.00116	L=U, L=D**, U=D**

Abbreviations as in Table 1.

**Net mediolateral impulses generated by the hindlimb were medially directed on the level, as indicated by the negative. They were laterally directed on the decline, as indicated by the positive. Thus these net mediolateral impulses in the hindlimb were very different between level and declined trackways, but the absolute values of these impulses were not significantly different.

2002), and the general pattern found for *M. domestica* is typical of terrestrial quadrupedal mammals. Given that body weight support is reflected by the magnitudes of vertical SRFs or impulses, then the forelimbs of *M. domestica* on level substrates support the majority of the body weight. The most likely (and unremarkable) explanation for this is that the center of mass of *M. domestica* is closer to the forelimbs than to the hindlimbs (37% of the glenohumeral–acetabular distance). A cranially oriented center of mass is a common feature among non-primate mammals (Schmitt and Lemelin, 2002).

With the animal’s center of mass located closer to the forelimbs than to the hindlimbs, we expected that fore- and hindlimbs would support approximately equal body weight on the 30° inclined substrate (Prediction 1). This was apparently the case. This finding can be explained by the direction of the

line of gravity passing through the center of mass (**G**). On the incline, this gravity vector typically intersects the substrate closer to a point roughly 50% of the glenohumeral–acetabular distance. On the decline, the opposite occurred, and the gravity vector **G** intersected the substrate more anteriorly. This explains why the vertical impulse exerted by the forelimb was so considerably and significantly greater on the decline. The animals were never observed to topple (pitch) over their forelimbs, which suggests that **G** usually intersected the substrate posterior to the forelimb contact on the substrate (but more anteriorly than was the case on the level trackway).

Shear forces and the required coefficient of friction

On the level trackway, both limb pairs have braking and propulsive components during level locomotion (Fig. 6).

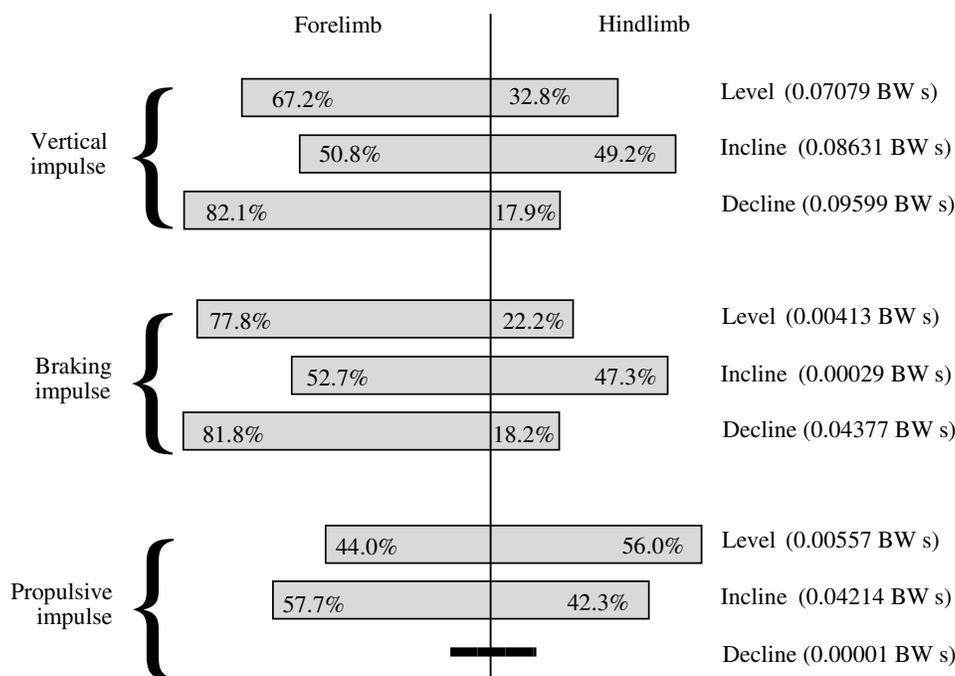


Fig. 7. Relative effort (%) of vertical, braking and propulsive impulses exerted by fore- and hindlimbs. Absolute values of total impulse (forelimb + hindlimb) are indicated to the right. Because the total propulsive impulse on the decline was extremely low, percent limb effort was not calculated. These percentages were calculated for illustrative purposes; because they were calculated from the mean vertical, braking and propulsive impulses for each substrate slope, testing for significant difference among groups was not possible. BW, body weight.

Thus neither fore- nor hindlimbs are exclusively responsible for decelerating or accelerating the center of mass with every step. The forelimbs of *M. domestica* are net braking whereas the hindlimbs are net propulsive, as is typical for terrestrial quadrupeds (Demes et al., 1994). It is noteworthy, however, that although the forelimbs take on a larger share of overall braking effort, forelimbs and hindlimbs share more equally the propulsive effort, as was observed in trotting dogs (Lee et al., 2004). This may be due to the greater range of motion of the forelimbs in *M. domestica*, although most mammals similarly have greater excursion angles in the forelimb compared with the hindlimb (Larson et al., 2001). A greater

limb excursion might allow that limb to apply braking or propulsive force over a longer time within a stride. Alternatively, the opossums in the sample may have been, on average, slightly accelerating during forelimb trials and/or slightly decelerating during the hindlimb trials, despite our best efforts to eliminate trials in which the opossums did not move at a steady speed.

Rocha-Barbosa et al. suggest that the hindlimbs of guinea pigs (*Cavia porcellus*) have a greater role in changing locomotor speed than the forelimbs (Rocha-Barbosa et al., 2005). This supposition is based on the observation that as speed increases, the hindlimb joints exhibit more kinematic changes than forelimbs (changes in joint angles and angular velocity). It is unknown if these differences between fore- and hindlimbs are accompanied by kinetic differences. In our experiments on substrate effects on opossum locomotion (this study), we observed an increased role of the forelimbs in generating propulsive impulse on the inclined trackway. This was an unexpected result, as we anticipated that the hindlimbs (which are net-propulsive on the level trackway) would exert greater propulsive effort relative to the normally net-braking forelimbs (Prediction 2). At the very least, given that the fore- and hindlimb supported approximately equal body weight on the incline, one might expect roughly equal propulsive impulses from fore- and hindlimbs. Lammers and Biknevicius found that on a narrow, horizontal, 'arboreal' support, the forelimbs similarly increased their propulsive role on the narrow trackway in comparison to the flat 'terrestrial' trackway (Lammers and Biknevicius, 2004). In *M. domestica*, the forelimbs may increase their role in locomotion (as measured by craniocaudal and mediolateral substrate reaction forces) on challenging substrates while the hindlimb function remains relatively unchanged. It is possible that this pattern is comprehensive among primitive quadrupedal mammals in general, but comparative force data are needed on additional species whose body plans resemble primitive mammals.

On the inclined trackway, the forelimbs generated greater propulsive impulse than the hindlimbs, but the role of the forelimbs in supporting body weight decreased. These results explain the high required coefficient of friction (μ_{req}) observed in the forelimb on the incline, which was the highest μ_{req} observed in this study. Shear forces were higher due to increased propulsive forces. Simultaneously, the normal forces (which are largely generated by body weight, even on a 30° incline) are decreased in the forelimbs. With greater shear and lower normal forces, the μ_{req} of the forelimbs is significantly greater on the incline.

Whereas fore- and hindlimbs had equivalently low median μ_{req} on the level substrate, the median μ_{req} is significantly higher in both limb pairs on both inclined and declined trackways. The substrate slope apparently causes the body weight to increase the shear forces and contribute less to normal forces. This is consistent with data on humans walking on gradients (McVay and Redfern, 1994), but there are no comparable data for animals roughly the size of *M. domestica*. Despite the increase in μ_{req} on the sloped terrain, the animals

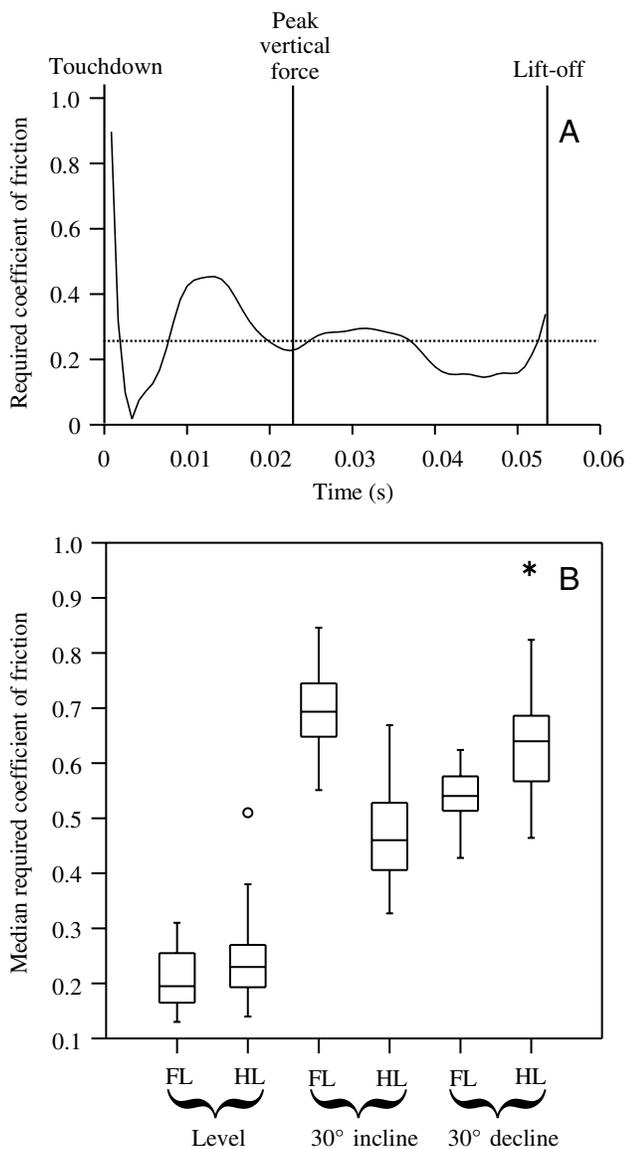


Fig. 8. Frictional conditions in locomotion. (A) Typical plot of the required coefficient of friction (μ_{req}) in *M. domestica* (1.78 m s^{-1}) on the level trackway. Broken line represents the median value of μ_{req} . (B) Box plots of the median required coefficient of friction for each substrate and limb pair. Asterisk, outlier; circle, extreme outlier.

never slipped in any of the trials used for this study, and rarely slipped during any trial. This is because the μ_{req} is lower than the true coefficient of friction (μ_s), which was not measured. Two other studies provide estimations of μ_s : Kinoshita et al. calculated μ_s between 220-grit sandpaper and human skin (thumb and index finger) to be above 1.5 (Kinoshita et al., 1997), and Cartmill estimated μ_s between the volar skin of primates and a plastic surface to be above 5 (Cartmill, 1979). Both of these values are substantially greater than the median μ_{req} computed for *M. domestica* on the sandpaper-covered trackways (maximum value=0.96). The animals' claws must also provide additional traction on the level and inclined trackways.

Mediolateral forces control yaw and provide some stability against rolling. Mediolateral impulses were medially directed in *M. domestica*, reflecting of laterally directed limb forces. The most striking feature of the mediolateral impulses is their magnitude: mediolateral impulses are nearly equivalent to craniocaudal impulses. The likely explanation for relatively high mediolateral impulses is that *M. domestica* maintains a moderately abducted limb as commonly found in non-cursorial mammals (Jenkins, Jr, 1971). By contrast, many terrestrial mammals, and especially those that are cursorial, have mediolateral forces that are so negligible that they are customarily ignored (e.g. Bertram et al., 2000). The mediolateral impulses of *M. domestica* are greater in comparison to mammals with erect limb posture, but low relative to tetrapods with more sprawled limb postures such as lizards (Christian, 1995) and alligators (Willey et al., 2004). Indeed, *M. domestica* maintains a moderately abducted limb, as commonly found in non-cursorial mammals (Jenkins, Jr, 1971). We conclude that high mediolateral forces may be a hallmark of tetrapods that move in non-parasagittal locomotion.

On both inclined and declined trackways, we predicted that the mediolateral impulses would not differ greatly from those observed on the level trackway (Prediction 4). This was not the case. On the inclined trackway, net mediolateral substrate reaction impulses remained medially directed, as they were on the level trackway. But they were about 19.8 times smaller in the forelimb, and about 3.6 times lesser in the hindlimb relative to their magnitude on the level. Thus, a greater amount of muscular effort was devoted to toward propulsion, and away from stability and ability to change direction. This is especially true in the forelimb, which had greater propulsive effort than the hindlimb, but less mediolateral effort. Substantial medially directed reaction impulses were commonly observed in the forelimbs during decline locomotion in *M. domestica*. Although the forelimbs tend to be somewhat more abducted on decline trials, they are not significantly more abducted than they were on the level or incline substrates. But the hindlimbs undergo considerable adduction during stance on all substrates, suggesting lateral undulation of the spine (Pridmore, 1992). This apparent lateral undulation is somewhat (but not significantly) greater on the decline, and this may partially explain the larger lateral

forelimb forces. Also, the hindlimbs exerted laterally directed net mediolateral impulses, which is the opposite direction of the forelimb net mediolateral impulse. But because these animals use primarily trotting gaits regardless of substrate slope (this study, Fig. 3), a medial SRF in the forelimb and a lateral SRF in the contralateral hindlimb have the effect of pushing the animal to one side or another. These mediolateral forces should cause the animal to move from side to side (right and left) as it moves downhill, which may serve to control the rate of descent.

Limb kinematics

Our results indicate that shoulder height is always lower than hip height, but we believe that shoulder and hip heights in *M. domestica* are probably more similar than our data indicate. This is because we measured the approximate location of the glenohumeral joint as the pivot point of the shoulder rather than the middle of the scapula (Fischer et al., 2002). Measuring the scapula was impossible using videography, but despite the lack of data on shoulder blade excursion, we believe our results comparing substrate effects on forelimb excursion are valid. Total forelimb angles were measured in the same way regardless of substrate, which means that relative differences among substrates are most likely real differences.

Our predictions of how limb protraction at touchdown, limb retraction at lift-off, and overall limb posture would change with substrate slope were based on the assumption that the locomotor behavior of the animals would maximize stability (Predictions 5 and 6). This was partially borne out. *M. domestica* assumes a high degree of crouching, with its forelimbs during incline locomotion, and hindlimbs during decline locomotion. These kinematic adjustments brought the center of mass somewhat closer the substrate, which causes **G** to remain closer to the center of the base of support. These adjustments to limb posture also had the effect of leveling the animal's body, a behavior commonly reported among primates moving on inclined and declined substrates (Vilensky et al., 1994; Stevens, 2000; Krakauer et al., 2002). Similar increased hindlimb crouching during substrate descent was reported for squirrel monkeys (Vilensky et al., 1994) and desert iguanas (Higham and Jayne, 2004). Because *M. domestica* did not crouch with the limb pair located lower on the trackway (hindlimbs on the incline, and forelimbs on the decline; see Fig. 4) the opossums maintained a relatively lower rotational moment about the hip/shoulder, thereby reducing the likelihood of toppling over the downslope limb pair.

As is the case with most mammals (Larson et al., 2001), the forelimbs of *M. domestica* undergo greater craniocaudal excursion than the hindlimbs. Although the amount of limb protraction and retraction differed on inclines and declines, this difference between forelimbs and hindlimbs was consistent.

We predicted that on the incline, both limb pairs would undergo greater retraction, especially at touchdown, in an effort to keep **G** located within the base of support (Prediction 6). On the decline, both limb pairs should protract more, especially at touchdown. The limbs did not behave as

predicted on the incline; this, in addition to the net mediolateral impulse results, suggests that 30° incline locomotion does not destabilize the opossums as much as decline locomotion. On the decline, both limb pairs were more protracted at touchdown, which will keep **G** located within the base of support. Furthermore, with the limbs more aligned with the gravity vector, the rotational moment about the shoulder may decrease. In summary, the relatively extreme kinematic adjustments, the considerable loading on the forelimbs, and the claws (which most likely are less effective on the decline) strongly suggest that moving downslope is more challenging than moving uphill.

In spite of changes in limb function during locomotion on the sloped trackways, the shoulder and hip movements (perpendicular to the surface of the trackway) of *M. domestica* continued to exhibit the 'bouncing' pattern similar to that described on the level trackway. This pattern suggests that the animals are running, e.g. converting gravitational potential energy and kinetic energy into stored elastic strain energy in their tendons during midstance (Cavagna et al., 1977). As with level locomotion, the storage and utilization of elastic energy during incline/decline locomotion may be limited in mammals as small as *M. domestica* (Ettema, 1996; Biewener and Roberts, 2000). Furthermore, recovery of external mechanical energy may not be universal on inclined substrates: whereas peak stresses measured from the tendons of leg muscles of guinea fowl moving on level and incline trackways suggest that elastic energy storage increases on inclines (Daley and Biewener, 2003), they are unchanged in the tammar wallaby (Biewener et al., 2004), so that enhanced recovery of external mechanical energy when running on inclined substrate is not universal.

Conclusion

Some of our results are explained by body weight support. The craniocaudal location of the center of mass accounted for the differences in relative magnitudes of vertical forces between fore- and hindlimbs and among substrates. Body weight support also seems to explain why the forelimbs exerted a much greater braking impulse than hindlimbs while descending a 30° decline. Second, the need to remain stable during locomotion appears to account for mediolateral impulses and the required coefficient of friction results, as well as limb excursion of shoulder/hip heights. However, craniocaudal impulses on the inclined trackway could not be explained by either body weight support or stability. There is also no outstanding morphological feature that gives a reason for this phenomenon: fore- and hindlimbs are approximately the same size, and they have the same number of digits (five). Also, all the digits (except the hallux) have claws. The craniocaudal impulses measured during incline locomotion imply that the locomotor behavior of forelimbs may be more malleable than hindlimbs, and that when an animal encounters a challenging substrate, its forelimbs might modify their locomotor behavior more than the hindlimbs (Lammers and Biknevicius, 2004).

List of symbols and abbreviations

COM	center of mass
F_{CC}	craniocaudal force
F_{DV}	dorsoventral force
F_{ML}	mediolateral force
F_V	vertical force
G	gravity vector through COM
<i>l</i>	distance between knife edges of reaction board
R_s	amount of weight supported by the reaction board knife edge over the weighing scale
SRF	substrate reaction force
W_p	weight of reaction board
W_s	weight of the animal specimen
Y_{com}	COM along the craniocaudal axis
μ_{req}	required coefficient of friction
μ_s	coefficient of static friction

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