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Analysis Of The Crested And Gargoyle Geckos' Locomotion And Toepad
Activity On Horizontal And Vertical Poles Of Varying Thickness

by

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A Paper Presented to the
Faculty of Mount Holyoke College in
Partial Fulfillment of the Requirements for
the Degree of Bachelors of Arts with
Honor

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May 2016

This paper was prepared
under the direction of
Professor Duncan Irschick and
Professor Craig Woodard
for eight credits.

ACKNOWLEDGEMENTS

I would like to thank my thesis advisor, Professor Craig T. Woodard, PhD, and my two committee members Professor Duncan J. Irschick, PhD and Professor Stan P. Rachootin, PhD for their continuous support throughout the course of this project, and for believing in me when I needed it most. I would like to express my sincerest gratitude to the Department of Biological Sciences for the opportunity to write a thesis. I am forever grateful to Professor Irschick for giving me the opportunity to pursue such interesting and engaging research in his lab and for teaching me countless lessons about independent research. It is because of his constant mentorship and guidance that I was able to complete this project. I would also like to thank Professor Woodard and Professor Rachootin for their invaluable input and suggestions, and for always encouraging me to view my thesis from different perspectives. Lastly, I would like to thank Rabya Saraf and Umme Lena, two individuals who were integral to the completion of this project.

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ABSTRACT

Various morphological traits and behaviors have evolved to facilitate a gecko's ability to climb vertically. The gecko relies on the structural elements of its toepads to maximize adhesive force and enable easy release from the substrate. Thus, toepad adhesion plays an important role in the locomotive behavior of the gecko and influences how it maximizes adhesion efficiency. The change from a horizontal surface to an incline prompts the geckos to alter their gaits to deploy their adhesive system which accommodates for the different gravitational and frictional forces acting on them. Current research on geckos has looked at gecko toepad properties and locomotion on flat surfaces, but there has been little to no research on how gecko locomotion compensates for the unique challenges of walking on curved surfaces. By analyzing the locomotion on poles (of varying thickness) for two species of geckos, *Rhacodactylus auriculatus* and the *Correlophus ciliates*, this study found that both the stride lengths and frequencies decreased as the diameter of the pole decreased, indicating that shorter, slower steps help the animal maintain balance. The gecko's body also moves closer to the surface of the substrate for increased stability while the tail acts as a fifth appendage when necessary.

INTRODUCTION

Geckos have a remarkable ability to walk and climb on different types of substrates, be they rough or smooth, wet or dry, horizontal or vertical (Gilman *et al.*, 2015). There are over a thousand species of geckos, each with its own morphological variations on toepad structures (Autumn *et al.*, 2006). The size, shape, and effect on surface adhesion of a gecko's toepad have long held a fascination for many in the scientific community, as it allows the gecko to run upside-down and maneuver complex three-dimensional environments (Hill *et al.*, 2011).

Of the terrestrial vertebrate lineages, geckos are some of the most species-rich, comprising 25% of all described lizard species (Gamble *et al.*, 2012). The thousands of species of geckos come with their own morphological variations on toepad structures (Autumn *et al.*, 2006). Scansorial pads preserved in amber-embedded gecko fossils suggest that the adhesives system of geckos has been present since at least the mid-Cretaceous era; today, about 60% of gecko species have adhesive toepads (Gamble *et al.*, 2012).

Looking at the origin, diversification and loss of adhesive toepads, Gamble *et al.*, (2012) found that environmental circumstances trigger these transitions. Geckos demonstrate elevated levels of morphological evolution when they lose their adhesive system, which leads to profound effects on their functional capacities (Higham *et al.*, 2015). Reduction in the adhesion system may allow geckos to achieve greater maximum speeds, burrow more effectively, or move on loose sand that could clog their setae (Higham *et al.*, 2015). Gamble *et al.* (2012) looked at molecular genetic data for 107 of 118 known genera of geckos and hypothesized that the adhesive capabilities of the gecko toepads have been lost and gained multiple times over the gecko's evolutionary history; specifically, their hypothesis suggested they may have evolved 11 times and been lost 9 times. The researchers used Maximum Likelihood (ML) in *RAxML* 7.2.6 and Bayesian analysis in *MrBayes* 3.1.2 to determine the phylogenetic relationships among the genera and estimated the independent gains and losses of the adhesive pad using ancestral state reconstruction based on parsimony and ML. There are lineage-specific differences evident in geckos from different genera, especially in the internal anatomy of the toepads, yet the similarities in external morphology is still prominent.

(Gamble *et al.*, 2012). The researchers, however, recognized that an incomplete phylogenetic record makes the process of determining the loss and gain of the adhesive system quite challenging (Gamble *et al.*, 2012).

Gecko Toepad: Setae and Spatulae

Geckos as a species demonstrate a wide range of foot adaptations and morphology (Gennaro 1969). Studies looking into gecko toepads have rejected previous hypotheses regarding suction or friction being involved in gecko adhesion (Gennaro, 1969). The gecko toepad contains a hierarchy of structures that decrease in size while increasing in surface area (Fig. 1). Tiny, hair-like structures, called setae, found at the base of the toepad allow the gecko to successfully attach its toepad to the substrate via frictional and van der Waals forces (Birn-Jeffery and Higham, 2014). The distal ends of setae further branch into hundreds of fibers that end in flat structures called 'spatulae' (Hill *et al.*, 2011). The increased surface area available for contact afforded by these spatulae contribute to the strong attachment forces generated by the toepad (Hill *et al.*, 2011). The spatular tips are 0.2 μm long, much smaller than the wavelength of visible light

(Hansen and Autumn, 2005). The forces produced by these miniscule structures are truly amazing. Each spatula can produce anywhere from 5 to 25 nN of force and thus each seta can produce an average force of approximately 200 μ N, at least for the Tokay gecko (*Gekko gecko*) (Autumn *et al.*, 2000). Since geckos range in body size anywhere from about 2 grams to over 250 grams, the force produced by their toepads varies significantly (Autumn *et al.*, 2000).

The gecko setae are composed of β -keratin that gives it a compliant quality and allows for the successful attachment of the toepad to the substrate (Autumn *et al.*, 2006). Microbeam X-ray diffraction analysis has shown conclusively the presence of these protein constituents, but other experimental techniques point to the presence of other proteins as well; specifically, Raman microscopy of individual setae shows the presence of α -keratins and electrophoretic analysis of setal proteins also supports this interpretation (Rizzo *et al.*, 2006).

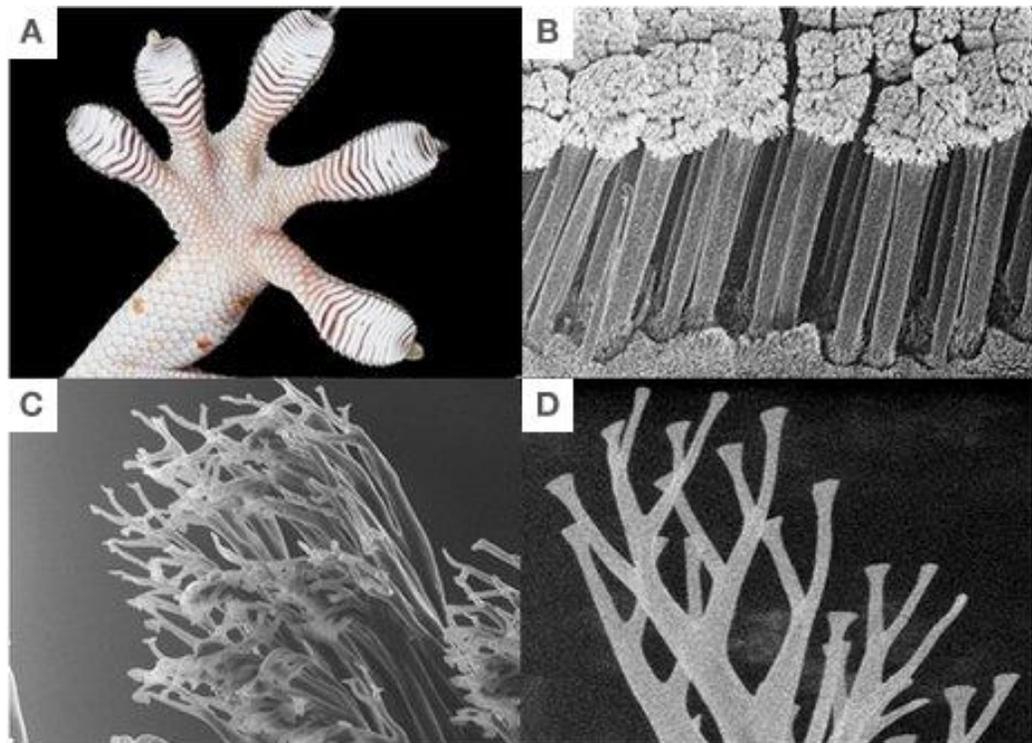


Figure 1. The various hierarchical structures found on a gecko toepad. (A) Ridge-like lamellae cover the toes of the gecko. (B) Millions of microscopic hair-like structures called setae cover each toe. (C) Each seta contains hundreds of spatulae at its tip. (D) The spatular tips are $0.2\ \mu\text{m}$ long, smaller than the wavelength of visible light. Adapted from BBC News.

These setae are outgrowths of the outer layer of the subdigital epidermis, evolving from the microscopic spinules present in the outer epidermis of all gekkotans, an infraorder of the order Squamata (or scaled reptiles) (Gamble *et al.*, 2012). Geckos have a stiff tendon tissue that is connected to the bone and integrated directly into the skin of the toepad, resulting in flaps known as scansors (King *et al.* 2014). These scansors allow for draping adhesion, a property that allows the adhesive to

conform to the surface it attaches to while maintaining in-plane stiffness, generating strong forces over centimeter length scales (King *et al.* 2014). The tendon exhibits extensional compliance, and works in conjunction with the pad and skin since compliance is additive (King *et al.* 2015). A pattern seen in many species of gecko indicate that the loss of adhesive capabilities is due to a reduction in the number of scansors and setal length, and not because of a complete dissolution of the microscopic structures themselves (Gamble *et al.*, 2012). Thus, setal elongation and enhancement is associated with a directional adhesive complex that also includes broadened scansors, or digital pads, and modified tendons/muscles that control these scansors (Johnson and Russell, 2009).

Gecko toepad adhesion is mechanically controlled, which is a reason why adhesion is not spontaneous and setae are not self-adhering (Autumn *et al.*, 2006). In their resting state, the setae are bent proximally (Autumn *et al.*, 2006). When the gecko takes a step, the setae are bent out of this resting state and the setal stalks are flattened against the substrate, creating a small preload and displacement of the scansor on the toepad (Autumn *et al.*, 2006). This is hypothesized to bring the spatula flush with the substrate, maximizing the area of contact (Autumn, 2006). Thus,

adhesion requires a loading force perpendicular to the substrate and a drag force parallel to it, which consequently requires an appropriate orientation of the toepad to maximize the adhesive forces, and hence is critical for successful locomotion (Hill *et al.*, 2011).

Six properties of the gecko setae lead to its functional versatility (Autumn *et al.*, 2006). These include possessing directionality, attaching with minimal preload, detaching quickly and easily, sticking almost without discrimination, self-cleaning, and being non-adhesive by default (Autumn *et al.*, 2006). Another impressive quality of gecko setae is their resistance to wear and tear despite constant use. Their setae stick more strongly the faster they slide, and do not wear out even after 30,000 cycles (Gravish *et al.*, 2010). This is remarkable since "friction between dry, hard, macroscopic materials" decreases as velocity increases and continues to decrease, partly due to wear. Indeed, for the non-molting Tokay geckos (*Gekko gecko*) used by Gravish *et al.* (2010), adhesive forces continued to increase from the onset of sliding as shear speed went from 500nm/s to 158mm/s.

There is an inverse relationship between body mass and the size of the spatula tip in lizards and arthropods (Arzt *et al.* 2003), a correlation

supporting the prediction by Autumn *et al.* (2002) that larger spatulae result in lower forces. Because geckos have a small spatular size, the adhesive forces produced by their toepads are far superior to other animals with setae (Autumn *et al.*, 2006). A microscopic study of the terminal elements of animals differing in weight by 6 orders of magnitude, from a beetle to fly to spider to gecko, has shown a strong inverse scaling effect between attachment devices and body mass (Fig. 2). The diameters of their spatula ends ranged from 0.2 μm (gecko) to 5.0 μm (beetle); the larger the animal, the smaller the terminal elements were to increase the surface area of contact with the substrate (Arzt *et al.*, 2003). The mass of the animal increases faster than the possible foot-to-substrate contact, and this is compensated by an increase in setal density (Arzt *et al.*, 2003). Thus, downscaling the contact elements, or the setae, multiplies the contact area as a whole and leads to more efficient attachment (Arzt *et al.*, 2003). Increasing setal density is also useful in situations where the inability of a few setae to make contact with the surface, due to a dirt particle or gaps in the substrate, minimally influence contact adhesion (Arzt *et al.*, 2003). In larger animals, a small surface-area-to-volume ratio is compensated by disproportionately large pads along with an increased

attachment efficiency (Labonte and Federle, 2014). Pad area demonstrates isometric scaling while pad efficiency increases with size, thus making attachment performance dependent on size (Labonte and Federle, 2014).

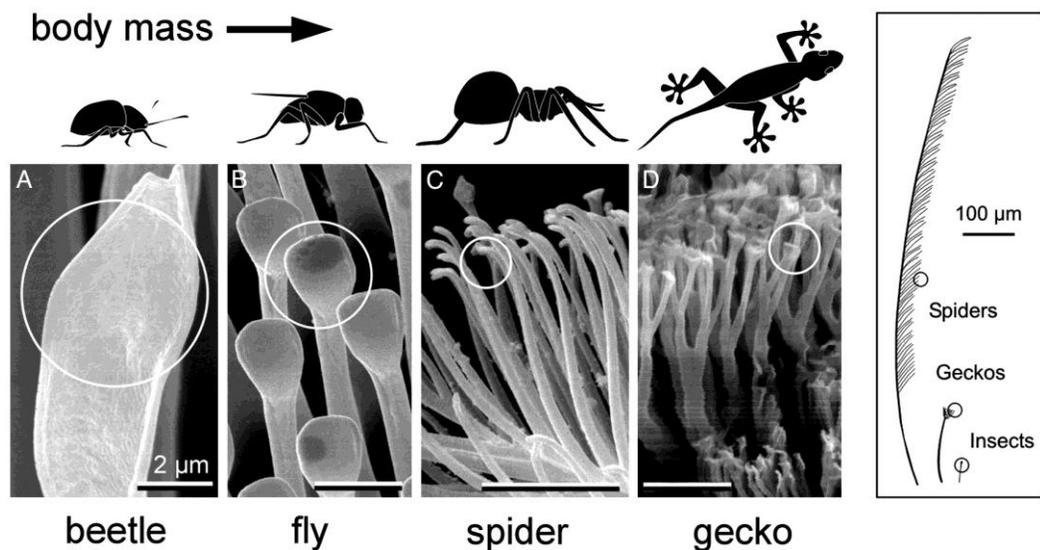


Figure 2. Terminal elements in animals with hair-like attachment mechanisms. The heavier animals possess finer adhesion structures. Taken from Arzt *et al.*, (2003).

Toepad Orientation, Adhesion and Locomotion

Previous studies have established a connection between the gecko's speed and toepad adhesion (Russell and Higham, 2009). Going from a flat surface to an incline showed a decrease in speed for the climbing gecko, indicating that adhesive capabilities were at work (Russell and Higham,

2009). Adhesion is driven by gravitational forces that indicate an incline, rather than the texture of the substrate itself, and comes with its own trade-offs: adhesion compromises speed but maximizes stability (Russell and Higham, 2009). However, acceleration is affected by substrate texture. When a gecko climbs a gap-filled substrate such as a wire, only part of the toepad adheres to the surface, resulting in a lower acceleration capacity (Vanhooydonck *et al.*, 2005). Thus, the smoother the surface, the greater the contact and the faster a gecko can accelerate (Vanhooydonck *et al.*, 2005).

Switching quickly between strong attachment and easy detachment is necessary for swift locomotion involving adhesion and has been a focus of much scientific study (Labonte and Federle, 2014). Both adhesive and frictional forces generated by the gecko can be changed by over three orders of magnitude to facilitate this switch, and require a tiny angular displacement within 0.25° of the proximal end of the lamellae (Tian *et al.*, 2006; Wu *et al.*, 2015). The adhesive capabilities of geckos are also multifunctional: while going uphill they stabilize the organism and avoid slippage, going downhill they account for a smooth descent, where the

geckos rotate their hind limbs posteriorly to allow the adhesive system to function as a break instead (Birn-Jeffery and Higham, 2014).

The specific movements of the limbs allow the geckos to produce forces to counter gravity while climbing. Wang and colleagues measured the three-dimensional reaction forces of geckos (*Gekko gecko*) climbing a vertical surface using a three-dimensional force-sensors-array to study gecko locomotion. They found that the gecko's speed had no relation to the attachment and detachment times of the toepad. Instead, speed was increased by an increase in the stride length or stride frequency, depending on the species of gecko (Wang *et al.*, 2011). This, however, contradicts the study done by Zaaf *et al.* (2001) which found that stride lengths did not vary with speed in climbing species, instead, faster climbing speeds correlated with increasing stride frequency. The change from a horizontal surface to an incline prompted the geckos to alter their gaits in order to accommodate for the different gravitational and frictional forces acting on them (Wang *et al.*, 2011). Studying this gait adaptation may contribute to the invention of gecko-inspired robots that could maneuver tough, complex surroundings, and may serve a variety of functions.

In addition to the role of the limbs, the gecko adapts its posture as well. When geckos move vertically, they use a sprawled posture where the limbs play a role in maintaining the sprawled posture for stability (Wang *et al.*, 2011). The gecko's body moves in an S-shape motion and the feet need to generate lateral forces to counter the inertia caused by the twisting. This is achieved by pulling the limbs to the midline of the body to prepare for the attachment mechanism (Wang *et al.*, 2011). These lateral forces are important in forming adequate adhesion with the vertical surface and also counter forces that disturb the gecko's balance, such as the overturning moment, the lateral inertia etc. (Wang *et al.*, 2011). Differential leg function is essential for effective locomotion: while moving upwards, the forelimbs and the hind limbs both contribute equally to stability and the driving motion forwards, in contrast, when moving downwards, the hind limbs are much more involved in maintaining stability than the forelimbs (Wang *et al.*, 2011). This suggests that the direction of motion forces the geckos to alter the function of their limbs to counteract destabilizing forces (Wang *et al.*, 2011). Looking at the vertical ascent of the Indo-Pacific gecko (*Hemidactylus garnotii*), Autumn *et al.* (2006) found that this species climbed at a speed of 77 cm/s with a

stride frequency of 15 Hz. During each step, the overall force acting on the body decreased to zero whenever the gecko attached and detached its toepad from the surface, while the peak overall force was twice the body weight at mid-step, suggesting their posture enables them to effectively counter the forces acting on them (Autumn *et al.*, 2006). Since geckos are energy efficient climbers, the total mechanical climbing energy is only 5-11% greater than the potential energy change because geckos do not generate decelerating forces on their center-of-mass while climbing (Autumn *et al.*, 2006).

Another Important Appendage: The Tail

Gecko tails serve a variety of functions. They not only allow the geckos to reorient themselves midair, by producing a greater tail inertia with respect to the body's inertia (Jusufi *et al.*, 2011), but also help with balance and locomotion by acting as a fifth limb when necessary (Yong, 2008). This function as a "control appendage" adds to the existing roles of the tail as a source of providing balance, grip, and serving as a passive store of fat (Jusufi *et al.*, 2008). Many species have evolved to possess setae

on the tips of their tails as well (Bartlett, 2004). For example, the Crested and Gargoyle geckos are a closely related species hailing from the rainforests of New Caledonia in the South Pacific (Hsu *et al.*, 2012). Both possess webbing on their legs and digits, and are mostly arboreal species; they also possess setae at the tips of their tails (Brusso, 2013).

The setae on the tails demonstrate the same properties as those on the gecko's toepads, allowing it to accomplish some more feats unique to its species (Vosjoli, 2005). Both the Crested and Gargoyle geckos have setae at the tip of their tails that are similar in surface morphology to the toes and used for a variety of functions (Bauer, 1998). The adhesive apparatus on the tail forms an observable scansorial pad with increasing complexity (Hansen and Autumn, 2005). The scansors on the tail resemble the toepads in terms of surface morphology, but lack the tendon and vascular system characteristic of the toepads (Hansen and Autumn, 2005). Nonetheless, the scansors on the toepads and the tails seem to be homologous structures (Hansen and Autumn, 2005).

According to Jusufi *et al.* (2008), the flat-tailed house gecko (*Cosymbotus platyurus*) actively uses its tail when climbing vertical surfaces. This species of gecko can run up a wall at speeds of 3 feet per

second, peeling their toepads from the surface approximately 30 times per second, thus making their quick recovery from slips even more impressive (Sanders, 2008). Losing traction with a limb causes the gecko to use the tail as a temporary substitute until it can regain its grip on the surface (Jusufi *et al.*, 2008). The flat-tailed gecko studied by this group had the ability to right itself within a tenth of a second after slipping and flailing off a vertical surface at a 60° angle. In contrast, geckos without a tail did not recover their footing in one of five slips (Jusufi *et al.*, 2008). The tail tip pushes against the vertical surface to counter the "pitch-back" of the head and upper body when it slips (Jusufi *et al.*, 2008). If the gecko loses traction with more than one foot, it flattens its tail against the surface as opposed to tapping it against the surface; both the "tail-tapping" and "tail-flattening" techniques aid the geckos in recovering from slippery patches on vertical surfaces (Sanders, 2008). How high the geckos keep their tails off a surface is determined by the anticipated slippage on that surface; when the flat-tailed geckos were made to run up a high traction vertical wall, their tails were held up off the wall (Thompson, 2008). In comparison, on a wall of intermediate traction the tails tended to be in

constant contact with the surface as the geckos' feet slipped slightly with each step (Thompson, 2008).

In addition to the tail's role in high speed vertical climbing, landing on a wall after a jump is also stabilized by the presence of a tail (Jusufi, 2013). Because of its generally small size, the flat-tailed house gecko does not have a highly controlled landing mechanism on a wall. Instead it uses the tail as a counter-lever to its body weight and reduces the individual forces acting on its feet without incurring serious damage (Jusufi, 2013). Looking at the locomotion of geckos that have lost their tails can help to assess the significance of the tail. Geckos can lose their tails by a process called autotomy, whereby an animal voluntarily sheds a part of its body in pursuit of self-preservation when threatened or attacked (Jagnandan *et al.*, 2014). After a gecko loses its tail, its center of mass shifts, forcing the gecko to compensate for this until a new tail is regenerated (Jagnandan *et al.*, 2014). Analyzing tail autotomy and subsequent regeneration, Jagnandan *et al.* (2014) found that in the Leopard gecko (*Eublepharis macularius*), although there were no changes in body kinematics, there were decreases in hind limb joint angles, leading to a more sprawled posture and greater hind limb ground reaction forces after autotomy.

These changes, however, were short-lived, lasting only until the tail was regenerated. This suggests that tail morphology significantly influences body posture and limb forces, and distributes the weight in a way that maximizes stability (Jagnandan *et al.*, 2014). Thus, the geckos may employ the tail in a similar manner while climbing a curved, vertical surface, and studying their locomotion on such a surface may provide more insights into their climbing behavior in the real world.

Commercial Breakthroughs

Bio-inspired technologies require understanding not only the molecular basis of the adhesive toepads, but also the biomechanics of the organism's body as a whole; these levels span seven orders of magnitude of size in a gecko and make commercial replications a demanding enterprise (Gamble *et al.*, 2012). In recent years, there have been commercial breakthroughs that have found a way to take advantage of the adhesive properties of gecko toepads and apply it to everyday use. GeckSkin™, a super-adhesive that was the culmination of a collaborative effort by two separate labs, the Irschick Lab and Crosby Lab, at the

University of Massachusetts at Amherst, is an example of the possibilities of such research (Crosby and Irschick 2016). An index-sized piece of this adhesive can hold 700 pounds on a smooth surface, and can easily be removed and reused without damaging surfaces (Crosby and Irschick 2016). While traditional pressure-sensitive adhesives rely on viscoelasticity, GeckSkin™ relies on draping adhesion, a property that allows the adhesive to conform to the surface it attaches to and distribute the weight evenly while maintaining high elastic stiffness, the same property that natural geckos exploit (Crosby and Irschick 2016). Continued research into this area, including studying whole body gecko locomotion on flat and curved surfaces, may facilitate further advances into this technology and beyond.

Purpose of My Research

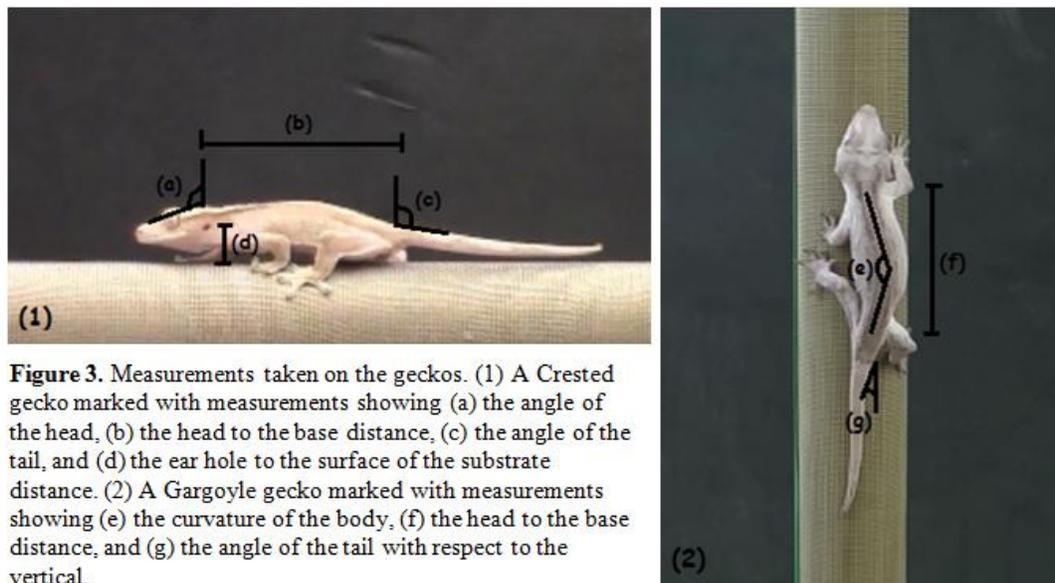
Current research on geckos has looked at gecko toepad properties and locomotion on different substrates and different inclines of flat surfaces, but there has been little to no research conducted on how gecko locomotion compensates for the unique challenges of walking on curved

surfaces like poles. Although a lot of research is already available on gecko toepad adhesion, which has led to commercial breakthroughs, there has not been enough attention devoted to how the toepad adhesion capabilities and the gecko's tail facilitate gecko locomotion on wide and narrow poles. With respect to previous findings, I hypothesized that as the locomotion became more challenging with a switch to a narrow pole, the geckos would decrease their stride lengths and frequencies, and move their center of mass closer to the pole for greater stability.

MATERIALS AND METHODS

This project involved the use of 14 individual geckos: 7 Crested geckos (*Correlophus ciliatus*) and 7 Gargoyle geckos (*Rhacodactylus auriculatus*), that were commercially bred for the purposes of lab research. This work was done under an IACUC protocol 2012-0064 from the University of Massachusetts Amherst. The individual Crested geckos will be referred to as CC1, CC2, CC4, CC5, CC6, CC7 and CC8, while the individual Gargoyle geckos will be referred to as RR1, RR2, RR4, RR5, RR6, RR7 and RR8. A standard digital video camera and a Cannon G16 recording at 30fps (frames per second) were used to record the motion of the 14 geckos as they made their way horizontally across and vertically up the two cylindrical poles of varying thickness (The thick pole had a diameter of 2.5 inches while the thin pole has a diameter of 0.5 inches). The geckos were made to walk 45-55cm along the pole to obtain complete strides that could be analyzed. For each gecko, three to four strides were analyzed in terms of stride lengths and frequencies, and in addition several lengths and angles on their body were also measured. These included the distances from the head to the base of the tail, from the ear

hole to the surface of the substrate, the angle of the head, and the angle of the tail relative to a vertical normal. *Figure 1* below illustrates the measurements taken for the vertical and horizontal trials.



There were a total of four conditions imposed on the geckos:

Horizontal Thick, Horizontal Thin, Vertical Thick and Vertical Thin. The vertical trials were further divided into Vertical (side view) and Vertical (top view), the 'side view' correspond to the view seen in (1) of Fig. 3, while the 'top view' corresponded to the view seen in (2) of Fig. 3. Thus, for the horizontal and the vertical (side view) trials four variables were

measured, while for the vertical (top view) trials three variables were measured.

The video recordings of the geckos were used to extract every frame from each video (the camera recorded at 30fps) to obtain a frame by frame picture series using a Video to JPG Converter program from DVDVideoSoft (a software downloading site). Four to five frames corresponding to successive strides of the same limb (as the toepad made contact with the substrate surface) were selected and the aforementioned variables were measured using the program *ImageJ*.

There were some ambiguities in the measurements because the frames did not always align with when the toepad was fully attached to the surface or the toepad itself was on the surface for a few consecutive frames. The measurements, thus, had to rely on the visual acumen and judgment of the researcher. The Snout-to-Vent length (cm) and Mass (g) of the geckos were also measured to account for the differences in their locomotion with respect to size (Table 1). All the data values from the frames are compiled in several tables and graphs and include the averages for each condition for the stride lengths, the stride frequencies and the various lengths along their bodies.

Table 1. The individual Mass (grams) and Snout-to-Vent length (cm) for the 14 geckos used in the experiments, and their averages

Crested Gecko			Gargoyle Gecko		
Gecko ID	Mass (g)	SVL (cm)	Gecko ID	Mass (g)	SVL (cm)
CC1	29.32	9.68	RA1	37.90	10.63
CC2	34.08	10.86	RA2	29.51	11.31
CC4	31.62	10.29	RA4	31.69	10.23
CC5	31.62	10.68	RA5	31.60	10.97
CC6	28.15	9.55	RA6	41.18	11.66
CC7	28.51	10.58	RA7	38.30	10.11
CC8	34.49	10.88	RA8	36.88	10.43
Average	31.11	10.36	Average	35.29	10.76

RESULTS

Stride lengths and frequencies were measured for all the geckos, as well as various lengths and angles along the geckos' bodies. For some of the geckos, there were some trials with no examinable videos produced; the data for those were left blank and therefore not included in the averages (Table 2).

Table 2. Individual geckos that did not produce any examinable videos of locomotion for each of the four trials.

Trial	Geckos with No Data
Horizontal Thick	-
Horizontal Thin	-
Vertical Thick	CC4, RA1
Vertical Thin	CC1, CC4, RA1

The averages for the horizontal thick trials were based on 10 frames per gecko, for a total of 70 frames per species. The averages for the horizontal thin trials were based on 5 frames per gecko (35 frames per species) due to a lack of analyzable data. The averages of vertical trials were based on an even lower number of frames, since they had to be divided up into the side and top views, and not every gecko produced

both views. The vertical thick (side) trial was based on 3 geckos per species and involved 12 frames per species; the vertical thick (top) trial was based on 5 geckos pr species and involved 20 frames per species; the vertical thin (side) trial was based on 4 geckos per species and involved 16 frames per species; and the vertical thin (top) trial was based on 3 and 6 geckos for the Crested and Gargoyle species, respectively, and involved 12 frames for the Crested and 24 frames for the Gargoyle geckos.

For each of the four trials, the head and tail angles were measured (in degrees) to determine how high off of the surface of the substrate the gecko's head and tail were during locomotion. Except for the Gargoyle gecko on the vertical trials, the angle of the head and the tail increased as the gecko went from the thick to the thin poles (Table 3). For the Crested gecko, both angles increased as it went from the horizontal thick to the horizontal thin pole as well as from the vertical thick to the vertical thin pole, suggesting that the gecko moved both its head and tail closer to the surface it was walking across as the pole's diameter decreased. The Gargoyle gecko moved its head and tail closer to the surface as it went from the horizontal thick to the horizontal thin pole, but actually raised them as it went from the vertical thick to the vertical thin pole (Table 3).

Table 3. The averages of the head and tail angles in (degrees) for the four conditions. Both the head and tail angles were measured against a vertical normal (Fig. 3). Not all the geckos gave analyzable data for each trial.

Gecko ID	Horizontal Thick*		Horizontal Thin*		Vertical Thick (Side)**		Vertical Thin (Side)***	
	Head Angle	Tail Angle	Head Angle	Tail Angle	Head Angle	Tail Angle	Head Angle	Tail Angle
CC	106.87	85.22	113.06	94.06	99.66	85.29	105.38	96.49
SE	2.16	7.44	1.69	6.83	0.40	13.14	1.93	5.53
RA	101.94	82.89	111.36	105.73	108.23	109.64	103.17	100.58
SE	2.41	2.71	2.42	1.67	3.66	2.77	1.25	6.13

*Data from all 14 geckos were used to derive the averages and their standard errors (SE)

**Data from CC1, CC5, CC8, RA2, RA4 and RA5 were used

***Data from CC2, CC5, CC6, CC8, RA2, RA4, RA6 and RA8 were used

Fig. 4 shows that the head angles for the Crested and Gargoyle geckos on the horizontal trials were much closer than the tail angles, as the Gargoyle geckos' tails moved a lot closer to the surface than the Crested geckos' tails. The Crested geckos started with their heads and tails closer to the surface on the horizontal trials than the vertical trials, while the Gargoyle geckos showed the same trend for the thin trials but the opposite trend for the thick trials (Fig. 4). The Gargoyle gecko had its tail high in the air for the horizontal thick trial which lowered on the

horizontal thin trial, while it had its tail closer to the surface on the vertical thick trial than the vertical thin one (Fig. 4).

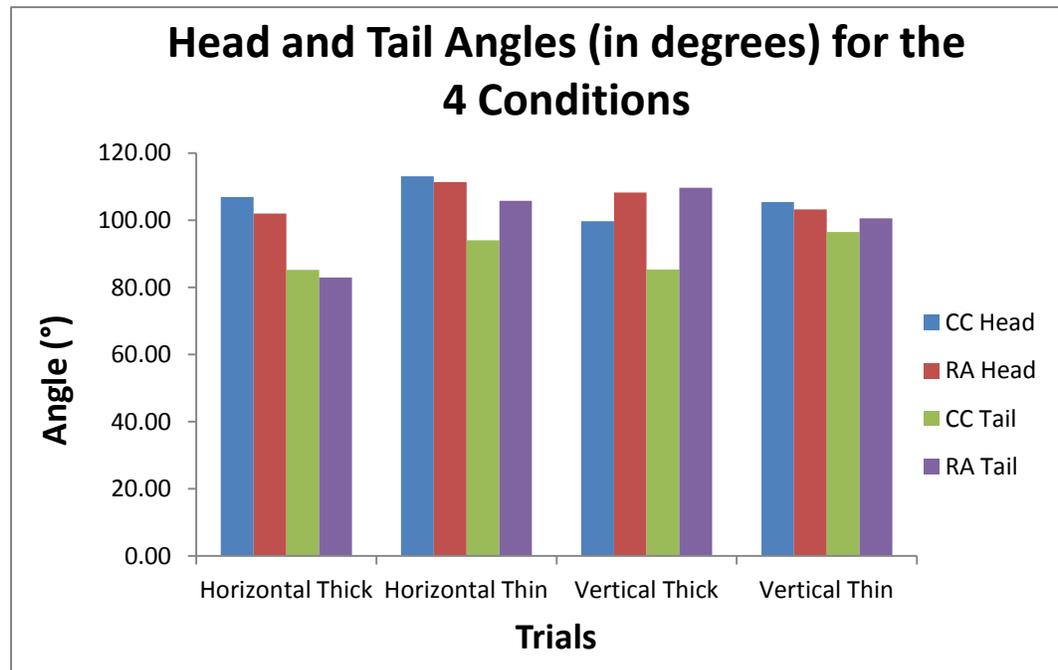


Figure 4. Head and tail angles (in degrees) measured for the four conditions, as shown in Fig. 3. For the horizontal trials, data from all 14 geckos was used to derive the averages and their standard errors (SE). For the vertical thick (side) trials, data from CC1, CC5, CC8, RA2, RA4 and RA5 were used, while for the vertical thin (side) trials data from CC2, CC5, CC6, CC8, RA2, RA4, RA6 and RA8 were used.

The distance from the earhole to the surface of the substrate also decreased as we went from the thick to the thin trials, within the horizontal and vertical trials (Table 4). Going from the horizontal thick to the horizontal thin to the vertical thick and to the vertical thin trials, the

distance across the body, measured straight down vertically from the base of the head to the base of the body where the tail started, progressively decreased for both species, indicating that the geckos were twisting their bodies more while walking and bringing their limbs closer to their body with each step (Table 4).

Table 4. The averages of the lengths (cm) measured for the four conditions, where ES = Ear to surface distance in cm, BD = Distance across the body in cm, and SL = Stride Length in cm. Not all the geckos gave analyzable data.

Gecko ID	Horizontal Thick*			Horizontal Thin*			Vertical Thick (Side)**			Vertical Thin (Side)***		
	ES	BD	SL	ES	BD	SL	ES	BD	SL	ES	BD	SL
CC	1.0	7.9	8.0	0.9	7.0	6.5	1.4	6.8	8.0	1.2	5.7	6.6
SE	0.1	0.2	0.3	0.1	0.2	0.4	0.1	0.2	0.3	0.1	0.4	0.8
RA	1.5	8.2	8.3	0.9	7.0	6.0	1.3	6.8	5.5	1.2	6.7	5.7
SE	0.1	0.3	0.5	0.1	0.1	0.3	0.1	0.2	0.5	0.1	0.3	0.3

*Data from all 14 geckos were used to derive the averages and their standard errors (SE)

**Data from CC1, CC5, CC8, RA2, RA4 and RA5 were used

***Data from CC2, CC5, CC6, CC8, RA2, RA4, RA6 and RA8 were used

According to Fig. 5, the Crested gecko had the highest stride length during the vertical thick trial, and stride length decreased going from a

thick to a thin pole. The same was observed for the Gargoyle geckos' strides for the horizontal trials, but their stride lengths for the vertical trials were consistent throughout (Fig. 5).

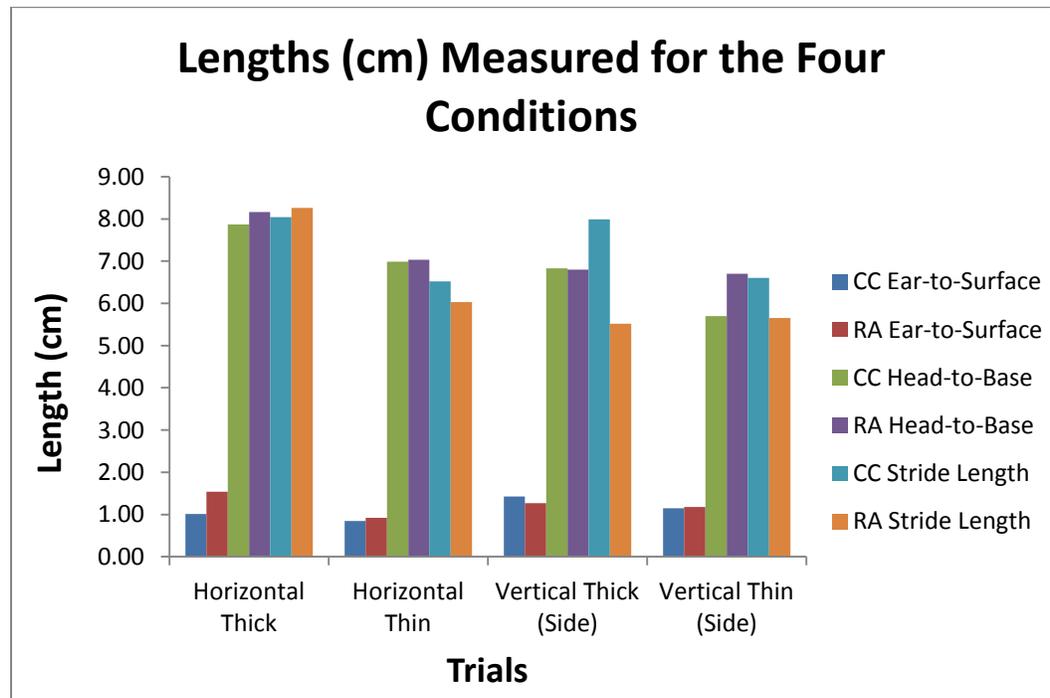


Figure 5. The averages of the lengths (cm) measured for each of the four trials for the Crested (CC) and Gargoyle (RA) geckos. The lengths measured include the distance from the earhole to the surface of the pole (Ear-to-Surface), the distance from the earhole to the base of the body where the tail begins (Head-to-Base), and the Stride lengths for each trial. To see which geckos were used to calculate these variables, refer to Table 4.

Another factor I looked at was stride frequency, which remained constant only for the Gargoyle geckos as they went from the vertical thick to the vertical thin trials (Table 5).

Table 5. Average stride frequencies (strides/sec) for each of the four conditions where S = Side View, T = Top View and A = Average of the side and top views.

Gecko ID	Stride Frequency (strides/sec)							
	Horizontal Thick ¹	Horizontal Thin ¹	Vertical Thick			Vertical Thin		
			S ²	T ³	A	S ⁴	T ⁵	A
CC	2.78	1.39	3.63	2.65	3.14	1.89	3.24	2.57
SE	0.52	0.20	1.86	0.43	1.15	0.38	0.45	0.42
RA	3.95	1.25	2.08	2.78	2.43	2.36	2.62	2.49
SE	0.46	0.07	0.67	0.78	0.73	0.65	0.48	0.57

¹Data from all 14 geckos were used to derive the averages and their standard errors (SE)

²Data from CC1, CC5, CC8, RA2, RA4 and RA5 were used

³Data from CC1, CC2, CC6, CC7, CC8, RA2, RA4, RA6, RA7 and RA8 were used

⁴Data from CC2, CC5, CC6, CC8, RA2, RA4, RA6 and RA8 were used

⁵Data from CC2, CC6, CC7, RA2, RA4, RA5, RA6, RA7 and RA8 were used

Fig. 6 shows that the Gargoyle geckos as a whole have a much greater variance in their stride frequencies than the Crested geckos. The Gargoyle geckos were thus the fastest on the horizontal thick trial and

about the same on the vertical trials. Both the Crested and Gargoyle geckos were slowest on the horizontal thin trials. The Crested gecko was faster on the vertical thick trial and had comparable speeds on the horizontal thick and vertical thin trials (Fig. 6).

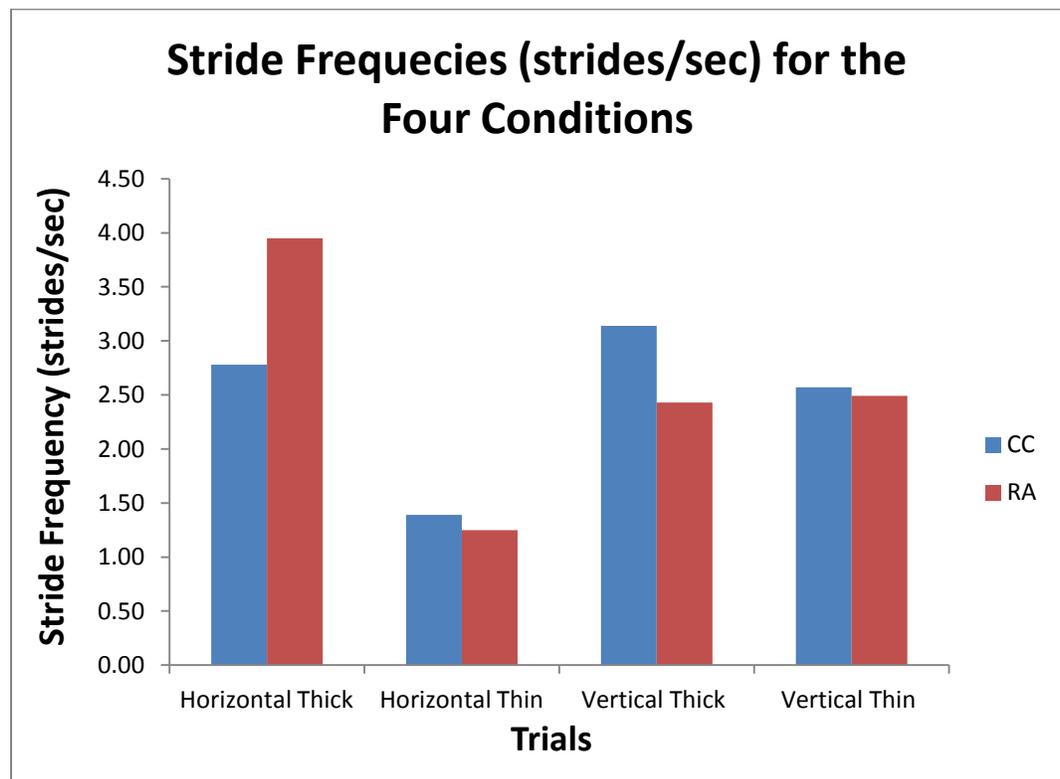


Figure 6. Average stride frequencies (Hz) for each of the four conditions, calculated using the average number of frames it took for a gecko to take one step, where 30 frames corresponded to one second. To see which geckos were used to calculate these variables, refer to Table 4.

For the top view, the body angle was measured when the left hind toepad made contact with the surface, ensuring that the angle measured

was always when the body formed a backwards "C" and the total angle had to be less than 180 °. For these frames, the tail would swing to the left and the angle measured was with respect to a vertical normal.

For both the Crested and Gargoyle geckos, the body angles slightly decreased going from the vertical thick to the vertical thin trials, indicating that the body was more curved with each step (Table 6). The tail angles also increased going from the vertical thick to the vertical thin trial, which meant that the tails had a higher swing angle as the diameter of the pole decreased (Table 6).

Table 6. The body and tail angles (in degrees) measured for the vertical (top) trials, as illustrated in Fig. 3.

Gecko ID	Vertical Thick (Top)*		Vertical Thin (Top)**	
	Body Angle	Tail Angle	Body Angle	Tail Angle
CC	156.75°	18.68°	153.58°	23.60°
SE	3.30°	3.84°	3.50°	2.66°
RA	158.98°	17.01°	155.10°	23.95°
SE	2.92°	2.70°	1.05°	1.47°

*Data from CC1, CC2, CC6, CC7, CC8, RA2, RA4, RA6, RA7 and RA8 were used to derive the averages and their standard errors (SE)

**Data from CC2, CC6, CC7, RA2, RA4, RA5, RA6, RA7 and RA8 were used

The lengths measured from the top views of the vertical trials did not show particular trends. The distances measured across the body of the geckos were consistent for the Crested geckos and slightly increased for the Gargoyle geckos going from the vertical thick to the vertical thin trials (Table 7). As for the stride lengths, the Crested geckos saw a slight increase while the Gargoyle geckos saw a slight decrease in the distances they put successive steps at.

Table 7. The average lengths (cm) measured for the vertical trials, as illustrated in Fig. 3.

Gecko ID	Vertical Thick (Top)*		Vertical Thin (Top)**	
	Distance across body (cm)	Stride Length (cm)	Distance across body (cm)	Stride Length (cm)
CC	6.20	7.50	6.19	7.95
SE	0.21	0.10	0.24	0.30
RA	5.86	6.63	6.13	6.10
SE	0.28	0.37	0.13	0.17

*Data from CC1, CC2, CC6, CC7, CC8, RA2, RA4, RA6, RA7 and RA8 were used to derive the averages and their standard errors (SE)

**Data from CC2, CC6, CC7, RA2, RA4, RA5, RA6, RA7 and RA8 were used

As seen in Fig. 7, the body postures remained relatively unaffected going from the vertical thick to the vertical thin trials for either species of gecko while the stride lengths changed slightly.

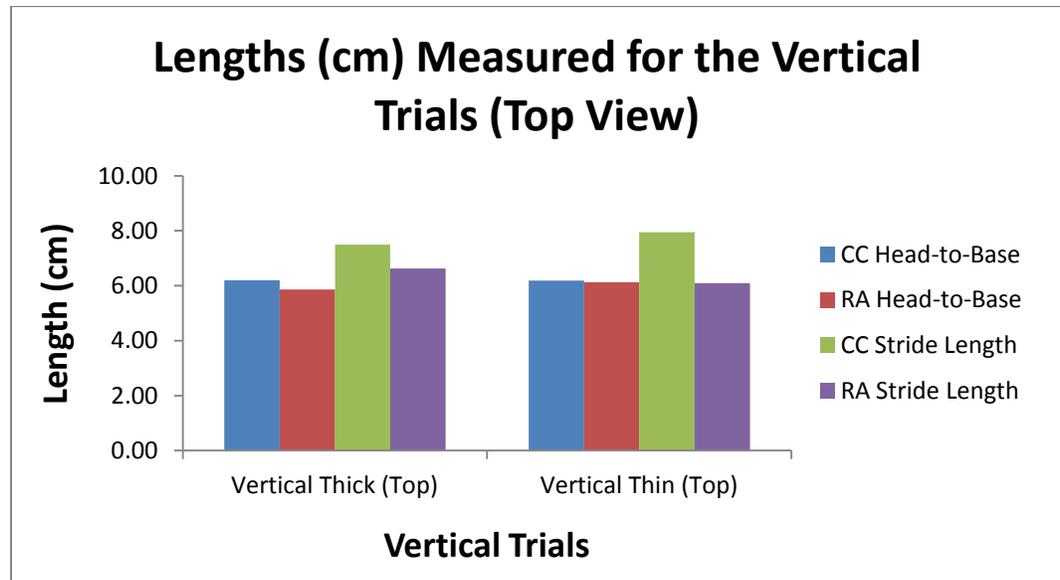


Figure 7. Average lengths (cm) measured for the vertical trials, including the distance from the earhole to the base of the body where the tail begins (Head-to-Base) and the Stride length, compiled from CC1, CC2, CC6, CC7, CC8, RA2, RA4, RA6, RA7 and RA8 for the vertical thick and CC2, CC6, CC7, RA2, RA4, RA5, RA6, RA7 and RA8 for the vertical thin trials.

DISCUSSION

In analyzing the locomotion of two species of geckos, the Crested and Gargoyle geckos, as they made their way across and up poles of varying thickness (3.5 inches and 0.5 inches in diameter), a quantitative record and qualitative observations were made. Differential climbing abilities were observed, although they did not so much correlate with the specific species of the gecko as it did with the individual gecko's overall performance itself. Some geckos did not produce any data that could be analyzed for a trial, while others were much more competent.

All 14 geckos recorded showed some usage of the tail for balance, especially on the narrow poles. When trying to get the geckos onto the poles, the geckos would wrap their tails around either the pole itself or the researcher's fingers for the extra stability it could afford them. This usage was more noticeable before the trials were conducted; once on the pole, the use of the tail became less noticeable and more varied for the geckos: some wrapped their tails around the pole, others let it graze the surface while they walked, while still others had theirs high in the air. As the geckos jumped off or onto the pole, their tails would become more

relevant for stabilizing them onto the new surface by relying on its prehensile abilities. For the horizontal thick trials the tails were draped across the poles while for the horizontal thin trials they wrapped around the pole as the gecko slowed down for greater balance.

Table 3 shows that both the head and tail angles increased for the Crested geckos as they went from the thick to the thin trials for both the horizontal and vertical poles, and for the Gargoyle geckos as they went from the horizontal thick to the horizontal thin trials. An increase in the angles corresponds to the head and tail being closer to the surface (refer to Fig. 3). How high the geckos keep their tails off a surface is determined by the anticipated slippage on that surface; when the flat-tailed geckos were made to run up a high traction vertical wall, their tails were held up off the wall, but when they had to walk on a wall with intermediate traction, the tails tended to be in constant contact with the surface (Thompson, 2008). Thus, if we disregard the vertical trials of the Gargoyle geckos, we see the same trend. In addition to the relative angle of the tail, when the geckos lost balance, they would use their tails as described by Jusufi *et al.* (2006), where the tail would flatten against the surface to avoid the gecko from slipping.

Not all the tail angles may be viable to use, however, since the measurement corresponded to the initial tail angle and did not account for those tails that drooped down right after (observed for many of the Crested geckos). Thus, the averages for the tail angle may be misleading.

Russell and Higham (2009) found that going from a flat surface to an incline showed a decrease in speed for the climbing gecko (*Tarentola mauritanica*), indicating that adhesive capabilities were at work. Although Wang *et al.* (2011) found that speed increased by an increase in the stride length or stride frequency, Zaaf *et al.* (2001) only found a correlation between stride frequency and speed. Going from the horizontal thick to horizontal thin to vertical thick to vertical thin trials, the stride lengths progressively decreased for both species in the experiment. Both the Crested and the Gargoyle geckos had a harder time balancing not only going from the horizontal to the vertical, but also from the thick to the thin trials and so took shorter steps. The stride length also decreased because there was a lower surface area and thus lower adhesion possible. We would expect that taking shorter, more frequent steps on inclined surfaces would enhance stability, yet my results only found stride lengths to follow this pattern. The stride frequencies varied quite dramatically, and with no

obvious patterns. The one consistent find from the stride frequencies was that both the Crested and Gargoyle geckos had the lowest stride frequency, and thus speed, on the horizontal thin trials (Fig. 6). On the vertical trials the geckos had to counter the force of gravity, and are already equipped for that; however, on the horizontal thin trial, the geckos had to avoid falling over to either side with each step, which significantly lowered their stride frequencies and speeds. The stride frequency remained constant for the Gargoyle geckos on the vertical trials while it decreased for the Crested geckos, suggesting that the Gargoyle geckos were better able to account for the different orientation by maintaining the same stride frequency.

The distance from the earhole to the surface and across the body were also measured (Table 4). The distance from the gecko's earhole to the surface of the substrate decreased consistently as we went from the thick to the thin trials, within the horizontal and vertical trials, possibly because the closer the gecko is to the surface, the greater control it retains and the less force it needs to impart for locomotion.

Wang *et al.* (2011) looked at the vertical motion of the Tokay gecko (*Gekko gecko*) and found that its body moved in an S-shape motion to

generate lateral forces that countered the destabilizing forces on the gecko. The vertical trials confirmed this, as not only the distance across the body, from the head of the gecko to the base where the tail started, decreased progressively across the trials (Table 4), but the body angles measured on the top view of the vertical trials (Fig. 3) decreased as well (Table 6). This suggests that the body was twisting more to generate the lateral forces necessary for effective locomotion up the pole.

A higher swing angle of the tail going from the vertical thick to the vertical thin trials also suggests that the geckos were twisting their bodies more to increase the lateral forces produced, using inertia to aid movement and counter the gravitational forces acting on their bodies (Table 6). Although both the Crested and Gargoyle geckos have very similar SVL, they differ in their masses (Table 1). Having more mass increases the body's inertia, yet there were no significant differences between the Crested or Gargoyle geckos' tail angles, as seen from the vertical top views (Table 6). The difference in their average masses, a mere 4.18g (calculated from Table 1), was too low to impact their bodies' inertia.

For what was assumed to be steady state locomotion, the geckos' footfall had a RF LH LF RH pattern, as limbs moved diagonally with each

step. As the geckos sped up when prompted, their diagonal limbs moved in unison to accommodate for the change in speed, on both the vertical and horizontal trials. The contact their toepads made with the surface also decreased significantly. It is interesting to note that only the gecko's posture changed as it switched from a horizontal to a vertical surface and not the footfall pattern itself.

A few sources of error due to the measurement technique as well as the sample size might have led to some of the findings being inconsistent with literature. The speed of the gecko affects its body angle, stride length and frequency. Since there was no way to standardize their speed, the data collected thus may not be reflective of steady state locomotion.

Another factor that may have led to some inconsistency in the results may be due to the individual gecko's response to being prompted to walk.

Most of the geckos did not walk across or up the poles without some perturbation on the part of the researcher. This may have impacted their posture, speed, stride frequencies, and stride lengths, as they ran across or up the poles after being provoked. There were also a different number of frames used to calculate the average lengths, angles and stride frequencies for each trial, ranging from 70 frames per species to a mere 12 frames per

species. Having a smaller sample size (the number of frames) makes it harder to compare results and generalize conclusions as a characteristic behavior of the species as a whole. Lastly, many of the trends observed did not follow for the vertical trials of the Gargoyle gecko. It is possible that the data for the vertical thick and vertical thin trials of the Gargoyle geckos might have been switched and caused inconsistencies in the data.

Future research should involve a greater number of trials and individuals in each species category. This would allow the researcher to draw conclusions that are more consistent with current literature and would provide greater confidence in the results as a whole. In addition to increasing sample size, standardizing the measurement system that does not rely solely on visual markers would also lead to a much greater accuracy in the data measurements. Pressure and force sensitive poles can also be used in the future to calculate the Ground Reaction Forces (GFRs) produced by the toepads and the angles at which these forces are applied since the curvature of the pole would influence the toepad orientation. This data would aid in understanding how geckos accommodate for the challenges imposed on their toepads by curved surfaces.

CONCLUSION

Gecko toepads have a remarkable ability to attach and detach from surfaces without wearing out, leaving a mark, or wasting energy. Geckos alter their gait by changing stride lengths, frequencies, and body movements to accommodate for diverse environments. Specifically, going from the thick to the thin poles, both the Crested and Gargoyle geckos used in the experiments decreased their stride lengths as they took shorter steps for greater stability, but had no observable pattern for stride frequencies. As the locomotion became more challenging with decreased pole diameter, the geckos in general brought their heads and tails closer to the surface of the pole to aid with balance. Further work on this topic would potentially reveal information that could add to commercial possibilities as well as to the collective knowledge of the scientific community.

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