

Dynamics of geckos running vertically

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Summary

Geckos with adhesive toe pads rapidly climb even smooth vertical surfaces. We challenged geckos (*Hemidactylus garnotii*) to climb up a smooth vertical track that contained a force platform. Geckos climbed vertically at up to 77 cm s⁻¹ with a stride frequency of 15 Hz using a trotting gait. During each step, whole body fore–aft, lateral and normal forces all decreased to zero when the animal attached or detached its toe pads. Peak fore–aft force was twice body weight at mid-step. Geckos climbed at a constant average velocity without generating decelerating forces on their center of mass in the direction of motion. Although mass-specific mechanical power to climb was ten times the value expected for level running, the total mechanical energy of climbing was only 5–11% greater than the potential energy change. Fore- and

hindlegs both pulled toward the midline, possibly loading the attachment mechanisms. Attachment and detachment of feet occupied 13% and 37% of stance time, respectively. As climbing speed increased, the absolute time required to attach and detach did not decrease, suggesting that the period of fore–aft force production might be constrained. During ascent, the forelegs pulled toward, while hindlegs pushed away from the vertical surface, generating a net pitching moment toward the surface to counterbalance pitch-back away from the surface. Differential leg function appears essential for effective vertical as well as horizontal locomotion.

Key words: locomotion, dynamics, climbing, leg function, mechanical stability, power, gecko, *Hemidactylus garnotii*.

Introduction

No general dynamic model of legged climbing exists. By contrast, a single mass-spring model of level running captures the dynamics of two-, four-, six- and eight-legged pedestrians differing greatly in phylogeny and morphology (Blickhan and Full, 1993; Cavagna et al., 1977; Farley et al., 1993; McMahon and Cheng, 1990). During a level trot, alternate sets of legs act as a single virtual leg spring that decelerates the center of mass (COM) in the fore–aft direction during compression in the first part of a step. In the second half of a step, the virtual spring accelerates the body forward. To maintain a constant average velocity, the sum of fore–aft accelerating forces and decelerating forces must equal zero. Oscillating normal ground reaction forces (GRFs) must sum over a step to support body weight (Fig. 1A).

Any template for rapid vertical climbing must meet at least three physical challenges. First, oscillating fore–aft GRFs must sum to equal to body weight over a step to maintain constant average speed climbing. Second, development of effective GRFs for climbing requires rapid engagement of an attachment mechanism. Third, the natural pitching moment rotating the head away from the vertical surface must be stabilized. To begin to construct a dynamic template (Full and Koditschek, 1999)

for climbing, we selected one of nature's most spectacular climbers (Irschick et al., 2003). Geckos run vertically up walls as fast as other legged creatures can run over level ground. This capability is accompanied by exceptional stability.

Accelerating effectively against gravity

Lizards locomoting on the level produce spring-mass dynamics typical of other legged runners (Farley and Ko, 1997; Reilly and Biknevicius, 2003; Reilly and Blob, 2003; Ritter, 1996). Geckos, including the subject of the present study (Chen et al., 2006), are no exception. In the direction of motion, the fore–aft direction, geckos first decelerate their COM at the beginning of the step and then accelerate it in the second half of the step. To maintain a constant average velocity on the level, acceleratory forces must sum to equal deceleratory forces.

During climbing the acceleratory forces applied over each step must sum to equal the deceleratory force of the legs plus that of gravity to maintain a constant average velocity up a wall. If both gravity and the gecko's legs decelerate during climbing with each step, as they do when moving on level ground, velocity fluctuations will increase the difference between the potential energy change and the total mechanical work required

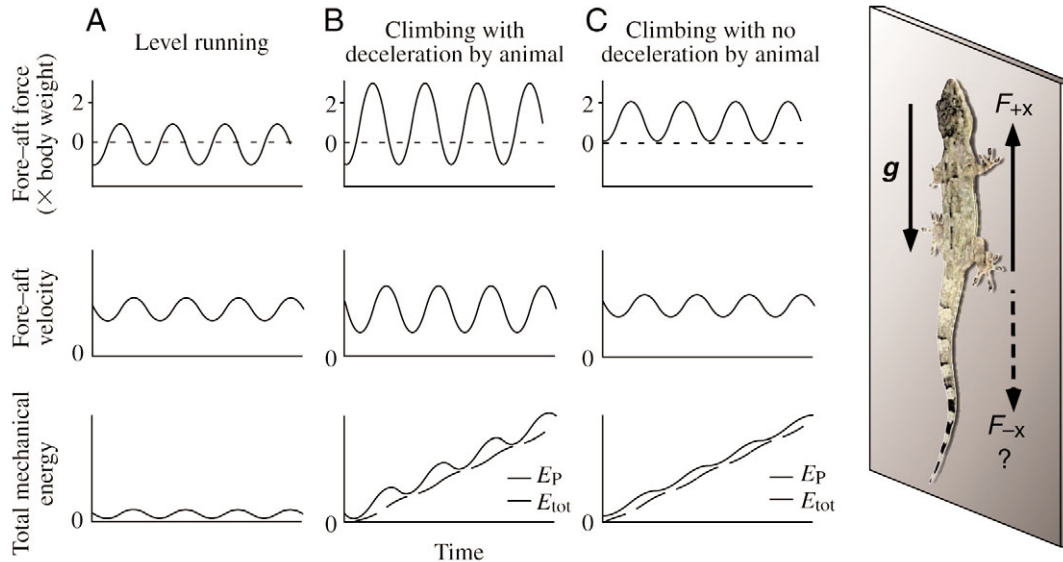


Fig. 1. Theoretical comparison of dynamics of running on level ground (A) vs climbing using two different models. In the first model (B), legs produce deceleratory fore–aft forces, F_{-x} , as an unavoidable consequence of foot attachment. Thus larger acceleratory forces, F_{+x} , are required to counteract the combined deceleration of the legs and gravity g . In the second model (C), legs do not produce deceleratory forces. Thus, acceleratory forces are reduced since only gravity decelerates the animal, and total mechanical energy (E_{tot}) required to climb approaches potential energy (E_P).

to climb (Fig. 1B). If this is the case, the total mechanical power produced during climbing will be significantly greater than the product of body weight and velocity, because additional mechanical work will be done to maintain a constant average velocity. Slow climbing tree frogs only generate fore–aft acceleratory forces (Hanna and Barnes, 1991); however, climbing chameleons may produce deceleratory forces as they reach forward to grasp with their fore feet (Higham and Jayne, 2004b). Decelerations may be an unavoidable outcome of foot contact when climbing at high speeds. If a rapid climbing gecko could reduce or eliminate the deceleratory force of the first phase of a step, the mechanical energy required to climb could be greatly decreased. Given a model of ideal climbing where the legs do not decelerate the body, as an animal climbs more rapidly, the total mechanical power produced would be close to the product of gravity and velocity (Fig. 1C).

Loading the attachment mechanism

Attachment to a vertical surface must be sufficient to allow feet to generate acceleratory forces. The varied attachment mechanisms observed in nature (Cartmill, 1985; Gorb et al., 2002; Nachtigall, 1974) may constrain the pattern of force development possible by individual legs. Static analyses show that attachment by gripping with claws or on curved surfaces with friction pads requires that legs pull toward the body's midline (Cartmill, 1979, 1985). Yet, sprawled-posture animals do just the opposite when running on the level (Blob and Biewener, 2001; Chen et al., 2006; Full et al., 1991; Full and Tu, 1990, 1991; Reilly and Delancey, 1997). In fact, legs pushing away from the midline generate lateral GRFs that couple with fore–aft forces to enhance self-stabilization in the

horizontal plane (Kubow and Full, 1999; Schmitt et al., 2002). We hypothesize that legs must reverse their function from level running to climb effectively. The dry adhesive on gecko toes is directional such that only pulling on toes toward the foot engages the adhesive (Autumn et al., 2000; Autumn and Peattie, 2002; Dellit, 1934; Russell, 2002). The adhesive may be more effective during climbing if legs pull toward the midline, even on flat surfaces.

Attachment and detachment of an adhesive mechanism may require additional force. Vertically walking tree frogs show transient normal forces when animals attach their toe pad (Hanna and Barnes, 1991). No normal detachment forces were measured because frogs effectively peel their toe from the surface. The remarkable adhesive capacity of gecko feet is achieved by hundreds of thousands of microscopic setae (Autumn and Peattie, 2002; Dellit, 1934; Maderson, 1964; Schmidt, 1904). Gecko setae branch at the tips to form spatulae as small as 200 nm wide (Ruibal and Ernst, 1965). The combined surface area of up to 10^9 spatulae is sufficient for weak intermolecular forces (Autumn and Peattie, 2002; Autumn et al., 2002) to sum to as much as 10 atm (~ 1 MPa) of adhesive pressure (Autumn et al., 2000). Adhesion of individual gecko setae requires precise orientation, preload, and micron-scale displacement (Autumn et al., 2000). The precise requirements of setal attachment raise the question of how geckos accomplish attachment of 10^3 – 10^6 setae during foot placement (Autumn and Peattie, 2002; Russell, 2002). If geckos must push their feet actively into the wall to preload their setae, the effect on the dynamics during climbing could be quite large. Because single setae have great adhesive and shear capacity (20–200 μ N; (Autumn et al., 2000), large

detachment forces could also present a significant challenge during rapid climbing. However, single setae can be detached without added force by increasing the angle between the setal shaft and the wall (Autumn et al., 2000). If geckos can increase rapidly the setal angle in all attached setae, detachment forces could be reduced.

Balancing overturning moments

Static analyses of climbing detail the challenge of preventing catastrophic overturning while station-keeping on a vertical surface (Cartmill, 1974). Because the COM is away from the vertical surface, a destabilizing moment results, which tends to rotate the head away from the vertical surface. The destabilizing moment is directly proportional to the animal's weight and the distance from the COM to the surface. Stabilizing moments can be generated in several ways. Forelegs can pull the anterior end of the body toward the vertical surface (Cartmill, 1974, 1985; Zaaf and Van Damme, 2001). Here, the stabilizing moment is proportional to the pulling force and the distance from the forefoot to the hindleg or pivot. Tails in birds such as treecreepers, balance the overturning moment from below the COM (Norberg, 1986). Large feet or feet with long toes represent other options.

When running on the level, geckos generate equal normal forces with their fore- and hindlegs in the same direction, as they support their body weight (Chen et al., 2006). Balancing an overturning moment during rapid climbing may demand normal GRFs in opposite directions for fore- and hindlegs. Although the tail has been hypothesized to stabilize against pitch-back, it remains unclear whether it contacts the surface or only exerts an effect through its inertia (Walter and Carrier, 2002).

The present study measured the dynamics of rapid vertical climbing in small geckos *Hemidactylus garnotii* (2 g mass), to test three sets of hypotheses concerning the differential leg function required for climbing. First, we hypothesize that rapid climbing animals necessarily decelerate their COM in the fore-aft direction as they attach their feet, adding to the deceleration exerted by gravity. Second, we hypothesize that rapid climbers must generate forces to engage their attachment mechanisms, and therefore that climbers will pull toward their midline in the plane parallel to the wall. Pulling toward the midline would generate lateral GRFs that are the reverse of those observed on the level. In addition, we hypothesize that rapid climbers generate identifiable normal forces associated with attachment and detachment of the toe pads. Third, we hypothesize that rapid climbers balance overturning moments that rotate an animal's anterior end away from the vertical surface by pulling their head toward the surface.

Materials and methods

Animals

Hemidactylus garnotii Duméril and Bibron 1836 (1.9±0.7 g mass, mean ± s.d., 4.6–5.8 cm snout-vent length, $N=9$) were obtained from a commercial collector (Glades Herp, Bushnell, FL, USA). Geckos were kept with 1–3 animals per cage and

housed in an environmental room illuminated for 12 h a day at 25±2°C. They were provided crickets, vitamin mineral supplement, and water once daily. Trials were conducted at 31°C.

Running track

We used a track with Plexiglas walls to contain the animals during filming and force measurements. The walls were polished with Brilliance (Chemical Products Co. Inc., Omaha, NE, USA) to prevent geckos from clinging to the side of the track. The floor was model aircraft plywood. A force platform was inserted into the floor of the track, flush with the running surface and 20 cm from the start of the track. The animals ran into a darkened plastic box placed 20 cm above the force platform.

Force measurements

We measured fore-aft, normal and lateral wall reaction forces using a force platform based on a design by Full and Tu (1990). A model aircraft plywood plate (10.7 cm×6 cm×0.06 cm) was mounted on four brass beams. Semiconductor strain gauges bonded to spring blades cut from the brass supporting beams responded to forces acting on the plywood cover. The force platform was inserted into the floor of a Plexiglas and model aircraft plywood track. Force signals were filtered using a Butterworth filter at a cut-off frequency of 150 Hz (unloaded natural frequency of the plate >400 Hz). Crosstalk between three axes of force measurement was less than 2%. Loads in the range 0.01–0.05 N produced a linear response with a maximum variation across the platform of less than 7%.

Data acquisition

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 Power Macintosh 9500 (Apple) computer at a frequency of 1000 Hz. Integration of force records and energy fluctuations were calculated with a spreadsheet (Microsoft Excel), and Igor Pro 5.05 software (Wavemetics, Portland, OR, USA) on a PowerBook G4 (Apple) computer.

Kinematic analysis

A total of twenty points on the body were marked with Wite-out (Gillette Co., Boston, MA, USA) to serve as landmarks for digitization (Fig. 2). Eight of these points lay on the dorsal midline of the gecko (one in the middle of the head, one between the shoulders, three on the main body, one between the hips, and two on the tail). Each leg contained three points, one on the shoulder/hip, one on the elbow/knee, and one on the wrist/ankle.

One dorsal and two dorso-lateral views were filmed simultaneously using video cameras capturing 500–1000 frames s⁻¹ (Redlake Motionscope, Tucson, AZ, USA; Kodak EktaPro SE, and Kodak EktaPro with image

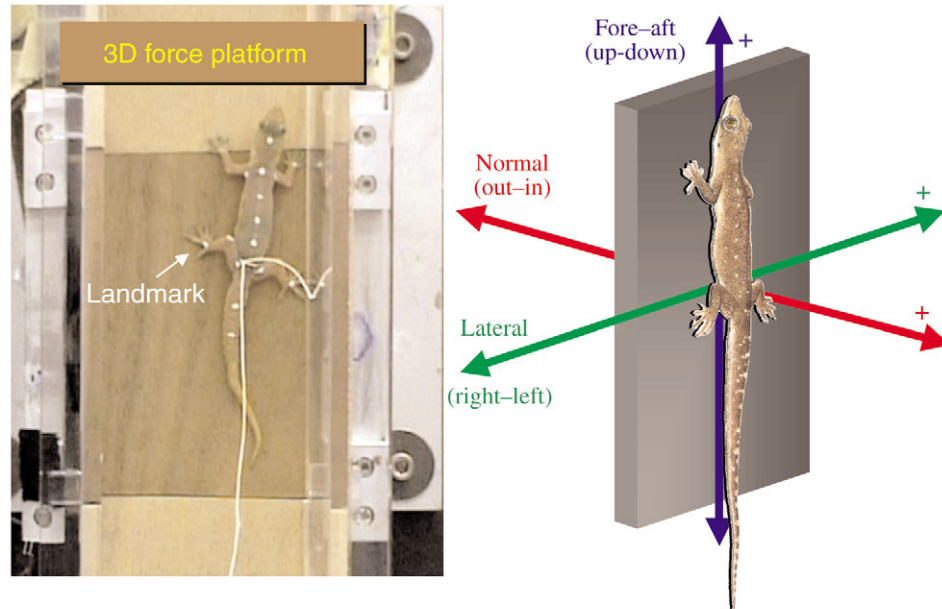


Fig. 2. (A) Force platform used to measure dynamics of climbing geckos *Hemidactylus garnotii*. (B) Axis conventions used in this study. Positive fore–aft forces (+ x ; blue) correspond to wall reaction forces that would accelerate a mass upwards. The force of gravity acts in the $-x$ direction. Positive normal forces (+ y ; red) correspond to wall reaction forces that would accelerate a mass away from the force plate, whereas negative normal forces ($-y$) correspond to wall reaction forces that would accelerate a mass towards the force plate. The z axis was the lateral dimension and corresponds to forces directed to the animals right or left. Positive lateral forces (+ z ; green) correspond to wall reaction forces that would accelerate a mass to the animal's right, whereas negative lateral forces ($-z$) correspond to wall reaction forces that would accelerate a mass to the animal's left.

intensifier). Video frames were grabbed and the coordinates of various positions on the body at each frame were digitized into a computer (Gateway 2000, Irvine, CA, USA) using a video analysis system (Motus, Peak Performance Technologies Inc., Lake Forest, CA, USA). Video frames were synchronized with each other and with the force data by means of a trigger switch that simultaneously lit an LED in view of the cameras while sending a signal to the data acquisition system. For the present study, we used the kinematic data for constant average speed, stride frequency, gait and characterization of toe attachment and detachment.

Velocity and displacement of the COM

We calculated the average speed of the animal from the video recordings by digitizing the point between the shoulders as it climbed the force platform. Segments of the force recordings were selected for analysis if they contained one or more complete strides in which the sum of the increases and decreases in fore–aft speed were within 10% of the average speed of the animal. We only accepted trials for which the integration of the fore–aft force over a stride equaled body weight as measured by a separate scale. The normal and lateral velocity of the COM were calculated by integrating the normal and lateral force recordings, respectively (Blickhan and Full, 1992). The fore–aft velocity of the COM was calculated from integration of the fore–aft force recording minus body weight. An additional integration

of the fore–aft velocity yielded the vertical displacement of the COM. The average speed of the animal was used as the integration constant for the fore–aft velocity of the COM. The integration constants for the normal and lateral components of velocity and for the vertical displacement of the COM were assumed to be zero.

Mechanical energy calculations

Calculations of the energy fluctuations of the COM were performed as in Blickhan and Full (1992). The fore–aft, normal, and lateral kinetic energy changes of the COM were calculated from the velocity changes of the COM. Gravitational potential energy of the COM was calculated from the vertical displacement. The power output of each individual component was determined by summing the positive increments over a stride and dividing by the duration of the stride. At each sampling period the fore–aft, normal and lateral kinetic and gravitational potential energies were summed to obtain the total energy of the COM. The power generated to lift and accelerate the COM was calculated from the sum of the positive increments of the total energy of the COM over a stride divided by the duration of the stride.

Statistics

We used a commercial statistics programs [Statview (SAS) and SuperANOVA; Abacus, Cary, NC, USA] on computers

(Apple Macintosh) for all statistical analysis. We present all values here as means \pm standard deviation (s.d.) unless otherwise noted.

Results

Kinematics

Geckos climbed vertically using a trotting gait at all speeds (Fig. 3A,B). Contralateral limbs moved nearly synchronously (leg phase=0.93 \pm 0.06), while ipsilateral limbs moved in antiphase (leg phase=0.45 \pm 0.05). Speed had no significant effect on leg phase (ANCOVA, $F=1.05$; d.f.=1,98; $P=0.3$). Geckos placed the heel of their feet first with toes hyperextended, then uncurled the toes and attached their toe pads prior to force generation. At the end of stance phase, geckos again hyperextended their toes, peeling their toe pads from the distal end prior to movement of the heel.

At climbing speeds ranging from 0.29–0.77 m s⁻¹, *Hemidactylus garnotii* had stride frequencies of 8.5–16.0 Hz, with an average stride frequency of 12.5 \pm 2.2 Hz. Stride frequency was not significantly affected by velocity, v (ANCOVA, $F=2.25$; d.f.=1,13; $P=0.16$), thus geckos increased velocity largely by increasing stride length (in m; stride length=0.01+0.00057 v , where v is in m s⁻¹); $r^2=0.70$; $P<0.0001$).

Stance period and swing period also lacked significant speed effects ($P>0.09$) and each required approximately the same amount of time (stance=42 \pm 11 ms; swing=39 \pm 8 ms). Duty factor for all four limbs averaged 0.5 \pm 0.06 and was unaffected by speed ($P>0.4$).

Detachment of the adhesive pads occurred by digital hyperextension (toe peeling from the tip) prior to the swing phase of fore- and hindlegs. Foot placement preceded attachment of the adhesive pads by uncurling of the toes from base to tip. Time required for attachment of the adhesive pads averaged 5 \pm 2 ms. Attachment occupied 6.5 \pm 1.3% of stride time, and 12.7 \pm 2.1% of stance time. Attachment time was not significantly affected by speed (ANOVA, $F=4.0$; d.f.=1,13; $P=0.07$). Time required for detachment of the adhesive pads averaged 15 \pm 4 ms. Detachment occupied 18.5 \pm 3.3% of stride time, and 36.4 \pm 7.3% of stance time. Detachment time was not significantly affected by speed (ANOVA, $F=2.8$; d.f.=1,13; $P=0.11$).

COM wall reaction forces

Geckos trotting vertically at all speeds generated a stereotyped wall reaction force pattern (Figs 3C, 4).

Fore–aft

Over the course of a complete stride the fore–aft (vertical, x -axis) wall reaction force pattern had two distinct maxima corresponding to mid-stance for each diagonal leg pair (Fig. 4B). At mid-stride, the fore–aft wall reaction forces attained a minimum that was not significantly different from zero (1.0 \pm 1.0 mN, mean \pm s.e.m.; $P=0.5$). Despite the periodic absence of acceleratory forces, geckos maintained constant average, positive vertical speeds with less than 10% variation

(Fig. 3D). Fore–aft wall reaction forces during mid-stride were negative in one quarter of the steps, indicating that footfalls were producing deceleratory forces. However, when deceleratory forces occurred, they were only $-16\pm 0.12\%$ of body weight, and did not add substantially to gravitational deceleration. Maximum fore–aft acceleratory force production was 2.1 times the average weight and did not vary with speed ($P=0.5$).

Lateral

Lateral wall reaction forces (z -axis) possessed two distinct patterns, depending on which diagonal leg pair was in contact with the wall (Fig. 3B). When the left-hindlimbs and right-forelimbs initially contacted the wall, the gecko bent such that the convex side pointed to the right. Throughout the stance phase of this leg pair the lateral wall reaction forces were negative, indicating that the COM was being accelerated to the left (Fig. 4C). This occurred as the gecko straightened its body through mid-stance and then began to bend such that the convex side pointed to the left. As the right-hindlimb and left-forelimbs were placed on the ground the lateral wall reaction forces changed sign, and the COM was then accelerated back to the right.

Unlike the fore–aft wall reaction forces, which displayed a single local force maximum for each leg pair, the lateral wall reaction forces were variable, but tended to show two local force maxima per leg pair (Figs 3B, 4C).

Normal

The normal wall reaction forces (perpendicular to the wall, y -axis) had a less stereotypical pattern than either the fore–aft or lateral wall reaction forces (Fig. 3B). Maximum normal forces for both pressing into ($+x$) and pulling away from ($-x$) the wall were equal in magnitude and 12% as large as maximum fore–aft forces. At the beginning of the stance period of each diagonal leg pair, normal wall reaction forces tended to be positive indicating that the gecko was pushing its COM away from the wall (Fig. 4A). This was then followed by a period during the stance phase where the normal forces were negative indicating that the gecko was pulling its COM toward the wall. The timing of the normal force peaks and when the force changed sign (changed from a pushing to a pulling force) varied considerably.

There was one consistent pattern in every trial regardless of speed. Despite the fact that all four feet were in contact with the wall at the transition between steps (double support), wall reaction forces fell to nearly zero in all three axes. Velocity remained high, indicating that the geckos were moving in a ballistic fashion as they bridged the gap between placement of leg pairs.

Mechanical energy and power of COM

The fore–aft kinetic energy fluctuated cyclically through the course of a stride (Fig. 3E), decreasing during early stance and then increasing through mid-stance as the gecko produced peak fore–aft acceleratory forces. When fore–aft force production began to decline prior to mid-stride, the fore–aft kinetic energy

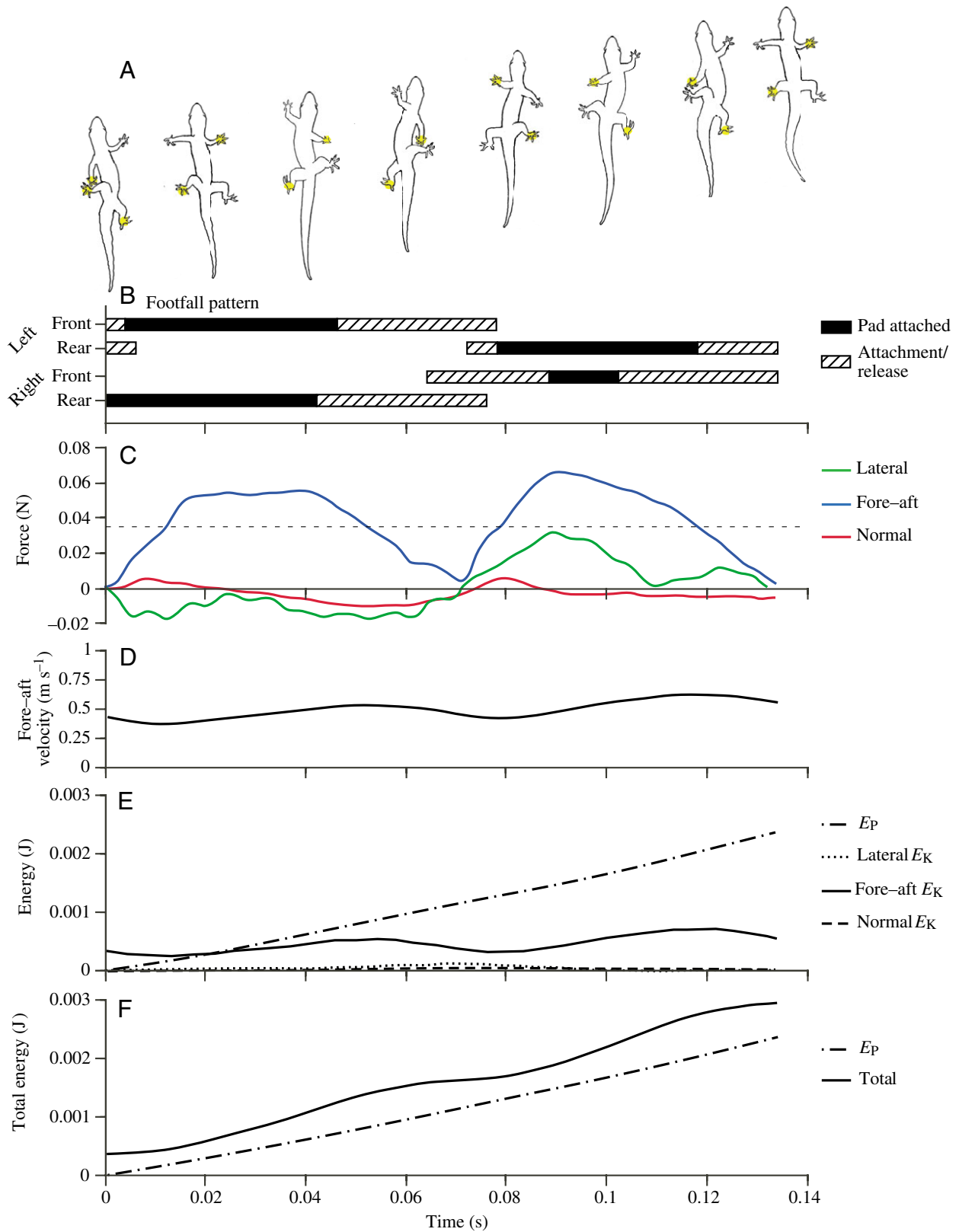


Fig. 3. For legend see p. 266.

declined as well, and continued to decline through mid-stride and early stance phase of the next diagonal leg pair (Fig. 3B,E) as the gecko slowed at a rate near that of gravity. The normal and lateral kinetic energies together contributed less than 10% of the total kinetic energy (Fig. 3E).

The gravitational potential energy of the gecko's COM increased monotonically over the course of a stride (Fig. 3E). The total mechanical energy of the COM also increased monotonically over the stride. Average total mechanical energy was only $8.5 \pm 6.9\%$ greater than the change in potential energy or for the minimum possible for a model of ideal climbing (no deceleratory forces; Figs 3F, 5).

Mechanical power (W kg^{-1}) of the COM increased as velocity increased (Fig. 5), as shown by the significant linear relationship ($\text{power} = 0.82 + 9.93v$, where v is in m s^{-1} ; $r^2 = 0.85$). The slope of the linear regression of power and speed was not significantly different from the value of gravity ($P > 0.05$). Average maximum mechanical power was $10.7 \pm 4.4 \text{ mW}$ (mean \pm s.d.; range: 5.0–19.4 mW), or $5.7 \pm 1.44 \text{ W kg}^{-1}$ mean \pm s.d. (range: 3.4–8.5 W kg^{-1}). The effect of speed on power was not due to individual effects (nested ANOVA, $F = 11.94$; d.f. = 6, 11; $P = 0.0003$).

Single leg wall reaction forces

Fore–aft

Geckos primarily produced acceleratory (positive) fore–aft forces during rapid climbing (Fig. 6E). Peak fore–aft forces occurred at mid-step. Peak fore–aft forces were fourfold greater than normal forces. Two out of 26 steps produced deceleratory peak fore–aft forces. Between steps in one-quarter of the trials, single leg non-peak forces summed to create small deceleratory whole body forces.

Lateral

In the lateral direction all legs pulled towards the midline of the body such that the left legs generated a lateral wall reaction

force to the right while the right legs generated a lateral wall reaction force to the left. Lateral wall forces peaked near mid-step (Fig. 6F). Lateral forces were over twice that of normal force.

Normal

Forelegs pulled the head toward, while hindlegs pushed the body away from the vertical surface (Fig. 6D). Normal wall forces were small, but sufficient to counter pitch-back. No measurable attachment or detachment forces were recorded at the beginning or end of a step. The tail did not contribute to the wall forces generated by feet when there was no perturbation.

Balancing overturning impulse moment

Geckos balanced their normal overturning and stabilizing impulse moments during climbing (Fig. 7C,D). We calculated the normal impulse as the integral of a single leg force (F_{leg}) over a stride period (Δt). The mean normal impulse of the

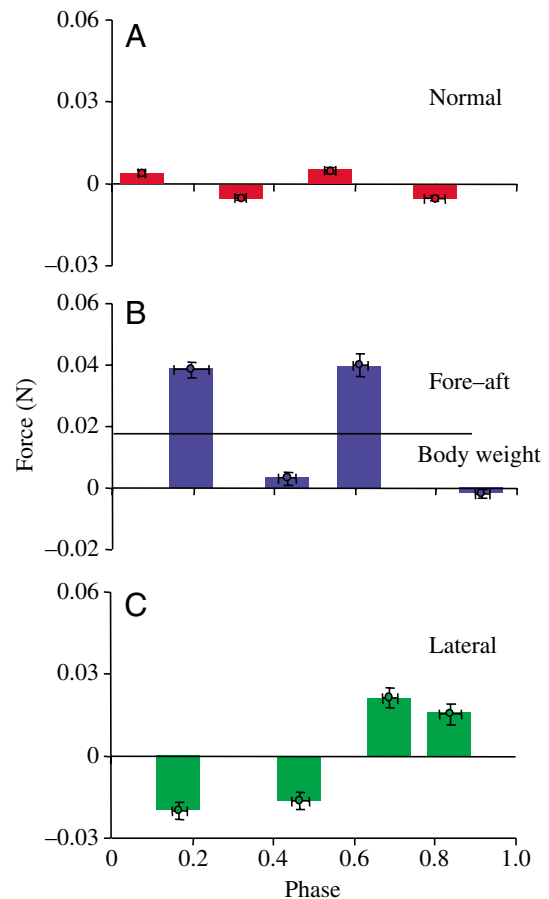


Fig. 4. Whole body peak GRF magnitudes and phases. Values are means \pm 1 s.e.m. One phase is equal to one complete stride or two steps. (A) Normal force showed two maxima, but was highly variable, representing the cancellation of individual leg forces. (B) Fore–aft force peaked once per step with magnitudes of approximately twice body weight (broken line). (C) Lateral force accelerated the COM to the left followed by an acceleration to the right. Two maxima per step were observed.

Fig. 3. Gait, force, velocity and energy of the COM vs time during one stride of a 3.6 g (0.035 N) gecko *Hemidactylus garnotii* climbing vertically at 0.44 m s^{-1} . (A) Tracing of gecko climbing. Yellow circles represent foot contact. (B) Gait pattern and timing of attachment and release for each foot. The initial striped portion of each box represents the time required for the toe pads to attach to the force plate. The filled portion indicates when toe pads were in contact with the force plate, and the second striped portion represents the time for the toes to detach before the foot was lifted from the force plate. (C) Fore–aft, normal and lateral forces of the COM. The horizontal broken line represents weight (35 mN). Force production decreased nearly to zero at mid-stride, despite the fact that all four feet were in contact with the force plate. (D) Fore–aft velocity calculated by integration of the force recording minus gravity. Velocity attained a minimum at the beginning of each step as forces decreased to zero, indicative of a period of ballistic movement. (E) Fore–aft kinetic, normal kinetic, lateral kinetic energy (E_K) and gravitational potential energy (E_P) fluctuations of the COM. (F) Total mechanical energy of the COM obtained by summation of the fore–aft kinetic, normal kinetic, lateral kinetic and gravitational potential energy components.

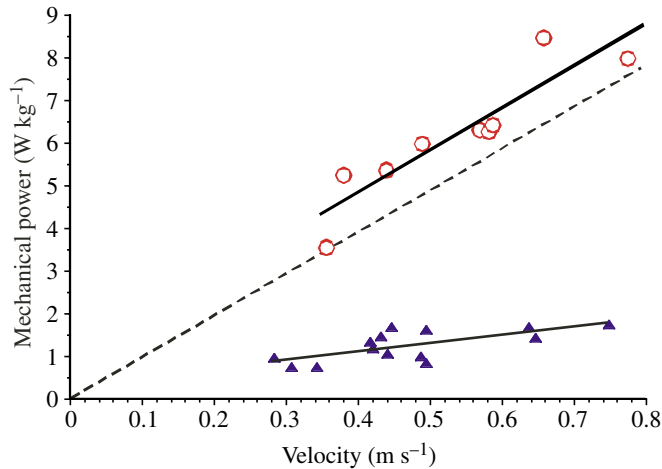


Fig. 5. Mass-specific mechanical power vs velocity in *Hemidactylus garnotii* climbing vertically and running on the level. Solid line (circles) is the linear least-squares regression ($\text{Power} = 0.9 + 9.9v$, where v is velocity in m s^{-1} ; $r^2 = 0.83$) for climbing. The broken line represents the product of gravity and velocity, the minimum mechanical power production possible. The solid line (triangles) represents the least-squares linear regression ($\text{Power} = 0.3 + 1.9v$; $r^2 = 0.48$) of geckos running on level ground (Chen et al., 2006).

foreleg (-0.11 ± 0.064 mN s, mean \pm s.d.) was not significantly different from the mean normal impulse of the hindleg (0.08 ± 0.037 mN s, mean \pm s.d.), thereby resulting in no net translation of the COM in the normal direction over a stride period. With respect to stability, we viewed the hindleg as a

pivot, based on the observation that when animals fail they overturn (pitch away) from the wall (Fig. 7D). The overturning impulse moment ($M_o = 0.0071$ mN m s) is a product of the distance of the COM from the wall ($r = 5.18 \pm 0.44$ mm, mean \pm s.d.), body mass (M_b), gravity (g) and stride period (Δt). The stabilizing impulse moment ($M_s = 0.0072$ mN m s) is the product of the normal foreleg impulse and is the stabilizing moment arm from the foreleg to the hindleg pivot ($R = 3.20 \pm 0.27$ cm, mean \pm s.d.; Fig. 7D).

Discussion

The COM data from the present study on geckos provide a foundation to build the first template (Full and Koditschek, 1999) of dynamic vertical climbing comparable to the spring-mass templates used to model pedestrians running on the level. By selecting an exceptional climber that also exhibits rapid running on the level, we had the opportunity to ask how a more anchored model with legs alters leg force production to seemingly defy gravity.

Accelerating effectively against gravity

While it would be advantageous to minimize active deceleration by the legs during climbing (Fig. 1C), it

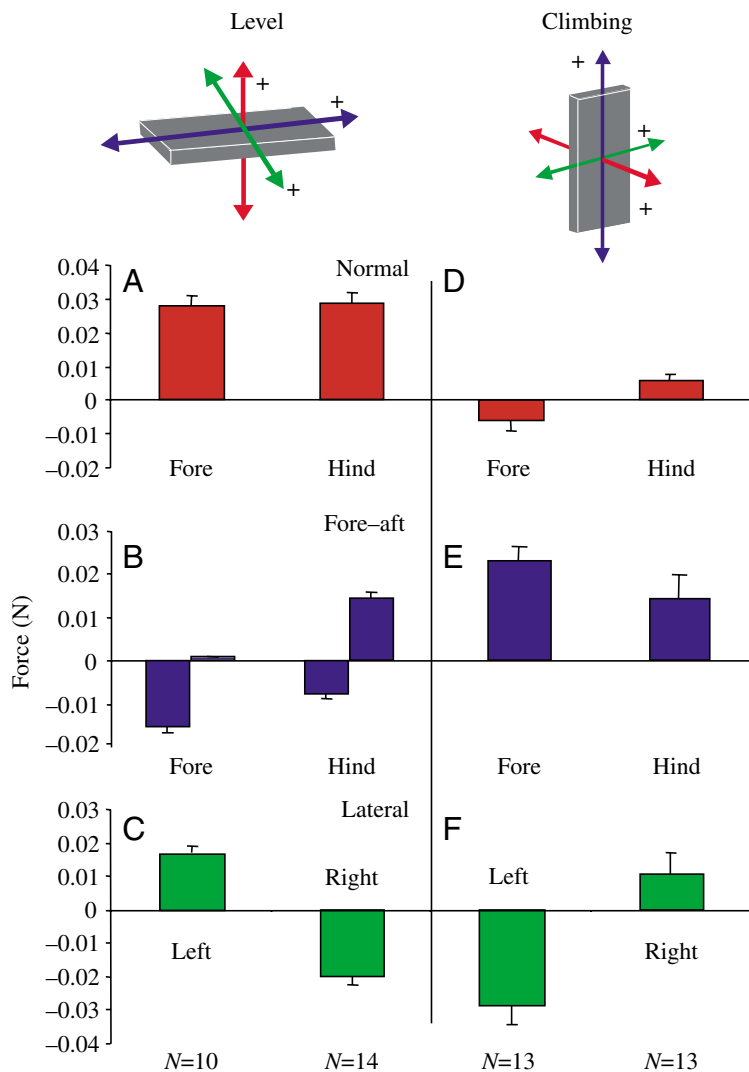


Fig. 6. Mean peak GRFs of single legs in geckos climbing (D–F) and running on level ground (A–C). (A) On a level, normal GRFs were always positive. (B) Geckos running over level ground used the forelegs to produce only deceleratory forces, while hindlegs first produced deceleratory forces during the first part of each step, and then produce acceleratory forces during the second part of each step. (C) All four legs pushed laterally away from the midline of the body such that the left legs produced forces that pushed the gecko to the right, while the right legs produced forces that pushed the gecko to the left. (D) In climbing geckos, forelegs produced forces that pushed the gecko away from the vertical surface, while hindlegs produced forces that pulled the gecko toward the vertical surface. (E) Climbing geckos produced positive fore-aft forces that propelled the gecko upwards. (F) During climbing, all four legs pulled laterally towards the midline of the body such that the left legs produced forces that pulled the gecko to the left, while the right legs produced forces that pulled the gecko to the right. The directions of lateral GRFs during climbing were opposite to those produced during level running.

is not a simple matter to attach feet without decelerating the COM. To accomplish foot attachment without active deceleration, the gecko would need to swing one pair of legs into place, rapidly attach the toe pads, and at the same time detach the toe pads of the other leg pair, and swing them away from the surface, while running at 15 body lengths per second (Russell, 1972, 1975, 2002). Surprisingly, this is precisely what the geckos did in the majority of steps (92% were acceleratory) as they attached and detached their adhesive

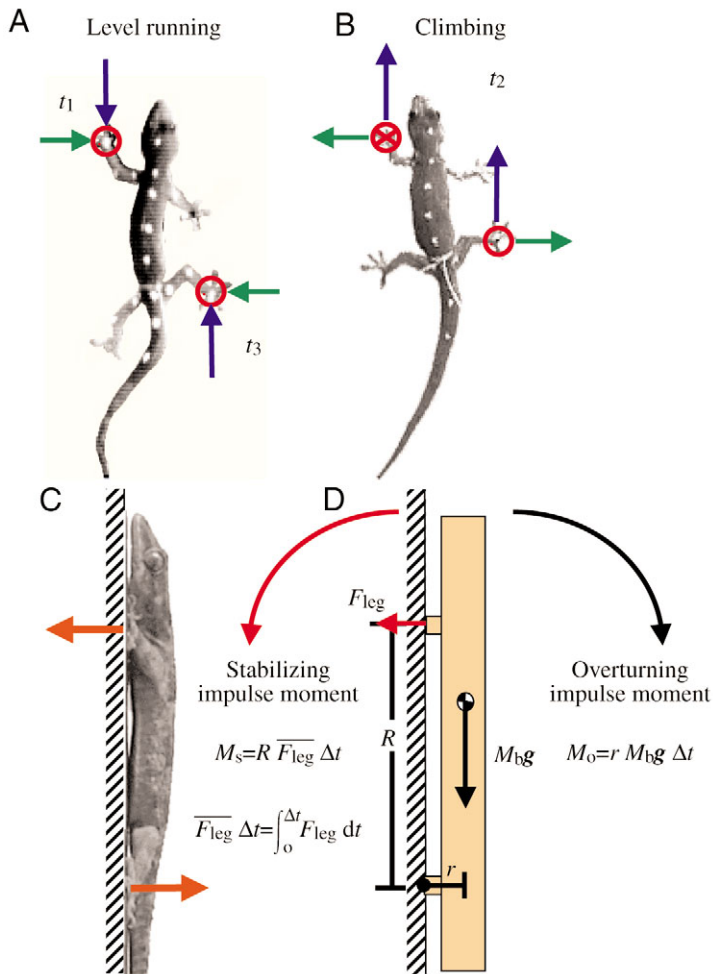


Fig. 7. Direction of single-leg round reaction forces in geckos climbing vertically (B–D) and (A) running on level ground. (A) Single leg GRFs during level running. Circle with a dot in the center represents a vector that points toward the reader. t_1 represents the time in the first half-step when the forces shown are generated. t_3 represents the time in the second half-step. (B) Single leg GRFs during climbing. Circle with an \times in the center represents a vector that points away from the reader. t_2 represents the time at mid-step when the forces shown are generated. (C) Lateral view of normal GRFs during climbing. (D) Lateral view of overturning (M_o) and stabilizing (M_s) impulse moments during climbing where F_{leg} is the mean normal force generated by the forelegs over a stride period (Δt), R is the stabilizing moment arm from the foreleg to the hindleg pivot, the integral of F_{leg} from 0 to Δt represents the foreleg impulse, g is acceleration due to gravity, M_b equals body mass, and r is the distance of the COM to the wall.

pads. Fore–aft deceleratory forces occurred at the transitions between steps when the forces were small (Fig. 4B). We found that forces in all three axes dropped to near zero as the geckos made the transition from attachment of one leg pair to the other. Zaaf et al. (2001) predicted that to avoid velocity fluctuations due to gravitational deceleration, climbing geckos should keep at least one leg on the substrate and produce acceleratory forces with at least one foreleg at all times. Our results support the absence of an aerial phase, but contradict the hypothesis of continuous acceleration. Even though four feet were in contact with the wall (Fig. 3B), geckos passed through a ballistic, pseudo-aerial phase in which fore–aft velocity remained positive and was sufficient to bridge the gap between steps. Thus, during the first phase of a step, each leg pair acted as a single virtual leg that accelerated the climbing gecko to overcome gravity. During the second phase of a step, gravity dominated by decelerating the gecko. The net effect resulted in a constant average vertical velocity of the COM mechanics (Fig. 3D).

Mechanical power output estimates

Even though individuals of *Hemidactylus garnotii* possess adhesive toe pads and are otherwise adapted to climbing, power output estimates for level running increased in proportion to velocity (Chen et al., 2006) as found for other lizards (Farley, 1997; Reilly and Biknevicius, 2003) and legged runners generally (Full, 1997). As a gecko climbs, it must produce mechanical power at least equal to the product of gravity and velocity to increase its potential energy (E_p). Geckos lost kinetic energy (E_k) as gravity slowed them down between steps during the ballistic, pseudo-aerial phase (Fig. 3E), but added additional mechanical energy to accelerate the COM at the beginning of the next step. These cyclic fluctuations in fore–aft E_k make it appear that rapid legged climbers require a great deal more mechanical power than a climber capable of producing power continuously (e.g. a tracked vehicle; Fig. 8). However, the mechanical power required for climbing geckos exceeded the product of gravity and velocity by less than 10% (Fig. 5). The minimal mechanical power requirement of the COM was nearly attained because geckos minimized decelerations of the body during leg placement.

The E_p increase of the COM during climbing comprised the largest component of the total increase in COM energy (Fig. 3E). Kinetic energy in the normal and lateral axes also fluctuated during a stride, but the amount of energy was low. Normal and lateral E_k together contributed less than 10% of the total kinetic energy. It is important to note that these mechanical power values are only gross approximations of what gecko muscle might be required to generate for rapid climbing. It remains exceedingly difficult to estimate total energy storage, return and transfer (Blickhan and Full, 1992). Energy generated to pitch, yaw and roll the body, swing the limbs, and undulate the body and tail could be

significant. Because legs push against one another, the extent to which energy is produced and absorbed is unclear (Alexander, 1980; Donelan et al., 2002). Nevertheless, studies adding loads to climbing geckos suggest that maximal power output may limit the maximal velocity of climbing (Irschick et al., 2003). Therefore, the geckos' ability to eliminate fore–aft decelerations of the COM during rapid vertical climbing may significantly affect performance.

Loading the attachment mechanism

Wall reaction force data on one of nature's surest-footed animals revealed that loading an attachment mechanism must be considered when creating a dynamic model of climbing. At the same time, mechanisms exist to decouple attachment and detachment from the COM.

Lateral wall reaction forces

Rapidly climbing geckos reversed the direction of lateral GRFs generated during running on the level. Geckos running on the level push away from the midline of the body (Figs 6C, 7A). Their COM during level running behaves as if it was bouncing from side to side. Formalization of this lateral leg spring template has shown how the coupling of lateral and fore–aft forces can lead to passive, self-stabilization and simplify control (Full et al., 2002; Schmitt and Holmes, 2000a,b). The self-stabilizing effects produced by the gains and losses of angular momentum may disappear when operating against gravity. Stability during climbing may depend more on the ability to secure a foothold.

Animals can cling to objects using friction if they can grasp by producing an adduction force at a sufficient central angle (Cartmill, 1974, 1985). Grasping the surface in this manner requires that legs pull toward the midline. When animals wrap their limbs around tree trunks, distally located claws may engage by interlocking as they are pulled toward the midline and down.

Geckos pulled their feet toward the midline of their body during climbing (Figs 6F, 7B). This action not only favors claw interlocking but also setal attachment, resulting in enhanced shear force (Dellit, 1934; Russell, 2002). Adhesion of individual gecko setae requires micron-scale displacements that pull the stalk toward the center of the foot (Autumn et al., 2000). Pushing away from the body as observed during level running tends to detach the dry adhesive and prevent attachment.

Attachment and detachment of adhesive toe pads

Transient normal forces resulting from attachment and detachment of the gecko's dry adhesive were not identifiable. Attachment and detachment of the toe pads appeared to be mechanically decoupled from the COM. Detachment of the strong adhesive was accomplished by digital hyperextension (Russell, 1975, 2002; Wagler, 1830), a mechanism analogous to the peeling of tape from a surface (Gay and Leibler, 1999; Kendall, 1975). Toe peeling appeared to reduce greatly the force required for detachment. Since the muscles responsible

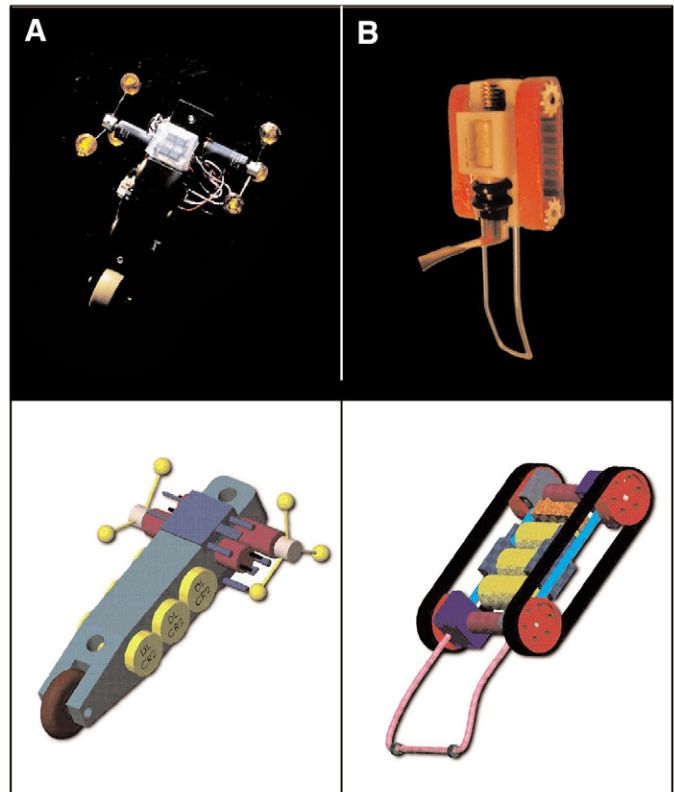


Fig. 8. (A) MechoGecko and (B) BullGecko, small (4 cm long), climbing robots designed by iRobot Corp. The designs of the feet and treads of the robots were inspired biologically by the toe-peeling mechanism of gecko toes. MechoGecko used pressure sensitive adhesive (PSA) feet. The spherical foot shape promoted peeling to reduce pull-off force. MechoGecko's trispoke legs caused significant velocity fluctuations during climbing. BullGecko used PSA tracks to peel as it climbed. The track design allowed BullGecko to exert a constant fore–aft force on the COM.

for digital hyperextension (interossei dorsales; Russell, 1975) are located in the toe, detachment does not have to be coupled mechanically to the COM, as would be the case if the gecko only used its leg musculature to break the adhesive bonds in the foot. Single setae can be detached without added force by increasing the angle between the setal shaft and the wall (Autumn et al., 2000). If the geckos increased the setal angle rapidly in all attached setae during toe peeling, detachment forces would be low or immeasurable.

Single setae require a preload force normal to the surface, and a small ($5\ \mu\text{m}$) proximal drag in shear for maximal attachment (Autumn et al., 2000). It is not clear how the preload and drag requirements of the setae during toe uncurling are accomplished without measurable forces acting on the COM. The setae may be preloaded and dragged simply as a consequence of force development during the stride. However, this is difficult to reconcile with the negative normal forces produced by the front feet. The force necessary to bend even thousands of setae into an adhesive orientation is probably quite small (at most 10 mN; Autumn and Peattie, 2002) and

possibly below the threshold of our force plate. Another possibility is that attachment is a reversal of the peeling process of toe detachment, which may be decoupled from the COM. The gecko's foot may approach the substrate without pressing into it and reapply the adhesive by unrolling its toes like tape, thus spreading out preload forces over time. The complex network of tendons acting on the scansors (Russell, 1975) might then drag the setae following preload (Russell, 2002).

Digital hyperextension may reduce detachment and attachment forces, but may limit the options to increase speed during vertical climbing. If we assume that toe peeling and uncurling in climbing geckos requires some minimum time, then speed cannot be increased by reducing contact time, as is typical in level running. Zaaf et al. (2001) argue that that stride frequency should be decreased so as to keep stride length and therefore the positioning of the adhesive feet constant. The relationship between stride frequency, stride length, duty factor and velocity for climbing geckos appears to be highly variable and is often restricted to small ranges in velocity. In the present study, *Hemidactylus garnotii* increased velocity by increasing stride length. Irschick et al. (2003) showed that two gecko species (*Gekko gecko* and *Hemidactylus garnotii*) increase speed primarily by increasing stride frequency, even when carrying additional loads. Zaaf et al. (2001) found that one climbing gecko (*Gekko gecko*) modulates speed almost entirely by changing stride frequency, whereas a similarly sized terrestrial gecko (*Eublepharis macularius*) changes speed primarily by changing stride length. Despite the variability in stride length, frequency and velocity in the present study, attachment and detachment occupied a constant value of approximately 20 ms.

Balancing overturning impulse moments

Geckos reduced the overturning impulse moment substantially by keeping their COM close to the vertical surface (r ; Fig. 7C,D). Their low weight was also a considerable advantage, but the impulse due to gravity was still sixfold greater than the foreleg stabilizing impulse. Geckos were able to balance the overturning impulse moment by generating a small normal adhesive force with their forelegs because the stabilizing moment arm (R) was sixfold longer than the overturning moment arm (Fig. 7D). This normal foreleg adhesive force was only one-quarter that of the fore-aft (shear) force required to generate vertical accelerations. Our finding that geckos' forelegs pulled toward, while hindlegs pushed away, from the vertical surface is consistent with predictions based on comparisons of hind- and forelimb musculature in climbing and ground-dwelling geckos (Zaaf et al., 1999). Results at the level of the foot during rapid climbing are consistent with data at the level of the seta as well. Autumn et al. (2000) discovered that the force generated by a single seta was tenfold greater in the fore-aft direction or shear than in the normal or perpendicular pull-off direction.

To balance forces with respect to the overturning moment, fore-aft GRFs must be sufficient to at least support weight, but the distribution among fore- and hindlegs is not fixed. Geckos

produced greater fore-aft support and propulsion with fore- as opposed to hindlegs ($P < 0.05$; Fig. 6E). Greater foreleg-hindleg differentiation is observed in climbing monkeys (Eishi et al., 2002; Hirasaki et al., 2000). The spider monkey uses its forelimbs to keep the body close to the substrate, rather than to generate fore-aft propulsion. The forelimb of the Japanese macaque, on the other hand, contributes more to propulsion.

Differential leg function

Within a single stride, geckos can transition from rapid running on the level to seemingly defying gravity without major changes in kinematics. In chameleons, changes in incline are associated with large changes in muscular activity, but not with substantial alterations in kinematics (Higham and Jayne, 2004a). Jayne and Irschick (1999) measured significant kinematic differences in lizards running on an incline vs those on a level. In contrast, Zaaf et al. (1997, 2001) reported very little adjustment in gait characteristics when climbing and non-climbing geckos were forced to move on a non-habitual substratum. Gait characteristics differed little between lizard species despite clear differences in ecological niche (Van Damme et al., 1997; Vanhooydonck et al., 2002; Zaaf et al., 2001). Climbing performance in lizards may (Losos and Irschick, 1996; Sinervo and Losos, 1991) or may not (Aerts et al., 2000; Van Damme et al., 1997; Vanhooydonck and Van Damme, 2001; Zaaf and Van Damme, 2001) be predicted by simple ecomorphological characters such as leg length. Our results suggest that kinematics are insufficient to explain the extraordinary scansorial behavior of geckos.

Major changes in force production do occur when pedestrians transition from the level to vertical locomotion. In geckos, the force production of single legs changed in magnitude and/or completely reversed in direction (Figs 6, 7A,B). Forelegs that support weight during level running (Chen et al., 2006) reversed the direction of normal force and pulled the body toward the surface during climbing. Forelegs that decelerate the body at the beginning of a step during level running (t_1) reverse the direction of fore-aft force and accelerated the body upward during climbing. Fore- and hindlegs that push outward during level running reversed the direction of lateral force and pulled toward the body during climbing. Hindlegs that support weight during level running reduced their normal force by one-sixth during climbing. Hindlegs that accelerate the body only at the end of a step during level running (t_3) accelerated the body upward in the fore-aft direction during the entire step when climbing. Major alterations in GRFs necessarily translate into changes in muscle function. Based on the present results, a comprehensive evaluation of muscle function comparing level running and vertical climbing is certainly warranted (Daley and Biewener, 2003; Higham and Jayne, 2004a). Differential leg function appears to be essential for both sprawled-posture running on the level and vertical climbing.

The individual leg force patterns in the gecko *Hemidactylus garnotii* could be specific to these adept climbers, but the physical constraints on vertical locomotion make this less

likely. Measuring the dynamics of vertical climbing in other species is needed to test the generality of the dynamics measured in the present study. To test if gecko dynamics represent a general template that serves as a target of control (Full and Koditschek, 1999), perturbation experiments, such as adding loads or impulses (Jindrich and Full, 2002), need to be conducted. The gecko's COM dynamics suggest a spring-mass template consisting of a spring that alternately pushes or pulls a mass along a rail or in a vertical plane.

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