Differential leg function in a sprawled-posture quadrupedal trotter

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Summary

Legs of sprawled-posture, quadrupedal trotting geckos (*Hemidactylus garnotii*) each functioned differently during constant average-speed locomotion. The center of mass decelerated in the first half of a step and accelerated in the second half, as if geckos were bouncing in fore–aft and side-to-side directions. Forelegs decelerated the center of mass only in the fore–aft direction. Hindlegs provided all the acceleration in the latter half of the step. Lateral ground reaction forces were always directed toward the midline and exceeded the magnitude of fore–aft forces. The differential leg function of sprawled-posture geckos resembled sprawled-posture hexapods more than upright-posture quadrupeds. The pattern of leg ground reaction forces observed may provide passive, dynamic stability while minimizing joint moments, yet allow high maneuverability. Integrating limb dynamics with whole body dynamics is required to resolve the trade-offs, if any, that result from stable sprawled-posture running with differential leg function.

Key words: biomechanics, locomotion, dynamics, leg function, mechanical stability, running, quadruped, gecko, *Hemidactylus garnotii*.

Introduction

Simple spring-mass templates effectively model the center of mass (COM) dynamics of diverse legged runners (Blickhan, 1989; Cavagna et al., 1977; Full and Koditschek, 1999; Herr et al., 2002; McMahon and Cheng, 1990). Initial decelerations of the body in the first half of a step are followed by comparable accelerations in the second half. Remarkably, two-, four-, six- and eight-legged runners produce similar whole body ground reaction force (GRF) patterns when bouncing at a constant average-speed (Blickhan and Full, 1987, 1993; Cavagna et al., 1977; Farley et al., 1993). Both horizontal and sagittal plane templates demonstrate the extraordinary capability to self-stabilize (Kubow and Full, 1999; Altendorfer et al., 2002; Schmitt et al., 2002; Schmitt and Holmes, 2000a,b; Seyfarth et al., 2002). To test hypotheses of control and energy management as they relate to diversity in form and function, we must anchor these simple templates in sufficiently elaborate models. Leg number and posture represent two of the most obvious differences in a runner's morphology. How leg number and posture interact to produce the common dynamics of the COM observed in diverse species remains a challenge.

A simple way to operate legs during running is to have them all function as passive springs that first decelerate and then accelerate the COM in the fore–aft direction (Fig. 1A). Similar spring-like leg function has been discovered in upright-trotting quadrupeds (Cavagna et al., 1977; Jayes and Alexander, 1978) and built into bouncing robots (Raibert et al., 1986). Peak force magnitudes vary depending on mass distribution and asymmetries, but decelerations followed by accelerations remain the general pattern in upright-posture, trotting quadrupeds (Alexander, 2003; Biewener, 2003; Lee et al., 1999; Witte et al., 2002). Full et al. (1991) discovered differential leg function in trotting, sprawled posture runners (Fig. 1B). Cockroaches use an alternating tripod as they bounce forward with individual legs producing large lateral and opposing GRFs. Forelegs only decelerate the COM during a step period, whereas hindlegs only accelerate the body. Middle legs first decelerate and then accelerate the COM, much like the pattern in upright-posture quadrupeds. Differential leg function in sprawled posture runners can minimize joint moments, but still enable maneuvers such as rapid turning (Jindrich and Full, 1999). Lateral forces generated as insects bounce from side to side can contribute to passive, dynamic self-stabilization in the horizontal plane (Kubow and Full, 1999; Schmitt et al., 2002; Schmitt and Holmes, 2000a,b; Seipel et al., 2004).

Upright-posture quadrupeds exhibit differential leg function during high-speed gaits and unsteady locomotion. During galloping and bounding the forelegs of dogs and horses (Cavagna et al., 1977; Gregersen et al., 1998; Heglund et al., 1982) and small therian mammals (Heglund et al., 1982; Witte et al., 2002) produce primarily decelerating forces, whereas the hindlegs accelerate the body. When speeding up, the hindlegs of trotting dogs generate more acceleratory force than the
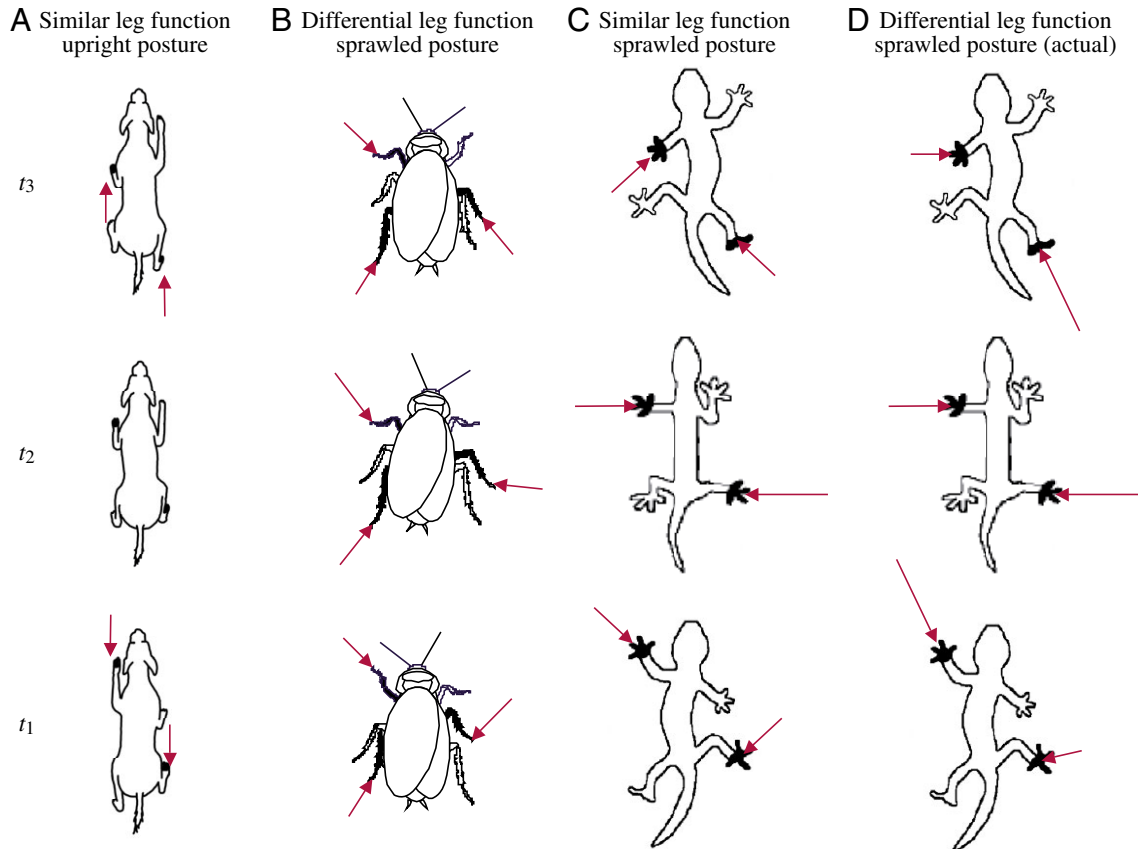
Fig. 1. Horizontal plane GRFs in upright- and sprawled-posture trotters during a step when running at a constant average speed. (A) Upright-posture quadruped running with similar leg function. Fore- and hindlegs first (t_1) both generate decelerating fore–aft forces (arrows) followed by an accelerating force later in the step (t_3). No lateral GRFs are present. (B) Sprawled-posture hexapod running with differential leg function. Fore- and middle legs first (t_1) both generate decelerating forces, while the hindleg generates an accelerating force (Full et al., 1991). All legs develop large lateral forces directed toward the midline. At midstep (t_2) forelegs continue to generate decelerating forces and the hindleg an accelerating force. The middle leg only develops a lateral force. At the end of the step (t_3), the foreleg generates a decelerating force. Hind- and middle legs both generate accelerating forces. (C) Hypothetical sprawled-posture quadruped running with similar leg function resulting from adding opposing lateral forces to the upright posture pattern in A. Fore- and hindlegs first (t_1) both generate decelerating forces followed by an accelerating force later in the step (t_3). Lateral GRFs were added assuming sprawled-posture animals tend to produce them. Horizontal forces sum to produce a clockwise yaw throughout the step. (D) Sprawled-posture quadruped running with differential leg function. GRFs approximate those measured in the present study on geckos. The foreleg first (t_1) generates the majority of fore–aft decelerating force. At midstep (t_2), fore- and hindlegs only generate lateral forces directed toward the midline. Later in the step (t_3) hindlegs generate all of the fore–aft accelerating force. The major decelerating force by the foreleg (t_1) and accelerating force by the hindleg (t_3) are directed to the animal's COM, reducing yaw, and are aligned axially along the leg, reducing joint moments.

forelegs (Lee et al., 1999). When slowing down, forelegs generate the majority of the deceleration. During constant average speed trotting, both fore- and hindlegs of dogs generate decelerations and accelerations, but the mean leg force can be deceleratory for the foreleg and acceleratory for the hindleg, demonstrating differential leg function in the sagittal plane (Lee et al., 2004). Simulations suggest that directionally compliant legs result in a fore–aft force bias that passively reduces pitch (Lee and Meek, 2005).

To determine the mechanical implications of posture and leg number, we measured leg function during trotting in a gecko, a sprawled-posture quadruped. We tested the hypothesis that sprawled-posture quadrupeds use fore- and hindlegs similarly to decelerate and subsequently accelerate the COM in the

fore–aft direction during each step. Alternatively, sprawled-posture quadrupeds could exhibit differential leg function with large lateral and opposing leg GRFs, like arthropods. If legs function differently, then we predict that forelegs will generate decelerations of the COM, hindlegs will produce accelerations and all legs will create large, opposing lateral forces during a step.

Sprawled-posture, trotting lizards produce spring-mass dynamics of the COM typical of other legged runners (Farley and Ko, 1997; Ritter, 1996). However, whole body GRF data are insufficient to make conclusions about single leg function if more than one leg is in contact with the ground simultaneously. The hindleg of lizards has been hypothesized to be the primary propulsor (Irschick and Jayne, 1999; Jayne

and Irschick, 1999; Reilly and Delancey, 1997a,b). However, single leg GRF data for the hindleg of iguanas show decelerations followed by accelerations, supporting the hypothesis of similarity in leg function (Blob and Biewener, 2001). To examine leg function in four-legged, sprawled-posture runners, we selected the gecko *Hemidactylus garnotii*. These geckos are rapid runners with masses similar to those of the hexapods studied to determine sprawled-posture leg function (Full et al., 1991). The geckos we selected here are also extraordinary at rapid vertical climbing (Autumn et al., 2005; Irschick et al., 2003). Our choice of experimental animal provides an opportunity to compare running directly with climbing, further elucidating the advantages and disadvantages of differential leg function, posture and leg number.

Materials and methods
Animals

Hemidactylus garnotii Diméril and Bibron 1836 (2.55±0.27 g body mass, mean ± s.d., N=5) snout–vent length 5.57±0.27 cm (mean ± s.d.) were obtained from a commercial collector (Glades Herp, Bushnell, FL, USA). Geckos were housed in individual containers in an animal care facility and fed with a diet of water, crickets and a vitamin mineral supplement. All animals were kept on a local photoperiod at ambient temperatures (25±2°C). Immediately prior to trials, geckos were kept in an environmental chamber set at 31.5±0.5°C.

Kinematics

Three high-speed digital cameras (Redlake Motionscope, Tucson, AZ, USA) operating at a rate of 1000 frames s^{-1} captured the geckos' motion. One camera recorded the dorsal view, and the other two cameras recorded the left and right dorso-ventral views. An external trigger simultaneously generated a pulse on the data acquisition system and lit LEDs in the three camera views to synchronize the video with the measured forces.

Twenty landmarks painted on each gecko with correction fluid to facilitate digitization. Eight of these points were on the dorsal midline of the gecko: one in the middle of the head (snout), one between the shoulders (pectoral), three on the trunk, one between the hips (pelvic) and two on the tail. Each leg contained three points: one on the shoulder/hip, one on the elbow/knee and one on the foot. Video frames were transferred and the coordinates of various positions on the body at each frame were digitized into a computer (Gateway 2000, Irvine, CA, USA) using a motion analysis system (Motus, Peak Performance Technologies, Inc., Lake Forest, CA, USA). The data were filtered using a low-pass Butterworth filter with a cut-off frequency of 30 Hz.

To calculate the average forward velocity of the animal, we digitized the pectoral or pelvic point from the dorsal camera view as the gecko ran across the force platform. Video recordings were used to gather footfall data. Relative phase

was calculated as the time elapsed between when a forelimb or hindlimb contacted the ground relative to the stride period. A stride period was defined as the time between consecutive footfalls of either the fore- or hindfoot when the animal was on the force platform. Legs contacting the ground at the same time have an equal relative phase, whereas legs in antiphase have relative phase values equal to 0.50.

Axial or lateral bending was calculated by using three of the points along the trunk of the gecko, the pectoral, the second point on the trunk and the pelvic point. We calculated joint moments using both kinematic and force platform data. The angles between the shoulder/hip and foot with respect to the horizontal plane were calculated in the anterior, lateral and dorsal planes. This was compared to the vector angle formed by GRFs in each plane.

Ground reaction force measurement

Geckos ran from a darkened box 0.55 m across a force platform into another darkened box 0.15 m away. The floor of the track was made out of balsa wood and walls were constructed from Plexiglas and polished with Brillianize (Chemical Products Co. Inc., Omaha, NE, USA) to prevent geckos from clinging to the side of the track. The track was long enough to allow the animals to achieve and maintain a constant average velocity for at least one stride across the length of a force platform. Trials were selected for analysis if they contained one complete stride in which the sum of the increases and decreases in velocity were less than 15% of the average forward velocity of the animal. The degree of divergence was determined by integrating fore–aft force at the time of data collection.

Vertical, fore–aft and lateral GRFs were measured using a force platform (0.11 m×0.06 m). The design and performance of the force platform have been described previously (Full et al., 1991; Full and Tu, 1991). Forces were measured from the signals produced by semi-conductor strain gauges bonded to spring blades at each corner of the force platform. Loads in the range 0.0001–0.1 N produced a linear response, and peak GRFs never exceeded 0.1 N. Signals from each force platform channel were amplified (Vishay, Measurements Group, Malvern, PA, USA) and collected by a 16-bit data acquisition system (National Instruments, Austin, TX, USA) on a computer (Apple Power Macintosh) at a frequency of 5000 Hz. Force signals were filtered using a Butterworth low-pass filter at a cut-off frequency of 150 Hz (unloaded natural frequency of the plate was greater than 400 Hz). Crosstalk between vertical, horizontal and lateral outputs was less than 5%.

Whole body dynamics
Velocity and position changes of the center of mass

Whole body GRFs were used to determine the velocities and position and energy changes of the center of mass (COM) over an integral number of strides (Biewener and Full, 1992; Cavagna, 1985). Integrating the fore–aft GRFs when the whole body of the animal was positioned on the force platform yielded the fluctuations of the fore–aft velocity of the COM.

The integration constant for the fore–aft velocity was the average speed over the force platform determined from the kinematic analysis. Fluctuations in the vertical velocity of the COM were found by integrating the vertical force minus the body weight. We only accepted trials for which the integration of vertical force over a stride equaled body weight as measured by a separate scale. Integrating the vertical velocity again yielded the vertical displacement of the COM, assuming the average height of the COM did not vary over an integral number of strides. Integrating the lateral forces gave the fluctuations of lateral velocity of the COM. Integrating the lateral velocity again yielded the lateral displacement of the COM, assuming the average position of the COM did not move left or right over an integral number of strides.

Energy changes of the center of mass

The kinetic and gravitational potential energy of the COM were calculated from the fore–aft velocity and vertical displacement of the COM, respectively (Blickhan and Full, 1992). The total external mechanical power used to lift and accelerate the COM over one stride was found by summing the positive increments in total mechanical energy for a stride and dividing by the stride period. The lateral kinetic energy of the COM was calculated from the lateral velocity by summing the positive increments in mechanical energy, assuming zero energy storage and return.

Single leg ground reaction forces

Single leg force data were collected from trials that began or ended with a single foot on the force platform. Single leg forces were included when the stride before or after was determined to be constant average speed. These forces were used to determine the alignment of the GRF relative to the position of the joint centers of the leg. Angles in the anterior view were determined at mid-stance, a phase of 0.5 within a step. Angles in the lateral and dorsal view were determined at a phase of 0.20 within a step for the forelegs and 0.70 for the hindlegs.

Statistical analysis

We used a nested analysis of variance model (NANOVA) to account for the effects of measuring individuals more than once. We used NANOVA instead of repeated-measures ANOVA since the number of measurements within individuals varied from 1 to 6. For all statistical analyses, we used a commercial statistical program (StatView 5.1, SAS, Cary, NC, USA) on a computer (Apple, Macintosh). Values are means ± standard deviations (s.d.) unless otherwise noted.

Results

Kinematics

Geckos ran with velocities ranging from $0.28\,\mathrm{m\,s^{-1}}$ and $0.75\,\mathrm{m\,s^{-1}}$, mean=$0.47\pm0.13\,\mathrm{m\,s^{-1}}$. Mean stride frequency was $13\pm2\,\mathrm{Hz}$, but varied with velocity, v (Fig. 2). Stride frequency (F_S) increased linearly as a function of velocity
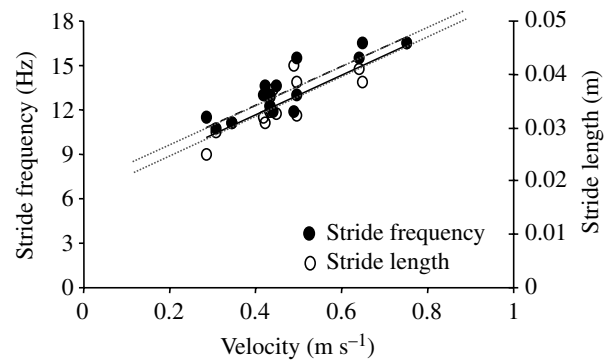

Fig. 2. Stride frequency and stride length as a function of velocity. Solid circles represent stride frequency and open circles represent stride length ($N=5$). Both stride frequency and stride length increased as velocity increased. Stride frequency is represented the solid line and stride length by the broken regression line. For regression equations, see text.

($F_S=6.09+13.7v$; $r^2=0.78$; ANCOVA, $F=42.5$; d.f.=1,13; $P<0.0001$). Stride length (L_S) increased linearly as a function of velocity ($L_S=0.02+0.04v$; $r^2=0.77$; $P<0.0001$). Duty factor (DF) for all four limbs averaged 0.43 ± 0.03 with no significant effect of speed (DF=$0.479-0.106v$; $r^2=0.203$; ANCOVA, $F=3.06$; d.f.=1,13; $P=0.106$). Duty factor (DF) for hindlegs (0.46 ± 0.06) was significantly longer then for forelegs (0.42 ± 0.05; $t=-2.52$; d.f.=39; $P=0.016$).

Geckos used a trotting gait characterized by pairs of diagonal limbs hitting the ground synchronously (Fig. 3). We measured phase shift as a value between 0 and 1, with 1 indicating an in-phase relationship and 0.5 indicating anti-phase. Diagonal limb phase averaged 0.92 ± 0.06 ($N=11$) for the right hindleg–left foreleg pair and 0.94 ± 0.03 ($N=12$) for the left hindleg–right foreleg pair. The contralateral limb pairs moved in antiphase with its diagonal pair (0.48 ± 0.07, $N=51$). Speed had no significant effect on limb phase (ANCOVA, $F=0.122$; d.f.=1,72; $P=0.73$; power=0.06).
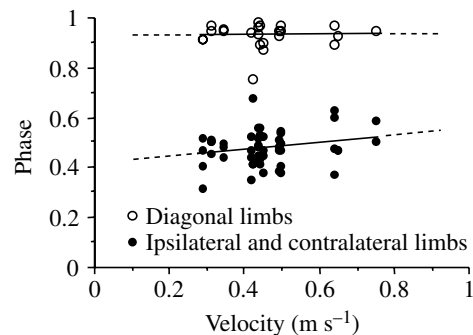

Fig. 3. Limb phase *vs* velocity. A phase of 1 indicates that limbs hit the ground synchronously; a phase of 0.5 indicates that limbs are in antiphase. Diagonal limbs were in phase whereas ipsilateral (left and right) limbs and contralateral (same side fore- and hind-) limbs were in antiphase. (Ipsilateral and contralateral limbs=$0.93+0.01v$; $r^2=0.001$. Diagonal limbs=$0.47+0.14v$; $r^2=0.55$).

Lateral flexion was greatest during the initial footfall at phase 0.03±0.04; the magnitude of bending was 20.1±6.32° (Fig. 4A). Lateral trunk bending became rectilinear through midstance and continued flexing attaining a maximum at phase 0.81±0.08 with 19.4±5.60°.

Whole body dynamics

Ground reaction forces

Normal. GRFs in the normal direction produced during the stance phase oscillated around the body weight and decreased to zero during an aerial phase (Fig. 4C; red line). No negative

normal reaction forces were produced, indicating that geckos did not exert dectectable detachment forces. Over one stride (two steps), two distinct force maxima occurred at phases 0.21±0.04 and 0.71±0.04, respectively for each diagonal couplet, and peak magnitudes attained 2× body weight (Fig. 5A).

Fore–aft. GRFs in the fore–aft direction showed a decelerating force driving the animal's COM rearwards followed by an accelerating force propelling the animal's COM forward (Fig. 4C; blue line). Peak fore–aft forces occurred at phases 0.10±0.04, 0.33±0.04, 0.60±0.07 and 0.83±0.03 (Fig. 5B). Peak magnitudes were one-third the normal force.

Lateral. Fore- and hindlegs summed to accelerate the COM in the lateral direction. Left foreleg and right hindleg couplets summed to produce a lateral GRF acting on the COM directed to the left (Figs 1D, 5C). Right foreleg and left hindleg couplets summed to produce a lateral GRF directed to the right (Fig. 5C). The lateral GRF pattern was more variable than the vertical and fore–aft force pattern. A single maximum per step occurred in the six trials. Nine trials with more variable footfall phases showed more than one lateral GRF peak per step. To make a general conclusion about the lateral GRF pattern, we examined additional data serving as a control for a separate study but using the same animals, equipment and experimental conditions (Irschick et al., 2003). Thirteen of a total of 15 trials displayed a lateral GRF pattern with a single maximum per step, as depicted in Fig. 5C. Peak magnitudes of the summed lateral force were one-half the peak normal force.

Velocity and energy changes of the center of mass

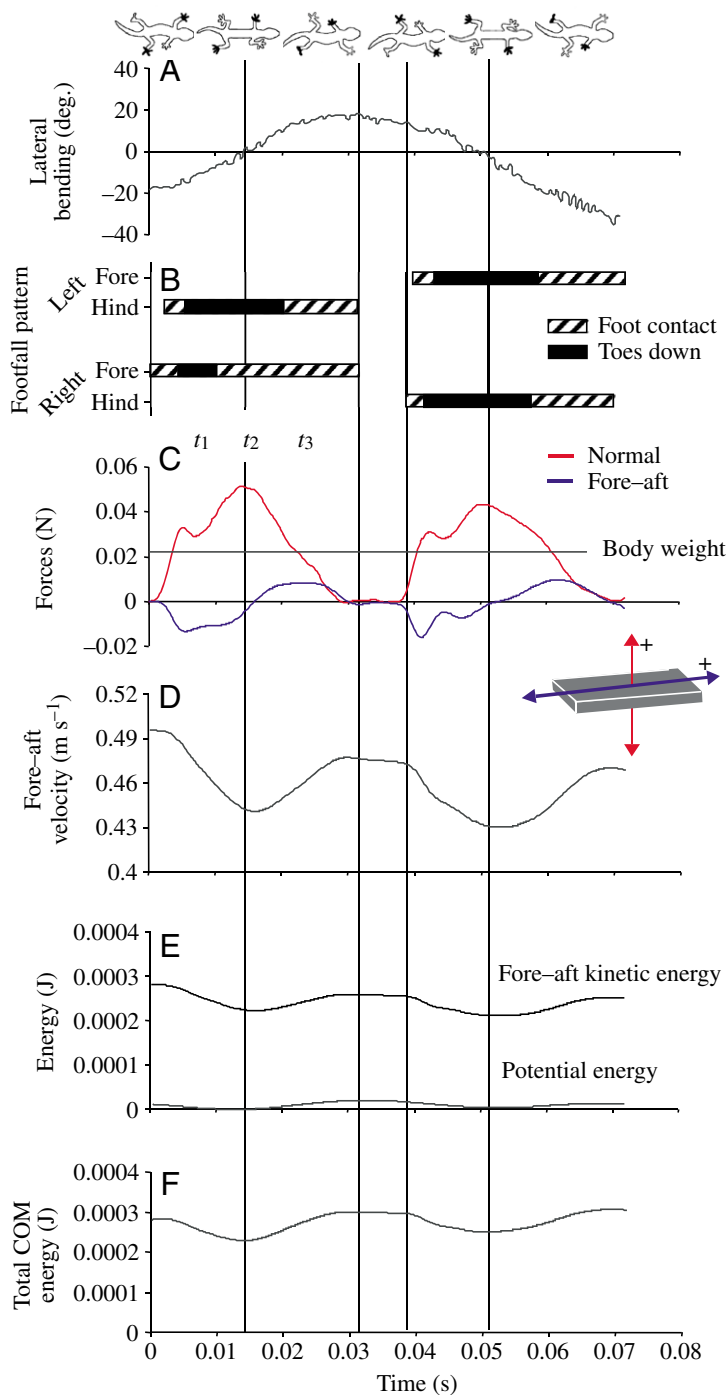Velocity in the fore–aft direction fluctuated as the

Fig. 4. Gait, lateral bending, force, velocity and energy of the COM over one stride (two steps) of a 2.3 g (0.023 N) *Hemidactylus garnotii* running on the level at 0.50 m s⁻¹. (A) Tracing of gecko running where a solid black foot represents a foot in contact with the substrate. Minimum lateral trunk bending occurred at midstep. (B) Footfall patterns indicated a trotting gait where a fore- and hindleg couplet hit the ground simultaneously followed by the opposite fore- and hindleg couplet. Solid areas in the bars represent toes down whereas striped bars show the time it takes to attach and detach feet. (C) Whole body GRFs of one stride from the force platform. Red lines, normal forces; blue lines, fore–aft forces. Normal forces fluctuate around body weight. A brief aerial phase was observed midstride. Fore–aft forces decelerate and accelerate the COM in each step similar to that of a forward-bouncing, spring-loaded, inverted pendulum. (D) Integration of fore–aft force yields fore–aft velocity of the COM. Velocity dropped to a minimum during midstep and was at a maximum during midstride. Despite the fluctuating velocity, the gecko maintained a constant average velocity of ±10%. (E) Fore–aft kinetic energy and gravitational potential energy of the COM fluctuated in phase. (F) Total energy of COM.
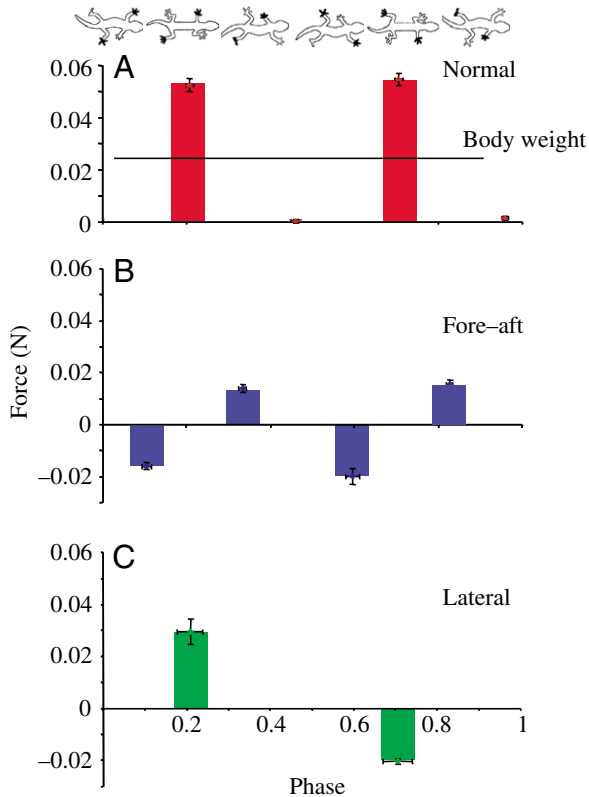
Fig. 5. Whole body peak GRF magnitudes and phases. Values are means ± 1 s.e.m. One phase is equal to one complete stride or two steps. (A) Normal force peaked at approximately twice body weight (broken line). (B) Peak fore–aft forces decelerated and then accelerated the COM at each step with forces about 40% of the normal forces. (C) Lateral force accelerated the COM to the right followed by an acceleration to the left.

COM decelerated and accelerated (Fig. 4D). Fore–aft kinetic energy and gravitational potential energy of the COM fluctuated in phase (Figs 4E, 6). Total mechanical energy of the COM fluctuated as the sum of fore–aft kinetic energy and gravitational potential energy (Fig. 4F). The mass-specific, mechanical power (E_{cm}) used to lift and accelerate the COM increased linearly with speed and was not significantly affected by individual (ANOVA; $E_{cm}= 0.24+1.89v$; $r^2=0.50$). Mass-
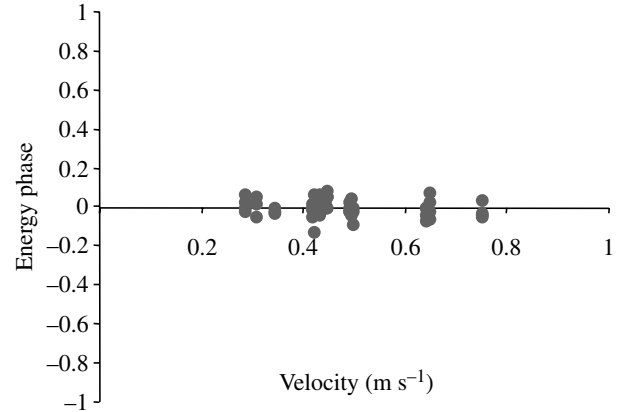

Fig. 6. Phase shift between peak gravitation potential energy and fore–aft kinetic energy *vs* velocity. A phase shift of zero means the fluctuations are in phase, whereas phase shifts of 0.5 shows that fluctuations are in antiphase.

specific, lateral mechanical power increased linearly with speed ($E_{lat}=0.042+2.36v$; $r^2=0.26$) and was on average 85±14% of E_{cm}.

Single leg forces

Measuring single leg forces at the beginning and end of a run when only one leg was in contact with the force platform demonstrated that geckos have differential leg functions. Right and left, and fore- and hindlegs generated different GRF patterns (Fig. 7; Table 1).

Normal. Peak normal GRFs were evenly distributed among fore- and hindlegs during trotting (Table 1; Fig. 7). Individual legs did not generate measurable detachment forces, shown by the absence of negative normal forces.

Fore–aft. Fore- and hindlegs summed to produce the COM pattern where a deceleration was followed by an acceleration in the fore–aft direction, but each leg functioned differently. Forelegs only produced decelerating forces early in the step at phase 0.20±0.01 (Table 1; Fig. 7A,C). Hindlegs produced both decelerating and accelerating forces in the fore–aft direction. Accelerating forces of the hindleg occurred late in the step (0.69±0.02) and were twice the magnitude of the decelerating forces.

Table 1. *Peak single leg ground reaction force magnitudes and phases during a step*

Leg	Normal		Fore–aft		Lateral	
	Phase	Force (mN)	Phase	Force (mN)	Phase	Force (mN)
Fore-	0.37±0.04 (10)	27.7±3.06 (10)	0.20±0.01 (10)	−15.0±1.50 (10)	0.34±0.04 (10)	15.7±2.77 (10)
Hind-	0.46±0.02 (14)	28.7±2.42 (14)	0.20±0.03 (13)	−6.97±1.28 (13)	0.45±0.03 (13)	21.7±1.89 (13)
			0.69±0.02 (14)	14.0±1.40 (14)		
Right					0.40±0.03 (8)	−20.0±2.50 (8)
Left					0.42±0.04 (16)	16.7±2.20 (16)

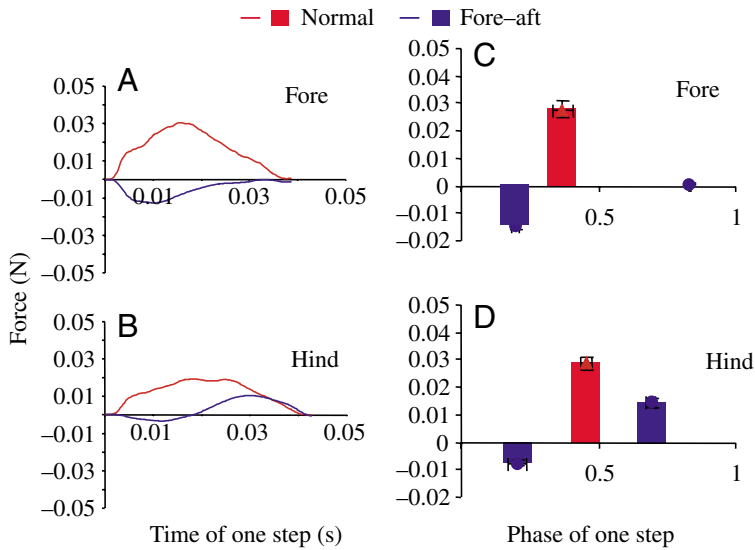Values are means ± s.e.m.; *N* values are given in parentheses.

Fig. 7. Single leg peak GRFs of one step measured when only one foot was on the force platform. Red lines and bars represent normal forces, whereas blue lines and bars represent fore–aft forces. Values are means ± s.e.m. (A) Forefoot GRF tracing from a single individual. (B) Hindfoot GRF tracing from a single individual. (C) Mean peak forefoot GRF magnitudes and phases (*N*=10). (D) Mean peak hindfoot GRF magnitudes and phases (*N*=14). Fore- and hindfeet both produce positive normal forces, showing geckos did not exert any detachment force.

Lateral. Whole body lateral forces showed that the gecko's COM oscillated from side to side each step as it ran forward. Single leg forces revealed that lateral GRFs always pointed toward the midline of the body (Table 1). Hindleg lateral forces exceeded those measured in the forelegs. The peak magnitude of single leg lateral forces was equal to or greater than the peak fore–aft forces.

GRF vector orientation. All peak single leg GRFs were directed axially along the leg toward the COM (Table 2). In Table 2, we compare the single leg force vector orientation with the position of the joints for fore- and hindlegs. The angles of the force vectors represented in Table 2 are shown in Fig. 8. There were no differences for left *vs* right sides.

Discussion

Legs of sprawled-posture, quadrupedal trotting geckos each functioned differently during constant average speed locomotion on the level (Fig. 1D). Whole body dynamics were typical of a spring-loaded, inverted pendulum template (Alexander, 2003; Blickhan, 1989; Schwind and Koditschek,

1997; Blickhan and Full, 1993; Farley et al., 1993; McMahon and Cheng, 1990; Raibert et al., 1986; Figs 4, 5, 8A). Forelegs only decelerated the COM in the fore–aft direction (Fig. 7; Table 1). Hindlegs provided all the acceleration in the latter half of the step. Lateral GRFs were always directed toward the midline and exceeded the magnitude of fore–aft forces. Thus, the differential leg function of sprawled-posture geckos resembled sprawled-posture hexapods more than upright-posture quadrupeds (Fig. 1A,B,D). The advantages and disadvantages of differential leg function as it relates to whole body stability, maneuverability and energetics remain to be explained.

Sprawled posture increases pitch and roll stability

Pitch

Differential leg function in upright-posture quadrupeds has been hypothesized to assist in the control of a body's pitch (Herr et al., 2002; Lee et al., 1999). The body axis tends to pitch nose-down in the sagittal plane when the COM is decelerated and nose-up during accelerations. Trotting labradors and greyhounds redistribute vertical impulses of their fore- and

Table 2. *Angles of individual leg ground reaction force and joint position vectors*

| | View (degrees) | | | | | | | |
| | Anterior | | | Lateral | | | Dorsal | |
Leg	Force vector	Shoulder/ hip joint	Elbow/ knee joint	Force vector	Shoulder/ hip joint	Force vector	Shoulder/ hip joint
Fore- (*N*=10)	63.8 ±16.3 (θ_A)	40.2±12.1	37.3±10.8	53.9±9.3 (θ_{LF})	30.9±11.1	54.6±13.0 (θ_{DF})	36.5±10.7
Hind- (*N*=14)	50.9±12.6 (θ_A)	31.0±8.7	31.0±11.3	50.7±11.3 (θ_{LH})	23.6±6.5	62.0±15.8 (θ_{DH})	38.5±12.1
All	57.3±15.6	35.6±11.3	34.2±11.2	52.3±10.2	27.3±9.6	58.3±14.5	37.5±11.1

Values are means ± s.e.m.
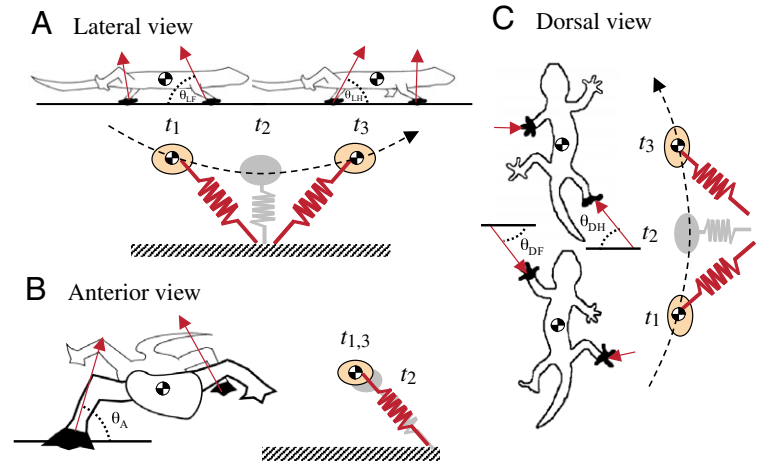See Fig. 8 for labeled angles.

Fig. 8. Single leg GRFs compared with the hypothesized templates for whole body dynamics. (A) Lateral or sagittal view. Individual leg GRFs represented by red arrows at the beginning of the step (t_1) and toward its end (t_3). Below is the corresponding spring-loaded inverted pendulum representing the COM dynamics. (B) Anterior view. Peak forces are represented by red vectors at midstep (t_2). To the right is a simple mass on top of a spring that represents the summed action of both legs as the animal's bounces down and to its left. (C) Dorsal view. Individual leg GRFs represented by red arrows at the beginning of the step (t_1) and toward its end (t_3). To the right is the corresponding lateral spring representing the COM dynamics.

hindlegs to stabilize the pitch moments created by fore–aft accelerating and decelerating forces (Lee et al., 1999). Both fore- and hindlegs generate decelerations followed by accelerations during trotting. However, the mean individual leg forces do not sum to zero. When slowing the body down, the dogs' forelegs produce the majority of the decelerating force. When speeding up, hindlegs generate the bulk of the accelerating force. Even during constant average-speed trotting, the mean leg force is deceleratory for the foreleg and acceleratory for the hindleg (Lee et al., 2004). Similar fore–hind patterns have been reported during trotting in sheep (Jayes and Alexander, 1978). Lee et al. (2004) successfully manipulated antero-posterior mass distribution in dogs by adding loads to the limb girdles. Added load to the pelvic girdle resulted in a greater foreleg braking bias and a lesser hindleg propulsive bias, in addition to an increase in the relative contact time of the experimentally loaded limb. Lee et al. (2004) predicted that lizards, which support more weight on their hindlegs, would show smaller hindleg propulsion biases and greater hindleg duty factors relative to the forelegs. In fact, this appears to be exactly what we observe in the present study on geckos.

Sprawled-posture locomotors can actively reduce pitching. Sideways-moving rock crabs increase their stance length in water relative to air, thereby increasing stability against overturning by hydrodynamic forces (Martinez et al., 1998). As velocity increases, trotting cockroaches reduce the destabilizing effects of increased momentum by moving their COM posteriorly within the triangle of support (Ting et al., 1994). This shift makes cockroaches less likely to tumble by being carried forwards and out of the base of support by inertial forces, should they stop abruptly. Although active adjustments have been observed, sprawled-posture animals appear to be far more passively stable than upright posture animals with respect to overturning moments in vertical planes. The low height of the COM of sprawled-posture runners increases stabilizing moments, while their long and wide support base decreases overturning moments (Alexander, 1971; Martinez et al., 1998; Ting et al., 1994). Because geckos such as *H. garnotii* have a very low COM,

long bodies and a tail, overturning in the sagittal plane is less likely than in upright-posture quadrupeds (Walter and Carrier, 2002). In gecko locomotion, deceleration of the COM by the foreleg early in the step that resulted in nose-down pitch appears to be easily corrected by the hindleg acceleration later in the step (Fig. 8A).

Roll

Stability in roll or lateral stability has received less attention than pitch, except in human posture and locomotion focusing on aging and disease (Zettel et al., 2002). Long bodies and a tail provide little resistance to roll. If a pedestrian's COM is low, then at least two options are available for rapid running. Short legs must operate at high frequencies or legs can produce longer stride lengths by projecting laterally. Laterally projecting legs decrease roll overturning moments. In cockroaches, peak rolling moments during unperturbed running can spin the body by more than 360° in the time it takes to complete one step (Ting et al., 1994). These moments cause the cockroach's body to roll toward the middle leg of the tripod at the end of each step. Moments generating roll to one side in one step are balanced by the opposite moment in the next step, maintaining dynamic stability over each stride.

Trotting quadrupeds do not have the advantage of a hexapod's statically stable tripod, nor can they roll to a side where two legs have an opportunity for a foothold (Ting et al., 1994). Still, we found that on ideal terrain, the laterally projecting legs in geckos dynamically balanced roll moments over the stride. Normal fore- and hindleg GRFs were equal to the animal's body weight (Fig. 7; Table 1). Should the gecko mis-step (i.e. significantly reduce foot GRF), substantial normal forces could produce significant roll moments if unbalanced. However, as in sprawled-posture cockroaches, geckos also generated large lateral forces directed toward their midline as they bounced from side to side (Table 1). If legs function as springs rather than struts (Fig. 8B), unrecoverable roll from a missed foot contact may be delayed or avoided. If geckos are rolling toward the side maintaining foot contact,

then that leg spring will take time to compress and return energy to reverse the roll.

Coupling lateral and fore–aft GRFs can stabilize running in the horizontal plane

To better elucidate differential leg function in sprawled-posture runners, we must look beyond the reference frame that humans are most familiar with. Sprawled-posture animals operate primarily in the horizontal plane (Kubow and Full, 1999). The negative consequences of falling in a sprawled-posture runner already so close to the substratum may be minor compared to the disruption of movement in the horizontal plane.

Assume that a sprawled-posture runner uses legs that function similarly, as in upright-posture quadrupeds, where each leg generates a fore–aft deceleration followed by an equal acceleration (Fig. 1A). If a sprawled-posture trotter generates lateral forces because its legs operate as springs to minimize roll instability (Fig. 8B), then these same GRFs will also alter moments in the horizontal plane. If we add the midline-directed lateral GRFs measured for geckos (Table 1) to the typical upright posture pattern (Fig. 1A) without changing fore–aft forces, then significant yaw moments result (Fig. 1C). Moreover, these yaw moments would produce unbalanced rotations in a single direction during a step. Instead, our data show an increased fore–aft decelerating force generated by the foreleg early in the step and a greater accelerating force produced by the hindlimb later in the step. Both fore–aft force alterations minimize yaw by directing these GRF vectors towards the COM (Fig. 1D).

The lateral GRFs measured in the gecko (Fig. 5), but absent in upright-posture trotters, can be critical for stability in the horizontal plane (Kubow and Full, 1999; Schmitt et al., 2002). Kubow and Full (1999) input the lateral and fore–aft leg forces measured in cockroaches into a six-legged anchored, dynamic model. Surprisingly, the model passively self-stabilized to perturbations without the aid of neural feedback. Perturbations to fore–aft, lateral and rotational velocity altered the translation and/or rotation of the body that consequently provided mechanical feedback by altering leg moment arms. Schmitt and Holmes (2000a,b) represented the synergistic behavior of the insect's legs by a simple horizontal plane template, termed the lateral leg spring, that is similar to the sagittal plane spring loaded inverted pendulum. The lateral leg spring model consists of a single leg spring (representing the summed force of individual legs) attached to a body free to yaw (Fig. 8C). Perturbation experiments showed that the model self-stabilizes as it runs forward bouncing side to side. Stability results from the gains and losses of angular moment in leg-to-leg transitions that couple lateral and fore–aft forces (Schmitt et al., 2002). Jindrich and Full (2002) tested the passive, dynamic stability hypothesis on running cockroaches by producing a rapid lateral impulse to the COM. Insects began recovering with spring-like behavior in less than 10 ms, challenging all but the fastest reflexes (Holtje and Hustert, 2003) and thereby simplifying control.

Geckos produced the step-to-step GRF patterns consistent with the operation of a lateral leg spring in the horizontal plane (Figs 5, 8C). This hypothesis requires testing to determine if passive stability results following perturbations. Our preliminary efforts suggest that a more anchored model may be required. Instead of using a single mass to represent the body, two or more segments attached by a passive rotational spring could generate novel hypotheses of lateral back bending (Ritter, 1996).

Differential leg function can increase maneuverability in the horizontal plane

The low COM and wide support base, which stabilize sprawled-posture runners against over-turning moments, place legs in positions to facilitate maneuvers such as rapid turning. Jindrich and Full (1999) measured single leg GRFs in cockroaches executing rapid turns. The force production necessary to turn required only minor alterations in the force hexapods generate during constant average velocity, straight-ahead locomotion. The lateral leg spring template predicts that just such minor alterations of the center of pressure could be effective in initiating maneuvers (Schmitt and Holmes, 2000b). Legs farther from the center of rotation on the outside of the turn contributed the majority of force and torque impulse. Forelegs contribute most effectively to turning by producing small forces nearly perpendicular to the heading, whereas middle and hindlegs must produce additional force parallel to the heading. The lateral and decelerating forces produced by the gecko's forelegs may facilitate rapid turning by requiring only small changes in force production. Turning dynamics in reptiles needs further investigation, since the role of body bending and tails is unknown. Walter and Carrier (2002) have shown that iguanas and monitor lizards have 3.0- to 4.9-fold greater rotational inertia than similarly sized murine rodents, but at least smaller lizards such as *Hemidactylus garnotii* appear to be highly maneuverable.

Differential leg function with joint moment minimization

A low COM with a broad base of support in all directions favors increased stability to overturning moments in pitch and roll caused by the animal's momentum or external perturbations to the body. Sprawled-posture pedestrians bounce when they locomote at high speeds. The initial deceleration at the beginning of a step in crabs (Blickhan and Full, 1987), insects (Full, 1993; Full et al., 1991) and now geckos (Table 1; Fig. 8A) is primarily produced by middle or forelegs, whereas accelerations later in the step are generated by middle and hindlegs. In insects (Ting et al., 1994), roll is balanced by coupling normal forces supporting weight with lateral forces directed toward the animal's midline. Sprawled-posture geckos appear to use the same strategy (Fig. 8B). Insects attain passive, dynamic stability in the yaw or horizontal plane by coupling initial fore–aft decelerations of middle and forelegs and later middle and hindleg accelerations with lateral forces directed toward the midline. The horizontal

plane GRFs of sprawled-posture geckos followed a similar pattern (Fig. 8B).

Remarkably, the GRF patterns generated by the individual legs of insects and geckos can be modeled by simple spring-mass systems characterized by axially aligned forces. The original dichotomy proposed by Gray (1968) of legs as levers or struts should be expanded to explicitly include springs. The same spring-like GRF patterns that stabilize sprawled posture runners to pitch, roll and yaw tend to minimize joint moments (Full, 1993; Full et al., 1991). GRFs tend to be directed axially along legs, much as they are found in upright-posture runners (Alexander, 2003; Full, 1993).

The tendency to minimize joint moments does not imply that all GRFs are directed through joint centers of rotation. In fact, multi-segment bent legs make this nearly impossible. Full et al. (1991) tested the hypothesis that deviations from the minimum moments in running cockroaches could be explained by considering the minimization of the summed muscle forces in several legs. The measured GRFs were within only 12% of that which would minimize muscle forces. In general, individual leg GRFs in running geckos tended to pass above shoulder/elbow and hip/knee joints (Table 2). Lateral and fore–aft forces were smaller than required to minimize joint moments.

Spring-mass models as templates vs an anchored model

Simply fitting a spring-mass model to data from an animal's COM is not conclusive proof of energy storage and return (Alexander, 1988). Full and Koditschek (1999) make a distinction between a template and a more anchored model. A template is the simplest model representing the system behavior and serving as a target of control. Templates are a necessary abstraction if we are to integrate mechanics with control. To determine how legs, joints and muscles function to produce the COM behavior, a more anchored model is needed. It is entirely possible that spring loaded inverted pendulum behavior results from one set of muscles absorbing energy and another generating it anew (Alexander, 1988). Although the geckos in this and another study (Farley and Ko, 1997) produce whole body GRFs consistent with a spring-mass template, examination of the individual leg forces make it more difficult to explain how the energy absorbed at the beginning of the step is stored and returned later by the hindlimb (Fig. 8A). Perhaps spring-mass templates will continue to show their value in understanding control rather than with respect to metabolic energetics. Clearly, more anchored models are required to test hypotheses of mechanism. For example, it remains to be discovered if energy storage and return can explain how the metabolic cost of transport in geckos can be one-fourth that predicted for an animal of its mass (Autumn, 1999; Autumn et al., 1999, 2002; Farley and Emshwiller, 1996). Integrating limb dynamics (e.g. Blob and Biewener, 2001; Reilly and Blob, 2003) and muscle force development with whole-body dynamics is required to resolve the trade-offs, if any, that result from stable sprawled-posture running with differential leg function.

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