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Author for correspondence:
Aleksandra V. Birn-Jeffery
e-mail: aleks.birnjeffery@ucr.edu

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Geckos significantly alter foot orientation to facilitate adhesion during downhill locomotion

Aleksandra V. Birn-Jeffery and Timothy E. Higham

Department of Biology, University of California, 900 University Avenue, Riverside, CA 92521, USA

Geckos employ their adhesive system when moving up an incline, but the directionality of the system may limit function on downhill surfaces. Here, we use a generalist gecko to test whether limb modulation occurs on downhill slopes to allow geckos to take advantage of their adhesive system. We examined three-dimensional limb kinematics for geckos moving up and down a 45° slope. Remarkably, the hind limbs were rotated posteriorly on declines, resulting in digit III of the pes facing a more posterior direction (opposite to the direction of travel). No significant changes in limb orientation were found in any other condition. This pes rotation leads to a dramatic shift in foot function that facilitates the use of the adhesive system as a brake/stabilizer during downhill locomotion and, although this rotation is not unique to geckos, it is significant for the deployment of adhesion. Adhesion is not just advantageous for uphill locomotion but can be employed to help deal with the effects of gravity during downhill locomotion, highlighting the incredible multi-functionality of this key innovation.

1. Introduction

Geckos are incredibly diverse; both in terms of morphology [1] and habitat [2]. They thrive in habitats that require climbing, such as trees and rocks, utilizing three-dimensional components of their habitat. The gecko adhesive system is a key innovation that facilitates climbing vertically, and even in inverted positions, on smooth surfaces. This has resulted in increased rates of diversification [1] and allows them to occupy areas of the habitat that are unsuitable for other animals.

Gecko adhesion occurs via a combination of van der Waals and frictional forces [3–5]. Setae, on the ventral side of their toes, provide the increased surface area and close contact between the foot and the substrate that permits successful attachment [6]. Digital hyperextension provides the attachment/release mechanism for the adhesive system, which is only employed on inclines of 10° or greater [7]. Gecko adhesion is directional [3], acting primarily along the long axis of the digit. This constrains how the foot must be orientated during locomotion. Although the adhesive system facilitates inclined locomotion, its function may be limited to uphill surfaces given that the manus or pes would have to be rotated posteriorly for adhesion to be effective on declines. This leads to a fundamental question about gecko adhesion: can geckos employ their adhesive system when moving downhill?

We use *Chondrodactylus bibronii* (Smith 1846) to investigate the modulation of fore- and hindlimb kinematics during downhill locomotion. We chose *C. bibronii* due to its varied habitat preference [8]; they also lack functional claws, so any advantage on declines would be from the adhesive system [9]. Although we cannot discount unique specializations for a non-terrestrial habitat, which could lead to unique kinematics, using an animal that is a generalist provides us with initial insight into how animals move downhill.
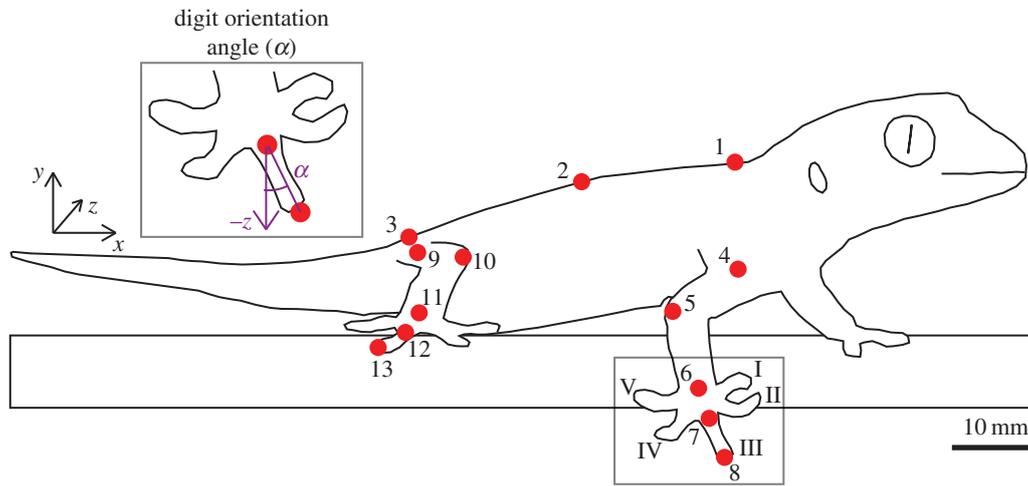
Figure 1. Schematic for marker locations, data coordinate system and calculation of digit orientation. 1–3: body markers; 4: shoulder; 5: elbow; 6: wrist; 7: metacarpalphalangeal joint (MCP); 8: digit III tip; 9: hip; 10: knee; 11: ankle; 12: metatarsalphalangeal joint (MTP); 13: digit III tip; letters I–V represent the digits.

2. Material and methods

Six adult *C. bibronii* (body mass = 13.4 ± 6.9 g [average ± s.d.]; snout-vent length = 72.8 ± 8.0 mm) were used. Prior to running trials, each animal had white markers placed on joint locations using nail polish (figure 1). Animals were run on a flat runway, covered in 60-grit sandpaper (Ra-value: 254 μm) that was inclined at 0°, +45° and −45°. Three synchronized high-speed video cameras (2 Phantom Miro M150, Vision Research Inc., NJ, USA; 1 Photron APX-RS, Photron, San Diego, CA, USA) were located to one side of the runway; one recording a direct lateral view, while the other two were set obliquely to the runway. Three good steady strides per limb, condition and individual were collected.

Markers were digitized using DLT_dv5 [10] and the data were processed using custom-written code in MATLAB (R2013b, The MathWorks, Natick, MA, USA). Joint angles were calculated following methods previously published [11–13]. Statistics and graphs were also produced using custom codes in MATLAB. ANOVAs were run using condition as a fixed factor and individual as a random factor, with the F-values subsequently adjusted using the interaction term between individual and condition [14].

3. Results

The forelimbs were more sprawled on inclines than during level locomotion (figure 2*b*; electronic supplementary material, table S1). Forelimb motion was only slightly adjusted during downhill locomotion; the digits did not move as far posteriorly nor as close to the floor compared with the other conditions (figure 2*a,b*; electronic supplementary material, table S1). The hindlimb digit trajectory was similar for the level and uphill conditions (figure 2*a,b*). However, digit III on the pes had significant changes in the fore–aft and vertical planes when moving downhill (electronic supplementary material, table S1). The total excursion in both the fore–aft and vertical direction around the hip was greatly reduced (figure 2*a*). Overall, the cyclical motion of the hindlimb exhibited a reduced circular arc on the decline.

Despite changes in incline, the orientation of the digits on the manus were unaffected during stance; with the tendency for digit III to be pointed nearly in line with the fore–aft plane—therefore, pointing anteriorly (figure 2*c*). On the other hand, the pes on the level and uphill conditions faced slightly laterally away from the body midline (figure 2*c*). The pes was rotated posteriorly (70° compared to level) and away from

the direction of travel on declines (figure 2*c*; ANOVA at footfall angle between metatarsalphalangeal joint (MTP) and digit: $F_{2,10} = 27.74$; $p < 0.005$; post hoc Dunn–Sidak both level and uphill versus downhill $p < 0.005$). Proximal femur rotation accounted for 14° (table 1) indicating that the remaining rotation occurred at distal joints.

4. Discussion

Geckos are extremely capable of climbing up steep, smooth surfaces. Here, we demonstrate that geckos have a remarkable ability to reverse the position of their hind feet in order to use adhesion as a brake and/or stabilizer when moving on steep downhill surfaces. Specifically, on the 45° downhill slope, geckos rotated their hindlimb up to 70° posteriorly (relative to level conditions—figure 2*c*). Use of the adhesive system on declines has previously been suggested [15], but not tested experimentally. We provide evidence for the multi-functionality of the gecko adhesive system, permitting effective locomotion on both uphill and downhill slopes. Without this ability, geckos would be effective at going up, but would be constrained by not being able to descend as easily. This critical component of locomotion (i.e. what goes up, must come down) has been achieved effectively using extreme degrees of joint rotation.

Animals often exhibit differential limb function on level and sloped terrain [16–20], and the amount of bodyweight support per limb often shifts between the fore- and hindlimbs depending on the type of terrain. Here, the significant rotation of the pes likely results in the forelimbs accounting for a much greater component of bodyweight support on the downhill condition than in other conditions. The forelimbs probably adopt a more significant role in braking [16,19], whereas the hindlimbs likely act as stabilizers (see the electronic supplementary video), analogous to stabilizer wheels on a child's bike to prevent them from toppling medio-laterally. It is probable that, although the hindlimbs may be providing medio-lateral stability, the adhesive system is also engaged to supply some braking, via increased friction, and fore–aft stability. Our data highlight the significant and context-dependent decoupling between limbs, as well as the large shifts in limb modulation. This shift has probably led to significant changes in the neural control of locomotion, but this requires further research. In addition, future studies
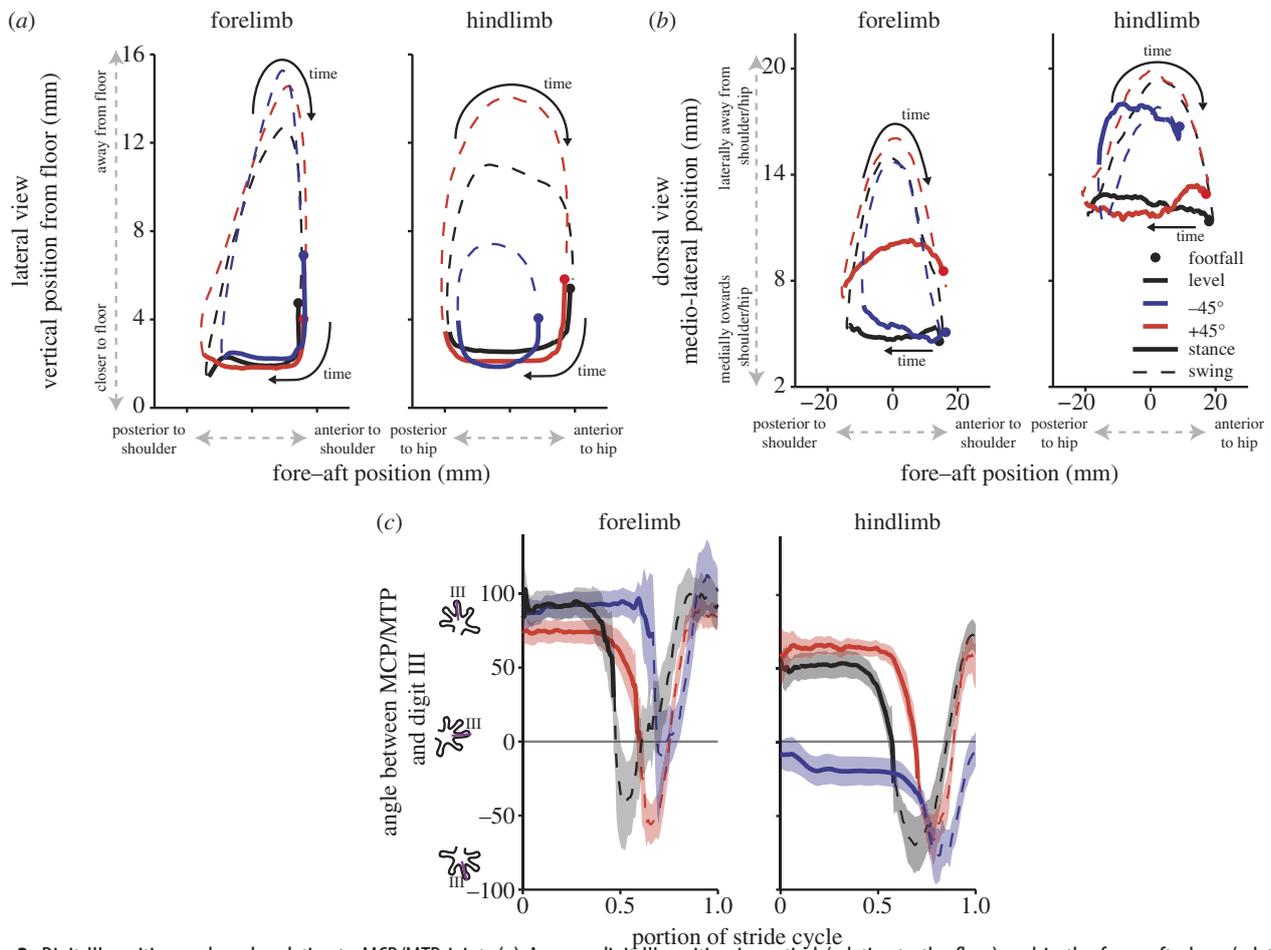
Figure 2. Digit III position and angle relative to MCP/MTP joint. (*a*) Average digit III position in vertical (relative to the floor) and in the fore–aft plane (relative to shoulder/hip marker). (*b*) Average digit III position in the medio-lateral and fore–aft planes relative to the shoulder/hip marker. (*c*) Average angle between MCP/MTP and digit III (figure 1 for calculation). Shaded regions represent the 95% confidence intervals.

Table 1. Average femur rotation for level condition, and average difference from level (negative values indicate increased clockwise rotation) on incline and decline conditions.

condition	level (degrees $\pm$ s.e.m.)	difference from level (degrees $\pm$ s.e.m.)		d.f. numerator	d.f. denominator
		+45°	−45°		
footfall	−28.94 $\pm$ 3.56	−12.12 $\pm$ 3.38[a]	−13.58 $\pm$ 3.03[a]	2	10
mid-stance	−38.16 $\pm$ 2.88	−10.87 $\pm$ 2.92[a]	−10.74 $\pm$ 3.05[a]	2	10
end stance	−67.29 $\pm$ 1.68	8.49 $\pm$ 7.14	2.53 $\pm$ 2.35	2	10

[a]Significant difference from the level condition. d.f.: degrees of freedom.

could confirm our interpretations by quantifying the patterns of force generation by the fore- and hindlimbs simultaneously.

The posterior rotation of the pes during downhill locomotion is not unique to *C. bibronii*. Several studies have noted this capability in mammals (e.g. [21–24]), but this potential functional change in the hindlimb has not been previously quantified during locomotion. For mammals that reverse their foot orientation, femoral rotation accounts for a very small portion of the total rotation. The majority of rotation stems from the crurotalar and subtalar joints [22–24]. This is similar to *C. bibronii*, where femoral rotation accounts for only 20% of the full foot reversal (table 1). As in mammals, we expect that the astragalocalcaneum (fused ankle bones) of the mesotarsal joint are providing the majority of the posterior

rotation in geckos. Lizards, however, exhibit differences in morphology of their astragalocalcaneum, which, in some cases, may preclude separate rotations between distal limb elements and the foot [25]. However, climbing geckos appear to possess an astragalocalcaneum that may allow greater rotation at the articulation with the tibia and fibula [26], particularly as there has been no mention of significant hindlimb reversal in lizards in the literature, although some rotation at the mesotarsal joint appears common among lizards [27]. Future work detailing ankle–foot morphology in *Gekkota* and other lizards will determine the extent of foot reversal capabilities and the link with an adhesive system.

In conclusion, we highlight the ability of climbing geckos to rotate their adhesive system to deal with declines. The

directionality of the system, in that adhesion only works when loaded in shear opposite to the direction of travel, has the potential to constrain locomotion in geckos, but the extreme rotation discovered in our study ameliorates this constraint and avoids a trade-off.

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