

# Whole-body mechanics and gaits in the gray short-tailed opossum *Monodelphis domestica*: integrating patterns of locomotion in a semi-erect mammal

Andrew J. Parchman<sup>1</sup>, Stephen M. Reilly<sup>1,\*</sup> and Audrone R. Biknevicius<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, College of Arts and Sciences and <sup>2</sup>Department of Biomedical Sciences, College of Osteopathic Medicine, Ohio University, Athens OH 45701, USA

\*Author for correspondence (e-mail: reilly@ohiou.edu)

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## Summary

Gaits (footfall patterns) and external mechanical energy patterns of the center of mass were quantified in a generalized, semi-erect mammal in order to address three general questions. First, do semi-erect mammals exhibit the walk/run gait transitions that have been proposed as the primitive condition for tetrapods? Second, do small, semi-erect mammals employ the energy-saving pendular and spring-based mechanics used by erect mammals? Third, how well do mechanical locomotor patterns of the center of mass correlate with gaits? *Monodelphis domestica* utilizes only fast walking and running trot gaits over a fivefold increase in speed, over which we could illicit constant velocity steps, although running trots were their preferred gait. In sustained level locomotion the opossums did not use other walking gaits presumed to be primitive for tetrapods. Across the full range of speeds their trotting gaits exhibited force patterns and in-phase mechanical energy fluctuations that are characteristic of spring-mass mechanics. Thus, opossums appear to prefer

trotting gaits with bouncing mechanics for sustained locomotion. Integration of center-of-mass *versus* footfall perspectives reveals that spring-mass mechanics is associated with both walking trot and running trot gaits. Furthermore, the onset of an aerial phase was not clearly associated with either the walk/run gait transition (50% duty factor) or a change in center-of-mass mechanics. The assumption that energy-saving mechanisms are ubiquitous among mammals is tenuous because small non-cursorial mammals do not appear to use pendular-based mechanics for sustained locomotion and, although they prefer spring-based mechanics, they probably lack clear musculoskeletal spring elements that could store energy during running. Thus, it appears that simply paying for locomotion with muscular work may be the primitive condition for mammals.

Key words: kinematics, kinetics, locomotion, opossum, *Monodelphis domestica*, marsupial.

## Introduction

Cursorially adapted vertebrates employ two basic patterns of locomotor mechanics that permit some degree of energy saving (Blickhan and Full, 1987; Cavagna et al., 1977; Heglund et al., 1982; Reilly and Biknevicius, 2003; Roberts et al., 1997). At slower speeds, the center of mass of these animals fluctuates in such a way that it may be modeled as an inverted pendulum. In its simplest expression, gravitational potential energy rises and then falls during the support phase as the center of mass vaults over the largely stiff supporting legs. Kinetic energy fluctuates out of phase relative to gravitational potential energy because forward velocity falls to its minimum at midstance. This pendulum-like exchange of energy used at slower speeds can decrease the external mechanical energy requirements of vertebrates with erect limb postures by as much as 70%, thereby reducing the amount of muscular work needed to maintain steady speed locomotion (Cavagna et al., 1977; Donelan et al., 2002). We refer to this pattern of center-of-mass mechanics as ‘pendular mechanics’ (Table 1). To save energy at higher

speeds, vertebrates shift to bouncing gaits (footfall patterns such as the running trot or gallop), in which limbs compress and then extend during each step. Here, gravitational potential and kinetic energies are in phase (as both decrease to their minima at midstance) so that energy savings by pendular mechanics are greatly diminished. Instead, components of the musculoskeletal system are thought to act as biological springs, storing and passively releasing elastic strain energy during each step (Biewener et al., 1981; Biewener and Blickhan, 1988; Blickhan, 1989). We refer to this pattern of center of mass mechanics as ‘spring mechanics’. Although the distinction between pendular and spring mechanics is not always clear (Lee and Farley, 1998; Full and Koditschek, 1999) among vertebrates, both pendular and spring mechanics have been described for cursorially adapted birds and mammals (e.g. large terrestrial birds, humans, dogs and ungulates; Cavagna et al., 1977). However, little is known about the locomotor mechanics of non-erect and non-cursorial vertebrates. While Farley and Ko (1997)

Table 1. *Terms used in this study to compare mechanical patterns of the center of mass to gait patterns of the limbs*

Whole-body mechanics (patterns of center-of-mass fluctuation) <sup>a</sup>	
Pendular mechanics	Inverted pendulum-like mechanism
Spring mechanics	Spring-mass mechanism
Gaits (patterns of footfalls) <sup>b</sup>	
Walk	Duty factor >50% (includes several possible walking gaits*)
Run	Duty factor <50% (includes several possible running gaits*)
Trot	Limb phase 50±10% (diagonal couplet gait)
Walking trot	Limb phase 50±10% (with >50% duty factor)
Running trot	Limb phase 50±10% (with <50% duty factor)
Strides	
Aerial	Steps separated by periods with no limb contact with the ground
Non-aerial	Steps overlapping – continuous ground contact by at least one limb

<sup>a</sup>Cavagna et al., 1977.  
<sup>b</sup>Hildebrand, 1976.  
 \*Determined by duty factor and limb phase.

showed that two lizards with sprawling postures used pendular and spring mechanics, only in-phase gravitational potential and kinetic energy exchange patterns (spring mechanics) have been reported for small, semi-erect mammals (Cavagna et al., 1977; Heglund et al., 1982).

Another way to quantify patterns of locomotion is by describing gaits; for centuries ‘gait’ has referred to footfall patterns (e.g. Gioffon and Vincent, 1779; see review in Reilly and Biknevičius, 2003). In the well-established gait model proposed by Hildebrand (1976, 1977, 1980, 1985), the walk/run transition occurs at a 50% duty factor (Table 1). Specific walking and running gaits are then defined by the phase relationships of the limbs (relative timing of fore- and hindfoot falls). From gait analyses of numerous species spanning the postural and phylogenetic range of terrestrial vertebrates, Hildebrand proposed that vertebrates almost universally use the more stable walking gaits at slower speeds and either transition into specific running gaits dominated by coordinated limb couplets (such as the trot, Table 1), or switch to asymmetrical gaits (such as the bound or gallop) to increase speed. Gait studies of lizards (White and Anderson, 1994; Reilly and Delancey, 1997), alligators (Reilly and Elias, 1998; Renous et al., 2002) and mammals (Dagg, 1973; Pridmore, 1992; White, 1990) have supported this hypothesis. Thus, vertebrate footfall patterns can be categorized as walking or running gaits based on duty factor (Table 1), and specific gaits are determined by limb phase. Note that ‘walk’ and ‘run’ are often used by students of mechanics as synonyms for pendular and spring mechanics, respectively. However, we retain Hildebrand’s formal definition for walk and run (Hildebrand, 1976) as they relate to footfall patterns, because of priority of formal definition (Reilly and Biknevičius, 2003) and because it has not been demonstrated how these mechanical patterns relate to gait patterns.

Remarkably, the two perspectives on quantifying locomotion (center-of-mass fluctuations *versus* footfall

patterns) have been largely explored independently (see Reilly and Biknevičius, 2003). Consequently, gaits used during mechanical energy studies are often vaguely described, and kinematic studies rarely obtain data appropriate for assessing locomotor mechanics. The relationships between gaits and mechanical energy patterns have not been examined in any quantitative way and therefore, we know little about how neuromuscular movements of axial and appendicular systems control movements of the center of mass. Neuromuscular control of the limbs produces the gait patterns that carry the center of mass. Thus, to understand locomotion we have to know more than what the center of mass is doing. Details of locomotor mechanics and gaits are particularly lacking in non-cursorial mammals. Therefore, the goal of this study is to quantify both the kinematic gaits and mechanical energy patterns employed by a generalized, semi-erect mammal as a means to address three general questions. First, do small, semi-erect mammals employ the energy-saving pendular and spring mechanics used by erect mammals? Second, do opossums exhibit the walk/run gait transitions proposed as the primitive condition for tetrapods by Hildebrand? Third, how well do mechanical locomotor patterns correlate with kinematic gaits? Specifically, we want to test the hypothesis (Reilly and Biknevičius, 2003) that gaits (walks, runs) correlate with mechanical patterns (pendular and spring mechanics, respectively).

### Materials and methods

Data were collected from seven specimens (mass 80–127 g) of the gray short-tailed opossum *Monodelphis domestica* (Wagner, 1942). *Monodelphis* was chosen because it is regarded phylogenetically, morphologically (size, shape) and behaviorally (terrestrial insectivore, semi-erect posture, lateral undulation) as a good model for a generalized primitive mammal (Lee and Cockburn, 1985; Novacek, 1992).

### Data collection

All procedures followed approved animal care and use protocols. Footfall data and ground reaction forces were collected simultaneously as possums moved down a trackway and across a force platform. During data collection, the opossums were allowed to freely choose the speed and gait with which they crossed the force platform. Our goal in recording kinematic and force data was to sample the full range of velocities (and therefore, we presumed, mechanical patterns and gaits) that the opossums would use. After numerous trials revealed the general range of speeds at which the opossums chose to move, we attempted to extend the range of speeds for analysis by chasing the animals with our hands to invoke faster trials. We also spent considerable time simply hiding and waiting for the animals to use even slower speeds. Neither of these approaches extended the range of speeds that the opossums would move at a steady speed.

Each trial was filmed at 120 Hz by a digital video camera (JVC GR-DVL 9800) mounted 0.85 m directly above the center of the force platform. Two Monarch-Nova strobe lights (233.3 Hz) provided adequate lighting to visualize all four feet. Two mirrors, mounted on the angled walls of each side of the platform, provided lateral views of the animals so that each video frame included a dorsal and two lateral views. The three separate views allowed us to verify whether or not the animal ran straight across the platform and to clearly visualize the interaction of each limb with the force platform. The videos were downloaded to a computer using Studio DV (version 1.04.100), and the motion analysis program APAS (version 1.0) was then used to review each trial in order to eliminate those in which opossums failed to move at a steady speed and direction. Footfall times of valid trials were recorded. For each trial, the touchdown time of the first limb to contact on the platform was aligned with the onset of vertical ground reaction forces on the platform to synchronize footfall data with force data.

The force platform was based on a spring-blade design similar to that described in Bertram et al. (1997). The platform surface measured 0.11 m wide by 0.36 m long, a length that allowed ground reaction forces to be recorded for 2–3 complete strides per trial. The platform was inserted flush to the surface of a 2.44 m trackway and then the platform and trackway were covered with a thin layer of fine grit sandpaper for traction. A dark enclosure was placed at the end of the trackway to entice the opossums to cross the platform.

Ground reaction forces were measured in the three orthogonal directions (vertical, craniocaudal and mediolateral) with four separate outputs: one each for craniocaudal and mediolateral and two for the verticals (at cranial and caudal ends of the platform). By assessing the relative output of each vertical sensor, the craniocaudal position of the center of pressure was determined. The movement of the position of the center of pressure during each step was used to calculate mean velocity for each step.

Ground reaction force data were collected at 500 Hz for 4 s periods. Analog outputs were amplified (National Instruments

SCXI 1000 and 1121) and then converted to a digital format (National Instruments NB-M10-16L). Voltage changes were recorded with a LabView 5.1 (National Instruments) virtual instrument data acquisition program. A second LabView program scaled the voltage data to forces (in N), based on calibration factors for the three directions of force and the craniocaudal position of center of pressure; our calibration protocols followed Bertram et al. (1997), adapted for a single platform. Finally, a third LabView program extracted ground reaction force data for each step and determined external mechanical energy profiles, phase shifts, and percentage energy recoveries for these steps (see below).

### Video data analysis

The gaits (footfall patterns) for each step analyzed were described using Hildebrand's model of symmetrical gaits (Hildebrand, 1976, 1977, 1980, 1985; Reilly and Biknevicius, 2003). Duty factor is the percentage of the stride that the reference hindlimb was on the ground: a 50% or greater duty factor defines a walking gait whereas running gaits have duty factors that fall below 50% (Table 1). Limb phase was determined as the duration between footfalls of the reference hindlimb to the ipsilateral forelimb, as a percentage of total stride duration. The limb phase variable very conveniently describes symmetrical gaits generally (diagonal *versus* lateral sequence) and in specific terms (pace, singlefoot and trot, as well as lateral and diagonal couplet walking gaits; see Reilly and Biknevicius, 2003 for details).

### External mechanical energy analysis

The change in the position of the center of pressure (distance traveled) during the step and step duration of the diagonal couplet (taken from the videos) were used to calculate the average velocity for each couplet step under analysis. From the initial sample of steps, only those in which the differences in velocity at the beginning and end of the step were within  $\pm 5\%$  of mean velocity were subjected to mechanical analysis. Consequently, a total of 90 steps were analyzed, representing individual samples of 16, 11, 20, 8, 15, 15 and 5 steps for the seven opossums.

External mechanical energy profiles for each diagonal couplet step were determined following procedures given by Blickhan and Full (1992). Accelerations of the center of mass in vertical, craniocaudal and mediolateral directions were obtained by dividing ground reaction forces by body mass (body weight was first subtracted in vertical records). Velocity changes of the center of mass for each direction were estimated by taking the first integration of acceleration. The integration constants for the craniocaudal direction were set to mean forward velocity (Cavagna et al., 1977; Blickhan and Full, 1992), and for the vertical and lateral records they were estimated as the mean values from calculated velocity profiles (Donelan et al., 2002). These velocities were then used to calculate kinetic energies ( $KE = 1/2mv^2$ , where  $m$  is body mass in kg) in the vertical ( $KE_V$ ), craniocaudal ( $KE_{CC}$ ) and mediolateral ( $KE_{ML}$ ) directions. Total kinetic energy of the

center of mass ( $KE_{TOT}$ ) during the step was then calculated as:

$$KE_{TOT} = KE_V + KE_{CC} + KE_{ML}. \quad (1)$$

Finally, changes in the vertical displacement of the center of mass ( $h$ ) were determined by integrating vertical velocity (integration constant estimated as the mean vertical displacement) and were used to determine changes in gravitational potential energy during the step ( $PE = mgh$ , where  $g$  is gravitational acceleration or  $9.81 \text{ m s}^{-2}$ ).

The phase shift between fluctuations in  $PE$  and  $KE_{TOT}$  was used to determine whether the center of mass exhibited pendular or spring mechanics during each step (Cavagna et al., 1977; Farley and Ko, 1997). Phase shifts were calculated as the time interval between minima in  $PE$  and  $KE_{TOT}$  divided by step duration and multiplied by  $360^\circ$ . Perfect pendular mechanics are characterized by a phase shift of  $180^\circ$ , indicating that the two energies are precisely out of phase, and spring mechanics are characterized by a phase shift around  $0^\circ$  (in phase).

The efficacy with which an animal was utilizing pendular mechanics was calculated as the percentage energy recovery (Cavagna et al., 1977; Farley and Ko, 1997):

% Recovery =

$$\left( \frac{(\Delta KE_{TOT}) + (\Delta PE) - (\Delta ME_{TOT})}{(\Delta KE_{TOT}) + (\Delta PE)} \right) \times 100\%, \quad (2)$$

where  $ME_{TOT}$  (total mechanical energy) is computed as  $KE_{TOT} + PE$ , and  $\Delta KE_{TOT}$ ,  $\Delta PE$  and  $\Delta ME_{TOT}$  are the sums of the positive increments of the  $KE_{TOT}$ ,  $PE$  and  $ME_{TOT}$  profiles, respectively (positive increments are those portions of an energy profile where there is a net gain of energy during a step). Once summed, the phase, shape and relative magnitudes of the  $PE$  and  $KE_{TOT}$  profiles determine the shape and magnitude of the total mechanical energy profile. If the  $PE$  and  $KE_{TOT}$  curves were perfectly out of phase (as in pendular mechanics) and of the same magnitude, the  $ME_{TOT}$  profile would be flat, and the recovery would be 100%. If the  $PE$  and  $KE_{TOT}$  profiles were perfectly in phase (as in spring mechanics) and of the same magnitude, the recovery would drop to 0%. Thus, low percent recoveries are generally considered to be indirect indicators of spring mechanics. An analysis of variance (ANOVA) with *post-hoc* Tukey's multiple comparison tests, was run to evaluate phase shifts and % energy recoveries for each gait type identified in the video analysis. In addition, both phase shift and % energy recovery were regressed against velocity in order to look for changes in mechanical patterns with speed.

## Results

A total of 90 steps of constant velocity were obtained over a range of speeds from  $0.323$  to  $1.795 \text{ m s}^{-1}$ . The fastest speed obtained freely was about twice the maximum speed we could entice opossums to match on a treadmill (S. M. Reilly,

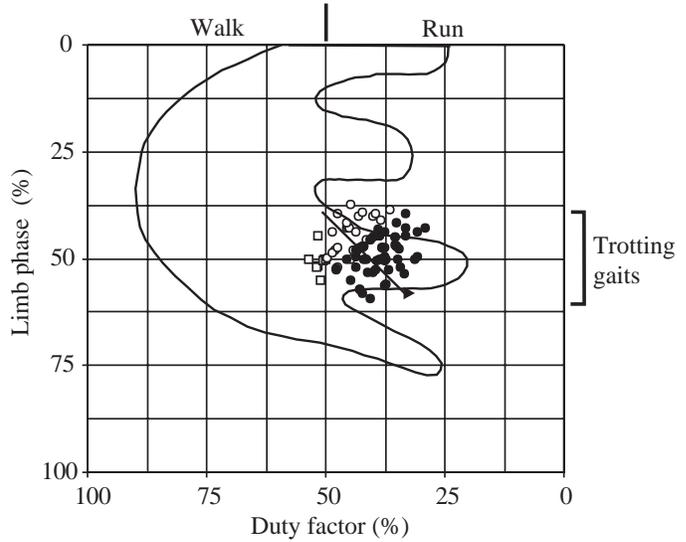


Fig. 1. Hildebrand gait plots for the 90 steps analyzed from seven *Monodelphis domestica*. Duty factor is the % of stride that the reference hind foot is on the ground; limb phase is the % of stride that the fore-foot follows the hind-foot on the same side. Gaits with duty factor  $\geq 50\%$  are classified as walking gaits (open squares), while those with duty factor  $< 50\%$  are classified as running gaits (open circles, non-aerial runs; filled circles, aerial runs). The limb-phase variable describes the general and specific footfall patterns associated with symmetrical gaits. Note that *Monodelphis* used only trotting gaits. The black triangle marks the velocity vector superimposed onto the Hildebrand plot from the three-dimensional plot of velocity, limb phase and duty factor. For comparison, the black outline encompasses 1178 symmetrical gait plots from 156 genera of tetrapods observed by Hildebrand (1985).

unpublished data), and thus we are confident that we have adequately sampled the high end of the range of speeds that these opossums will perform. At the slowest speeds the opossums tended to move in series of very short bursts, with frequent bouts of turning, stopping, starting and smelling the substrate. Steady-speed locomotion (sets of unidirectional, constant-velocity steps) could not be obtained at speeds slower than  $0.323 \text{ m s}^{-1}$ . Therefore, the more than fivefold increase in speed that we successfully sampled is likely to represent the range of locomotor behaviors naturally used by opossums for sustained locomotion on a level substrate.

## Gaits

Gait plots for all steps analyzed in *Monodelphis domestica* are presented in Fig. 1 and means for velocity, duty factor and limb phase are presented in Table 2. Duty factors ranged from 29.0% to 53.6% and averaged 41.45%. Only eight (Fig. 1, squares) of the 90 steps had duty factors of 50% or higher, thus, according to the Hildebrand (1980) model, only these steps were defined as walks and the remainder were scored as runs (Fig. 1, circles). The limb-phase relationship between the reference hindlimb and ipsilateral forelimb was 37.4–59.2%, mean 47.81% (Table 2). The majority of the trials (76 of 90)

Table 2. Locomotor dynamics in *Monodelphis domestica*

	All (N=90)	<i>P</i>	Walks (N=8)	Non-aerial runs (N=28)	Aerial runs (N=54)
Velocity (m s <sup>-1</sup> )	0.948±0.039	<0.0001	0.642±0.100	0.658±0.054	1.144±0.039*
Duty factor (%)	41.5±0.6	<0.0001	51.4±1.3*	44.5±0.7	38.4±0.5
Limb phase (%)	47.8±0.5	<0.0001	50.6±1.5	44.8±0.8*	49.0±0.6
% Recovery	3.4±0.3	0.437	3.4±0.9	3.1±0.5	3.8±0.3
Phase shift (degrees)	13.7±0.2	0.643	7.4±7.2	17.7±3.9	14.7±2.8

\*Significantly different *post-hoc* comparison at  $P < 0.0001$ .

Values are means ± S.E.M. for all 90 steps analyzed, and *P* values and *post-hoc* tests for ANOVA comparing walking (duty factors 50% or greater), non-aerial and aerial running (duty factors less than 50%) gaits.

had limb-phase variables between 44% and 56% and were clearly categorized as trots (with the footfalls and lift-offs of diagonal couplets tightly coordinated in time, following Hildebrand's model). 14 trials had limb-phase variables between 44% and 37.4%, which indicates that the footfall and lift-off times of the feet of the diagonal couplet were becoming less synchronized.

Aerial phases (identified from gait diagrams or when vertical force records decrease to zero between steps) were never observed in walking strides. Among the 82 running strides, 54 contained aerial phases between steps (Fig. 1, solid circles). In the remaining 28 running strides, the forelimb–hindlimb couplets were sufficiently unsynchronized that no aerial phases were recorded even though the duty factors for these trials were less than 50% (Fig. 1, open circles).

The velocity vector, indicating how speed increases in the sample of steps analyzed, is also presented in Fig. 1. This is the superimposition of the direction of velocity increase, taken from a velocity *versus* duty factor *versus* limb phase plot, onto the 2-D Hildebrand plot. Comparison of the velocity vector with the appearance of an aerial phase indicates that the aerial/non-aerial transition lies perpendicular to the velocity vector.

#### Ground reaction forces and step mechanics

The typical ground reaction forces observed during the support duration of a diagonal couplet are illustrated in Fig. 2A. Vertical forces during a diagonal couplet tended to either start at 0 N, if there was an aerial phase between the two couplets, or very close to 0 N. The vertical force increased throughout the first half of the step to reach about one and a half times body weight around midstance and then decreased more rapidly back towards 0 N during the second half of the step. The craniocaudal forces show an initial breaking impulse during the first half of the step, followed by an equivalent propulsive impulse throughout the last half of the stance phase. Mediolateral forces observed over a diagonal couplet were small in comparison to the vertical and craniocaudal forces and fluctuated slightly around zero with no discernable pattern across the sample.

Among the velocities, craniocaudal velocities, which fluctuated about the mean forward velocity, were of greatest

magnitude (Fig. 2A). In every step, the center of mass started at its maximum height relative to the ground, decreased to its minimum height at midstance, and then increased back to its maximum height throughout the remainder of the stance phase. Vertical fluctuations in the center of mass ranged between 1 and 4 mm.

Consistent patterns of fluctuations in total kinetic, gravitational potential and total mechanical energies were found across all trials (Fig. 2B). Kinetic and gravitational potential energies decreased to their minima at midstance and then increased throughout the remainder of the stance phase. Consequently, total mechanical energy profiles similarly displayed maxima at the beginning and ending of a step with minima at midstep. Fluctuations in total kinetic and gravitational potential energies of the center of mass remained closely in phase with one another across the full range of velocities (Fig. 3A, Table 2). The phase shift between the minimum values of kinetic and potential energies ranged from  $-44.00^\circ$  to  $46.96^\circ$ , mean  $13.72^\circ$ . No significant change in phase shift was seen with velocity ( $P=0.797$ ), thus, all 90 steps were categorized as spring mechanics.

A trivial amount of external mechanical energy was recovered through pendular mechanisms during the support phase of each diagonal couplet that was analyzed (Fig. 3B, Table 2). Percentage recovery ranged from 0 to 9.41%, mean 3.42%; such low values are indicative of spring mechanics. In addition, no significant change in percentage recovery was seen with velocity ( $P=0.630$ ).

#### Effects of an aerial phase

No significant differences were found in percentage recovery or phase shift in the ANOVA comparing steps grouped into walking, non-aerial running and aerial running gaits (Table 2; three groups in Fig. 1). Walks and non-aerial runs occurred at the same speed while aerial runs occurred at significantly higher velocities (Table 2), as indicated by the velocity vector (Fig. 1). Walks and aerial runs maintained coordinated limb couplets (limb phases near 50%, Table 2). The non-aerial runs differed from walks and aerial runs in having significantly lower limb phase values, indicating that the limb couplets were less tightly coordinated. Thus, as duty factor decreased, walks changed to aerial runs when more

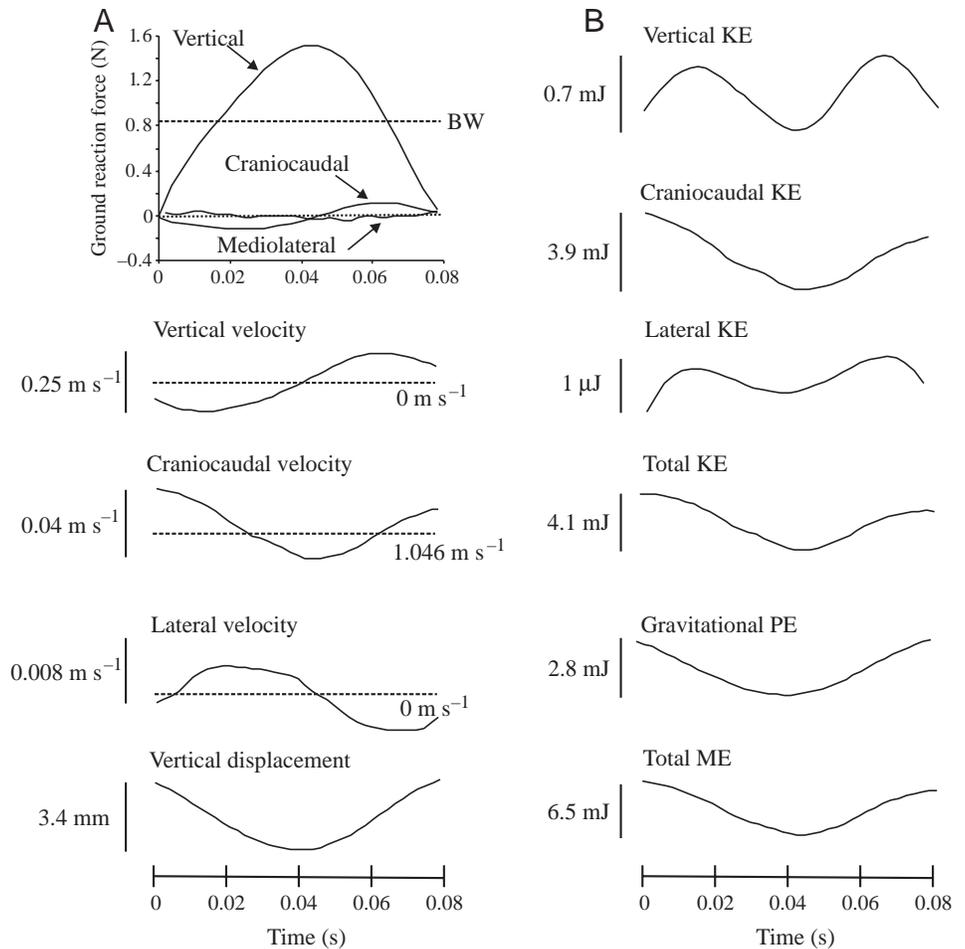


Fig. 2. Spring mechanics (vertical, craniocaudal and lateral) in *Monodelphis domestica* typical of all steps analyzed over a fivefold increase in speed ( $0.3\text{--}1.8\text{ m s}^{-1}$ ). (A) Ground reaction forces, velocities of the center of mass, and vertical displacement of the center of mass. BW is body weight ( $0.833\text{ N}$ ). Negative values in the craniocaudal record reflect braking effort whereas positive values are propulsive. The broken line indicates mean velocity. (B) Three-dimensional kinetic energies (KE), gravitational potential energy (PE), and total mechanical energy (ME) of the center of mass. Data are for a single diagonal couplet step from a 85 g individual moving at  $1.046\text{ m s}^{-1}$  with a duty factor of 43.75, limb phase of 52.08, % recovery of 1.36%, and total KE–PE phase shift of  $8.18^\circ$ . The diagonal couplet step began when the first limb of the couplet touched the ground and ended when the last limb of the couplet was lifted off.

synchronized trotting gaits were maintained. Non-aerial runs occur in slower runs with less coordinated limb contact times.

## Discussion

### *Locomotor gaits in Monodelphis*

Based on Hildebrand's (1976, 1977, 1980, 1985) broad phylogenetic sample, it is clear that the generalized condition for quadrupedal vertebrates is to use walking gaits (with footfalls more equally spaced for stability and maneuverability) at slower speeds and then switch to running gaits (primarily trots, with diagonal couplets coordinated) to attain higher speeds. We expected to find this pattern of gait change with speed in *Monodelphis domestica*, not only because of its unspecialized body form and semi-erect posture, but also because gait data for other marsupials with similar body shapes show a clear transition from non-trot walking gaits to trotting gaits to increase speed (Hildebrand, 1980; Pridmore, 1992; White, 1990). Moreover, marsupials in these studies rarely used running gaits (duty factors under 50%) thus, we postulated that *Monodelphis* might favor walking gaits and limit, or even avoid, running gaits.

Contrary to these predictions, our results show that *Monodelphis domestica* preferentially utilizes running trots for

steady-speed locomotion on flat surfaces. Over the fivefold range of speeds where the opossums used uniform linear locomotion, limb phases of most strides were around 50%, indicating that diagonal limbs were tightly coordinated; that is, they were trotting. And while limb phases of 14 strides were slightly lower (44–37%, with less synchronized touch-downs and lift-offs of the fore- and hindlimbs), these runs were still dominated by diagonal couplet movements. All but eight steps analyzed had duty factors that fell below 50%, and thus 90% of the steps were characterized as running trots. The remaining steps fell just into the zone describing walking trots (50–54% duty factor; 45–55% limb phase). Although it is clear that opossums are dedicated to trotting gaits across their full range of speeds, evidence for a clear gait transition between walking and running is not obvious given the round shape of the overall cloud of steps in Fig. 1.

We are not suggesting that *Monodelphis* is incapable of performing other walking gaits (besides trots). Indeed, *Monodelphis* moved at slower speeds on the trackway but these locomotor bouts were brief and erratic, never lasting for more than a step or two before the animal turned or stopped. This intermittent locomotor behavior resembled foraging activity (as opposed to steady-state locomotion as when *Monodelphis* preferentially ran with coordinated diagonal limb couplets).

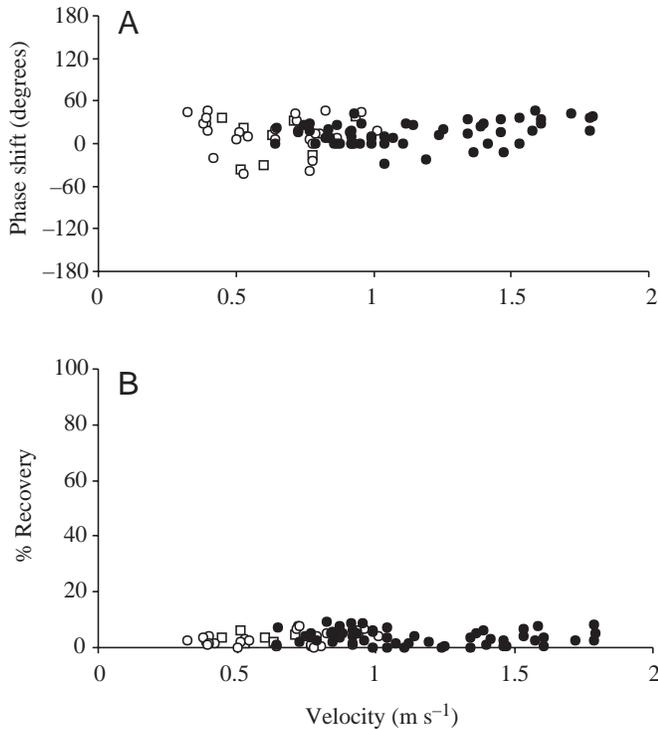


Fig. 3. (A) Phase shift between the fluctuations in total kinetic energy and gravitational potential energy *versus* velocity. Phase shifts around 0° indicate that the two energies are in phase with one another and thus all steps analyzed exhibit spring mechanics. (B) Percentage recovery (measuring the efficiency of pendular mechanics) *versus* velocity. Low values indicate little to no pendular exchange of mechanical energy characteristic of spring mechanics. Note that neither variable changes significantly with speed, indicating that the opossums consistently use spring mechanics over the full range of speeds that they will perform sustained locomotion. Kinematic gaits are indicated by symbols: walking trots, open squares; non-aerial running trots, open circles; aerial running trots, filled circles.

Intermittent locomotion at slow speeds has been reported for squirrels, chipmunks and even cockroaches (Biewener, 1983; Full and Tu, 1990; Heglund et al., 1982). Interestingly, non-trotting walks (lateral-sequence diagonal-couplets walks and singlefoot walks) have been observed in *Monodelphis* during slow treadmill locomotion (Pridmore, 1992; S. M. Reilly and T. D. White, unpublished data). It is possible that the movement of the belt on the treadmill inspired more linear locomotion, but it is also important to note that kinematic stride variables of treadmill locomotion are not precisely equivalent to overground locomotion. For example, horses on treadmills tend to increase stance duration, have earlier forelimb footdowns, and greater fore- and hindlimb retractions (Buchner et al., 1994). If these also characterize slow treadmill locomotion in *Monodelphis*, then greater stance durations would yield higher duty factors (walks) and earlier forelimb footdowns would shift walking gaits further into the lateral sequence singlefoot range of the Hildebrand gait plot. In addition, observations of arboreal locomotion in *Monodelphis*

have verified that lateral sequence diagonal couplets walks and singlefoot walks are normal parts of their locomotor repertoire (Lammers, 2001). In terms of Hildebrand's hypothesis that primitive tetrapods should transition from walking to running gaits with speed, it appears that opossums do transition from singlefoot and lateral-sequence diagonal-couplets walks (when moving intermittently and at low unsustained speeds) to fast walking and running trots for more continuous locomotion and higher speeds.

Finally, aerial phases were not a necessary characteristic of running gaits. In our sample, about a third of the running strides lacked aerial phases. These trials had duty factors that fell below 50%, but were, on average, equivalent in speed to the walking strides (Table 2). The aerial phases were lost when forelimb–hindlimb couplets became slightly unsynchronized during the slower running trots. This is comparable to the condition found among gaited horses (such as the Tennessee walking horse breed), which employ a variety of 4-beat symmetrical gaits and also lose aerial phases at the lower running speeds (Hildebrand, 1965; Harris, 1993). As gaited horses run faster, the duty factor of each limb decreases further and an aerial phase is achieved.

#### *Locomotor mechanics in walking and running gaits*

Our analysis of whole-body ground reaction forces clearly shows that *Monodelphis domestica* preferentially utilized the spring mechanics at all speeds of steady state locomotion on level terrestrial substrates. The force and velocity patterns seen over the duration of a diagonal couplet were similar to those that have been observed in spring mechanics in larger, erect animals such as horses, dogs and kangaroos (Biewener et al., 1981; Budsberg et al., 1987; Cavagna et al., 1977; Kimura and Endo, 1972). Phase shifts between the minima of total kinetic and gravitational potential energies were scattered around 0°, ranging from –42 to 47°, clearly indicating the in-phase relationships of spring mechanics. In addition, percentage recoveries across trials were small (mean 3.5%), indicating that the animals were not utilizing pendular mechanics as an effective energy-saving mechanism, even in walking trots. Furthermore, neither percentage recovery nor phase shift changed with speed (Table 2), revealing that *Monodelphis domestica* maintained the same locomotor mechanics over the fivefold range of speeds used for sustained locomotion. Thus, there was no evidence that they were beginning to transition out of spring mechanics at either end of the speed range. Consequently, very little kinetic–gravitational energy transfer took place in *Monodelphis* during walking trots. The intermittent locomotor behavior of *Monodelphis* at even slower speeds probably interrupts pendular mechanisms so that these, too, would be likely to lack efficient energy exchange and transfer.

This is the first study to explore the relationship between whole body mechanics and Hildebrand gaits explicitly, so we can examine how these two locomotor paradigms can be integrated. Reilly and Biknevicius (2003) predicted that running trots should be associated with spring mechanics and

that spring mechanics may extend into the walking trot gait as well. Both of these predictions are true for opossums. In *Monodelphis*, the Hildebrand trotting gaits from fast walking trots to running trots are clearly associated with spring mechanics (Table 2).

The prediction that fast walking trots might have characteristics in common with spring mechanics (Reilly and Biknevičius, 2003) was based on data displayed in previous studies that suggest that this apparent inconsistency may not be unusual. For example, the fastest walking trials of skinks, rams and turkeys recover very little mechanical energy through pendular mechanisms (see fig. 7 in Cavagna et al., 1977; figs 6 and 7 in Farley and Ko, 1997). Unfortunately these studies did not report gaits, so the relationship between gait and changes in mechanics cannot be directly examined. Among invertebrates, slow and fast locomotion of cockroaches have been variously described as 'walking' or 'running' (Hughes, 1952; Kozacik, 1981) yet only the energy fluctuation patterns associated with bouncing gaits have been reported (Blickhan and Full, 1987; Full and Tu, 1990), suggesting that cockroaches use spring mechanics at nearly all speeds as well. Additionally, lizards use spring mechanics in trots with greater than 50% duty factors (S. M. Reilly and K. L. Hickey, unpublished data) and non-aerial spring mechanics can be obtained in humans when they 'Groucho walk' (McMahon et al., 1987). Furthermore, locomotor data on *Monodelphis*, together with those on lizards (S. M. Reilly and K. L. Hickey, unpublished data) and cockroaches (Full and Tu, 1990), reveal that while steps with aerial phases are usually associated with spring mechanics, the lack of an aerial phase does not exclude a gait from having in-phase energy fluctuations. Thus, the time course of mechanical energy fluctuations characteristic of spring mechanics can occur in both walking and running trotting gaits. Further work is needed to examine how far spring mechanics can extend into slower walking, trotting gaits and if slower trots can have pendular mechanics.

#### *Why is Monodelphis dedicated to spring mechanics and trotting gaits?*

The key to saving energy with spring-like limbs is the use of elastic elements of the musculoskeletal system, and several have been identified (Biewener and Baudinette, 1995; Biewener and Roberts, 2000). Although elastic recoil of cross-bridges in muscles may save some mechanical energy, the most likely sources of elastic energy recovery are tendons and ligaments in the limbs (Alexander et al., 1982; Biewener and Baudinette, 1995; Cavagna et al., 1977). The tendons and ligaments of species that display the greatest specialization for elastic energy recovery (ungulates, dogs, hopping kangaroos and humans) are typically long and slender (Biewener et al., 1998; Cavagna et al., 1977; Ker et al., 1987, 1988), a condition that also increases locomotor efficiency by reducing distal limb mass (Biewener and Baudinette, 1995). Elastic strain energy, stored and then released from these 'biological springs', reduces significantly the amount of work that muscles must supply in order to efficiently locomote at high speeds and for

long distances. Energy savings *via* elastic recoil may be as high as 30–50% (Biewener et al., 1995, 1998; Farley et al., 1993).

Although the spring-mass model has gained general acceptance for larger, cursorial mammals, it is believed that the tendons of smaller and less cursorially adapted mammals may not be capable of storing large amounts of elastic strain energy as their shortness and relative thickness render them poor springs at best (Biewener et al., 1981). Furthermore, to date, there is no empirical support for significant energy savings by summing small amounts of potential energy stored in serially arranged elastic elements. Acknowledging that *Monodelphis* is a small mammal (<150 g) with a semi-erect, crouched posture, it seems improbable that their tendons are capable of storing sufficient energy for useful elastic energy recovery when running. Nonetheless, *Monodelphis* clearly prefer to use spring mechanics with coordinated diagonal couplets over their entire range of steady-state locomotor speeds. One possible explanation is that *Monodelphis* does not use biological springs for energy recovery to any significant extent, that is, it may simply pay for running with muscular work.

Support for this hypothesis comes from recent studies of abdominal muscle function during locomotion in marsupials. Didelphid opossums (and probably most marsupials possessing epipubic bones) have a unique cross-couplet body stiffening mechanism powered by muscles (Reilly and White, 2003). Electromyographical patterns of abdominal muscles (extending from the rib cage on one side through the midline to the contralateral epipubic bone and femur) are activated asymmetrically across a couplet in concert with the stance period of the diagonal limbs of that couplet. The asymmetrical firing of these muscles in conjunction with the elevation of the movable epipubic bone effectively forms a tightening sling across each diagonal limb couplet as the animal bounces on it. This functional mechanism appears to stiffen the trunk across each couplet during the step. Perhaps *Monodelphis* prefers the running trot gait rather than other possible gaits because it employs this unique cross-couplet firing mechanism. It is possible that the cross-couplet support mechanism largely restricts *Monodelphis* to using couplet-dominated trotting gaits for any kind of sustained locomotion. Indeed, *Monodelphis* in this study continued to use a running trot at speeds three times greater than the speed at which rats shift to a gallop (Gillis and Biewener, 2001). We hypothesize that use of the cross-couplet muscle linkage produces the mechanical energy patterns characteristic of a spring mechanics. Thus, *Monodelphis* appears to simply pay for locomotion with muscular activity, and this involves both appendicular and abdominal muscles.

Spring mechanics are highly correlated with a running gait in *Monodelphis*, but the assumption that spring mechanics are associated with passive spring storage appears to be tenuous for non-cursorial mammals with semi-erect postures. Paying for locomotion with muscular work may be the primitive condition for mammals. Further work on animal locomotor dynamics should look for other possible ways that semi-erect and sprawling forms may be choosing gaits and coping with the costs typically associated with bouncing mechanics. Future

studies integrating mechanics with gaits will begin to illuminate the energetic consequences of particular gaits, why certain gaits are preferred, and how the neural control of an array of musculoskeletal systems can move the limbs to modulate patterns of whole body mechanics.

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