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The role of the tail in stability and maneuverability during running, climbing, mid-air orientation and gliding in both animals and robots.

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by

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Thesis Committee:

Professor Robert J. Full, Chair
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Professor Robert Dudley
Professor Benson Tongue

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Abstract

The role of the tail in stability and maneuverability during running, climbing, mid-air orientation and gliding in both animals and robots.

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Doctor of Philosophy in Integrative Biology

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Professor Robert J. Full, Chair

Life above ground requires that animals navigate a highly three-dimensional world. Both cursorial and arboreal animals must rapidly negotiate a myriad of complex and often unpredictable substrata within their habitats (e.g. dense vegetation; forest canopy) in which discontinuous supports challenge secure footholds. Traveling rapidly through such demanding terrain necessitates a behavioral repertoire that consists of both terrestrial and aerial modes of locomotion. Lizards represent an important model system in the study of general principles of how animals move. Moreover, developing capabilities of ambulation in cluttered environments to assist in search and rescue operations is in demand in robotics. Within the scope of this dissertation, I investigate whether multiple coordinated tail reflexes and responses are necessary for the successful navigation of a highly three-dimensional environment that challenges animals' locomotor systems with numerous obstacles, discontinuous supports and slippery surfaces.

In *Chapter One*, I present data on challenging single footholds in wall-running geckos, which lead to the discovery of a control structure the significance of which had not been previously recognized. Although the remarkable climbing performance of geckos has traditionally been attributed to specialized feet, I showed that a gecko's tail functions as an emergency fifth leg to prevent falling during rapid climbing. A response initiated by slipping causes the tail tip to push against the vertical surface, thereby preventing pitch-back of the head and upper body. When confronted with insurmountable gaps the lizards exhibited tail movement as they recovered from free fall. Lizards could also control body pitch and induce turning during simulated aerial descent. These experiments suggested that the secret to the gecko's arboreal acrobatics includes an active tail.

In the context of measuring locomotor performance as a function of foot-substrate interaction, I perturbed geckos even further and found that when a gecko falls with its back to the ground, a swing of its tail induces the most rapid air-righting response yet measured. *Chapter Two* investigates the tail as an effective torque source first attempting to generate simple, low parameter models of the system, then developing thee-dimensional analytical models of multi-body systems to investigate righting performance in two species of lizard, and how it is affected by variations in tail length, mass distribution, tail placement and orientation. These results suggest that large, active tails can function as effective control appendages. Lizards gliding in a vertical wind tunnel could use appendage inertia to induce turns in yaw whereby tails twice the

torso length have better yield. Robots can also serve as physical models to test our understanding of animal locomotion. In this spirit, a physical model and robot prototype tests the model's predictive capacity further, while also demonstrating feasibility of tail use in robots.

In *Chapter Three*, I present data from field research conducted in Southeast Asian lowland tropical rainforest, the natural habitat of my model system *H. platyurus.* A species heretofore not known to glide exhibits considerable horizontal transit of over 4m. Geckos with tails that glided to the tree trunk were able to remain attached to it upon landing in the majority of trials, whereas geckos without tails generally became dislodged upon impact. Moreover, I present how they carry out landing on vertical tree trunks despite approaching them at very high speeds. I propose a mechanically-mediated solution to how landing on a wall could be stabilized by the caudal appendage.

In *Chapter Four,* I explore whether representatives of lizard taxa other than Gekkonidae night utilize their tails for improving the stability, maneuverability and overall robustness of a mode of terrestrial locomotion: Rapid climbing on tree bark. Observations from the field in Malaysian lowland tropical rainforest, where I observed these animals' behavior initiated this study. I discovered that they have specialized subcaudal scales which are keeled such as to engage with a rough substrate. I present materials testing measurements using an Instron machine, where we determined that each scale can support one to several times body weight, depending on species. *Acanthosaurus crucigera*, *Gonocephalus grandis* and *Iguana iguana* were sampled. When the scales are prevented from engaging the animals' performance decreases dramatically.

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I am also very much indebted to Marvalee H. Wake and Robert Dudley, who have been there for me and helped to expand my horizons on a variety of subjects ranging from my first ever pilot field trip to the rainforest to their sharing of invaluable knowledge in physiology, functional morphology and evolution. My thanks to them go beyond what words can express. I want to also very much thank Benson Tongue, who in the classroom has stunned students with revolutionary techniques to conveying general principles of mechanics, which I've treasured. Benson has also taught me to think different. Last but not least, I have learned from these remarkable individuals very important lessons not just about being a scientist or an engineer, but perhaps just as importantly about life experience in general. They are great personalities and I hold them in high regard. I appreciated the conversations with all of them. They have had a lasting impact on my development which I daresay has been life-changing.

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Chapter I Role of 'Fifth Leg' in Rapid Locomotion Above Ground

The subject of study described in Chapters One through Chapter Three is an arboreal lizard commonly known as the "Flat-Tailed House Gecko" with its original habitat located in the tropical rainforests of South-East Asia from which it has radiated considerably, perhaps in part due to its locomotor apparatus allowing it to access niches that may not be as accessible to other lizard taxa with fewer arboreal specializations.

Studying how animals respond to perturbations can yield important insights about the range of capabilities encompassed by their parameter space for locomotion (*sensu* Bennett, 1992). For example, we found that when confronted with a natural ledge, geckos can run near top speed atop a leaf of the Giant Bird's Nest Fern in a South-East Asian rainforest. Having approached the edge at 12 to 15 body lengths per second of without decelerating they dive off the ledge, attach their rear feet like a "grappling hook" and use pendulum-like motion to swiftly swing around to the underside of the natural ledge, and out of sight (Mongeau *et al.,* 2012). Such dynamic behaviors could help them escape from predators in their natural habitat.

Active tails enhance arboreal acrobatics in geckos[1]

Summary

Geckos are nature's elite climbers. Their remarkable climbing feats have been attributed to specialized feet with hairy toes that uncurl and peel in milliseconds. Here we report that the secret to the gecko's arboreal acrobatics includes an active tail. We examine the tail's role during rapid climbing, aerial descent and gliding. We show that a gecko's tail functions as an emergency fifth leg to prevent falling during rapid climbing. A novel response initiated by slipping causes the tail tip to push against the vertical surface, thereby preventing pitch-back of the head and upper body. When pitch-back cannot be prevented, geckos avoid falling by placing their tail in a posture similar to a bicycle's kickstand. Should a gecko fall with its back to the ground, a swing of its tail induces the most rapid, zero angular momentum air-righting response yet measured. Once righted to a sprawled gliding posture, circular tail movements control yaw and pitch as the gecko descends. Our results suggest that large, active tails can function as effective control appendages. These results have provided biological inspiration toward the design of an active tail on a climbing robot and we anticipate their use in non-flapping aerial vehicles and multi-segment spacecraft.

I.1 Introduction

In a single second of vertical running, geckos travel fifteen body lengths and take thirty steps (Autumn *et al*., 2006). During rapid climbing, their toes attach in 5 msec and detach in only 15 msec. To explain their climbing agility, research has focused on the fibrillar adhesives found on their toes that function by van der Waals forces (Autumn *et al*., 2006). Despite morphological and behavioral adaptations that enhance stability (Cartmill, 1985), lizards, such as *Sceloperus occidentalis*, can fall frequently in experimental (Sinervo and Losos, 1991) as well as natural conditions (Schlesinger *et al*., 1993). During our initial explorations of climbing on realistic surfaces we noticed that a gecko's agility involved far more than just secure footholds. Here we pursue our observations by testing the hypothesis that the gecko's tail enhances its scansorial and arboreal performance.

Reptilian tails have been shown to affect running speed (Ballinger *et al*., 1979; Daniels 1983; Lin *et al*., 2006), maneuverability (Carrier *et al*., 2001), and endurance (Chapple and Swain, 2002) on level ground. In arboreal environments, prehensile tails (Emmons and Gentry, 1983) facilitate resting balance and slow climbing. However, tail function during rapid climbing, aerial descent and gliding is largely unknown (Chapple and Swain, 2002; Brown *et al*., 1995; Essner, 2002). To examine the tail's role in each behavior, we studied the flat-tailed house gecko, *Cosymbotus platyurus,* because it is agile and has a sizeable, active tail. Moreover, the dynamics of house geckos' horizontal running (Chen *et al*., 2006) and vertical climbing (Autumn *et al*., 2006) are well characterized. Our results suggest that large tails not only serve as passive structures that store fat (Lin *et al*., 2006; Bustard, 1967), provide balance and give a grip, but also function as highly active control appendages.

I.2 Materials and Methods

I.2.1 Rapid Vertical Ascent – Climbing

Animals

Flat-tailed house geckos, *Cosymbotus platyurus,* were purchased from commercial vendors (California Zoological Supply, CA; The Reptile Company, NY, USA). The majority of kinematic measurements were conducted with trials from nine individuals (3.25 ±0.2 g, 5.3 ±0.07 cm snout-vent length; mean ± 1 s.e.) and force measurements were made on six individuals (2.91 ±0.2 g, 5.4 ±0.08 cm snout-vent length). Geckos were housed in individual containers in an animal care facility and fed with a diet of water, crickets and vitamin/mineral supplements. Animals were kept in an environmental room illuminated for 12 hours a day at 25 ±2 °C. Trials were conducted at an average temperature of 29 °C and average humidity of 28 %. The Animal Care and Use Committee at U.C. Berkeley, whose activities are mandated by the U.S. Animal Welfare Act and Public Health Service Policy, approved all experimental procedures described in these research projects.

When possible, we used geckos that had already let go of their tails. To induce caudal autotomy, we followed well-established procedures in the literature (e.g. Ballinger *et al.*,1979; Daniels, 1983; Lin *et al.*, 2006; Chapple and Swain, 2002; Brown *et al.*, 1995), in which autotomy was initiated by holding the base of the tail past the biologically predetermined breaking point upon which lizards release their tail voluntarily to escape. There was usually no or very minor blood loss when geckos shed their tails. To avoid infections the area was covered with Silver Sulfadiazene Cream. The animals were not used for locomotion experiments for 48 hours following shedding of the tail. Each individual that experienced caudal autotomy began to regenerate their tail.

Climbing substrata

High traction substrate. To develop a substrate providing the most secure foothold that enabled both claw and toe pad engagement (Figure 1(a)), we manufactured a perforated track (560x75 mm) using a laser cutter (VersaLaser-200, Universal Laser Systems Inc.) that drilled 1.7 mm deep holes through a polyethylene plate in a hexagonal fashion (center-center 2.5 mm). Conceptual drawings were done in SolidWorks2005® and sent into the laser cutter to create two concentric circles of 0.8 and 0.37 mm diameter, which yielded perforations of 1 mm diameter in the plastic plate. The perforated track was coated with latex-based paint after having cooled down to room temperature.

High traction substrate with slippery patch. To induce single foot displacements, we inserted a slippery horizontal gap (width 1.7 - 3.4 cm) into the high traction substrate (Figure 1(a)). Geckos were unable to attain foothold on a patch made from commercial dry erase board (QUARTET®) that was coated with dry erase marker (EXPO® and AVERY®).

Intermediate traction substrate with slippery patch. We coated an aluminum plate with glass beads (diameter = 0.7 mm), which were applied using glue that consisted of 90% acetone (ACE®) and 10% cement (Duco®). We again inserted a dry erase board slippery patch.

I.2.2 Kinetics measurements of climbing lizards

A force platform was inserted into the floor of the track-way. Semiconductor strain gauges (bonded to spring blades cut from the brass supporting beams) embedded in a force-sensitive instrument (1, 14, 31; Figure 1(g)); platform dimensions 105 x 68 x 1.3 mm) responded to fore-aft, lateral and normal forces that geckos exerted onto the wall. Force signals were filtered using a 5th order Butterworth filter at a cut-off frequency of 100 Hz (unloaded natural frequency of the plate > 200 Hz in all channels). Crosstalk between three axes of force measurement was less than 5 %. Loads in the range 0.005 - 0.069 N produced a linear response with a maximum variation across the platform of less than 2 %. Signals from each force platform channel were amplified (Vishay Measurements Group) and collected by a 16 bit data acquisition system (National Instruments) on a computer (Power Macintosh 9500) at a frequency of 9500 Hz. Results from force measurements are shown in Figure 1(f).

I.2.2.1 Kinematics measurements of climbing lizards

We video recorded one dorsal and one sagittal view simultaneously using digital video cameras capturing 500 frames s^{-1} (Redlake®; Kodak® EktaPro, HG Imager, Model 2000; Fastcam PCI, Photron®). Video frames were acquired and the coordinates of various landmarks (white-out LiquidPaper®, SANFORD®) on the body at each frame were digitized into a computer using video analysis programs in Matlab 6.5 (TheMathWorks). A trigger switch synchronized video frames from both camera views with the force data. We measured the extent of foot slippage from the video. The unit for foot displacements measurements on various substrates was individual foot lengths. One individual foot length was defined as the distance from the claw tip of the middle toe to the heel of the forefoot that was subjected to perturbation. Assuming that foot slippage could be detected immediately upon contact by means of digital mechano-sensors, we measured the response time from initial contact of the forefoot with the slippery surface until the tail tip touched the wall or a substantial increase in production of tail force was detected.

I.2.3 Recovery from Free Fall

Animals

The average weight of the *C. platyurus* used in aerial descent experiments was 3.17 ±0.1 g (*n*=11). Their tails weighed approximately 0.29 ±0.1 g which represents approximately 10 % of their entire body mass. Caudotomy was initiated and the animals were housed as described earlier in Materials and Methods section on climbing.

I.2.3.1 Experimental Design for Analysis of Air-righting

Take-off site: horizontal platform

To study how geckos self-right during aerial descent, they were placed onto the bottom of a platform in a supine or inverted posture 2 m above a padded 1x1 m landing area. We observed the first 23 cm of their aerial descent. For this experiment, we held a rectangular polyethylene foil in a horizontal position with four fishing lines that were tied to each corner. The platform was loosely mounted to reduce the possibility of geckos introducing a lateral momentum by pushing off prior to release. The platform was 12 cm x 10 cm and weighed only 4.5 g. The transparent platform allowed a mirror mounted above it to provide us with a top view of the falling animal. One additional mirror was mounted at an angle next to the experimental set up and perpendicular to the optical lens such that a sagittal view of the animal's falling behavior could be captured. Usually geckos lost their foothold on their own after just a few minutes. If not, we gently vibrated the platform to induce the gecko to release. All geckos landed safely in a prone posture on a soft landing zone.

I.2.3.2 Kinematics measurements

We operationally defined a successful air-righting trial as one in which the gecko: 1) released and began to fall in a supine position, 2) the fall was followed by motion of body segments, such as feet, head or limbs, relative to the rest of the body leading to postural changes, and 3) all feet left the platform symmetrically and simultaneously. We defined simultaneous release as all four feet detaching from the platform within 0.02 s of one another. Trials in which animals released asymmetrically, i.e. first left forefoot and left hind foot followed by right fore and right hind foot or first with their forefeet followed by hind feet, were excluded. The air-righting behavior was recorded with digital high-speed video cameras (Redlake®) operating at 500 frames s^{-1}. The time was measured from release to the beginning of reorientation and from beginning of reorientation until the body attained a prone (horizontal, skydiving) posture, after which the air-righting behavior was completed. We measured tail position and rotation angle as well as the shoulder and pelvis position and rotation angles for each trial as a control to check the contributions of twisting to air-righting. By suitable camera placement and positioning of the gecko before the fall, we ensured that the body axis of the gecko was normal to the plane of cranial camera view during fall to within ± 5 degrees. This alignment allowed accurate resolution of body and tail angle using projected views onto a single imaging plane.

I.2.3.3 Planar Air-Righting Model

The angular momentum ***L*** of an object is expressed as the product of its moment of inertia *I* and its angular velocity vector [$\mathbf{\Delta}\theta/\mathbf{\Delta}t$; equation 1].

$$L = I\left(\frac{\Delta\theta}{\Delta t}\right) \tag{1}$$

When a gecko is free falling without external torques acting on its body, the sum of the angular momentum of the body segment ($\boldsymbol{I}_B(\Delta\theta_B/\Delta t)$) and the tail ($\boldsymbol{I}_T(\Delta\theta_T/\Delta t)$) equals zero, thus, total angular momentum is conserved [Equation 2].

$$I_B\left(\frac{\Delta\theta_B}{\Delta t}\right)+I_T\left(\frac{\Delta\theta_T}{\Delta t}\right)=0 \tag{2}$$

We calculated individual moments of inertia of the gecko's body, $\boldsymbol{I}_B$, assuming an object with a fixed mass and the principal rotation occurring about the fixed, longitudinal body axis.

The total moment of inertia of the tail $\boldsymbol{I}_T$ was estimated by treating the tail as a cone rotating perpendicular to the body about one end. Given equation (3), the ratio of change in tail rotation angle to the change in body rotation angle $\Delta\theta_T/\Delta\theta_B$ equals the ratio of the moment of inertia of the body to the moment of inertia of the tail $\boldsymbol{I}_B/\boldsymbol{I}_T$.

$$\left(\frac{\Delta\theta_T}{\Delta\theta_B}\right)=-\left(\frac{I_B}{I_T}\right) \tag{3}$$

I.2.4 Aerial descent: gliding, turning and translation

Simulated gliding in the wind tunnel

The airflow moving past a gecko skydiving in a vertically tilted wind tunnel is not different from the airflow around a gecko parachuting or gliding through still air (McCay, 2001), where the air moves relative to the gecko. Instead of pursuing an experimental approach that involves dropping animals from large heights (e.g. McCay, 2001), we utilized a vertically tilted wind tunnel (Midimaster Eco, Siemens) to simulate the conditions of aerial descent. Terminal falling velocity is reached when the aerodynamic drag and lift forces balance the force of gravity. Depending on individual mass and surface area, *C. platyurus* attained terminal velocity at ventral airflow speeds between 4.0 and 7.0 msec^{-1}, consistent with our prediction of 6 msec^{-1}. The wind tunnel was set such that it contained fields of identified flow rates ranging from 2.5 – 8.0 msec^{-1}. We mounted transparent Plexiglas sidewalls around the opening of the wind tunnel. This prevented geckos from maneuvering sideways out of the test section and enabled high-speed video recording at 250 and 300 frames s^{-1}. To prevent animals from contacting the expansion chamber of the wind tunnel, we installed a safety net in the test section. Anemometers (Velocicalc, TLC Inc.) were used to determine an area of uniform airflow. We marked the area on the safety net with white paint and only used this section for video recording.

Kinematics measurements of turning and translation

We placed the gecko in the wind tunnel and they began to hover. Animals were positioned toward the uniform flow in our marked area using a feathered brush. We operationally defined a successful turning trial as one in which the gecko: 1) adopted a skydiving posture, 2) remained stable in pitch, yaw and roll and then 3) yawed more than 20°. We analyzed kinematics of the body and tail that occurred before the maneuver. We defined translation as when the gecko: 1) adopted a skydiving posture, 2) remained stable in pitch, yaw and roll and then 3) moved horizontally.

I.3 Results and Discussion

I.3.1 Rapid Vertical Wall Running

We began by investigating tail use during rapid vertical climbing. In nature, swift climbers must respond rapidly to discontinuous supports, obstacles and slippery surfaces. We challenged geckos with three vertical surfaces that produced different degrees of foot slippage. First, we ran geckos up a high traction vertical track built from perforated board. Geckos running up vertical surfaces that provide a good grip balance the tendency to pitch back by pulling their head toward the wall with their foreleg on each step (Autumn *et al*., 2006).
We noticed that the gecko's tail was held off the surface (tail tip to wall distance 7.7 ±2.2 mm, mean ±s.e.) when footholds were secure. Next, we inserted a slippery patch into the high traction vertical track. When geckos reached the patch, their forefeet slipped toward their body (undergoing large displacements of 2.2 ±0.3 foot lengths). Foot slippage initiated a tail response that appeared to compensate for the lost grip of the forefoot. Geckos running on a vertical high-traction surface began to move their tail tip towards the wall approximately 28.9 ±6.3 msec after forefoot contact with the low traction patch (see Materials and Methods for characteristics of experimental substrata). The latency and consistency of response suggest it might be a reflex. The tail tip of *C. platyurus* contacted the surface in 47.0 ±11.0 msec to stabilize the body from impending pitch-back (Figure 1 (a) – (c)).

To test the hypothesis that tails adjust contact force actively and sufficiently to counter the animal's body pitch-back, we ran geckos up another vertical surface of intermediate traction (moderate displacements of 0.4 ±0.1 foot lengths). For these trials, we embedded a sensitive scale into the track that could measure force. In contrast to the surface with secure footholds, geckos running up a substrate that resulted in moderate foot slippage at each step kept their tails in contact with the substrate at all times. We again inserted the slippery patch into the track. We measured a significant increase in stabilizing impulse moment (0.007 ±0.002 mN-m-s, $n=7$, $P<0.05$) shortly (16.9 ±4.7 msec) after the forefoot slipped (Figure 1 (d) – (f)).

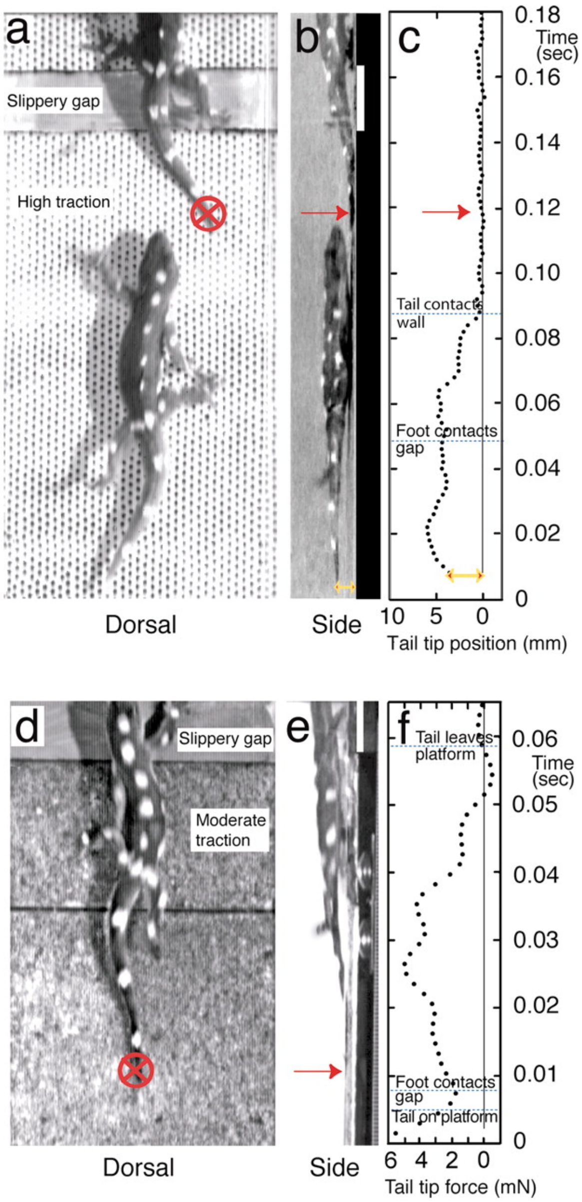

Figure 1: Gecko tail response activated during rapid vertical climbing. (a) Dorsal view of a gecko running up a high traction vertical track with a slippery gap lacking traction.

(b) Side view demonstrates that the tail remains clear of the surface before slipping, but contacts the surface shortly after the forefoot slips.

(c) Plot of tail tip position as a function of time shows tail response activation after the forefoot slips and subsequent depression of the tail tip.

(d, e) Dorsal and side view of gecko climbing a moderate traction surface with an embedded force platform.

(f) Plot shows tail tip normal force as a function of time. Substantial normal forces were measured when geckos pushed their tail into the wall after a forefoot slip (red arrow).

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Calculations showed that the tail response induced a stabilizing impulse moment (0.007 ±0.002 mN-m-s) that counterbalanced the natural pitch-back impulse moment (0.012 ±0.003 mN-m-s, P>0.05, n=7). The latter was determined from the product of the animal's body mass (3.15 ±0.3 g), distance from the center of mass to the wall (d = 4.9 ±0.5 mm), stride period (0.08 ±0.01 s) and gravity. The tail's stabilizing impulse moment calculated as tail force normal to the wall integrated over time increased in proportion to the distance (r=0.64, P=0.01; n=14) and duration (r=0.63, P=0.02, n=14) that the forefeet slipped suggesting active control.

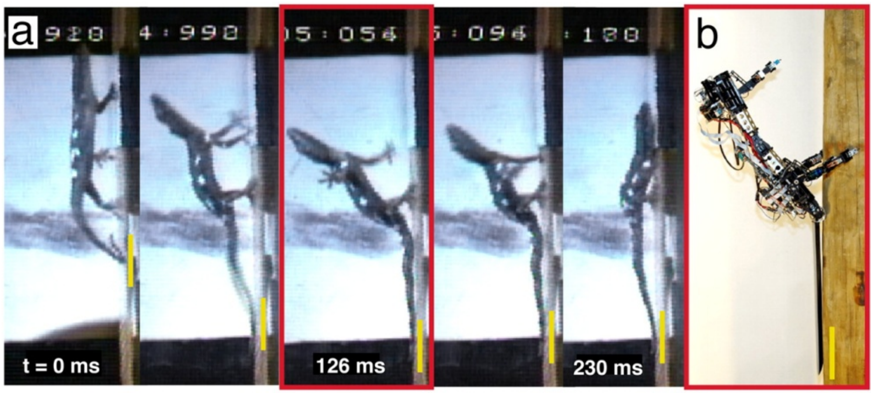

Figure 2: Tail use in a running gecko and a legged climbing robot in response to a large pitch-back. (a) Repeated, large foot slips (t = 0 msec) resulted in pitch-back. To prevent over-turning, an extreme posture similar to that of a bicycle kickstand was used by geckos (t = 126 msec) which enabled them to avoid falls and regain contact with the wall (t = 230 msec) to traverse gaps. (b) RiSE (Robot in Scansorial Environment), a quadrupedal, bio-inspired robot, will use an active tail as an emergency fifth limb to assist in climbing. From Jusufi *et al.* 2008. Copyright (2008) by the National Academy of Sciences, U.S.A.

The tail response could not correct for large repeated slips. When the tail response was insufficient, geckos tolerated pitch-back up to sixty degrees, eventually preventing over-turning by placing their tail in a posture where the last two-thirds of the tail pressed against the wall similar to that of a bicycle's kickstand (Figure 2(a)).

Gecko tails stopped the backwards pitching within ~129 msec and managed to regain hold of the wall in only ~124 msec more (both durations approximately 1.6 of a stride period). Even during these extreme perturbations tailed animals never fell off the wall (*n*=30). In contrast, catastrophic pitch-back resulting in falling was observed in nearly 20% of animals without tails. Despite no difference in average climbing velocity between tailed (0.78 msec^{-1} ±0.03, *n*=23) and tailless animals (0.77 msec^{-1} ±0.02, n=34, *P*=0.64), in over 60% of the trials, tailless animals failed to cross the slippery patch, whereas less than 15% of the tailed animal trials were unsuccessful.

I.3.2 Recovery from Free Fall

We observed that rapidly climbing geckos that fell or jumped off the wall always landed with the ventral side facing the ground independent of the initial posture at take-off. To examine how geckos executed quick air-righting reactions, we placed them upside-down (in supine position) on a light, loosely-mounted platform that mimicked the underside of a flexible plant leaf. Upon loss of foothold, geckos immediately spread their feet out laterally and fell in a supine posture (Figure 3 (a); average latency 45 msec ±5, *n* = 16). Next, the tail pitched into a position perpendicular to the longitudinal axis of the torso (Figure 3 (b)). Simultaneously, the head pitched slightly. A cyclic rotation of the tail about the longitudinal axis produced a counter-rotation of the body (Figure 3 (b)-(c)). The transition from supine to prone (right-side up) body posture was marked by inflation of the lateral membranes along the body of *Cosymbotus*. As the geckos attained prone posture, tail rotation stopped, thus terminating body rotation (Figure 3 (d)).

The average time to reorient was only 106 msec ±6 (*n* = 16; Figure 3 (f)), the shortest duration yet reported for air-righting animals (McDonald, 1960; Laouris *et al.,* 1990a; Pellis *et al.,* 1989; Schoenfelder, 1984). Finally, the tail was realigned with the longitudinal body axis, which compensated for the initially generated pitch. After a prone posture was attained, geckos began to parachute in the characteristic skydiving posture (Wassersug *et al.,* 2005; Figure 3 (d)). When *C. platyurus'* horizontally sprawled body deviated from the horizontal posture in roll during subsequent free fall after completion of air-righting (first order response), they generated second order corrections by way of partial counter-rotations of the tail to regain the preferred body posture of descent. In nearly 70% of the trials, the tail alone generated air-righting without head-shoulder or shoulder-pelvis rotations.

All geckos that induced reorientation with their tails recovered from a supine posture to attain a near prone posture (approximately 140° – 180° of rotation). Fully prone posture was attained in half the trials within the vertical distance investigated (approximately 4 snout-vent lengths). In contrast, none of the geckos without tails attained a fully prone posture within the same vertical falling distance (*n* = 19). In nearly half the trials, tailless geckos rotated only half way (Figure 3 (g)) to the prone position by twisting. In the few trials where tailed geckos did not rotate their tails (9.8 %) during free fall, reorientation performance was similar to that of tailless geckos.

Beginning with the study of the falling cat (Marey, 1894) in 1894, the mechanical explanation of air-righting with zero angular momentum has intrigued biologists, engineers, mathematicians, and physicists alike for over one hundred years. Mammalian air-righting responses are generally characterized by twists and flexions of the spine that change shape (McDonald, 1960; Laouris *et al*., 1990; Pellis *et al*., 1989; Schönfelder, 1984; Marey, 1894) and therefore the instantaneous moment of inertia (Marsden and Ostrowski, 1998). No difference is apparent between the air-righting performance of tailed and tailless cats (McDonald, 1960).

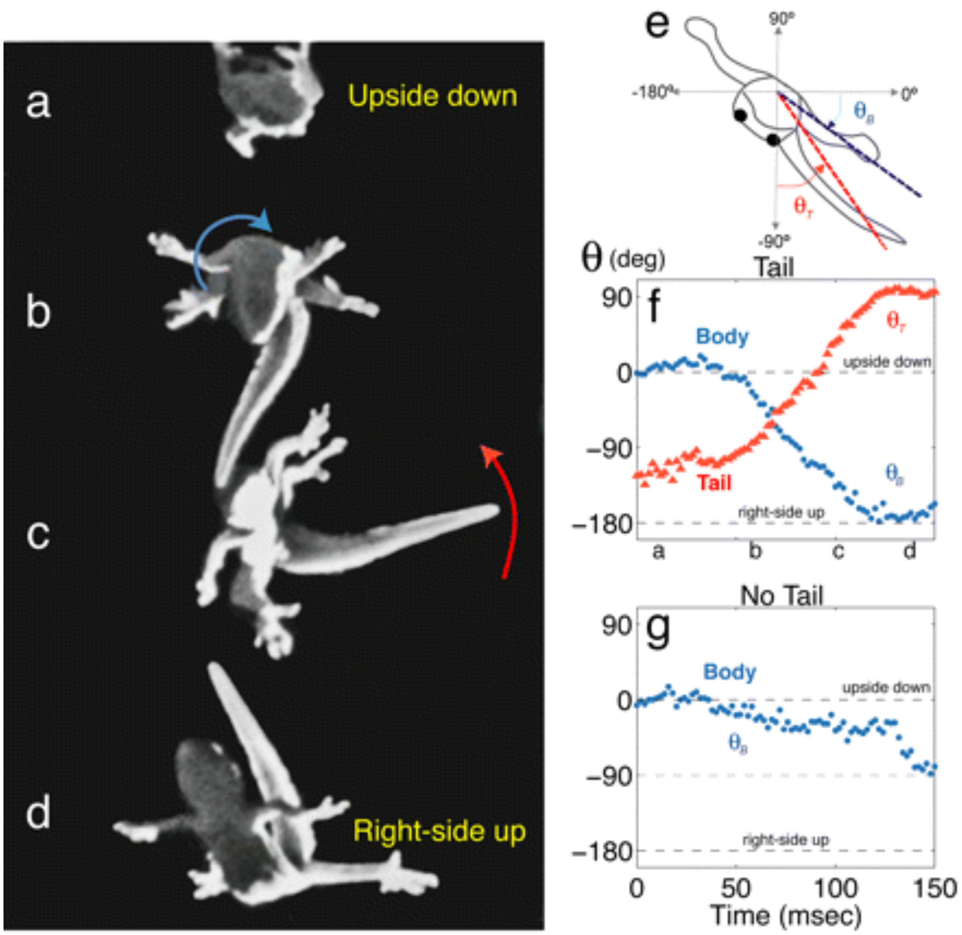

Figure 3: Tail-induced air-righting maneuver in geckos. (a) At takeoff the gecko released from an upside down (supine) posture. (b) and (c) Counterclockwise tail rotation (red arrow; θ_T) induced a clockwise rotation of the body (blue arrow; θ_B). (d) As the gecko's body attained right-side up (prone) posture, the tail stopped rotating. The animal maintained a skydiving posture during the subsequent free fall. (e) Schematic of a supine gecko falling to show angle convention. (f and g) Rotation of body and tail segments as a function of time in tailed (f) and tailless animals (g). From Jusufi *et al.* 2008. Copyright (2008) by the National Academy of Sciences, U.S.A.

Rats are unable to execute air-righting responses if head-torso and torso-pelvis rotation is prevented, leaving only the tail free to move (Laouris *et al*., 1990). Tail cycling during free fall of the "flying gecko" *Ptychozoon kuhli* has been associated with changes in posture such as somersaulting (Young *et al*., 2002). Tail motion in lizards has also been observed in microgravity on parabolic flights (Wassersug *et al*., 2005) and in jumps during above-ground acrobatics (Higham *et al*., 2001). Lizards appear unusual in their ability to perform the change in shape using their relatively large tails.

To test the hypothesis that geckos self-right by swinging their tail, we demonstrated that angular momentum of body and tail about the central axis is conserved (Young B *et al.*, 2002) during the righting maneuver. We acquired the rotation angle of both segments ($\Delta\theta_B$, $\Delta\theta_T$) experimentally and calculated the moments of inertia (I_B, I_T) using data approximating *Cosymbotus*' morphology (see Methods – Air-righting model). The moment of inertia ratios predicted by this model (1.44 ± 0.26) were not significantly different from our direct kinematic measurements of rotation (1.26 ± 0.20**,** *n*=6, *P*=0.29, t-test of paired means), thus suggesting that the gecko's tail is capable of generating sufficient rotational impulse moments to account for a reorientation of its body.

I.3.3 Simulated Gliding

After rapid self-righting, we noticed that *C. platyurus* adopted a skydiving posture and glided to a safe landing site. In nature*,* *Cosymbotus* representatives have been reported to parachute and glide (Honda *et al.*, 1997). To test whether an active tail plays a role in the control of gliding, we used a vertically tilted wind tunnel (McCay, 2001).

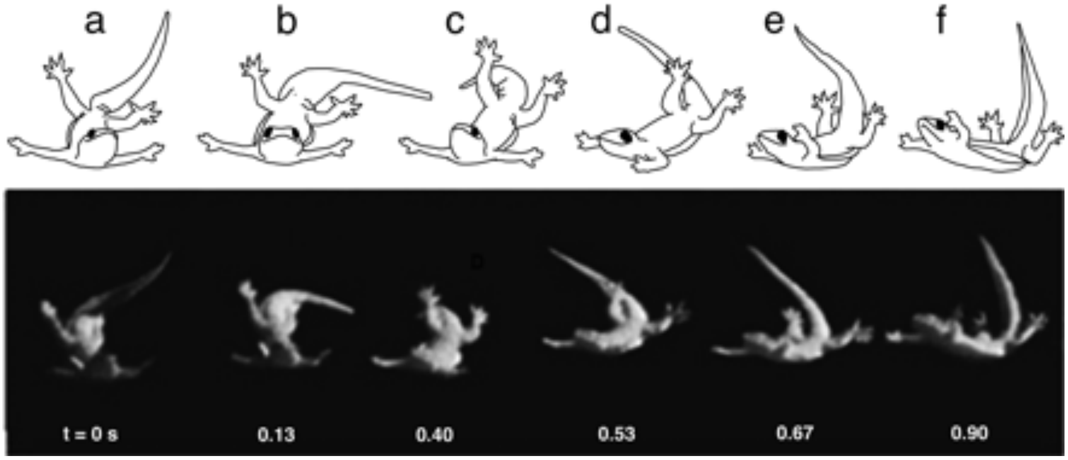

Figure 4: Tail-based turning meneuver of gecko during an equilibrium glide in a vertical wind tunnel that moved air upward. Time sequence from left to right of postural stages during a right turn while gliding. When viewed head-on, the tail rotated in a clockwise manner starting from the 12 o'clock position at *t* = 0 s (*a*) and sweeping to the right (3 o'clock position; *b*), down (near 6 o'clock; *c*), and swinging back past the 9 o'clock position (*d* and *e*), and finally stopping near the 12 o'clock position at *t* = 0.9 s (*f*). Geckos that rotated their partially dorsi-flexed tail in this clockwise direction initiated a clockwise turn to the right in yaw when viewed from above. From Jusufi *et al*. 2008. Copyright (2008) by the National Academy of Sciences, U.S.A.

Airflow at the calculated terminal velocities of approximately 6 m/sec for *C. platyurus* induced an equilibrium glide. We discovered that circular tail motion was coupled with yaw maneuvers of the body. Geckos that rotated their partially dorsi-flexed tail in a clockwise direction when viewed head-on (Figure 4) initiated a clockwise turn to the right in yaw (n = 8) when viewed from above. A clockwise tail rotation when viewed head-on produced a counter-clockwise rotation of the tail's center of mass motion when projected onto the plane of the body. As the conservation of angular momentum predicts, when the tail's motion was counter-clockwise in the plane of the body, the body rotated in the opposite direction by yawing to the right. Tail rotations in the counter-clockwise direction caused a counter-clockwise turn in yaw to the left (n = 7). The sharpest turns in yaw (Figure 4) occurred when the tail rotated predominantly in the plane perpendicular to *Cosymbotus platyurus'* sprawled torso, thereby projecting the largest circular motion on the body plane. Flat-tailed house geckos parachuting at terminal velocity controlled body pitch by moving their tail in the dorso-ventral plane. Ventral flexion of the tail accompanied pitch-down (n = 4) and dorsi-flexion accompanied pitch up (n = 9). We found that geckos were capable of moving parallel to the ground while gliding. They generated translation in cranial direction by oscillating the tail in the sagittal plane alternating positive and negative pitch with the corresponding tail motions (n = 3).

I.4 Conclusions

Discovering that active tails allow arboreal acrobatics in geckos opens the door for future studies of its neuromechanical control, evolution and effectiveness in the gecko's natural environment. The novel tail response that prevents catastrophic pitch-back during rapid climbing has already provided biological inspiration for the design of a new active tail, in the legged-robot named RiSE (Autumn *et al.,* 2005) that can climb brick walls, fences and trees (Figure 2 (b)). Similarly, biological inspiration could result in small, highly maneuverable unmanned aerial vehicles. Finally, the investigation of zero angular momentum maneuvers in biological systems may provide inspiration for energy-efficient attitude control (Kane and Scher, 1969) in multi-segment space vehicles as well as the astronauts who pilot them (Kane and Scher, 1970; Passerello and Huston, 1971).

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Chapter II Transitions during Rapid Locomotion in Complex Terrain

In *Chapter Two* the salient features of air-righting in two reptile representatives are explored in depth. Because reptiles tend to have larger and more massive caudal appendages than mammals, their tails could be used to change body orientation. Given substantial diversity of body morphology, anatomical features, and mass distribution is evident when compared across lizard taxa, we investigated how lizards with different body plans might solve the problem of aerial righting. To investigate mechanical effects, we compared righting performance of two lizard species that have approximately the same body size but differ in relative length of the tail. Specifically, the righting performance of the Flat-tailed House Gecko, *Hemidactylus platyurus,* is compared with that of the Green Anole, *Anolis carolinensis*. To better understand how morphological features (e.g. tail length) and behavioral variation, such as placement and orientation of tail movement, affect air-righting performance we developed a three-dimensional computational model. This approach allowed the comparison of model predictions with the measured kinematic results from air-righting lizards.

The scientific name identifying the "Flat-Tailed House Gecko" (in Chapter One referred to as *Cosymbotus platyurus*) has been subject to change. A determination based on morphological and anatomical characteristics had identified features that set it apart from species of *Cosymbotus* such that it had been placed it in its own genus *Cosymbotus* with workers referring to this particular species as *C. platyurus* (e.g. Chou and Leong, 1984). However, on the grounds of more recent molecular, phylogenetic analysis *Cosymbotus* is no longer a valid genus according to most systematists (Zug *et al.*, 2007) as the aforementioned genus was collapsed and species that belonged to it are now considered to be part of *Cosymbotus* (Carranza and Arnold, 2006). For these reasons, the species with common name Flat-Tailed House Gecko, formerly known as *Cosymbotus platyurus*, is referred to as *Hemidactylus platyurus* from here on in this work.

Righting and turning in mid-air using appendage inertia: Reptile tails, analytical models and bio-inspired robots.[2]

Summary

Unlike the falling cat, lizards can right themselves in mid-air by a swing of their large tails in one direction causing the body to rotate in the other. Here, we developed a new three-dimensional analytical model to investigate the effectiveness of tails as inertial appendages that change body orientation. We anchored our model using the morphological parameters of the Flat-tailed House Gecko *Hemidactylus platyurus*. The degree of roll in air righting and the amount of yaw in mid-air turning directly measured in house geckos matched the model's results. Our model predicted an increase in body roll and turning as tails increase in length relative to the body. Tails that swung from a near orthogonal plane relative to the body (i.e. 0–30° from vertical) were the most effective at generating body roll, whereas tails operating at steeper angles (i.e. 45–60°) produced only half the rotation. To further test our analytical model's predictions,

we built a bio-inspired robot prototype. The robot reinforced how effective attitude control can be attained with simple movements of an inertial appendage.

II.1 Introduction

Animals in arboreal habitats can lose footholds and fall as a consequence of challenging terrain, predator-prey interactions, fighting behavior or mating (Jurmain, 1997; Nakai, 2003; Sinervo and Losos, 1991; Knops *et al*., 1993). While in free fall many can reorient themselves to a posture in which their ventral side faces the ground, thereby decreasing the possibility of injury, permitting effective maneuvering and/or avoiding undesirable environments. The notion that animals can perform righting in mid-air without pushing themselves off the substrate beforehand or without changes in net angular momentum was contested in the 19th century. The dispute was first experimentally addressed in 1894 by a study of the falling cat (Marey, 1894). The cat's air-righting responses are generally characterized by twisting and bending between the anterior and the posterior parts of the torso (Marey, 1894; Magnus, 1922; McDonald, 1960; Kane and Scher, 1969; Edwards, 1989; Arabyan and Tsai, 1998; Marsden and Ostrowski, 1998), changing shape and instantaneous moment of inertia (Schönfelder, 1984). The study of air-righting reactions has mainly focused on mammals, such as cats, monkeys, guinea pigs, rabbits and rats (Marey, 1894; Magnus, 1922: McDonald, 1960; Kane and Scher, 1969; Edwards, 1989; Arabyan and Tsai, 1998; Marsden and Ostrowski , 1998; Schönfelder, 1984; Laouris *et al*., 1990; Pellis *et al*., 1989). Animals can use mass-redistribution by their appendages to induce zero-angular momentum reorientations in mid-air (e.g. Kane and Scher, 1969; Edwards, 1989; Arabyan and Tsai, 1998; Marsden and Ostrowski, 1998; Kane and Scher, 1970). The extent to which the limbs contribute to self-righting in falling cats is still under-explored (Arabyan and Tsai, 1998). Because it was observed that the tail rotates when the cat rights itself, it was proposed that the tail could be used for at least the fine-tuning of the air-righting reaction. However, in a comparison between the air-righting performance of tailed and tailless cats, no difference could be found (McDonald, 1960). Mammals with relatively small tails, such as rabbits and guinea pigs, appear to right themselves predominately by twisting (Laouris *et al*., 1990; Pellis *et al*., 1989). Mammals with longer tails, such as rats, can still perform aerial righting if either head-torso or torso-pelvis remains free for rotation. However, if head-torso and torso-pelvis rotation is prevented, leaving only the tail free to move, the rats are incapable of attaining a right-side-up posture (Laouris *et al*., 1990). Righting with the tail alone has not yet been found in mammals. Primates have been hypothesized to use rotation of their tails to assist in leaping maneuvers (Dunbar, 1988; Demes *et al*., 1996) and more generally to maintain balance during arboreal locomotion on narrow branches (Larson and Stern, 2006). Whether "flying squirrels" use their tail as a steering device during gliding is unknown (Essner, 2002).

Because reptiles tend to have larger and more massive caudal appendages than mammals, their tails could be used to change body orientation. Tail motion in lizards has been observed during simulated (Wassersug *et al*., 2005) and actual free fall (Oliver, 1951). Tail cycling during free fall of the "flying gecko" has been associated with changes in posture such as somersaulting (Young *et al*., 2002). Movement of the tail has been reported to affect the turning ability of tailed (Higham *et al*., 2001) and tailless (Gillis *et al*., 2009) jumping green anoles, *Anolis carolinensis*. From free fall in an upside-down posture, flat-tailed house geckos *Hemidactylus platyurus* swing their tail nearly perpendicular to their body 180° in one direction to cause their body to rotate 180° in the other (Figure 3, Chapter One). By conserving angular momentum, house geckos can right themselves rapidly in mid-air, attaining a right-side-up, gliding posture (*Chapter I*). While descending in the gliding posture, house geckos can yaw to produce a turn by further swings of their tail.

Here, we develop an analytical model to investigate the effectiveness of tails as inertial appendages that can change body orientation. We anchored our model by measuring the relevant morphological parameters for the well-studied, flat-tailed house gecko *H. platyurus.* This approach allowed direct testing of the model with previously measured kinematic results from mid-air righting and turning (Jusufi *et al*., 2008). Using the house gecko as a starting point, we then explored the parameter space reflecting the variation we see in this species. We examined the model's air-righting and turning performance as we varied two parameters – tail length and inclination angle relative to the body. By extending beyond this space, we speculate about the effectiveness of designs that begin to represent other species that can use their tails for reorientation. Finally, we applied the model predictions to a robot prototype of one of the most successful legged, climbing robots (Kim *et al*., 2007) yet built to test if it could right in mid-air using only its tail.

II.2.1 Model design and parameters

To investigate the feasibility of righting the body from upside-down to right-side-up posture by way of circular tail motion in the plane orthogonal to the axis of body roll, we developed a simple theoretical model anchored in the morphology of the house gecko, *Hemidactylus platyurus.*

Multi-segment models that conserve angular momentum while righting in mid-air have been discussed in the literature to describe the motion of falling cats (Kane and Scher, 1969; Arabyan and Tsai, 1998; Marsden and Ostrowski, 1998; Fernandes, Gurvits and Li, 1994), robots of various designs (Mather and Yim, 2009; Li and Montgomery, 1990), humans in space (Kane and Scher, 1970; Passerello and Huston, 1971), and even cell phones (Yang *et al*., 2011). The models presented in these papers range from two jointed rigid bodies (Fernandes *et al.* 1994, Li Z and Montgomery R 1990, Yang *et al*., 2011) to elaborate multi-segment and multi-jointed bodies (Arabyan andTsai, 1998; Passerello and Huston, 1971), with some focusing on the design of a specific physical robot (Mather and Yim, 2009) or specializing in the morphology of cats (Arabyan and Tsai, 1998) or humans (Passerello and Huston, 1971). Several of these studies (Arabyan and Tsai, 1998; Fernandes *et al.* 1994; Li and Montgomery, 1990; Yang *et al*., 2011) are control oriented, often concerned with determining an optimal control sequence to produce a desired air-righting response. Consequently, the derivations of the associated equations of motion (differential-algebraic equations (Arabyan and Tsai, 1998), a Lagrangian approach (Yang *et al*., 2011), etc., geared toward an optimal control problem, often lack the simplicity we desire to simply verify experimental observations of gecko righting and then use experimental findings to predict righting behavior. We chose a jointed two-body model of the gecko righting (similar to the models in (Fernandes *et al.* 1994) and (Yang *et al*., 2011) for its ease of formulation, and where the equations of motion are most efficiently obtained through basic vector mechanics by conserving angular momentum about the system's mass center (see equation (2) in (Passerello and Huston, 1971, replacing 10 with 2 for the number of jointed bodies). Our model is, in essence, a simplified 2-body version of the 10-body human model in (Passerello and Huston, 1971), with one of the bodies tailored to the morphology of the house gecko's body (torso and legs) and the other body representing the tail.

We represented the gecko as two rigid bodies, one for the torso and legs, and the other for the tail (Figure 5 (a)).

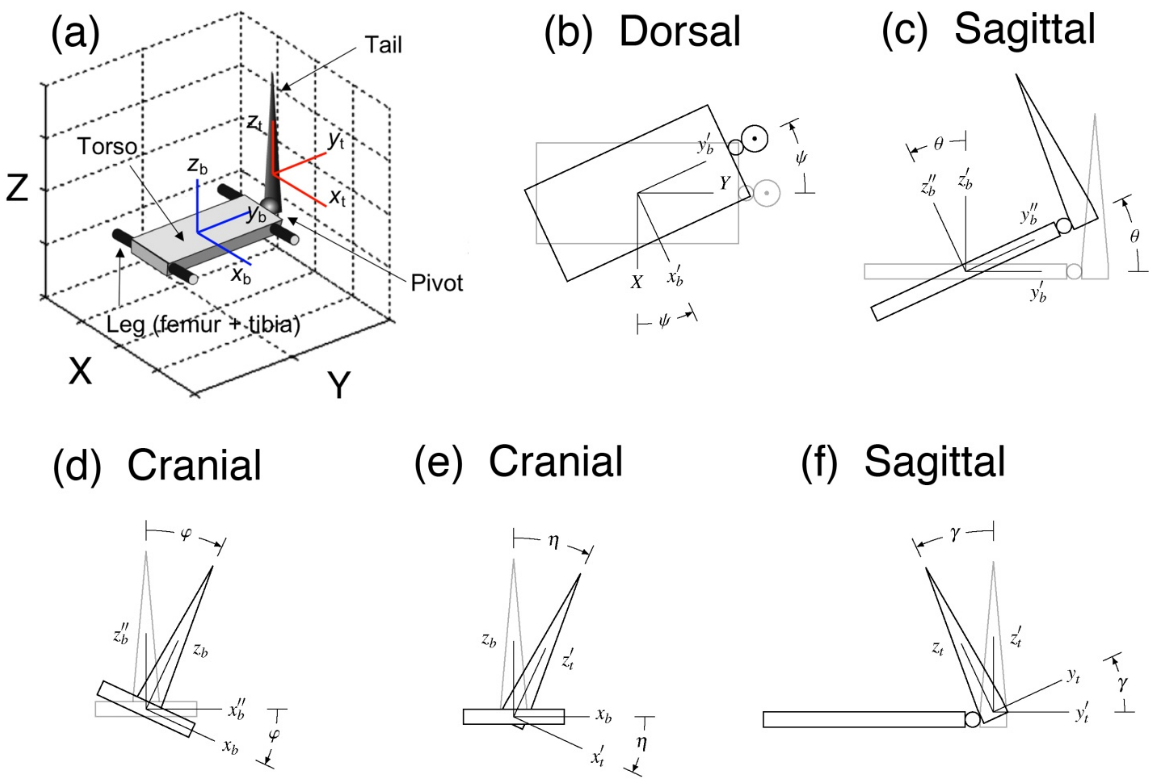

Figure 5: Analytical model planar views illustrating the sequence of rotations for the gecko model's body. Analytical model planar views illustrating the sequence of rotations for the gecko model's body and tail from the fixed *XYZ* frame to the body-fixed $x_b y_b z_b$ frame and tail-fixed frame $x_t y_t z_t$. (a) 3D view of the analytical model of the house. (b) Dorsal view of body yaw ψ. (c) Sagittal view of body pitch θ. (d) Cranial view of body roll φ. (e) Cranial view of tail side sweep η relative to the body. (f) Sagittal view of tail inclination γ relative to the body. From Jusufi *et al.* 2010.

Based on experimental observations of geckos righting in mid-air, we believe that treating the body as a single rigid component is a reasonable approximation, since significant flexing of the gecko's torso does not occur, unlike the traditional problem of the falling cat. The body (torso and legs) and tail were connected by a small universal joint that prohibited lengthwise spin of the tail. We assumed momentum was completely transferred from the tail to the body across the joint. We modeled the tail as a cone. The torso was modeled as an elliptical slab with widths (the major axis) and heights (the minor axis) measured directly from the animals. The value for the major axis takes into account variations in torso width from snout to tail base. We used cadavers to determine the effective radii at the snout, forehead, neck, shoulder, breast, rib-cage, pelvis, and tail base. To explore the inertial properties of the limbs, we modeled the front and rear legs as cylinders and we assumed that the femoral segments were protracted maximally away from the longitudinal body axis. We chose the body-fixed axes $x_b y_b z_b$ and tail-fixed axes $x_t y_t z_t$ so that the body and tail were symmetric relative to their respective axes (i.e., there are no products of inertia for the body and tail (see Figure 5(a)).

To obtain the theoretical model, we derived an expression for the total angular momentum **H** about the gecko's mass center using vector mechanics (equation (2) in (Passerello and Huston, 1971), except there are only two bodies). We calculated the angular momenta about the mass centers of the body and tail by considering a rotation sequence of yaw ψ, then pitch θ, then roll φ of the body and tail (i.e., a 3-1-2 set of Euler angles), followed by side sweep η and incline γ of the tail relative to the body (see Figures 5(b) - (f)) for an illustration of the rotation sequence).

We assumed that when a gecko performs self-righting during free fall, no external torques are acting on the system and therefore angular momentum is conserved: $\mathbf{H} = \text{constant} = \mathbf{0}$ when the gecko is released from rest. Aerodynamic effects were assumed to be negligible in the model due to the following considerations. To investigate the possibility of aerodynamic forces affecting the air-righting maneuver, we performed calculations that were based on conservative overestimates, such as the cross-sectional area subjected to airflow and the drag coefficient (see appendix *II.6.1.* for details). The calculations suggest that the maximum drag moment from aerodynamic forces acting on the tail could account for only 3.6% of the total moment that the geckos require to perform air-righting successfully. The low percentage for the drag moment relative to the inertial moment indicates that non-inertial torques do not play a major role in this behavior.

Writing the three components of the angular momentum vector with respect to the body-fixed frame $x_b y_b z_b$ in matrix-vector form, the gecko model's aerial rotation is governed by

$$\mathbf{A}\dot{\mathbf{y}} = \mathbf{f}_1\dot{\eta} + \mathbf{f}_2\dot{\gamma},$$

$$\begin{bmatrix} A_{11} & A_{12} & A_{13} \\ A_{21} & A_{22} & A_{23} \\ A_{31} & A_{32} & A_{33} \end{bmatrix}\begin{bmatrix} \dot{\psi} \\ \dot{\theta} \\ \dot{\phi} \end{bmatrix} = \begin{bmatrix} f_{11} \\ f_{12} \\ f_{13} \end{bmatrix}\dot{\eta} + \begin{bmatrix} f_{21} \\ f_{22} \\ f_{23} \end{bmatrix}\dot{\gamma}, \tag{4}$$

for which the superposed dot denotes a time derivative. The components A_{ik} (i, k = 1, 2, 3) of the coefficient matrix **A**, f_{1i} (i = 1, 2, 3) of the vector $\mathbf{f}_1$ associated with tail side sweep and f_{2i} (i = 1, 2, 3) of the vector $\mathbf{f}_2$ associated with tail inclination for equation (1) are derived in appendix II.6.2. We show the model's inputs and outputs in Table 1. We performed all calculations with standard software (Mathematica and MATLAB). We determined the moments of inertia using dimensions taken from cadavers (Table 2). We measured the torso and tail mass, snout-vent length, tail length and radius from six *Hemidactylus platyurus* individuals. We measured leg lengths from four individuals. We performed statistics using standard software (JMP and Microsoft Excel).

To calculate the moment of inertia of the torso, we modeled the body as an elliptical slab with major axis and minor axis. The dorso-ventral body height (minor axis) was approximately uniform across the torso. To determine the lateral width (major axis), we used an average value from the snout to tail base. In *Hemidactylus platyurus* the maximum lateral radius (major axis) was measured at the rib-cage whereas the minimum values were found at the snout and the tail base. We dissected cadavers of *Hemidactylus platyurus* to investigate the inertial properties of the geckos' legs and measured the masses and dimensions of the femora and tibiae of each fore and rear leg (n = 4).

From the average and standard deviation of the estimated moments of inertia for the body and tail calculated from biometric data (see Table 2), we observed that there was significant variation in the moments of inertia associated with roll of the gecko body (J_{b2}) and turning of the tail (J_{t1} and J_{t2}).

Table 1: Input and output parameters of analytical model for testing tail-induced body reorientation

Property	Description
Input Parameters:	
J_{bi} (i = 1, 2, 3)	Body moments of inertia
J_{ti} (i = 1, 2, 3)	Tail moments of inertia
m	Ratio of body mass × tail mass to total mass
L_1	Body mass center to tail base center distance
L_2	Tail base center to tail mass center distance
$\eta(t)$	Tail side sweep profile
$\gamma(t)$	Tail incline profile
ψ_0, θ_0, φ_0	Initial body orientation
Output Parameters:	
$\psi(t)$	Body yaw over time
$\theta(t)$	Body pitch over time
$\varphi(t)$	Body roll over time

Of the system's six moments of inertia, these three have the greatest effect on the gecko's aerial righting performance because they primarily govern the reorientation (i.e., roll). By using average values for the moments of inertia, we would obtain results that are not representative of the actual performance of the individual specimens.

Table 2: Masses, dimensions and inertial properties of geckos' torso, tail and legs

Property	Mean	Standard deviation
Torso mass (kg)	2.9×10^{-3}	$\pm 5.1\times10^{-4}$
Tail mass	2.9×10^{-4}	$\pm 8.9\times10^{-5}$
Fore leg mass	9.8×10^{-5}	$\pm 7.3\times10^{-6}$
Rear leg mass	1.9×10^{-4}	$\pm 1.2\times10^{-5}$
Body length (m)	5.4×10^{-2}	$\pm 6.4\times10^{-3}$
Body semi-major axis	4.2×10^{-3}	$\pm 3.8\times10^{-4}$
Body semi-minor axis	3.7×10^{-3}	$\pm 3.6\times10^{-4}$
Tail length	5.0×10^{-2}	$\pm 8.2\times10^{-3}$
Tail base radius	4.0×10^{-3}	$\pm 4.0\times10^{-4}$
Fore leg femur length	7.6×10^{-3}	$\pm 6.8\times10^{-4}$
Fore leg femur width	3.1×10^{-3}	$\pm 2.0\times10^{-4}$
Fore leg shank length	7.5×10^{-3}	$\pm 1.8\times10^{-4}$
Fore leg shank width	2.8×10^{-3}	$\pm 3.6\times10^{-4}$
Rear leg femur length	9.0×10^{-3}	$\pm 6.6\times10^{-4}$
Rear leg femur width	5.9×10^{-3}	$\pm 5.1\times10^{-4}$
Rear leg shank length	8.6×10^{-3}	$\pm 3.9\times10^{-4}$
Rear leg shank width	2.8×10^{-3}	$\pm 8.5\times10^{-5}$
Body pitch moment of inertia (MOI), J_{b1} (kg-m2)	1.1×10^{-6}	$\pm 4.4\times10^{-7}$
Body roll MOI, J_{b2}	6.6×10^{-8}	$\pm 1.0\times10^{-8}$
Body yaw MOI, J_{b3}	1.2×10^{-6}	$\pm 4.4\times10^{-8}$
Tail pitch MOI, J_{t1}	3.0×10^{-8}	$\pm 1.8\times10^{-8}$
Tail roll MOI, J_{t2}	3.0×10^{-8}	$\pm 1.8\times10^{-8}$
Tail yaw MOI, J_{t3}	1.4×10^{-9}	$\pm 6.4\times10^{-10}$

For this reason, in our investigation of the effect of relative tail length and tail incline we chose to focus on model results for a single specimen whose body morphology (i.e., ratio of tail length to snout-vent length) was nearest to the average values across all individuals (1.08 ± 0.18, $n = 6$).

To ground our speculation of how other species with varying body and tail lengths may perform mid-air righting and turning, we collected morphological data on anoles. The average body length of the *Anolis carolinensis* was 5.3×10^{-2} m $\pm 1.3 \times 10^{-3}$ m ($n = 3$, snout-vent length). We measured tail lengths that well exceed the snout-vent length of the animals: 9.53×10^{-2} m with a standard deviation of 6.7×10^{-3} m ($n = 3$). The average body mass of the anoles was 3.0×10^{-3} kg $\pm 1.1 \times 10^{-3}$ kg.

II.2.2 Air-righting

The initial conditions for the aerial righting simulation correspond to the house gecko starting upside down with no pitch and yaw: $\varphi_0 = \theta_0 = 0^o$, $\varphi_0 = -180°$. To ensure that the gecko has no initial angular momentum, the profiles for the tail side sweep $\eta(t)$ and tail incline $\gamma(t)$ must be chosen so that they yield zero initial angular velocity (i.e., $\dot{\eta}(0) = \dot{\gamma}(0) = 0$). Since angular momentum is conserved, it follows that the final values of angular velocity must also be zero so that the gecko stops rotating. We examined the aerial righting motion of the house gecko (*H. platyurus*) by first making a direct comparison with the air-righting data and then by varying two parameters – tail length relative to body length and tail incline angle.

II.2.2.1 Varying tail length relative to body length

We studied the effect of tail length on the righting behavior of a house gecko (*Hemidactylus platyurus*) of representative dimensions with a nominal tail length of 5.4 cm and body length of 4.59 cm. The tail length was varied from the shortest measured gecko tail length of 4 cm to the longest measured value of 6.1 cm. We extended the simulation results by including tail to body length ratios that fall within the range of *Anolis carolinensis*. We varied tail lengths for a tail rotating one revolution relative to the body when the tail was held orthogonal to the body. In the case where there was no tail incline ($\gamma = 0°$), we prescribed the relative sweep of the tail by a half cosine with a duration of 110 msec (an average value based on experimental observations) to approximate the experimentally determined tail sweep trajectory in Figure 3 (f).

II.2.2.2 Varying tail incline

We next explored how the body roll, as a function of tail length, would be affected if the tail was not held orthogonal to the body plane, but rather at a fixed incline so that the tail swept out a cone relative to the body. We examined the roll performance for various tail to body length ratios using tail incline angles of $15°$, $30°$, $45°$, and $60°$.

II.2.3 Turning

To examine turning of the gecko's body due to tail sweep in the horizontal *XY* plane, we set the first tail angle η to a constant $-90°$ so that the tail was constrained to rotate in the *XY* plane according to $\gamma(t)$ which then described planar yaw of the tail instead of incline as before. We used a half cosine profile for $\gamma(t)$ to ensure conservation of (zero) angular momentum (Figure 3 (f)). The initial conditions were chosen so that the body had no initial yaw in the *XY* plane (i.e., $\psi_0 = \theta_0 = \varphi_0 = 0°$).

II.2.3.1 Varying tail length relative to body length

We studied how the planar yaw of the gecko was affected by both tail to body length ratio and the amount of relative sweep of the tail. We varied the tail length from 4 cm to 6.1 cm (i.e., the range of measured values for the house gecko specimens), and the relative motion of the tail ranged from $30°$ to $180°$ in increments of $180°$. In all cases, the tail was initially held orthogonal to the length of the body.

II.2.4 Model scaling

To compare body reorientation across different tail lengths, we scaled the tail length and the tail base radius isometrically to keep density constant (see section 3.3, as mass scales cubically with the tail length ratio α). A cylinder tapering toward one tip was a reasonable shape to approximate the moment of inertia of the tail, assuming constant density across the various tissues that make up the caudal appendage. We also reasoned through the effects of isometric scaling on air-righting and turning performance to both make predictions about lizards as well as our larger robot prototype.

II.2.5 Robot prototype

To test the hypothesis that righting could be accomplished with a purely zero angular momentum approach, we built a simple, scaled-up robot prototype (Figure 5(d)). The robot consisted of a solid body constructed from laser-cut acrylic and aluminum sheet connected to an acrylic tail via a single revolute joint. We actuated the tail by using a torsion spring-loaded shaft which was preloaded and locked with a pin. The robot was a scaled and proportioned version of a bio-inspired quadrupedal robot (Kim *et al.*, 2007) designed to climb. We used a tail stroke relative to the body of approximately 360°, as was observed in the house geckos (*H. platyurus*). The tail moment of inertia was made sufficiently large by placing a 14 g lead weight 22 cm from the body axis.

During initial testing, the final position of the mass was modulated to fine-tune body rotation. The robot was dropped and video recorded with a high-speed video camera (AOS X-PRI, AOS Technologies AG). If under- or over-rotation of the body was observed, we modulated the moment of inertia of the tail by changing the moment arm of the mass on the tail. Time course of rotation was controlled via the strength of the torsion spring. To end the maneuver, we employed a damped bump-stop (i.e., a sticky tack on steel) to halt the rotation without a rebound. A viscoelastic foam pad prevented damage to the robot on landing.

Table 3: Mass, dimensions and inertial properties of robot prototype

Property	Body	Tail
Mass (kg)	2.14×10^{-1}	4.80×10^{-2}
Center of mass distance from joint (m)	1.65×10^{-1}	1.95×10^{-1}
Pitch moment of inertia (MOI) (kg-m2)	2.4×10^{-3}	6.0×10^{-4}
Roll (MOI)	6.5×10^{-4}	6.0×10^{-4}
Yaw (MOI)	2.9×10^{-3}	5.0×10^{-6}

A delayed release pin controlled initiation of righting as follows. We preloaded the tail, hung the robot upside down and secured it with a release pin. We locked the preloaded tail using a pin tied to a length of string. Both release mechanisms consisted of a steel pin in a Teflon bearing to keep friction at a minimum as the pin slides out. When the body pin was removed, the robot fell, and at a distance of 10 cm, the string pulled the tail release pin, initiating tail rotation. This approach ensured that no external torques would be introduced during the release. If the tail accelerated while the body was contacting the substrate, net angular momentum would be introduced and the righting would not be stable. For the same reason, the release pin bearing was positioned at the center of mass of the model such that friction forces could not impart a moment on the body.

We used the same analytical model described previously (see section *II.2.1*) to make predictions about the robot's performance. Because the robot's mass distribution varied significantly from the animals, we directly measured its physical parameters rather than estimating them from segment lengths. We measured the mass, centers of mass, and mass moments of inertia about the three principal axes of both the body and tail of the physical model (see Table 3). We measured moments of inertia with a bifilar pendulum constructed by suspending the robot by lengths of string. We fixed the tail incline angle at 35° from vertical. We chose the tail side-sweep kinematics to be a half-cosine as in the animal model. However, we used a duration of 250 msec (based on experimental observations) and the actual measured tail stroke of 309° relative to the body's rotation instead of a complete rotation.

II.3 Results and discussion

Lizards, such as geckos, can use their tails to perform maneuvers at the interface of terrestrial and aerial locomotion with exceptional precision and agility (Higham *et al*., 2001; Jusufi *et al*., 2008). Contrary to the falling cat (Marey, 1894; Marsden and Ostrowski, 1998) and other quadrupedal mammals (Schönfelder, 1984; Laouris *et al.,* 1990), no head-shoulder or shoulder-pelvis twist appears to be required for sufficient air-righting in flat-tailed house geckos *Hemidactylus platyurus*. We define sufficient righting to be body roll that falls within the range of 140° to 180° as was observed in all experimental trials in geckos (n = 16; Jusufi *et al.,* 2008). Preliminary results in anoles indicate that they also fall in this range. Examining the experimentally measured angular position of the pelvis and shoulder over time in the house gecko reveals that the body does not twist (Figure 3) in most trials. By making the fore and hind portion of the body rigid and coplanar in an analytical model and a robot prototype, we show that sufficient mid-air righting is possible.

Not only does our analytical model and robot prototype show that tail movement alone is sufficient for aerial maneuvers, but they also raise the hypothesis that external forces, such as aerodynamic lift and drag, are not required. Because air-righting occurs within a vertical height of less than two body lengths, well before the animal achieves terminal velocity, lift- and drag-based mechanisms for righting appear less likely. However, as both the tail and body can achieve high angular velocities during the maneuver, significant drag may act on both segments. Yet, the kinematics of air-righting in both animals and the robot showed little or no change in angular momentum during maneuvers, suggesting that the net impulse due to drag is negligible. In addition, conservative overestimates of the maximum moment that could be induced by drag forces acting on the tail indicate that aerodynamic effects are small (see section *II.2.1*). The drag moment could account for only 3.6% of the total maximal moment necessary to reorient the body (see appendix *II.6.1*), thus suggesting that inertia is the main component. Although challenging, a next step in model development should include drag forces.

II.3.1 Air-righting model

Our analytical model of a representative flat-tailed house gecko predicted the air-righting performance measured in the animals. Rotation of the tail in one direction elicited righting behavior (roll) in the body in the opposite direction. As observed in the animals, rotations about other axes (pitch and yaw) were small in comparison to the roll achieved, and angular momentum was zero both before and after the maneuver. To make comparisons between individuals and the model, we normalized absolute tail rotation by absolute body rotation.

The ratio of absolute tail rotation to absolute body rotation ($\Delta\varphi_T / \Delta\varphi_B$) expresses the tail effort required for righting – animals that use more tail rotation to achieve righting will have a higher ratio. If conservation of angular momentum is the primary mechanism for righting in lizards, the model should predict the ratio of rotation observed in the experimental trials. We used a t-test of paired means to determine the match of the experimental results to the model prediction. The difference between the two ratios was not statistically significant ($P > 0.2$, t-test of paired means, $n = 6$; and is further supported by $P > 0.2$ with a Wilcoxon test). This suggests that the gecko's tail is capable of generating sufficient moment to account for a reorientation of its body. The model predicted a ratio of 1.24 ± 0.22 (mean ± s.e., $n = 6$), whereas the experiments on geckos produced a value of 1.26 ± 0.20 ($n = 6$).

II.3.1.1 Varying tail length relative to body length

Because the house gecko *H. platyurus,* and lizards in general, vary in the length of their tail relative to the length of their body, we used our analytical model to predict the degree of reorientation or roll as the tail length to body length ratio varied (Figure 6(a)). The model predicts that the degree of body roll during air-righting will increase as tail length relative to body length increases.

First, we used the model to examine the effect of the natural variation in house gecko tail to body length ratio (i.e., 0.8 to 1.33) on air-righting performance. If average house geckos *H. platyurus* (tail length 5.4 cm, tail length/body length = 1.18) can sweep their tail 360° relative to the body, then the model predicts that they should be able to right themselves sufficiently from an upside-down to a near right side-up pose for landing as long as they keep their tail incline angle less than 45° (Figure 6 (b); see cross). The tails of house geckos that are 20% longer (tail length = 6.1 cm, tail length/body length = 1.33) and swung at a zero degree incline angle (i.e., orthogonal to the body plane) are predicted to generate 50° more body roll (i.e., 229°) with one tail swing.

Second, we explored the parameter space beyond the house gecko to predict how further increases in tail length might affect righting performance (Figure 6 (a)). If the lizard tail were nearly twice as long as the body (tail length = 10.5 cm, tail length/body length = 2.29) and made one revolution with respect to the body, then the body roll would nearly double to 341°. Preliminary observations suggest that much smaller rotations of the tail (less than 45° absolute rotation) are sufficient to effect righting in lizards with tail lengths substantially greater than body lengths, such as in green anoles (average tail length = 9.35 cm, tail length/body length = 1.8).

Thus, our model predicts and preliminary experiments suggest that a longer tail will be a considerably more effective inertial appendage for reorientation, as lizards require less effort to achieve aerial righting of their body.

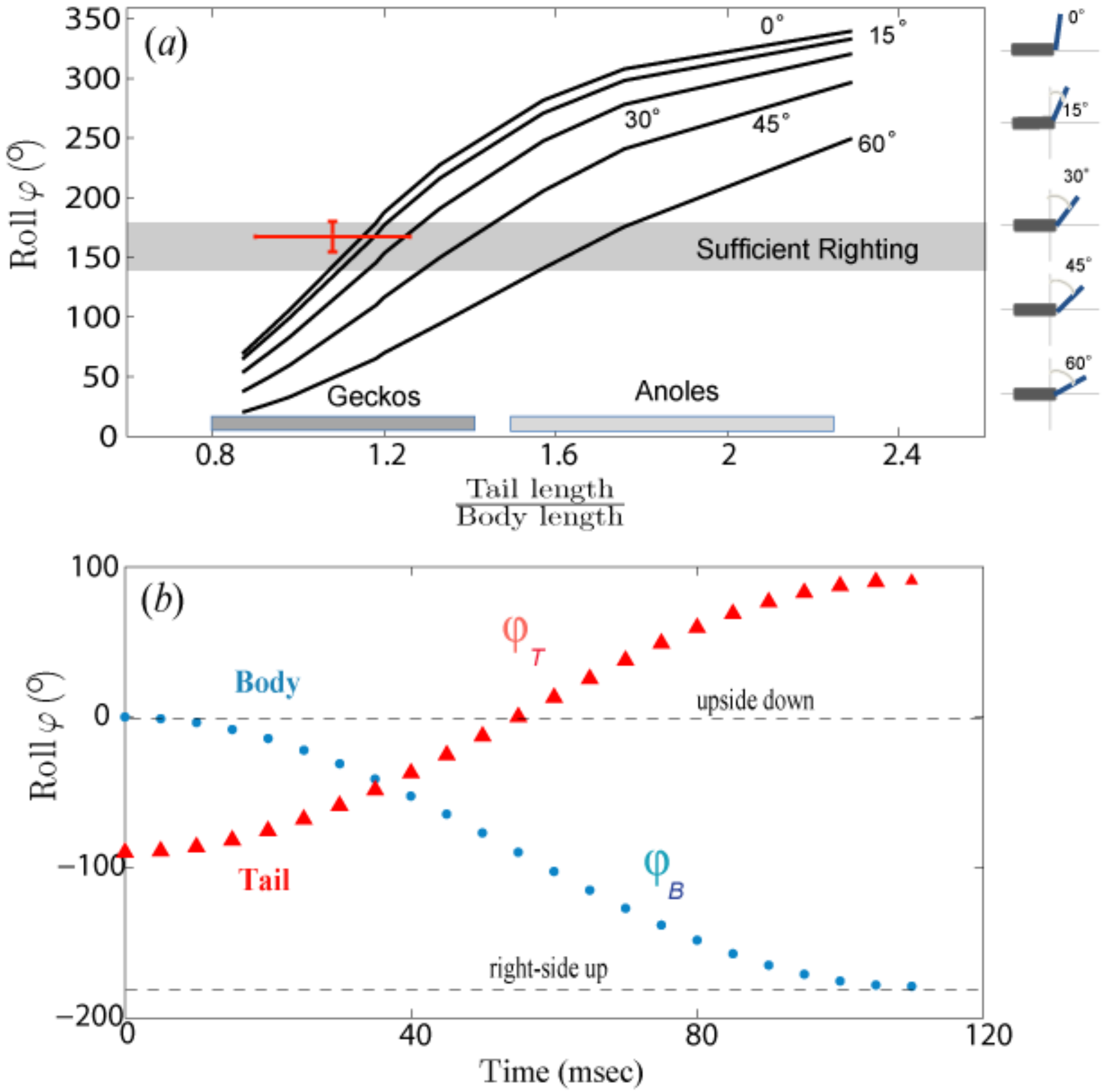

Figure 6: Tail induced body roll as a function of tail length to body length ration and tail inclination angle. (a) Tail-induced body roll as a function of tail length to body length ratio for the tail held at an angle of 0°, 15°, 30°, 45° and 60° from vertical, from top to bottom, respectively (as depicted by the icons). The shaded region denotes the range of near prone posture for sufficient air-righting to right-side-up posture. The red cross represents measurements from the air-righting experiments with house geckos (*Hemidactylus platyurus*). The vertical red line indicates the final position of the body relative to the horizontal during air-righting (mean ± one s.d.). The horizontal red line indicates the tail length to body length ratios observed in house geckos (mean ± one s.d.). The grey bars show the range of tail to body lengths found in house geckos and green anoles. The plot shows the variation in body roll for a gecko of average dimensions when the tail makes one full revolution relative to the body. All other body parameters were held fixed. Tail lengths used for calculation span the range of measured house gecko tail lengths to hypothetical lengths that approach those in lizards such as anoles. We scaled the tail length and the tail base radius isometrically to keep density constant. (b) Depicted is the righting performance of the average house gecko as predicted by the analytical model. The rotation of the body (blue) and the tail (red) is plotted as a function of time (see Figure 3(f)). From Jusufi *et al.,* 2010.

II.3.1.2 Varying tail incline γ

We noticed that house geckos *H. platyurus* did not always hold their tail in a plane orthogonal to the body when swinging it to perform air-righting. When the tail is not held orthogonal to the body (i.e., more than 0°), it sweeps out a more conical trajectory. Our analytical model showed that a lizard's ability to generate roll during air-righting decreased if its rotating tail was not held perpendicular to the body (Figure 6 (a)). The model predicts that if the tail of the average gecko is not held orthogonal to the axis of rotation, but is inclined by 15°, then the body will still reorient sufficiently to a 170° roll angle. If the tail is inclined by 30°, then the model predicts that the body will reorient to a 146° roll angle, which will be just sufficient to allow for a successful landing or transition to gliding. However, the model predicts that if the tail of the average house gecko is inclined by 45° or more, then air-righting will be unsuccessful as the body will reorient to only 110° or less. Righting is unsuccessful even with this longest gecko tail (tail length/body length = 1.33) if it is inclined by 60°, since the model predicts that the body will reorient only half-way to 95°, as can be seen in simulation. The house gecko with the shortest tail (tail length = 4 cm, tail length/body length = 0.8) will roll only 70° if the tail only makes one revolution with respect to the body. By contrast, a lizard tail that is twice as long (tail length = 8.1 cm, median length for green anoles, tail length/ body length ratio of 1.76) permits the animal to hold it at an incline of 60° and still fully reorient its body to 176°, as can be seen in simulation.

In preliminary mid-air righting experiments using the Green Anole, *Anolis carolinensis,* we observed the tail being held at a particularly exaggerated angle (i.e., more than 45° from vertical). Our model predicts that if a lizard with a long tail (tail length/body length = 1.57), such as the green anole, makes one revolution with respect to the body, it can incline the tail at a steep angle of 60° and still reorient its body to 141° of roll, thus attaining a sufficient near-prone posture (Figure 6 (a)). Our observations of righting in anoles indicate that they achieve complete righting despite their relatively large tail inclination.

Green anoles may be restricted in the extent to which they can position and swing their tail. The hind legs of *Anolis carolinensis* are nearly twice as long as the fore legs. The ratio of hind leg to fore leg length is much larger than in the house gecko *Hemidactylus platyurus.* Further study is needed to test the hypothesis that lizards, such as anoles, might be constrained in their tail movements to avoid collisions with their hind legs.

II.3.2 Turning

Upon completion of air-righting, we observed that flat-tailed, house geckos used movements of the tail during aerial descent (*Chapter One*). To test whether tail activity played a role, we simulated equilibrium gliding conditions by using a vertical wind tunnel (see *Chapter One*) for more details about the wind tunnel experiments). *H. platyurus* attained terminal velocity at ventral airflows ranging from 4.0 m/s to 7.0 m/s. We observed that tail movements occurred simultaneously with systematic turning maneuvers. In addition to large 90° turns that correlated with circular tail motion, we found that geckos could also generate smaller turns of the body in the yaw plane. For these smaller turns, geckos kept both the body and tail in the horizontal plane (i.e., XY plane), thus conserving momentum about an axis perpendicular to that plane. A similar use of the tail for turning has been proposed for *Anolis* lizards in the airborne phase of jumping (Kane and Scher, 1969). Therefore, to investigate the effectiveness of tails to induce mid-air turning, we viewed our analytical model in an XY plane projection and set the initial conditions for zero yaw.

II.3.2.1 Effect of tail length relative to body length

First, we used our analytical model to predict the degree of mid-air turning (yaw) as we varied the length of the tail relative to the length of the body within the natural variation measured in the house gecko *H. platyurus* (Figure 7). The model predicts that the degree of body yaw during air-righting will increase as tail length relative to body length increases. For the average gecko (tail length 5.4 cm, tail length/body length = 1.18) the model predicts that if the tail sweeps 180° in one direction relative to the body, the gecko will complete a turn of about 20° in the other direction (Figure 7), which is consistent with the observed results. Geckos with the largest relative tail lengths could generate nearly twice as much body yaw than geckos with the shortest tails.

Second, we explored the parameter space beyond the house gecko to predict how further increases in tail length might affect turning (Figure 7).

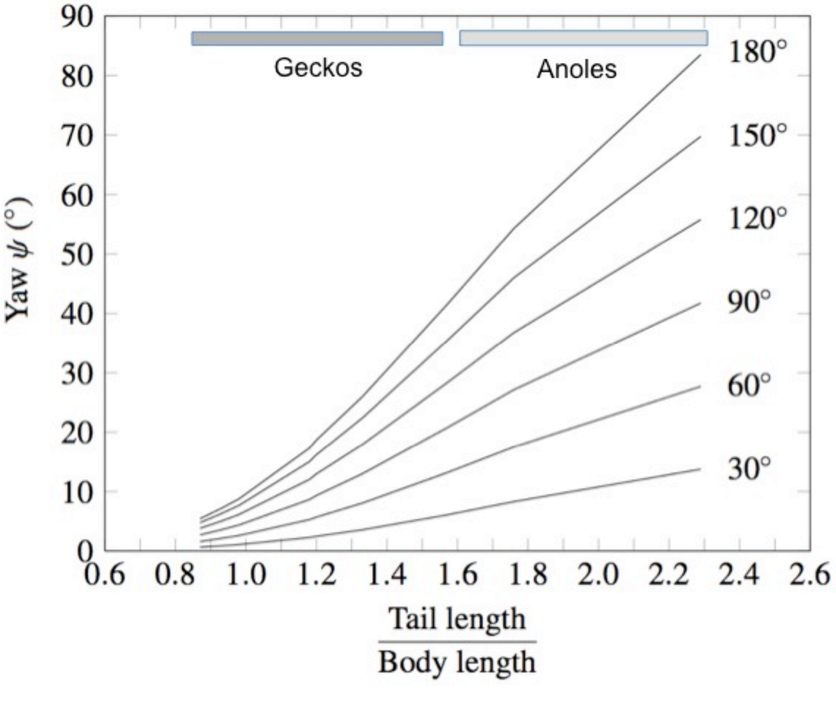

Figure 7: Mid-air turning performance as a function of tail length relative to body length and the degree of tail sweep. The plot shows the variation in body yaw for a gecko of average dimensions when the tail is swung in the plane of the body. The tail sweeps from 30° to 180° in 30° intervals. Tail lengths used for calculation span the range of measured house gecko tail

lengths to hypothetical lengths that approach those in lizards such as anoles, as indicated by the grey bars. All other body parameters were held fixed. From Jusufi *et al.,* 2010.

Anoles with short tails (tail length/body length = 1.57) would need to sweep their tail by 90° to turn their body by about 20°. If, however, they swing their tail 180°, then the body should turn by over 40°. By contrast, if the tail is nearly twice as long as the average house gecko, similar to that found in the green anole *A. carolinensis* (tail length = 10.5 cm, tail length/body length = 2.29) and it is swung 90°, then the body should yaw over 40°. A tail swing of 180° for the same morphology should yield a turn of the body of over 80°. Again, the model predicts the increased effectiveness of a relatively longer caudal appendage.

II.3.3 Model scaling

We used our analytical model to speculate on the effects scaling has on aerial maneuvers and to assist in the design of our robot prototype. Suppose we scale lengths by a length ratio $\alpha = L'/L$, where L is the nominal length and L' is the scaled length. Clearly $L' = \alpha L$. Assuming constant density across all size scales, mass is proportional to volume, and hence the scaled mass m' is related to the nominal mass m by $m' = \alpha^3 m$. Since moment of inertia has units of mass times length squared, the inertias of the body and tail scale as $J' = \alpha^5 J$. From equations (1) and (B.6-B.20), we observe that every term of the coefficient matrix $\mathbf{A}$ and coefficient vectors $\mathbf{f}_1$ and $\mathbf{f}_2$ is multiplied by a moment of inertia (J_{b1}, J_{t1}, etc.) or an inertia-like term (e.g., mL_1L_2). The scaling appears on both sides of the equations of motion as α^5 and thus cancels out, from which we conclude that isometric scaling has no effect on the dynamical response of the system. A given tail rotation should elicit a corresponding body rotation irrespective of size.

Assuming no storage/return of energy in elastic tissues, the total work required to complete the maneuver must equal twice the maximum rotational kinetic energy (proportional to mass moment of inertia) of the body and tail and hence scales as α^5. To maintain constant righting duration, the average mass-specific power supplied by the actuator must increase as α^2 and hence we hypothesize that time of righting will increase at larger size scales.

II.3.4 Robot prototype

Rather than produce a physical model the size of the house gecko, *H. platyurus,* we chose to explore the analytical model's predictions by building a relevant robot prototype with the size and morphology of the most effective climbing robot (Figure 8). Stickybot, a quadrupedal robot inspired by the morphology and dynamics of house geckos, can climb smooth vertical surfaces (Kim *at al*., 2007). We anticipate that one of the next steps in its development will be mid-air reorientation, perhaps allowing directed aerial descent. The tail was rotated about the robot's longitudinal axis. (a) Free falling robot begins in upside-down pose.

Our robot prototype completed a mid-air righting behavior similar to that observed in the geckos and predicted by our analytical model. As the tail of the robot accelerated, the body rotated in the opposite direction by 180° in 250-300 ms (Figures 8 (a) - (c) and (e)). After the maneuver ended with the tail at rest with respect to the body, no further rotation was observed (Figure 8 (d)) before the model collided with the ground, indicating that no net angular momentum was introduced by the release process or by drag.

Analytical model predictions agreed with observed robot behavior even though the analytical model differed in morphology (Tables 2 and 3). Using the nominal measured physical parameters, the model predicted a body roll of 148.7° and residual nose-up pitch of 34.2°. The observed roll of the robot prototype was 168° with approximately 30° of pitch. Flexing of the body and tail in the physical model during the rotation may account for some of the differences between the predicted and observed rotation. The robot prototype was designed with an inclined tail angle (35°) to avoid potential collisions with the hind legs in the real robot. To achieve complete righting with the inclined tail, we used a relatively large tail moment of inertia.

The tail moment of inertia taken about its base for the gecko (6.8×10^{-8} kg-m^2) was nearly equal to the body roll moment of inertia. In our robot, the moment of inertia about the base was 2.4×10^{-3} kg-m2, nearly four-fold larger than the roll moment of inertia. The necessarily larger tail moment of inertia in the robot is consistent with the analytical model's prediction that longer tails would be necessary in animals using inclined tails. However, since the tail was not constrained to conical morphology, we were able to effect the necessary change in moment of inertia without lengthening the tail or increasing mass significantly.

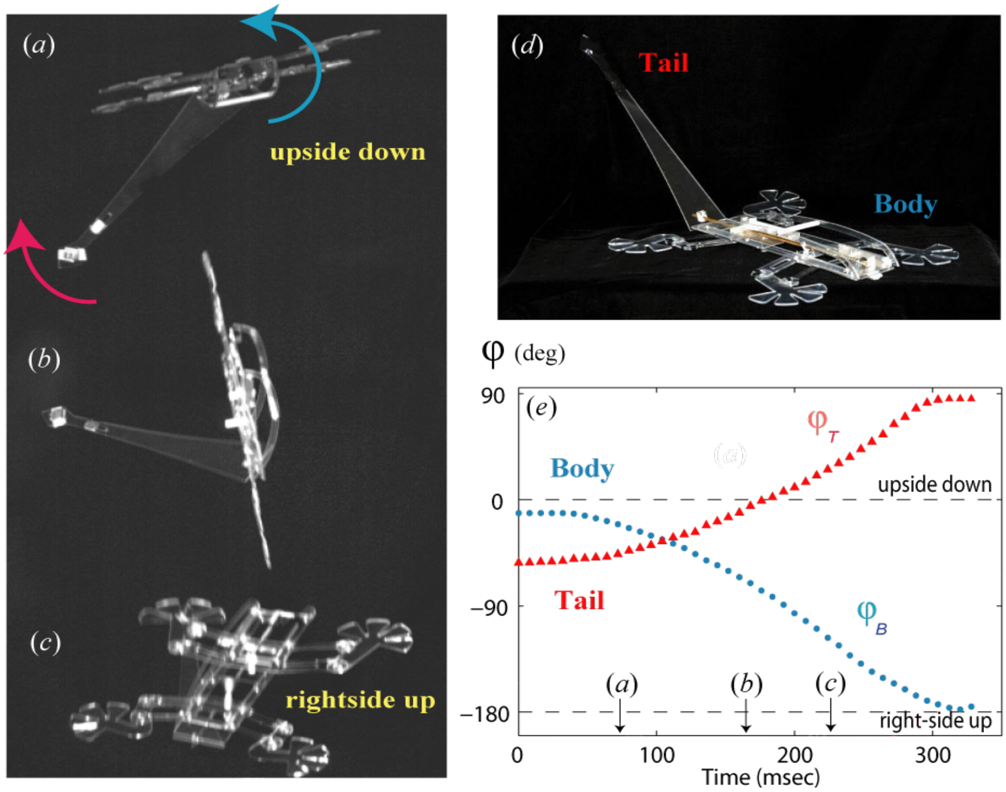

Figure 8: Air-righting maneuver performed by the robot prototype. The tail (red arrow) rotates clockwise and the body (blue) anti-clockwise. Reorientation is initiated after a characteristic latency upon take-off. (b) Robot mid-way during air-righting. (c) Robot attained right-side up posture more favorable for collision with the ground. (d) Dorso-lateral view of the robot prototype showing its similarity to Stickybot (Kim *et al*., 2007). (e) Plot depicts robot's body (blue) and tail (red) rotation as a function of time (see Figures 3 (f) and 6 (b)). From Jusufi *et al.* 2010.

If a conical tail morphology were used in the robot with the same mass and dimensions, the moment of inertia about the tail base would be 5.64×10^{-4} kg-m^2, less than 25% of the value needed for complete righting. If the robot's tail were orthogonal to the body, as in the average gecko, the predicted roll by the analytical model increases to 221°.

The performance of our robot prototype underscores the effectiveness of air-righting with redistribution of mass using tail rotation, thus complementing the results of our theoretical analysis. By contrast, Mather and Yim's (Mather and Yim, 2009) analysis of a modular robot's controlled fall led them to conclude that "tail type inertias are not potentially useful." Their two-joint robot, with essentially a flexible spine, self-rights via cat-like back bending rotations. The authors speculate that tail-like devices attached to the end of a body will be ineffective because of the large inertial load that they must move. We agree that segmenting a body and reorienting by cat-like twisting could reduce the inertial load. However, our animal and robot prototype data do not support the assertion that tails are necessarily useless because body bending has a particular advantage. Tails provide an opportunity for simple body attitude control with a single swing or sweep, whereas back twisting from an arbitrary initial orientation is a far more challenging control problem, may take longer to execute and is less likely to attain the desired body position with all the legs from each segment safely on the ground or wall. Also, as pointed out in Mather and Yim (Mather and Yim, 2009), "tail type inertia loads do have a significant advantage in that their final orientation is usually unimportant to the system." Moreover, tails can be easily added to current platforms and have been shown to have the added benefit of vertical climbing stabilization (Kim *et al.*, 2007).

Finally, we observe that tail-like structures can be economical with respect to mass; in geckos, the tail was on average only 1/10th of the body mass, yet still enabled the fastest air-righting yet observed in an animal or robot. In fact, a solution using inertial appendages could simplify control of a variety of unmanned aerial and space vehicles, because it allows for reorientation without the need to implement complex, multi-axis bending or twisting of the trunk (Kane and Scher, 1969).

II.4 General conclusions

Addition of an appendage to a body allows rapid rotations about a chosen axis. Our model predictions indicate that a simple two-link system (i.e., body and tail) with a two degree-of-freedom joint enables effective attitude control of the body without the need for external work. Such a system can maintain rotational control authority in the absence of an environment on which it can generate forces. An airborne animal or robot could maintain control authority at zero airspeed or high angles of attack, where lift-based control mechanisms can generate little or no force.

The utility of an inertial appendage extends beyond the aerial rotations illustrated here. Undesired angular momentum injected by disturbances could be temporarily directed to the appendage, allowing the body to remain stable until substrate interactions allow dissipation of the perturbation energy. Modulating the mechanical properties of the joint could effect large changes in the dynamical behaviour of the system. For example, traditional aircraft with fixed body structures must compromise between stability and maneuverability. By varying the stiffness and position of an appendage such as a tail, the aircraft could modulate the moment of inertia about arbitrary axes of rotation, allowing it to rapidly change from a stable mode to a maneuverable mode. Terrestrial or scansorial robots could use such an appendage to generate transient torques to maintain body attitude in the face of unsteady or unpredictable surface forces.

II.5 Literature cited

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II.6 Appendix

II.6.1 Estimating the maximum drag moment acting on the gecko during air-righting

To estimate the maximum drag moment acting on the gecko while it performs its air-righting maneuver, we consider the simplified case in which the body and tail are held orthogonal to each other. The effects of pitch and yaw are very small for this alignment of tail and body, so we assume that rotation occurs solely in the vertical XZ plane. Also, it is assumed that the gecko executes a perfect reorientation: the body rotates $180°$. The passive falling speed of the body at the beginning of free fall is small relative to the body and tail rotation by muscle power. Moreover, the tail is rotating upward and in the opposite direction of the downward falling body. Consequently, we ignore the oncoming airflow due to free fall and consider just the airflow tangent to the rotating tail and body. In essence, we are calculating our estimate of the drag moment from a model in which the body and tail rotate about a common pivot fixed in space, where the pivot coincides with the base of the tail and the centerline of the body. For brevity, we detail here the analytical methods for estimating the maximum drag moment acting on the tail only – the drag moment acting on the body (torso and legs) is determined in a similar fashion. We then compare the tail drag moment to the moment associated with air-righting.

Because of the geometry of the projected (frontal) area of the tail and the variation in speed of the oncoming airflow, the applied drag force will vary along the rotating tail. Since the tail is modeled as a cone, its projected area is an isosceles triangle with base width 2R (where R is the tail base radius) and height L_t (tail length), and hence the projected area varies linearly in width from base to tip. The tail spins about its base with angular speed ω , and so the speed of the oncoming tangential airflow increases linearly from the base, where the air speed is zero, to the tail tip, where the air speed is a maximum at ωL_t . Let h denote the distance along the tail's length from its base. The differential aerodynamic drag force dF_D acting on the tail is

$$dF_D = \frac{1}{2}\rho C_D v(h)^2 dA \,, \tag{5}$$

where the air density $\rho = 1.2$ kg/m3, C_D is the drag coefficient (assumed constant), $v(h)$ is the variation in oncoming airflow, and dA is the differential projected area:

$$v(h) = \omega h \,, \tag{6}$$

$$dA = 2R\left(1 - \frac{h}{L_t}\right)dh \,. \tag{7}$$

The corresponding net drag moment M_D acting at the tail pivot is determined by integration over the tail length:

$$M_D = \int h\,dF_D\,. \tag{8}$$

For simulation, we used a half cosine profile for the absolute rotation of the tail based on the experimental data for tail sweep trajectory in Figure 3 (f):

$$\phi_T(t) = -\frac{\pi}{2}\cos\left(\frac{\pi}{t_f}t\right), \tag{9}$$

where $t_f = 110\,\text{ms}$ is the average duration of air-righting based on experimental observations. Differentiation of equation (9) gives a maximum angular speed and acceleration of $\omega_{\max} = \pi^2/(2t_f)$ and $\dot{\omega}_{\max} = \pi^3/(2t_f^2)$, respectively. Integrating equation (8) and evaluating at the maximum angular speed, the maximum drag moment acting at the tail pivot is

$$M_{D,\max} = \frac{\rho C_D R(\pi L_t)^4}{80t_f^2}\,. \tag{10}$$

Using a drag coefficient $C_D = 1$ for a smooth cylinder and the average parameter values given in table 2, we obtain $M_{D,\max} = 3.02\times10^{-6}$ N-m. This value is an overestimate for several reasons. First, we used a drag coefficient for a cylinder, not a cone. Because of the taper of the cone, the drag coefficient is not uniform across the tail and decreases toward the tip (since the tail becomes more like a thin plate). Second, looking at the compressed tail of the flat-tailed house gecko from the side, its base width is a fraction of *2R*. Since the flatter side of the tail is presented to the oncoming airflow during air-righting, using the maximal width *2R* for calculation gives an overestimate of $M_{D,\max}$. The maximum drag moment acting on the torso and legs can be approximated in the same manner as for the tail, yielding a value of $M_{b,\max} = 1.79\times10^{-7}$ N-m, an order of magnitude lower than the maximum drag moment exerted on the tail.

Next we compare the maximum value of the drag moment to the maximum moment needed to spin the body around by 180°. This air-righting moment $M_{I,\max}$ is obtained by a moment balance on the body around the mutual pivot for the body and tail:

$$M_I = J_{\text{body, pivot}}\dot{\omega} = J_{b2}\dot{\omega}\ , \tag{11}$$

where J_{b2} is the moment of inertia of the body about its mass center. The drag moment M_b acting on the body would normally be added to the right-hand side of equation (11), but it has been neglected because its maximum value $M_{b,\max}$ is two orders of magnitude smaller than the maximum inertial term $J_{b2}\dot{\omega}_{\max}$, implying that body drag is an insignificant effect. Using the average value of J_{b2} listed in table 2, an estimate of the maximum moment exerted for air-righting is $M_{I,\max} = 8.47\times10^{-5}$ N-m. Comparing the drag and inertial moments, we find that $M_{D,\max} = 0.036 M_{I,\max}$, or the maximum moment induced by tail drag is estimated to be 3.6% of the maximum moment that the geckos require to perform air-righting.

II.6.2 Derivation of the equation of motion

Let $\{\mathbf{E}_1, \mathbf{E}_2, \mathbf{E}_3\}$ be a set of basis vectors for the ground-fixed frame XYZ. Likewise, take $\{\mathbf{b}_1, \mathbf{b}_2, \mathbf{b}_3\}$ to be a set of basis vectors for the frame $x_b y_b z_b$ attached to and rotating with the gecko body. Using a set (ψ, θ, ϕ) of 3-1-2 Euler angles to parameterize the rotation of the gecko body, the ground-fixed vectors are rotated into the body-fixed vectors according to

$$\begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{b}_3 \end{bmatrix} = \begin{bmatrix} C_\phi & 0 & -S_\phi \\ 0 & 1 & 0 \\ S_\phi & 0 & C_\phi \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 \\ 0 & C_\theta & S_\theta \\ 0 & -S_\theta & C_\theta \end{bmatrix} \begin{bmatrix} C_\psi & S_\psi & 0 \\ -S_\psi & C_\psi & 0 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} \mathbf{E}_1 \\ \mathbf{E}_2 \\ \mathbf{E}_3 \end{bmatrix}, \tag{12}$$

where $S_\alpha = \sin\alpha$ and $C_\alpha = \cos\alpha$ for any angle α. The body's total angular velocity vector $\boldsymbol{\omega}_b$ has components $\omega_{bi} = \boldsymbol{\omega}_b \cdot \mathbf{b}_i$ (i = 1, 2, 3) in the body-fixed basis given by

$$\begin{aligned} \omega_{b1} &= -\dot{\psi} S_\phi C_\theta + \dot{\theta} C_\phi, \\ \omega_{b2} &= \dot{\psi} S_\theta + \dot{\phi}, \\ \omega_{b3} &= \dot{\psi} C_\phi C_\theta + \dot{\theta} S_\phi . \end{aligned} \tag{13}$$

Let $\{\mathbf{t}_1, \mathbf{t}_2, \mathbf{t}_3\}$ be a set of basis vectors for the frame $x_t y_t z_t$ fixed on the tail. Based on the sequence of rotations depicted in Figures 5 (e) and (f) for side sweep η and incline γ of the tail relative to the body, the tail-fixed vectors are related to the body-fixed vectors by the transformation

$$\begin{bmatrix} \mathbf{t}_1 \\ \mathbf{t}_2 \\ \mathbf{t}_3 \end{bmatrix} = \begin{bmatrix} 1 & 0 & 0 \\ 0 & C_\gamma & S_\gamma \\ 0 & -S_\gamma & C_\gamma \end{bmatrix} \begin{bmatrix} C_\eta & 0 & -S_\eta \\ 0 & 1 & 0 \\ S_\eta & 0 & C_\eta \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{b}_3 \end{bmatrix}, \tag{14}$$

and so the total angular velocity vector of the tail is

$$\boldsymbol{\omega}_t = \boldsymbol{\omega}_b + \dot{\gamma} C_\eta \mathbf{b}_1 + \dot{\eta} \mathbf{b}_2 - \dot{\gamma} S_\eta \mathbf{b}_3 \,. \tag{15}$$

From equation (2) in (Passerello and Huston, 1971), the total angular momentum of the torso-tail system about its mass center takes the form

$$\mathbf{H} = \mathbf{J}_b \boldsymbol{\omega}_b + \mathbf{J}_t \boldsymbol{\omega}_t + \frac{m_b m_t}{m_b + m_t} \left(\boldsymbol{\xi} \times \dot{\boldsymbol{\xi}} \right), \tag{16}$$

where the inertia tensors $\mathbf{J}_b$ and $\mathbf{J}_t$ are symmetric, and m_b and m_t are the total body mass (torso and legs) and tail mass, respectively. The vector $\boldsymbol{\xi} = L_1 \mathbf{b}_2 + L_2 \mathbf{t}_3$ is the relative position vector between the centers of mass of the body and tail. The distance along the body's length between its mass center and the center of the tail's base is L_1, and L_2 is the distance between the center of the tail's base and its center of mass. By setting equation (16) to zero to conserve angular momentum and taking components in the body-fixed frame $x_b y_b z_b$, we obtain the equation of motion (1) with components A_{ik} (i, k = 1, 2, 3) of the coefficient matrix A given by

$$\begin{aligned} A_{11} = \; & \frac{1}{4}[2S_\eta (J_{t2} - J_{t3} + mL_2^2)(S_{2\gamma} S_\theta - C_{2\gamma} C_{\varphi\eta} C_\theta) + 4mL_1 L_1 (2C_\theta S_\gamma S_\varphi - C_\gamma S_\eta S_\theta) \\ & - C_\theta (4C_\eta S_{\varphi\eta} J_{t1} + 4S_\varphi (J_{b1} + mL_1^2) - 2C_{\varphi\eta} S_\eta (J_{t2} + J_{t3}) + mL_2^2 (S_{2\eta\varphi} + 3S_\varphi))], \end{aligned} \tag{17}$$

$$\begin{aligned} A_{12} = {} & C_{\varphi} J_{b1} + C_{\eta} C_{\varphi\eta} J_{t1} + m[C_{\eta} C_{\varphi\eta} (C_{\gamma} L_2)^2 + C_{\varphi} (L_1 - L_2 S_{\gamma})^2] \\ & + S_{\eta} S_{\varphi\eta} (J_{t3} C_{\gamma}^2 + J_{t2} S_{\gamma}^2), \end{aligned} \tag{18}$$

$$A_{13} = C_{\gamma} S_{\eta} [(J_{t2} - J_{t3} + mL_2^2) S_{\gamma} - mL_1 L_2], \tag{19}$$

$$\begin{aligned} A_{21} = {} & J_{t2} C_{\gamma} (C_{\gamma} S_{\theta} + C_{\varphi\eta} C_{\theta} S_{\gamma}) + J_{t3} S_{\gamma} (S_{\gamma} S_{\theta} - C_{\varphi\eta} C_{\theta} C_{\gamma}) + mL_2 C_{\gamma} [L_2 (C_{\gamma} S_{\theta} \\ & + C_{\varphi\eta} C_{\theta} S_{\gamma}) - C_{\varphi\eta} C_{\theta} L_1] + J_{b2} S_{\theta}, \end{aligned} \tag{20}$$

$$A_{22} = C_{\gamma} S_{\varphi\eta} [(J_{t2} - J_{t3} + mL_2^2) S_{\gamma} - mL_1 L_2], \tag{21}$$

$$A_{23} = J_{b2} + (J_{t2} + mL_2^2) C_{\gamma}^2 + J_{t3} S_{\gamma}^2, \tag{22}$$

$$\begin{aligned} A_{31} = {} & \frac{1}{4} [2C_{\eta} (J_{t2} - J_{t3} + mL_2^2)(S_{2\gamma} S_{\theta} - C_{2\gamma} C_{\varphi\eta} C_{\theta}) - 4mL_1 L_1 (C_{\gamma} C_{\eta} S_{\theta} + 2C_{\theta} S_{\gamma} C_{\varphi}) \\ & + C_{\theta} (4S_{\eta} S_{\varphi\eta} J_{t1} + 4C_{\varphi} (J_{b3} + mL_1^2) + 2C_{\varphi\eta} C_{\eta} (J_{t2} + J_{t3}) - mL_2^2 (C_{2\eta\varphi} - 3C_{\varphi}))], \end{aligned} \tag{23}$$

$$\begin{aligned} A_{32} = {} & S_{\varphi} J_{b3} - S_{\eta} C_{\varphi\eta} J_{t1} + m[S_{\varphi} (L_1 - L_2 S_{\gamma})^2 - S_{\eta} C_{\varphi\eta} (C_{\gamma} L_2)^2] \\ & + C_{\eta} S_{\varphi\eta} (J_{t3} C_{\gamma}^2 + J_{t2} S_{\gamma}^2), \end{aligned} \tag{24}$$

$$A_{33} = C_{\gamma} C_{\eta} [(J_{t2} - J_{t3} + mL_2^2) S_{\gamma} - mL_1 L_2]. \tag{25}$$

The components f_{1i} (i = 1, 2, 3) of the vector $\mathbf{f}_1$ associated with tail side sweep are

$$f_{11} = -C_{\gamma} S_{\eta} [(J_{t2} - J_{t3} + mL_2^2) S_{\gamma} - mL_1 L_2], \tag{26}$$

$$f_{12} = -(J_{t2} + mL_2^2) C_{\gamma}^2 - J_{t3} S_{\gamma}^2, \tag{27}$$

$$f_{13} = -C_{\gamma} C_{\eta} [(J_{t2} - J_{t3} + mL_2^2) S_{\gamma} - mL_1 L_2]. \tag{28}$$

The components f_{2i} (i = 1, 2, 3) of the vector $\mathbf{f}_2$ associated with tail inclination are

$$f_{21} = -C_{\eta} [J_{t1} + mL_2 (L_2 - L_1 S_{\gamma})], \tag{29}$$

$$f_{22} = 0, \tag{30}$$

$$f_{23} = S_{\eta} [J_{t1} + mL_2 (L_2 - L_1 S_{\gamma})]. \tag{31}$$

In these equations, $S_{2\alpha} = \sin 2\alpha$, $C_{2\alpha} = \cos 2\alpha$, $S_{\alpha\beta} = \sin(\alpha + \beta)$, $C_{\alpha\beta} = \cos(\alpha + \beta)$, $S_{2\alpha\beta} = \sin(2\alpha + \beta)$, and $C_{2\alpha\beta} = \cos(2\alpha + \beta)$ for any two angles α and β. Also, J_{bi} (i = 1, 2, 3) and J_{ti} denote the moments of inertia for the body and tail, respectively, about their mass centers, where $J_{t1} = J_{t2}$ for the conical tail. In addition, $m = m_b m_t / (m_b + m_t)$ for convenience.

Chapter III Landing on a Tree Trunk assisted by Active Tails

Summary

Passive mechanical stability is critical to terrestrial locomotion. Here we show that a similar control strategy improves landing stability in an unspecialized gliding lizard. Video footage obtained in the field shows *H. platyurus* is a capable glider, traveling significant horizontal distances in excess of 4m. However, unlike specialized gliders, does not undergo a stereotypical landing maneuver to substantially decrease velocity prior to impact. Instead, the geckos their tails as a "shock-absorbers" to reduce the forces acting on the limbs during hard landings, allowing controlled perching at high speeds. Strategies incorporating such mechanical integration can be applied successfully to enhance perching robustness in aerial and terrestrial robots. We measured geckos, *H. platyurus,* in a Southeast Asian rainforest to study tail function during aerial descent and gliding in nature. Field video revealed that geckos traveled horizontal distances from tree to tree of up to 4m. Prior to landing, geckos pitched their body up by ca. 27° and decelerated to approximately 5m/s. Near head-on collisions with the tree trunk pitched the torso vertically as high landing forces were absorbed by the body and tail. After vertical alignment with the tree trunk, geckos exhibited enormous pitch-back of their torso away from the tree to an average angle of 103° ±34° (n=3) toward the forest floor. When geckos halted the backwards pitching at enormous peak angles of up to 125° they maintained these extreme postures for an average duration of 19msec ±3, anchored by only the hind limbs and tail. Of the gliding geckos that reached the tree target (n=7), the majority (86% of trials) alighted safely on the vertical target. By contrast, tailless that these geckos experienced catastrophic falls in 75% of trials after crashing into the tree (n=4). Results reveal geckos use tails as shock-absorbers and stabilizers to reduce and control high impact forces acting on the limbs allowing effective landing at high speeds. Gecko's perching behavior could be initiated by the same reflex discovered during climbing where forefoot slippage stimulates tail depression. Strategies incorporating tail assisted responses can improve the vertical landing performance and stability of both animals and robot planes.

III.1 Introduction

Landing on a vertical target is an emerging challenge in multi-modal robots (Desbiens, *et al.* 2010). In nature, the highest landing stability is achieved by integrating sensory feedback to alter aerodynamic forces as seen in birds (e.g. Bonser, 1999) and specialized mammalian gliders (Paskins, 2007; Byrnes *et al.* 2008). However, passive mechanical control systems have been shown to be important in the terrestrial locomotion of both animals and robots. Here we report an alternative method to heavily learned sensory feedback control of landing, one that relies on a mechanically mediated solution.

A successful landing maneuver onto a vertical substrate hinges on the reliable attachment of the legs upon first impact. Gliding animals approach targets at relatively high speeds and experience enormous peak forces at landing (Byrnes *et al.,* 2008). A critical aspect of this process is that the animal uses their feet to cling to the wall. Any mechanism that acts to relieve the strain on the animal will contribute towards a safe attachment to the wall. We propose that systems can alight safely on vertical substrates by simple integration of the mechanics.

Quantitative studies addressing landing on a solid vertical substrates have been explored only in few gliding mammals, such as flying squirrels (Paskins, 2007) and flying lemurs (Byrnes *et al*., 2008). Landing stability is better for long glides in which considerable horizontal distances are covered since animals have more time to use aerodynamic forces acting on its control surfaces to decelerate prior to impact. But what to do if the desired landing target is located too far for a leap and is also too close for a glide? Even gliding specialists such as flying squirrels and flying lemurs avoid "hard landings" by choosing to not attempt a glide. Observations of squirrels released onto a tree trunk at breast height show that they did not climb and glide, and instead chose to jump to the ground and run to the nearby tree (Scheibe *et al*., 2006). Higher landing forces increase the probability of damage in robots and of injury in animals. Ando and Shiraishi (1993) proposed that free-ranging flying squirrels avoid short glides in order to limit the landing forces. It is possible that the squirrels may have a sense for a maximum speed at which they can safely or comfortably land on a stiff or unknown substrate for a given approach angle (Paskins 2007). It has been suggested that if a glide is too short to effectively reduce body momentum or allow the animal to adjust its posture for landing, short glides could result in the highest peak landing forces, and this has been experimentally confirmed for the Malayan flying lemur (Byrnes *et al.* 2008). Lizards with extended ribcages and cutaneous flaps, such as the flying gecko *Ptychozoan kuhli* (e.g. Young *et al.* 2002) and the gliding lizard *Draco* (McGuire and Dudley, 2007) are known to be capable of gliding by employing these aerodynamic surfaces and performing a controlled landing on solid vertical structures, much like their gliding mammalian counterparts. However, how landing is accomplished in unspecialized gliding animals remains under-explored.

To discover how lizards are able to land on a tree after gliding, we carried out field experiments in Southeast Asian lowland tropical rainforest, the native environment of *Hemidactylus platyurus.* By investigating the flight of geckos as they move from tree to tree, we discovered a common phenomenon where a successful landing is accomplished significantly more often when the individual gecko has a tail. Here we provide new insight, bridging the problem of hard landings between leaping and gliding by increasing landing stability.

III.2 Materials and Methods

Choice of field research locality

Being home to more than 30 species of gliding animals from three vertebrate orders, South-East Asian rain forests harbor by far the highest biodiversity of gliding flight. By contrast, we find far fewer gliding vertebrates in the lowland tropical rain forests of Africa or South and Central America. The architecture of vegetation is likely the primary selective pressure driving the evolution of vertebrate gliders. Liana density was found to be lowest in Indo-Malaya, higher in the New World and highest in Africa. Due to the lack of lianas interconnecting vegetation, Indo-Malayan forests can be assumed to contain comparatively larger open spaces, thus providing increased relative selective pressure for animals that engage in aerial locomotion (Emmons and Gentry, 1983). Moreover, the significantly greater height of lowland Indo-Malayan rain forests is believed to increase the diversity of vertebrate gliders. Canopy heights of African and South American rain forests are significantly lower (Dudley and DeVries, 1990).

Animals

Our model system, the Flat-tailed House Gecko, *Hemidactylus platyurus,* is native to The Republic of Singapore (e.g. Chan and Corlett 1997; Lim and Lim 1992; Chou 1978). The National Parks Board of The Republic of Singapore approved a research proposal to study the locomotion of geckos with a field research permit. The Wildlife Reserves Singapore allowed us to capture house geckos *H. platyurus* (Specimen Collection Permit # NP/RP955A). When we collected lizards no harm was done to the animals or surrounding landscape. All animals were released shortly after capture if they were deemed not suitable for the study. No detrimental effects resulted from the short confinement. All methods of capture and handling are well-established standard techniques used by herpetologists. Our study of perching behavior was based on eight wild-caught *Hemidactylus platyurus.* The average body weight of the lizards was 3.56 ±0.3g (mean ±1 s.e.). All animals were released after conclusion of the locomotion experiments. Most lizards were released after a period of just two days in captivity. We made sure that animals were provided with water at all times. We feed crickets to the geckos. We temporarily accommodated lizards in portable terraria with ambient humidity (ca. 85%) and temperature (ca. 38°C) for the shortest duration possible at our field site in the Wildlife Reserves.

Field experiment protocol and measurements

We used generators, extension cords, and power strips to power three digital video cameras (X-PRI, AOS Technologies). To prevent damage of electronic equipment at humidity of ca. 85% and prevent over-heating at temperatures ~38° Celsius, we mounted heat sinks on the high-speed video cameras. to keep high speed video cameras. Video frames from all three camera views were synchronized with a trigger switch connected via BNC cables. The data were stored on a portable lap top computer. The cameras were placed on the ground in orthogonal fashion. One 35 m away from the drop test zone and with a 50 mm objective. The other 12 m away from the drop test zone and a 25mm objective. The lighting conditions in the forest often changed rapidly. Changing light conditions forces us to adapt recording at different frame rates ranging from 120 to 500 frames per second. We frequently adjusted the aperture on one 50 mm and two 25 mm lenses to ensure an adequate amount of light be made available to the high-speed video cameras.

Lizards were placed on a vertical platform at a height of 6.6m from which they voluntarily took off. Many lizards climbed around the platform instead of jumping off. The majority of lizards that jumped off moved toward a tree trunk that was situated a horizontal distance of 4.3m away from the origin. Of the lizards which did not reach the tree trunk, but landed short of it, most were seen to walk up to the tree trunk via the forest floor. This observation was encouraging in that the tree trunk proved to be a successful stimulus in triggering not only aerial but also subsequent terrestrial locomotor behavior. Field site flora and fauna were discussed with Dr. George Staples from the Singapore Botanic Garden.

We performed motion tracking analysis using Xcitex ProAnalyst as well as ImageJ. We performed kinematics analysis using MATLAB and statistics using standard software (JMP and Microsoft Excel). The geckos' angle of attack during gliding was measured relative to the horizontal. The duration for geckos‘ to complete fall-arresting response was measured as the onset of pitch-back of the torso away from the tree and toward the forest floor until it recovered and returned the body to the tree trunk such that forefeet could establish contact with the tree. The geckos pitch-back angle throughout the fall arresting response was measured relative to the tree trunk. The duration that geckos remained at peak pitch-back angle (apex) was measured as the time window in which the instantaneous angular position of the body relative to the tree did not deviate form the peak angle by more than 2° which was considered to be within measurement error.

Dynamic model

The rigid body rotates about the pin joint through an angle θ with respect to the world frame ($\{\mathbf{E}_x, \mathbf{E}_y\}$).

Denote the vector from the foot to the torso center of mass by $\boldsymbol{b}$ (see equation 1).

$$\boldsymbol{b} = l_b(cos\theta\ \boldsymbol{E_x} + sin\theta\ \boldsymbol{E_y}) \tag{32}$$

where l_b represents the distance from the point of rotation to the body center of mass.

The center of mass velocity $\boldsymbol{v}$ is described by (see equation 2).

$$\boldsymbol{v} = -l_b\dot{\theta}\ sin\theta\ \boldsymbol{E_x} + l_b\dot{\theta}\ cos\theta\ \boldsymbol{E_y} \tag{33}$$

The acceleration is described by equation 3.

$$\boldsymbol{a} = -l_b\ddot{\theta}sin\theta\boldsymbol{E_x} - l_b\dot{\theta}^2cos\theta\boldsymbol{E_x} + l_b\ddot{\theta}cos\theta\boldsymbol{E_y} - l_b\dot{\theta}^2sin\theta\boldsymbol{E_y} \tag{34}$$

$$a_y = \boldsymbol{a} \cdot \boldsymbol{E_y} = l_b\ddot{\theta}cos\theta - l_b\dot{\theta}^2sin\theta \tag{35}$$

The linear and rotational dynamics arise from Newton's equations of motion. The normal component of foot force (see Table 4) follows from the balance of linear momentum in the $\mathbf{E}_y$ direction,

$$F_y + C_y = m\ a_y \tag{36}$$

The contact force can be found from the rotational dynamics, as follows:

$$I\ddot{\theta} = mgl_b sin\theta - l_t C_y \tag{37}$$

Solving for C_y reveals the contact force required to accelerate body rotation:

$$C_y = \frac{mgl_b \sin\theta - I\ddot{\theta}}{l_t} \tag{38}$$

Substituting equations (4) and (7) into the linear dynamics (5) reveals the relationship between foot force and righting kinematics. The normal force at the rear leg point of attachment (see Figure 13) is expressed in equation 8:

$$F_y = ml_b(\ddot{\theta}cos\theta - \dot{\theta}^2 sin\theta) - \frac{mgl_b sin\theta - I\ddot{\theta}}{l_t} \tag{39}$$

$$F_y = D_y - \frac{mgl_b sin\theta - I\ddot{\theta}}{l_t} \tag{40}$$

III.3 Results and Discussion

Transitions during locomotion in complex arboreal habitats and changes of body orientation in mid-air (e.g. Jusufi *et al.,* 2008; Gillis *et al.,* 2009) can determine gliding outcomes (Dudley and Yanoviak, 2011; Jusufi *et al.,* 2011). Laboratory studies of aerial righting and equilibrium gliding revealed that Geckos and Anoles could use tail movements for maneuvering (Jusufi *et al.,* 2010). We measured geckos, *H. platyurus*, in a Southeast Asian rainforest to study tail function during aerial descent and gliding in nature. We examined the glide trajectories and landing of geckos that had no obvious specializations for flight. In contrast to the Flying Gecko, *Ptychozoan kuhli,* which has been reported to glide in numerous studies, representatives of the gekkonid genus *Hemidactylus platyurus* are generally considered to be terrestrial lizards that live in arboreal habitats. Despite this, *H. platyurus* were capable of traveling a horizontal distance of 4m with a glide angle less than 60˚ (see Figure 9 (a)).

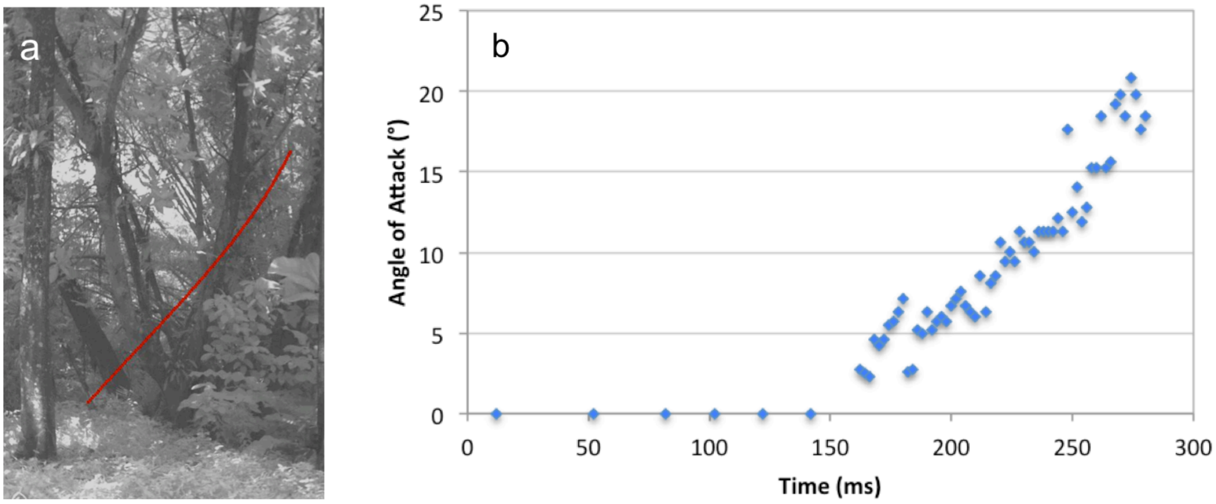

Figure 9: Glide trajectory and angle of attack. (a) Field locality in the rainforest at the Wildlife Reserves Singapore. Take-off is at the top right and the tree trunk stimulus for perching is on the bottom left-hand side. The gecko's glide trajectory is marked by the red trace. Distances are 4.3m of horizontal and 6.6m of vertical transit. (b) The gecko's torso angle relative to the horizontal is depicted from mid-glide to landing.

Classical gliders can alight safely on a tree trunk in part because they exhibit large aerodynamic control surfaces in the form of flaps (e.g. flying lemurs) that allow them to stall. By contrast, geckos lack such structures and reach the tree trunk at substantially higher speeds consequently experiencing hard landings. We complement our own field observations with kinematics analysis of landing to test the prediction that tails could be used as shock-absorbers thus stabilizing hard landings to and control high impact forces acting on the limbs allowing effective landing on vertical targets at high speeds. *H. platyurus* exhibited postural changes during gliding from angles of attack of approximately -15° to -20° after take-off and then leveled off to near horizontal in mid-flight (Figure 9 (b)) with speeds ranging from 5.4m/s to 7.5m/s. As they approached the tree target geckos pitched up to positive angles relative to horizontal ranging from 15° to 35° as the lizards prepared for landing, suggesting a dedicated landing maneuver. Geckos decelerated to speeds from 4.4m/s to 6.3m/s. Geckos were landing at higher speeds than other gliding animals. The average landing velocities of mammalian gliders were lower than in geckos despite their much larger size (Byrnes *et al.*, 2008). However, the capabilities of these unspecialized animals go beyond transit of a horizontal distance. Recent work on arthopods has shed light to the directed aerial descent capabilities of insects heretofore not known to possess capabilities to control descent (Dudley and Yanoviak, 2011; Yanoviak *et al.* 2005; Yanoviak *et al.,* 2009). Some vertebrates without obvious specializations for flight, such as wings or patagia, have been found to glide (e.g. Oliver, 1951), but how they accomplish landing is under-explored. Snakes can glide (Socha, 2002) but they can alight safely in compliant canopy foliage only. Snakes apparently do not land on solid vertical tree trunks.

Here we show original footage from the field in South-East Asia revealing that geckos gliding in the lowland tropical rainforest can use their tails in conjunction with their rear legs to land safely on a tree trunk (see Figure 10). This remarkable landing behavior is executed successfully even if animals approach it at high impact speeds. The animal's landing maneuver can be characterized as follows. As the animal concludes its aerial descent first contact is established with anterior portion of the torso (Figure 10 (a)).

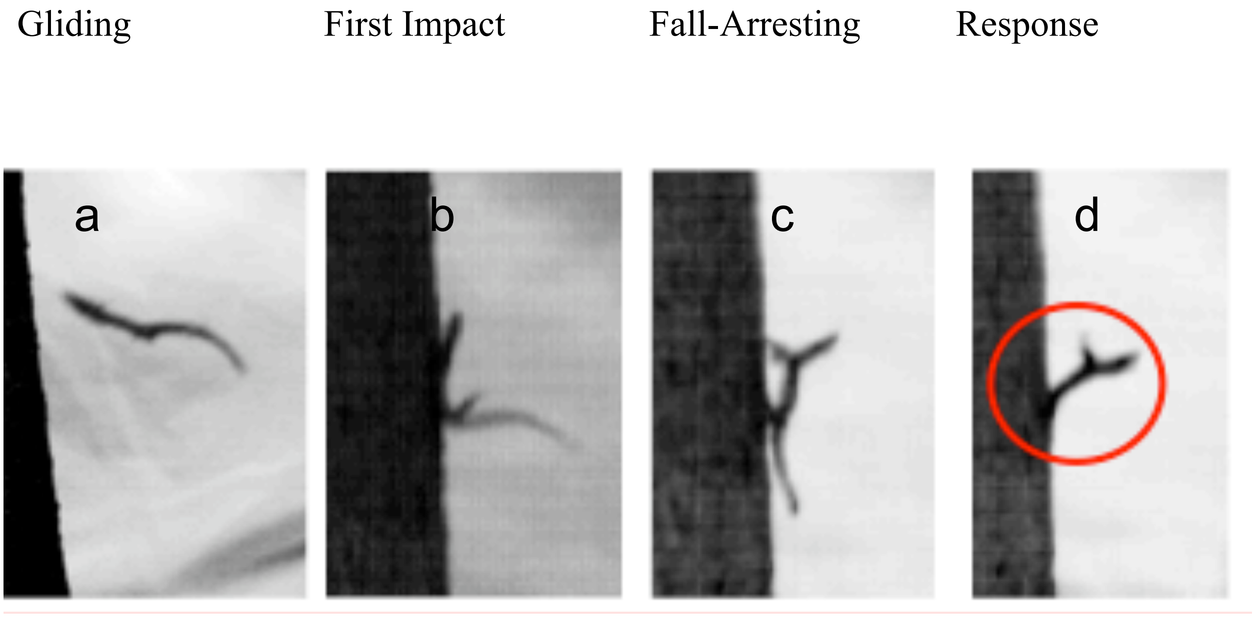

Figure 10: Landing maneuver. Gecko *Hemidactylus platyurus* gliding in Southeast Asian lowland tropical rainforest. Sagittal view with close-up footage of the landing site with motion sequence from left to right. (a) Animal rears up in preparation of landing on vertical tree trunk after having covered a horizontal distance of 4m. (b) First impact occurs with fore and then with hind quarters. (c) Next, the tail is pressed against the tree while the trunk is dislodged as the animal loses contact with the fore legs. (d) Gecko’s torso exhibits remarkable pitching backwards (circle) while still attached with rear legs and with tail placed adjacent to the tree trunk.

Next, the rear legs contact the vertical substrate. With all four feet on the vertical target the animal does not regress backwards towards the forest floor (Figure 10 (b)). The distal tail tip is observed to arch over in ventral direction. Both of the fore feet now begin to slip (Figure 10 (c)) potentially as a result of high impact forces transferred internally. Pitch-back cannot be prevented, however, and the animal's torso begins to fall back on the initial point of landing on tree trunk (Figure 10 (d)).

The most extreme landings observed are illustrated in Figure 11. Near head-on collisions with the tree trunk pitched the torso vertically as high landing forces were absorbed by the body and tail (Figure 11 (b)). Next the hind limbs contact the vertical substrate and the distal tail tip was observed to ventri-flex (Figure 11 (c)). After vertical alignment with the tree trunk, the anterior section of the body pitched over 125°, anchored by only the hind limbs and tail (Figure 11 (d), (e)). The ventri-flexion could be related to the tail response initiated by slippage in rapid climbing (Jusufi *et al.* 2008).

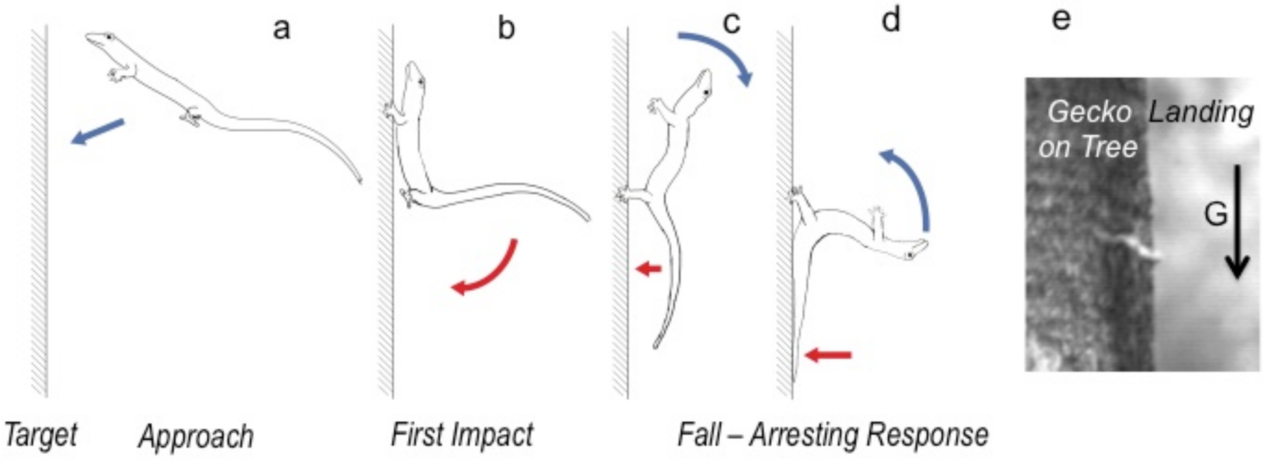

Figure 11: Postural sequence of the landing maneuver. Blue arrows illustrate motion of the torso and red arrows show tail rotation. (a) Motion sequence of the gecko approaching the vertical target at positive angle of attack and (b-e) alighting on it. (b) First impact occurs with the front legs and the trunk. Red arrow indicates onset of the ventral flexion of the tail. (c) Rear legs attach to the tree trunk. Front legs slip off and the gecko rotates with its back towards the forest floor as the tail makes contact with the wall. (d) Maximum pitch-back is reached and the animal momentarily comes to rest (e) before it's torso returns to the tree trunk so that the front legs regain foothold.

This enormous response (Figure 11 (d), (e)) is nearly double the amount of pitch back that we observed in the Kickstand response during rapid wall running (*Chapter One*). Moreover, as they arrested the fall geckos appeared to momentarily stand still as they sustained these extreme peak angles for a duration ranging from 15 msec to 25 msec (n = 3 individuals) with an average of 19msec ±3. During this stationary period the animals appeared to momentarily stop rotating backwards. During hard landings geckos must dissipate very large impact forces. The salient features of the Fall-Arresting Response that is critical to a successful landing is revealed in the kinematic analysis presented in Figures 12 and 13.

The torso's angular position as a function of time throughout the response is depicted in Figure 12 for a characteristic trial. At first impact the trunk peels onto the tree from anterior to posterior, being effectively pressed against it. Next, the front legs are dislodged from the tree, leaving only the rear legs gripping the vertical substrate. Within 15msec we measured a rapid increase to 45° in body pitch-back (see Figure 12), as the anterior part of the torso bounces back off the tree trunk, apparently as a consequence of the very large impact forces. The torso then rotates past a right angle of 90° of pitch-back at 37msec as the rotation about the rear leg pivot and toward the forest floor continues unabated (Figure 12).

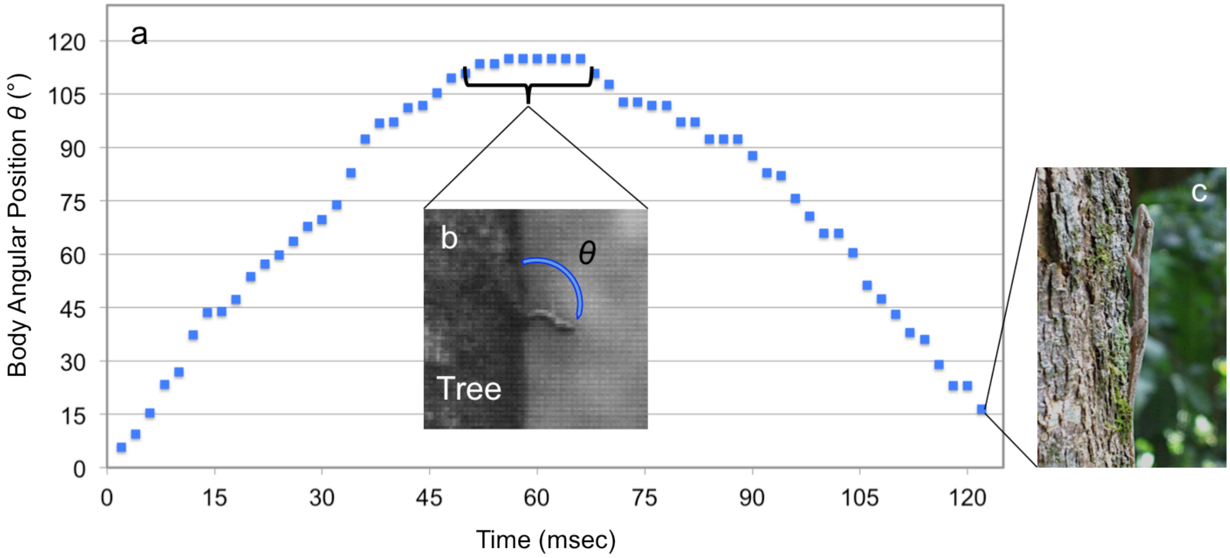

Figure 12: Body pitch-back over time. (a) Angular position of the torso relative to the tree trunk throughout the Fall-Arresting Response. (b) Inset from field high-speed videography depicts landing *H. platyurus* at peak pitch-back angle of 115° which it maintains for a duration of 18 msec. (c) Field photo inset shows a gecko perched on the tree upon completion of the landing maneuver.

Within 50 msec into the response the gecko approached it's peak excursion relative to the tree when the animal appeared to have arrested the torso's fall at last and came to a halt (Figure 12 (b)) at an enormous peak pitch-back angle of 115°. Surprisingly, once the gecko reached its maximum excursion, it maintained the posture nearly unchanged for a period of 18 msec, before it began to rotate its torso back toward the tree trunk.

At time T = 70msec the gecko's trunk begins to move away from the forest floor and back toward the tree to attain a more vertical posture and finally return within reach for its forefeet to regain hold (Figure 12 (c)) of the tree bark which occurred circa 120 msec after it was lost.

The kinematics analysis in Figure 13 confirm the observation of such a stationary period. The data in Figure 13 reveal that when geckos were at peak pitch-back excursion their body angular velocity is at minimum or goes to zero (see Figure 13 (b)).

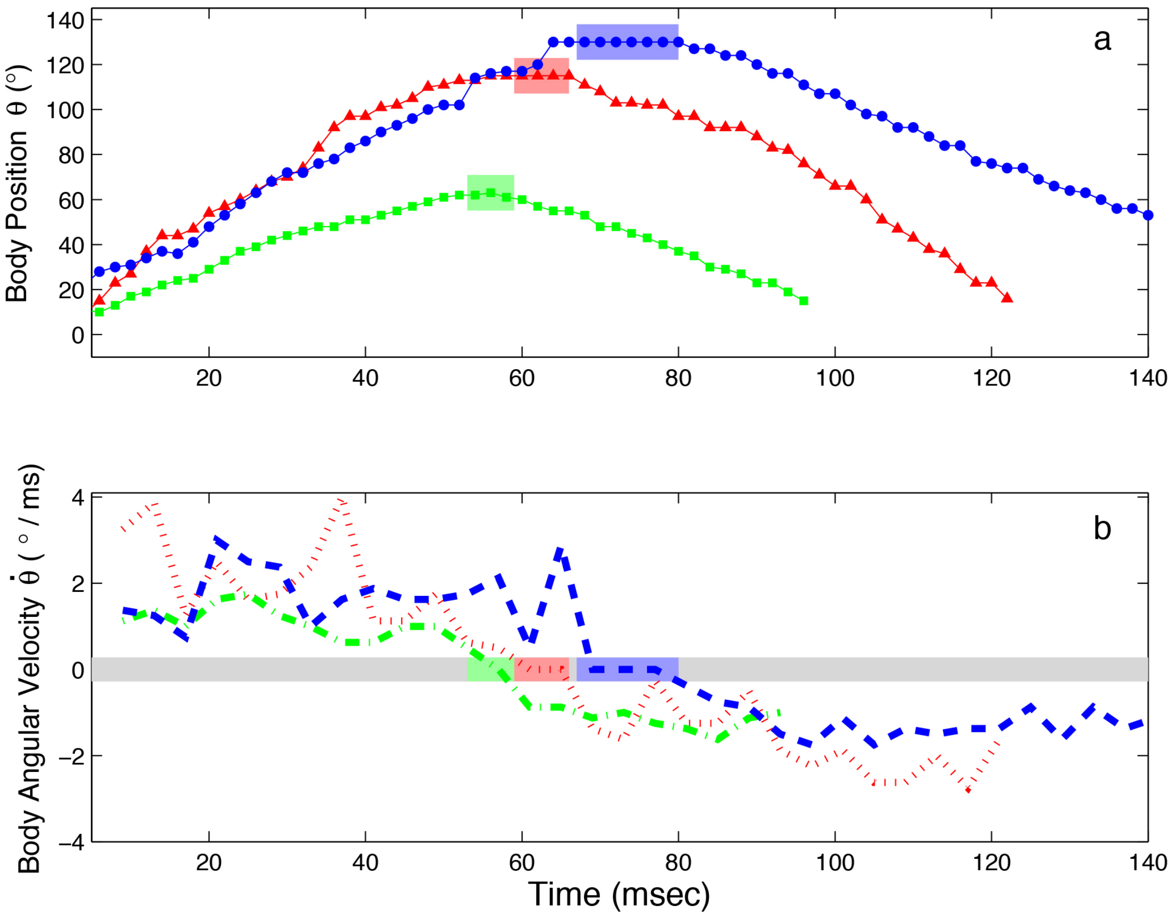

Figure 13: Fall-Arresting Behavior in response to Hard Landings in Flat-Tailed House Geckos. (a) Body position over time. High-speed video footage captured the *H. platyurus* landings and then body angle was measured on a frame by frame basis. The time is reconstructed from the frame rate and is in msec. As excess impact energy from landing was dissipated it caused the geckos' trunk to fall back toward the forest floor, while only rear legs and tail maintain contact with the tree. In this process geckos pitch back to average peak angles of 103° which are sustained for a duration forming a plateau as highlighted by the shaded color regions. The behavioral variation arising from performance measured from multiple geckos (n = 3 individuals) is shown in the lines represented by the symbols triangle, square and circle. (b) Body position rate of change over time for each individual. The data in (a) are interpolated to a 4 msec sample rate. The body angular velocity is defined as the difference in body position per interpolated time interval (4msec). In each graph the body rate change is positive in the approach to the tree as the lizard pitches backwards, then drops to near zero, next it becomes negative as the lizard returns to the tree trunk. The horizontal, shaded area y = 0 ± 0.2 °/msec indicates that no significant change in body position rate occurs in this region, which lasts approximately between 10 and 30 msec. The shaded, colored boxes indicate that average maximum body position [in (a)] occurs when the rate of body position change is closest to zero.

It is evident from Figure 13 that the least change in angular position occurred in the region of maximum pitch-back angle, where angular velocity dropped to zero. Another characteristic feature that emerges is that body rate of change (see Figure 13 (b)) is positive before peak excursion (apex) and negative thereafter, coinciding with the aforementioned ‘plateau’. When geckos halted the backwards pitching they appeared to maintain these extreme excursions for an average duration of 19 msec ±3 (n=3). The pitch-back moment induced by gravity is near maximal in this situation. So is the angular acceleration.

Geckos exhibited enormous pitch-back of their torso away from the tree to an average angle of 103° ±34 toward the forest floor (n = 3). We find a mean duration of 131 msec ±23 for completing the fall-arresting response from the gecko’s trunk becoming dislodged to regaining tree contact with front legs.

A comparison of landing performance revealed that while the majority of gliding geckos (86% of trials) landed safely on the vertical target (n = 7). By contrast, tailless geckos experienced catastrophic falls in 75% of trials after crashing into the tree (n = 4).

To get insight into the mechanistic basis of the possible effect of tail in the difference in mostly landing success observed in tailed geckos as opposed to failure in tailless animals in landing, we consider the following planar rigid body dynamics analysis (see model in Materials and Methods). To study the Fall-Arresting Response we represent the gecko’s torso by a single rigid body (blue oval “Body” in Figure 14).

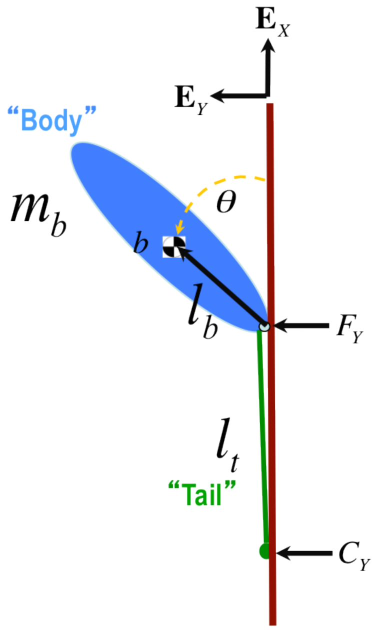

Figure 14: Free Body Diagram depicts the forces acting on the system during Peak Excursion during the Fall Arresting Response.

Body position θ corresponds to the pitch-back angle that is enclosed by the geckos’ torso and the tree trunk (Angular position over time is reflected in Figure 13).

m_b	mass of body.
l_t	is the radius of the tail or the moment arm.
F_y	Foot force component
C_y	Tail or Caudal normal force

We propose that this system can be simplified by assuming negligible friction forces from the tail and the tree (Figure 14), as well as a ridge transfer of forces through the spinal vertebrae and the axial and hypaxial musculature (Figure 14). From the video footage taken in the rainforest in South-East Asia, we observe that the geckos hind legs do not regress or slip during the landing maneuver. The forces required at the foot, ***F***, can therefore be represented as a pin joint, whereby it will exhibit a normal and a tangential component.

By contrast, compared to the gecko adhesive system in the foot gripping the tree, the friction that the smooth, large, unspecialized, subcaudal scales can generate is orders of magnitude lower and therefore negligible for the outcome of this behavior. For this reason, the tangential component of the tail contact force, **C**, is assumed to be zero and we only concern ourselves with its normal component C_y.

Table 4: Model Parameters

Property	Description
m_b	mass of body.
θ	Torso angle of rotation
l_t	Radius of tail
l_b	Radius from feet to center of mass
F_y	Foot attachment force
C_y	Tail contact center of pressure, normal component
D_y	Centripetal force and angular acceleration force

Calculations suggest that the tail contact force is the sum of deceleration of body and countering gravity as a reasonable first model for the fall-arresting response (see methods for derivation of the equation of motion). We solved for normal forces experienced by the animal at the rear leg point of attachment ***F*** (see Table 5) as expressed in equation 8:

$$F_y = ml_b\left(\ddot{\theta}cos\theta - \dot{\theta}^2 sin\theta\right) - \frac{mgl_b sin\theta - I\ddot{\theta}}{l_t} = D_y - \frac{mgl_b sin\theta - I\ddot{\theta}}{l_t} \tag{41}$$

The first linear dynamics term in equation 8 represents centripetal forces and angular acceleration forces. When the gecko's body angular position is in the region of average peak near orthogonal relative to the tree trunk the component $cos\theta$ is goes to zero. The kinematics analysis represented in Figure 13 suggest that geckos remained in a stationary period at peak pitch-back angles which coincided with the body angular velocity dropping to zero or a minimum (see Figure 13 (b)). The dynamic model predicts that when the angular velocity $\dot{\theta}$ is zero and the torso is at peak excursion, the first term containing centripetal force and tangential acceleration D_y is negligible (see equation 9). The remaining term due to the tail contact is inversely proportional to tail length. Therefore, forces experienced at the foot F_y are inversely proportional to tail length l_t which is expressed in the simplified equation 9:

$$F_y = D_y - \frac{mgl_b sin\theta - I\ddot{\theta}}{l_t} \tag{42}$$

Under these circumstances the rear foot force F_y required to keep the lizard attached to the vertical substrate would be inversely proportional to tail length. This is consistent with our findings that tailless animals fall more frequently.

This implies that animals with large tails can effectively reduce F_y required to keep the gecko attached to the tree by its rear legs as it counteracts large over-turning moments. By contrast, tailless lizards' l_t << than in lizards with intact tails. Thus it follows from the remaining term in equation (9) that larger foot forces F_y are required to ensure a successful landing in tailless geckos, potentially exceeding the critical strain of what the rear legs can sustain. According to this prediction, the consequence specifically for *H. platyurus* is that foot forces required to keep a tailless gecko attempting to land from falling off were about five times greater than those for tailed geckos. While we do not know the critical F_y or the maximum force with which the rear legs would be able to cling to the tree before becoming dislodged, it does appear that for a given landing on vertical substrate the F_y in tailless animals is more likely to exceed this threshold, thus causing the rear legs to lose foothold. This prediction from the model provides a mechanistic explanation for the function of the tail in stabilizing the landing maneuver. Moreover, it is consistent with the performance difference observed in the field whtere successful landings were found in the vast majority of trials with tailed geckos that glided to the tree (n=7) compared to 75% of catastrophic falls in tailless animals (n=4) which lost stability upon collision with the same, fell head over heels, thus, alighting on the forest floor in an uncontrolled fashion. Experiments with geckos being confronted with perturbations while running vertically revealed that they can push into the wall to counter pitch-back induced by foot slippage while tailless animals can fall head over heels (see *Chapter One,* Figure 1). Geckos with intact tails were also able to use the larger moment arm to effectively overcome even larger gaps as they exhibited the 'kickstand response' (*Chapter One*, Figure 2) that allowed recovery from dramatic pitch-back angles of up to 60°.

These results support the hypothesis that we have advanced based on field observations that tails are used as shock-absorbers to stabilize hard landings and control high impact forces acting on the limbs allowing effective perching on vertical targets at high speed.

We find that there is a low probably of recovery from a slip by a tailless gecko in comparison to a tailed gecko, since tailless geckos fell experienced catastrophic falls in 75% of trials. Results from the kinematics analysis of data collected in the field (Figure 13) appears to support the predictions from our hypothesized dynamic model (Figure 14; equations (1) to (9)) and suggests that tail-type structures provide stability and could be important to making hard landings possible. By contrast, gliding mammals (e.g. flying squirrels; Ando and Shiraishi, 1993) avoid hard landings and short glides since the steeper approach angles inhibit their ability to employ air braking by pitching up and to dissipate the high impact energy across all four limbs simultaneously (Paskins *et al*., 2007). If the animal does not have sufficient time to pitch its body up substantially for a landing with all four limbs, then peak forces acting on the forelimbs are thought to be even greater (Byrnes *et al*., 2008).

III.4 Conclusions

Geckos do not appear to use a highly controlled stall with a substantial deceleration for landing of short glides. Small size permits a simple mechanically-mediated solution for landing – a head-on collision. Considering the effect of size, a small lizard of ~4g might be able to crash-land into a tree without getting hurt whereas a ~2kg flying lemur might experience injury and damage to tissues. Tail increases landing stability by acting as a counter lever to the gecko's body weight and likely reducing foot forces. Therefore, they can use mechanically mediated solution to make landing control simpler.

Tail responses during the landing behavior of geckos could be initiated by the same reflex discovered during climbing where forefoot slippage stimulates ventral flexion of the tail (Jusufi *et al.* 2008) to provide support.

Strategies incorporating tail-assisted responses can improve the vertical landing performance and stability of both animals and robots. Landing on a wall is an emerging challenge in engineering robotics. For the design of aerial robots we can learn from nature how to solve the problem of a vertical landing situations in the face of temporary a loss of aerodynamic control. Despite aerodynamic control surfaces (airfoils), when micro-aerial vehicles pitch up, they lose control authority via Bernoulli. Here too, a three point landing can allow robots to alight safely on a vertical target (Desbiens *et al.*, 2010). Moreover, these results demonstrate feasibility of landing stability enhanced by mechanical integration as observed in unspecialized arboreal lizards and terrestrial and aerial robots, and propose that these structures could complement the heavily aerodynamically-controlled landings seen in birds.

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Chapter IV Scales Assist Scaling

Keeled, subcaudal scale arrays engage substrate during rapid vertical climbing.

Summary

To explore substrate interactions between locomotor appendages such as feet and tails, we video recorded lizards *Iguana iguana, Acanthosaurus crucigera* and *Gonocephalus grandis* as they scaled substrates of varying traction (tree bark, sandpaper, wire mesh). In addition, we observed how Forest Dragons climb trees in their natural habitats in South-East Asian tropical rainforests and Green Iguanas in Central America. Analysis revealed that lizards are continuously perturbed by natural substrata and frequently experience foot displacement. Lizards held their tail tip in constant contact with the substratum. Previously, using a force platform embedded in wall, we showed that tails pushing against the substrate can stabilize the body against overturning during rapid, vertical running (Jusufi *et al.,* 2008). The lizard species investigated here possess subcaudal scales that are keeled and therefore have the potential to anchor in the substrate. To experimentally determine whether these structures could arrest a fall to avoid climbing failure, we mounted cadaver tails from deceased lizards in a materials testing machine (Instron). We performed friction tests to determine the toughness of the subcaudal structures to a simulated fall by pulling the tail parallel to the substrate. We discovered that engagement of only one or a few caudal scales with the substrate allowed support of 1 to 2 times body weight. Preliminary experiments with lizards running on rough vertical substrata suggest that utilizing the passive attachment properties of scales increases fault tolerance from foot slippage and could significantly simplify the control of climbing unpredictable environments. Robots could increase the robustness of dynamic climbing by using keeled scale arrays on their tails.

IV.1 Introduction

Animals navigating a highly three-dimensional world must respond rapidly to gaps, obstacles and slippery surfaces to negotiate complex scansorial terrains, lest they experience predation or injury from catastrophic falls (Jurmain 1997; Nakai 2003).

Squamate tails have been implicated in aspects of horizontal locomotion, such as running velocity (Brown *et al.,* 1979; Daniels 1983; Goodman 2006), maneuverability and endurance (Chaple *et al.,* 2004). Tails can also affect jumping performance in *Anolis* lizards (Gillies *et al.,* 2009; Kuo, Gillis, and Irschick, 2012) and have also been implicated to influence mid-air body orientation (Higham *et al.* 2001). During free fall geckos and anoles have been shown to use tails as inertial appendages to reorient their bodies dorso-ventrally to recover form an upside down to a right-side up posture (*Chapter Two*; Jusufi *et al.,* 2011). Tails can also be used as a torque source for pitch-control during running and leaping in agamas (Libby *et al*., 2012).

We tested the hypothesis that active tail use can increase stability during rapid vertical running on challenging terrain (*see Chapter One*). Having found that active tail responses are used in geckos *H. platyurus* prevent pitch-back and falls in the face of single foot slippage to push off the substrate when footholds are perturbed during rapid running, I sought to explore whether these active tail responses are used in other taxa of arboreal lizards as well, and how wide-spread the behavior might be. One promising indicator of tail use in other lizard taxa would be the presence of traction-enhancing features in the caudal region.

To enhance traction during arboreal locomotion on irregular and unpredictable terrain, numerous squamate taxa also exhibit specialized morphological features, such as claws and adhesive pads (e.g. Russell 1975; Bloch and Irschick, 2004). Limbless squamates, can utilize their flexible and elongated ventral scales to help engage the substrate with (e.g. Hu *et al*., 2009) and ultimately for traversing horizontal terrain and inclines in conjunction with their hypaxial and axial musculature. In addition, snakes can also utilize keeled scales to assist in digging (Mosauer, 1932) in conjunction with side-to-side movement of the body.

There exists remarkable diversity in reptilian scales. For example, variation in scale numbers has been proposed to effect how natural selection acts on squamate taxa in an inter- and conspecific context (e.g. Calsberg, Knouft, and Smith, 2006).

When it comes to traction enhancing structures on tails, promising morphological features have been identified in form of fibrillar adhesives on the tails geckos in the genus *Phelsuma* (Hiller, 1968) and *Rhacodactylus* (Bauer, 1992), but their roles in the whole-body climbing dynamics of the relevant species are under-explored.

To get a sense of the relevance of active tail use as an integral aspect of the rapid arboreal locomotion in squamates, I sought to study arboreal lizards that are not closely related to Geckos and that do not possess adhesive feet. *Acanthosaurus crucigera, Gonocephalus grandis and Iguana iguana.*were sampled initially for subcaudal morphological specializations. Next, microscopy was performed, which was followed by materials testing of scales using an Instron Materials testing machine. And finally, the lizards were run on vertical trackways to explore whether rapid scaling of rough terrains, such as tree bark or rock outcrops, could be assisted by specializations in spine-like scale structures that could have a traction generating function and may enhance stability.

IV.2.1 Microscopy and Materials Testing Machine

Microscopy was performed without damaging specimens from the Museum of Vertebrate Zoology at the University of California, Berkeley. Magnification of 10x to 50x revealed the morphological features of the subcaudal scales. Photographs were taken from the microscopy for comparison of morphology.

Measurements of single scale peak force were performed using a standard Instron Materials Testing Machine (Type 5544). Experiments were carried out at an average temperature of 23.7° Celsius ±2.1° in the lab where the Instron machine was located. We performed standard extension to failure tests to measure peak forces that a single scale could sustain. Specimens of preserved tails were obtained from deceased lizards. They were mounted, rigidly clamped, to a V-shaped beam that was bolted to the base of the machine, ensuring no movement. The upper head of the Instron apparatus containing the load cell was responsible for the linear extension. A thin rod with a spatula tip of 2mm was mounted to securely clamped onto it (see Figure 15). As it engaged one individual scale in a typical trial, we measured a distinct increase of from 0 to 1 N with which the scale resisted the linear extension imparted on it by the Instron until peak force was reached.

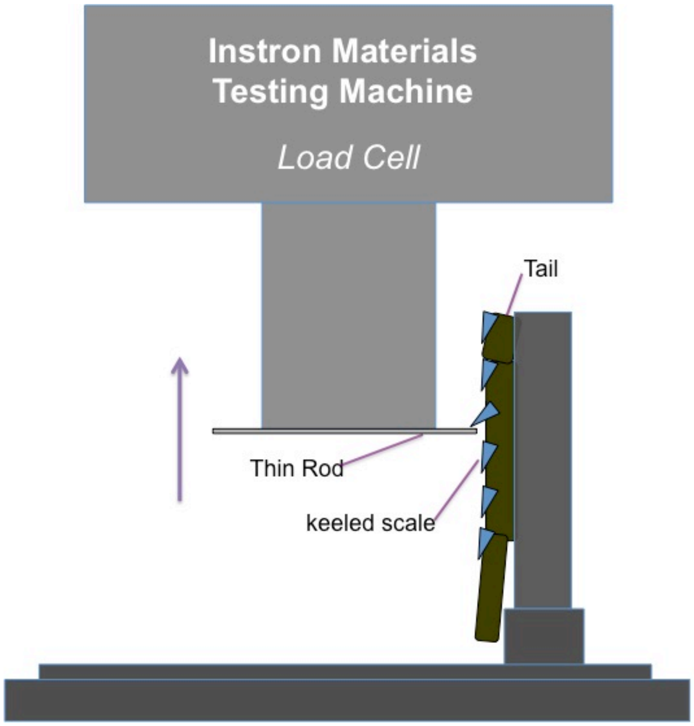

Figure 15. Sketch represents the Experimental Design with preserved tail preparate mounted in the Instron Materials Testing Machine. Specimens were rigidly clamped to a beam that was bolted to the base to ensure that it was not moving. The upper head of the Instron performs the continuous linear extension upwards thereby engaging just one keeled subcaudal scale via a spatula mounted on a thin rod. Not drawn to scale.

IV.2.2 Climbing Experiments

Green Iguanas *Iguana iguana,* as well as the Mountain Horned Dragons *Acanthosaurus crucigera* and *Gonocephalus grandis* were purchased from a commercial vendor California Zoological Supply, Los Angeles, CA, USA, and The Reptile Company, Endicott, NY, USA.

They were housed in an animal care facility with a 12 hour light cycle per day. Special consideration was taken for the Mountain Horned Dragons to ensure they have adequate temperature and high humidity, and flowing water was provided, according to observations form habitat in the field, and it was found to be important to keep them in good health. We performed locomotion experiments of climbing on vertical trackways with these lizards. The trackways (e.g. mesh similar to cages) provided asperities for the claws to engage and traction to rapidly climb. Vertical perches were placed in the animals cages. Mountain Horned Dragons were fed crickets dusted with vitamins and minerals and iguanas were also fed fresh vegetables.

IV.3 Results and Discussion

IV.3.1 Microscopy and Materials Testing Machine

Previous studies of the material properties of biological tissues and their mechanical behavior, such as determination of fracture properties of disassociated fingernails (Farren, Shayler, and Ennos, 2003), stress the importance of differential strength based on the direction from which the force is applied. In this spirit, our examination is based on direct observations of behaviors relevant to the ecology of the animal.

We have gained new insight on rapid scaling of challenging terrains assisted by specializations in traction generating appendages that could enhance stability via distributed mechanical feedback. Based on initial observations from the field, which revealed how Mountain Horned Dragons, such as *Acanthosaurus crucigera* climb trees in their natural habitats in South-East Asian lowland tropical rainforest, we carried out microscopy, laboratory experiments with trackways involving wire mesh and slippery substrata using high-speed videography, as well as materials testing of the mechanical properties of the tails in question.

The presence of specialized morphological features for enhanced interaction with the substrate is a possible indicator for locomotor function of tails in lizard taxa. Investigation of tail function in geckos using both kinematics and force platform measurements had tested the hypothesis that tails increase stability during obstacle negotiation in rapid climbing (see Chapter One). Using sandpaper to model rough substrata animals might encounter in their natural habitat such as rough tree bark, I first performed simple friction tests (see Figure 16) with tails from live animals.

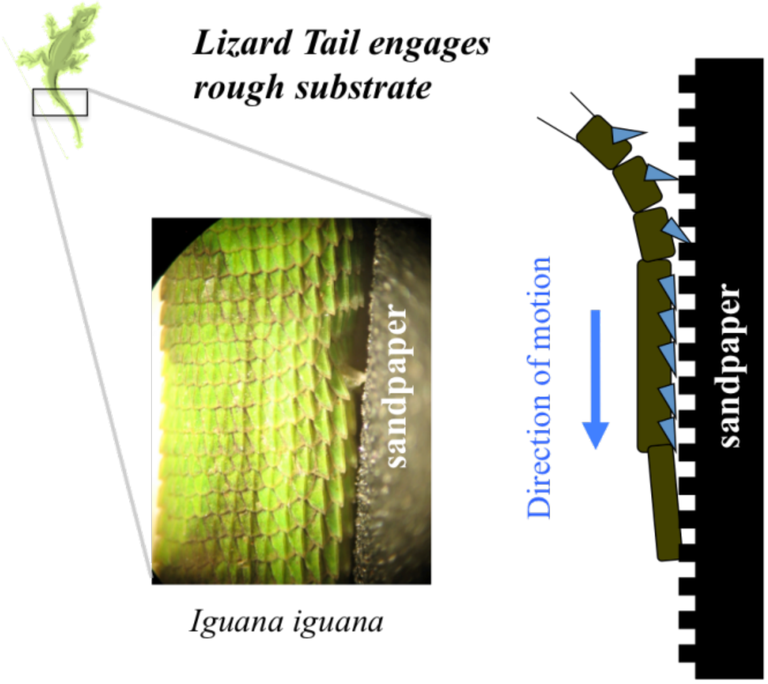

Figure 16: Morphological features interlock with substrate asperities. *Iguana iguana* subcaudal scale engages with sandpaper. Friction tests were performed to determine whether these subcaudal structures do engage when in contact with a rough substrate and if they could potentially sustain forces relevant to a simulated fall by pulling the tail parallel to the substrate.

Although it was found that multiple scales can indeed engage and exhibit directionality by resisting movement in the animal's caudal direction, these initial tests were not continued because it was not possible to reliably tell the number of scales which were engaged with a multitude of asperities. To experimentally address the question whether these structures could arrest a fall to avoid climbing failure, we mounted cadaver tails from deceased lizards in a materials testing machine (Instron).

I found that some arboreal lizard species possess subcaudal scales that are keeled and therefore have the potential to anchor in the substrate. To explore whether other squamate taxa might also use their tails in a locomotion capacity I examined specimens from the collections of the Museum of Vertebrate Zoology located at the University of California Berkeley under the microscope.

Microscopy revealed that highly arboreal species of Mountain Horned Dragon, *A.crucigera* possess large keeled, subcaudal scales with directional properties (Figure 17).

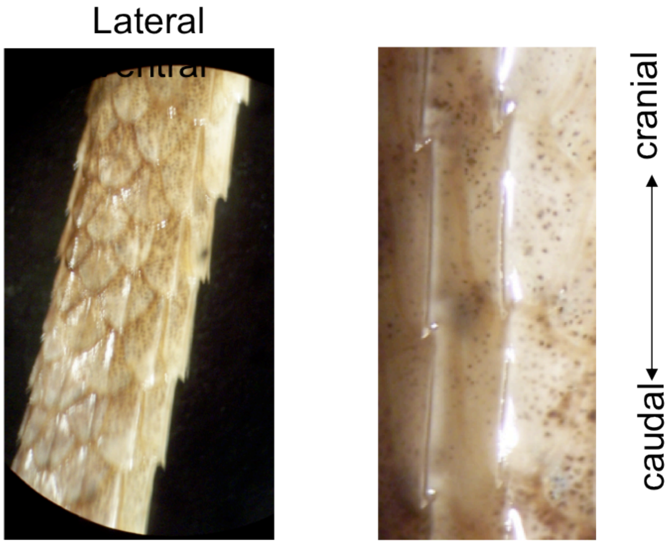

Figure 17: Mountain Horned Dragon tail with subcaudal keeled scales. Microscopy revealed keeled subcaudal scales in contrast to doral and lateral scales that were more smooth.

Because of their cranio-caudal orientation, we hypothesized that they could collapse onto themselves if the tail is pressed against the surface to reduce friction, thus allowing continuous tail contact during climbing (see Figure 17).

More importantly, these keeled scales could contribute an attachment point by interlocking with the substrate. Photographs taken in the field (Figure 18) of *G. grandis* revealed the largest, macroscopically visible spines yet.

Following up on this initial microscopy work, we sought to test the hypothesis that keeled, specialized subcaudal scales could anchor in the substrate. To experimentally determine whether these structures could arrest a fall to avoid climbing failure, we mounted the tails from preserved lizard specimens in a materials testing machine (Instron). We performed friction tests to determine the single scale peak forces associated with a simulated fall by pulling the tail parallel to the substrate.

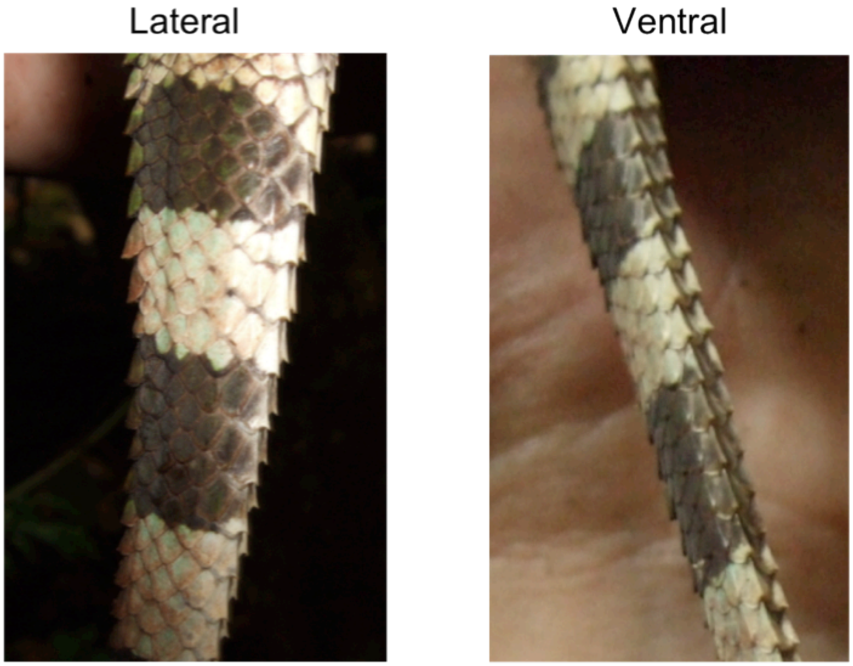

Figure 18: Photos of macroscopic keeled spines. Lateral and ventral view of subcaudal scale rows**.** Scales appear to be bent towards the substrate.

We employed a comparative approach, in which repeated tests are performed to study the peak forces generated by individual scales in a multiple species from several specimens. This experiment could be considered as a simulation of a lizard experiencing locomotor failure while running in the wild and falling head over heels whereby the tail could be dragged parallel to the substrate, and complements the work with live lizard locomotion.

Mounting the tails from the arboreal *Acanothosauraus crucigera*, in a materials testing machine (Instron) we carried out friction tests in order to measure the single scale peak forces (Figure 19) that scales could sustain when engaged.

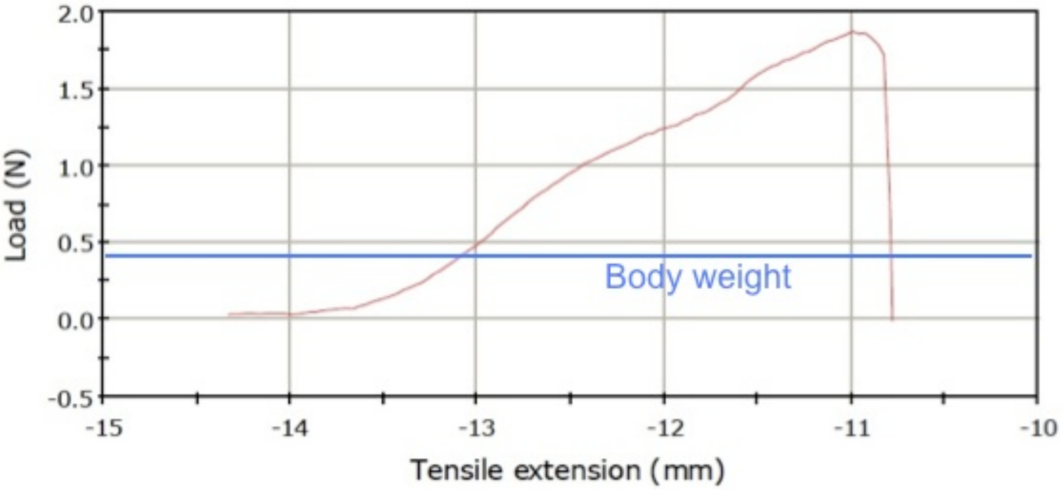

Figure 19: Measurement of single peak force in Mountain Horned Dragon *Acanthosaurus crucigera*. One scale is engaged with a spatula in an Instron materials testing machine in order to perform a linear extension until failure test. It takes about 1mm of extension before the scale develops force comparable to body weight an another 2mm before it reaches peak force. We measured a peak force of 1.7 N in an experiment carried out with proximal individual keeled scales *Acanthosaurus crucigera* with a body mass of 38.85g.

We can see in Figure 19 that as the spatula is linearly extended it was at first not engaged with the scale in the the preparete, thus covering a short distance in which the load was zero until contact was established after which the scale pushed back on the device, thereby resisting the motion in proximal direction (toward tail base) or cranial direction (whole animal perspective).

The average peak forces measured in three scales yielded 1.97 N ±0.22 in *Acanthosaurus crucigera.* It an sustain forces above body weight for over 2mm of extension and the entire linear extention to failure trial typically extends to a total of 3mm.

Based on preliminary experiments with *Acanthosaurus crucigera* we estimate that proximal individual keeled scales could sustain approximately four to five times body weight. Such a large safety factor would allow for compensation of larger than expected overturning moments as a function of gravity, as is the case when carrying prey or overcoming obstacles. Therefore utilizing the passive attachment properties of scales could increase lizards fault tolerance from foot slippage and could significantly simplify the control of climbing.

We find that while the peak force sustained by *G.grandis* (3.5 to 7x body weight) and *Acanthosaurus crucigera* (4 to 5x body weight) are comparable, the behavior of the scales in response to linear extension appears to be different.

Comparing the force profile between species, we find that as soon as the spatula engages a scale in *G.grandis* we measure that force is developed very rapidly and reaches a peak before breaking. This can occur within just one millimeter of extension by the spatula, which is shorter than the length of the scale.

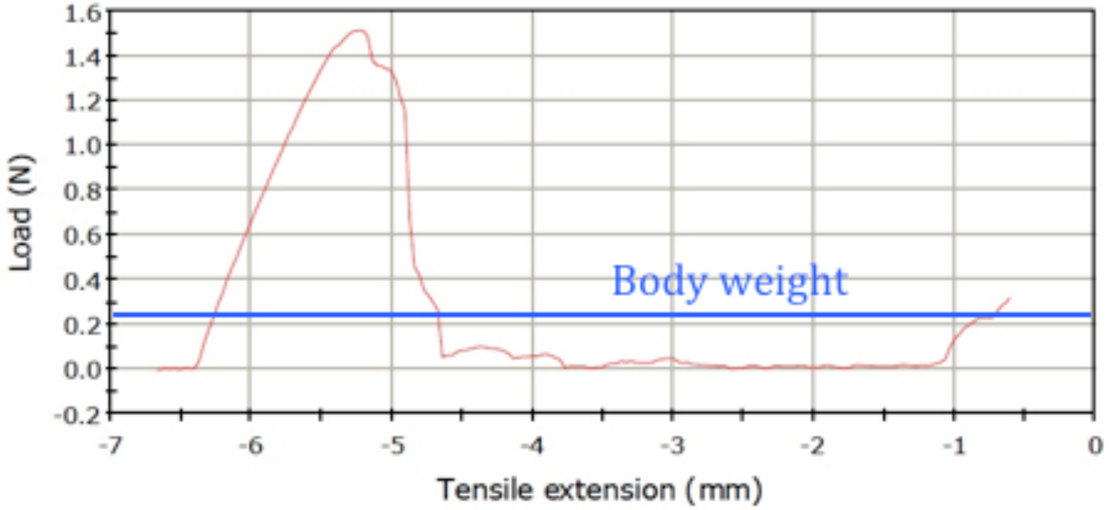

Figure 20: Single scale capability in *G. grandis* exceeds body weight. A large subcaudal, keeled scale in the proximal tail base is engaged. The peak force of 1.52 N is attained by extending by a distance of 1.25 mm. A further extension of just 0.6 mm causes the line drop off to near 0 N.

We can see in Figure 20 that force was developed very rapidly by the large, subcaudal scales near *G. grandis* tail base. Forces exceeding the animal's body weight within an extension of just 0.2mm. Peak forces are developed by extending another 1.2mm beyond that. Although these scales are larger, these peak forces are observed in less than half the distance extended in *A. crucigera* as shown in Figure 19 suggesting that scales in *G.grandis* could be more robust and stiffer structures not just in relative but also in absolute terms. The drop off from peak to zero occurs within 0.5mm from the peak force measured here. The average peak forces measured in *G. grandis* across five proximal scales was approximately 1.53 N ±0.22. While the lineare extension to failure profile extends to a total of 2mm. It's scales are able to sustain forces above body weight for an extension of circa 1.5mm.

By contrast, as we can see in Figure 19 with the equivalent test in *A. crucigera*, where the scale could be extended up to 3 millimeters before breaking. Forces above body weight appear to be sustained over a larger extenion. These scales appear to be more flexible. If the tail base was assumed to be identical, then these initial measurements suggest that the scales of *Acanthasaurus crucigera* could potentially allo greater pitch-back angles relative to the tree trunk. This could have advantages during stationkeeping, as the lizard's flexible scales would potentially allow the lizard to lean out further and extend its torso further away from the tree trunk. This could allow for a greater preview distance along the tree trunk. Having the capability to be 'elevated' from the substrate may be advantageous for spotting conspecifics, or potential predators earlier. By contrast, being able to sustain larger loads several times your body weight bay be advantageous for carrying food, or fighting or other interactions. It is not immediately obvious which animal would be more robust to rejecting perturbations, though it does appear that the kickstand response to perturbations and obstacles would be larger *in A. crucigera*. Moreover, allowing the animal to pitch back further during and could potentially provide better amortization in response to abrupt falls from the animal during cyclic behaviors such as rapid vertical running.

Lizards have smaller scales at the distal tail tip with the scale size increasing along the tail in proximal direction. Proximal tail portion in contact *G. grandis* with body mass 23g as Figure 21 shows.

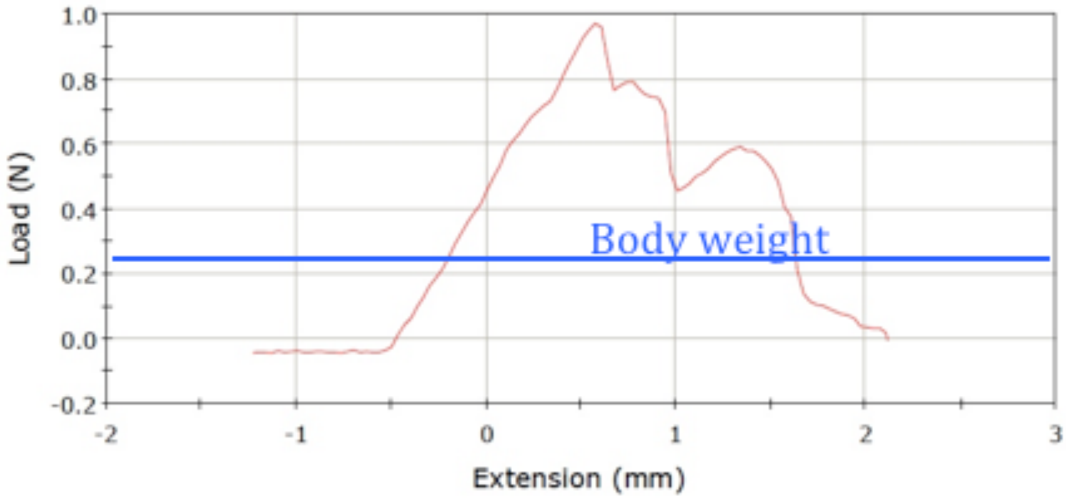

Figure 21: Distal tail portion spines in contact extension to failure test. A keeled, subcaudal scale in the distal tail portion of a *G. grandis* tail is tested here. The line of force over extension is approximately at zero before the spatula engages with the scale at -0.5mm extension when the force rapidly increases to positive values, exceeding body weight within an extension of just 0.3mm. Peak force recorded was 0.97 N. The load remained above body weight for an extension of nearly 2mm.

Larger, distal keeled scales (see Figure 21) support peak forces that appear to be by approximately 30% higher when compared to smaller, more distal scales. The number of asperities available increases inversely with radius (Asbeck *et al.,* 2006). Different sized scales could be used for different purposes and make accessible a number of terrains of varying roughness. Proximal scales may be more for stationkeeping while distal tail tip is in contact during rapid tree running and obstacle negotiation where the radius is larger.

The safety factor well exceeds body weight in *A. crucigera.* as is also the case with *G. grandis*. It is possible that engagement of just one or a few of these scales allow these lizard species to carry additional loads such as prey or other items. Preview distance could also be enhanced by allowing the animals to lean back on the rear legs and tail in order to observe terrain located ahead or behind the animal.

It is important to consider that the measurement of the force that scales are capable of sustaining can be influenced by several factors, including and not limited to: Selecting the correct orientation of the specimen and selecting the appropriate direction from which the force is applied (e.g. Farren, Shayler, and Ennos, 2003) such that it is relevant to the biological hypothesis to be tested. More specifically in this case, the caudal anatomy of the model system (e.g. how the scale to be tested is anchored to the appendage and whether scales are embedded in an overlapping array); the state of preservation that the scales are in; the developmental state of the animal (juvenile vs adult); shedding cycles for scales; variations in body weight; and terrains on which they were utilized prior to being subjected to further damage during materials testing. All this in addition to experimental conditions such as temperature and humidity at the time of the materials test can have a large effect on the measurements and experimental outcomes (Farren *et al.,* 2009).

Nevertheless the initial preliminary experiments in this study suggest feasibility for the scales potentially being capable of sustaining forces relevant to behaviors that are relevant to the lizard in it's arboreal lifestyle, such as station-keeping while perched on the tree trunk against gravity in an efficient posture, or perhaps more importantly preventing overturning during rapid climbing on the tree trunk at large heights above ground. Future work will likely identify more variables.

Therefore utilizing the passive attachment and interlocking properties of subcaudal keeled scales could increase these highly arboreal lizards' fault tolerance from foot slippage and could significantly simplify the control of dynamic climbing.

IV.3.2 Climbing Experiments

Having found that the highly arboreal lizards keeled subcaudal scales have the potential to stabilize locomotion, we sought to test that in lizards climbing experiments.

We found that the lizards possess keeled, subcaudal scales (Figure 22) and could provide an additional point of attachment in the substrate. We tested experimentally if lizards employ these structures in real running.

We measured the rapid vertical running performance of lizards that are highly adapted for arboreal terrains. Nevertheless their appendages are still continuously perturbed by natural substrata such as tree bark where I observed continuous small foot slippage.

We hypothesized that these structures, in and of themselves, could generate sufficient force to sustain the body weight in more than one species and potentially arrest a fall. In a live locomotion test we covered the subcaudal scales in the tail region of the lizards with a flexible material to prevent them from engaging with the substrate. We ran the animals on a rough substrate that was made of wire mesh where in which claws could engage.

In this spirit, we measured perturbation response mechanisms employed by Mountain Horned Dragons *A. crucigera* during locomotion by using obstacles and surfaces of varying probability of contact (e.g. mesh) or traction (e.g. slippery surfaces).

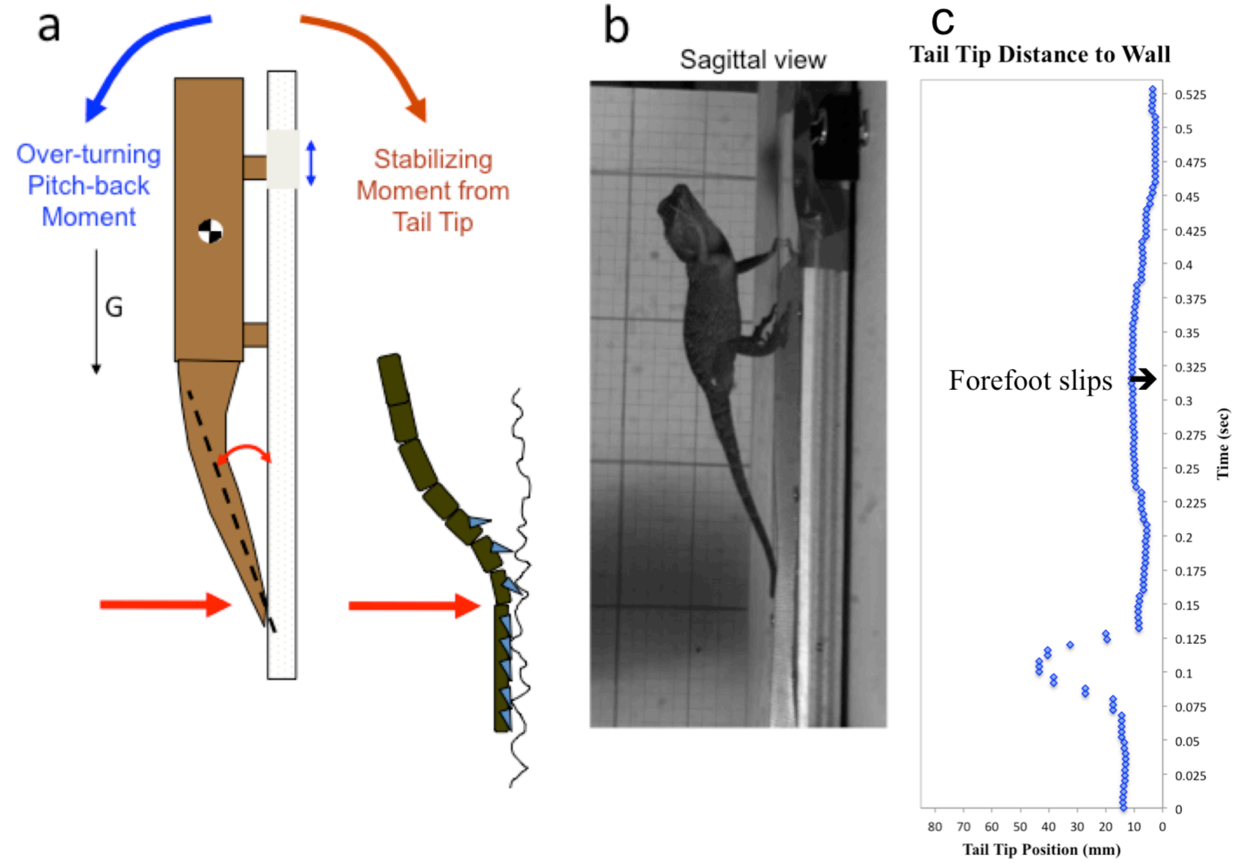

Figure 22: Climbing experiments with *Acanthasaurus crucigera*. Model representation (a) of moments acting on the lizard encountering a perturbation while climbing rapidly (b) with tail and possessing subcaudal rows of keeled scales engaged on the substrate as depicted on the inset. High-speed videography of Mountain Horned Dragons *Acanthasaurus crucigera* preventing extreme pitch back by pushing the tail into the substrate as it runs up on perforated aluminum mesh when it encounters a slippery patch. (c) Tail tip trajectory in representative lizard trial as a function of time shows that the tail is is in contact with the wall after in response to forefoot slippage (b).

We ran lizards on a vertical trackway of wire mesh which models natural substrates in terms of small contact area and few asperities (Figure 22 (a)). The three lizards used for climbing experiments had an average snout-vent length of 12.7 cm ±0.9cm and a body mass of 60gram ±5). We observed that the lizard does not fall off after being confronted with a perturbation when the tail is intact (see Figure 22 (a), (b)). Climbing kinematics revealed that lizards held their tail tip in constant contact with the substratum (Figure 22 (b)) When forefeet were perturbed with a slippery patch (Figure 22 (c)) they appeared to lean back on the tail to a greater extent. In experiments described in *Chapter One* we had embedded a force platform in a vertical wall trackway and we showed that tails pushing against the substrate can stabilize the body against overturning during rapid, vertical running (see Figure 1).

Next, we performed a preliminary experiment in which we not only confronted the lizards with the aforementioned trackway, but also wrapped their tails with sheer bandages (Brand CVS Pharmacy (sterile) Sheer Bandages), thus still permitting tail contact but greatly reducing the friction.

When confronted with a perturbation to their fore legs during rapid vertical running (n=3), we found that lizards with blocked scales attempted to push the tail into the wire mesh but had difficulty to remain attached to wall and fell off the wall. By contrast, in the control experiment in which lizards were unrestrained (n = 5) they used their tails to push down on the substrate and engage with the subcaudal region (Figure 22 (b), (c)), potentially interlocking with the asperities of the substrate thus preventing falls. Considering that the number of asperities available increases inversely with radius (Asbeck *et al.,* 2006) the relatively smaller scales of *Acanthasaurus crucigera* may be advantageous in that they could allow these lizards to climb smoother surfaces in addition to rough ones. Their being less rigid could also allow them to tolerate greater pitch-back angles providing greater support as they traverse obstacles, slippery surfaces and discontinuous terrain (e.g. branches in the forest canopy).

Previously, we found that when geckos were confronted with large, repeated slips they tolerated pitch-back by placing their tail in a posture where the tail was pressed against the wall similar to that of a bicycle's kickstand (Jusufi *et al.* 2008). *Acantahsaurus crucigera* appeard to utilize a very similar behavior. We observed that while in captivity the lizards could engage their scales in their cage walls made of wire mesh. This could allow for a fairly convenient method of station-keeping or maintaining upright posture on a vertical surfaces that could potentially require different muscle groups to be recruited, or a smaller number thereof, than if the animal had smooth subcaudal scales.

IV.4 Conclusions

The orientation and characteristics of morphological features supports the hypothesis that tails could assist locomotion. Preliminary measurements of force capability suggests that keeled, subcaudal scales can support several times body weight in three species of arboreal lizards. Lizards running on rough terrain keep the tail in contact with the ground and could utilize such subcaudal structures in dynamic climbing. Morphological specializations such as keeled scale array structures could simplify the control of rapid climbing in multiple lizard taxa by providing distributed mechanical feedback (Spagna *et al.,* 2007). Experimental manipulations to understand the relative roles of specialized traction enhancing structures (e.g. change in surface area of the body) are now required in a comparative context. Analogous self-locking mechanisms could benefit the performance of bio-inspired robots scaling uneven terrain (Asbeck *et al.,* 2006), increasing the robustness of dynamic climbing by using keeled scale arrays on their tails.

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Chapter V Synthesis and Concluding Remarks

V.1 General Conclusions

Numerous studies on caudal autotomy have been performed in lizards (e.g. Bateman and Fleming 2009) with focus on the obvious function of predator-avoidance but also associated locomotor costs. Tails were not primarily seen as appendages that are critical to several modes of locomotion. The results presented in each of the above chapters, however, suggest that tails are critical appendages that are integral to transitions in several modes of locomotion necessary (Jusufi *et al.,* 2011) for the successful and dynamic navigation of complex, changing and ultimately unpredictable terrain. Tails provide stability and allow lizards to reject perturbations such as obstacles, slippery surfaces, discontinuous perches that abound in their natural habitats. Animals depend on a behavioral repertoire of perturbations response mechanisms for traversing dense arboreal habitats requires such as rapid running (Libby *et al.*, 2012), jumping (Gillis *et al.*, 2009), leaping, mid-air righting (Jusufi *et al.*, 2011), and turning during gliding (Jusufi *et al.*, 2010) and landing on vertical targets, all of which depend on dynamic tail responses.

Despite the important locomotor function of the caudal appendage for lizards demonstrated in this work, we must remind ourselves that the tail shapes present in extant taxa do not necessarily allow us to directly infer that these shapes are optimal in their mass distribution for a particular task. For one reason, of all the tail shapes that an optimality parameter sweep would yield, we would expect different task-dependent shapes and distributions of mass for inertial appendages, if we consider what tail morphologies are expressed in extant taxa are constrained to a to a subset of phenotypes by evolutionary history. Perhaps more importantly, selection pressures of multiple kinds are at work to determine the length, shape and mass distribution of tails. For example, extrapolating from *Chapter II*, where several advantages with respect to tail-induced change of body attitude are associated with the larger tails of *Anolis*, one might be tempted to say that based on moment of inertia considerations tails could be made double or triple their length. However, there could well be disadvantages associated with very long tails, such as providing predators with a large area upon which to focus pursuit (e.g. prosimians) or getting entangled in very dense arboreal habitats (Peters and Preuschoft, 1984; Günther *et al*., 1991). Heavily ossified structures in slow cursorial dinosaurs could indeed have limited maneuverability (Carrier *et al.*, 2001).

V.2 Outlook and Applications

This work proposes that active tails enable effective transitions in difficult locomotion tasks, both as appendages that work a a "fifth leg" directly pushing into the substrate in rapid wall running of geckos and RiSE (Jusufi *et al.* 2008), as well as inertial appendages that facilitate mid-air reorientation in geckos and RightingBot (Jusufi *et al.* 2010). We have also advanced the proposition that they play an important role in pitch control of more cursorial lizards during running on discontinuous terrains and in a tailed robot car TailBot (see Libby *et al.*, 2012).

There is great potential for design of multi-modal robots inspired by this work, and we have already seen transfer and increasing activity in this area of experimental robotics in recent years. We must remind ourselves that although critical functions of tails will continue to be found in the control and mechanics of vertebrate locomotion, the transfer of these capabilities in terms of to human-made locomotion devices could have more effective solutions for redistribution of mass that are better suited for a particular task at hand.

V.3 Literature cited

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