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Function, Morphology, and Evolution of Gecko Locomotion: The Importance of Ecology and Substrate

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Function, Morphology, and Evolution of Gecko Locomotion: The Importance of Ecology and Substrate

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

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in

Evolution, Ecology, & Organismal Biology

by

Emily R. Naylor

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ABSTRACT OF THE DISSERTATION

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by

Emily R. Naylor

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Locomotion is a central tenet of life for many organisms that is inherently tied to the surrounding physical environment. Geckos represent a speciose and phenotypically diverse clade of lizards that are found within many habitats and move on a variety of substrates. Although much is now known about the integration and mechanics of the highly adept frictional adhesive toe pads from intensive laboratory study within model species, the functional and evolutionary significance of phenotypic diversity within geckos is ripe for investigation. This dissertation thus brings ecological context to the foreground to begin to address this large gap. In Chapter 1, we collected field observations and locomotor trials of surface compliance transitions in a cursorial day gecko, *Rhoptropus afer*, to examine how this species responds to sudden changes in substrate conditions encountered in nature. This species maintained high-speed running while altering its posture and stance time when transitioning into and out of sand collected from its habitat. In Chapter 2, we used experimental claw manipulation (i.e., partial removal) in the arboreal species, *Thecadactylus rapicauda*, to assess the functional interplay of adhesive toe pads and claws on natural and artificial surfaces of different roughness. After partial claw removal, static clinging

performance significantly declined on non-smooth surfaces, and geckos tended to adjust their foot kinematics to increase contact duration on smooth and rough surfaces at both horizontal and low incline, although their ability to accelerate from a stationary position was not significantly altered. Finally, in Chapter 3, we took a phylogenetic comparative approach (112 gecko species) to test if morphological variation in toe pads and claws represents adaptive evolution to general habitat use. We found that species using more scansorial habitats tended to have larger, longer pads and more curved claws, with saxicolous species having longer setae than all other groups.

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INTRODUCTION

For many organisms, to exist is to move, as fitness often demands the active pursuit of food and mates, the defense of territory, and/or avoidance of predation and other threats (Darwin 1859; Biewener 2003). Elucidating how organisms move successfully within their environments requires an understanding of multiple levels of integrated traits that comprise the emergent whole-organism phenotype (Dickinson et al. 2000; Garland and Kelly 2006).

At the upper end of this hierarchy of biological organization, morphology and functional properties underly performance (i.e., an organism's capacity to do something), which in turn shapes behavior (i.e., "what an animal actually does" in nature); selection acts most directly upon behavior to determine fitness (Arnold 1983; Garland 1994; Garland and Losos 1994). Along with biotic interactions, the abiotic environment can impose strong selective pressures on behavior, as well as on performance and functional traits (Simpson 1953; Garland and Losos 1994). In many cases the surrounding air, water, or land that an organism intimately interacts with (i.e., substrate) can challenge propulsion and/or station holding, thus driving phenotypic modifications for more effective navigation of the environment (Moody et al. 2015; Donihue et al. 2018; Dufour et al. 2019).

Geckos are a diverse and speciose clade of lizards found within a variety of habitats, including forest canopies, boulder fields, and sandy deserts (Vitt and Caldwell 2013; Uetz et al. 2020) and display an array of limb and autopodial morphologies that are linked (putatively in many cases) with their particular environments (Bauer et al. 1996; Zhuang et al. 2019). Some geckos are primarily ground-dwelling, but many are scansorial and able to cling and climb on a variety of surface textures and orientations (Russell 2002; Autumn et al. 2014). While most species bear digital claws, this attachment ability has been credited more to their highly integrated frictional adhesive toe pads, which generate intermolecular and frictional adhesive force between microscopic hairs of the ventral toes and a surface (Ruibal and Ernst 1965; Russell 2002; Autumn 2006).

This attachment apparatus has garnered decades of investigation from both engineering and biological perspectives (Autumn et al. 2014; Niewiarowski et al. 2016; Russell et al. 2019), elucidating its microstructural and mechanistic basis (e.g., Ruibal and Ernst 1965; Russell 1975; Autumn et al. 2000; Autumn and Peattie 2002; Russell 2002; Autumn 2006) and aspects of gecko evolutionary morphology (Gamble et al. 2012; Higham et al. 2015; Russell et al. 2015; Russell and Gamble 2019). However, our knowledge base of gecko attachment and locomotor is still largely comprised of studies on isolated aspects of morphology and performance measured under optimal laboratory conditions, and within only a few model species. Much remains to be understood regarding the functional significance of digital morphological diversity, including the functional relationship between toe pads and claws (Autumn et al. 2014; Bauer 2019; Russell and Gamble 2019). Moreover, how geckos move and use substrates within their natural habitats is extremely understudied, despite the necessity of this information to fully understand how selection has and continues to act on gecko attachment and locomotion (Higham and Russell 2010; Niewiarowski et al. 2016; Higham et al. 2019). This dissertation attempts to begin addressing these gaps through a combination of performance and behavioral experiments on wild geckos under different substrate conditions and phylogenetic morphological comparisons with respect to habitat use.

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CHAPTER 1

Impacts of substrate compliance transitions on locomotion in a cursorial gecko (*Rhoptropus afer*)

Abstract

Animal movement is often largely determined by abiotic conditions of the environment, including substrate. While a large body of work has improved our understanding of how different substrate properties can impact locomotor performance and behavior, few of these studies have investigated this relationship during a single locomotor event. In nature, terrestrial animals are likely to encounter substrate transitions, or changes in substrate level, incline, texture, and/or compliance during a single bout of movement, which occur suddenly for high-speed animals. High-speed animals often adjust their posture and kinematics during transitions, and in some cases also lose forward velocity. We examined the occurrence and effect of non-elastic compliance transitions in *Rhoptropus afer*, a cursorial day gecko known for its ability to sprint rapidly for several meters at a time when evading a threat. In addition to collecting field observations of substrate use, we conducted locomotor trials on a level trackway featuring a transition into and out of sand, as well as a on a solid trackway. During escapes from an approaching simulated predator, *R. afer* appeared to use substrates of different compliance and transitioned to and from more compliant surfaces fairly equally. Sprint speed was not affected by acute changes in compliance, which was likely facilitated by an increased body angle and duty factor upon entering the sand. Further study is needed to determine if these alterations represent an active behavioral strategy versus a passive mechanical response, as well as the actual deformability of sand relative to the ground reaction forces produced by this species. This study provides important insight as to how geckos and other animals accommodate natural, often heterogeneous, substrate conditions during critical locomotor events.

Introduction

An organism's capacity and propensity to move (or not move) is tied to the intrinsic properties of the media with which it interacts, such as water temperature (Fry and Hart 1948), airflow turbulence (Combes and Dudley 2009), or perch diameter (Losos and Sinervo 1989). A multitude of studies have demonstrated the significance of substrate properties with respect to locomotion and/or attachment, as well as ways in which animals respond to challenging conditions, such as low-friction (Wheatley et al. 2018) or rough surfaces (Crawford et al. 2016). However, most studies have examined these relationships by evaluating one or more performance or behavioral traits under discrete sets of substrate conditions. Far fewer studies have examined how organisms respond to variable substrate properties within a single locomotor event, a scenario that likely occurs frequently in nature, particularly for terrestrial animals found in what are often complex and heterogenous habitats (Dickinson et al. 2000; Higham et al. 2019).

A locomotor perturbation, or a sudden disturbance in motion, can be caused by a substrate transition, which we define broadly as a change in mechanical substrate properties along the path of movement during a locomotor event. Transitions by this definition include (but are not limited to) obstacles (i.e., physical barriers within the locomotor path) or other changes in substrate level, as well as changes in incline, texture (e.g., friction), and compliance (see Full et al. 2002; Jindrich and Full 2002; Daley 2008),

Locomotor perturbations, including those induced by transitions, are best studied in fast-running animals. For example, guinea fowl are able to avoid falling and continue their pattern and trajectory of motion after experiencing an unexpected drop in substrate height and loss of friction during running (i.e., maintain dynamic stability) by altering their limb posture, angle of contact, and center of mass (Daley et al. 2006; Clark and Higham 2011). In terms of obstacle negotiation, many lizards elevate the head and trunk when approaching a barrier, thus shifting their center of mass over the hindlimbs (particularly in bipedal gaits), which provides greater propulsive force for quickly clearing the obstacle (Kohlsdorf and Biewener 2006; Parker and McBrayer 2016); this response is accompanied by a loss in forward velocity for some lizards (e.g., *Sceloporus malachiticus*; Kohlsdorf and Biewener 2006) but not others (e.g., *Aspidoscelis sexlineata*, Olberding et al. 2012; *S. woodi*, Parker and McBrayer 2016).

Compliant surfaces incur greater mechanical energetic costs to locomotion, as the limbs must do more work to generate propulsive force (Lejeune et al. 1998; Li et al. 2012). Many animals that move on sand and other deformable surfaces exhibit morphological specializations of the autopodia to prevent sinking, such as toe fringes seen in sand (e.g., *Uma*; Carothers 1986) and aquatic specialist lizards (e.g., *Basiliscus*; Laerm 1973). Body and limb posture can also be altered to maximize force generation, namely through aligning the limb elements beneath the center of mass (Biewener 1989), as seen in basilisk lizards running on a compliant liquid surface versus a solid one (Laerm 1973; Hsieh 2003); while it has not been directly examined, rapid kinematic adjustments likely occur when these lizards transition between water and land.

Some animals appear to avoid a reduction in velocity and acceleration when locomoting over a compliant substrate. For example, neither *Callisaurus draconoides* or *Uma scoparia* exhibited performance differences when sprinting on packed wash sand versus fine dune sand (Korff and McHenry 2011). Moreover, cockroaches maintained running speed and step frequency while running between artificial rigid and elastic surfaces by lowering their body to shorten stride swing time, as well as by sustaining multi-limb contact and propulsive force production (also aided by the elastic properties of the surface; Spence et al. 2010). Studies of actual compliance transitions centered around ecologically relevant conditions, however, are very limited.

We explored the effects of non-elastic compliance transitions within *Rhoptropus afer*, the Namib Day Gecko (Peters 1869), a well-known species among gekkonids for its unique cursorial morphology (i.e., elongated hindlimb elements (Bauer et al. 1996; Johnson et al. 2005), high running performance, and ecology. Unlike its scansorial congeners, *R. afer* occupies open and low incline rocky habitats, and when provoked, can run continuously for several meters at a time at upward speeds of 3 meter per second (Odendaal 1979; Lamb and Bauer 2006; Higham and Russell 2010; Collins et al. 2015). Moreover, we know from previous work that *R. afer* habitats are structurally heterogeneous (i.e., variable incline and "rockiness") and that incline not only impacts sprint speed performance, but also alters limb mechanics and relative contributions to forward velocity (Collins et al. 2015; Collins and Higham 2017). We observed substrate use and transitions in the field and conducted field-informed transition experiments in the lab to investigate how *R. afer* alter their locomotor speed, timing, and/or posture in response to shifts in substrate compliance. Understanding how this species experiences and accommodates such abrupt changes along their locomotor paths will better contextualize the function and evolution of their specialized locomotor behavior and morphology among geckos, as well as that of other high-speed terrestrial animals.

Methods

Study site and field recordings

We conducted our study at the Gobabeb Research and Training Centre (Namib-Naukluft Park, Namibia) in January 2016. We collected data from wild *R. afer* at a single site south of the field station across the Kuiseb River, a granitic outcrop interspersed with fine sand blown in from the nearby dunes (see **Figure 1.1**).

After making preliminary observations of diverse substrate use during high-speed locomotion at the study site, we provoked "escapes" (i.e., continuous running for at least one meter) by approaching an individual upon sighting at a steady walking pace while using a GoPro

Hero4 camera (120 frames/s) to record the focal animal's' escape trajectory. Geckos would frequently run for a few meters before taking refuge within or under rock, and so we recorded additional bouts from the same individual if it could be induced to flee from its refuge (e.g., lifting the rock). We recorded 51 total escape bouts from 26 encounters. As we could not identify specific individuals through these recordings, we cannot say if or how frequently we repeated observations on the same geckos, however the purpose of these recordings was simply to document general patterns of substrate use and transitions in nature.

Locomotor trials & video processing

We constructed a two-meter horizontal trackway for our locomotor trials that featured approximately 20 centimeters of unpacked level dune sand at its center, thus representing two transitions (into sand and out of sand); the trackway could also be configured as a continuous solid surface (i.e., no transition; see **Figure 1.2**). Sand was collected from the field site, and the solid portions of the trackway were lined with 60-grit sandpaper, an artificial surface found to be fairly representative of the microtopographies of natural rock sampled within the biogeographical range of *Rhoptropus* (Russell and Johnson 2014).

Ten individuals captured from the study site were induced to run down the trackway (always from the same starting point) into a "refuge" box while we recorded from lateral view using Phantom Miro M110 high-speed camera at 500 frames/s (~60cm field of view at the center of the trackway). We measured body temperature with an infrared thermal sensor aimed at the cloaca of the gecko immediately before placing it on the trackway; all body temperatures recorded fell within the normal field active temperature range (30-35ºC (Brain 1962; Higham and Russell 2010). While we attempted to elicit high-speed sprinting down the trackway, obtaining maximum performance was not the objective of this study.

We conducted multiple trials per individual per trackway configuration in random order during daylight hours; geckos were rested after initial capture and between trials. We also collected standard morphometric (i.e., snout-vent-length, limb element lengths) and body mass data from all individuals (**S1.1**). Geckos were kept in breathable cotton bags between experiments and were returned to their capture site within 48 hours. All handling procedures were in accordance with approved IACUC protocols for the University of California, Riverside (AUP 20170039).

From these recordings (~80 in total), we digitized the frame-by-frame movement of lateral body points (i.e., snout tip, shoulder, and hip) with the DLTdv5 package (Hedrick 2008) in MATLAB (version R2015b; MathWorks Inc., USA) and documented the sequence and timing of ipsilateral strides (right side) for each trial; we excluded entire trials and series of strides within trials where geckos did not run straight or deviated from typical quadrupedal and bipedal gait patterns (e.g., "leaping" between strides), leaving a total of 26 sand transition trials and 30 non-transition trials. We used IGOR PRO (version 4.0; Wavemetrics, Inc, USA) to plot and smooth the raw 2D coordinate data from these trials with standard smoothing splines (smoothing factor = 3). With the smoothed coordinate data and record of kinematic events for each trial, we calculated instantaneous velocity (frame by frame displacement over time), stride velocity (total distance travel over the time of a single stride), duty factor (the proportion of time in stance over the total stride time), and maximum body pitch angle (angle between the substrate and a straight line connecting the shoulder and pelvic joints).

Analyses

Field recordings

From each recorded escape, we documented the sequence and frequency of substrate use, which we divided into three categories: solid rock (the least compliant), gravel (a mixture of dune sand and eroded granite pebbles), and pure sand (the most compliant). We tallied the total number of specific substrate transitions (e.g., sand to rock), including transitions into and out of sand. We used Chi-squared tests to determine if our observed proportions significantly deviated from the null hypothesis of even probabilities.

Locomotor trials

We ran linear mixed-effects (LME) models using the lme function in the {nlme} package (v3.1-148; Piñheiro et al. 2020) in R (v4.0.2; R Foundation for Statistical Computing, Vienna, Austria) via RStudio (v1.2.5001; RStudio, Inc., Boston, MA) to test the impact of substrate transitions on our variables. This approach allowed us to incorporate multiple fixed effects, including covariates, and nested random effects, thus accounting for repeated measurements and uneven numbers of observations within trials and trials within geckos (Lindstrom and Bates 1990; Harrison et al. 2018).

We first attempted to capture potential changes in speed (i.e., acceleration) and posture as geckos ran over the entire sand portion of the transition trials. We used five "checkpoints" (CPs) from which we sampled and averaged 2D coordinates from five frames (0.01 total seconds) immediately preceding sand contact (CP 1), from the onset of initial sand contact (CP 2), midway through the sand portion of the trackway (CP 3), immediately preceding secondary contact with the solid trackway (CP 4), and the onset of secondary contact with the solid trackway (CP 5) (see **Figure 1.2**). We compared instantaneous velocity and body angle between these checkpoints, and also between analogous points within the non-transition trials, which were based on the approximate position of the sand within the field of view. This parallel dataset gave us a base from which to contextualize patterns detected within the sand-transition trials (see **S1.2a** for observation totals)

We first evaluated the separate predictive relationships between our covariates and response variables, as well as correlations among covariates; variables were normalized via log-transformation and removal of extraneous data points prior to analyses. A litany of previous work has shown that size and temperature are significant predictors of sprint speed among squamates (e.g., Hertz et al. 1983; Bauwens et al. 1995; Herrel et al. 2007); we verified these relationships between body temperature, SVL, and instantaneous velocity within our trial datasets via simple ordinary least squares (OLS) regressions. With respect to body pitch angle, OLS regressions with these three variables showed that velocity was the only significant predictor. As expected, we found significant correlations between covariates through simple OLS correlations, although the relationship between velocity and body temperature was negative ($r_{(128)}$= -0.489, p=3.69e^{-9}) for sand transition trials (n=26 with five CP observations per trial; relationships summarized in **S1.3a**). Given these relationships and the issue of collinearity (Harrison et al. 2018), we chose to exclude body temperature from the body pitch angle models and instead include velocity, which we deemed more biologically relevant based on previous studies (e.g., Aerts et al. 2003),

We ran saturated (i.e., included all fixed effects) and reduced nested models (observations within trials and trials within geckos) for velocity and body angle within the two sets of trials. We primarily compared model fit using Akaike Information Criterion (AIC) scores, with the difference between the lowest-scoring model and other models (ΔAIC). If ΔAIC between the next lowest-scoring model was greater than 4, we considered the lowest-scoring model to be the single best model, while ΔAIC<4 meant that we could not reject the other model(s) (Burnham and Anderson 2002).

We also used the ‘anova’ function in R to perform in likelihood-ratio tests between the lowest-scoring model and the other models with different degrees of freedom (i.e., number of effects); a significant test indicates that the primary model explains significantly more variability than the other model (Bolker et al. 2009). This approach was also used to assess the significance of our nested random effects in model fit by comparing the lowest-scoring model with a model containing only the main fixed effect (generalized least-squares model).

To more closely examine acute kinematic responses to shifts in substrate compliance, we focused our second set of analyses on capturing variation between sequential strides at each of the two transition sites. We designated “limb one” as making the first stride within sand at transition 1 (T1; solid to sand) and making the first stride on solid trackway at transition 2 (T2; sand to solid); “limb two” made the second stride on sand (T1) or solid trackway (T2). Within in each limb, we compared the stride of new substrate contact with its predecessor. For example, in limb one of T1 we compared the first sand stride to the penultimate stride on solid trackway, and within limb two of T1 we compared the second sand stride to the ultimate stride on solid trackway (see **Figure 1.2**). Thus, we analyzed two stride pairs per transition, which totaled four sets of models per kinematic response variable: stride velocity, duty factor, and maximum body pitch angle (see **S1.2b** for stride counts).

We used the same approach and covariates for our LME models as in the first group of analyses for instantaneous velocity and body pitch angle, including first examining individual relationships between variables (summarized in **S1.3b**). Along with body pitch angle, duty factor was also significantly predicted by stride velocity, and so we again elected to use this variable as a covariate within these models and not body temperature. As before, we nested observations (i.e., strides) within trials and trials within geckos for our random effects and compared fits of saturated and reduced models.

Results

Field observations of substrate use

We found that *R. afer* individuals used all three substrate types in 30 out of our 51 recorded escape bouts and used at least two types within 12 escapes (only rock used in the other 9 bouts). Of the total tallied instances of substrate use (331), proportions between rock, gravel, and sand did not significantly deviate from the null hypothesis of even probabilities ($\chi^2_{(2)}$ =0.011, p=0.99). In terms of movement between substrate types, we observed a total of 261 transitions, 204 of which represented transitions into or out of sand. There was no significant deviation from even probabilities for total transitions to a more compliant versus a less compliant substrate ($\chi^2_{(1)}$ =0.002, p=0.97), or specifically within sand transition trials ($\chi^2_{(1)}$ =1.0e^{-4}, p=0.99) (see **S1.4** for summarized counts).

Locomotor trials

LME models for response variables as predicted by checkpoint (CP) in the sand transition and non-transition trials are summarized in **Table 1.1**, with full model outputs in **S1.5**. We observed a significant effect of CP on instantaneous velocity in both sets of trials; geckos slowed down between the first two and the last two CPs. Body pitch angle was significantly predicted by CP and velocity within the sand-transition trials, and the two models with both of these fixed effects showed the best overall fit and explained significantly more variability than those without. Parameter estimates show that geckos increased their pitch between the first CPs and CP3 (mid-sand) and sustained this posture through the last two CPs. The non-transition trials did not a show a significant effect of CP or velocity. However, linear mixed model-based repeatability, R_m (i.e., estimated intraclass correlation coefficient), was rather low for body pitch angle ($0.15 \leq R_m \leq 0.25$). In contrast, velocity showed very high repeatability ($R_m > 0.95$).

LME models for response variables as predicted by stride pairs about the two sand transitions sites (T1 and T2), stride velocity, duty factor, and body pitch angle, are summarized in **Tables 1.2-4**, with full model outputs in **S1.6-8**. Echoing our previous results for instantaneous velocity over the entire sand portion of the trackway, we did not find a significant change in velocity between pairs of sequential strides (for limb one or limb two) at the transition into sand (T1) or the transition out of sand (T2), but there was a significant effect of temperature on stride velocity at T2 for limb 1. Again, velocity showed high repeatability within all model sets (R_m>0.97).

As a covariate, velocity significantly predicted duty factor at both transition sites; models with velocity as a fixed effect for both limbs at T1 and T2 showed better overall fit and explained significantly more variability than the other models. There was a significant effect of the limb two stride pair on duty factor for T1, in which the relative proportion of contact time increased between the ultimate stride on solid trackway and the second stride into sand. Furthermore, we observed that the same stride pair of T1 also had a significant effect on body pitch angle, with geckos exhibiting increased pitching in the second sand stride. Limb one and limb two stride pairs at T2 also had a significant effect on body pitch angle, in which the trunk of the geckos lowered between the last two strides in sand and the first two strides on solid trackway. However, body pitch angle again showed fairly low repeatability ($0.34 \leq R_m \leq 0.51$), while R_m was the most variable within and between model sets for duty factor ($0.18 \leq R_m \leq 0.68$). Only in the T1, limb 1 model set for body pitch angle did we observe that the model containing only the main fixed effect did not have the worst overall fit or explain significantly less variability than the other models.

Discussion

Field observations of substrate use, including transitions, indicate that this population of *R. afer* uses all three substrate types, rock, gravel, and sand with relatively equal frequency during escape bouts. Moreover, geckos transitioned between more and less compliant substrates almost equally, including transitions into and out of sand. These patterns demonstrate the ecological relevance of our experiments and bring important context to our results for velocity, duty factor, and body pitch angle.

That we did not find a significant effect of the transitions on instantaneous or stride velocity immediately before, during, or immediately after the sand was encountered, suggests that like some other lizards (see Introduction), *R. afer* is able to maintain its forward velocity over a range of substrate compliances. This apparent lack of a performance cost may explain why *R. afer* escaped over different substrates with fairly equal frequency. In both the sand transition and non-transition trials, geckos did decelerate between the first and last checkpoints, although this is more likely to be a consequence of the geckos perceiving the end of the trackway and/or a decrease in lighting within this region; the inside of the refuge box at the end of the trackway was dark, and the box itself casted a slight shadow on the end of the trackway. A study published after this data was collected showed that *R. afer* (a diurnal gecko) does reduce speed in lower light conditions, likely due to loss of visual acuity (Birn-Jeffery and Higham 2016). Given the significant predictive relationship of velocity with respect to duty factor, we originally expected to see parallel changes in these variables, specifically an increase in duty factor and decrease in velocity due to sinking into the sand. Increased relative contact time between the strides of the second sand-contacting without a loss of between-stride speed suggests that *R. afer* may instead increase stride length (i.e., the distance travelled during stance and swing phases of a stride) to maintain forward velocity when transitioning to a more compliant substrate.

Body pitch angle increased from sand entry through the middle of sand contact and decreased between the last sand strides and first strides on solid substrate at the transition 2. While increased trunk elevation has been observed within multiple lizard species during obstacle transitions, it remains unclear the extent to which this postural change, both within *R. afer* and among lizards in general, represents a behavioral response (i.e., under active neuromuscular control) versus a passive response (i.e., reflexes and mechanical self-stabilization) (Full and Koditschek 1999; Daley 2008; Grimmer et al. 2008). There are clear advantages of increasing body pitch angle when encountering many types of substrate transitions (e.g., enhanced vantage point of the locomotor path and greater loading of the hindlimbs for propulsion), which therefore point to trunk elevation (and tail lifting) as an adaptive behavioral response (Kohlsdorf and Biewener 2006; Parker and McBrayer 2016).

However, it has also been hypothesized that body pitching represents a mechanical consequence of a rapid caudal shift of the center of mass onto the hindlimbs during accelerative bursts, with tail elevation representing a consequence of pitching (Aerts et al. 2003; Van Wassenbergh and Aerts 2013; Clemente and Wu 2018). As we did not detect significant acceleration events between checkpoints or between strides within the sand transition trials, the latter explanation seems insufficient to explain the observed sustained increase in body pitch angle that occurred within the first half of sand contact. Further investigation of passive self-stabilization (see Moritz and Farley 2004 and Grimmer et al. 2008) and of tail action during high-speed pitched and bipedal locomotion within lizards would seem pertinent to resolve this question (see Parker and McBrayer 2016 and Clemente and Wu 2018). Regardless of the nature of the response for this increase in body pitch angle, this change likely contributes to *R. afer*'s ability to sustain high-speed locomotion during shifts in substrate compliance.

Given its small body size (1.5-3.5g), it's possible that *R. afer* did not generate enough force to greatly deform the sand during locomotion, as was posited as an explanation for no observed difference in hard-packed versus soft sand running performance in *Calisaurus draconoides* or *Uma scoparia*, even though *U. scoparia* is considered a specialist of the latter (Korff and McHenry 2011). Measurements of the surface strength of the sand and force generated by *R. afer* would be needed to test this hypothesis. Moreover, it is likely that additional alterations in timing and kinematics occur within this species for velocity to be maintained during compliance transitions, such as increased effective hindlimb length (i.e., increased knee extension) in order to potentially offset the force-dampening effect of the sand. Moreover, quantification of the mechanical properties of the substrates used by this population of *R. afer* would enhance our ability to make inferences regarding substrate use and transitions within other populations, which have already been shown to vary in incline use and adhesive toe pad morphology (Collins et al. 2015). This is thus a ripe system to test multiple layers within the expanded the morphology-performance-behavior-fitness paradigm (Arnold 1983; Garland and Losos 1994).

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Tables & Figures

Table 1.1. Model summaries for instantaneous velocity and body pitch angle

Table 1.1 shows results of LME models (R package {nlme}) of sand transition (n=26) and non-transition trials (n=30) for instantaneous velocity (Vel) and body pitch angle (BPA) as predicted by the main effect of checkpoint (CP), the covariates of body temperature (body temp), SVL, and/or velocity (Vel), and random nested effects (observations within trials, trials within geckos); significant model terms are bolded at the $p<0.05$ level. Models with only the main fixed effect (italicized GLS models) were included to observe the impact of random effects on fit. Akaike Information Criterion (AIC) scores, ΔAIC scores (the difference between each model and the lowest-scoring AIC model), and model weights are shown; if ΔAIC >4, then the lowest-scoring model was interpreted as the single best model. Bayesian Information Criterion (BIC) and log Likelihoods (logLik) with degrees of freedom (df) are also shown for each model; the log Likelihood ratio (lL ratio) is shown between the lowest-scoring model and other models (bolded terms are significant at the $p<0.05$ level). Estimated marginal R-squared and linear mixed model-based repeatability (R_m) are also included.

Model	R^2	AIC	ΔAIC	Weight	BIC	df	logLik	lLratio	Rm
Sand transition trials									
Vel ~ **CP**, random = ~1|geckoID/trial	0.14	-469.58	0	0.366	-446.64	8	242.79		0.98
Vel ~ temp + **CP**, random = ~1|geckoID/trial	0.66	-469.06	0.53	0.281	-443.25	9	243.53	1.47	0.98
Vel ~ SVL + **CP**, random = ~1|geckoID/trial	0.831	-468.31	1.27	0.194	-442.50	9	243.15	0.73	0.98
Vel ~ temp + SVL + **CP**, random = ~1|geckoID/trial	0.874	-467.91	1.67	0.159	-439.24	10	243.96	2.33	0.98
Vel ~ CP		*-82.25*	*387.34*	*2.8E-85*	*-65.04*	*6*	*47.12*	***391.33***	
BPA ~ **Vel** + **CP**, random = ~1|geckoID/trial	0.294	-68.49	0	0.630	-42.68	9	43.25		0.18
BPA ~ **Vel** + SVL + **CP**, random = ~1|geckoID/trial	0.295	-66.76	1.73	0.265	-38.09	10	43.38	0.27	0.18
BPA ~ **CP**, random = ~1|geckoID/trial	0.226	-64.21	4.28	0.074	-41.27	8	40.11	**6.28**	0.25
BPA ~ SVL + **CP**, random = ~1|geckoID/trial	0.227	-62.30	6.19	0.029	-36.49	9	40.15		0.24
BPA ~ CP		*-56.25*	*12.24*	*1.4E-03*	*-39.04*	*6*	*34.13*	***18.24***	
Non-transition trials									
Vel ~ **CP**, random = ~1|geckoID/trial	0.224	-523.30	0	0.472	-499.21	8	269.65		0.96
Vel ~ SVL + **CP**, random = ~1|geckoID/trial	0.552	-521.89	1.40	0.234	-494.80	9	269.95	0.60	0.96
Vel ~ temp + **CP**, random = ~1|geckoID/trial	0.241	-521.54	1.75	0.196	-494.45	9	269.77	0.25	0.96
Vel ~ temp + SVL + **CP**, random = ~1|geckoID/trial	0.555	-520.14	3.16	0.097	-490.03	10	270.07	0.84	0.96
Vel ~ CP		*-177.97*	*345.33*	*4.9E-76*	*-159.90*	*6*	*94.98*	***349.33***	
Vel~ BPA+ CP, random = ~1|geckoID/trial	0.079	-111.63	0	0.345	-84.54	9	64.82		0.16
BPA~ CP, random = ~1|geckoID/trial	0.051	-111.56	0.07	0.334	-87.48	8	63.78	2.07	0.19
BPA~ SVL + CP, random = ~1|geckoID/trial	0.063	-110.13	1.50	0.163	-83.03	9	64.06		0.17
BPA~ Vel+ SVL + CP, random = ~1|geckoID/trial	0.087	-109.93	1.71	0.147	-79.82	10	64.96	0.29	0.15
BPA ~ CP		*-104.73*	*6.90*	*0.011*	*-86.67*	*6*	*58.37*	***12.90***	

Table 1.2. Model summaries for stride velocity with respect to transition 1 and 2

Table 1.2 shows results of LME models (R package {nlme}) for stride velocity (Vel) about sand transition 1 (T1; 112 total strides) and 2 (T2; 96 total strides) as predicted by the main effect of stride (i.e., preceding or commencing the transition) within limb 1 (L1) or 2 (L2), the covariates of body temperature (temp) and snout-vent-length (SVL), and random nested effects (observations within trials, trials within geckos); significant model terms are bolded at the $p<0.05$ level. Models with only the main fixed effect (italicized GLS models) were included to observe the impact of random effects on fit. Akaike Information Criterion (AIC) scores, ΔAIC scores (the difference between each model and the lowest-scoring AIC model), and model weights are shown; if ΔAIC >4, then the lowest-scoring model was interpreted as the single best model. Bayesian Information Criterion (BIC) and log Likelihoods (logLik) with degrees of freedom (df) are also shown for each model; the log Likelihood ratio (lL ratio) is shown between the lowest-scoring model and other models (bolded terms are significant at the $p<0.05$ level). Estimated marginal R-squared and linear mixed model-based repeatability (R_m) are also included.

Model	R^2	AIC	ΔAIC	Weight	BIC	df	logLik	lLratio	Rm
T1_L1									
Vel ~ T1_L1, random = ~1|geckoID/trial	0.02	-126.96		0.350	-117.20	5	68.48		0.99
Vel ~ SVL + T1_L1, random = ~1|geckoID/trial	0.93	-126.92	0.04	0.343	-115.21	6	69.46	1.96	0.98
Vel ~ temp + T1_L1, random = ~1|geckoID/trial	0.36	-125.42	1.54	0.162	-113.71	6	68.71	0.46	0.98
Vel ~ temp + SVL + T1_L1, random = ~1|geckoID/trial	0.93	-125.20	1.76	0.145	-111.54	7	69.60	2.24	0.98
Vel ~ T1_L1		*-17.55*	109.40	6.1E-25	*-11.70*	*3*	*11.78*	***113.40***	
T1_L2									
Vel ~ T1_L2, random = ~1|geckoID/trial	0.00	-158.92		0.403	-148.45	5	84.46		0.99
Vel ~ SVL + T1_L2, random = ~1|geckoID/trial	0.94	-158.50	0.42	0.327	-145.93	6	85.25	1.58	0.99
Vel ~ temp + T1_L2, random = ~1|geckoID/trial	0.01	-156.92	2.00	0.148	-144.36	6	84.46	0.004	0.99
Vel ~ temp + SVL + T1_L2, random = ~1|geckoID/trial	0.94	-156.54	2.38	0.122	-141.88	7	85.27	1.62	0.99
Vel ~ T1_L2		*-20.95*	137.96	4.4E-31	*-14.67*	*3*	*13.48*	***141.96***	
T2_L1									
Vel ~ **temp** + T2_L1, random = ~1|geckoID/trial	0.87	-141.46		0.435	-129.75	6	76.73		0.99
Vel ~ **temp** + SVL + T2_L1, random = ~1|geckoID/trial	0.97	-141.23	0.22	0.389	-127.57	7	77.62	1.78	0.99
Vel ~ SVL + T2_L1, random = ~1|geckoID/trial	0.96	-138.44	3.02	0.096	-126.73	6	75.22		0.99
Vel ~ T2_L1, random = ~1|geckoID/trial	0.05	-138.07	3.38	0.080	-128.32	5	74.04	**5.38**	0.99
Vel ~ T2_L1		*-29.02*	112.44	1.7E-25	*-23.17*	*3*	*17.51*	***118.44***	
T2_L2									
Vel ~ ***temp*** + T2_L2, random = ~1|geckoID/trial	0.85	-123.12		0.419	-112.28	6	67.56		0.99
Vel ~ ***temp*** + SVL + T2_L2, random = ~1|geckoID/trial	0.95	-122.26	0.86	0.272	-109.61	7	68.13	1.14	0.99
Vel ~ T2_L2, random = ~1|geckoID/trial	0.03	-121.32	1.80	0.170	-112.29	5	65.66	3.80	0.99
Vel ~ SVL + T2_L2, random = ~1|geckoID/trial	0.93	-120.92	2.20	0.139	-110.08	6	66.46		0.99
Vel ~ T2_L2		*-39.97*	83.15	3.7E-19	*-34.55*	*3*	*22.99*	***89.15***	

Table 1.3. Model summaries for duty factor with respect to transition 1 and 2

Table 1.3 shows results of LME models (R package {nlme}) for duty factor (DF) about sand transition 1 (T1; 112 total strides) and 2 (T2; 96 total strides) as predicted by the main effect of stride (i.e., preceding or commencing the transition) within limb 1 (L1) or 2 (L2), the covariates of velocity (Vel) and snout-vent-length (SVL), and random nested effects (observations within trials, trials within geckos); significant model terms are bolded at the $p<0.05$ level. Models with only the main fixed effect (italicized GLS models) were included to observe the impact of random effects on fit. Akaike Information Criterion (AIC) scores, ΔAIC scores (the difference between each model and the lowest-scoring AIC model), and model weights are shown; if ΔAIC >4, then the lowest-scoring model was interpreted as the single best model. Bayesian Information Criterion (BIC) and log Likelihoods (logLik) with degrees of freedom (df) are also shown for each model; the log Likelihood ratio (lL ratio) is shown between the lowest-scoring model and other models (bolded terms are significant at the $p<0.05$ level). Estimated marginal R-squared and linear mixed model-based repeatability (R_m) are also included.

Model	R^2	AIC	ΔAIC	Weight	BIC	df	logLik	lLratio	Rm
T1_L1									
DF ~ **Vel** + T1_L1, random = ~1|geckoID/trial	0.49	-52.44		0.720	-40.74	6	32.22		0.57
DF ~ **Vel** + SVL + T1_L1, random = ~1|geckoID/trial	0.49	-50.46	1.99	0.267	-36.80	7	32.23	0.01	0.57
DF ~ T1_L1, random = ~1|geckoID/trial	0.00	-43.10	9.34	6.7E-03	-33.34	5	26.55	**11.34**	0.68
DF ~ SVL + T1_L1, random = ~1|geckoID/trial	0.14	-42.79	9.65	5.8E-03	-31.08	6	27.39		0.66
DF ~ T1_L1		*-31.20*	21.25	1.8E-05	*-25.34*	*3*	*18.60*	***27.25***	
T1_L2									
DF ~ **Vel** + **T1_L2**, random = ~1|geckoID/trial	0.55	-98.27		0.581	-85.70	6	55.13		0.34
DF ~ **Vel** + SVL + **T1_L2**, random = ~1|geckoID/trial	0.56	-97.60	0.67	0.415	-82.94	7	55.80	1.33	0.31
DF ~ **T1_L2**, random = ~1|geckoID/trial	0.12	-87.61	10.65	2.8E-03	-77.14	5	48.81	**12.65**	0.65
DF ~ SVL + **T1_L2**, random = ~1|geckoID/trial	0.16	-85.90	12.37	1.2E-03	-73.33	6	48.95		0.64
DF ~ T1_L2		*-67.59*	30.68	1.3E-07	*-61.30*	*3*	*36.79*	***36.68***	
T2_L1									
DF ~ **Vel** + T2_L1, random = ~1|geckoID/trial	0.61	-79.33		0.619	-67.62	6	45.67		0.20
DF ~ **Vel** + SVL + T2_L1, random = ~1|geckoID/trial	0.61	-78.36	0.97	0.381	-64.70	7	46.18	1.03	0.18
DF ~ T2_L1, random = ~1|geckoID/trial	0.04	-54.94	24.39	3.1E-06	-45.18	5	32.47	**26.39**	0.65
DF ~ SVL + T2_L1, random = ~1|geckoID/trial	0.22	-54.39	24.94	2.4E-06	-42.68	6	33.19		0.61
DF ~ T2_L1		*-43.69*	35.64	1.1E-08	*-37.84*	*3*	*24.85*	***41.64***	
T2_L2									
DF ~ **Vel** + T2_L2, random = ~1|geckoID/trial	0.41	-87.67		0.719	-76.83	6	49.84		0.36
DF ~ **Vel** + SVL + T2_L2, random = ~1|geckoID/trial	0.41	-85.68	1.99	0.266	-73.04	7	49.84	0.01	0.36
DF ~ T2_L2		*-78.52*	9.15	7.4E-03	*-69.49*	*3*	*44.26*	***18.63***	
DF ~ SVL + T2_L2, random = ~1|geckoID/trial	0.13	-78.12	9.56	6.1E-03	-67.28	6	45.06		0.51
DF ~ T2_L2, random = ~1|geckoID/trial	0.04	-75.04	12.63	1.3E-03	-69.62	5	40.52	**26.39**	0.54

Table 1.4. Model summaries for body pitch angle with respect to transition 1 and 2

Table 1.4 shows results of LME models (R package {nlme}) for body pitch angle (BPA) about sand transition 1 (T1; 112 total strides) and 2 (T2; 96 total strides) as predicted by the main effect of stride (i.e., preceding or commencing the transition) within limb 1 (L1) or 2 (L2), the covariates of velocity (Vel) and snout-vent-length (SVL), and random nested effects (observations within trials, trials within geckos); significant model terms are bolded at the p<0.05 level. Models with only the main fixed effect (italicized GLS models) were included to observe the impact of random effects on fit. Akaike Information Criterion (AIC) scores, ΔAIC scores (the difference between each model and the lowest-scoring AIC model), and model weights are shown; if ΔAIC >4, then the lowest-scoring model was interpreted as the single best model. Bayesian Information Criterion (BIC) and log Likelihoods (logLik) with degrees of freedom (df) are also shown for each model; the log Likelihood ratio (lL ratio) is shown between the lowest-scoring model and other models (bolded terms are significant at the p<0.05 level). Estimated marginal R-squared and linear mixed model-based repeatability (R_m) are also included.

Model	R^2	AIC	ΔAIC	Weight	BIC	df	logLik	lLratio	Rm
T1_L1									
BPA ~ SVL + T1_L1, random = ~1|geckoID/trial	0.14	-59.65		0.313	-48.18	6	35.82		0.35
BPA ~ T1_L1, random = ~1|geckoID/trial	0.03	-58.91	0.74	0.217	-49.35	5	34.46	2.74	0.39
BPA ~ T1_L1		*-58.81*	0.84	0.206	*-53.08*	*3*	*32.41*	*6.84*	
BPA ~ Vel + T1_L1, random = ~1|geckoID/trial	0.08	-57.97	1.68	0.135	-46.50	6	34.98		0.36
BPA ~ Vel + SVL + T1_L1, random = ~1|geckoID/trial	0.14	-57.87	1.78	0.129	-44.48	7	35.93	0.22	0.34
T1_L2									
BPA ~ Vel + **T1_L2**, random = ~1|geckoID/trial	0.27	-81.13		0.337	-68.57	6	46.57		0.35
BPA ~ SVL + **T1_L2**, random = ~1|geckoID/trial	0.26	-80.23	0.91	0.214	-67.66	6	46.11		0.37
BPA ~ **T1_L2**, random = ~1|geckoID/trial	0.19	-80.01	1.12	0.192	-69.54	5	45.01	3.12	0.40
BPA ~ Vel + SVL + **T1_L2**, random = ~1|geckoID/trial	0.30	-79.99	1.14	0.190	-65.33	7	46.99	0.86	0.34
BPA ~ T1_L2		*-77.92*	3.22	0.067	*-71.64*	*3*	*41.96*	***9.22***	
T2_L1									
BPA ~ Vel + **T2_L1**, random = ~1|geckoID/trial	0.30	-90.71		0.536	-79.01	6	51.36		0.37
BPA ~ Vel + SVL + **T2_L1**, random = ~1|geckoID/trial	0.29	-88.86	1.85	0.212	-75.20	7	51.43	0.15	0.36
BPA ~ **T2_L1**, random = ~1|geckoID/trial	0.17	-88.53	2.18	0.180	-78.78	5	49.27	**4.18**	0.41
BPA ~ SVL + **T2_L1**, random = ~1|geckoID/trial	0.18	-86.66	4.06	0.070	-74.95	6	49.33		0.41
BPA ~ T2_L1		*-78.99*	11.72	1.5E-03	*-73.14*	*3*	*42.50*	***17.72***	
T2_L2									
BPA ~ Vel + T2_L2, random = ~1|geckoID/trial	0.26	-73.97		0.370	-63.00	6	42.99		0.50
BPA ~ T2_L2, random = ~1|geckoID/trial	0.18	-73.90	0.07	0.358	-64.76	5	41.95	2.07	0.51
BPA ~ Vel + SVL + T2_L2, random = ~1|geckoID/trial	0.25	-72.00	1.97	0.138	-59.20	7	43.00	0.03	0.50
BPA ~ SVL + T2_L2, random = ~1|geckoID/trial	0.18	-71.93	2.04	0.133	-60.96	6	41.97		0.51
BPA ~ T2_L2		*-59.61*	14.36	2.8E-04	*-54.12*	*3*	*32.80*	***20.36***	

Figure Legends

Figure 1.1 a) *Rhoptropus afer* individual (study average SVL ~45mm); b) image from study site at Gobabeb Research & Training Centre showing dark granitic rock interspersed with fine red sand (from adjacent dunes) and a more light-colored gravel mixture of eroded rock and sand.

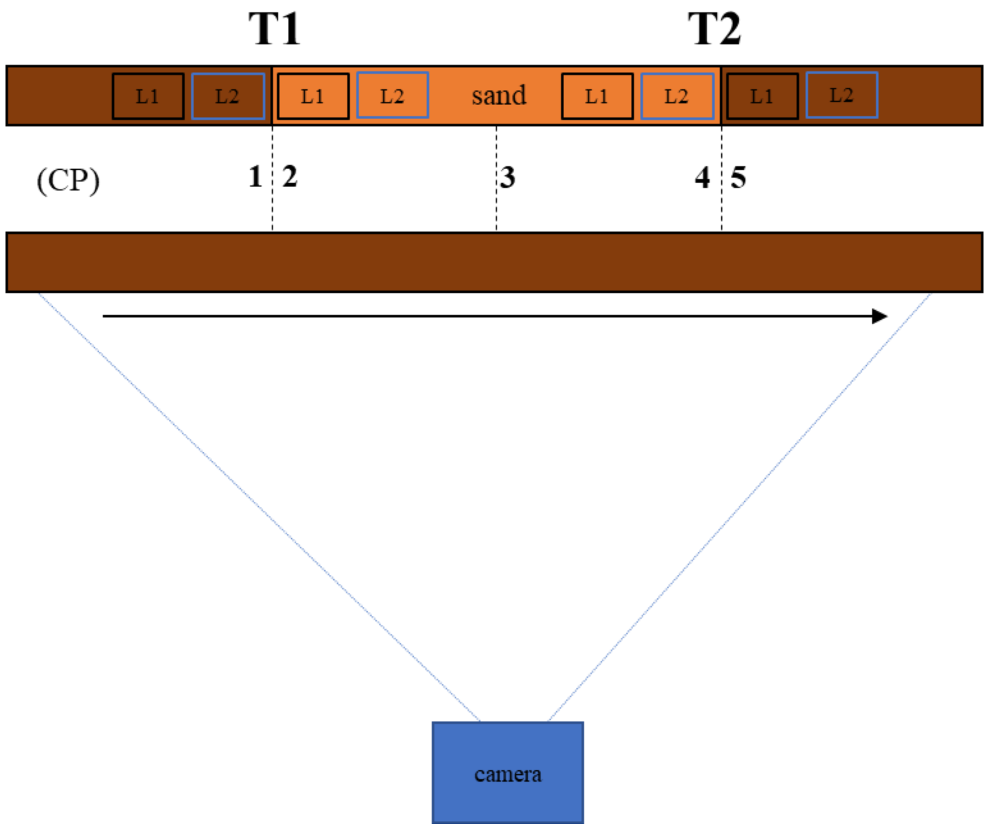
Figure 1.2 Schematic of the experimental set-up showing the two trackway configurations (sand transition and non-transition) within the camera field of view with the 5 checkpoints (CPs) and sequence of strides pairs within limb 1 (L1) and 2 (L2) about transition 1 (T1) and transition 2 (T2).

Figure 1.1. *Rhoptropus afer* and study site

A)

B)

Figure 1.2 Schematic drawing of experimental set-up



CHAPTER 2

Attachment beyond the adhesive system: the contribution of claws to gecko clinging and locomotion

Abstract

Attachment is imperative for many biological functions, such as holding position and climbing, but can be challenged by natural conditions. Adhesive toe pads and claws have evolved in multiple terrestrial lineages as important dynamic attachment mechanisms, and some clades (e.g., geckos) exhibit both features. The functional relationship of these features that comprise a complex attachment system is not well-understood, particularly within lizards (i.e., if pads and claws are redundant or multifunctional). Geckos exhibit highly adept frictional adhesive toe pads that continue to fuel biological inquiry and inspiration. However, gecko claws (the ancestral lizard clinging condition) have received little attention in terms of their functional or evolutionary significance. We assessed claw function in *Thecadactylus rapicauda* using assays of clinging performance and locomotor trials on different surfaces (artificial and natural) and inclines with claws intact, then partially removed. Area root mean square height (Sq), a metric of 3D surface roughness, was later quantified for all test surfaces, including acrylic, sandpaper, and two types of leaves (smooth and hairy). Maximum clinging force significantly declined on all non-acrylic surfaces after claw removal, indicating a substantial contribution to static clinging on rough and soft surfaces. With and without claws, clinging force exhibited a negative relationship with Sq. However, claw removal had relatively little impact on locomotor function on surfaces of different roughness at low inclines ($\leq 30^{\circ}$). High static and dynamic safety factor estimates support these observations and demonstrate the species' robust frictional adhesive system. However, maximum station-holding capacity significantly declined on the rough test surface after partial claw removal, showing that geckos rely on their claws to maintain purchase on rough, steeply inclined surfaces. Our results point to a context-dependent complex attachment system within geckos, in which pads dominate on relatively smooth surfaces and claws on relatively rough surfaces, but also that these features function redundantly, possibly synergistically, on surfaces that allow

attachment of both the setae and the claw (as in some insects). Our study provides important novel perspectives on gecko attachment, which we hope will spur future functional studies, new evolutionary hypotheses, and biomimetic innovation, along with collaboration and integration of perspectives across disciplines.

Introduction

Permanent or temporary attachment to a surface can occur within and between animals, and between an animal and a substrate (Nachtigall 1974; Emerson and Diehl 1980; Flammang 1996; Gorb 2008; Bullock and Federle 2009; Kovalev et al. 2014). This attachment often entails overcoming certain challenges of the environment, such as wave action (e.g., Carrington et al. 2009), gravity (e.g., Foster and Higham 2012), and slippery (Clark and Higham 2011), heterogeneous (Gorb and Gorb 2009), or friable (Russell and Delaugerre 2017) surfaces.

Within terrestrial animals, the ability to successfully attach and detach from surfaces repeatedly, or dynamic attachment, is critical to avoid slipping and falling during rest and during movement on non-horizontal surfaces (Cartmill 1985; Barnes 2006). Two prevalent structures within and across animal groups that confer this ability are adhesive pads and claws (Nachtigall 1974; Gorb 2008; Labonte and Federle 2015).

Adhesive pads, the sites of animal-surface interactions, are classified by their structure and nature of adhesive forces produced (see Barnes 2007; Gorb 2008). Some insects and arachnids exhibit tiny hair-like structures, or setae, projecting from a glandular ('wet') pad that intimately contact a surface to generate intermolecular forces (i.e., van der Waal's) along with fluid-based forces (Beutel and Gorb 2001; Gorb 2001; Bullock et al. 2008; Wolff and Gorb 2016). Dry adhesion is based only on forces associated with the setae, and is prevalent in spiders (e.g., Kesel et al. 2003) and lizards (Ruibal and Ernst 1965; Williams and Peterson 1982). The shearing of densely arranged setae over a surface can yield substantial frictional adhesive forces, best exemplified by geckos (see Autumn et al. 2000; Autumn and Peattie 2002).

Claws represent another dynamic attachment feature convergent within and between arthropods and tetrapod vertebrates (Gorb 2001, 2008; Alibardi 2009; Pattrick et al. 2018). As the composition and development of these structures vary across clades, we use a simple functional definition of claws: pointed, often recurved projections of the distal aspect of a limb or digit that attach via penetration (soft surfaces) or mechanical interlocking (surface asperities are larger than the claw tip), and/or friction (surface asperities are smaller than the claw tip) (see Cartmill 1974; Dai et al. 2002; Labonte and Federle 2015). Some clades exhibit adhesive pads as well as claws, including insects, spiders, and lizards (Gorb 2008; Labonte and Federle 2015), posing further questions about the evolutionary relationships between and the functional significance of these concurrent attachment morphologies. Do they confer different functions or redundancy?

The combination of adhesive toe pads and claws represents what we consider a 'complex attachment system', with multiple attachment morphologies and/or multiple attachment functions *within an individual*. We can conceptualize different relationships of form and function within these systems using interspecific perspectives from Wainwright et al. (2005). When multiple features confer one attachment function within an individual (i.e., 'many-to-one mapping'), this can be considered a redundant, possibly synergistic, attachment system. Such a system may enhance performance within a particular context, as well as provide maintenance of overall function if one feature fails. For example, atelid primates have prehensile tails bearing a friction-enhancing volar pad which, along with the autopodial volar pads, provide grip during suspension and locomotion (Meldrum 1998). Converse to this scenario, an organism could exhibit a multifunctional attachment system in which one feature serves multiple functions (i.e., 'one-to-many mapping'), or multiple features may confer different functions within an individual (i.e., 'one-to-one' or 'many-to-many mapping'). Functional partitioning allows structures to become optimized for different roles (e.g., tube feet in some sea cucumbers; Santos et al. 2009). Although this may lead to vulnerability to a perturbation, it may also allow an organism to effectively perform a variety of tasks, such as locomoting on diverse surfaces. Where do adhesive pads and claws fall with respect to these categories?

Within lizards, anoles and geckos are the only groups with frictional adhesive digital pads (Ruibal and Ernst 1965; Russell 1972, 1979; Peterson 1983). In geckos, the pads comprise a particularly hierarchical and integrated suite of external and internal structures that finely modulate setal-surface contact and enable strong, repeated attachment on vertical and inverted surfaces (Russell 1972, 1975, 1979, 1981, 2002, 2016; Autumn et al. 2000; Autumn 2006). Approximately two-thirds of gecko species exhibit this putative evolutionary key innovation, with multiple independent origins of diverse pad forms across the phylogeny (Russell 1976; Pianka and Sweet 2005; Gamble et al. 2012, 2017; Russell and Gamble 2019). Geckos are thus a rich source of biological interest and inspiration (Autumn et al. 2014; Patek 2014; Niewiarowski et al. 2016).

Claws are the ancestral clinging condition exhibited by all modern lizard groups (Pianka and Vitt 2003) but have received relatively little attention within geckos. Interestingly, claws have been lost or reduced (i.e., become vestigial or lost on some digits) within pad-bearing and secondarily padless gecko lineages on multiple occasions (Khannoon et al. 2015). Much remains to be explored concerning the apparent diversity of autopodia across the clade, including patterns of evolution and the ecological significance of different morphologies. **Figure 2.1** outlines possible selective regimes for phenotypic combinations of toe pads and claws, ignoring potential effects of non-adaptive evolutionary processes (e.g., phylogenetic constraint or pleiotropy).

Within three gecko genera, Zani (2000) reported positive correlations between pad area, claw curvature, and clinging force on smooth surfaces; taller claws were correlated with higher performance on rough surfaces. Crandell et al. (2014) found positive relationships between pad area, claw size, and arboreality in anoles, but a negative relationship of claw curvature that conflicts with other padless lizards (Tulli et al. 2009; D’Amore et al. 2018). These studies suggest that pads and claws have evolved in concert within these clades, potentially driven by functional demands. Experimental studies are rare, but Mahendra (1941) used claw amputation to qualitatively examine clinging and climbing ability within a house gecko, *Hemidactylus flaviviridis*, which appeared to decline on rough, but not smooth surfaces. Garner et al. (2017) instead used partial claw removal (i.e., trimming the distal keratinized aspect to avoid tissue damage; see (Bloch and Irschick 2005) and evaluated its effect on clinging performance in *Anolis sagrei*. Clinging force was maintained on smooth artificial surfaces, but performance was not tested on rough or natural surfaces. How do claws contribute to clinging ability and locomotion on different substrates?

In this study, we assessed claw function in *Thecadactylus rapicauda* (Turnip-tailed gecko; Houttuyn 1782), an arboreal species that uses a variety of natural surfaces (e.g., tree bark, bromeliad leaves) and humanmade structures throughout neotropical and southern Caribbean island forests (Vitt and Zani 1997; Russell and Bauer 2002). This species exhibits sharp, "sheathed" claws (i.e., recessed in subdigital sulci) between divided lamellae of the toe pad (Russell and Bauer 1988, 2002; Bergmann and Russell 2003), and previous studies have demonstrated strong frictional adhesive capabilities relative to other lizards (Higham et al. 2017a,b). If gecko claws contribute to static and dynamic attachment via mechanical interlocking and friction, then we expect that partial claw removal in *T. rapicauda* will 1) confer lower clinging performance on rough surfaces (but not smooth surfaces), and 2) alter locomotor kinematics on rough surfaces, particularly those that are inclined.

Methods

Study site, individuals, and claw removal

Wild geckos were captured at two camps within the Nouragues Ecological Research Station (Centre National de la Recherche Scientifique, French Guiana), 'Inselberg' (4805′ N, 52841′ W) and ‘Saut Pararé’ (4802′ N, 52841′ W), in February 2018. We obtained the mass of each individual using a Pesola scale, and standard morphological measurements (snout-vent-length and limb element lengths) were taken with calipers or later from photographs in ImageJ (version 1.51j8; National Institutes of Health, USA; **Table 2.1**). Individuals underwent clinging performance and locomotor trials before and after we trimmed the claw tips from all digits (precluding any living tissue; *sensu* Garner et al. 2017); digit I lacks claws (Russell and Bauer 1988). Individuals were given several hours to recover before subsequent trials. Ambient temperature and relative humidity were recorded for all trials; body temperature was also determined from digital infrared thermometer readings of the ventral surface for all locomotor trials. Geckos were released at their site of capture after trials were completed. All handling procedures were in accordance with approved IACUC protocols for the University of California, Riverside (AUP 20170039).

Test surfaces

Both natural and artificial surfaces were used in our experiments. Two types of tree leaves, one “smooth”, the other “rough” (i.e., hairy with trichomes) were selected from habitat typical of the species, although we did not observe *T. rapicauda* occupying these specific leaves or tree species. Based on observations of geckos utilizing wooden shelters around both camps, we also included a treated wood sample. Finally, acrylic and 60-grit sandpaper (samples from two manufacturers) were selected as standardized surfaces of extreme smoothness and roughness. All samples were retained for surface analyses (described in a later section).

Clinging Performance

Maximum clinging force

In the first clinging performance assay, we determined maximum peak tension force from 14 individuals. As conducted in previous field studies (e.g., Higham et al. 2017a), geckos freely placed the right manus onto a test surface affixed to a portable force gauge (Mark-10 Series 5) and were steadily pulled in parallel opposition until slipping occurred. A maximum force value (newtons) was recorded from five trials per individual per test surface before and after partial claw removal; test surface order was randomized. The setae achieved exceptionally high contact and frictional adhesion on acrylic, so we attempted to avoid damaging the toe pads (i.e., separation of the lamellae from the toe pad) for subsequent performance and locomotor trials. Therefore, "true" maximum clinging force on acrylic was not likely obtained in our study (see **S1.1** for raw force data).

Station-holding capacity

We tested station-holding capacity within a subset of individuals (n=5) by placing a gecko on a horizontal platform and slowly rotating it from 0 to roughly 180˚ (i.e., level to inverted; *sensu* Huber et al. 2007). From video recordings of three to four trials per individual (before and after partial claw removal), we determined the maximum angle achieved before the gecko began to fall. This assay was conducted only on acrylic and 60-grit 'sandpaper 2' (see **S2.2** for raw fall angle data).

Locomotor behavior

Finally, 7 geckos were recorded from lateral view using an Edgertronic SC1 monochrome high-speed camera (250 frames/second) while running on acrylic and sandpaper 2 at level and 30˚ inclines before and after partial claw removal. These inclines were selected to capture running and climbing behavior; 30˚ was based on previous gecko locomotor studies (Russell and Higham 2009; Collins and Higham 2017) and to ensure that geckos would be able to successfully ascend all substrates. Two to four trials were conducted per individual and substrate treatment (four total treatments; random order) with claws intact and removed.

From videos in which the gecko exhibited sequential, straight, and clean (i.e., did not run into trackway walls) strides, we digitized multiple points along the body using the DLTdv5 package (Hedrick 2008) in MATLAB (version R2015b; MathWorks, Inc., USA). These data were then imported into IGOR PRO (version 4.0; Wavemetrics, Inc, USA), where smoothing splines (smoothing factor = 2) were applied. We then extracted multiple variables that encompassed aspects of timing, posture, and forward movement (see **S2.3** for variable list and definitions).

Analyses

Surface microtopography

Area root mean square height (Sq), a metric of 3D roughness, was determined for each test surface (i.e., acrylic, wood, 60-grit sandpaper samples 1 and 2, and smooth and rough leaves) using a confocal laser scanning microscope (CSLM; LEXT OLS4000, Olympus Corporation, Japan) and 3D topographical reconstructions in MountainsMap Premium 7.2 software (Digital Surf, France). Unlike 2D metrics of roughness derived from a single transect through the sample, such as mean roughness (Ra) and root mean square (RMS), our area roughness values were derived from numerous surface transects (see Higham et al. 2019 for further details).

Clinging performance

We ran linear mixed-effects (LME) models using the lme4 and lmerTest packages (Bates et al. 2015; Kuznetsova et al. 2017) in R Studio (version 1.1.456; RStudio, Inc., USA) to test the contribution of claws to clinging performance (both clinging force and station-holding angle). For each surface model, claw status, body mass, and ambient conditions (i.e., temperature and relative humidity) were coded as fixed effects with maximum performance trials nested within geckos (i.e., random effect). Log transformation was used to normalize performance and body mass data prior to analyses.

We also calculated an average static clinging safety factor for each surface before and after partial claw removal by multiplying an individual's maximum clinging force on each surface by four (representing whole-organism performance) and dividing by body weight. We ran paired samples t-tests to compare static clinging safety factor on each surface before and after partial claw removal in SPSS (version 24; IBM Corp., USA).

Locomotor behavior

All locomotor variables were normalized via log transformation prior to analysis; forelimb and hindlimb strides were analyzed separately. To remove the effect of speed, kinematic variables were regressed with average stride velocity; for all significant regressions ($\alpha \leq 0.1$), residuals were obtained and used in subsequent analyses. To test the effect of claws on each of the kinematic variables within each substrate treatment, we ran LME models (see previous section); multiple, unequal numbers of strides (and initial acceleration observations) per individual per test surface (1-4 strides each) were incorporated. Each model had the following structure: the response variable as predicted by claw status, body size (body mass, SVL, fore/hindlimb length, or humerus/femur length), body temperature, and ambient conditions (i.e., fixed effects), with strides nested within treatment and treatment nested within individual geckos (i.e., random effects).

Furthermore, we tallied the number of strides (of those analyzed) in which the distal toes appeared to remain a least partially hyperextended (i.e., all or some toes in hyperextended position) throughout the stride.

Locomotor safety factor

Using maximum initial acceleration values and body mass measurements, we estimated the amount of force that geckos exerted in order to move from a stationary position on both a level and inclined surface, or their 'locomotor force'. True maximum clinging force values on acrylic were estimated from a regression of body mass and clinging force (per manus, claws intact) with data published for this species captured at the same locality in Higham et al. (2017b). These estimates and the per manus measurements for 60-grit sandpaper were then multiplied by four to provide a whole-organism estimate of maximum clinging force. By then dividing clinging force by locomotor force, we calculated an average 'locomotor safety factor' for each surface-incline treatment before and after partial claw removal. Because we did not observe a significant difference in clinging performance on acrylic after partial claw removal in our study, we used the maximum clinging performance estimates from the Higham et al. (2017b) data in our calculations for both "claws intact" and "claws removed". We also ran paired samples t-tests in SPSS to compare locomotor safety factors for each substrate treatment before and after partial claw removal.

<u>Results</u>

Roughness of test surfaces & distal toe morphology

The six test surfaces are here listed by their Sq value from smoothest to roughest: acrylic (0.0 µm), smooth leaf (6.4 µm), wood (29.3 µm), 60-grit sandpaper 2 (87.6 µm), rough leaf (94.1 µm), and 60-grit sandpaper 1 (105.2 µm). 3D microtopographical reconstructions for the smooth leaf and sandpaper 2, as well as a micrograph of the rough leaf trichomes can be viewed in **S2.4**.

To gain a sense of the scale of interactions between the surfaces and the attachment structures, we measured the fourth pedal digit of a single preserved *T. rapicauda* individual (ZFMK 85463) to obtain maximum setal length (109.6 µm; *sensu* (Russell and Johnson 2007), claw length (1.34 mm; sensu Zani 2000), and claw tip diameter (13 µm). **Figure 2.3** shows a simple 2D schematic of the distal toe with the setae (length) and claw at approximate scale with one another.

Clinging performance – maximum clinging force

LME models showed that clinging force was maintained on acrylic (t (9.2) = -1.35, p = 0.21) after partial claw removal, but was significantly lower on the smooth leaf (t (13.0) = -3.75, p = 2.4 x 10^{-3}), wood (t (14.0) = -2.63, p = 0.020), sandpaper 2 (t (12.7) = -11.90, p = 2.87 x 10^{-8}), rough leaf (t (28) = -4.80, p = 4.79 x 10^{-5}), and sandpaper 1 (t (14.8) = -7.77, p = 1.37 x 10^{-6}) surfaces (**Figure 2.4**); ambient predictors (temperature and relative humidity) found be to non-significant in initial models were excluded from final LME models (LME model output summaries can be found in **S2.5a**).

Average static clinging safety factor estimates (**Table 2.2**) were highest on acrylic (claws intact: 67.0 ± 6.05; claws removed: 56.5 ± 17.2) and lowest on the rough leaf (claws intact: 5.2 ± 0.9; claws removed: 1.1 ± 0.4). Paired samples t-tests of log transformed static clinging safety factor values showed a significant decline after partial claw removal on the smooth leaf (t (12) = 3.10, p = 9.0 x 10^{-3}), sandpaper 2 (t (11) = 7.87, p = 8.0 x 10^{-6}) , rough leaf (t (13) = 5.40, p = 1.2 x 10^{-4}, and sandpaper 1 (t (13) = 5.41, p = 1.2 x 10^{-4}), with a non-significant decline on wood (t (13) = 2.12, p = 0.054). Safety factor was maintained on acrylic (t (7) = 1.09, p = 0.31).

When maximum clinging force was mass adjusted, pooled across individuals for each surface, and regressed with Sq values, we observed a significant negative relationship both with claws intact (R^2 = 0.687; p = 0.042) and after partial claw removal (R^2 = 0.770; p = 0.022), the latter showing a stronger relationship.

Clinging performance – maximum station-holding angle

LME models showed that station-holding capacity after claw removal was maintained on acrylic (t (10) = 1.74, p = 0.11), but significantly declined on sandpaper 2 (t (10) = -4.61, p = 9.62 x 10^{-4}) (**Figure 2.5**); ambient predictors (temperature and relative humidity) found be to non-significant in initial models were excluded from final LME models (LME model output summaries can be found in **S2.5b**).

Locomotor behavior – kinematics and initial acceleration

LME models showed that claw status had a significant effect on some kinematic variables under specific substrate treatments within forelimb and hindlimb strides (see **S2.5c, d** for LME model output summaries). Unless otherwise indicated, the proceeding results describe significant changes that occurred after partial claw removal. Within the forelimb strides, there was a significant increase in duty factor on level sandpaper (t (19.3) = 2.54, p = 0.020). Time to toe unfurling decreased on inclined sandpaper (t (13.3) = -2.21, p = 0.045) but increased on level acrylic (t (29.0) = 2.26, p = 0.032); time to hyperextension increased on level sandpaper (t (20.3) = 2.53, p = 0.020). In terms of posture, body pitch angle significantly increased on level acrylic (t (29.0) = 2.89, $p = 7.28 \times 10^{-3}$); the humerus showed a greater extent of retraction on inclined sandpaper (t (22.0) = 5.62, $p = 1.20 \times 10^{-5}$) and greater protraction on level acrylic (t (29.0) = -2.156, p = 0.040).

For timing variables of the hindlimb strides, duty factor increased on both inclined (t (24.0) = 2.44, p = 0.024) and level (t (7.9) = 4.82, $p = 1.39 \times 10^{-3}$) acrylic. The duration of toe relaxation (t (25.9) = 2.17, p = .040) and time to hyperextension (t (26.0) = 2.63, p = 0.014) increased on level sandpaper, but the duration of hyperextension declined on this surface (t (26.0) = -2.70, p = 0.012) and on level acrylic (t (17.5) = -2.52, p = 0.022). Finally, the extent of femur depression increased on level sandpaper (t (26.0) = 3.01, $p = 5.81 \times 10^{-3}$); a non-significant trend of greater femur retraction was observed on level acrylic (t (9.0) = -2.17, p = 0.060). In terms of forward movement, step length decreased on these two surfaces (level sandpaper: (t (26.0) = -2.80, $p = 9.54 \times 10^{-3}$; acrylic: (t (16.2) = -2.58, p = 0.020)). The extent of hindfoot slippage was significantly greater before partial claw removal on level acrylic (t (7.5) = -5.52, $p = 6.95 \times 10^{-4}$).

Finally, LME models for initial acceleration did not indicate a significant effect of claw status (see **S2.5e**).

Of the strides analyzed, a higher percentage of the total forelimb strides (52%) showed at least partial hyperextension of the toes throughout the stride than the total hindlimb strides (25%). The percentage of partially hyperextended forelimb and hindlimb strides declined after partial claw removal (forelimbs: 74% to 34%; hindlimbs: 37% to 13%); this trend was observed within each substrate treatment (see **S2.6**).

Locomotor safety factor estimates

Average locomotor safety factor estimates (**Table 2.3**) were highest on level acrylic (claws intact: 307.9 ± 59.3; claws removed: 331.7 ± 58.8) and lowest on inclined sandpaper (claws intact: 38.9 ± 14.8; claws removed: 7.5 ± 1.31). Paired samples t-tests of log transformed locomotor safety factor values showed a significant decline on inclined sandpaper after partial claw removal (t (4) = 3.56, p = 0.024). Locomotor safety factor was maintained for the level (t (5) = -1.45, p = .206) and inclined (t (5) = 0.26, p = 0.80) acrylic substrates; a non-significant decline was observed on level sandpaper (t (4) = 2.21, p = 0.092) (**Figure 2.6**).

Discussion

We found that the claws of *T. rapicauda* are critical to maintaining clinging function on non-smooth surfaces but observed limited impacts of claw removal on locomotor dynamics. The latter can likely be attributed to this species' ability to generate sufficient force on experimental surfaces and inclines. More demanding inclines, however, likely limit net frictional adhesive force, thereby placing greater importance on the claws for friction and mechanical interlocking on rough surfaces. Overall, claw and adhesive function in geckos appears context-dependent.

Surface roughness and interactions

A grand challenge in the field of gecko adhesion is to better incorporate and quantify "roughness" in a consistent and meaningful way (see Russell and Johnson 2007, 2014; Johnson et al. 2009; Higham et al. 2019; Niewiarowski et al. 2019). The artificial and natural test surfaces used in this study showed a wide range of root mean square height values (Sq). As anticipated, acrylic, frequently used to elicit maximum frictional adhesive performance (e.g., Higham et al. 2017a), was completely smooth. Surprisingly, the two samples of 60-grit sandpaper showed a nearly 20 µm difference in Sq. Caution should be exercised when using surfaces from different natural and manufactured sources; analysis and quantification of surface characteristics is advisable to ensure consistency and to contextualize organism-surface interactions.

It appears that the claws could interlock with the asperities of wood and the two sandpaper samples, as well as the trichomes of the rough leaf. The largest asperities of the smooth leaf are similar in size to the claw tip, and therefore friction between the two would be more likely than mechanical interlocking (Dai 2013; Prüm et al. 2013). Estimating contact interactions between surfaces and attachment structures can be useful for establishing an upper bound on clinging capacity (Russell and Johnson 2014), while performance measurements provide a more realistic representation of clinging function (Irschick et al. 1996).

Clinging performance

As predicted, maximum clinging force significantly decreased on all non-acrylic surfaces after partial claw removal, with the most dramatic declines occurring on the three roughest surfaces (60-grit sandpapers and rough leaf). We assumed that claw interlocking would be limited on the smooth leaf (supported by low Sq), so we suspect that the significant decline in force after claw removal may reflect surface compliance and penetration by the claws. In-depth study of biological puncturing from a claw-substrate perspective is wanting (see Anderson 2018).

Regardless of claw status, a significant negative relationship between clinging force and roughness was observed. This aligns with previous studies showing that increasing surface heterogeneity diminishes setal contact area and thereby limits frictional adhesive force (Russell and Johnson 2007, 2014), while claws help to maintain clinging ability on rougher surfaces (Betz 2002; Bullock and Federle 2011). This was further supported by the decline in station-holding capacity (i.e., maximum fall angle) on 60-grit sandpaper (but not acrylic) after partial claw removal. However, other substrate properties, such as surface chemistry and polarizability, should also be considered in future studies using artificial (Autumn 2006; Badge et al. 2014) and natural surfaces (Gorb and Gorb 2009; Prüm et al. 2013).

Locomotion

Deployment of the gekkotan adhesive system can result in a loss of locomotor performance, as each step requires time to unfurl the toe pads, establish and break frictional adhesive bonding, and distoproximally peel the pads from the substrate via hyperextension (Russell 1975; Autumn et al. 2006a; Russell and Higham 2009). Russell & Higham (2009) found that running speed in *Tarentola mauritanica* (claws intact) was greater in individuals that kept their toes hyperextended on rough inclines but was lesser on smooth inclined surfaces, indicating a trade-off between forward velocity and maintaining purchase. Moreover, unfurling of the toe pads was induced at 10˚ inclines (30˚ in all individuals), while toes were held in hyperextension on level surfaces, regardless of surface texture. However, it is unclear if these patterns are representative of all pad-bearing geckos.

Our study examined locomotor behavior before and after partial claw removal on smooth and rough surfaces at level and 30˚ inclines. We found that some aspects of footfall (including toe movement) timing, body posture, and forward movement were impacted by claw status on certain substrate treatments, but this was not consistent between the forelimbs and hindlimbs. We observed a substantial difference in the frequency of partial toe hyperextension between analyzed forelimb and hindlimb strides; a reduction in the proportion of hyperextended strides was observed after partial claw removal for both regions across all treatments.

Within forelimb strides, duty factor and time to toe hyperextension from the onset of stance increased on level sandpaper after claw removal. We observed a 38% decrease in the number of partially hyperextended strides for this treatment, meaning that the distal toes overall appeared to be more flexed, and therefore in greater contact with the substrate more frequently after claw removal. Increased duty factor and delayed hyperextension may represent a compensatory response to reduced stability, as might occur if an attachment modality is lost. More rapid initiation of toe unfurling and greater humerus retraction on inclined sandpaper may also relate to a perceived loss of purchase. Although we observed kinematic changes on level acrylic (i.e., increased time to toe unfurling, body pitch angle, and humerus protraction) after partial claw removal, their functional significance is unclear.

The hindlimbs exhibit different responses to claw removal and substrate treatments relative to the forelimbs; only 25% of all strides exhibited partial toe hyperextension. On level sandpaper, the duration of distal toe contact and time to onset of hyperextension increased (as in forelimb strides), with a lower duration of hyperextension. This again may suggest that geckos behaviorally compensate for grip loss after claw removal by increasing distal toe contact. Moreover, greater femur depression on this treatment could coincide with a pedal adjustment, but more detailed mechanical analyses are needed to test this. Step length decreased on level sandpaper after claw removal, again suggesting a reduction in purchase. Increased duty factor on both inclined and level acrylic may correspond with the decreased frequency of hyperextended strides observed after claw removal and potentially increased surface contact (i.e., greater frictional adhesion), with the duration of hyperextension also lower on level acrylic. We are unsure why decreased step length and greater hindfoot slippage were observed on this surface given the apparent reduction of toe hyperextension.

It should be noted that we cannot confirm when and if the pads and claws were actually engaged during locomotion, only when distal toes appeared to contact the substrate. Many geckos, including *T. rapicauda*, exhibit cartilaginous paraphalanges integrated with other digital features that confer precise control of pad placement and adhesion (Russell and Bauer 1988; Russell 2002). Moreover, this species appears to be able to withdraw its claws into the digital sulci (pers. obs.), but the extent of control of this behavior is not known. Future gecko attachment studies should consider ways in which to confirm claw-substrate interaction.

Differences between forelimb and hindlimb characteristics in response to claw removal may point to a division in their function during locomotion on different surfaces and inclines; the latter has been observed in *Chondrodacylus bibronii* when comparing uphill and downhill strides (Birn-Jeffery and Higham 2014). Zaaf et al. (2001) found little difference between fore and hindlimb kinematics during horizontal running or vertical climbing on cork in *Gekko gecko* (claws intact) but noted that the degree of sprawling was greater in the hindlimb on the level substrate and greater in the forelimb on vertical substrate (along with duty factor and step length). Moreover, we know in other quadrupeds that hindlimbs tend to confer propulsion on level surfaces, while forelimbs are dominant on inclines (e.g., Lammers et al. 2006). More distinct adjustments of both fore and hindlimb kinematics within *T. rapicauda* may be observed at steeper inclines. We did not detect a significant effect of claw status on initial acceleration for any substrate treatment, but we did not attempt to elicit maximum sprint speed performance during trials.

Clinging performance and locomotion

High static clinging safety factors for pad-bearing geckos on artificial smooth surfaces in the lab (e.g., Autumn et al. 2000) led to a short-lived notion that geckos are "overbuilt". However, we now appreciate that application of the adhesive system under non-static and/or suboptimal conditions can substantially depress this margin of safety (Stark et al. 2015; Niewiarowski et al. 2016; Higham, et al. 2017a, b; Higham et al. 2019; Stark and Mitchell 2019). Rougher or more irregular surfaces pose greater challenges to attachment, particularly at greater inclines (Huber et al. 2007). Our study demonstrates that claws enhance static clinging and locomotor safety factor on relatively rough, inclined surfaces in *T. rapicauda*. We observed a significant negative effect of partial claw removal on clinging performance, including leaves and sandpaper. However, partial claw removal induced little locomotor alteration on surfaces orientated at 30˚ or below. These observations and our high estimates of both clinging and locomotor safety factors suggest that the toe pads are able to maintain function under these conditions. Given that the adept adhesive system of this species is hypothesized to have evolved for the acute and extreme demands of defensive canopy leaping and high impact forces during landing (Higham et al. 2017b), our results are perhaps unsurprising. However, we did observe falling on inverted surfaces, which was exacerbated by roughness and claw removal. Comparisons of locomotor kinematics under more challenging substrate conditions in this species would help further elucidate the functional and evolutionary significance of gecko claws.

Pads & claws: a functionally redundant or multifunctional attachment system?

As observed in some insects, we saw within a padded gecko a substantial loss of static clinging ability on the roughest surfaces after claw removal that points towards a multifunctional, or division of labor system, in which pads dominate on smooth, solid surfaces and claws dominate on rough and penetrable surfaces (Betz 2002; Bullock and Federle 2011; Voigt et al.

2012). However, that clinging performance declined with increasing surface roughness when claws were intact also indicates that there is some functional redundancy and potential synergism within this system, where together the pads and claws confer greater attachment on surface topographies that allow both features to attach; such synergism has been reported in beetles (Betz 2000) and an insect mimic (Song et al. 2016).

When we consider the role of gecko claws under dynamic conditions, we see that locomotor behavior is largely conserved after removal across treatments. This again supports functional redundancy between attachment structures at inclines below 30˚. However, if claw removal had a larger impact on rough surfaces at greater inclines, it would suggest a division of labor. In another study, Russell and Delaugerre (2017) observed that on horizontal and inclined friable schist substrate, *Euleptes europaea* (European Leaf-toed gecko) appeared to engage its claws while holding the pads in hyperextension, presumably to avoid fouling during locomotion (Hu et al. 2012). On concrete, however, the geckos appeared to fully unfurl the toes while engaging their claws. We surmise that gecko and some insect attachment systems are context-specific; redundant or multifunctional qualities can be exhibited depending on the conditions under which the organism employs its attachment system. This may also extend to reproductive functions (e.g., egg gluing and positioning in geckos; Bauer 2013).

Implications & future directions

Manipulating the toe pad as to neutralize its function while leaving the claws intact would be an ideal next step to better understand gecko attachment. Although this has been successfully conducted in beetles (see Betz 2002), the complexity and high concentration of sensory structures of the gekkotan adhesive system makes completely isolating functional effects rather difficult. Such experiments using biomimics (as in Song et al. 2016) may prove to be an informative alternative to live animal manipulation, also highlighting how material science research can help advance our understanding of a biological system. As Niewiarowski et al. (2016) articulated, continued advancement of adhesion research fundamentally requires not only data on wild geckos under ecologically relevant conditions, but also the integration of perspectives from multiple disciplines.

Although we recognize the standing diversity of gekkotan autopodial form beyond a few model species (Russell 1972, 1976; Gamble et al. 2012; Bauer 2019; Russell and Gamble 2019; Zhuang et al. 2019) and are beginning to illuminate the genomic underpinnings of this diversity (e.g., Gamble 2019), we must continue to increase our efforts to investigate how this diversity actually functions under "real-world" conditions (Higham and Russell 2010; Collins et al. 2015; Russell and Delaugerre 2017). The present study contributes important perspectives towards this goal, including novel perspectives regarding gecko claw function. Moreover, this work serves as a launching point for new hypotheses aimed at understanding the evolution of gecko attachment. For example, the loss and reduction of claws in some species may be driven by selection and modification of the adhesive system and/or habitat conditions, such as substrate availability (**Fig. 2.1**). Linking ecology with the extent of correlated morphological evolution between claws and toe pads is an important aim moving forward, as is testing biomechanical properties of particular morphologies. This will also lend itself to understanding complex functional systems and evolutionary key innovations at large.

We highlight an additional attachment feature as a potential source of inspiration for biomimetics and related endeavors. From Favi et al. (2014), "nature has shown, with striking examples, how diverse strategies can be used to generate adhesion in nearly all environmental extremes." We posit that looking to "diverse strategies" *within* an organism may be fruitful for finding solutions to complex problems and dreaming up new technologies. In other words, geckos may have more to offer than just their toe pads. Could combinations of features within synthetic materials or robots, such as claws and adhesive structures, enhance their performance and/or universality? We look forward to both the intellectual and practical rewards of synergism between diverse research groups to come.

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Tables and Figures

Table 2.1. *T. rapicauda* morphological data

Individual No.	Body mass (g)	Snout-vent-length (cm)	Forelimb length (cm)	Humerus length (cm)	Hindlimb length (cm)	Femur length (cm)
1	11.2	8.68	1.83	0.96	2.28	1.13
2	16.6	9.43	2.15	1.18	2.46	1.26
3	20	9.64	2.41	1.22	2.37	1.27
4	21.2	9.75	2.40	1.21	2.42	1.27
5	15	8.77	2.00	1.07	2.53	1.24
6	14.5	8.85	2.12	1.12	2.22	1.19
7	23.2	9.67	2.40	1.22	2.67	1.37
8	15.2	9.35	1.95	1.08	2.36	1.26
9	17	9.64	2.19	1.02	2.64	1.34
10	11	8.64	1.76	0.77	2.05	1.06
11	14.4	8.60	1.92	0.96	2.27	1.17
12	20.5	9.83	2.56	1.29	2.74	1.42
13	14	8.87	1.99	1.02	2.43	1.14
14	10.9	7.63	1.83	0.90	2.04	1.05

Table 2.2. Average static clinging safety factor estimate on each test surface

	Average Safety Factor		
Test Surface	**Claws Intact**	**Claws Removed**	Δ
acrylic	67.01 ± 6.51	56.49 ± 17.20	
smooth leaf	53.89 ± 4.75	36.3 ± 4.57	**
wood	23.75 ± 3.38	14.46 ± 2.70	
sandpaper 2	21.44 ± 2.74	5.56 ± 1.01	***
rough leaf	5.20 ± 0.88	1.09 ± 0.44	***
sandpaper 1	25.33 ± 2.71	7.56 ± 1.78	***

Δ significance: $*p < 0.05$, $**p < 0.01$, $***\ p < 0.001$

Table 2.3. Average locomotor safety factor estimates on each substrate treatment

	Average Safety Factor		
Substrate Treatment	**Claws Intact**	**Claws Removed**	Δ
level (0˚) acrylic	307.93 ± 59.25	331.73 ± 58.84	
inclined (30˚) acrylic	96.11 ± 5.97	94.48 ± 3.70	
level (0˚) sandpaper	78.98 ± 21.40	44.33 ± 14.97	
inclined (30˚) sandpaper	38.90 ± 14.80	7.55 ± 1.31	*

Δ significance: *$p < 0.05$, **$p < 0.01$, *** $p < 0.001$

Figure Legends

Figure 2.1. Potential selective regimes, including abiotic factors (i.e., substrate), that could result in the four pad-claw character combinations seen within the Gekkota (non-adaptive evolutionary processes are not considered here). Top left: The presence of both pads and claws may enhance attachment ability or maintain function if one mechanism fails (i.e., redundancy), or it may accommodate various inclined substrates within its environment (i.e., multifunctional). Top right: Claw loss or reduction could reflect relaxed selection (see Lahti et al. 2009) if surfaces are regularly encountered that optimize the adhesive system but not the interlocking of claws. Claws may also pose a risk of becoming caught or a physical impediment to the flush placement of the pads, as previously speculated (previously speculated in anoles; Garner et al. 2017) and may be selected against. Bottom left: Claws without pads represents the ancestral phenotype. However, relaxed and/or negative selection is hypothesized to have led to the secondary loss of pads and subsequent radiation within some lineages (see Higham et al. 2015). Pads pose a potential fouling and injury risk, as well as a locomotor speed cost (Autumn et al. 2006a; Russell and Higham 2009). Bottom right: Both structures may be lost within lizards occupying surfaces that do not require attachment and/or present an injury risk.

Figure 2.2. Photos of *Thecadactylus rapicauda*. A) Dorsal view of individual on treated wood (field station shelter), B) Ventral view of manus on acrylic showing divided scansors of the toe pads with arrow pointing to a “sheathed” claw, C) Lateral-oblique view of pes on 60-grit sandpaper with arrow pointing to a claw contacting the surface.

Figure 2.3. Schematic drawings of attachment structures and surface interactions to approximate scale. A) Overview of distal toe with claw tip (white) projecting from sulcus (light gray) and setae projecting from ventral surface of the toe (dark gray) onto a surface (black). B)/C) Closer view of setae (length to scale) and a surface with low (top) and high (bottom) roughness. D)/E) Closer view of claw tip (diameter to scale) and a surface with a low (top) and high (bottom) roughness. B) Most setae make contact on a surface with small asperities (as in the smooth leaf); C) Some setae are precluded from making contact on a surface with large, irregular asperities (as in 60-grit sandpaper); D) The claw tip slides over the surface, rather than mechanically interlocking with small asperities; E) The claw tip mechanically interlocks with large surface asperities.

Figure 2.4. Maximum clinging force (N) of the right manus averaged across individuals ($n = 14$) on each test surface before and after partial claw removal. Surfaces are arranged by increasing area root mean square height (Sq; µm) values: AC (acrylic), SL (smooth leaf), WD (wood), SP2 (60-grit sandpaper sample 2), RL (rough leaf), SP1 (60-grit sandpaper sample 1). Each plot shows the median (center line), interquartile ranges (box), and the range of values (within whiskers) that are not outliers (open circles and small star). Significant differences from LME models are indicated by asterisks: *$p < 0.05$, **$p < 0.01$, *** $p< 0.001$.

Figure 2.5. Maximum fall angle (˚) averaged across individuals ($n = 5$) on acrylic (AC) and 60-grit sandpaper (SP2) before and after partial claw removal. Each plot shows the median (center line), interquartile ranges (box), and the range of values (within whiskers). Significant differences from LME models are indicated by asterisks: *$p < 0.05$, **$p < 0.01$, *** $p< 0.001$.

Figure 2.6. Average locomotor safety factor estimates with standard error bars before and after partial claw removal for each substrate treatment: LA (level acrylic), IA (inclined acrylic), LS (level sandpaper), IS (inclined sandpaper). Significant differences from paired-samples t-tests are indicated by asterisks: *$p < 0.05$, **$p < 0.01$, *** $p< 0.001$.

Figure 2.1. Potential selective regimes for pad-claw character combinations

	+ Claws	- Claws
+ Pads	**Positive selection for both:** *Redundancy & synergism* • Retain function if one fails • Enhance attachment ability *Division of labor* • Cope with different conditions <u>Substrate</u> • Varied: rough, smooth, soft, hard • Inclines prevalent	**Negative selection against claws:** • Impede placement of pad • Constrain pad size • Injury risk **Relaxed selection on claws:** • Attachment inferior to pads <u>Substrate</u> • Specific: smooth, soft • Inclines prevalent
- Pads	**Negative selection against pads:** • Reduce locomotor speed • Fouling/injury risk **Relaxed selection on pads:** • Attachment inferior to claws <u>Substrate</u> • Specific: rough, hard friable • Inclines variable	**Negative selection against both:** • Fouling/injury risk **Relaxed selection on both:** • Attachment ability inconsequential <u>Substrate</u> • Specific: soft friable • Inclines few

Figure 2.2. *Thecadactylus rapicauda* plate

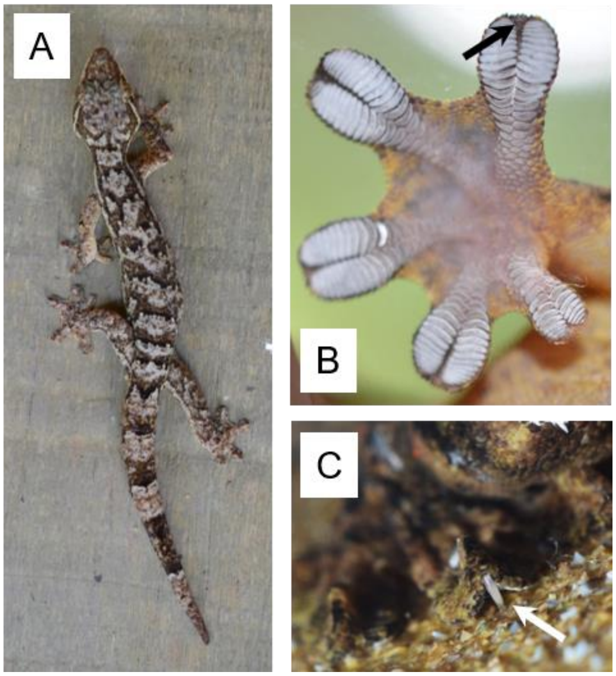


Figure 2.3. Schematic drawing of attachment structures and surface interactions

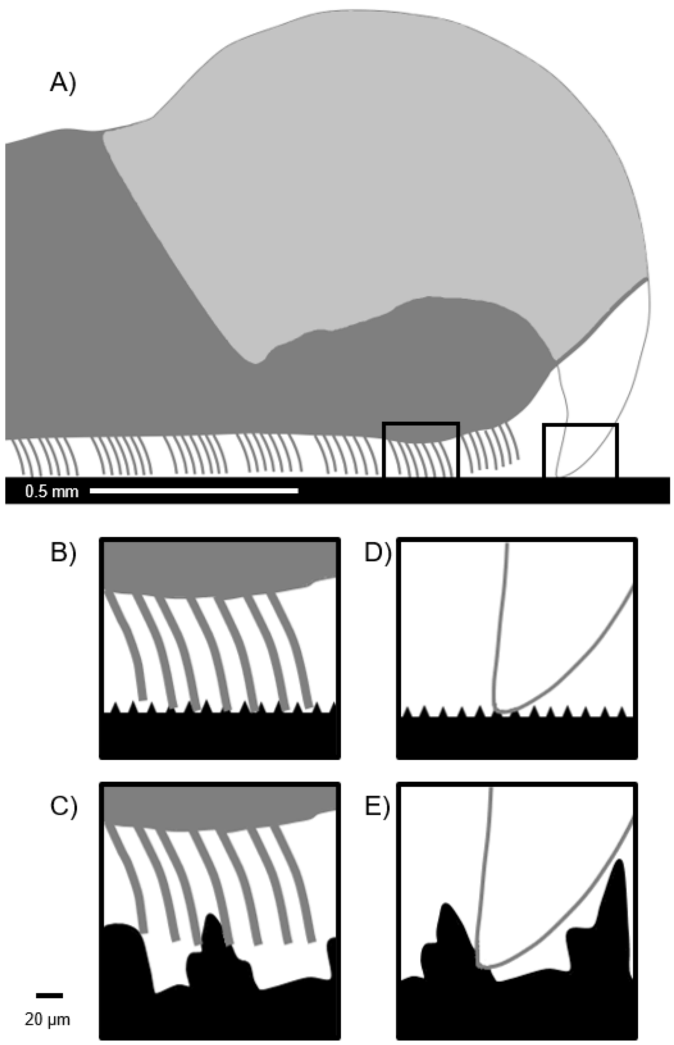


Figure 2.4. Boxplots of maximum clinging forces before and after partial claw removal on all test surfaces

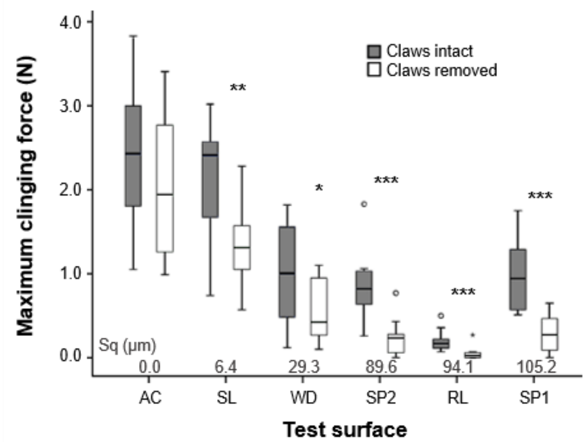


Figure 2.5. Boxplots of maximum fall angle before and after partial claw removal on acrylic and sandpaper

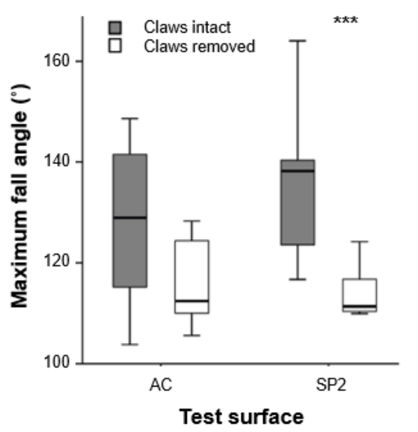
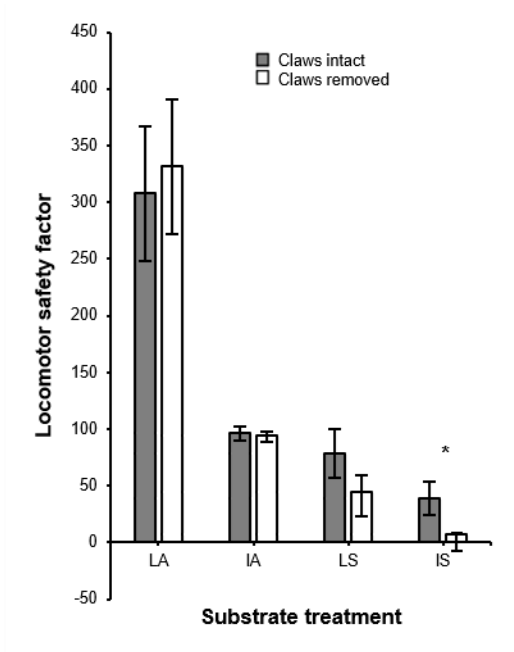


Figure 2.6. Bar graphs of average locomotor safety factor estimates before and after partial claw removal on all surface treatments



CHAPTER 3

Does variation in gecko toe pad and claw morphology reflect adaptive evolution to habitat?

Abstract

Geckos represent a speciose and diverse lizard clade, both ecologically and morphologically. In terms of attachment phenotypes, some geckos exhibit frictional adhesive toe pads and claws, while some lack one or both of these features. However, the extent and adaptive significance of variation in toe morphology has not been formally investigated within this group. For 112 gecko species, we imaged and measured multiple traits of the toe pad and claw and used habitat use data from the literature to categorize each as belonging to one of five groups: arboreal, saxicolous, mixed scansorial, generalist, or terrestrial. To test for an effect of habitat use and body size on the variation within these traits while accounting for species' relatedness, ANCOVA models were run as phylogenetic generalized least squares regressions with Pagel's λ branch length transformation. To assess covariation among the morphometric traits, we used ordinary least squares pairwise correlations and principal component analysis with the correlation matrix. Most traits were significantly predicted by body size, and model estimates of λ indicated that variation structure in the residuals due to phylogenetic relatedness was moderate to high for most traits. We found evidence for adaptive evolution of toe pad and claws, with the more scansorial groups showing greater pad area, pad aspect ratio, and inner claw curvature relative to the more ground-dwelling species, and saxicolous species showing higher maximum setal lengths than the other groups. Significant univariate OLS correlations were detected within but not between toe pads and claws, while the multivariate PCA showed that setal length and claw traits loaded strongly on the same principal components. While further steps are needed to more directly examine signatures of selection and to assess covariation within a phylogenetic context, this study represents an important first step in understanding the ecological context and evolution of locomotor morphology within geckos.

Introduction

How traits covary and evolve within and across taxa to produce phenotypic diversity remains a fundamental question in biology. While phylogenetic relatedness often contributes to phenotypic similarity among species (i.e., phylogenetic signal – Blomberg & Garland 2002; Symonds & Blomberg et al. 2014), divergent selection drives phenotypic variation in traits that could directly or indirectly promote reproductive isolation (Simpson 1953; Nosil 2012). Selection on morphology often occurs as a downstream effect of selection on fitness-relevant functions, including an organism's ability to perform a task and its actual behavior (Arnold 1983; Garland and Carter 1994). Morphological diversity may thus arise when environmental conditions vary among populations and favor different functions, or under similar environmental conditions across populations if multiple morphological configurations yield the same functional "solution" (Nosil 2012; Higham et al. 2017). Habitat, including the structural habitat, can apply directional selective pressures (e.g., Slabbekoorn and Smith 2002), as well as directly source the "ecological opportunity" needed for adaptive radiation to occur, such as new arboreal substrates to exploit in the case of *Anolis* lizards (Simpson 1953; Schluter 2000; Losos 2010). Morphological adaptations of the locomotor apparatus of this clade have been well-documented with respect to specific structural habitat niche space (Schoener 1974; Moermond 1979; Losos 1990; Elstrott and Irschick 2004; Kolbe et al. 2011; Wollenberg et al. 2013; Crandell et al. 2014b; Yuan et al. 2019)

Similar to anoles, the gekkotan attachment system is often (but not always) comprised of two apparatuses: frictional adhesive toe pads and claws. These two apparatuses confer dynamic attachment on surfaces of various textures and inclines. Gecko exhibit toe pads with highly branched setae, which are finely coordinated by a hierarchical suite of underlying tissues to generate intermolecular and frictional forces with a surface at points of contact (see Russell 2002; Autumn 2006). Claws penetrate soft surfaces, mechanically interlock with asperities, and/or generate shear friction (Cartmill 1974, 1985; Dai et al. 2002). While the biology and application of frictional adhesive toe pads in geckos continues to be the focus of much multidisciplinary research (Autumn et al. 2014; Niewiarowski et al. 2016; Drotlef et al. 2019), an adequate grasp of the functional and evolutionary significance of claws and of the relationship between toe pads and claws is lacking (Higham 2015; Naylor and Higham 2019; Russell et al. 2019).

In a qualitative study, Mahendra (1941) amputated the claws of house geckos (*Hemidactylus flaviviridis*) and observed that individuals were no longer able to locomote on highly rough or inverted surfaces. Naylor and Higham (2019) also investigated the functional interplay of toe pads and claws through experimental manipulation in an arboreal species (*Thecadactylus rapicauda*), but partial claw removal was used to avoid potential confounding effects of soft-tissue damage (*sensu* Garner et al. 2017)). Consistent with similar empirical studies in other pad and claw-bearing clades (e.g., arthropods, Betz 2002; Song et al. 2016b) and *Anolis* lizards (Garner et al. 2017), toe pads of *T. rapicauda* were dominant on highly smooth surfaces that maximized setal contact, while claws were dominant on the roughest surfaces that allowed for mechanical interlocking, pointing to functional partitioning or one-to-one mapping within the gekkotan attachment system. However, intermediately rough surfaces provided purchase for both apparatuses, suggesting functional redundancy or many-to-one mapping. Given this evidence for substrate dependence of form-function relationships, how might ecological context shape the evolution of the gekkotan attachment system?

Autopodial diversity among geckos (over 1900 described species; Uetz et al. 2020) is striking, particularly with respect to the external and internal anatomy of the digits and frictional adhesive system (Russell 1972, 1976; Russell and Bauer 1988; Russell and Delaugerre 2017; Russell and Gamble 2019; Zhuang et al. 2019) and in comparison to *Anolis* lizards (Russell 1979, 2016). Patterns of gross morphological variation support the evolutionary hypothesis of multiple independent acquisitions (14 occurrences estimated within Gekkonidae, Phyllodactylidae, Sphaerodactylidae, and Diplodactylidae) and secondary losses (6 occurrences estimated within Gekkonidae and Diplodactylidae) of toe pads, which occur in roughly two-thirds of all species (Gamble et al. 2012, 2017; Russell and Gamble 2019). With the exception of the model species *Gekko gecko* (Delannoy 2006) and *Rhoptropus*, whose species' setal arrays have been well-studied in relation to substrate use (i.e., Russell and Johnson 2007, 2014; Johnson and Russell 2009), *in situ* pad micromorphology has been relatively undersurveyed within geckos (Autumn et al. 2014; Bauer 2019); but see Peattie 2007 and Peattie and Full 2007).

Our understanding of gecko claw morphology and the extent of interspecific variation is even more limited, with patchy cladistic observations (e.g., Russell 1972; Kluge and Nussbaum 1995), some qualitative descriptions and contextualization of fossil specimens (Simões et al. 2017; Fontanarrosa et al. 2018), and one quantitative comparative assessment (Zani 2000). Zani's study found surface-dependent relationships between claw shape and pull-off force, with curvature (and lamellae count) positively correlated with higher performance on a smooth surface, and claw height positively correlated with performance on rough surfaces. However, the study sample contained only ten gecko species (6 padded) out of 68 total species (representing multiple lizard families), and data was not linked to natural habitat use.

Comparative morphological and ecological evaluations of claws in padless lizards (e.g., iguanians, Tulli et al. 2009, 2011; monitor lizards, D'Amore et al. 2018; lacertids, Baeckens et al. 2019) and other vertebrates (e.g., mammals and birds; Tulli et al. 2016 and Cobb and Sellers 2020) generally point to shorter, more curved claws within scansorial species relative to more terrestrial species. Studies within pad and claw-bearing anoles, however, have presented results that both support (Yuan et al. 2019) and conflict (Crandell et al. 2014; Muñoz et al. 2015) with this pattern (see also Yuan et al. 2020). Moreover, patterns of covariation between claw and toe pad morphology in *Anolis* also differ between studies and subgroupings, with Greater Antillean anoles exhibiting strong covariation driven by habitat type (Yuan et al. 2019) and Lesser Antillean anoles exhibiting little to no covariation between apparatuses along ecomorph partitions (Yuan et al. 2020); Crandell et al. (2014) and Muñoz et al. (2015) observed correlations between pad and claw shape within mixed samples.

Morphological covariation within and between gecko toe pads and claws and their presumed adaptive evolutionary linkage with ecology has yet to be investigated. More complex relationships might be expected as claws have been entirely lost or reduced (i.e., absence of functional claws on one or more digits of the manus or pes) in multiple pad-bearing lineages (11 occurrences estimated within Gekkonidae, Phyllodactylidae, and Diplodactylidae; Pianka and Vitt 2003; Khannoon et al. 2015; Russell and Gamble 2019). Moreover, patterns of reduction and loss vary within families, such as complete loss of claws in the *Pachydactylus* radiation versus loss only on digit I of the manus and pes within the *Gekko* clade (*sensu lato*) of Gekkonidae (Khannoon et al. 2015). The occurrence of multiple pad and claw phenotypes across the gekkotan phylogeny raises the fundamental question of whether this variation represents adaptive evolution to the abiotic environment (see Figure 1 of Naylor and Higham 2019 on scenarios of selection with respect to substrate properties).

In this study, we seek to determine patterns of correlated evolution among gecko toe pads, claws, and ecology. We quantified body size and multiple aspects morphometric traits (including micromorphometric traits) and gathered habitat use data to perform phylogenetically-informed analyses to determine if variation in gecko toe pad and claw morphology represents adaptive evolution and if these structures covary. Examining patterns of variation within the gekkotan attachment system with respect to species relatedness and habitat use will allow us to better understand and make predictions about the evolution of morphological diversity, as well as how these phenotypes might translate to function.

Methods

Sampling

We sampled 112 species within Gekkomorpha (i.e., families Gekkonidae, Phyllodactylidae, Sphaerodactylidae, and Eublepharidae). Study specimens came from the Museum Koenig (ZFMK; Bonn, Germany) and the collection of T.E. Higham at the University of California, Riverside (HLC; Riverside, California). We used digital calipers (error ± 0.01 mm) to measure snout-vent-length (SVL) and noted pad and claw presence/absence and condition for digits of the manus and pes. The distal portion of the fourth pedal digit was selected for subsequent imaging of the toe pad and claw, as in previous studies (Russell and Johnson 2007; Johnson et al. 2009; Crandell et al. 2014; Yuan et al. 2019); data for some species was taken from the literature (see **S3.1** for specimen information and SVLs).

Phylogeny

We used R (v3.6.1; R Foundation for Statistical Computing, Vienna, Austria) running in RStudio (v1.2.5; RStudio, Inc., Boston, MA) for most of the phylogenetic tree manipulation. The time-calibrated tree from Zheng and Wiens (2016) was pruned using the R package {ape} (v5.3; Paradis and Schliep 2018), and species were added based on other published topologies in Mesquite (v3.6; Maddison and Maddison 2019) to match our taxonomic sampling (**Figure 3.1**; see **S3.2** for citations).

Imaging

Toe pads

Digits bearing subdigital pads were first imaged using either a microphotography set-up (Canon EOS 7D DSLR operated with P-51 CamLift) or stereomicroscope (Nikon SMZ800 with Nikon D7000 DSLR) to capture the entire pad surface (*sensu* Russell & Johnson 2007; Crandell et al. 2014).

Pads were sectioned and prepared for scanning electron microscopy (SEM) based on established methods (e.g., Russell & Johnson 2007; Johnson & Russell 2009). Toe pads exhibit one of three recurring scansor arrangements (*sensu* Russell & Gamble 2019): 1) a single row of transverse widened scansors running from the base to the tip of the digit ('basal' padded), 2) distally situated leaf-like scansor pairs ('leaf-toed'), and 3) a distal bisected terminal fan of scansors (often also grouped within 'leaf-toed'; Gamble et al. 2012; Russell and Gamble 2019); basal pads were sectioned longitudinally at the midline or just medial to the midline (when claws and/or a cleft was present; e.g., *Hemidactylus)*, and leaf-like and terminal fan pads were sectioned longitudinally at the midline of each lobe. Two SEMs were used: a Zeiss Gemini Sigma 300VP SEM at the Museum Koenig Central Research Facilities and a Hitachi TM 1000 tabletop SEM at the University of California, Riverside (UCR) Microscopy Core Facility. Sectioned pads were either critical point-dried or air-dried, then mounted with double-sided carbon tape onto stubs with the cut sagittal edge facing upwards. Specimens imaged at the Museum Koenig were gold-sputtered after mounting, while mounted specimens were placed directly into the SEM at UCR. We observed negligible differences in image quality between preparation methods and machines.

Claws

Digital scales and other tissues that form the "claw sheath" (i.e., the claw boundary) in lizards can be lost or damaged during preservation, thereby confounding standard measurements (exemplified in Fontanarrosa et al. 2018; see also Cobb and Sellers 2020 concerning this issue in theropods). In geckos, claw visibility can also be impeded by the frictional adhesive toe pads and/or the extent to which the claw is recessed in soft tissue at a given moment (e.g., subdigital sulci in *Thecadactylus rapicauda*, Russell and Bauer 2002; Naylor and Higham 2019). Moreover, claw position relative to the toe pads is variable among genera (e.g., distalmost projection in *Gekko* versus more proximal and wedged between pad lobes in *Phyllodactylus*). It was therefore necessary to dissect and expose the entire extent of the claw (i.e., the ungual) for both padded and padless species in our study. Claws were imaged laterally using the aforementioned microphotography set-up or stereomicroscope.

Measurements

All toe pad and claw morphometric traits (see **Figure 3.2**) were measured using Image J (v1.51j8; National Institutes of Health, USA). Total toe pad area and pad aspect ratio (entire basal pad or single pad lobe in leaf-toed species) were measured from gross pad images. From SEM images, we measured maximum length, average aspect ratio, and density of setae (*sensu* Russell and Johnson 2007; Peattie 2008; Johnson and Russell 2009); measurements were taken within the distalmost 25% of the total pad length. We modified approaches established by Zani (2000) and Tinius & Russell (2017) to quantify claw length and inner claw curvature from fully exposed claws (see **S3.1** for raw measurements and **S3.3** for detailed variable definitions).

Habitat Use

We took habitat data predominantly from the literature and field guides; in some cases we relied on ‘Habitat and Ecology’ accounts from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. Common structural habitat occupancy for a species was categorized as one of five types: arboreal (i.e., scansorial on vegetation and wood substrate), saxicolous (i.e., scansorial on rocky substrate), mixed scansorial (i.e., both vegetation and rocky scansorial substrates), terrestrial (i.e., predominantly ground-dwelling), or generalist (i.e., commonly uses both scansorial and terrestrial substrates) (see **S3.2** for species' categorizations and citations and **Table 3.1** for summary tallies of our sample).

Analyses

Size relationships

To first examine the relationships between body size and our morphometric traits, we fit ordinary least squares (OLS) log-log regressions with SVL in SPSS (v26; IBM Corporation, Armonk, NY); statistical outlier species (i.e., data points that caused non-normality of the distribution of residuals) were dropped from certain variables prior to running the models, which was based on visual inspection of scatterplots and the histograms for each trait (**S3.4**) and scatterplot (with SVL). To assess if the scaling relationship between SVL and maximum setal length, pad area, and claw length deviated from isometry, we determined if the isometric slope fell within the range of the observed slope's 95% confidence intervals. Size regressions for all variables were plotted in the R package {ggplot2} (v3.3.2; Wickham 2016) with 95% confidence intervals, in which we also color-coded species by habitat use; we retained the unstandardized residuals from significant regressions to use in later analyses of continuous trait covariation.

Attachment morphology with respect to phylogeny, habitat use, and body size

Missing values were prevalent in our study due to the inherent lack of toe pads or claws and/or incomplete preservation, which created different sample sizes for each trait. Univariate analyses allowed us to retain as many species for each trait as possible, and within a phylogenetic context. We used ANCOVA models to determine if habitat use, along with body size, significantly predicted each morphometric trait while incorporating species relatedness. Log-transformed values were used for morphometric traits and SVL, and habitat use was coded such that arboreal geckos, the most speciose group within our sample (and likely within Gekkota at large; Pianka and Vitt 2003; Bauer 2013), were the base group (analogous to dummy variable "0"), with the parameter estimates being relative to this group for saxicolous, mixed scansorial, generalist, and terrestrial groups.

We ran our ANCOVAs as PGLS regression models such that model parameters were estimated simultaneously with a branch length transformation parameter to optimize model fit and interpretation of phylogenetic signal among the residuals (Grafen 1989; Revell 2010). We used the 'pgls' function in the R package {caper} (v1.0.1; Orme et al. 2012) to apply Pagel's λ transformation (Pagel 1997) to the total shared branch lengths between species (i.e., multiplying λ to the off-diagonal elements of the variance-covariance matrix of the model) while also obtaining a maximum likelihood (ML) estimate of λ (lower bound=0; upper bound adjusted between 1.25 and 2 to allow ML estimation to exceed 1). When $\lambda = 1$, the covariance structure for that trait is identical to one of a Brownian motion evolutionary process (i.e., trait variation increases proportionally along the branches over time) and indicates a strong effect of phylogenetic relatedness on the model residuals. When $\lambda < 1$, internal branches are shortened while terminal branches are elongated (i.e., increasing time since divergence); therefore, when $\lambda = 0$, there is no phylogenetic structure among the residuals (i.e., variation is not influenced by relatedness; Pagel 1997; Freckleton et al. 2002; Kamilar and Cooper 2013). As visual representations of the ML estimation process, log likelihood profiles (i.e., the distribution of log likelihood estimates of the parameter applied to the model of over a range of possible values) were also examined as a qualitative confirmation of the optimal estimate of λ.

We then ran the model again with the 'gls' function ({ape} and {nlme}, v3.1; Pinheiro et al. 2019), in which we set the starting value for the ML estimation of λ equal to the value obtained in {caper} in order to 1) verify the parameter ML estimate, and 2) to obtain the AIC (Akaike information criterion) score and log-likelihood estimate of model fit under this transformation, as well as the Type III estimate of sums of squares for the model. Estimated marginal means (i.e., least squares means) were obtained using {emmeans} (v1.4.8; Lenth 2020); when habitat was a significant predictor, we also retained results of Tukey post-hoc tests from this function. If SVL did not significantly explain the model, it was dropped, and λ was again simultaneously estimated and applied to the new model with habitat alone.

We attempted but were unable to apply an Ornstein-Uhlenbeck (OU) branch length transformation and simultaneous parameter estimation in R, as this process would provide a better picture of how variation within these traits is structured by relatedness and selection (Martins 1994). The {caper} package does not include this transformation, and the aforementioned 'gls' function ({ape}, {nlme}) did not yield reliable results. Specifically, this function requires a "starting value" to be inputted into the script for the ML estimation, which should then run unbounded in both directions (as with λ). However, the output for OU models consistently returned the inputted value as the parameter (alpha) estimate. Moreover, when the model was run through a large range of alpha values and the log-likelihood profile plotted, the peak did not line up with the estimate. We attempted to implement other packages to perform the transformation and estimation, however, {phylolm} (v2.6.3; Ho and Ané 2014) could not be installed correctly, and we were unable to get the 'pglmm' function in {phyr} (v1.0.2; Li et al. 2020) to run.

Covariation of toe pads and claws

With the unstandardized residuals (i.e., body size-corrected) and log-transformed values (i.e., trait not significantly predicted by SVL) of our morphometric traits, we plotted pairwise scatterplots in SPSS to visually inspect for bivariate normal distributions; points that clearly fell outside of the distribution of the rest of the sample were dropped for that particular variable (e.g., *Colopus wahlbergii* consistently fell far from other species in plots with maximum setal length).

We then ran pairwise correlations in SPSS, excluding species pairwise in cases of missing data to maximize our sample size within each correlation and extract a correlation matrix.

This correlation matrix was then used to run a principal components analysis (PCA) in SPSS (i.e., 'Factor Analysis' with no rotation). Using a correlation matrix again allowed us to include as much of our data as possible in the analysis; listwise exclusion (i.e., dropping species with any missing data) would be required to use individual observations in a PCA.

Results

Size relationships

OLS log-log regressions showed that all but one of the seven morphometric traits (i.e., average setal aspect ratio) were significantly predicted by SVL, with significant ($p<0.05$) positive relationships observed for maximum setal length, total pad area, pad aspect ratio, and claw length (claw curvature showed a marginally significant relationship); density exhibited a significant negative relationship with body size (parameters summarized in **Table 3.2**; regressions are plotted in **Figure 3.3**). Furthermore, we observed a significant negative allometric relationship for maximum setal length ($0.186 < 0.377 < 0.567$) and a significant positive allometric relationship for pad area ($2.236 < 2.613 < 2.990$); claw length did not significantly deviate from isometry ($0.933 < 1.044 < 1.156$).

Effects of phylogeny, habitat, and body size on attachment morphology

From our PGLS regressions with Pagel's λ transformation, we found that variation in almost all of the morphometric traits as predicted by habitat and SVL was structured by phylogenetic relatedness; ML estimates of λ values for models with both predictors ranged from 0.684 to 1.00, with the exception of average setal aspect ratio ($\lambda = 0.282$). Moreover, residuals for the setal aspect ratio, setal density, and claw length models were not significantly explained by habitat use. Conversely, residuals for the inner claw curvature model were not significantly explained by body size; both predictors were significant for maximum setal length, total pad area, and pad aspect ratio; R^2, λ, and model likelihood estimates are summarized in **Table 3.3**, while all other output for these models can be found in **S3.5**.

With respect to setal length, parameter estimates for saxicolous species were significant (i.e., saxicolous species exhibited significantly longer setae than the arboreal base group). From the estimated marginal (least squares) means of all groups (**S3.5a**), saxicolous setae appear longer relative to the other groups as well, although pairwise post-hoc tests did not show significant differences between groups (**Figure 3.4a**). For pad area and pad aspect ratio, parameter estimates for generalist and terrestrial species were significantly lower than those for the arboreal base group. Least squares means pointed to smaller and less elongate pads within these groups relative to the other scansorial groups (**Figure 3.4b,c**; **S3.5d,e**); post-hoc tests for pad area confirmed this pattern for saxicolous species, and mixed scansorial species were significantly different from terrestrial, but not generalist species. Post-hoc tests also showed that terrestrial species had significantly lower pad aspect ratios than all other groups. Inner claw curvature parameter estimates (after dropping SVL) were once again significantly lower for generalist and terrestrial species, and least square means and post-hoc tests supported this pattern relative to the other scansorial groups (**Figure 3.4d**; **S3.5g**).

Covariation of pad and claw morphology

Non-phylogenetic pairwise correlations between our morphometric traits showed some significant relationships within pads and claws, but not between them. Within toe pads, average setal aspect ratio was positively correlated with maximum setal length ($r_{(59)}$ = 0.45, p=2.75e^{-4}), setal density ($r_{(56)}$ = 0.35, p=6.54e^{-3}), and pad area ($r_{(60)}$ = 0.02, p=0.021); pad area was positively correlated with pad aspect ratio ($r_{(65)}$ = 0.78, p=0.1.5e^{-14}). The two claw variables, claw length and inner claw curvature, showed a significant negative correlation ($r_{(94)}$ = -0.40, p=5.84e^{-5}; the full correlation matrix is presented in **Table 3.4**).

We extracted four principal components from our non-phylogenetic PCA (using eigenvalues >1 and scree plot criteria), which collectively accounted for 85.6% percent of the total variance (see **Table 3.5**). PC1, which accounted for 30.4% of the total variance, was strongly positively correlated with pad area, pad aspect ratio, and average setal aspect ratio, while PC2 (23.7% of total variance) was strongly negatively correlated with claw length and maximum setal length. Density was strongly positively correlated with PC3 (17.3% of total variance), and inner claw curvature was strongly correlated with PC4 (14.4% of total variance).

Discussion

This study provided evidence for adaptive evolution within the gecko attachment system. Habitat use significantly explained morphological variation within several traits, however, not exclusively; many traits were also significantly predicted by body size and showed a significant effect of phylogenetic relatedness. Finally, we observed significant morphological correlations within toe pads and claws, but the extent to which these apparatuses covary with one another and evolutionary implications of that relationship remain unclear.

Numerous comparative studies have documented adaptive morphology within the lizard locomotor apparatus with respect to habitat (Garland and Losos 1994; Herrel et al. 2000), including claws (see Introduction). However, geckos and anoles are the only lizard clades to exhibit two attachment-conferring apparatuses. The occurrence of claws and frictional adhesive toe pads (and overall autopodial variation), as well as the species richness of geckos make them an ideal system for investigating the evolution of phenotypic diversity and complex functional systems (Autumn et al. 2014; Russell et al. 2019). This of course necessitates understanding the contexts under which these structures are used and subjected to selective pressures, both separately and collectively (Higham et al. 2019; Naylor and Higham 2019).

Surfaces encountered in nature can pose many challenges to frictional adhesion, such as wetness (Stark et al. 2015), dustiness (Russell and Delaugerre 2017), and roughness (Naylor and Higham 2019), and to claw action, such as low friction and tearing surfaces (e.g., thin leaves). Many natural surfaces are highly irregular and at multiple length scales, such as the long trichomes of leaves (Higham et al. 2019) and most rocky surfaces, which can greatly reduce potential setal contact area (see Russell and Johnson 2007, 2014; Johnson et al. 2009). We therefore expected to see signatures of selection on both apparatuses with respect to habitat use.

Toe pads

This study is the first to investigate the adaptive significance of toe pad macro and micromorphology in lizards. Within our sample, maximum setal length, pad area, and pad aspect ratio showed a significant effect of both habitat use and body size. The distribution of species on the log-log plots of these traits reinforce these patterns, with scansorial-dominant species tending to occupy space above and along the size-regression slopes and generalist and terrestrial species tending to fall beneath the slopes within a more limited (and smaller) body size range.

In particular, saxicolous species would appear to exhibit a steeper slope between setal length and SVL, which also supports model results of significantly longer setae in this group. Longer setae would indeed be theoretically optimal for maximizing contact on rocky surfaces, as the setal tips could potentially reach further into depressions, and increased length without a proportional change in diameter would decrease stiffness, thus conferring greater deformability and conformation to a rough surface for maximizing attachment (Persson and Gorb 2003; Autumn et al. 2006b; Persson 2007). Moreover, larger, more elongate pads in scansorial species relative to more terrestrial species, a pattern also observed in anoles (e.g., Elstrott and Irschick

2004; Crandell et al. 2014b; Yuan et al. 2019), likely reflects positive directional selection on these correlated traits to meet greater functional demands during climbing (i.e., maximizing contact area with the substrate; see Autumn et al. 2006), and potentially relaxed selection in non-climbers.

Pad traits that did not show a significant effect of habitat (i.e., setal aspect ratio and density) also do not show obvious clustering patterns about their respective size regression slopes, but we do note that there were overall few generalist and terrestrial representatives for these setal traits. However, setal density was significantly and negatively predicted by SVL; implications for performance and variation in other correlated traits of setal morphology (i.e., setal aspect ratio and setal length) warrant further investigation (Johnson and Russell 2009).

With respect to λ, we observed that residuals of most pad models showed an effect of phylogeny, with the pad area and inner claw curvature models exhibiting the closest fit to a BM evolutionary process ($\lambda \geq .91$) of any of the other pad traits; model residuals for average setal aspect ratio showed less fit to a Brownian motion evolutionary process.

Claws

Claw length and inner claw curvature were significantly and negatively correlated within our sample but showed opposite patterns with respect to the effect of habitat use and body size, which are also reflected in the OLS regression plots. Short and highly curved claws are thought to be adaptive for scansorial habitats, as they are more biomechanically advantageous for mechanically interlocking with a substrate during climbing, as the out-lever is shorter and the claw tip is more perpendicular to the force generated by flexor muscles of the digits (Cartmill 1974, 1985). In contrast, longer, less curved claws are thought to be adaptive for terrestrial habitats, as they extend the effective length of the limb (i.e., longer mechanical strut) and thus confer a lower cost of transport during relatively level locomotion (Kram and Taylor 1990;

Pontzer 2007). Multiple studies have observed this inverse morphological and ecological claw relationship (e.g., Tulli et al. 2011; Birn-Jeffery et al. 2012; Baeckens et al. 2019), with our study in partial support.

However, limited studies of lizard claw function have found that performance correlations with claw morphology were substrate-dependent; claw curvature correlated with pull-off force only on smooth surfaces, and claw length was not significantly correlated with performance on rough or smooth surfaces (Zani 2000; Tulli et al. 2011). As it is for the frictional adhesive system (Klittich et al. 2017), surface compliance may also be important to claw function and evolution; arboreal habitat surfaces, for example, are likely to be more penetrable than saxicolous habitat surfaces (Autumn et al. 2014; Russell et al. 2019).

In terms of phylogenetic effects, the model residuals of inner claw curvature as predicted by habitat and body size converged on a λ of 1 (also when SVL was dropped from the model), the strongest possible support for a BM evolutionary process based on this parameter; claw length model residuals showed slightly weaker phylogenetic signal and fit to a BM process.

Correlated evolution of attachment morphology and future directions

Given previous experimental work in geckos (Mahendra 1941; Naylor and Higham 2019), as well as findings within *Anolis* lizards (Crandell et al. 2014; Yuan et al. 2019), we were surprised not find stronger evidence of covariation between toe pads and claws, although we did observe some overlap between traits in their correlations with two of the PCs (collectively explained ~1/3 of the total variance). Low levels of morphological covariation between these apparatuses points to their independent evolutionary origins (see Fontanarrosa et al. 2018) and possibly their continuing evolution under different selective regimes; this may be driving or reinforcing functional partitioning (Hulsey et al. 2006). High levels of covariation within apparatuses may be explained by phylogenetic or developmental constraint, genetic integration (e.g., pleiotropy), ecology, or a combination of these (Klingenberg 2014; Yuan et al. 2020).

Model-fitting with other evolutionary processes that are more representative of strong selection, namely OU, will allow us to better test specific hypotheses regarding the correlated evolution, and potentially convergent evolution, of traits towards phenotypic (e.g., ecological) optima (Butler and King 2004). However, complications related to missing data and subsequent unequal sample sizes and different tree topographies among traits (as in the present study) limit multivariate analytical approaches.

Beyond improving our estimations of phylogenetic structure and modes and tempo of evolution, finer species ecological data (i.e., specific surface use), as well as *in situ* and *in vivo* assessment of clinging performance across the gekkotan phylogeny are needed to test the putative link between attachment form and function (Autumn et al. 2014; Niewiarowski et al. 2016; Higham et al. 2019). There is a dearth of field-based performance and ecological behavior studies in geckos, which are necessary to get at this relationship, and ultimately to determine their relevance to fitness within species and across species (Garland and Losos 1994; Irschick and Garland 2001; Irschick 2003; Calsbeek and Irschick 2007).

Conclusion

This study marks the first ecologically and phylogenetically-informed evaluation of the functional and evolutionary significance of gecko attachment morphology. Along with phylogenetic signal, we found evidence for adaptation to habitat use in both pad and claw traits, which also showed significant relationships with body size. This study not only advances our knowledge of the complex functional and evolutionary morphology of gecko toes, but it also emphasizes the need to look through multiple lenses to begin to crack the code of observed diversity among modern clades.

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Tables & Figures

Table 3.1. Summary of study sample counts ($n_{species}$=112)

Habitat Use	**A**	**S**	**M**	**G**	**T**	*Total*
	27	26	19	16	24	***112***
Pad Status						
P	25	17	15	9	9	75
A	2	9	4	7	15	37
Claw Condition						
F	10	20	12	10	20	72
R/A	17	6	7	6	4	40

Habitat) A=arboreal, S=saxicolous, M=mixed scansorial, G=generalist, T=terrestrial
Pad Status) P=present, A=absent
Claw Condition) F=full claws, R/A=reduction or absence claws

Table 3.2. OLS regressions of log-transformed morphometric traits and snout-vent-length

Variables	**R^2**	**SE**	**N**	**int.**	**SE**	**b**	**SE**	***t***	**p**	**Lower**	**Upper**	**iso. b***
Max. Setal Length	0.201	0.133	64	1.281	0.171	**0.377**	0.095	3.95	**2.050E-04**	0.186	0.567	**1**
Ave. Setal Aspect Ratio	0.005	0.122	63	1.584	0.160	-0.049	0.089	-0.55	0.586	-0.227	0.130	
Setal Density	0.258	0.273	61	6.142	0.376	**-0.943**	0.208	-4.53	**2.930E-05**	-1.359	-0.526	
Pad Area	0.726	0.286	74	-4.155	0.338	**2.613**	0.189	13.83	**5.917E-22**	2.236	2.990	**2**
Pad Aspect Ratio	0.568	0.208	69	-2.143	0.267	**1.412**	0.150	9.39	**7.699E-14**	1.112	1.712	
Claw Length	0.783	0.100	98	-1.821	0.099	**1.044**	0.056	18.59	**1.429E-33**	0.933	1.156	1
Inner Claw Curvature	0.044	0.053	96	-2.232	0.055	**0.065**	0.031	2.07	**0.041**	0.003	0.126	

Regression parameters and standard errors (SE), including 95% confidence intervals (lower and upper bounds); the slopes of and p-values of significant models are bolded ($p<0.05$)

*****signifies the predicted isometric slope of some variables based on geometric scaling relationships

Table 3.3. Summary of ANCOVA models via PGLS with λ transformation in the R packages {caper} and {ape}+{nlme}

Model	R^2	AIC	BIC	logLik	lower	lamda*	upper	df total	df resid
Max. Setal Length ~ Habitat + SVL	0.308	-89.266	-71.995	52.633	0.381	0.755	1.130	64	58
Ave. Setal Aspect Ratio ~ Habitat + SVL	0.022	-81.692	-64.547	48.846	0.000	0.282	1.000	63	57
Ave. Setal Aspect Ratio ~ Habitat	0.017	-85.159	-72.300	48.580	0.000	0.440	1.020	63	58
Setal Density ~ Habitat + SVL	0.226	12.428	29.315	1.786	0.351	0.761	1.172	61	55
Pad Area ~ Habitat + SVL	0.822	-19.183	-0.751	17.592	0.656	0.906	1.155	74	68
Pad Aspect Ratio ~ Habitat + SVL	0.694	-50.510	-32.637	33.255	0.367	0.684	1.001	69	63
ClawL ~ Habitat + SVL	0.805	-189.198	-168.518	102.599	0.635	0.872	1.108	98	92
Inner Claw Curvature ~ Habitat + SVL	0.889	-343.878	-323.363	179.939	1.001	1.002	1.004	96	90
Inner Claw Curvature ~ Habitat	0.958	-337.460	-319.509	175.730	1.002	1.002	1.003	96	91

*transformation parameter with 95% confidence intervals (lower and upper bound)

'Habitat' indicates the five habitat use categories (arboreal, saxicolous, mixed scansorial, generalist, terrestrial)

Response variable and SVL (snout-vent-length) were log-transformed prior to analyses

Table 3.4. OLS correlation matrix for morphometric traits (non-phylogenetic)

Morphometric Variable		**Max. Setal Length**	**Ave. Setal Aspect Ratio**	**Setal Density**	**Pad Area**	**Pad Aspect Ratio**	**Claw Length**	**Inner Claw Curvature**
Max. Setal Length								
Ave. Setal Aspect Ratio	***r***	**0.45**						
	p	***2.75E-04***						
	N	61						
Setal Density	***r***	-0.22	**0.35**					
	p	*0.095*	***6.54E-03***					
	N	58	58					
Pad Area	***r***	0.19	**0.29**	0.01				
	p	*0.149*	***0.021***	*0.918*				
	N	62	62	59				
Pad Aspect Ratio	***r***	-0.01	0.23	0.06	**0.77**			
	p	*0.961*	*0.082*	*0.642*	***1.50E-14***			
	N	58	60	56	69			
Claw Length	***r***	0.24	0.19	-0.20	-0.16	-0.13		
	p	*0.097*	*0.187*	*0.177*	*0.217*	*0.342*		
	N	50	51	47	60	57		
Inner Claw Curvature	***r***	-0.18	-0.12	-0.05	-0.21	-0.13	**-0.40**	
	p	*0.222*	*0.395*	*0.746*	*0.117*	*0.322*	***5.84E-05***	
	N	48	49	45	58	56	96	

Parameters of two-tailed correlations shown:

(r) Pearson's correlation coefficient; bolded if significant
(p) p-values; bolded if significant ($p<0.05$)
(N) sample size for each pairwise relationship

Table 3.5. OLS PCA results (correlation matrix used)

a) Component matrix

	PC Component						
	1	**2**	**3**	**4**	**5**	**6**	**7**
Max. Setal Length	.466	**-.560**	-.039	**.570**	-.300	.226	-.047
Setal Density	.166	.351	**.851**	-.250	-.075	.234	.051
Ave Setal Aspect Ratio	**.671**	-.189	**.549**	.301	.186	-.290	-.048
Pad Area	**.819**	.361	-.311	.002	-.034	-.010	.319
Pad Aspect Ratio	**.737**	.461	-.295	-.132	.229	.123	-.268
Claw Length	.136	**-.806**	-.018	-.291	.467	.140	.093
Inner Claw Curvature	-.444	.441	.039	**.655**	.400	.113	.069

Correlation values (***r***) > |.5| are bolded

b) Total variance explained (initial eigenvalues; equivalent to extraction sums of squared loadings)

Component	**Total**	**% of Variance**	**Cumulative %**
1	**2.125**	**30.362**	**30.362**
2	**1.659**	**23.704**	**54.067**
3	**1.213**	**17.331**	**71.398**
4	**1.009**	**14.414**	**85.812**
5	**.562**	**8.026**	**93.838**
6	**.238**	**3.394**	**97.231**
7	**.194**	**2.769**	**100.000**

Figure Legends

Figure 3.1. Phylogenetic relationships of the study taxa within the four families of Gekkomorpha (phylogeny modified from Zheng and Wiens 2016) with habitat use denoted. 118 species are represented, but six species are shown here for visual purposes only (4 outgroup species: *Anolis carolinensis*, *Aspidoscelis sexlineata*, *Dipsosaurus dorsalis*, *Meroles cuneirostris*; 2 padless, clawless species: *Chondrodactylus anguilifer*, *Pachydactylus rangei*).

Figure 3.2. Morphometric variables of the toe pad (A) and claw (B), including sectioned pad (C) micromorphology (D): total pad area, pad aspect ratio (*a*/*b*), claw length (*c*+*d*), inner claw curvature (θ), maximum setal length (maximum *d*), average setal aspect ratio (mean *d*/*e*), and setal density (see S.3 for detailed variable definitions).

Figure 3.3. OLS regressions of morphometric traits with snout-vent-length (log-transformed) color-coded by habitat use; slopes are shown with 95% confidence interval bands for maximum setal length, average setal aspect ratio, setal density, total pad area, pad aspect ratio, claw length, and inner claw curvature.

Figure 3.4. Plots of estimated marginal (least squares) means for habitat use groups estimated at the grand mean of the covariate (SVL) with standard error bars for phylogenetic ANCOVA models where there was a significant predictive effect of habitat use on the morphometric trait; a) maximum setal length (grand $mean_{SVL}$=1.79); b) pad area (grand $mean_{SVL}$=1.78); c) pad aspect ratio (grand $mean_{SVL}$=1.77); d) inner claw curvature (grand $mean_{SVL}$=1.75). A=arboreal, S=saxicolous, M=mixed scansorial, G=generalist, T=terrestrial

Figure 3.1. Phylogeny of study taxa

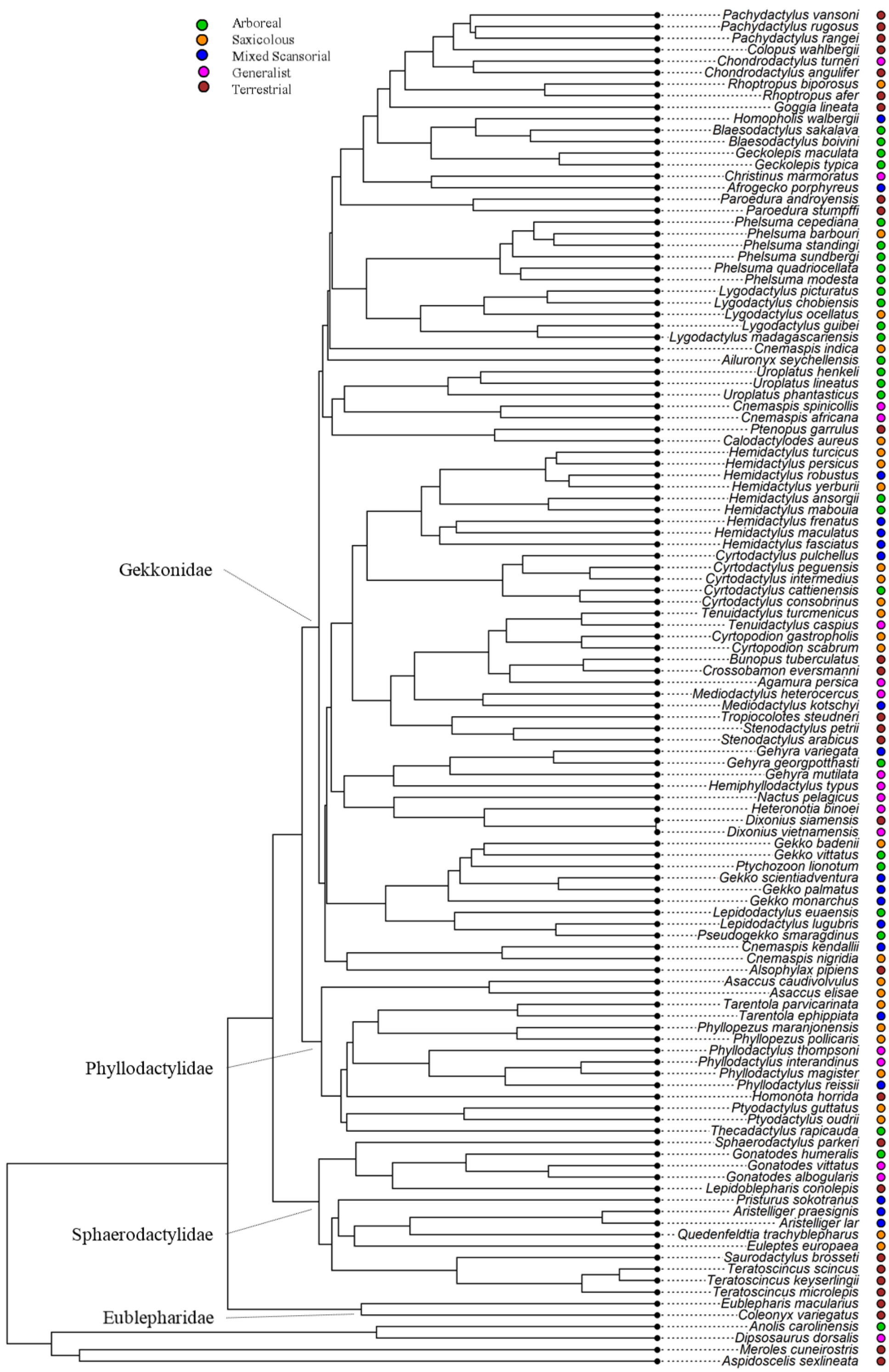


Figure 3.2. Morphometric variables of the toe pad and claw

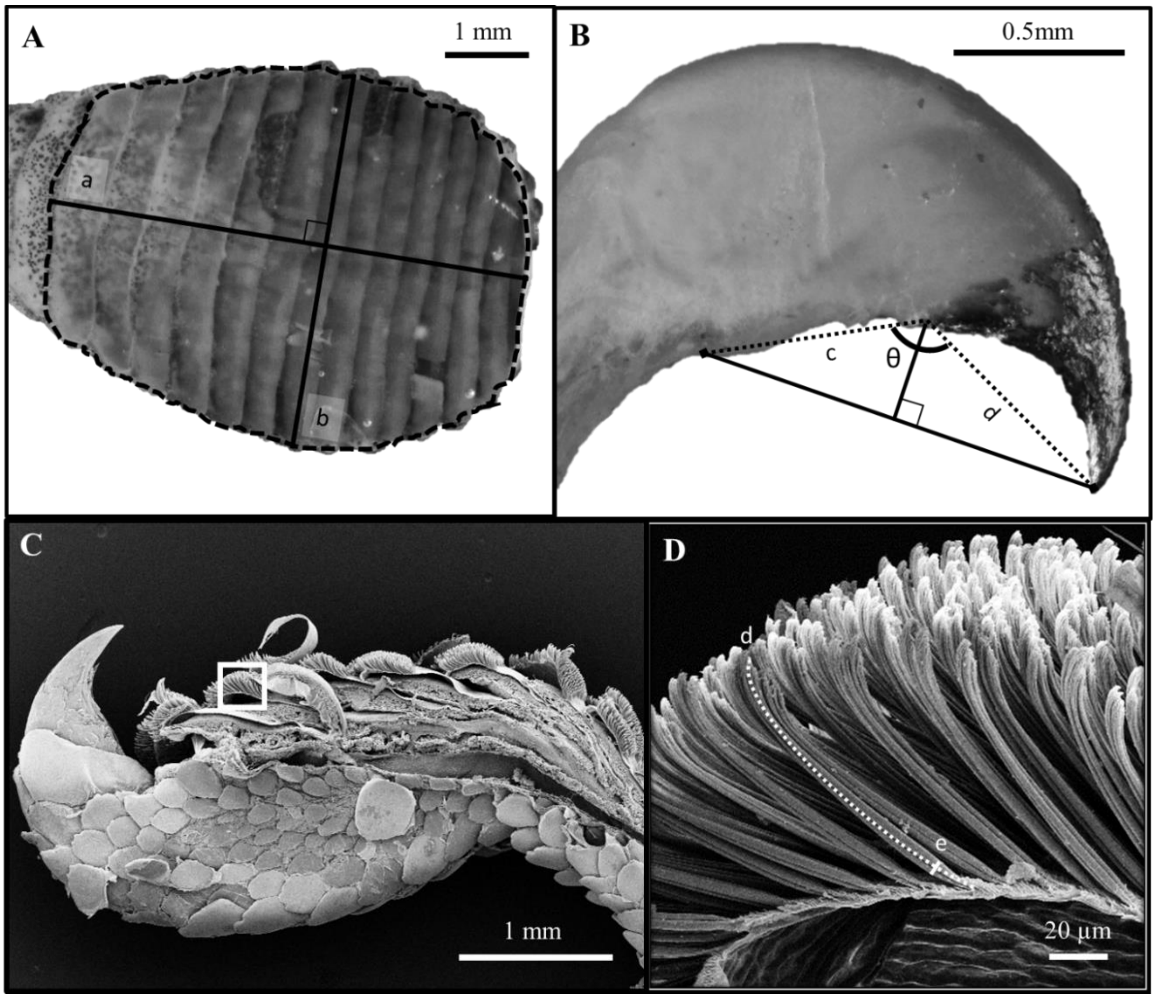


Figure 3.3. OLS regressions of log-transformed morphometric traits with snout-vent-length color-coded by habitat use.

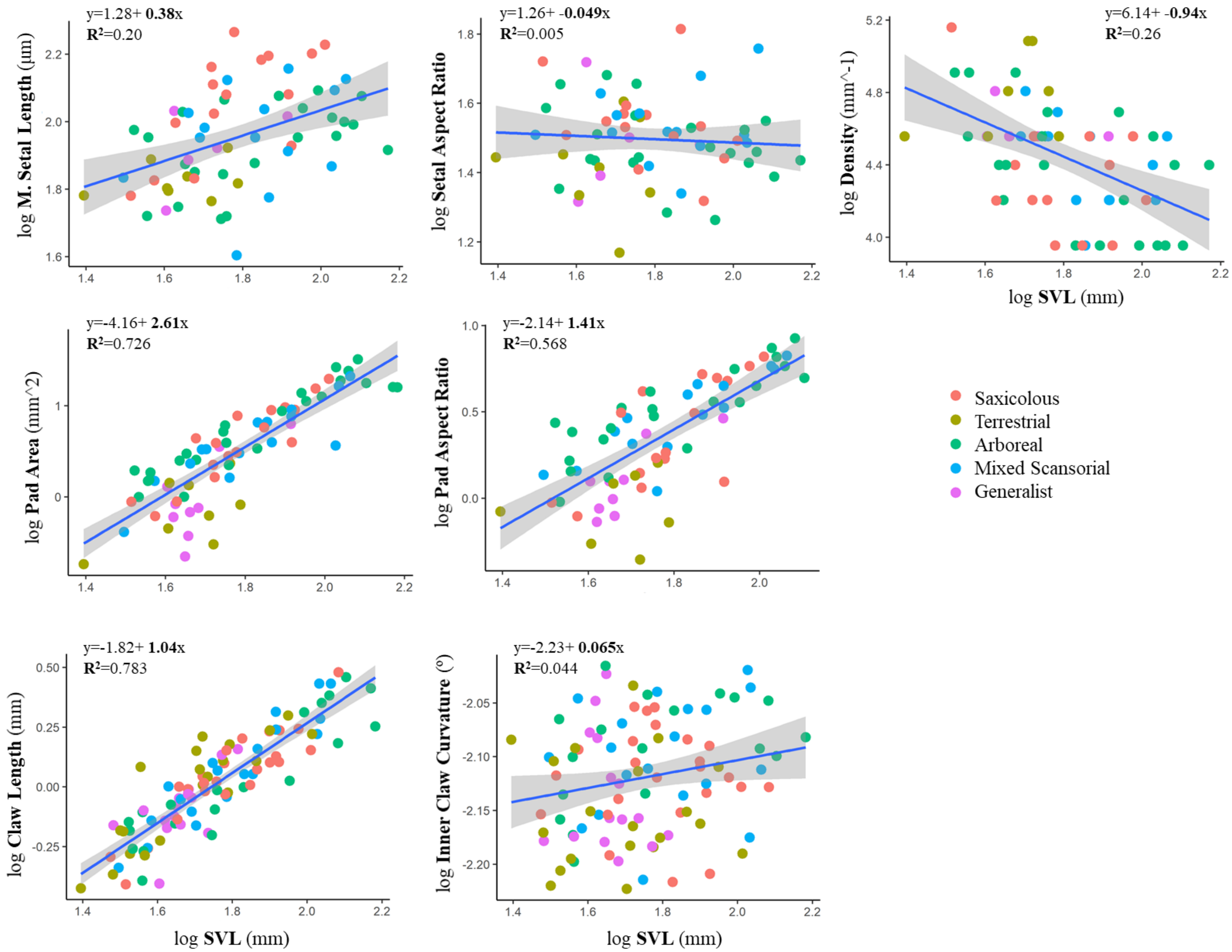
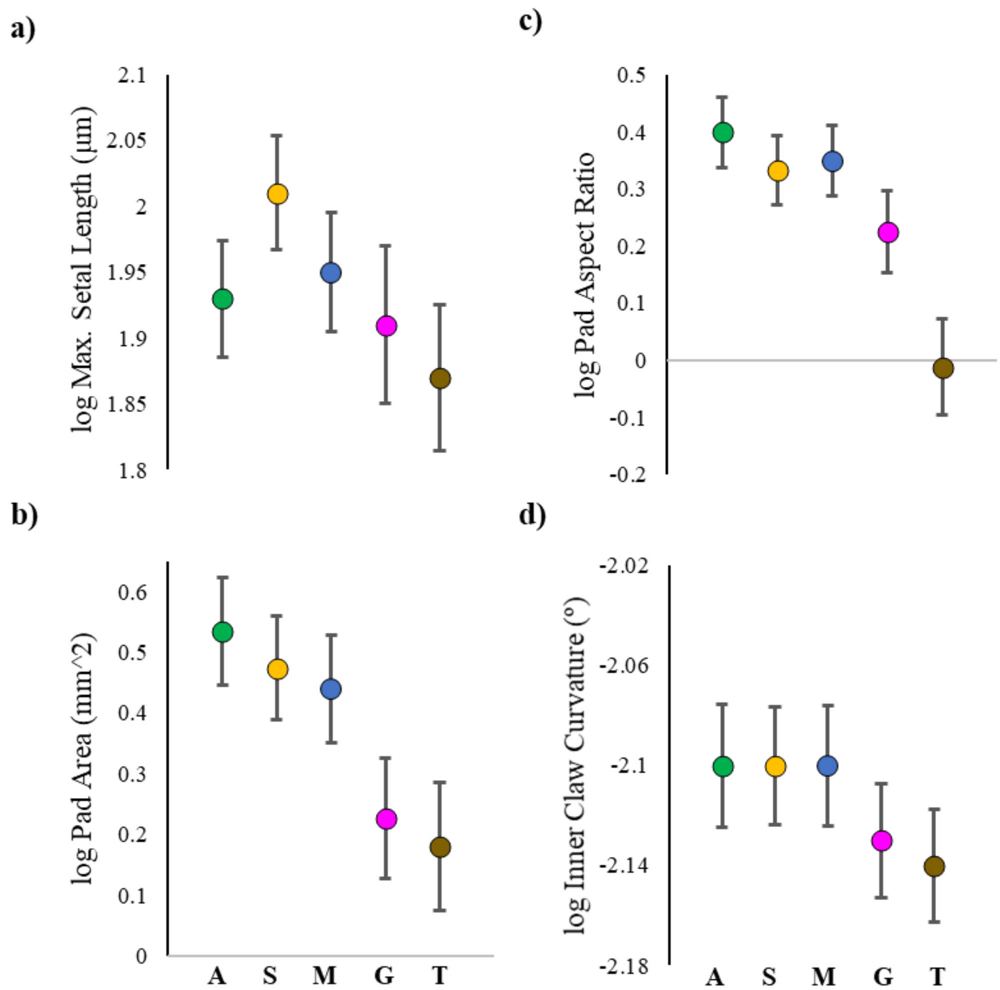


Figure 3.4. Plots of estimated marginal means for habitat use for significant phylogenetic ANCOVA models



CONCLUSION

Although it is often clear *why* animals move, *how* they move and do so successfully within their specific environments continues to be an active area of inquiry through many disciplinary lenses (Dickinson et al. 2000; Sponberg 2017). While gecko adhesion has been intensively studied for the past several decades, only a small portion of this work has attempted to address the ecology of gecko attachment and locomotion (Russell et al. 2019). My dissertation work provides much needed and new perspectives on this relationship.

Chapter 1 showed that the secondarily cursorial gecko species, *Rhoptropus afer*, maintained high-speed performance during acute changes in substrate compliance, specifically transitions into and out of sand, which aligned with behavioral observations of frequent substrate transitions within its habitat. This species appears to alter its body posture by elevating the trunk, presumably aligning its center of mass over the hindlimbs and allowing it to compensate for an otherwise reduced ability to generate propulsive force in sand. However, it is unclear if this adjustment represents an active behavioral strategy or a passive mechanical response to high acceleration. This study is one of few compliance transition studies within non-humans and was conducted under ecologically relevant experimental conditions. Pairing our experimental results with direct observations from the field allows us to make more informed inferences regarding the biological significance of *R. afer*'s unique locomotor phenotype.

Chapters 2 and 3 focused on the function and evolution of gecko toe pads and claws. In Chapter 2, claw manipulation (i.e., partial claw removal) revealed a substrate-dependent functional relationship between toe pads and claws with respect to static clinging performance in the arboreal species *Thecadactylus rapicauda*; pads were dominate on smooth surfaces (including smooth natural surfaces), while claws more significantly contributed to attachment on surfaces with asperities that allow for mechanical interlocking and shear friction, illustrating functional partitioning. On surface with intermediate roughness, these structures are functionally redundant and potentially synergistic. The frictional adhesive system of *T. rapicauda* appears sufficient for scaling low incline rough surfaces, as it exhibits high attachment safety factors and locomotor behavior was not appreciably altered by claw removal. This study quantitatively demonstrated the functional significance of gecko claws and provides a foundation from which to conduct future manipulation studies, including isolating the relative contribution of toe pads.

Through phylogenetic comparative analyses, Chapter 3 found evidence for adaptive evolution of gecko attachment morphology with respect to habitat use. Geckos that predominantly use scansorial habitats had significantly larger, longer toe pads and more curved claws than more terrestrial species. These patterns mostly aligned with studies in other lizard species and also support general biomechanical predictions of climbing versus level locomotion. Variation in these and most other traits was also explained by phylogenetic relatedness (Brownian motion process) and body size. Based on our set of morphometric traits, toe pads and claws did not co-vary with one another, however, significant covariation was detected within these apparatuses. Future analyses should fit models with additional evolutionary processes, including those that transform tree topologies under expectations of selection, which would provide a fuller picture of the evolutionary trajectory of these structures. In light of findings from Chapter 2, we would expect to observe signatures of natural selection in toe pad and claw variance.

Collectively, this work provides important ecological and functional grounding for currently held assumptions and future hypotheses regarding the evolution of gecko attachment and locomotion, as well as other complex systems.

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APPENDICES

Chapter 1

S1.1. Individual morphometric data and trial counts

Indiv.	Mass	SVL	Femur	Tibia	Pes	Digit IIIp	Humerus	Ulna	Manus	Digit IIIm	Sand Trans.	Non-Trans.
	g	mm	mm	mm	mm	mm	mm	mm	mm	mm	#trials	#trials
1	2.75	45.58	12.39	11.98	11.36	6.8	8.43	7.78	6.99	5.83	4	5
2	3.25	45.66	12.89	12.96	11.61	7.54	8.5	8.04	7.39	5.91	4	2
3	2.9	47.54	13.71	13.21	12.57	8.06	8.76	8.09	7.72	6.85	4	1
4	2.55	47.01	13.22	12.56	10.78	6.55	8.57	7.42	7.48	5.75	2	3
5	1.45	38.29	11.03	11.23	9.97	6.5	6.3	6.77	6.41	5.12	4	4
6	3	49.43	13.55	13.75	12.03	7.83	8.38	7.97	8.02	6.93	3	4
7	2.7	45.4	13.04	12.33	11.44	7.1	7.57	7.09	7.04	5.98	3	3
8	2	42.6	10.94	11.38	10.32	6.83	7.16	7.19	6.72	5.14	3	5
9	3.2	43.91	12.81	13.06	12.37	6.69	7.85	7.35	6.73	5.84	3	4
10	1.5	35.97	10.14	10.97	9.51	6.07	6.3	3.61	6.1	4.84	5	2
mean	2.53	44.14	12.37	12.34	11.20	7.00	7.78	7.13	7.06	5.82		
max.	3.25	49.43	13.71	13.75	12.57	8.06	8.76	8.09	8.02	6.93		
min.	1.45	35.97	10.14	10.97	9.51	6.07	6.30	3.61	6.10	4.84		

S1.2. Summary of model sample sizes

a) Total number observations and trials for instantaneous velocity and body pitch angle (five observations for five checkpoints per trial)

	Sand Transition	**Non-transition**
Obs.	130	150
Trials	26	30

b) Total number of strides within limb 1 and 2 for transition 1 and 2

stride pair	**Velocity**	**Duty Factor**	**Body Pitch Angle**
T1 L1	52	52	50
T1 L2	60	60	60
T2 L1	52	52	52
T2 L2	44	44	46

S1.3. Summary results of simple OLS variable regressions and covariate correlations

a) Dependent and independent variable relationships for models of checkpoint (CP): instantaneous velocity (Vel), BPA (body pitch angle), body temperature (temp), snout-vent-length (SVL). Regression and correlation parameters, including R-squared (R^2) and Pearson's correlation coefficient (R) are shown. Bolded terms indicate significance at the p<0.05 level.

y	x	R^2	int.	SE	b	SE	t	p	df	Resid. SE
Sand Trans.										
Vel	SVL	0.122	2.041	0.040	0.111	0.026	4.220	**4.60E-05**	128	0.159
Vel	temp	0.239	12.356	1.602	-6.713	1.059	-6.339	**3.63E-09**	128	0.148
BPA	SVL	0.002	0.964	0.052	0.016	0.034	0.475	0.635	128	0.207
BPA	temp	0.022	4.733	2.213	-2.476	1.462	-1.693	0.092	128	0.205
BPA	Vel	0.058	0.341	0.230	0.294	0.105	2.812	**0.0057**	128	0.201
Non-trans.										
Vel	SVL	0.058	0.855	0.434	0.794	0.264	3.006	**0.00311**	148	0.126
Vel	temp	0.001	2.519	1.056	-0.240	0.699	-0.342	0.7325	148	0.130
BPA	SVL	0.025	-0.064	0.572	0.676	0.348	1.940	*0.0543*	148	0.167
BPA	temp	0.005	2.224	1.366	-0.781	0.905	-0.864	0.389	148	0.168
BPA	Vel	0.025	0.603	0.227	0.205	0.105	1.946	*0.0535*	148	0.167

Correlation pair			
Sand Trans.	**R**	**p**	**N**
Vel, SVL	0.349	**4.60E-05**	128
Vel, temp	-0.489	**3.63E-09**	128
Non-trans.			
Vel, SVL	0.240	**0.003**	148
Vel, temp	-0.028	0.733	148

b) Dependent and independent for models of stride pairs within limb 1 and 2 (L1 and 2) for transitions 1 and 2 (T1 and 2): stride velocity (Vel), duty factor (DF), BPA (body pitch angle), body temperature (temp), snout-vent-length (SVL). Regression and correlation parameters, including R-squared (R^2) and Pearson's correlation coefficient (R) are shown. Bolded terms indicate significance at the p<0.05 level.

(stride pair)	**y**	**x**	**R^2**	**int.**	**SE**	**b**	**SE**	**t**	**p**	**df**	**Resid. SE**
T1_L1	Vel	temp	0.074	7.636	2.802	-3.634	1.852	-1.96	*0.056*	48	0.184
	Vel	SVL	0.132	-0.470	0.966	1.596	0.591	2.70	**0.009**	48	0.178
	DF	Vel	0.230	0.482	0.238	-0.419	0.111	-3.79	**4.22E-04**	48	0.147
	DF	SVL	0.036	0.776	0.889	-0.728	0.544	-1.34	0.187	48	0.164
	BPA	Vel	0.033	0.830	0.208	0.124	0.097	1.28	0.206	48	0.128
	BPA	SVL	0.066	-0.161	0.684	0.768	0.419	1.84	0.073	48	0.126
T1_L2	Vel	temp	0.082	7.654	2.408	-3.632	1.593	-2.28	**0.026**	58	0.188
	Vel	SVL	0.160	-0.698	0.862	1.751	0.527	3.32	**0.002**	58	0.180
	DF	Vel	0.401	0.574	0.153	-0.440	0.071	-6.23	**5.61E-08**	58	0.106
	DF	SVL	0.015	0.222	0.648	-0.366	0.396	-0.92	0.359	58	0.136
	BPA	Vel	0.070	0.767	0.182	0.176	0.084	2.09	**0.041**	58	0.126
	BPA	SVL	0.047	0.113	0.609	0.633	0.372	1.70	0.095	58	0.127
T2_L1	Vel	temp	0.260	11.236	2.167	-6.001	1.432	-4.19	**1.13E-04**	50	0.152
	Vel	SVL	0.228	-0.775	0.731	1.798	0.449	4.01	**2.05E-04**	50	0.153
	DF	Vel	0.529	0.936	0.183	-0.636	0.085	-7.49	**1.02E-09**	50	0.106
	DF	SVL	0.074	0.975	0.708	-0.865	0.434	-1.99	*0.052*	50	0.148
	BPA	Vel	0.093	0.736	0.190	0.199	0.088	2.26	**0.028**	50	0.110
	BPA	SVL	0.000	1.152	0.548	0.007	0.337	0.02	0.983	50	0.115
T2_L2	Vel	temp	0.169	8.294	2.094	-4.079	1.382	-2.95	**0.005**	43	0.136
	Vel	SVL	0.147	0.174	0.712	1.194	0.438	2.73	**0.009**	43	0.137
	DF	Vel	0.288	0.431	0.186	-0.366	0.088	-4.17	**1.45E-04**	43	0.086
	DF	SVL	0.036	0.486	0.511	-0.510	0.315	-1.62	0.112	43	0.112
	BPA	Vel	0.055	0.698	0.267	0.199	0.126	1.58	0.122	43	0.123
	BPA	SVL	0.001	1.234	0.654	-0.072	0.403	-0.18	0.859	43	0.126

(stride pair)	**Correlation pair**	**R**	**p**	**N**
T1_L1	Vel, SVL	0.036	**0.009**	50
	Vel, temp	-0.272	*0.056*	50
T1_L2	Vel, SVL	0.400	**0.002**	60
	Vel, temp	-0.287	**0.026**	60
T2_L1	Vel, SVL	0.493	**2.05E-04**	52
	Vel, temp	-0.510	**1.13E-04**	52
T2_L2	Vel, SVL	0.384	**0.009**	45
	Vel, temp	-0.411	**0.005**	45

S1.4. Summary tables of substrate use and transitions from field observations (GoPro recordings)

Substrate types used by *R. afer* during escapes

All types used	Rock and Gravel	Rock and Sand	Gravel and Sand	Rock only	**Total Escapes**
30	4	3	5	9	**51**

Total instances of *R. afer* using each substrate type during escapes

Rock	Gravel	Sand	**Total Instances**
125	96	110	**331**

Total instances of sand transitions by *R. afer* during escapes

Into sand	Out of sand	**Total Sand Transitions**
103	101	**204**

Total instances of compliance transitions by *R. afer* during escapes

To more compliant	To less compliant	**Total Transitions**
136	125	**261**

S1.5. R {nmle} output: instantaneous velocity (Vel) and body pitch angle (BPA) models for sand transition (sa) and non-transition (ns) trials

a) Velocity: sand-transition

```
saV = lme(Vel ~  temp + SVL + CP, random = ~1|geckoID/trial,
+                    SA, method="ML")
> summary(saV)
Linear mixed-effects model fit by maximum likelihood
 Data: SA
        AIC       BIC   logLik
  -467.9136 -439.2383 243.9568

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1243546

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.08238217 0.02266129

Fixed effects: Vel ~ temp + SVL + CP
                Value Std.Error  DF   t-value p-value
(Intercept)  5.959489 2.9337180 100  2.031378  0.0449
temp        -2.578440 1.9337095  15 -1.333416  0.2023
SVL          0.089764 0.0966014   8  0.929221  0.3800
CP2    0.003961 0.0064615 100  0.612954  0.5413
CP3   -0.009273 0.0064615 100 -1.435102  0.1544
CP4   -0.020751 0.0064615 100 -3.211422  0.0018
CP5   -0.014573 0.0064615 100 -2.255296  0.0263
 Correlation:
          (Intr) temp   SVL    Intrv2 Intrv3 Intrv4
temp      -0.999
SVL       -0.076  0.027
CP2 -0.001  0.000  0.000
CP3 -0.001  0.000  0.000  0.500
CP4 -0.001  0.000  0.000  0.500  0.500
CP5 -0.001  0.000  0.000  0.500  0.500  0.500

> VarCorr(saV)
            Variance     StdDev
geckoID =
(Intercept) 0.0154640663 0.12435460
trial =
(Intercept) 0.0067868218 0.08238217
Residual    0.0005135342 0.02266129

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.9210518 -0.7445191  0.2032380  0.6446408  1.7893077

Number of Observations: 130
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> CPs(saV, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower         est.        upper
(Intercept)  0.297948114  5.959489491 11.621030868
temp        -6.587542569 -2.578439900  1.430662769
SVL         -0.126918782  0.089764051  0.306446884
CP2   -0.008508894  0.003960588  0.016430071
CP3   -0.021742365 -0.009272883  0.003196600
CP4   -0.033220024 -0.020750541 -0.008281059
CP5   -0.027042039 -0.014572557 -0.002103074
attr(,"label")
[1] "Fixed effects:"

> anova(saV, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1   100 4.126495  0.0449
temp            1    15 1.777999  0.2023
SVL             1     8 0.863451  0.3800
CP         4   100 4.962426  0.0011

> #estimated marginal means (least squares)
> emmls = emmeans(saV, pairwise ~ CP,      mode="containment")
> summary(emmls)
$emmeans
 CP temp  SVL emmean     SE df lower.CL upper.CL
```

```
 1        1.51 1.42   2.19 0.0451  8     2.08      2.29
 2        1.51 1.42   2.19 0.0451  8     2.09      2.29
 3        1.51 1.42   2.18 0.0451  8     2.07      2.28
 4        1.51 1.42   2.17 0.0451  8     2.06      2.27
 5        1.51 1.42   2.17 0.0451  8     2.07      2.28

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                                   estimate      SE  df t.ratio p.value
 1 1.51304377907692 1.42255125953846 - 2 1.51304377907692 1.42255125953846 -0.00396 0.00646 100 -0.613  0.9727
 1 1.51304377907692 1.42255125953846 - 3 1.51304377907692 1.42255125953846  0.00927 0.00646 100  1.435  0.6067
 1 1.51304377907692 1.42255125953846 - 4 1.51304377907692 1.42255125953846  0.02075 0.00646 100  3.211  0.0150
 1 1.51304377907692 1.42255125953846 - 5 1.51304377907692 1.42255125953846  0.01457 0.00646 100  2.255  0.1684
 2 1.51304377907692 1.42255125953846 - 3 1.51304377907692 1.42255125953846  0.01323 0.00646 100  2.048  0.2511
 2 1.51304377907692 1.42255125953846 - 4 1.51304377907692 1.42255125953846  0.02471 0.00646 100  3.824  0.0021
 2 1.51304377907692 1.42255125953846 - 5 1.51304377907692 1.42255125953846  0.01853 0.00646 100  2.868  0.0395
 3 1.51304377907692 1.42255125953846 - 4 1.51304377907692 1.42255125953846  0.01148 0.00646 100  1.776  0.3931
 3 1.51304377907692 1.42255125953846 - 5 1.51304377907692 1.42255125953846  0.00530 0.00646 100  0.820  0.9238
 4 1.51304377907692 1.42255125953846 - 5 1.51304377907692 1.42255125953846 -0.00618 0.00646 100 -0.956  0.8739

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates




saV2 = lme(Vel ~  SVL + CP, random = ~1|geckoID/trial,
+            SA, method="ML")
> summary(saV2)
Linear mixed-effects model fit by maximum likelihood
 Data: SA
        AIC       BIC   logLik
  -468.3078 -442.4999 243.1539

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1422284

 Formula: ~1 | trial %in% geckoID
        (Intercept)  Residual
StdDev:  0.08079735 0.0226613

Fixed effects: Vel ~ SVL + CP
                 Value  Std.Error  DF   t-value p-value
(Intercept)  2.0530923 0.16940887 100 12.119154  0.0000
SVL          0.0923115 0.10839397   8  0.851629  0.4192
CP2     0.0039606 0.00643538 100  0.615440  0.5397
CP3    -0.0092729 0.00643538 100 -1.440923  0.1527
CP4    -0.0207505 0.00643538 100 -3.224449  0.0017
CP5    -0.0145726 0.00643538 100 -2.264445  0.0257
 Correlation:
          (Intr) SVL    Intrv2 Intrv3 Intrv4
SVL       -0.956
CP2 -0.019  0.000
CP3 -0.019  0.000  0.500
CP4 -0.019  0.000  0.500  0.500
CP5 -0.019  0.000  0.500  0.500  0.500

> VarCorr(saV2)
            Variance     StdDev
geckoID =
(Intercept) 0.0202289207 0.14222841
trial =
(Intercept) 0.0065282124 0.08079735
Residual    0.0005135343 0.02266130

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.9261395 -0.7448131  0.2182990  0.6322782  1.8048179

Number of Observations: 130
Number of Groups:
           geckoID trial %in% geckoID
                10                 26

> CPs(saV2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower         est.        upper
(Intercept)  1.724837701  2.053092252  2.381346804
SVL         -0.151809087  0.092311484  0.336432055
CP2    -0.008508896  0.003960588  0.016430072
CP3    -0.021742367 -0.009272883  0.003196602
CP4    -0.033220025 -0.020750541 -0.008281057
CP5    -0.027042041 -0.014572557 -0.002103072
```

```
attr(,"label")
[1] "Fixed effects:"

> anova(saV2, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1   100 146.87390  <.0001
SVL             1     8   0.72527  0.4192
CP        4   100   5.00277  0.0010

> #estimated marginal means (least squares)
> emmls = emmeans(saV2, pairwise ~ CP + SVL, mode="containment")
> summary(emmls)
$emmeans
 CP  SVL emmean     SE df lower.CL upper.CL
 1        1.42    2.18 0.0503  8     2.07     2.30
 2        1.42    2.19 0.0503  8     2.07     2.30
 3        1.42    2.18 0.0503  8     2.06     2.29
 4        1.42    2.16 0.0503  8     2.05     2.28
 5        1.42    2.17 0.0503  8     2.05     2.29


Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                  estimate      SE  df t.ratio p.value
 1 1.42255125953846 - 2 1.42255125953846 -0.00396 0.00644 100 -0.615  0.9723
 1 1.42255125953846 - 3 1.42255125953846  0.00927 0.00644 100  1.441  0.6029
 1 1.42255125953846 - 4 1.42255125953846  0.02075 0.00644 100  3.224  0.0144
 1 1.42255125953846 - 5 1.42255125953846  0.01457 0.00644 100  2.264  0.1652
 2 1.42255125953846 - 3 1.42255125953846  0.01323 0.00644 100  2.056  0.2474
 2 1.42255125953846 - 4 1.42255125953846  0.02471 0.00644 100  3.840  0.0020
 2 1.42255125953846 - 5 1.42255125953846  0.01853 0.00644 100  2.880  0.0383
 3 1.42255125953846 - 4 1.42255125953846  0.01148 0.00644 100  1.784  0.3889
 3 1.42255125953846 - 5 1.42255125953846  0.00530 0.00644 100  0.824  0.9228
 4 1.42255125953846 - 5 1.42255125953846 -0.00618 0.00644 100 -0.960  0.8723

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates




> saV3 = lme(Vel ~  temp + CP, random = ~1|geckoID/trial,
+              SA, method="ML")
> summary(saV3)
Linear mixed-effects model fit by maximum likelihood
 Data: SA
        AIC       BIC   logLik
  -469.0563 -443.2485 243.5282

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1328587

 Formula: ~1 | trial %in% geckoID
        (Intercept)  Residual
StdDev:  0.08178935 0.0226613

Fixed effects: Vel ~ temp + CP
                 Value Std.Error  DF   t-value p-value
(Intercept)  5.900459 2.9245807 100  2.017540  0.0463
temp        -2.451225 1.9325496  15 -1.268389  0.2240
CP2     0.003961 0.0064354 100  0.615440  0.5397
CP3    -0.009273 0.0064354 100 -1.440923  0.1527
CP4    -0.020751 0.0064354 100 -3.224449  0.0017
CP5    -0.014573 0.0064354 100 -2.264445  0.0257
 Correlation:
          (Intr) temp   Intrv2 Intrv3 Intrv4
temp      -1.000
CP2 -0.001  0.000
CP3 -0.001  0.000  0.500
CP4 -0.001  0.000  0.500  0.500
CP5 -0.001  0.000  0.500  0.500  0.500

> VarCorr(saV3)
            Variance     StdDev
geckoID =
(Intercept) 0.0176514327 0.13285869
trial =
(Intercept) 0.0066894979 0.08178935
Residual    0.0005135343 0.02266130

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
```

```
-1.9218975 -0.7450121  0.2009656  0.6462377  1.7943810

Number of Observations: 130
Number of Groups:
           geckoID trial %in% geckoID
                10                26
> CPs(saV3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower          est.        upper
(Intercept)  0.233654675  5.900458889 11.567263102
temp        -6.474177230 -2.451225027  1.571727176
CP2    -0.008508896  0.003960588  0.016430072
CP3    -0.021742367 -0.009272883  0.003196601
CP4    -0.033220025 -0.020750541 -0.008281057
CP5    -0.027042041 -0.014572557 -0.002103073
attr(,"label")
[1] "Fixed effects:"
> anova(saV3, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1   100 4.070468  0.0463
temp            1    15 1.608811  0.2240
CP        4    100 5.002770  0.0010

> #estimated marginal means (least squares)
> emmls = emmeans(saV3, pairwise ~ CP+temp, mode="containment")
> summary(emmls)
$emmeans
 CP temp emmean     SE df lower.CL upper.CL
 1        1.51   2.19 0.0469  9     2.09     2.30
 2        1.51   2.20 0.0469  9     2.09     2.30
 3        1.51   2.18 0.0469  9     2.08     2.29
 4        1.51   2.17 0.0469  9     2.06     2.28
 5        1.51   2.18 0.0469  9     2.07     2.28

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                estimate      SE  df t.ratio p.value
 1 1.51304377907692 - 2 1.51304377907692 -0.00396 0.00644 100  -0.615  0.9723
 1 1.51304377907692 - 3 1.51304377907692  0.00927 0.00644 100   1.441  0.6029
 1 1.51304377907692 - 4 1.51304377907692  0.02075 0.00644 100   3.224  0.0144
 1 1.51304377907692 - 5 1.51304377907692  0.01457 0.00644 100   2.264  0.1652
 2 1.51304377907692 - 3 1.51304377907692  0.01323 0.00644 100   2.056  0.2474
 2 1.51304377907692 - 4 1.51304377907692  0.02471 0.00644 100   3.840  0.0020
 2 1.51304377907692 - 5 1.51304377907692  0.01853 0.00644 100   2.880  0.0383
 3 1.51304377907692 - 4 1.51304377907692  0.01148 0.00644 100   1.784  0.3889
 3 1.51304377907692 - 5 1.51304377907692  0.00530 0.00644 100   0.824  0.9228
 4 1.51304377907692 - 5 1.51304377907692 -0.00618 0.00644 100  -0.960  0.8723

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates



saV4 = lme(Vel ~ CP, random = ~1|geckoID/trial,
+             SA, method="ML")
> summary(saV4)
Linear mixed-effects model fit by maximum likelihood
 Data: SA
        AIC       BIC  logLik
  -469.5821 -446.6418 242.791

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1490874

 Formula: ~1 | trial %in% geckoID
        (Intercept)  Residual
StdDev:  0.08057177 0.0226613

Fixed effects: Vel ~ CP
                 Value  Std.Error  DF  t-value p-value
(Intercept)  2.1907998 0.05150671 100 42.53426  0.0000
CP2     0.0039606 0.00640958 100  0.61792  0.5380
CP3    -0.0092729 0.00640958 100 -1.44672  0.1511
CP4    -0.0207505 0.00640958 100 -3.23742  0.0016
CP5    -0.0145726 0.00640958 100 -2.27356  0.0251
 Correlation:
          (Intr) Intrv2 Intrv3 Intrv4
CP2 -0.062
CP3 -0.062  0.500
CP4 -0.062  0.500  0.500
```

```
CP5 -0.062  0.500  0.500  0.500

> VarCorr(saV4)
            Variance     StdDev
geckoID =
(Intercept) 0.0222270386 0.14908735
trial =
(Intercept) 0.0064918094 0.08057177
Residual    0.0005135343 0.02266130

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.9263265 -0.7450025  0.2158932  0.6344441  1.8080584

Number of Observations: 130
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> CPs(saV4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower         est.        upper
(Intercept)  2.090596363  2.190799793  2.291003222
CP2   -0.008508896  0.003960588  0.016430073
CP3   -0.021742367 -0.009272883  0.003196602
CP4   -0.033220025 -0.020750541 -0.008281057
CP5   -0.027042041 -0.014572557 -0.002103072
attr(,"label")
[1] "Fixed effects:"
> anova(saV4, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1   100 1809.1632  <.0001
CP        4   100    5.0431   0.001
> #estimated marginal means (least squares)
> emmls = emmeans(saV4, pairwise ~ CP,     mode="containment")
> summary(emmls)
$emmeans
 CP emmean     SE df lower.CL upper.CL
 1          2.19 0.0515  9     2.07     2.31
 2          2.19 0.0515  9     2.08     2.31
 3          2.18 0.0515  9     2.07     2.30
 4          2.17 0.0515  9     2.05     2.29
 5          2.18 0.0515  9     2.06     2.29

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast estimate      SE  df t.ratio p.value
 1 - 2    -0.00396 0.00641 100 -0.618  0.9719
 1 - 3     0.00927 0.00641 100  1.447  0.5992
 1 - 4     0.02075 0.00641 100  3.237  0.0139
 1 - 5     0.01457 0.00641 100  2.274  0.1622
 2 - 3     0.01323 0.00641 100  2.065  0.2437
 2 - 4     0.02471 0.00641 100  3.855  0.0019
 2 - 5     0.01853 0.00641 100  2.891  0.0371
 3 - 4     0.01148 0.00641 100  1.791  0.3847
 3 - 5     0.00530 0.00641 100  0.827  0.9217
 4 - 5    -0.00618 0.00641 100 -0.964  0.8706

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates
```

S1.5. R {nmle} output: velocity (Vel) and body pitch angle (BPA) models for sand transition (sa) and non-transition (ns) trials

a) Velocity: non-transition

```
nsV = lme(Vel ~  temp + SVL + CP, random = ~1|geckoID/trial,
+            NS, method="ML")
> summary(nsV)
Linear mixed-effects model fit by maximum likelihood
 Data: NS
        AIC       BIC   logLik
  -520.1398 -490.0335 270.0699

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
```

```
StdDev:  0.08976395

 Formula: ~1 | trial %in% geckoID
        (Intercept)    Residual
StdDev:  0.08348524 0.02558829

Fixed effects: Vel ~ temp + SVL + CP
                 Value Std.Error  DF   t-value p-value
(Intercept)  1.5737836 1.6115521 115  0.976564  0.3308
temp        -0.2896615 0.5804997 115 -0.498987  0.6187
SVL          0.6387952 0.8324789   8  0.767341  0.4649
CP2    0.0046750 0.0067715 115  0.690391  0.4913
CP3   -0.0099485 0.0067855 115 -1.466149  0.1453
CP4   -0.0321506 0.0068077 115 -4.722689  0.0000
CP5   -0.0212603 0.0068374 115 -3.109417  0.0024
 Correlation:
          (Intr) temp   SVL    Intrv2 Intrv3 Intrv4
temp      -0.530
SVL       -0.839 -0.016
CP2  0.018 -0.038  0.001
CP3  0.037 -0.074  0.001  0.501
CP4  0.056 -0.110  0.002  0.501  0.504
CP5  0.074 -0.143  0.002  0.500  0.504  0.508

> VarCorr(nsV)
            Variance     StdDev
geckoID =
(Intercept) 0.0080575662 0.08976395
trial =
(Intercept) 0.0069697859 0.08348524
Residual    0.0006547605 0.02558829

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.35371152 -0.62647180  0.05018317  0.61968952  1.85703239

Number of Observations: 150
Number of Groups:
           geckoID trial %in% geckoID
                10                 30
> CPs(nsV, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower         est.        upper
(Intercept) -1.543016994  1.573783556  4.690584106
temp        -1.412369119 -0.289661522  0.833046074
SVL         -1.235576516  0.638795185  2.513166885
CP2   -0.008421333  0.004674979  0.017771290
CP3   -0.023071790 -0.009948480  0.003174829
CP4   -0.045316863 -0.032150560 -0.018984258
CP5   -0.034484115 -0.021260333 -0.008036550
attr(,"label")
[1] "Fixed effects:"
> anova(nsV, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1   115 0.953677  0.3308
temp            1   115 0.248988  0.6187
SVL             1     8 0.588812  0.4649
CP         4   115 9.845265  <.0001
> #estimated marginal means (least squares)
> emmls = emmeans(nsV, pairwise ~ CP,      mode="containment")
> summary(emmls)
$emmeans
 CP temp  SVL emmean     SE df lower.CL upper.CL
 1        1.51 1.64   2.19 0.0342  8     2.11     2.26
 2        1.51 1.64   2.19 0.0342  8     2.11     2.27
 3        1.51 1.64   2.18 0.0342  8     2.10     2.25
 4        1.51 1.64   2.15 0.0342  8     2.07     2.23
 5        1.51 1.64   2.16 0.0342  8     2.08     2.24

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                                    estimate      SE  df t.ratio p.value
 1 1.50942971514 1.64136459453333 - 2 1.50942971514 1.64136459453333 -0.00467 0.00677 115 -0.690  0.9582
 1 1.50942971514 1.64136459453333 - 3 1.50942971514 1.64136459453333  0.00995 0.00679 115  1.466  0.5864
 1 1.50942971514 1.64136459453333 - 4 1.50942971514 1.64136459453333  0.03215 0.00681 115  4.723  0.0001
 1 1.50942971514 1.64136459453333 - 5 1.50942971514 1.64136459453333  0.02126 0.00684 115  3.109  0.0196
 2 1.50942971514 1.64136459453333 - 3 1.50942971514 1.64136459453333  0.01462 0.00677 115  2.160  0.2026
 2 1.50942971514 1.64136459453333 - 4 1.50942971514 1.64136459453333  0.03683 0.00678 115  5.428  <.0001
 2 1.50942971514 1.64136459453333 - 5 1.50942971514 1.64136459453333  0.02594 0.00681 115  3.811  0.0021
 3 1.50942971514 1.64136459453333 - 4 1.50942971514 1.64136459453333  0.02220 0.00677 115  3.279  0.0118
 3 1.50942971514 1.64136459453333 - 5 1.50942971514 1.64136459453333  0.01131 0.00678 115  1.668  0.4580
 4 1.50942971514 1.64136459453333 - 5 1.50942971514 1.64136459453333 -0.01089 0.00677 115 -1.608  0.4951

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates
```

```
> nsV2 = lme(Vel ~  SVL + CP, random = ~1|geckoID/trial,
+             NS, method="ML")
> summary(nsV2)
Linear mixed-effects model fit by maximum likelihood
 Data: NS
       AIC       BIC   logLik
  -521.8944 -494.7987 269.9472

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.08808059

 Formula: ~1 | trial %in% geckoID
        (Intercept)  Residual
StdDev:  0.08506685 0.0255546

Fixed effects: Vel ~ SVL + CP
                 Value Std.Error  DF   t-value p-value
(Intercept)  1.1447917 1.3500663 116  0.847952  0.3982
SVL          0.6336944 0.8220290   8  0.770891  0.4629
CP2    0.0045471 0.0067342 116  0.675226  0.5009
CP3   -0.0102004 0.0067342 116 -1.514710  0.1326
CP4   -0.0325230 0.0067342 116 -4.829504  0.0000
CP5   -0.0217499 0.0067342 116 -3.229754  0.0016
 Correlation:
          (Intr) SVL    Intrv2 Intrv3 Intrv4
SVL       -1.000
CP2 -0.002  0.000
CP3 -0.002  0.000  0.500
CP4 -0.002  0.000  0.500  0.500
CP5 -0.002  0.000  0.500  0.500  0.500

> VarCorr(nsV2)
            Variance     StdDev
geckoID =
(Intercept) 0.0077581906 0.08808059
trial =
(Intercept) 0.0072363695 0.08506685
Residual    0.0006530377 0.02555460

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.3524990 -0.6376058  0.0382869  0.6160979  1.8645773

Number of Observations: 150
Number of Groups:
           geckoID trial %in% geckoID
                10                 30
> CPs(nsV2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower         est.         upper
(Intercept) -1.475159375  1.144791702  3.764742778
SVL         -1.223608973  0.633694444  2.490997860
CP2   -0.008521383  0.004547125  0.017615632
CP3   -0.023268912 -0.010200405  0.002868102
CP4   -0.045591497 -0.032522990 -0.019454482
CP5   -0.034818408 -0.021749900 -0.008681393
attr(,"label")
[1] "Fixed effects:"
> anova(nsV2, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1   116  0.719023  0.3982
SVL             1     8  0.594272  0.4629
CP        4   116 10.334087  <.0001
> #estimated marginal means (least squares)
> emmls = emmeans(nsV2, pairwise ~ CP,      mode="containment")
> summary(emmls)
$emmeans
 CP  SVL emmean     SE df lower.CL upper.CL
 1        1.64   2.18 0.0338  8     2.11     2.26
 2        1.64   2.19 0.0338  8     2.11     2.27
 3        1.64   2.17 0.0338  8     2.10     2.25
 4        1.64   2.15 0.0338  8     2.07     2.23
 5        1.64   2.16 0.0338  8     2.09     2.24

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                estimate      SE  df t.ratio p.value
```

```
 1 1.64136459453333 - 2 1.64136459453333 -0.00455 0.00673 116 -0.675  0.9614
 1 1.64136459453333 - 3 1.64136459453333  0.01020 0.00673 116  1.515  0.5551
 1 1.64136459453333 - 4 1.64136459453333  0.03252 0.00673 116  4.830  <.0001
 1 1.64136459453333 - 5 1.64136459453333  0.02175 0.00673 116  3.230  0.0137
 2 1.64136459453333 - 3 1.64136459453333  0.01475 0.00673 116  2.190  0.1908
 2 1.64136459453333 - 4 1.64136459453333  0.03707 0.00673 116  5.505  <.0001
 2 1.64136459453333 - 5 1.64136459453333  0.02630 0.00673 116  3.905  0.0015
 3 1.64136459453333 - 4 1.64136459453333  0.02232 0.00673 116  3.315  0.0106
 3 1.64136459453333 - 5 1.64136459453333  0.01155 0.00673 116  1.715  0.4288
 4 1.64136459453333 - 5 1.64136459453333 -0.01077 0.00673 116 -1.600  0.5006

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates
```

```
> nsV3 = lme(Vel ~  temp + CP, random = ~1|geckoID/trial,
+             NS, method="ML")
> summary(nsV3)
Linear mixed-effects model fit by maximum likelihood
 Data: NS
       AIC       BIC  logLik
  -521.544 -494.4483 269.772

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.09382732

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.08336819 0.02558841

Fixed effects: Vel ~ temp + CP
                 Value Std.Error  DF   t-value p-value
(Intercept)  2.6240142 0.8736480 115  3.003514  0.0033
temp        -0.2902941 0.5785991 115 -0.501719  0.6168
CP2    0.0046753 0.0067480 115  0.692839  0.4898
CP3   -0.0099479 0.0067619 115 -1.471176  0.1440
CP4   -0.0321497 0.0067840 115 -4.739020  0.0000
CP5   -0.0212593 0.0068137 115 -3.120086  0.0023
 Correlation:
          (Intr) temp   Intrv2 Intrv3 Intrv4
temp      -0.999
CP2  0.034 -0.038
CP3  0.071 -0.074  0.501
CP4  0.106 -0.110  0.501  0.504
CP5  0.140 -0.144  0.500  0.504  0.508

> VarCorr(nsV3)
            Variance     StdDev
geckoID =
(Intercept) 0.0088035655 0.09382732
trial =
(Intercept) 0.0069502553 0.08336819
Residual    0.0006547666 0.02558841

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.35293897 -0.62980350  0.05316597  0.61965580  1.85365544

Number of Observations: 150
Number of Groups:
           geckoID trial %in% geckoID
                10                 30
> CPs(nsV3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower         est.        upper
(Intercept)  0.928449465  2.624014165  4.319578865
temp        -1.413231751 -0.290294075  0.832643602
CP2   -0.008421119  0.004675258  0.017771635
CP3   -0.023071316 -0.009947930  0.003175455
CP4   -0.045316143 -0.032149747 -0.018983351
CP5   -0.034483163 -0.021259264 -0.008035364
attr(,"label")
[1] "Fixed effects:"
> anova(nsV3, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1   115 9.021098  0.0033
temp            1   115 0.251722  0.6168
CP        4   115 9.913496  <.0001
> #estimated marginal means (least squares)
> emmls = emmeans(nsV3, pairwise ~ CP,      mode="containment")
```

```
> summary(emmls)
$emmeans
 CP temp emmean     SE df lower.CL upper.CL
 1       1.51   2.19 0.0352  9     2.11     2.27
 2       1.51   2.19 0.0352  9     2.11     2.27
 3       1.51   2.18 0.0352  9     2.10     2.26
 4       1.51   2.15 0.0352  9     2.07     2.23
 5       1.51   2.16 0.0352  9     2.08     2.24

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                            estimate      SE  df t.ratio p.value
 1 1.50942971514 - 2 1.50942971514 -0.00468 0.00675 115 -0.693  0.9577
 1 1.50942971514 - 3 1.50942971514  0.00995 0.00676 115  1.471  0.5832
 1 1.50942971514 - 4 1.50942971514  0.03215 0.00678 115  4.739  0.0001
 1 1.50942971514 - 5 1.50942971514  0.02126 0.00681 115  3.120  0.0190
 2 1.50942971514 - 3 1.50942971514  0.01462 0.00675 115  2.167  0.1997
 2 1.50942971514 - 4 1.50942971514  0.03682 0.00676 115  5.447  <.0001
 2 1.50942971514 - 5 1.50942971514  0.02593 0.00678 115  3.824  0.0020
 3 1.50942971514 - 4 1.50942971514  0.02220 0.00675 115  3.290  0.0114
 3 1.50942971514 - 5 1.50942971514  0.01131 0.00676 115  1.673  0.4544
 4 1.50942971514 - 5 1.50942971514 -0.01089 0.00675 115 -1.614  0.4915

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates
```

```
> nsV4 = lme(Vel ~ CP, random = ~1|geckoID/trial,
+              NS, method="ML")
> summary(nsV4)
Linear mixed-effects model fit by maximum likelihood
 Data: NS
        AIC       BIC   logLik
  -523.2977 -499.2126 269.6489

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.09215546

 Formula: ~1 | trial %in% geckoID
        (Intercept)  Residual
StdDev:  0.08494835 0.0255546

Fixed effects: Vel ~ CP
                 Value  Std.Error  DF  t-value p-value
(Intercept)  2.1856884 0.03478567 116 62.83301  0.0000
CP2     0.0045471 0.00671097 116  0.67757  0.4994
CP3    -0.0102004 0.00671097 116 -1.51996  0.1312
CP4    -0.0325230 0.00671097 116 -4.84624  0.0000
CP5    -0.0217499 0.00671097 116 -3.24095  0.0016
 Correlation:
          (Intr) Intrv2 Intrv3 Intrv4
CP2 -0.096
CP3 -0.096  0.500
CP4 -0.096  0.500  0.500
CP5 -0.096  0.500  0.500  0.500

> VarCorr(nsV4)
            Variance     StdDev
geckoID =
(Intercept) 0.0084926286 0.09215546
trial =
(Intercept) 0.0072162218 0.08494835
Residual    0.0006530377 0.02555460

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.35172229 -0.64099503  0.04011716  0.61511684  1.86118812

Number of Observations: 150
Number of Groups:
           geckoID trial %in% geckoID
                10                 30
> CPs(nsV4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower         est.        upper
(Intercept)  2.117949062  2.185688441  2.253427819
CP2    -0.008521382  0.004547125  0.017615632
CP3    -0.023268912 -0.010200405  0.002868102
CP4    -0.045591497 -0.032522990 -0.019454482
```

```
CP5   -0.034818408 -0.021749900 -0.008681393
attr(,"label")
[1] "Fixed effects:"
> anova(nsV4, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1   116 3947.988  <.0001
CP              4   116   10.406  <.0001
> #estimated marginal means (least squares)
> emmls = emmeans(nsV4, pairwise ~ CP,      mode="containment")
> summary(emmls)
$emmeans
 CP emmean     SE df lower.CL upper.CL
 1      2.19 0.0348  9     2.11     2.26
 2      2.19 0.0348  9     2.11     2.27
 3      2.18 0.0348  9     2.10     2.25
 4      2.15 0.0348  9     2.07     2.23
 5      2.16 0.0348  9     2.09     2.24

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast estimate      SE  df t.ratio p.value
 1 - 2    -0.00455 0.00671 116 -0.678  0.9609
 1 - 3     0.01020 0.00671 116  1.520  0.5517
 1 - 4     0.03252 0.00671 116  4.846  <.0001
 1 - 5     0.02175 0.00671 116  3.241  0.0132
 2 - 3     0.01475 0.00671 116  2.198  0.1880
 2 - 4     0.03707 0.00671 116  5.524  <.0001
 2 - 5     0.02630 0.00671 116  3.919  0.0014
 3 - 4     0.02232 0.00671 116  3.326  0.0102
 3 - 5     0.01155 0.00671 116  1.721  0.4252
 4 - 5    -0.01077 0.00671 116 -1.605  0.4971

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates
```

S1.5. R {nmle} output: velocity (Vel) and body pitch angle (BPA) models for sand transition (sa) and non-transition (ns) trials

b) Body Pitch Angle: sand-transition

```
saBA = lme(BPA ~  Vel + SVL + CP, random = ~1|geckoID/trial,

+            SA, method="ML")
> summary(saBA)
Linear mixed-effects model fit by maximum likelihood
 Data: SA
        AIC       BIC   logLik
  -66.76204 -38.0867 43.38102

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.02641224

 Formula: ~1 | trial %in% geckoID
        (Intercept)  Residual
StdDev:  0.07068779 0.1609995

Fixed effects: BPA ~ Vel + SVL + CP
                 Value  Std.Error DF   t-value p-value
(Intercept)  0.1253598 0.28815898 99  0.435037  0.6645
Vel      0.3555446 0.13617953 99  2.610852  0.0104
SVL         -0.0230541 0.04537388  8 -0.508091  0.6251
CP2     0.0052414 0.04590943 99  0.114168  0.9093
CP3     0.1833103 0.04592363 99  3.991635  0.0001
CP4     0.1923393 0.04599315 99  4.181911  0.0001
CP5     0.1822624 0.04594914 99  3.966612  0.0001
 Correlation:
          (Intr) X5fVav SVL    Intrv2 Intrv3 Intrv4
Vel   -0.969
SVL        0.111 -0.324
CP2 -0.068 -0.012  0.004
CP3 -0.106  0.027 -0.009  0.499
CP4 -0.139  0.061 -0.020  0.498  0.501
```

```
CP5 -0.121  0.043 -0.014  0.499  0.501  0.501

> VarCorr(saBA)
            Variance     StdDev
geckoID =
(Intercept) 0.0006976067 0.02641224
trial =
(Intercept) 0.0049967637 0.07068779
Residual    0.0259208352 0.16099949

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-4.2382902 -0.5140875  0.1774810  0.6717018  1.9187041

Number of Observations: 130
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> CPs(saBA, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.      upper
(Intercept) -0.43080332  0.12535981 0.68152294
Vel      0.09271038  0.35554458 0.61837878
SVL         -0.12483042 -0.02305408 0.07872227
CP2    -0.08336640  0.00524140 0.09384920
CP3     0.09467515  0.18331035 0.27194555
CP4     0.10356986  0.19233925 0.28110864
CP5     0.09357797  0.18226240 0.27094683
attr(,"label")
[1] "Fixed effects:"
> anova(saBA, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    99 0.189257  0.6645
Vel         1    99 6.816547  0.0104
SVL             1     8 0.258157  0.6251
CP        4    99 9.530803  <.0001
> #estimated marginal means (least squares)
> emmls = emmeans(saBA, pairwise ~ CP + SVL, mode="containment")
> summary(emmls)
$emmeans
 CP Vel  SVL emmean     SE df lower.CL upper.CL
 1            2.2 1.42  0.874 0.0366  8    0.790    0.959
 2            2.2 1.42  0.879 0.0367  8    0.795    0.964
 3            2.2 1.42  1.058 0.0366  8    0.973    1.142
 4            2.2 1.42  1.067 0.0367  8    0.982    1.151
 5            2.2 1.42  1.057 0.0367  8    0.972    1.141

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                                                          estimate     SE df t.ratio p.value
 1 2.19855111299231 1.42255125953846 - 2 2.19855111299231 1.42255125953846 -0.00524 0.0459 99 -0.114  1.0000
 1 2.19855111299231 1.42255125953846 - 3 2.19855111299231 1.42255125953846 -0.18331 0.0459 99 -3.992  0.0012
 1 2.19855111299231 1.42255125953846 - 4 2.19855111299231 1.42255125953846 -0.19234 0.0460 99 -4.182  0.0006
 1 2.19855111299231 1.42255125953846 - 5 2.19855111299231 1.42255125953846 -0.18226 0.0459 99 -3.967  0.0013
 2 2.19855111299231 1.42255125953846 - 3 2.19855111299231 1.42255125953846 -0.17807 0.0459 99 -3.876  0.0018
 2 2.19855111299231 1.42255125953846 - 4 2.19855111299231 1.42255125953846 -0.18710 0.0460 99 -4.065  0.0009
 2 2.19855111299231 1.42255125953846 - 5 2.19855111299231 1.42255125953846 -0.17702 0.0460 99 -3.850  0.0019
 3 2.19855111299231 1.42255125953846 - 4 2.19855111299231 1.42255125953846 -0.00903 0.0459 99 -0.197  0.9997
 3 2.19855111299231 1.42255125953846 - 5 2.19855111299231 1.42255125953846  0.00105 0.0459 99  0.023  1.0000
 4 2.19855111299231 1.42255125953846 - 5 2.19855111299231 1.42255125953846  0.01008 0.0459 99  0.219  0.9995

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates




> saBA2 = lme(BPA ~  SVL + CP, random = ~1|geckoID/trial,
+              SA, method="ML")
> summary(saBA2)
Linear mixed-effects model fit by maximum likelihood
 Data: SA
        AIC       BIC   logLik
  -62.30245 -36.49464 40.15123

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.03817735

 Formula: ~1 | trial %in% geckoID
        (Intercept)  Residual
StdDev:  0.08358153 0.1615503
```

```
Fixed effects: BPA ~ SVL + CP
                Value  Std.Error  DF   t-value p-value
(Intercept) 0.8540289 0.08222608 100 10.386350  0.0000
SVL         0.0148417 0.05028000   8  0.295181  0.7754
CP2   0.0066496 0.04587720 100  0.144943  0.8850
CP3   0.1800134 0.04587720 100  3.923810  0.0002
CP4   0.1849615 0.04587720 100  4.031665  0.0001
CP5   0.1770812 0.04587720 100  3.859896  0.0002
 Correlation:
          (Intr) SVL    Intrv2 Intrv3 Intrv4
SVL       -0.881
CP2 -0.279  0.000
CP3 -0.279  0.000  0.500
CP4 -0.279  0.000  0.500  0.500
CP5 -0.279  0.000  0.500  0.500  0.500

> VarCorr(saBA2)
            Variance     StdDev
geckoID =
(Intercept) 0.001457510  0.03817735
trial =
(Intercept) 0.006985873  0.08358153
Residual    0.026098495  0.16155028

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-4.1878348 -0.5485717  0.2418694  0.5786481  1.7401266

Number of Observations: 130
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> CPs(saBA2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.      upper
(Intercept)  0.69470378 0.854028879 1.01335398
SVL         -0.09839692 0.014841685 0.12808029
CP2    -0.08224424 0.006649565 0.09554337
CP3     0.09111962 0.180013424 0.26890723
CP4     0.09606771 0.184961509 0.27385531
CP5     0.08818740 0.177081206 0.26597501
attr(,"label")
[1] "Fixed effects:"
> anova(saBA2, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1   100 107.87627  <.0001
SVL             1     8   0.08713  0.7754
CP        4   100   8.98030  <.0001
> #estimated marginal means (least squares)
> emmls = emmeans(saBA2, pairwise ~ CP+ SVL, mode="containment")
> summary(emmls)
$emmeans
 CP  SVL emmean     SE df lower.CL upper.CL
 1       1.42  0.875 0.0389  8    0.786    0.965
 2       1.42  0.882 0.0389  8    0.792    0.971
 3       1.42  1.055 0.0389  8    0.966    1.145
 4       1.42  1.060 0.0389  8    0.970    1.150
 5       1.42  1.052 0.0389  8    0.963    1.142

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                estimate     SE  df t.ratio p.value
 1 1.42255125953846 - 2 1.42255125953846 -0.00665 0.0459 100 -0.145  0.9999
 1 1.42255125953846 - 3 1.42255125953846 -0.18001 0.0459 100 -3.924  0.0015
 1 1.42255125953846 - 4 1.42255125953846 -0.18496 0.0459 100 -4.032  0.0010
 1 1.42255125953846 - 5 1.42255125953846 -0.17708 0.0459 100 -3.860  0.0018
 2 1.42255125953846 - 3 1.42255125953846 -0.17336 0.0459 100 -3.779  0.0024
 2 1.42255125953846 - 4 1.42255125953846 -0.17831 0.0459 100 -3.887  0.0017
 2 1.42255125953846 - 5 1.42255125953846 -0.17043 0.0459 100 -3.715  0.0030
 3 1.42255125953846 - 4 1.42255125953846 -0.00495 0.0459 100 -0.108  1.0000
 3 1.42255125953846 - 5 1.42255125953846  0.00293 0.0459 100  0.064  1.0000
 4 1.42255125953846 - 5 1.42255125953846  0.00788 0.0459 100  0.172  0.9998

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates



> saBA3 = lme(BPA ~  Vel + CP, random = ~1|geckoID/trial,
+             SA, method="ML")
> summary(saBA3)
Linear mixed-effects model fit by maximum likelihood
```

```
 Data: SA
        AIC       BIC   logLik
  -68.49226 -42.68445 43.24613

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.02842852

 Formula: ~1 | trial %in% geckoID
        (Intercept)  Residual
StdDev:  0.07071106 0.1610209

Fixed effects: BPA ~ Vel + CP
                Value  Std.Error DF  t-value p-value
(Intercept) 0.1386680 0.28803302 99 0.481431  0.6313
Vel     0.3344877 0.12962549 99 2.580416  0.0113
CP2   0.0053248 0.04572975 99 0.116441  0.9075
CP3   0.1831151 0.04574267 99 4.003157  0.0001
CP4   0.1919023 0.04580591 99 4.189466  0.0001
CP5   0.1819555 0.04576587 99 3.975791  0.0001
 Correlation:
          (Intr) X5fVav Intrv2 Intrv3 Intrv4
Vel   -0.992
CP2 -0.068 -0.011
CP3 -0.105  0.026  0.500
CP4 -0.137  0.059  0.498  0.501
CP5 -0.120  0.041  0.499  0.500  0.501

> VarCorr(saBA3)
            Variance     StdDev
geckoID =
(Intercept) 0.0008081807 0.02842852
trial =
(Intercept) 0.0050000546 0.07071106
Residual    0.0259277398 0.16102093

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-4.1790658 -0.5222237  0.1718678  0.6750203  1.8831045

Number of Observations: 130
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> CPs(saBA3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.      upper
(Intercept) -0.41950727 0.138668013 0.69684330
Vel      0.08328823 0.334487718 0.58568720
CP2    -0.08329427 0.005324797 0.09394387
CP3     0.09447100 0.183115090 0.27175918
CP4     0.10313565 0.191902310 0.28066897
CP5     0.09326649 0.181955547 0.27064461
attr(,"label")
[1] "Fixed effects:"
> anova(saBA3, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    99 0.231776  0.6313
Vel         1    99 6.658548  0.0113
CP        4    99 9.573331  <.0001

> #estimated marginal means (least squares)
> emmls = emmeans(saBA3, pairwise ~ CP + Vel , mode="containment")
> summary(emmls)
$emmeans
 CP Vel emmean     SE df lower.CL upper.CL
 1           2.2  0.874 0.0367  9    0.791    0.957
 2           2.2  0.879 0.0367  9    0.796    0.962
 3           2.2  1.057 0.0367  9    0.974    1.140
 4           2.2  1.066 0.0367  9    0.983    1.149
 5           2.2  1.056 0.0367  9    0.973    1.139

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                  estimate     SE df t.ratio p.value
 1 2.19855111299231 - 2 2.19855111299231 -0.00532 0.0457 99 -0.116  1.0000
 1 2.19855111299231 - 3 2.19855111299231 -0.18312 0.0457 99 -4.003  0.0011
 1 2.19855111299231 - 4 2.19855111299231 -0.19190 0.0458 99 -4.189  0.0006
 1 2.19855111299231 - 5 2.19855111299231 -0.18196 0.0458 99 -3.976  0.0012
 2 2.19855111299231 - 3 2.19855111299231 -0.17779 0.0458 99 -3.885  0.0017
 2 2.19855111299231 - 4 2.19855111299231 -0.18658 0.0458 99 -4.070  0.0009
 2 2.19855111299231 - 5 2.19855111299231 -0.17663 0.0458 99 -3.857  0.0019
```

```
 3 2.19855111299231 - 4 2.19855111299231 -0.00879 0.0458 99 -0.192  0.9997
 3 2.19855111299231 - 5 2.19855111299231  0.00116 0.0457 99  0.025  1.0000
 4 2.19855111299231 - 5 2.19855111299231  0.00995 0.0457 99  0.217  0.9995

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates



> saBA4 = lme(BPA ~ CP, random = ~1|geckoID/trial,
+             SA, method="ML")
> summary(saBA4)
Linear mixed-effects model fit by maximum likelihood
 Data: SA
        AIC       BIC   logLik
  -64.21236 -41.27208 40.10618

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.0394488

 Formula: ~1 | trial %in% geckoID
        (Intercept)  Residual
StdDev:  0.08338482 0.1615503

Fixed effects: BPA ~ CP
                Value  Std.Error  DF   t-value p-value
(Intercept) 0.8753393 0.03882696 100 22.544626  0.0000
CP2   0.0066496 0.04569332 100  0.145526  0.8846
CP3   0.1800134 0.04569332 100  3.939600  0.0002
CP4   0.1849615 0.04569332 100  4.047889  0.0001
CP5   0.1770812 0.04569332 100  3.875429  0.0002
 Correlation:
          (Intr) Intrv2 Intrv3 Intrv4
CP2 -0.588
CP3 -0.588  0.500
CP4 -0.588  0.500  0.500
CP5 -0.588  0.500  0.500  0.500

> VarCorr(saBA4)
            Variance     StdDev
geckoID =
(Intercept) 0.001556208  0.03944880
trial =
(Intercept) 0.006953028  0.08338482
Residual    0.026098495  0.16155029

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-4.2223818 -0.5422054  0.2281856  0.5743880  1.7490244

Number of Observations: 130
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> CPs(saBA4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.      upper
(Intercept)  0.79980361 0.875339291 0.95087497
CP2   -0.08224424 0.006649565 0.09554337
CP3    0.09111962 0.180013424 0.26890723
CP4    0.09606771 0.184961509 0.27385531
CP5    0.08818740 0.177081206 0.26597501
attr(,"label")
[1] "Fixed effects:"
> anova(saBA4, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1   100 508.2602  <.0001
CP         4   100   9.0527  <.0001
> #estimated marginal means (least squares)
> emmls = emmeans(saBA4, pairwise ~ CP,     mode="containment")
> summary(emmls)
$emmeans
 CP emmean     SE df lower.CL upper.CL
 1         0.875 0.0388  9    0.788    0.963
 2         0.882 0.0388  9    0.794    0.970
 3         1.055 0.0388  9    0.968    1.143
 4         1.060 0.0388  9    0.972    1.148
 5         1.052 0.0388  9    0.965    1.140

Degrees-of-freedom method: containment
Confidence level used: 0.95
```

```
$contrasts
 contrast estimate     SE  df t.ratio p.value
 1 - 2    -0.00665 0.0457 100 -0.146  0.9999
 1 - 3    -0.18001 0.0457 100 -3.940  0.0014
 1 - 4    -0.18496 0.0457 100 -4.048  0.0010
 1 - 5    -0.17708 0.0457 100 -3.875  0.0017
 2 - 3    -0.17336 0.0457 100 -3.794  0.0023
 2 - 4    -0.17831 0.0457 100 -3.902  0.0016
 2 - 5    -0.17043 0.0457 100 -3.730  0.0029
 3 - 4    -0.00495 0.0457 100 -0.108  1.0000
 3 - 5     0.00293 0.0457 100  0.064  1.0000
 4 - 5     0.00788 0.0457 100  0.172  0.9998

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates
```

S1.5) R {nmle} output: velocity (Vel) and body pitch angle (BPA) models for sand transition (sa) and non-transition (ns) trials

b) Body Pitch Angle: non-transition

```
nsBA = lme(BPA ~  Vel + SVL + CP, random = ~1|geckoID/trial,

+            NS, method="ML")
> summary(nsBA)
Linear mixed-effects model fit by maximum likelihood
 Data: NS
       AIC       BIC   logLik
  -109.9256 -79.81921 64.96278

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.04936149

 Formula: ~1 | trial %in% geckoID
        (Intercept)  Residual
StdDev:  0.03818312 0.1486338

Fixed effects: BPA ~ Vel + SVL + CP
                  Value Std.Error  DF    t-value p-value
(Intercept)  0.09093618 0.9142366 115  0.0994668  0.9209
Vel       0.19417168 0.1432275 115  1.3556868  0.1779
SVL           0.31336427 0.5568683   8  0.5627260  0.5890
CP2    -0.03710901 0.0393106 115 -0.9439960  0.3472
CP3     0.05110895 0.0393323 115  1.2994141  0.1964
CP4     0.06416362 0.0395802 115  1.6211028  0.1077
CP5     0.02594219 0.0394284 115  0.6579566  0.5119
 Correlation:
          (Intr) X5fVav SVL    Intrv2 Intrv3 Intrv4
Vel    -0.169
SVL        -0.941 -0.172
CP2 -0.019 -0.017  0.003
CP3 -0.028  0.037 -0.006  0.499
CP4 -0.041  0.118 -0.020  0.495  0.501
CP5 -0.035  0.079 -0.014  0.497  0.501  0.504

> VarCorr(nsBA)
            Variance     StdDev
geckoID =
(Intercept) 0.002436557  0.04936149
trial =
(Intercept) 0.001457951  0.03818312
Residual    0.022092010  0.14863381

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-7.0725230 -0.4305789  0.1524447  0.5277481  1.9295361

Number of Observations: 150
Number of Groups:
          geckoID trial %in% geckoID
               10                 30
> CPs(nsBA, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.      upper
```

```
(Intercept) -1.67723072  0.09093618 1.85910309
Vel      -0.08283561  0.19417168 0.47117897
SVL          -0.94045518  0.31336427 1.56718371
CP2   -0.11313706 -0.03710901 0.03891905
CP3   -0.02496116  0.05110895 0.12717907
CP4   -0.01238599  0.06416362 0.14071323
CP5   -0.05031381  0.02594219 0.10219819
attr(,"label")
[1] "Fixed effects:"
> anova(nsBA, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1   115 0.0098936  0.9209
Vel         1   115 1.8378866  0.1779
SVL             1     8 0.3166605  0.5890
CP        4   115 2.1030597  0.0849
> #estimated marginal means (least squares)
> emmls = emmeans(nsBA, pairwise ~ CP,     mode="containment")
> summary(emmls)
$emmeans
CP Vel  SVL emmean     SE df lower.CL upper.CL
 1          2.16 1.64  1.024 0.0335  8    0.947     1.10
 2          2.16 1.64  0.987 0.0335  8    0.910     1.06
 3          2.16 1.64  1.075 0.0334  8    0.998     1.15
 4          2.16 1.64  1.088 0.0333  8    1.011     1.17
 5          2.16 1.64  1.050 0.0333  8    0.973     1.13

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                                estimate     SE  df t.ratio p.value
 1 2.15708532863333 1.64136459453333 - 2 2.15708532863333 1.64136459453333   0.0371 0.0393 115   0.944  0.8790
 1 2.15708532863333 1.64136459453333 - 3 2.15708532863333 1.64136459453333  -0.0511 0.0393 115  -1.299  0.6921
 1 2.15708532863333 1.64136459453333 - 4 2.15708532863333 1.64136459453333  -0.0642 0.0396 115  -1.621  0.4871
 1 2.15708532863333 1.64136459453333 - 5 2.15708532863333 1.64136459453333  -0.0259 0.0394 115  -0.658  0.9648
 2 2.15708532863333 1.64136459453333 - 3 2.15708532863333 1.64136459453333  -0.0882 0.0394 115  -2.241  0.1722
 2 2.15708532863333 1.64136459453333 - 4 2.15708532863333 1.64136459453333  -0.1013 0.0397 115  -2.553  0.0862
 2 2.15708532863333 1.64136459453333 - 5 2.15708532863333 1.64136459453333  -0.0631 0.0395 115  -1.597  0.5025
 3 2.15708532863333 1.64136459453333 - 4 2.15708532863333 1.64136459453333  -0.0131 0.0394 115  -0.331  0.9974
 3 2.15708532863333 1.64136459453333 - 5 2.15708532863333 1.64136459453333   0.0252 0.0393 115   0.640  0.9682
 4 2.15708532863333 1.64136459453333 - 5 2.15708532863333 1.64136459453333   0.0382 0.0393 115   0.972  0.8674

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates



> nsBA2 = lme(BPA ~  SVL + CP, random = ~1|geckoID/trial,
+             NS, method="ML")
> summary(nsBA2)
Linear mixed-effects model fit by maximum likelihood
 Data: NS
        AIC       BIC   logLik
  -110.1282 -83.03245 64.06408

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.0503514

 Formula: ~1 | trial %in% geckoID
        (Intercept)  Residual
StdDev:  0.04593377 0.1480791

Fixed effects: BPA ~ SVL + CP
                 Value Std.Error  DF    t-value p-value
(Intercept)  0.2903714 0.9291376 116  0.3125171  0.7552
SVL          0.4496716 0.5656742   8  0.7949303  0.4496
CP2   -0.0362261 0.0390223 116 -0.9283437  0.3552
CP3    0.0491283 0.0390223 116  1.2589814  0.2106
CP4    0.0578486 0.0390223 116  1.4824501  0.1409
CP5    0.0217190 0.0390223 116  0.5565788  0.5789
 Correlation:
          (Intr) SVL    Intrv2 Intrv3 Intrv4
SVL       -0.999
CP2 -0.021  0.000
CP3 -0.021  0.000  0.500
CP4 -0.021  0.000  0.500  0.500
CP5 -0.021  0.000  0.500  0.500  0.500

> VarCorr(nsBA2)
            Variance     StdDev
geckoID =
(Intercept) 0.002535263  0.05035140
trial =
(Intercept) 0.002109911  0.04593377
Residual    0.021927428  0.14807913
```

```
Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-7.0905893 -0.3759005  0.1569667  0.5247903  1.8998500 

Number of Observations: 150
Number of Groups: 
           geckoID trial %in% geckoID 
                10                 30 
> CPs(nsBA2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.      upper
(Intercept) -1.51272164  0.29037139 2.09346443
SVL         -0.82842029  0.44967158 1.72776345
CP2   -0.11195308 -0.03622608 0.03950091
CP3   -0.02659867  0.04912832 0.12485531
CP4   -0.01787841  0.05784858 0.13357557
CP5   -0.05400802  0.02171897 0.09744596
attr(,"label")
[1] "Fixed effects:"
> anova(nsBA2, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1   116 0.0976669  0.7552
SVL             1     8 0.6319142  0.4496
CP        4   116 1.9156153  0.1124
> #estimated marginal means (least squares)
> emmls = emmeans(nsBA2, pairwise ~ CP,     mode="containment")
> summary(emmls)
$emmeans
 CP  SVL emmean     SE df lower.CL upper.CL
 1       1.64  1.028 0.0336  8    0.951     1.11
 2       1.64  0.992 0.0336  8    0.915     1.07
 3       1.64  1.078 0.0336  8    1.000     1.16
 4       1.64  1.086 0.0336  8    1.009     1.16
 5       1.64  1.050 0.0336  8    0.973     1.13

Degrees-of-freedom method: containment 
Confidence level used: 0.95 

$contrasts
 contrast                                estimate    SE  df t.ratio p.value
 1 1.64136459453333 - 2 1.64136459453333  0.03623 0.039 116  0.928  0.8854
 1 1.64136459453333 - 3 1.64136459453333 -0.04913 0.039 116 -1.259  0.7167
 1 1.64136459453333 - 4 1.64136459453333 -0.05785 0.039 116 -1.482  0.5759
 1 1.64136459453333 - 5 1.64136459453333 -0.02172 0.039 116 -0.557  0.9809
 2 1.64136459453333 - 3 1.64136459453333 -0.08535 0.039 116 -2.187  0.1918
 2 1.64136459453333 - 4 1.64136459453333 -0.09407 0.039 116 -2.411  0.1197
 2 1.64136459453333 - 5 1.64136459453333 -0.05795 0.039 116 -1.485  0.5743
 3 1.64136459453333 - 4 1.64136459453333 -0.00872 0.039 116 -0.223  0.9994
 3 1.64136459453333 - 5 1.64136459453333  0.02741 0.039 116  0.702  0.9556
 4 1.64136459453333 - 5 1.64136459453333  0.03613 0.039 116  0.926  0.8864

Degrees-of-freedom method: containment 
P value adjustment: tukey method for comparing a family of 5 estimates 



> nsBA3 = lme(BPA ~  Vel + CP, random = ~1|geckoID/trial,
+             NS, method="ML")
> summary(nsBA3)
Linear mixed-effects model fit by maximum likelihood
 Data: NS 
       AIC       BIC   logLik
  -111.632 -84.53625 64.81599

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.05424794

 Formula: ~1 | trial %in% geckoID
        (Intercept) Residual
StdDev:  0.03555126 0.148681

Fixed effects: BPA ~ Vel + CP 
                 Value  Std.Error  DF    t-value p-value
(Intercept)  0.5744893 0.31232280 115  1.8394086  0.0684
Vel       0.2084288 0.14233312 115  1.4643732  0.1458
CP2   -0.0371738 0.03918623 115 -0.9486455  0.3448
CP3    0.0512544 0.03920777 115  1.3072506  0.1937
CP4    0.0646273 0.03945339 115  1.6380673  0.1041
CP5    0.0262523 0.03930299 115  0.6679461  0.5055
 Correlation: 
          (Intr) X5fVav Intrv2 Intrv3 Intrv4
```

```
Vel   -0.994
CP2 -0.046 -0.017
CP3 -0.099  0.037  0.499
CP4 -0.179  0.117  0.495  0.501
CP5 -0.141  0.079  0.497  0.501  0.504

> VarCorr(nsBA3)
            Variance     StdDev
geckoID =
(Intercept) 0.002942839  0.05424794
trial =
(Intercept) 0.001263892  0.03555126
Residual    0.022106036  0.14868099

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-7.1019547 -0.4285920  0.1665706  0.5386046  1.9007874

Number of Observations: 150
Number of Groups:
           geckoID trial %in% geckoID
                10                30
> CPs(nsBA3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.      upper
(Intercept) -0.03166282  0.57448925 1.18064132
Vel     -0.06780948  0.20842881 0.48466710
CP2   -0.11322596 -0.03717384 0.03887828
CP3   -0.02483956  0.05125438 0.12734831
CP4   -0.01194332  0.06462731 0.14119793
CP5   -0.05002645  0.02625228 0.10253101
attr(,"label")
[1] "Fixed effects:"
> anova(nsBA3, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1   115 3.383424  0.0684
Vel          1   115 2.144389  0.1458
CP        4   115 2.135678  0.0808
> #estimated marginal means (least squares)
> emmls = emmeans(nsBA3, pairwise ~ CP,     mode="containment")
> summary(emmls)
$emmeans
 CP Vel emmean     SE df lower.CL upper.CL
 1          2.16  1.024 0.0341  9    0.947     1.10
 2          2.16  0.987 0.0342  9    0.910     1.06
 3          2.16  1.075 0.0340  9    0.998     1.15
 4          2.16  1.089 0.0339  9    1.012     1.17
 5          2.16  1.050 0.0339  9    0.974     1.13

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                 estimate     SE  df t.ratio p.value
 1 2.15708532863333 - 2 2.15708532863333   0.0372 0.0392 115   0.949  0.8771
 1 2.15708532863333 - 3 2.15708532863333  -0.0513 0.0392 115 -1.307  0.6873
 1 2.15708532863333 - 4 2.15708532863333  -0.0646 0.0395 115 -1.638  0.4764
 1 2.15708532863333 - 5 2.15708532863333  -0.0263 0.0393 115 -0.668  0.9629
 2 2.15708532863333 - 3 2.15708532863333  -0.0884 0.0392 115 -2.254  0.1678
 2 2.15708532863333 - 4 2.15708532863333  -0.1018 0.0395 115 -2.575  0.0818
 2 2.15708532863333 - 5 2.15708532863333  -0.0634 0.0394 115 -1.611  0.4932
 3 2.15708532863333 - 4 2.15708532863333  -0.0134 0.0393 115 -0.340  0.9971
 3 2.15708532863333 - 5 2.15708532863333   0.0250 0.0392 115   0.638  0.9686
 4 2.15708532863333 - 5 2.15708532863333   0.0384 0.0392 115   0.979  0.8643

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates



> nsBA4 = lme(BPA ~ CP, random = ~1|geckoID/trial,
+             NS, method="ML")
> summary(nsBA4)
Linear mixed-effects model fit by maximum likelihood
 Data: NS
        AIC       BIC   logLik
  -111.5627 -87.47762 63.78135

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.05773217

 Formula: ~1 | trial %in% geckoID
```

```
        (Intercept)  Residual
StdDev:  0.04326927 0.1480791

Fixed effects: BPA ~ CP
                 Value  Std.Error  DF   t-value p-value
(Intercept)  1.0292091 0.03467360 116 29.682790  0.0000
CP2   -0.0362261 0.03888748 116 -0.931562  0.3535
CP3    0.0491283 0.03888748 116  1.263345  0.2090
CP4    0.0578486 0.03888748 116  1.487589  0.1396
CP5    0.0217190 0.03888748 116  0.558508  0.5776
 Correlation:
          (Intr) Intrv2 Intrv3 Intrv4
CP2 -0.561
CP3 -0.561  0.500
CP4 -0.561  0.500  0.500
CP5 -0.561  0.500  0.500  0.500

> VarCorr(nsBA4)
            Variance     StdDev
geckoID =
(Intercept) 0.003333004  0.05773217
trial =
(Intercept) 0.001872229  0.04326927
Residual    0.021927427  0.14807912

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-7.1268689 -0.4175671  0.1779955  0.5500182  1.8635707

Number of Observations: 150
Number of Groups:
           geckoID trial %in% geckoID
                10                 30
> CPs(nsBA4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.      upper
(Intercept)  0.96168795  1.02920909 1.09673022
CP2   -0.11195307 -0.03622608 0.03950090
CP3   -0.02659867  0.04912832 0.12485531
CP4   -0.01787841  0.05784858 0.13357557
CP5   -0.05400802  0.02171897 0.09744596
attr(,"label")
[1] "Fixed effects:"
> anova(nsBA4, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1   116 881.0680  <.0001
CP          4   116   1.9289  0.1102
> #estimated marginal means (least squares)
> emmls = emmeans(nsBA4, pairwise ~ CP,     mode="containment")
> summary(emmls)
$emmeans
 CP emmean     SE df lower.CL upper.CL
 1         1.029 0.0347  9    0.951     1.11
 2         0.993 0.0347  9    0.915     1.07
 3         1.078 0.0347  9    1.000     1.16
 4         1.087 0.0347  9    1.009     1.17
 5         1.051 0.0347  9    0.972     1.13

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast estimate     SE  df t.ratio p.value
 1 - 2     0.03623 0.0389 116  0.932  0.8841
 1 - 3    -0.04913 0.0389 116 -1.263  0.7141
 1 - 4    -0.05785 0.0389 116 -1.488  0.5726
 1 - 5    -0.02172 0.0389 116 -0.559  0.9807
 2 - 3    -0.08535 0.0389 116 -2.195  0.1890
 2 - 4    -0.09407 0.0389 116 -2.419  0.1175
 2 - 5    -0.05795 0.0389 116 -1.490  0.5710
 3 - 4    -0.00872 0.0389 116 -0.224  0.9994
 3 - 5     0.02741 0.0389 116  0.705  0.9550
 4 - 5     0.03613 0.0389 116  0.929  0.8851

Degrees-of-freedom method: containment
P value adjustment: tukey method for comparing a family of 5 estimates
```

S1.6. R {nmle} output: stride velocity (Velstride) models for transition 1 and 2 (T1, T2) within limbs 1 and 2 (L1, L2)

a) T1 L1

```
#######Transition 1: solid solid-sand########
> ##T1_Limb1

T1L1Velstride = lme(Velstride ~  temp + SVL + T1_L1, random = ~1|geckoID/trial,
+               T1, method="ML")
> summary(T1L1Velstride)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -125.2005 -111.5418 69.60026

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1468574

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.08114095 0.02270451

Fixed effects: Velstride ~ temp + SVL + T1_L1
                 Value Std.Error DF    t-value p-value
(Intercept)  0.7303186  3.662988 25  0.1993778  0.8436
temp        -0.9041639  1.743223 15 -0.5186738  0.6116
SVL          1.7073195  1.278189  8  1.3357327  0.2184
T1_L11       0.0069229  0.006554 25  1.0562495  0.3010
 Correlation:
       (Intr) temp   SVL
temp   -0.826
SVL    -0.707  0.186
T1_L11 -0.001  0.000  0.000

> VarCorr(T1L1Velstride)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.0215670866 0.14685737
trial =     pdLogChol(1)
(Intercept) 0.0065838542 0.08114095
Residual    0.0005154948 0.02270451


Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.8808363 -0.3677872  0.1239551  0.4724108  1.8161288

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> CPs(T1L1Velstride, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower       est.      upper
(Intercept) -6.517785462  0.7303186 7.97842262
temp        -4.473988365 -0.9041639 2.66566059
SVL         -1.124556704  1.7073195 4.53919576
T1_L11      -0.006046217  0.0069229 0.01989202
attr(,"label")
[1] "Fixed effects:"
> anova(T1L1Velstride, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    25 0.0397515  0.8436
temp            1    15 0.2690225  0.6116
SVL             1     8 1.7841819  0.2184
T1_L1           1    25 1.1156630  0.3010
> #estimated marginal means (least squares)
> emmls = emmeans(T1L1Velstride, pairwise ~ T1_L1 + temp + SVL,  mode="containment")
> summary(emmls)
$emmeans
 T1_L1 temp  SVL emmean     SE df lower.CL upper.CL
 0     1.51 1.63   2.15 0.0526  8     2.03     2.27
 1     1.51 1.63   2.16 0.0526  8     2.04     2.28

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                        estimate      SE df t.ratio p.value
 0 1.51226884873077 1.63400780646154 - 1 1.51226884873077 1.63400780646154 -0.00692 0.00655 25 -1.056  0.3010
```

```
Degrees-of-freedom method: containment


> T1L1Velstride2 = lme(Velstride ~ SVL + T1_L1, random = ~1|geckoID/trial,
+                      T1, method="ML")
> summary(T1L1Velstride2)
Linear mixed-effects model fit by maximum likelihood
 Data: T1 
        AIC      BIC   logLik
  -126.9195 -115.212 69.45975

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1506216

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:   0.0807376 0.02270451

Fixed effects: Velstride ~ SVL + T1_L1 
                 Value Std.Error DF    t-value p-value
(Intercept) -0.8355430  2.086773 25 -0.4003995  0.6923
SVL          1.8282521  1.270690  8  1.4387867  0.1882
T1_L11       0.0069229  0.006487 25  1.0671955  0.2961
 Correlation: 
       (Intr) SVL  
SVL    -1.000      
T1_L11 -0.002  0.000

> VarCorr(T1L1Velstride2)
            Variance     StdDev    
geckoID =   pdLogChol(1)           
(Intercept) 0.0226868681 0.15062161
trial =     pdLogChol(1)           
(Intercept) 0.0065185605 0.08073760
Residual    0.0005154947 0.02270451

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-1.8863927 -0.3645799  0.1449310  0.4597727  1.8105729 

Number of Observations: 52
Number of Groups: 
           geckoID trial %in% geckoID 
                10                 26 
> CPs(T1L1Velstride2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower       est.      upper
(Intercept) -5.007516948 -0.8355430 3.33643097
SVL         -1.016183488  1.8282521 4.67268760
T1_L11      -0.006046215  0.0069229 0.01989201
attr(,"label")
[1] "Fixed effects:"
> anova(T1L1Velstride2, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    25 0.1603197  0.6923
SVL             1     8 2.0701073  0.1882
T1_L1           1    25 1.1389062  0.2961
> #estimated marginal means (least squares)
> emmls = emmeans(T1L1Velstride2, pairwise ~ T1_L1, mode="containment")
> summary(emmls)
$emmeans
 T1_L1  SVL emmean     SE df lower.CL upper.CL
 0     1.63   2.15 0.0532  8     2.03     2.27
 1     1.63   2.16 0.0532  8     2.04     2.28

Degrees-of-freedom method: containment 
Confidence level used: 0.95 

$contrasts
 contrast                               estimate      SE df t.ratio p.value
 0 1.63400780646154 - 1 1.63400780646154 -0.00692 0.00649 25 -1.067  0.2961 

Degrees-of-freedom method: containment


> T1L1Velstride3 = lme(Velstride ~ temp + T1_L1, random = ~1|geckoID/trial,
+                      T1, method="ML")
> summary(T1L1Velstride3)
Linear mixed-effects model fit by maximum likelihood
 Data: T1 
```

```
        AIC       BIC   logLik
  -125.4164 -113.709 68.70821

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1616049

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.08135364 0.02270449

Fixed effects: Velstride ~ temp + T1_L1
                Value Std.Error DF    t-value p-value
(Intercept)  3.942914  2.596951 25  1.5182860  0.1415
temp        -1.174935  1.716881 15 -0.6843428  0.5042
T1_L11       0.006923  0.006487 25  1.0671962  0.2961
 Correlation:
       (Intr) temp
temp   -1.000
T1_L11 -0.001  0.000

> VarCorr(T1L1Velstride3)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.026116141  0.16160489
trial =     pdLogChol(1)
(Intercept) 0.006618415  0.08135364
Residual    0.000515494  0.02270449

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.8742646 -0.3687905  0.1229922  0.4763070  1.8227035

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> CPs(T1L1Velstride3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower       est.      upper
(Intercept) -1.249030156  3.9429141 9.13485831
temp        -4.727251689 -1.1749352 2.37738121
T1_L11      -0.006046207  0.0069229 0.01989201
attr(,"label")
[1] "Fixed effects:"
> anova(T1L1Velstride3, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    25 2.3051924  0.1415
temp            1    15 0.4683251  0.5042
T1_L1           1    25 1.1389078  0.2961
> #estimated marginal means (least squares)
> emmls = emmeans(T1L1Velstride3, pairwise ~ T1_L1, mode="containment")
> summary(emmls)
$emmeans
 T1_L1 temp emmean     SE df lower.CL upper.CL
 0     1.51   2.17 0.0557  9     2.04     2.29
 1     1.51   2.17 0.0557  9     2.05     2.30

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                               estimate      SE df t.ratio p.value
 0 1.51226884873077 - 1 1.51226884873077 -0.00692 0.00649 25 -1.067  0.2961

Degrees-of-freedom method: containment




> T1L1Velstride4 = lme(Velstride ~ T1_L1, random = ~1|geckoID/trial,

+                     T1, method="ML")
> summary(T1L1Velstride4)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -126.9559 -117.1997 68.47794

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1690316
```

```
 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.08048917 0.02270456

Fixed effects: Velstride ~ T1_L1
                Value  Std.Error DF  t-value p-value
(Intercept) 2.1662592 0.05736698 25 37.76143  0.0000
T1_L11      0.0069229 0.00642182 25  1.07803  0.2913
 Correlation:
       (Intr)
T1_L11 -0.056

> VarCorr(T1L1Velstride4)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.0285716955 0.16903164
trial =     pdLogChol(1)
(Intercept) 0.0064785057 0.08048917
Residual    0.0005154969 0.02270456

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.8819339 -0.3639943  0.1408211  0.4583949  1.8150236

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> CPs(T1L1Velstride4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower      est.      upper
(Intercept)  2.050404052 2.1662592 2.28211429
T1_L11      -0.006046244 0.0069229 0.01989204
attr(,"label")
[1] "Fixed effects:"
> anova(T1L1Velstride4, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    25 1425.9257  <.0001
T1_L1           1    25    1.1621  0.2913
> #estimated marginal means (least squares)
> emmls = emmeans(T1L1Velstride4, pairwise ~ T1_L1, mode="containment")
> summary(emmls)
$emmeans
 T1_L1 emmean     SE df lower.CL upper.CL
 0       2.17 0.0574  9     2.04      2.3
 1       2.17 0.0574  9     2.04      2.3

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast estimate      SE df t.ratio p.value
 0 - 1    -0.00692 0.00642 25 -1.078  0.2913

Degrees-of-freedom method: containment
```

S1.6. R {nmle} output: stride velocity (Velstride) models for transition 1 and 2 (T1, T2) within limbs 1 and 2 (L1, L2)

a) T1 L2

```
##T1_Limb2

> T1L2Velstride = lme(Velstride ~   + temp + SVL + T1_L2, random = ~1|geckoID/trial,
+               T1, method="ML")
> summary(T1L2Velstride)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -156.5366 -141.8762 85.26829

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:    0.161633

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.07811179 0.01994323

Fixed effects: Velstride ~ +temp + SVL + T1_L2
                 Value Std.Error DF    t-value p-value
(Intercept) -1.1172034  3.356394 29 -0.3328582  0.7416
temp         0.2755645  1.420500 19  0.1939912  0.8482
SVL          1.7503713  1.369721  8  1.2779038  0.2371
T1_L21      -0.0016272  0.005330 29 -0.3052967  0.7623
 Correlation:
       (Intr) temp   SVL
temp   -0.750
SVL    -0.775  0.165
T1_L21 -0.001  0.000  0.000

> VarCorr(T1L2Velstride)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.0261252282 0.16163300
trial =     pdLogChol(1)
(Intercept) 0.0061014519 0.07811179
Residual    0.0003977323 0.01994323

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.79215945 -0.50548752 -0.03899858  0.59236123  1.50463110

Number of Observations: 60
Number of Groups:
           geckoID trial %in% geckoID
                10                 30
> CPs(T1L2Velstride, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower         est.       upper
(Intercept) -7.74903385 -1.117203423 5.514627003
temp        -2.59676196  0.275564536 3.147891036
SVL         -1.30110838  1.750371284 4.801850949
T1_L21      -0.01215879 -0.001627247 0.008904293
attr(,"label")
[1] "Fixed effects:"
> anova(T1L2Velstride, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    29 0.1107946  0.7416
temp            1    19 0.0376326  0.8482
SVL             1     8 1.6330382  0.2371
T1_L2           1    29 0.0932061  0.7623
> #estimated marginal means (least squares)
> emmls = emmeans(T1L2Velstride, pairwise ~ T1_L2, mode="containment")
> summary(emmls)
$emmeans
 T1_L2 temp  SVL emmean     SE df lower.CL upper.CL
 0      1.51 1.63   2.16 0.0564  8     2.03     2.29
 1      1.51 1.63   2.16 0.0564  8     2.03     2.29

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                         estimate      SE df t.ratio p.value
 0 1.5118385102 1.63445981143333 - 1 1.5118385102 1.63445981143333  0.00163 0.00533 29 0.305    0.7623
```

```
> T1L2Velstride2 = lme(Velstride ~ SVL  + T1_L2, random = ~1|geckoID/trial,
+                 T1, method="ML")
> summary(T1L2Velstride2)
Linear mixed-effects model fit by maximum likelihood
 Data: T1 
        AIC      BIC   logLik
  -158.4981 -145.932 85.24903

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1603005

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.07847875 0.01994323

Fixed effects: Velstride ~ SVL + T1_L2 
                 Value Std.Error DF    t-value p-value
(Intercept) -0.6309961 2.1835999 29 -0.2889706  0.7747
SVL          1.7080402 1.3294346  8  1.2847869  0.2348
T1_L21      -0.0016272 0.0052831 29 -0.3080105  0.7603
 Correlation: 
       (Intr) SVL   
SVL    -1.000       
T1_L21 -0.001  0.000

> VarCorr(T1L2Velstride2)
            Variance     StdDev    
geckoID =   pdLogChol(1)           
(Intercept) 0.0256962639 0.16030054
trial =     pdLogChol(1)           
(Intercept) 0.0061589148 0.07847875
Residual    0.0003977325 0.01994323

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-1.78597121 -0.50357201 -0.03679938  0.59602154  1.50287535 

Number of Observations: 60
Number of Groups: 
           geckoID trial %in% geckoID 
                10                 30 
> CPs(T1L2Velstride2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                 lower         est.       upper
(Intercept) -4.98387862 -0.630996114 3.721886389
SVL         -1.28001673  1.708040175 4.696097083
T1_L21      -0.01215879 -0.001627248 0.008904295
attr(,"label")
[1] "Fixed effects:"
> anova(T1L2Velstride2, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    29 0.0835040  0.7747
SVL             1     8 1.6506774  0.2348
T1_L2           1    29 0.0948705  0.7603
> #estimated marginal means (least squares)
> emmls = emmeans(T1L2Velstride2, pairwise ~ T1_L2, mode="containment")
> summary(emmls)
$emmeans
 T1_L2  SVL emmean     SE df lower.CL upper.CL
 0     1.63   2.16 0.0555  8     2.03     2.29
 1     1.63   2.16 0.0555  8     2.03     2.29

Degrees-of-freedom method: containment 
Confidence level used: 0.95 

$contrasts
 contrast                                estimate      SE df t.ratio p.value
 0 1.63445981143333 - 1 1.63445981143333  0.00163 0.00528 29 0.308   0.7603 

Degrees-of-freedom method: containment 



> T1L2Velstride3 = lme(Velstride ~ temp  + T1_L2, random = ~1|geckoID/trial,
+                     T1, method="ML")
> summary(T1L2Velstride3)
Linear mixed-effects model fit by maximum likelihood
 Data: T1 
        AIC       BIC   logLik
```

```
  -156.9214 -144.3553 84.46068

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1766595

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.07807236 0.01994323

Fixed effects: Velstride ~ temp + T1_L2
                 Value Std.Error DF    t-value p-value
(Intercept)  2.0301476 2.1139278 29  0.9603675  0.3448
temp         0.0948343 1.3975153 19  0.0678592  0.9466
T1_L21      -0.0016272 0.0052831 29 -0.3080105  0.7603
 Correlation:
       (Intr) temp
temp   -1.000
T1_L21 -0.001  0.000

> VarCorr(T1L2Velstride3)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.0312085810 0.17665951
trial =     pdLogChol(1)
(Intercept) 0.0060952935 0.07807236
Residual    0.0003977325 0.01994323

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.79954866 -0.50594267 -0.03663807  0.60135344  1.50644385

Number of Observations: 60
Number of Groups:
           geckoID trial %in% geckoID
                10                 30
> CPs(T1L2Velstride3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower         est.       upper
(Intercept) -2.18384759  2.030147560 6.244142713
temp        -2.75613531  0.094834259 2.945803827
T1_L21      -0.01215879 -0.001627248 0.008904296

 [1] "Fixed effects:"
> anova(T1L2Velstride3, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    29 0.9223057  0.3448
temp            1    19 0.0046049  0.9466
T1_L2           1    29 0.0948705  0.7603

> #estimated marginal means (least squares)
> emmls = emmeans(T1L2Velstride3, pairwise ~ T1_L2, mode="containment")
> summary(emmls)
$emmeans
 T1_L2 temp emmean     SE df lower.CL upper.CL
 0      1.51   2.17 0.0596  9     2.04     2.31
 1      1.51   2.17 0.0596  9     2.04     2.31

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                       estimate      SE df t.ratio p.value
 0 1.5118385102 - 1 1.5118385102  0.00163 0.00528 29 0.308   0.7603

Degrees-of-freedom method: containment



> T1L2Velstride4 = lme(Velstride ~ T1_L2, random = ~1|geckoID/trial,
+                     T1, method="ML")
> summary(T1L2Velstride4)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -158.9169 -148.4451 84.45844

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1759863
```

```
 Formula: ~1 | trial %in% geckoID
        (Intercept)    Residual
StdDev:  0.07821853 0.01994324

Fixed effects: Velstride ~ T1_L2
                 Value  Std.Error DF  t-value p-value
(Intercept)  2.1735427 0.05889664 29 36.90436  0.0000
T1_L21      -0.0016272 0.00523735 29 -0.31070  0.7583
 Correlation:
       (Intr)
T1_L21 -0.044

> VarCorr(T1L2Velstride4)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.030971169  0.17598627
trial =     pdLogChol(1)
(Intercept) 0.006118139  0.07821853
Residual    0.000397733  0.01994324

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.79728599 -0.50481102 -0.03586682  0.60255164  1.50582958

Number of Observations: 60
Number of Groups:
           geckoID trial %in% geckoID
                10                 30
> CPs(T1L2Velstride4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                 lower         est.       upper
(Intercept)  2.0551102  2.173542749 2.291975268
T1_L21      -0.0121588 -0.001627248 0.008904301
attr(,"label")
[1] "Fixed effects:"
> anova(T1L2Velstride4, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    29 1361.9317  <.0001
T1_L2           1    29    0.0965  0.7583
> #estimated marginal means (least squares)
> emmls = emmeans(T1L2Velstride4, pairwise ~ T1_L2, mode="containment")
> summary(emmls)
$emmeans
 T1_L2 emmean     SE df lower.CL upper.CL
 0       2.17 0.0589  9     2.04     2.31
 1       2.17 0.0589  9     2.04     2.31

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast estimate      SE df t.ratio p.value
 0 - 1     0.00163 0.00524 29 0.311   0.7583

Degrees-of-freedom method: containment
```

S1.6. R {nmle} output: stride velocity (Velstride) models for transition 1 and 2 (T1, T2) within limbs 1 and 2 (L1, L2)

a) T2 L1

```
#Transition 2: sand sand-solid

>
> #T2_Limb1

> T2L1Velstride = lme(Velstride ~  temp + SVL + T2_L1, random = ~1|geckoID/trial,
+              T2, method="ML")
> summary(T2L1Velstride)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
       AIC       BIC   logLik
  -141.2335 -127.5748 77.61676

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1219455
```

```
 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.08348735 0.01780142

Fixed effects: Velstride ~ temp + SVL + T2_L1
                Value Std.Error DF   t-value p-value
(Intercept)  4.318937 2.8918624 25  1.493479  0.1478
temp        -2.982999 1.3510763 16 -2.207869  0.0422
SVL          1.441476 1.0703388  7  1.346747  0.2200
T2_L11      -0.008040 0.0051388 25 -1.564606  0.1302
 Correlation:
       (Intr) temp   SVL
temp   -0.800
SVL    -0.716  0.154
T2_L11 -0.001  0.000  0.000

> VarCorr(T2L1Velstride)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.0148706980 0.12194547
trial =     pdLogChol(1)
(Intercept) 0.0069701369 0.08348735
Residual    0.0003168906 0.01780142

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.64655225 -0.39408030  0.04570341  0.39696696  1.83807802

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                 9                 26
> CPs(T2L1Velstride, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.        upper
(Intercept) -1.40330866  4.31893694 10.041182539
temp        -5.73478929 -2.98299933 -0.231209372
SVL         -0.99018131  1.44147583  3.873132967
T2_L11      -0.01820865 -0.00804024  0.002128167
attr(,"label")
[1] "Fixed effects:"
> anova(T2L1Velstride, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    25 2.230481  0.1478
temp            1    16 4.874685  0.0422
SVL             1     7 1.813728  0.2200
T2_L1           1    25 2.447992  0.1302
> #estimated marginal means (least squares)
> emmls = emmeans(T2L1Velstride, pairwise ~ T2_L1, mode="containment")
> summary(emmls)
$emmeans
 T2_L1 temp  SVL emmean     SE df lower.CL upper.CL
 0     1.51 1.63   2.15 0.0477  7     2.04     2.26
 1     1.51 1.63   2.14 0.0477  7     2.03     2.26

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                                 estimate      SE df t.ratio
p.value
 0 1.51368667296154 1.62800471042308 - 1 1.51368667296154 1.62800471042308  0.00804 0.00514 25 1.565
0.1302

Degrees-of-freedom method: containment



> T2L1Velstride2 = lme(Velstride ~  SVL + T2_L1, random = ~1|geckoID/trial,
+                T2, method="ML")
> summary(T2L1Velstride2)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC      BIC   logLik
  -138.4385 -126.731 75.21925

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1298599

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.09285938 0.01780145
```

```
Fixed effects: Velstride ~ SVL + T2_L1
                  Value Std.Error DF    t-value p-value
(Intercept) -0.7904531 1.8378601 25 -0.4300943  0.6708
SVL          1.8069615 1.1205210  7  1.6126083  0.1509
T2_L11      -0.0080402 0.0050861 25 -1.5808171  0.1265
 Correlation:
       (Intr) SVL
SVL    -1.000
T2_L11 -0.001  0.000

> VarCorr(T2L1Velstride2)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.0168636012 0.12985993
trial =     pdLogChol(1)
(Intercept) 0.0086228638 0.09285938
Residual    0.0003168917 0.01780145

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.63165115 -0.39384250  0.03630413  0.37238468  1.85297279

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                 9                26
> CPs(T2L1Velstride2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.       upper
(Intercept) -4.46478795 -0.79045307 2.883881818
SVL         -0.76508315  1.80696151 4.379006174
T2_L11      -0.01820867 -0.00804024 0.002128185
attr(,"label")
[1] "Fixed effects:"
> anova(T2L1Velstride2, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    25 0.1849811  0.6708
SVL             1     7 2.6005057  0.1509
T2_L1           1    25 2.4989826  0.1265
> #estimated marginal means (least squares)
> emmls = emmeans(T2L1Velstride2, pairwise ~ T2_L1, mode="containment")
> summary(emmls)
$emmeans
 T2_L1  SVL emmean     SE df lower.CL upper.CL
 0     1.63   2.15 0.0505  7     2.03     2.27
 1     1.63   2.14 0.0505  7     2.02     2.26

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                estimate      SE df t.ratio p.value
 0 1.62800471042308 - 1 1.62800471042308  0.00804 0.00509 25 1.581   0.1265

Degrees-of-freedom method: containment




> T2L1Velstride3 = lme(Velstride ~ temp  + T2_L1, random = ~1|geckoID/trial,
+                     T2, method="ML")
> summary(T2L1Velstride3)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC       BIC   logLik
  -141.4559 -129.7484 76.72794

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1373974

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.08331931 0.01780142

Fixed effects: Velstride ~ temp + T2_L1
                 Value Std.Error DF   t-value p-value
(Intercept)  6.928369 2.0038332 25  3.457558  0.0020
temp        -3.145411 1.3249503 16 -2.373984  0.0305
T2_L11      -0.008040 0.0050861 25 -1.580820  0.1265
 Correlation:
       (Intr) temp
```

```
temp   -1.000
T2_L11 -0.001  0.000

> VarCorr(T2L1Velstride3)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.0188780513 0.13739742
trial =     pdLogChol(1)
(Intercept) 0.0069421078 0.08331931
Residual    0.0003168904 0.01780142

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.64725652 -0.39516083  0.05499732  0.39422014  1.83737471

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                 9                 26
> CPs(T2L1Velstride3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.        upper
(Intercept)  2.92221277  6.92836874 10.934524709
temp        -5.87195484 -3.14541134 -0.418867838
T2_L11      -0.01820864 -0.00804024  0.002128164
attr(,"label")
[1] "Fixed effects:"
> anova(T2L1Velstride3, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    25 11.954705  0.0020
temp            1    16  5.635802  0.0305
T2_L1           1    25  2.498993  0.1265
> #estimated marginal means (least squares)
> emmls = emmeans(T2L1Velstride3, pairwise ~ T2_L1, mode="containment")
> summary(emmls)
$emmeans
 T2_L1 temp emmean     SE df lower.CL upper.CL
 0     1.51   2.17 0.0506  8     2.05     2.28
 1     1.51   2.16 0.0506  8     2.04     2.28

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                               estimate      SE df t.ratio p.value
 0 1.51368667296154 - 1 1.51368667296154  0.00804 0.00509 25 1.581   0.1265

Degrees-of-freedom method: containment



> T2L1Velstride4 = lme(Velstride ~ T2_L1, random = ~1|geckoID/trial,
+                      T2, method="ML")
> summary(T2L1Velstride4)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
       AIC       BIC   logLik
  -138.074 -128.3178 74.03701

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1536313

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.09226602 0.01780144

Fixed effects: Velstride ~ T2_L1
                 Value  Std.Error DF   t-value p-value
(Intercept)  2.1728462 0.05580111 25 38.93912  0.0000
T2_L11      -0.0080402 0.00503501 25 -1.59687  0.1229
 Correlation:
       (Intr)
T2_L11 -0.045

> VarCorr(T2L1Velstride4)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.0236025732 0.15363129
trial =     pdLogChol(1)
(Intercept) 0.0085130176 0.09226602
Residual    0.0003168913 0.01780144
```

```
Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-1.63273510 -0.39457309  0.02980887  0.37138241  1.85189095 

Number of Observations: 52
Number of Groups: 
           geckoID trial %in% geckoID 
                 9                 26 
> CPs(T2L1Velstride4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.       upper
(Intercept)  2.06015345  2.17284623 2.285539011
T2_L11      -0.01820866 -0.00804024 0.002128179
attr(,"label")
[1] "Fixed effects:"
> anova(T2L1Velstride4, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    25 1516.255  <.0001
T2_L1           1    25    2.550  0.1229
> #estimated marginal means (least squares)
> emmls = emmeans(T2L1Velstride4, pairwise ~ T2_L1,   mode="containment")
> summary(emmls)
$emmeans
 T2_L1 emmean     SE df lower.CL upper.CL
 0       2.17 0.0558  8     2.04     2.30
 1       2.16 0.0558  8     2.04     2.29

Degrees-of-freedom method: containment 
Confidence level used: 0.95 

$contrasts
 contrast estimate      SE df t.ratio p.value
 0 - 1     0.00804 0.00504 25 1.597   0.1229 

Degrees-of-freedom method: containment 
```

S1.6. R {nmle} output: stride velocity (Velstride) models for transition 1 and 2 (T1, T2) within limbs 1 and 2 (L1, L2)

a) T2 L2

```
#T2_Limb2


> T2L2Velstride = lme(Velstride ~ temp + SVL + T2_L2, random = ~1|geckoID/trial,
+               T2, method="ML")
> summary(T2L2Velstride)
Linear mixed-effects model fit by maximum likelihood
 Data: T2 
       AIC       BIC   logLik
  -122.258 -109.6114 68.12902

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1067004

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.08139315 0.01635654

Fixed effects: Velstride ~ temp + SVL + T2_L2 
                Value Std.Error DF   t-value p-value
(Intercept)  4.139988 2.7700316 20  1.494563  0.1506
temp        -2.457524 1.3518037 15 -1.817959  0.0891
SVL          1.046353 0.9868934  6  1.060249  0.3298
T2_L2       -0.005313 0.0052814 20 -1.005925  0.3265
 Correlation: 
      (Intr) temp   SVL   
temp  -0.816              
SVL   -0.681  0.133       
T2_L2 -0.004  0.002  0.003

> VarCorr(T2L2Velstride)
            Variance     StdDev    
geckoID =   pdLogChol(1)           
(Intercept) 0.0113849724 0.10670039
trial =     pdLogChol(1)           
```

```
(Intercept) 0.0066248441 0.08139315
Residual    0.0002675362 0.01635654

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-1.88759888 -0.49043098  0.01516762  0.52239056  1.57960731 

Number of Observations: 45
Number of Groups: 
           geckoID trial %in% geckoID 
                 8                 24 
> CPs(T2L2Velstride, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower         est.       upper
(Intercept) -1.37541274  4.139988173 9.655389082
temp        -5.20778826 -2.457524378 0.292739509
SVL         -1.25866515  1.046352523 3.351370200
T2_L2       -0.01582843 -0.005312677 0.005203073
attr(,"label")
[1] "Fixed effects:"
> anova(T2L2Velstride, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    20 2.233720  0.1506
temp            1    15 3.304977  0.0891
SVL             1     6 1.124127  0.3298
T2_L2           1    20 1.011885  0.3265
> #estimated marginal means (least squares)
> emmls = emmeans(T2L2Velstride, pairwise ~ T2_L2, mode="containment")
> summary(emmls)
$emmeans
 T2_L2 temp  SVL emmean     SE df lower.CL upper.CL
 0     1.52 1.62   2.12 0.0452  6        2     2.23
 1     1.52 1.62   2.11 0.0452  6        2     2.22

Degrees-of-freedom method: containment 
Confidence level used: 0.95 

$contrasts
 contrast                                                                estimate      SE df t.ratio
p.value
 0 1.51521652293333 1.62349833657778 - 1 1.51521652293333 1.62349833657778  0.00531 0.00528 20 1.006
0.3265

Degrees-of-freedom method: containment 



> T2L2Velstride2 = lme(Velstride ~ SVL + T2_L2, random = ~1|geckoID/trial,
+                T2, method="ML")
> summary(T2L2Velstride2)
Linear mixed-effects model fit by maximum likelihood
 Data: T2 
        AIC       BIC   logLik
  -120.9192 -110.0792 66.45959

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1080333

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.08929668 0.01635574

Fixed effects: Velstride ~ SVL + T2_L2 
                 Value Std.Error DF    t-value p-value
(Intercept)  0.0233381  1.620978 20  0.0143975  0.9887
SVL          1.2887932  0.990887  6  1.3006460  0.2411
T2_L2       -0.0052710  0.005219 20 -1.0099724  0.3246
 Correlation: 
      (Intr) SVL  
SVL   -1.000      
T2_L2 -0.004  0.003

> VarCorr(T2L2Velstride2)
            Variance     StdDev    
geckoID =   pdLogChol(1)           
(Intercept) 0.0116711879 0.10803327
trial =     pdLogChol(1)           
(Intercept) 0.0079738963 0.08929668
Residual    0.0002675102 0.01635574

Standardized Within-Group Residuals:
         Min          Q1         Med          Q3         Max 
```

```
-1.838669803 -0.489917368  0.002478732  0.533630643  1.626158722

Number of Observations: 45
Number of Groups:
           geckoID trial %in% geckoID
                 8                24
> CPs(T1L1Velstride2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower       est.      upper
(Intercept) -5.007516948 -0.8355430 3.33643097
SVL         -1.016183488  1.8282521 4.67268760
T1_L11      -0.006046215  0.0069229 0.01989201
attr(,"label")
[1] "Fixed effects:"
> anova(T2L2Velstride2, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    20 0.0002073  0.9887
SVL             1     6 1.6916799  0.2411
T2_L2           1    20 1.0200442  0.3246
> #estimated marginal means (least squares)
> emmls = emmeans(T2L2Velstride2, pairwise ~ T2_L2, mode="containment")
> summary(emmls)
$emmeans
 T2_L2  SVL emmean     SE df lower.CL upper.CL
 0     1.62   2.12 0.0458  6        2     2.23
 1     1.62   2.11 0.0458  6        2     2.22

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                estimate      SE df t.ratio p.value
 0 1.62349833657778 - 1 1.62349833657778  0.00527 0.00522 20 1.010   0.3246

Degrees-of-freedom method: containment



> T2L2Velstride3 = lme(Velstride ~ temp  + T2_L2, random = ~1|geckoID/trial,
+                    T2, method="ML")
> summary(T2L2Velstride3)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
       AIC       BIC  logLik
  -123.1208 -112.2808 67.5604

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1171483

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.08111247 0.01635836

Fixed effects: Velstride ~ temp + T2_L2
                Value Std.Error DF   t-value p-value
(Intercept)  6.059734 2.0027007 20  3.025781  0.0067
temp        -2.595152 1.3225801 15 -1.962189  0.0686
T2_L2       -0.005330 0.0052187 20 -1.021327  0.3193
 Correlation:
      (Intr) temp
temp  -1.000
T2_L2 -0.003  0.001

> VarCorr(T2L2Velstride3)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.013723732  0.11714834
trial =     pdLogChol(1)
(Intercept) 0.006579233  0.08111247
Residual    0.000267596  0.01635836

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.90045618 -0.50097511  0.01824924  0.51068807  1.56741907

Number of Observations: 45
Number of Groups:
           geckoID trial %in% geckoID
                 8                24
> CPs(T2L2Velstride3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs
```

```
 Fixed effects:
                  lower         est.        upper
(Intercept)  2.02382700  6.059733794 10.095640590
temp        -5.31857681 -2.595151667  0.128273472
T2_L2       -0.01584675 -0.005329952  0.005186843
attr(,"label")
[1] "Fixed effects:"
> anova(T2L2Velstride3, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    20 9.155351  0.0067
temp            1    15 3.850184  0.0686
T2_L2           1    20 1.043110  0.3193
> #estimated marginal means (least squares)
> emmls = emmeans(T2L2Velstride3, pairwise ~ T2_L2,   mode="containment")
> summary(emmls)
$emmeans
 T2_L2 temp emmean     SE df lower.CL upper.CL
 0     1.52   2.13 0.0466  7     2.02     2.24
 1     1.52   2.12 0.0466  7     2.01     2.23

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                estimate      SE df t.ratio p.value
 0 1.51521652293333 - 1 1.51521652293333  0.00533 0.00522 20 1.021   0.3193

Degrees-of-freedom method: containment



> T2L2Velstride4 = lme(Velstride ~ T2_L2, random = ~1|geckoID/trial,
+                      T2, method="ML")
> summary(T2L2Velstride4)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC       BIC   logLik
  -121.3218 -112.2884 65.66088

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.1241435

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.08869616 0.01635703

Fixed effects: Velstride ~ T2_L2
                Value  Std.Error DF  t-value p-value
(Intercept)  2.131076 0.04903067 20 43.46415  0.0000
T2_L2       -0.005290 0.00515826 20 -1.02555  0.3173
 Correlation:
      (Intr)
T2_L2 -0.054

> VarCorr(T2L2Velstride4)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.0154116057 0.12414349
trial =     pdLogChol(1)
(Intercept) 0.0078670088 0.08869616
Residual    0.0002675523 0.01635703

Standardized Within-Group Residuals:
         Min           Q1          Med           Q3          Max
-1.851859088 -0.470951108  0.002715519  0.523350965  1.613859136

Number of Observations: 45
Number of Groups:
           geckoID trial %in% geckoID
                 8                 24
> CPs(T2L2Velstride4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower         est.       upper
(Intercept)  2.03109875  2.131076297 2.231053847
T2_L2       -0.01580814 -0.005290037 0.005228069
attr(,"label")
[1] "Fixed effects:"
> anova(T2L2Velstride4, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    20 1889.1322  <.0001
T2_L2           1    20    1.0517  0.3173
> #estimated marginal means (least squares)
```

```
> emmls = emmeans(T2L2Velstride4, pairwise ~ T2_L2, mode="containment")
> summary(emmls)
$emmeans
 T2_L2 emmean    SE df lower.CL upper.CL
     0   2.13 0.049  7     2.02     2.25
     1   2.13 0.049  7     2.01     2.24

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast estimate      SE df t.ratio p.value
 0 - 1     0.00529 0.00516 20 1.026   0.3173

Degrees-of-freedom method: containment
```

S1.7. R {nlme} output: duty factor (DF) models for transition 1 and 2 (T1, T2) within limbs 1 and 2 (L1, L2)

a) T1 L1

```
#######Transition 1: solid solid-sand########
> ##T1_Limb1

> T1L1DF = lme(DF ~  Vstride + SVL + T1_L1, random = ~1|geckoID/trial,
+                     T1, method="ML")
> summary(T1L1DF)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -50.45726 -36.79855 32.22863

Random effects:
 Formula: ~1 | geckoID
         (Intercept)
StdDev: 8.336475e-07

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:   0.1078566 0.09447535

Fixed effects: DF ~ Vstride + SVL + T1_L1
                 Value Std.Error DF   t-value p-value
(Intercept)  0.6987364 0.9781452 24  0.714348  0.4819
Vstride     -0.4672628 0.1445624 24 -3.232257  0.0036
SVL         -0.0752955 0.6465130  8 -0.116464  0.9102
T1_L11       0.0123668 0.0272910 24  0.453144  0.6545
 Correlation:
        (Intr) Vstrid SVL
Vstride  0.106
SVL     -0.956 -0.391
T1_L11  -0.018 -0.037  0.014

> VarCorr(T1L1DF)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 6.949681e-13 8.336475e-07
trial =     pdLogChol(1)
(Intercept) 1.163305e-02 1.078566e-01
Residual    8.925592e-03 9.447535e-02

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.8844155 -0.3312485  0.1246988  0.3754725  1.6701937

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> CPs(T1L1DF, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.       upper
(Intercept) -1.24085667  0.69873636  2.63832938
Vstride     -0.75391993 -0.46726284 -0.18060574
SVL         -1.50766897 -0.07529552  1.35707792
T1_L11      -0.04174944  0.01236677  0.06648299
attr(,"label")
[1] "Fixed effects:"

> anova(T1L1DF, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    24  0.510294  0.4819
Vstride         1    24 10.447483  0.0036
SVL             1     8  0.013564  0.9102
T1_L1           1    24  0.205340  0.6545

> #estimated marginal means (least squares)
> emmls = emmeans(T1L1DF, pairwise ~ T1_L1, mode="containment")
> summary(emmls)
$emmeans
 T1_L1 Vstride  SVL emmean     SE df lower.CL upper.CL
 0        2.14 1.63 -0.426 0.0293  8   -0.494   -0.359
 1        2.14 1.63 -0.414 0.0293  8   -0.481   -0.346

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                    estimate     SE df t.ratio p.value
```

```
 0 2.14426120738462 1.63400780646154 - 1 2.14426120738462 1.63400780646154 -0.0124 0.0273 24 -0.453
0.6545

Degrees-of-freedom method: containment
```

```
> T1L1DF2 = lme(DF ~ SVL + T1_L1, random = ~1|geckoID/trial,
+                    T1, method="ML")
> summary(T1L1DF2)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -42.78885 -31.08139 27.39442

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  1.8295e-06

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:   0.1336309 0.09625662

Fixed effects: DF ~ SVL + T1_L1
                Value Std.Error DF    t-value p-value
(Intercept)  1.034556 1.1378573 25  0.9092139  0.3719
SVL         -0.893000 0.6960620  8 -1.2829317  0.2354
T1_L11       0.009132 0.0275019 25  0.3320485  0.7426
 Correlation:
       (Intr) SVL
SVL    -1.000
T1_L11 -0.012  0.000

> VarCorr(T1L1DF2)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 3.347071e-12 0.0000018295
trial =     pdLogChol(1)
(Intercept) 1.785722e-02 0.1336308950
Residual    9.265336e-03 0.0962566174

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-3.73139749 -0.20685233  0.09266566  0.38870365  1.76975058

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> CPs(T1L1DF2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower         est.      upper
(Intercept) -1.24030126  1.034555718 3.30941270
SVL         -2.45113248 -0.893000017 0.66513245
T1_L11      -0.04585109  0.009131961 0.06411501
attr(,"label")
[1] "Fixed effects:"
> anova(T1L1DF2, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    25 0.8266700  0.3719
SVL             1     8 1.6459138  0.2354
T1_L1           1    25 0.1102562  0.7426
> #estimated marginal means (least squares)
> emmls = emmeans(T1L1DF2, pairwise ~ T1_L1, mode="containment")
> summary(emmls)
$emmeans
 T1_L1  SVL emmean     SE df lower.CL upper.CL
 0     1.63 -0.425 0.0333  8   -0.501   -0.348
 1     1.63 -0.415 0.0333  8   -0.492   -0.339

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                estimate     SE df t.ratio p.value
 0 1.63400780646154 - 1 1.63400780646154 -0.00913 0.0275 25 -0.332  0.7426

Degrees-of-freedom method: containment
```

```
> T1L1DF3 = lme(DF ~ Vstride + T1_L1, random = ~1|geckoID/trial,
+                     T1, method="ML")
> summary(T1L1DF3)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -52.44258 -40.73512 32.22129

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev: 8.36344e-07

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:   0.1079328 0.09445848

Fixed effects: DF ~ Vstride + T1_L1
                 Value  Std.Error DF   t-value p-value
(Intercept)  0.5898380 0.28349114 24  2.080622  0.0483
Vstride     -0.4738655 0.13172942 24 -3.597264  0.0014
T1_L11       0.0124125 0.02700354 24  0.459661  0.6499
 Correlation:
        (Intr) Vstrid
Vstride -0.995
T1_L11  -0.014 -0.034

> VarCorr(T1L1DF3)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 6.994712e-13 8.363440e-07
trial =     pdLogChol(1)
(Intercept) 1.164949e-02 1.079328e-01
Residual    8.922404e-03 9.445848e-02

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.8847497 -0.3248983  0.1205393  0.3691600  1.6701414

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> CPs(T1L1DF3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.      upper
(Intercept)  0.02186952  0.58983796  1.1578064
Vstride     -0.73778262 -0.47386554 -0.2099485
T1_L11      -0.04168853  0.01241248  0.0665135
attr(,"label")
[1] "Fixed effects:"
> anova(T1L1DF3, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    24  4.328989  0.0483
Vstride         1    24 12.940311  0.0014
T1_L1           1    24  0.211289  0.6499
> #estimated marginal means (least squares)
> emmls = emmeans(T1L1DF3, pairwise ~ T1_L1, mode="containment")
> summary(emmls)
$emmeans
 T1_L1 Vstride emmean    SE df lower.CL upper.CL
 0        2.14 -0.426 0.029  9   -0.492   -0.361
 1        2.14 -0.414 0.029  9   -0.479   -0.348

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                estimate    SE df t.ratio p.value
 0 2.14426120738462 - 1 2.14426120738462  -0.0124 0.027 24 -0.460  0.6499

Degrees-of-freedom method: containment



> T1L1DF4 = lme(DF ~ T1_L1, random = ~1|geckoID/trial,
+                     T1, method="ML")
> summary(T1L1DF4)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -43.09834 -33.34212 26.54917
```

```
Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  7.3746e-06

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:   0.1391693 0.09625662

Fixed effects: DF ~ T1_L1
                 Value  Std.Error DF   t-value p-value
(Intercept) -0.4246133 0.03384283 25 -12.54663  0.0000
T1_L11       0.0091320 0.02722548 25   0.33542  0.7401
 Correlation:
       (Intr)
T1_L11 -0.402

> VarCorr(T1L1DF4)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 5.438472e-11 0.0000073746
trial =     pdLogChol(1)
(Intercept) 1.936809e-02 0.1391692851
Residual    9.265336e-03 0.0962566175

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-3.71536721 -0.17733334  0.09282397  0.42128923  1.78578086

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> CPs(T1L1DF4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower         est.       upper
(Intercept) -0.49296035 -0.424613282 -0.35626621
T1_L11      -0.04585109  0.009131961  0.06411501
attr(,"label")
[1] "Fixed effects:"
> anova(T1L1DF4, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    25 157.41780  <.0001
T1_L1           1    25   0.11251  0.7401
> #estimated marginal means (least squares)
> emmls = emmeans(T1L1DF4, pairwise ~ T1_L1, mode="containment")
> summary(emmls)
$emmeans
 T1_L1 emmean     SE df lower.CL upper.CL
 0     -0.425 0.0338  9   -0.501   -0.348
 1     -0.415 0.0338  9   -0.492   -0.339

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast estimate     SE df t.ratio p.value
 0 - 1    -0.00913 0.0272 25 -0.335  0.7401

Degrees-of-freedom method: containment
```

S1.7. R {nlme} output: duty factor (DF) models for transition 1 and 2 (T1, T2) within limbs 1 and 2 (L1, L2)

a) T1 L2

```
##T1_Limb2

>
> T1L2DF = lme(DF ~  Vstride + SVL + T1_L2, random = ~1|geckoID/trial,
+                    T1, method="ML")
> summary(T1L2DF)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -97.59737 -82.93696 55.79869

Random effects:
```

```
 Formula: ~1 | geckoID
        (Intercept)
StdDev: 4.104872e-06

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.05489625 0.08115829

Fixed effects: DF ~ Vstride + SVL + T1_L2
                 Value Std.Error DF   t-value p-value
(Intercept) -0.1389788 0.5594666 28 -0.248413  0.8056
Vstride     -0.4762644 0.0844565 28 -5.639167  0.0000
SVL          0.4676308 0.3709519  8  1.260624  0.2430
T1_L21       0.0567279 0.0216909 28  2.615288  0.0142
 Correlation:
        (Intr) Vstrid SVL
Vstride  0.105
SVL     -0.953 -0.399
T1_L21  -0.019  0.006 -0.003

> VarCorr(T1L2DF)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 1.684998e-11 4.104872e-06
trial =     pdLogChol(1)
(Intercept) 3.013598e-03 5.489625e-02
Residual    6.586667e-03 8.115829e-02

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.0082155 -0.6375267  0.1754385  0.5518011  1.9737483

Number of Observations: 60
Number of Groups:
           geckoID trial %in% geckoID
                10                 30
> CPs(T1L2DF, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.       upper
(Intercept) -1.24613487 -0.13897882  0.96817723
Vstride     -0.64339953 -0.47626438 -0.30912923
SVL         -0.35878021  0.46763080  1.29404181
T1_L21       0.01380275  0.05672794  0.09965313
attr(,"label")
[1] "Fixed effects:"
> anova(T1L2DF, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    28  0.06171  0.8056
Vstride         1    28 31.80021  <.0001
SVL             1     8  1.58917  0.2430
T1_L2           1    28  6.83973  0.0142
> #estimated marginal means (least squares)
> emmls = emmeans(T1L2DF, pairwise ~ T1_L2, mode="containment")
> summary(emmls)
$emmeans
 T1_L2 Vstride  SVL emmean     SE df lower.CL upper.CL
 0        2.16 1.63 -0.405 0.0185  8   -0.448   -0.362
 1        2.16 1.63 -0.348 0.0185  8   -0.391   -0.306

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                                         estimate     SE df t.ratio
p.value
 0 2.16358362288333 1.63445981143333 - 1 2.16358362288333 1.63445981143333  -0.0567 0.0217 28 -2.615
0.0142

Degrees-of-freedom method: containment



> T1L2DF2 = lme(DF ~ SVL  + T1_L2, random = ~1|geckoID/trial,
+                    T1, method="ML")
> summary(T1L2DF2)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -85.90056 -73.33449 48.95028

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.08982552
```

```
 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.05622462 0.07910723

Fixed effects: DF ~ SVL + T1_L2
                 Value Std.Error DF    t-value p-value
(Intercept)  0.2879785 1.3196443 29  0.2182244  0.8288
SVL         -0.4252816 0.8040755  8 -0.5289076  0.6112
T1_L21       0.0575029 0.0209560 29  2.7439823  0.0103
 Correlation: 
       (Intr) SVL  
SVL    -1.000      
T1_L21 -0.008  0.000

> VarCorr(T1L2DF2)
            Variance     StdDev    
geckoID =   pdLogChol(1)           
(Intercept) 0.008068623  0.08982552
trial =     pdLogChol(1)           
(Intercept) 0.003161208  0.05622462
Residual    0.006257954  0.07910723

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-2.1397296 -0.4730702  0.1547478  0.4896752  1.8189854 

Number of Observations: 60
Number of Groups: 
           geckoID trial %in% geckoID 
                10                 30 

> CPs(T1L2DF2, level=0.95, which=c("fixed"))

Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.      upper
(Intercept) -2.34265757  0.28797854 2.91861464
SVL         -2.23253361 -0.42528161 1.38197039
T1_L21       0.01572831  0.05750294 0.09927757
attr(,"label")
[1] "Fixed effects:"

> anova(T1L2DF2, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    29 0.047622  0.8288
SVL             1     8 0.279743  0.6112
T1_L2           1    29 7.529439  0.0103
> #estimated marginal means (least squares)
> emmls = emmeans(T1L2DF2, pairwise ~ T1_L2, mode="containment")
> summary(emmls)
$emmeans
 $emmeans

 T1_L2  SVL emmean     SE df lower.CL upper.CL
 0     1.63 -0.407 0.0351  8   -0.488   -0.326
 1     1.63 -0.350 0.0351  8   -0.431   -0.269

Degrees-of-freedom method: containment 
Confidence level used: 0.95 

$contrasts
 contrast                               estimate    SE df t.ratio p.value
 0 1.63445981143333 - 1 1.63445981143333  -0.0575 0.021 29 -2.744  0.0103 
Degrees-of-freedom method: containment



> T1L2DF3 = lme(DF ~ Vstride  + T1_L2, random = ~1|geckoID/trial,
+                     T1, method="ML")
> summary(T1L2DF3)
Linear mixed-effects model fit by maximum likelihood
 Data: T1 
        AIC       BIC   logLik
  -98.26729 -85.70122 55.13364

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.02688503

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.05216647 0.08090811
```

```
Fixed effects: DF ~ Vstride + T1_L2
                 Value  Std.Error DF   t-value p-value
(Intercept)  0.5233913 0.18791423 28  2.785267  0.0095
Vstride     -0.4291680 0.08616147 28 -4.980973  0.0000
T1_L21       0.0568046 0.02143354 28  2.650266  0.0131
 Correlation: 
        (Intr) Vstrid
Vstride -0.994       
T1_L21  -0.064  0.007

> VarCorr(T1L2DF3)
            Variance     StdDev    
geckoID =   pdLogChol(1)           
(Intercept) 0.0007228051 0.02688503
trial =     pdLogChol(1)           
(Intercept) 0.0027213407 0.05216647
Residual    0.0065461224 0.08090811

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-1.9300758 -0.6173812  0.2064065  0.5058088  2.0228420 

Number of Observations: 60
Number of Groups: 
           geckoID trial %in% geckoID 
                10                 30 
> CPs(T1L2DF3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.       upper
(Intercept)  0.14821294  0.52339129  0.89856963
Vstride     -0.60119285 -0.42916800 -0.25714314
T1_L21       0.01401165  0.05680458  0.09959751
attr(,"label")
[1] "Fixed effects:"
> anova(T1L2DF3, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    28  7.757711  0.0095
Vstride         1    28 24.810096  <.0001
T1_L2           1    28  7.023908  0.0131
> #estimated marginal means (least squares)
> emmls = emmeans(T1L2DF3, pairwise ~ T1_L2, mode="containment")
> summary(emmls)
$emmeans
 T1_L2 Vstride emmean     SE df lower.CL upper.CL
 0        2.16 -0.405 0.0202  9   -0.451   -0.359
 1        2.16 -0.348 0.0202  9   -0.394   -0.303

Degrees-of-freedom method: containment 
Confidence level used: 0.95 

$contrasts
 contrast                                 estimate     SE df t.ratio p.value
 0 2.16358362288333 - 1 2.16358362288333   -0.0568 0.0214 28 -2.650  0.0131 

Degrees-of-freedom method: containment 



> T1L2DF4 = lme(DF ~ T1_L2, random = ~1|geckoID/trial,
+                    T1, method="ML")
> summary(T1L2DF4)
Linear mixed-effects model fit by maximum likelihood
 Data: T1 
       AIC       BIC   logLik
  -87.6131 -77.14138 48.80655

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.09208407

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.05597824 0.07910723

Fixed effects: DF ~ T1_L2 
                 Value  Std.Error DF    t-value p-value
(Intercept) -0.4097587 0.03509624 29 -11.675285  0.0000
T1_L21       0.0575029 0.02077458 29   2.767948  0.0097
 Correlation: 
       (Intr)
T1_L21 -0.296

> VarCorr(T1L2DF4)
```

```
             Variance     StdDev
geckoID =    pdLogChol(1)
(Intercept) 0.008479476  0.09208407
trial =      pdLogChol(1)
(Intercept) 0.003133563  0.05597824
Residual    0.006257954  0.07910723

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.1512555 -0.4527546  0.1483590  0.4790968  1.8074596

Number of Observations: 60
Number of Groups:
           geckoID trial %in% geckoID
                10                 30
> CPs(T1L2DF4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.       upper
(Intercept) -0.48033208 -0.40975868 -0.33918527
T1_L21       0.01572831  0.05750294  0.09927757
attr(,"label")
[1] "Fixed effects:"
> anova(T1L2DF4, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    29 136.31229  <.0001
T1_L2           1    29   7.66153  0.0097
> #estimated marginal means (least squares)
> emmls = emmeans(T1L2DF4, pairwise ~ T1_L2, mode="containment")
> summary(emmls)
$emmeans
 T1_L2 emmean     SE df lower.CL upper.CL
 0     -0.410 0.0351  9   -0.489   -0.330
 1     -0.352 0.0351  9   -0.432   -0.273

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast estimate     SE df t.ratio p.value
 0 - 1     -0.0575 0.0208 29 -2.768  0.0097

Degrees-of-freedom method: containment
```

S1.7. R {nlme} output: duty factor (DF) models for transition 1 and 2 (T1, T2) within limbs 1 and 2 (L1, L2)

a) T2 L1

```
> #Transition 2: sand sand-solid

>
> #T2_Limb1

> T2L1DF = lme(DF ~  Vstride + SVL + T2_L1, random = ~1|geckoID/trial,
+                   T2, method="ML")
> summary(T2L1DF)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC       BIC   logLik
  -78.36023 -64.70153 46.18012

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev: 1.38495e-06

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.04252113 0.09092443

Fixed effects: DF ~ Vstride + SVL + T2_L1
                 Value Std.Error DF   t-value p-value
(Intercept)  0.4621132 0.5468672 24  0.845019  0.4064
Vstride     -0.6901004 0.1045085 24 -6.603294  0.0000
SVL          0.3754471 0.3814934  7  0.984151  0.3578
T2_L11      -0.0432165 0.0262611 24 -1.645650  0.1129
 Correlation:
        (Intr) Vstrid SVL
```

```
Vstride  0.147
SVL     -0.933 -0.493
T2_L11  -0.019  0.032 -0.016

> VarCorr(T2L1DF)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 1.918085e-12 1.384950e-06
trial =     pdLogChol(1)
(Intercept) 1.808047e-03 4.252113e-02
Residual    8.267251e-03 9.092443e-02

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-3.06120810 -0.44515317 -0.08889564  0.49895341  2.38106455

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                 9                 26
> CPs(T2L1DF, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.        upper
(Intercept) -0.62228603  0.46211317  1.546512364
Vstride     -0.89733347 -0.69010043 -0.482867397
SVL         -0.49125139  0.37544714  1.242145666
T2_L11      -0.09529036 -0.04321652  0.008857332
attr(,"label")
[1] "Fixed effects:"
> anova(T2L1DF, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    24  0.71406  0.4064
Vstride         1    24 43.60349  <.0001
SVL             1     7  0.96855  0.3578
T2_L1           1    24  2.70816  0.1129
> #estimated marginal means (least squares)
> emmls = emmeans(T2L1DF, pairwise ~ T2_L1, mode="containment")
> summary(emmls)
$emmeans
 T2_L1 Vstride  SVL emmean     SE df lower.CL upper.CL
 0        2.15 1.63 -0.412 0.0205  7   -0.461   -0.364
 1        2.15 1.63 -0.455 0.0205  7   -0.504   -0.407

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                                 estimate     SE df t.ratio
p.value
 0 2.15247291648077 1.62800471042308 - 1 2.15247291648077 1.62800471042308   0.0432 0.0263 24 1.646
0.1129

Degrees-of-freedom method: containment




> T2L1DF2 = lme(DF ~  SVL + T2_L1, random = ~1|geckoID/trial,
+                     T2, method="ML")
> summary(T2L1DF2)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC       BIC   logLik
  -54.38662 -42.67916 33.19331

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.07559854

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.08684062 0.09181012

Fixed effects: DF ~ SVL + T2_L1
                 Value Std.Error DF    t-value p-value
(Intercept)  1.1243538 1.2578543 25  0.8938665  0.3799
SVL         -0.9445969 0.7683527  7 -1.2293794  0.2586
T2_L11      -0.0376679 0.0262315 25 -1.4359834  0.1634
 Correlation:
       (Intr) SVL
SVL    -1.00
T2_L11 -0.01   0.00
```

```
> VarCorr(T2L1DF2)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.005715139  0.07559854
trial =     pdLogChol(1)
(Intercept) 0.007541293  0.08684062
Residual    0.008429097  0.09181012

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.0772269 -0.2629174  0.1237013  0.4812890  2.1312993

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                 9                 26
> CPs(T2L1DF2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                 lower        est.      upper
(Intercept) -1.3904067  1.12435377 3.63911423
SVL         -2.7082741 -0.94459692 0.81908029
T2_L11      -0.0901111 -0.03766794 0.01477521
attr(,"label")
[1] "Fixed effects:"
> anova(T2L1DF2, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    25 0.7989973  0.3799
SVL             1     7 1.5113737  0.2586
T2_L1           1    25 2.0620482  0.1634
> #estimated marginal means (least squares)
> emmls = emmeans(T2L1DF2, pairwise ~ T2_L1, mode="containment")
> summary(emmls)
$emmeans
 T2_L1  SVL emmean     SE df lower.CL upper.CL
 0     1.63 -0.413 0.0374  7   -0.502   -0.325
 1     1.63 -0.451 0.0374  7   -0.540   -0.363

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                 estimate     SE df t.ratio p.value
 0 1.62800471042308 - 1 1.62800471042308   0.0377 0.0262 25 1.436   0.1634

Degrees-of-freedom method: containment



> T2L1DF3 = lme(DF ~ Vstride  + T2_L1, random = ~1|geckoID/trial,
+               T2, method="ML")
> summary(T2L1DF3)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC       BIC   logLik
  -79.33139 -67.62393 45.66569

Random effects:
 Formula: ~1 | geckoID
         (Intercept)
StdDev: 1.868912e-06

 Formula: ~1 | trial %in% geckoID
        (Intercept)  Residual
StdDev:  0.04523122 0.0909333

Fixed effects: DF ~ Vstride + T2_L1
                 Value  Std.Error DF   t-value p-value
(Intercept)  0.9641501 0.19901914 24  4.844510  0.0001
Vstride     -0.6394660 0.09179654 24 -6.966123  0.0000
T2_L11      -0.0428094 0.02599143 24 -1.647059  0.1126
 Correlation:
        (Intr) Vstrid
Vstride -0.995
T2_L11  -0.093  0.028

> VarCorr(T2L1DF3)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 3.492832e-12 1.868912e-06
trial =     pdLogChol(1)
(Intercept) 2.045863e-03 4.523122e-02
Residual    8.268866e-03 9.093330e-02

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
```

```
-2.9947671 -0.4241013 -0.1005552  0.5075515  2.4335476

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                 9                26
> CPs(T2L1DF3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower       est.        upper
(Intercept)  0.56541953  0.9641501  1.362880715
Vstride     -0.82337843 -0.6394660 -0.455553613
T2_L11      -0.09488267 -0.0428094  0.009263862
attr(,"label")
[1] "Fixed effects:"
> anova(T2L1DF3, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    24 23.46927  0.0001
Vstride         1    24 48.52687  <.0001
T2_L1           1    24  2.71280  0.1126
> #estimated marginal means (least squares)
> emmls = emmeans(T2L1DF3, pairwise ~ T2_L1, mode="containment")
> summary(emmls)
$emmeans
 T2_L1 Vstride emmean     SE df lower.CL upper.CL
 0        2.15 -0.412 0.0205  8   -0.460   -0.365
 1        2.15 -0.455 0.0205  8   -0.502   -0.408

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                         estimate    SE df t.ratio p.value
 0 2.15247291648077 - 1 2.15247291648077   0.0428 0.026 24 1.647   0.1126

Degrees-of-freedom method: containment



> T2L1DF4 = lme(DF ~ T2_L1, random = ~1|geckoID/trial,
+                    T2, method="ML")
> summary(T2L1DF4)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC       BIC   logLik
  -54.93873 -45.18251 32.46937

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.08950527

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.08549337 0.09181012

Fixed effects: DF ~ T2_L1
                 Value  Std.Error DF    t-value p-value
(Intercept) -0.4222606 0.03985973 25 -10.593663  0.0000
T2_L11      -0.0376679 0.02596782 25  -1.450562  0.1593
 Correlation:
       (Intr)
T2_L11 -0.326

> VarCorr(T2L1DF4)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.008011194  0.08950527
trial =     pdLogChol(1)
(Intercept) 0.007309116  0.08549337
Residual    0.008429097  0.09181012

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.1212819 -0.2618166  0.1281964  0.4774221  2.0872443

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                 9                26
> CPs(T2L1DF4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                 lower        est.       upper
```

```
(Intercept) -0.5027591 -0.42226058 -0.34176211
T2_L11      -0.0901111 -0.03766794  0.01477521
attr(,"label")
[1] "Fixed effects:"
> anova(T2L1DF4, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    25 112.22569  <.0001
T2_L1           1    25   2.10413  0.1593
> #estimated marginal means (least squares)
> emmls = emmeans(T2L1DF4, pairwise ~ T2_L1, mode="containment")
> summary(emmls)
$emmeans
 T2_L1 emmean     SE df lower.CL upper.CL
 0     -0.422 0.0399  8   -0.514   -0.330
 1     -0.460 0.0399  8   -0.552   -0.368

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast estimate    SE df t.ratio p.value
 0 - 1      0.0377 0.026 25 1.451   0.1593

Degrees-of-freedom method: containment
```

S1.7. R {nlme} output: duty factor (DF) models for transition 1 and 2 (T1, T2) within limbs 1 and 2 (L1, L2)

a) T2 L2

```
> #T2_Limb2

>
> T2L2DF = lme(DF ~ Vstride + SVL + T2_L2, random = ~1|geckoID/trial,
+                  T2, method="ML")
> summary(T2L2DF)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC       BIC   logLik
  -85.68405 -73.03741 49.84203

Random effects:
 Formula: ~1 | geckoID
         (Intercept)
StdDev: 1.989792e-06

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.04945694 0.06609426

Fixed effects: DF ~ Vstride + SVL + T2_L2
                 Value Std.Error DF   t-value p-value
(Intercept)  0.4838135 0.5141542 19  0.940989  0.3585
Vstride     -0.3570538 0.1101661 19 -3.241049  0.0043
SVL         -0.0347070 0.3453397  6 -0.100501  0.9232
T2_L2       -0.0296223 0.0209218 19 -1.415856  0.1730
 Correlation:
        (Intr) Vstrid SVL
Vstride -0.016
SVL     -0.909 -0.402
T2_L2   -0.051  0.034  0.014

> VarCorr(T2L2DF)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 3.959270e-12 1.989792e-06
trial =     pdLogChol(1)
(Intercept) 2.445988e-03 4.945694e-02
Residual    4.368451e-03 6.609426e-02

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.4066400 -0.1967409  0.1900083  0.5032305  1.3157803

Number of Observations: 45
Number of Groups:
           geckoID trial %in% geckoID
                 8                 24

> CPs(T2L2DF, level=0.95, which=c("fixed"))
```

```
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.       upper
(Intercept) -0.54338238  0.48381345  1.51100928
Vstride     -0.57714765 -0.35705377 -0.13695990
SVL         -0.84129277 -0.03470699  0.77187879
T2_L2       -0.07142061 -0.02962227  0.01217607
attr(,"label")
[1] "Fixed effects:"

> anova(T2L2DF, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    19  0.885460  0.3585
Vstride         1    19 10.504397  0.0043
SVL             1     6  0.010100  0.9232
T2_L2           1    19  2.004649  0.1730

> #estimated marginal means (least squares)
> emmls = emmeans(T2L2DF, pairwise ~ T2_L2, mode="containment")
> summary(emmls)
$emmeans
 T2_L2 Vstride  SVL emmean     SE df lower.CL upper.CL
 0        2.11 1.62 -0.327 0.0184  6   -0.372   -0.282
 1        2.11 1.62 -0.357 0.0180  6   -0.401   -0.313

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                                     estimate     SE df t.ratio
p.value
 0 2.11281992302222 1.62349833657778 - 1 2.11281992302222 1.62349833657778   0.0296 0.0209 19 1.416
0.1730

Degrees-of-freedom method: containment



> T2L2DF2 = lme(DF ~ SVL + T2_L2, random = ~1|geckoID/trial,
+                     T2, method="ML")
> summary(T2L2DF2)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
       AIC       BIC  logLik
  -78.1178 -67.27783 45.0589

Random effects:
 Formula: ~1 | geckoID
         (Intercept)
StdDev: 4.973342e-06

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.06772728 0.06696252

Fixed effects: DF ~ SVL + T2_L2
                 Value Std.Error DF    t-value p-value
(Intercept)  0.4357254 0.6122246 20  0.7117085  0.4849
SVL         -0.4712264 0.3765996  6 -1.2512663  0.2574
T2_L2       -0.0274133 0.0210344 20 -1.3032609  0.2073
 Correlation:
      (Intr) SVL
SVL   -0.999
T2_L2 -0.045  0.028

> VarCorr(T2L2DF2)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 2.473413e-11 4.973342e-06
trial =     pdLogChol(1)
(Intercept) 4.586984e-03 6.772728e-02
Residual    4.483980e-03 6.696252e-02

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.3446369 -0.2420248  0.1555573  0.4070190  1.1928363

Number of Observations: 45
Number of Groups:
           geckoID trial %in% geckoID
                 8                 24
> CPs(T1L1DF2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
```

```
                   lower         est.      upper
(Intercept) -1.24030126  1.034555718 3.30941270
SVL         -2.45113248 -0.893000017 0.66513245
T1_L11      -0.04585109  0.009131961 0.06411501
attr(,"label")
[1] "Fixed effects:"
> anova(T2L2DF2, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    20 0.506529  0.4849
SVL             1     6 1.565667  0.2574
T2_L2           1    20 1.698489  0.2073
> #estimated marginal means (least squares)
> emmls = emmeans(T2L2DF2, pairwise ~ T2_L2, mode="containment")
> summary(emmls)
$emmeans
 T2_L2  SVL emmean     SE df lower.CL upper.CL
 0     1.62 -0.329 0.0208  6   -0.380   -0.278
 1     1.62 -0.357 0.0204  6   -0.407   -0.307

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                estimate    SE df t.ratio p.value
 0 1.62349833657778 - 1 1.62349833657778   0.0274 0.021 20 1.303   0.2073

Degrees-of-freedom method: containment



> T2L2DF3 = lme(DF ~ Vstride  + T2_L2, random = ~1|geckoID/trial,
+                     T2, method="ML")
> summary(T2L2DF3)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC       BIC   logLik
  -87.67311 -76.83314 49.83656

Random effects:
 Formula: ~1 | geckoID
         (Intercept)
StdDev: 1.610811e-06

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:   0.0496489 0.06601009

Fixed effects: DF ~ Vstride + T2_L2
                 Value  Std.Error DF   t-value p-value
(Intercept)  0.4368094 0.21237057 19  2.056827  0.0537
Vstride     -0.3614809 0.09978832 19 -3.622478  0.0018
T2_L2       -0.0295935 0.02064465 19 -1.433469  0.1680
 Correlation:
        (Intr) Vstrid
Vstride -0.996
T2_L2   -0.093  0.043

> VarCorr(T2L2DF3)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 2.594710e-12 1.610811e-06
trial =     pdLogChol(1)
(Intercept) 2.465013e-03 4.964890e-02
Residual    4.357332e-03 6.601009e-02

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.4104493 -0.2144467  0.1874583  0.5072910  1.3038158

Number of Observations: 45
Number of Groups:
           geckoID trial %in% geckoID
                 8                 24
> CPs(T2L2DF3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower        est.       upper
(Intercept)  0.00738481  0.43680942  0.86623403
Vstride     -0.56325823 -0.36148093 -0.15970364
T2_L2       -0.07133804 -0.02959346  0.01215112
attr(,"label")
[1] "Fixed effects:"
> anova(T2L2DF3, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    19  4.230536  0.0537
```

```
Vstride         1    19 13.122343  0.0018
T2_L2           1    19  2.054833  0.1680
> #estimated marginal means (least squares)
> emmls = emmeans(T2L2DF3, pairwise ~ T2_L2, mode="containment")
> summary(emmls)
$emmeans
 T2_L2 Vstride emmean     SE df lower.CL upper.CL
 0        2.11 -0.327 0.0181  7   -0.370   -0.284
 1        2.11 -0.357 0.0178  7   -0.399   -0.314

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                estimate     SE df t.ratio p.value
 0 2.11281992302222 - 1 2.11281992302222   0.0296 0.0206 19 1.433   0.1680

Degrees-of-freedom method: containment



> T2L2DF4 = lme(DF ~ T2_L2, random = ~1|geckoID/trial,
+                     T2, method="ML")
> summary(T2L2DF4)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC       BIC   logLik
  -78.51949 -69.48618 44.25974

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.01274999

 Formula: ~1 | trial %in% geckoID
        (Intercept) Residual
StdDev:  0.07064106 0.066681

Fixed effects: DF ~ T2_L2
                 Value  Std.Error DF    t-value p-value
(Intercept) -0.3302056 0.02148540 20 -15.368835  0.0000
T2_L2       -0.0267367 0.02071075 20  -1.290957  0.2114
 Correlation:
      (Intr)
T2_L2 -0.497

> VarCorr(T2L2DF4)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.0001625624 0.01274999
trial =     pdLogChol(1)
(Intercept) 0.0049901599 0.07064106
Residual    0.0044463559 0.06668100

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-3.3857364 -0.2766785  0.1350214  0.4288218  1.2231746

Number of Observations: 45
Number of Groups:
           geckoID trial %in% geckoID
                 8                 24
> CPs(T2L2DF4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.       upper
(Intercept) -0.37401607 -0.33020558 -0.28639509
T2_L2       -0.06896759 -0.02673668  0.01549423
attr(,"label")
[1] "Fixed effects:"
> anova(T2L2DF4, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    20 236.20110  <.0001
T2_L2           1    20   1.66657  0.2114
> #estimated marginal means (least squares)
> emmls = emmeans(T2L2DF4, pairwise ~ T2_L2, mode="containment")
> summary(emmls)
$emmeans
 T2_L2 emmean     SE df lower.CL upper.CL
     0 -0.330 0.0215  7   -0.381   -0.279
     1 -0.357 0.0212  7   -0.407   -0.307

Degrees-of-freedom method: containment
Confidence level used: 0.95
```

```
$contrasts
 contrast estimate     SE df t.ratio p.value
 0 - 1      0.0267 0.0207 20 1.291   0.2114

Degrees-of-freedom method: containment
```

S1.8. R output: body pitch angle (BPA) models for transition 1 and 2 (T1, T2) within limbs 1 and 2 (L1, L2)

a) T1 L1

```
> #######Transition 1: solid solid-sand########
> ##T1_Limb1
>
> T1L1BPA = lme(BPA ~  Vstride + SVL + T1_L1, random = ~1|geckoID/trial,
+               T1, method="ML")
> summary(T1L1BPA)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -57.86599 -44.48183 35.93299

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.01836934

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.06831349 0.09875741

Fixed effects: BPA ~ Vstride + SVL + T1_L1
                 Value Std.Error DF    t-value p-value
(Intercept) -0.2206629 0.8159509 22 -0.2704365  0.7893
Vstride      0.0564114 0.1201723 22  0.4694211  0.6434
SVL          0.7205078 0.5367067  8  1.3424608  0.2163
T1_L11       0.0356196 0.0294038 22  1.2113967  0.2386
 Correlation:
        (Intr) Vstrid SVL
Vstride  0.094
SVL     -0.956 -0.380
T1_L11  -0.041 -0.064  0.039

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.98657685 -0.61077277 -0.06873982  0.69599810  1.68166160

Number of Observations: 50
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> VarCorr(T1L1BPA)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.0003374328 0.01836934
trial =     pdLogChol(1)
(Intercept) 0.0046667329 0.06831349
Residual    0.0097530265 0.09875741

> CPs(T1L1BPA, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.      upper
(Intercept) -1.84374357 -0.22066292 1.40241773
Vstride     -0.18263396  0.05641139 0.29545675
SVL         -0.46660248  0.72050775 1.90761799
T1_L11      -0.02287004  0.03561964 0.09410931
attr(,"label")
[1] "Fixed effects:"
> anova(T1L1BPA, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    22 0.0731359  0.7893
Vstride         1    22 0.2203562  0.6434
SVL             1     8 1.8022009  0.2163
T1_L1           1    22 1.4674819  0.2386
> #estimated marginal means (least squares)
> emmls = emmeans(T1L1BPA, pairwise ~ T1_L1+ Vstride + SVL, mode="containment")
> summary(emmls)
$emmeans
 T1_L1 Vstride  SVL emmean     SE df lower.CL upper.CL
 0        2.14 1.63   1.08 0.0263  8     1.02     1.14
 1        2.14 1.63   1.11 0.0254  8     1.05     1.17

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                    estimate     SE df t.ratio p.value
```

```
 0 2.1395499195 1.63480550494 - 1 2.1395499195 1.63480550494  -0.0356 0.0294 22 -1.211  0.2386

Degrees-of-freedom method: containment


> T1L1BPA2 = lme(BPA ~ SVL + T1_L1, random = ~1|geckoID/trial,
+                T1, method="ML")
> summary(T1L1BPA2)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -59.64766 -48.17552 35.82383

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.02590594

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:   0.0672108 0.09852228

Fixed effects: BPA ~ SVL + T1_L1
                 Value Std.Error DF    t-value p-value
(Intercept) -0.2949882 0.8354297 23 -0.3530976  0.7272
SVL          0.8399367 0.5103995  8  1.6456456  0.1385
T1_L11       0.0362754 0.0289631 23  1.2524690  0.2230
 Correlation:
       (Intr) SVL
SVL    -0.999
T1_L11 -0.033  0.015

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.02930810 -0.60727381 -0.06549166  0.69840104  1.66753310

Number of Observations: 50
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> VarCorr(T1L1BPA2)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.0006711179 0.02590594
trial =     pdLogChol(1)
(Intercept) 0.0045172910 0.06721080
Residual    0.0097066387 0.09852228

> CPs(T1L1BPA2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.      upper
(Intercept) -1.97055771 -0.29498821 1.38058128
SVL         -0.30119102  0.83993672 1.98106446
T1_L11      -0.02181413  0.03627542 0.09436496
attr(,"label")
[1] "Fixed effects:"
> anova(T1L1BPA2, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    23 0.1246779  0.7272
SVL             1     8 2.7081495  0.1385
T1_L1           1    23 1.5686786  0.2230
> #estimated marginal means (least squares)
> emmls = emmeans(T1L1BPA2, pairwise ~ T1_L1+ SVL, mode="containment")
> summary(emmls)
$emmeans
 T1_L1  SVL emmean     SE df lower.CL upper.CL
 0     1.63   1.08 0.0266  8     1.02     1.14
 1     1.63   1.11 0.0257  8     1.06     1.17

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                          estimate    SE df t.ratio p.value
 0 1.63480550494 - 1 1.63480550494  -0.0363 0.029 23 -1.252  0.2230

Degrees-of-freedom method: containment


> T1L1BPA3 = lme(BPA ~ Vstride + T1_L1, random = ~1|geckoID/trial,
+                T1, method="ML")
> summary(T1L1BPA3)
Linear mixed-effects model fit by maximum likelihood
```

```
 Data: T1 
       AIC       BIC   logLik
  -57.96847 -46.49633 34.98423

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.01267428

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.07381545 0.09925832

Fixed effects: BPA ~ Vstride + T1_L1 
                Value  Std.Error DF  t-value p-value
(Intercept) 0.8266683 0.24006054 22 3.443583  0.0023
Vstride     0.1176773 0.11175883 22 1.052958  0.3038
T1_L11      0.0340578 0.02922994 22 1.165168  0.2564
 Correlation: 
        (Intr) Vstrid
Vstride -0.994       
T1_L11  -0.011 -0.053

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-1.8505161 -0.4614186 -0.1601835  0.7064342  1.7508071 

Number of Observations: 50
Number of Groups: 
           geckoID trial %in% geckoID 
                10                 26 
> VarCorr(T1L1BPA3)
            Variance     StdDev    
geckoID =   pdLogChol(1)           
(Intercept) 0.0001606374 0.01267428
trial =     pdLogChol(1)           
(Intercept) 0.0054487213 0.07381545
Residual    0.0098522138 0.09925832
> 
> CPs(T1L1BPA3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                 lower       est.      upper
(Intercept)  0.3439799 0.82666833 1.30935674
Vstride     -0.1070355 0.11767733 0.34239020
T1_L11      -0.0247147 0.03405779 0.09283028
attr(,"label")
[1] "Fixed effects:"
> anova(T1L1BPA3, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    22 11.858262  0.0023
Vstride         1    22  1.108720  0.3038
T1_L1           1    22  1.357616  0.2564
> #estimated marginal means (least squares)
> emmls = emmeans(T1L1BPA3, pairwise ~ T1_L1+ Vstride , mode="containment")
> summary(emmls)
$emmeans
 T1_L1 Vstride emmean     SE df lower.CL upper.CL
 0        2.14   1.08 0.0263  9     1.02     1.14
 1        2.14   1.11 0.0254  9     1.05     1.17

Degrees-of-freedom method: containment 
Confidence level used: 0.95 

$contrasts
 contrast                        estimate     SE df t.ratio p.value
 0 2.1395499195 - 1 2.1395499195  -0.0341 0.0292 22 -1.165  0.2564 

Degrees-of-freedom method: containment 



> T1L1BPA4 = lme(BPA ~ T1_L1, random = ~1|geckoID/trial,
+               T1, method="ML")
> summary(T1L1BPA4)
Linear mixed-effects model fit by maximum likelihood
 Data: T1 
       AIC      BIC   logLik
  -58.91121 -49.3511 34.45561

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.0330853

 Formula: ~1 | trial %in% geckoID
```

```
        (Intercept)   Residual
StdDev:  0.07189373 0.09889486

Fixed effects: BPA ~ T1_L1
                Value  Std.Error DF  t-value p-value
(Intercept) 1.0800228 0.02773289 23 38.94376  0.0000
T1_L11      0.0353324 0.02878592 23  1.22742  0.2321
 Correlation:
       (Intr)
T1_L11 -0.547

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.9324575 -0.5378699 -0.1206516  0.7304337  1.7231621

Number of Observations: 50
Number of Groups:
           geckoID trial %in% geckoID
                10                 26
> VarCorr(T1L1BPA4)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.001094637  0.03308530
trial =     pdLogChol(1)
(Intercept) 0.005168708  0.07189373
Residual    0.009780194  0.09889486

> CPs(T1L1BPA4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower       est.      upper
(Intercept)  1.02381209 1.08002283 1.13623357
T1_L11      -0.02301271 0.03533237 0.09367746
attr(,"label")
[1] "Fixed effects:"
> anova(T1L1BPA4, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    23 1516.6162  <.0001
T1_L1           1    23    1.5066  0.2321
> #estimated marginal means (least squares)
> emmls = emmeans(T1L1BPA4, pairwise ~ T1_L1, mode="containment")
> summary(emmls)
$emmeans
 T1_L1 emmean     SE df lower.CL upper.CL
 0       1.08 0.0277  9     1.02     1.14
 1       1.12 0.0269  9     1.05     1.18

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast estimate     SE df t.ratio p.value
 0 - 1     -0.0353 0.0288 23 -1.227  0.2321

Degrees-of-freedom method: containment



> T1L1BPAfe = gls(BPA ~ T1_L1, T1, method="ML")
> summary(T1L1BPAfe)

Generalized least squares fit by maximum likelihood
  Model: BPA ~ T1_L1
  Data: T1
        AIC       BIC   logLik
  -58.81168 -53.07561 32.40584

Coefficients:
                Value  Std.Error  t-value p-value
(Intercept) 1.0761695 0.02636623 40.81621  0.0000
T1_L11      0.0371116 0.03656338  1.01499  0.3152

 Correlation:
       (Intr)
T1_L11 -0.721

Standardized residuals:
        Min          Q1         Med          Q3         Max
-2.27701821 -0.71753335 -0.08141359  0.68329417  2.16067462

Residual standard error: 0.1265579
Degrees of freedom: 50 total; 48 residual

> CPs(T1L1BPAfe, level=0.95)
Approximate 95% confidence CPs
```

```
 Coefficients:
                  lower       est.     upper
(Intercept)  1.02315664 1.07616950 1.1291824
T1_L11      -0.03640404 0.03711157 0.1106272
attr(,"label")
[1] "Coefficients:"

 Residual standard error:
    lower      est.     upper
0.1058922 0.1265579 0.1573214

> anova(T1L1BPAfe, type="marginal")
Denom. DF: 48
            numDF   F-value p-value
(Intercept)     1 1665.9626  <.0001
T1_L1           1    1.0302  0.3152

$emmeans
 T1_L1 emmean     SE df lower.CL upper.CL
 0       1.08 0.0277  9     1.02     1.14
 1       1.12 0.0269  9     1.05     1.18

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast estimate     SE df t.ratio p.value
 0 - 1     -0.0353 0.0288 23 -1.227  0.2321

Degrees-of-freedom method: containment
```

S1.8. R output: body pitch angle (BPA) models for transition 1 and 2 (T1, T2) within limbs 1 and 2 (L1, L2)

a) T1 L2

```
> ##T1_Limb2


> T1L2BPA = lme(BPA ~  Vstride + SVL + T1_L2, random = ~1|geckoID/trial,
+               T1, method="ML")
> summary(T1L2BPA)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -79.98977 -65.32935 46.99488

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.0325069

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.05808547 0.09306549

Fixed effects: BPA ~ Vstride + SVL + T1_L2
                Value Std.Error DF  t-value p-value
(Intercept) 0.0468249 0.7688722 28 0.060901  0.9519
Vstride     0.1426080 0.1087510 28 1.311326  0.2004
SVL         0.4562604 0.5067385  8 0.900386  0.3942
T1_L21      0.0891062 0.0248734 28 3.582385  0.0013
 Correlation:
        (Intr) Vstrid SVL
Vstride  0.115
SVL     -0.959 -0.391
T1_L21  -0.015  0.007 -0.003

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.4299227 -0.6674973  0.1648580  0.4671068  2.3836405

Number of Observations: 60
Number of Groups:
          geckoID trial %in% geckoID
               10                 30
> VarCorr(T1L2BPA)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.001056698  0.03250690
```

```
trial =     pdLogChol(1)
(Intercept) 0.003373922  0.05808547
Residual    0.008661186  0.09306549

> CPs(T1L2BPA, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower      est.     upper
(Intercept) -1.47473413 0.0468249 1.5683839
Vstride     -0.07260467 0.1426080 0.3578206
SVL         -0.67265744 0.4562604 1.5851783
T1_L21       0.03988295 0.0891062 0.1383295
attr(,"label")
[1] "Fixed effects:"
> anova(T1L2BPA, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    28  0.003709  0.9519
Vstride         1    28  1.719576  0.2004
SVL             1     8  0.810696  0.3942
T1_L2           1    28 12.833483  0.0013
> #estimated marginal means (least squares)
> emmls = emmeans(T1L2BPA, pairwise ~ T1_L2+ Vstride + SVL, mode="containment")
> summary(emmls)
$emmeans
 T1_L2 Vstride  SVL emmean     SE df lower.CL upper.CL
 0        2.16 1.63   1.10 0.0236  8     1.05     1.16
 1        2.16 1.63   1.19 0.0236  8     1.14     1.24

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                               estimate     SE df t.ratio
p.value
 0 2.16358362288333 1.63445981143333 - 1 2.16358362288333 1.63445981143333  -0.0891 0.0249 28 -3.582
0.0013

Degrees-of-freedom method: containment



> T1L2BPA2 = lme(BPA ~ SVL  + T1_L2, random = ~1|geckoID/trial,
+                T1, method="ML")
> summary(T1L2BPA2)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
       AIC       BIC   logLik
  -80.22889 -67.66283 46.11445

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.03835149

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.05950075 0.09321764

Fixed effects: BPA ~ SVL + T1_L2
                 Value Std.Error DF   t-value p-value
(Intercept) -0.1038780 0.8116585 29 -0.127982  0.8990
SVL          0.7371718 0.4955476  8  1.487590  0.1752
T1_L21       0.0888741 0.0246940 29  3.599024  0.0012
 Correlation:
       (Intr) SVL
SVL    -1.000
T1_L21 -0.015  0.000

> VarCorr(T1L2BPA2)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.001470837  0.03835149
trial =     pdLogChol(1)
(Intercept) 0.003540339  0.05950075
Residual    0.008689529  0.09321764

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.4011595 -0.6461802  0.1251788  0.4991122  2.4777147

Number of Observations: 60
Number of Groups:
           geckoID trial %in% geckoID
                10                 30
> CPs(T1L2BPA2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs
```

```
 Fixed effects:
                 lower        est.     upper
(Intercept) -1.72187324 -0.10387802 1.5141172
SVL         -0.37662830  0.73717181 1.8509719
T1_L21       0.03964814  0.08887414 0.1381001
attr(,"label")
[1] "Fixed effects:"
> anova(T1L2BPA2, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    29  0.016379  0.8990
SVL             1     8  2.212925  0.1752
T1_L2           1    29 12.952973  0.0012
> #estimated marginal means (least squares)
> emmls = emmeans(T1L2BPA2, pairwise ~ T1_L2+ SVL, mode="containment")
> summary(emmls)
$emmeans
 T1_L2  SVL emmean     SE df lower.CL upper.CL
 0     1.63   1.10 0.0245  8     1.04     1.16
 1     1.63   1.19 0.0245  8     1.13     1.25

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                estimate     SE df t.ratio p.value
 0 1.63445981143333 - 1 1.63445981143333  -0.0889 0.0247 29 -3.599  0.0012

Degrees-of-freedom method: containment



> T1L2BPA3 = lme(BPA ~ Vstride  + T1_L2, random = ~1|geckoID/trial,
+                T1, method="ML")
> summary(T1L2BPA3)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -81.13398 -68.56792 46.56699

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.03300802

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.06002081 0.09303938

Fixed effects: BPA ~ Vstride + T1_L2
                Value  Std.Error DF  t-value p-value
(Intercept) 0.7104662 0.21958860 28 3.235442  0.0031
Vstride     0.1809298 0.10067082 28 1.797242  0.0831
T1_L21      0.0891686 0.02464728 28 3.617785  0.0012
 Correlation:
        (Intr) Vstrid
Vstride -0.994
T1_L21  -0.063  0.007

> VarCorr(T1L2BPA3)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.001089529  0.03300802
trial =     pdLogChol(1)
(Intercept) 0.003602498  0.06002081
Residual    0.008656326  0.09303938

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.39266313 -0.65140477  0.08434535  0.55223574  2.22864394

Number of Observations: 60
Number of Groups:
           geckoID trial %in% geckoID
                10                 30
> CPs(T1L2BPA3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                 lower       est.     upper
(Intercept)  0.27204874 0.71046623 1.1488837
Vstride     -0.02006353 0.18092981 0.3819232
T1_L21       0.03995927 0.08916856 0.1383778
attr(,"label")
[1] "Fixed effects:"
> anova(T1L2BPA3, type="marginal")
```

```
            numDF denDF   F-value p-value
(Intercept)     1    28 10.468087  0.0031
Vstride         1    28  3.230079  0.0831
T1_L2           1    28 13.088370  0.0012
> #estimated marginal means (least squares)
> emmls = emmeans(T1L2BPA3, pairwise ~ T1_L2+ Vstride , mode="containment")
> summary(emmls)
$emmeans
 T1_L2 Vstride emmean     SE df lower.CL upper.CL
 0        2.16   1.10 0.0236  9     1.05     1.16
 1        2.16   1.19 0.0236  9     1.14     1.24

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                 estimate     SE df t.ratio p.value
 0 2.16358362288333 - 1 2.16358362288333  -0.0892 0.0246 28 -3.618  0.0012

Degrees-of-freedom method: containment



> T1L2BPA4 = lme(BPA ~ T1_L2, random = ~1|geckoID/trial,
+                T1, method="ML")
> summary(T1L2BPA4)
Linear mixed-effects model fit by maximum likelihood
 Data: T1
        AIC       BIC   logLik
  -80.01283 -69.54111 45.00641

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.04450952

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev:  0.06226398 0.09321765

Fixed effects: BPA ~ T1_L2
                Value  Std.Error DF  t-value p-value
(Intercept) 1.1031767 0.02560721 29 43.08070  0.0000
T1_L21      0.0888741 0.02448015 29  3.63046  0.0011
 Correlation:
       (Intr)
T1_L21 -0.478

> VarCorr(T1L2BPA4)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 0.001981098  0.04450952
trial =     pdLogChol(1)
(Intercept) 0.003876804  0.06226398
Residual    0.008689530  0.09321765


Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.33119743 -0.62151438  0.04447058  0.57085885  2.27814161

Number of Observations: 60
Number of Groups:
           geckoID trial %in% geckoID
                10                 30
> CPs(T1L2BPA4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                 lower       est.     upper
(Intercept) 1.05168432 1.10317667 1.1546690
T1_L21      0.03964814 0.08887414 0.1381001
attr(,"label")
[1] "Fixed effects:"
> anova(T1L2BPA4, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    29 1855.9470  <.0001
T1_L2           1    29   13.1802  0.0011
> #estimated marginal means (least squares)
> emmls = emmeans(T1L2BPA4, pairwise ~ T1_L2, mode="containment")
> summary(emmls)
$emmeans
 T1_L2 emmean     SE df lower.CL upper.CL
 0       1.10 0.0256  9     1.05     1.16
 1       1.19 0.0256  9     1.13     1.25

Degrees-of-freedom method: containment
```

```
Confidence level used: 0.95

$contrasts
 contrast estimate     SE df t.ratio p.value
 0 - 1     -0.0889 0.0245 29 -3.630  0.0011

Degrees-of-freedom method: containment
```

S1.8. R output: body pitch angle (BPA) models for transition 1 and 2 (T1, T2) within limbs 1 and 2 (L1, L2)

a) T2 L1

```
> #Transition 2: sand sand-solid

>
> #T2_Limb1
>
> T2L1BPA = lme(BPA ~  Vstride + SVL + T2_L1, random = ~1|geckoID/trial,
+               T2, method="ML")
> summary(T2L1BPA)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC       BIC   logLik
  -88.85949 -75.20079 51.42975

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.05984639

 Formula: ~1 | trial %in% geckoID
         (Intercept)   Residual
StdDev: 1.513006e-06 0.07959732

Fixed effects: BPA ~ Vstride + SVL + T2_L1
                 Value Std.Error DF   t-value p-value
(Intercept)  1.0604114 0.8984997 24  1.180202  0.2495
Vstride      0.2276893 0.1120992 24  2.031141  0.0535
SVL         -0.2161038 0.5819034  7 -0.371374  0.7213
T2_L11      -0.0707085 0.0229954 24 -3.074893  0.0052
 Correlation:
        (Intr) Vstrid SVL
Vstride  0.099
SVL     -0.967 -0.349
T2_L11  -0.009  0.039 -0.014

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.5305951 -0.5426621  0.1360589  0.5939925  2.0250549

Number of Observations: 52
Number of Groups:
          geckoID trial %in% geckoID
                9                 26
> VarCorr(T2L1BPA)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 3.581590e-03 5.984639e-02
trial =     pdLogChol(1)
(Intercept) 2.289188e-12 1.513006e-06
Residual    6.335734e-03 7.959732e-02
> CPs(T2L1BPA, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower       est.       upper
(Intercept) -0.721250352  1.0604114  2.84207306
Vstride      0.005404482  0.2276893  0.44997402
SVL         -1.538105296 -0.2161038  1.10589770
T2_L11      -0.116306837 -0.0707085 -0.02511017
attr(,"label")
[1] "Fixed effects:"
> anova(T2L1BPA, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    24 1.392877  0.2495
Vstride         1    24 4.125535  0.0535
SVL             1     7 0.137919  0.7213
T2_L1           1    24 9.454964  0.0052
> #estimated marginal means (least squares)
> emmls = emmeans(T2L1BPA, pairwise ~ T2_L1+ Vstride + SVL, mode="containment")
```

```
> summary(emmls)
$emmeans
 T2_L1 Vstride  SVL emmean     SE df lower.CL upper.CL
 0        2.15 1.63   1.20 0.0272  7     1.13     1.26
 1        2.15 1.63   1.13 0.0272  7     1.06     1.19

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                                     estimate    SE df t.ratio
p.value
 0 2.15247291648077 1.62800471042308 - 1 2.15247291648077 1.62800471042308   0.0707 0.023 24 3.075
0.0052

Degrees-of-freedom method: containment



> T2L1BPA2 = lme(BPA ~  SVL + T2_L1, random = ~1|geckoID/trial,
+                T2, method="ML")
> summary(T2L1BPA2)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC       BIC   logLik
  -86.65525 -74.94779 49.32763

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.06756163

 Formula: ~1 | trial %in% geckoID
         (Intercept)   Residual
StdDev: 1.761724e-06 0.08186089

Fixed effects: BPA ~ SVL + T2_L1
                 Value Std.Error DF    t-value p-value
(Intercept)  0.8676079 0.9815652 25  0.8839025  0.3852
SVL          0.2032402 0.5986215  7  0.3395136  0.7442
T2_L11      -0.0725392 0.0233888 25 -3.1014461  0.0047
 Correlation:
       (Intr) SVL
SVL    -1.000
T2_L11 -0.012  0.000

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.4184194 -0.5747785  0.1258525  0.5312693  2.0780713

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                 9                 26
> VarCorr(T2L1BPA2)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 4.564574e-03 6.756163e-02
trial =     pdLogChol(1)
(Intercept) 3.103671e-12 1.761724e-06
Residual    6.701205e-03 8.186089e-02

> CPs(T2L1BPA2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                 lower        est.       upper
(Intercept) -1.0947826  0.86760790  2.82999839
SVL         -1.1708362  0.20324015  1.57731646
T2_L11      -0.1192992 -0.07253918 -0.02577916
attr(,"label")
[1] "Fixed effects:"
> anova(T2L1BPA2, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    25 0.781284  0.3852
SVL             1     7 0.115269  0.7442
T2_L1           1    25 9.618968  0.0047
> #estimated marginal means (least squares)
> emmls = emmeans(T2L1BPA2, pairwise ~ T2_L1+  SVL,   mode="containment")
> summary(emmls)
$emmeans
 T2_L1  SVL emmean     SE df lower.CL upper.CL
 0     1.63   1.20 0.0294  7     1.13     1.27
 1     1.63   1.13 0.0294  7     1.06     1.20

Degrees-of-freedom method: containment
```

```
Confidence level used: 0.95

$contrasts
 contrast                                estimate     SE df t.ratio p.value
 0 1.62800471042308 - 1 1.62800471042308   0.0725 0.0234 25 3.101   0.0047

Degrees-of-freedom method: containment



> T2L1BPA3 = lme(BPA ~ Vstride  + T2_L1, random = ~1|geckoID/trial,
+                T2, method="ML")
> summary(T2L1BPA3)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC       BIC   logLik
  -90.71294 -79.00548 51.35647

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.06082007

 Formula: ~1 | trial %in% geckoID
         (Intercept)   Residual
StdDev: 1.387166e-06 0.07953352

Fixed effects: BPA ~ Vstride + T2_L1
                 Value  Std.Error DF   t-value p-value
(Intercept)  0.7373560 0.22857508 24  3.225881  0.0036
Vstride      0.2133837 0.10456851 24  2.040611  0.0524
T2_L11      -0.0708235 0.02273941 24 -3.114571  0.0047
 Correlation:
        (Intr) Vstrid
Vstride -0.993
T2_L11  -0.086  0.037

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.5233219 -0.5405002  0.1042207  0.6121359  2.0403031

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                 9                 26
> VarCorr(T2L1BPA3)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 3.699081e-03 6.082007e-02
trial =     pdLogChol(1)
(Intercept) 1.924229e-12 1.387166e-06
Residual    6.325581e-03 7.953352e-02


> CPs(T2L1BPA3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                   lower        est.      upper
(Intercept)  0.279410668  0.73735597  1.1953013
Vstride      0.003882875  0.21338366  0.4228844
T2_L11      -0.116381448 -0.07082352 -0.0252656
attr(,"label")
[1] "Fixed effects:"
> anova(T2L1BPA3, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    24 10.406307  0.0036
Vstride         1    24  4.164093  0.0524
T2_L1           1    24  9.700555  0.0047
> #estimated marginal means (least squares)
> emmls = emmeans(T2L1BPA3, pairwise ~ T2_L1+ Vstride , mode="containment")
> summary(emmls)
$emmeans
 T2_L1 Vstride emmean     SE df lower.CL upper.CL
 0        2.15   1.20 0.0266  8     1.14     1.26
 1        2.15   1.13 0.0266  8     1.06     1.19

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                estimate     SE df t.ratio p.value
 0 2.15247291648077 - 1 2.15247291648077   0.0708 0.0227 24 3.115   0.0047

Degrees-of-freedom method: containment
```

```
> T2L1BPA4 = lme(BPA ~ T2_L1, random = ~1|geckoID/trial,
+                T2, method="ML")
> summary(T2L1BPA4)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
        AIC       BIC   logLik
  -88.53324 -78.77702 49.26662

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.06788586

 Formula: ~1 | trial %in% geckoID
         (Intercept)   Residual
StdDev: 1.781678e-06 0.08191047

Fixed effects: BPA ~ T2_L1
                 Value  Std.Error DF  t-value p-value
(Intercept)  1.2007249 0.02850442 25 42.12417  0.0000
T2_L11      -0.0725392 0.02316778 25 -3.13104  0.0044
 Correlation:
       (Intr)
T2_L11 -0.406

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.4123390 -0.5858136  0.1311860  0.5420919  2.0814299

Number of Observations: 52
Number of Groups:
           geckoID trial %in% geckoID
                 9                 26
> VarCorr(T2L1BPA4)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 4.608490e-03 6.788586e-02
trial =     pdLogChol(1)
(Intercept) 3.174377e-12 1.781678e-06
Residual    6.709325e-03 8.191047e-02

> CPs(T2L1BPA4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                 lower        est.       upper
(Intercept)  1.1431590  1.20072495  1.25829086
T2_L11      -0.1193275 -0.07253918 -0.02575084
attr(,"label")
[1] "Fixed effects:"
> anova(T2L1BPA4, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    25 1774.4461  <.0001
T2_L1           1    25    9.8034  0.0044
> #estimated marginal means (least squares)
> emmls = emmeans(T2L1BPA4, pairwise ~ T2_L1, mode="containment")
> summary(emmls)
$emmeans
 T2_L1 emmean     SE df lower.CL upper.CL
 0       1.20 0.0285  8     1.13     1.27
 1       1.13 0.0285  8     1.06     1.19

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast estimate     SE df t.ratio p.value
 0 - 1      0.0725 0.0232 25 3.131   0.0044

Degrees-of-freedom method: containment
```

S1.8. R output: body pitch angle (BPA) models for transition 1 and 2 (T1, T2) within limbs 1 and 2 (L1, L2)

a) T2 L2

```
> #Transition 2: sand sand-solid

>
> #T2_Limb2
```

```
>
> T2L2BPA = lme(BPA ~ Vstride + SVL + T2_L2, random = ~1|geckoID/trial,
+               T2, method="ML")
> summary(T2L2BPA)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
       AIC       BIC   logLik
  -72.0023 -59.20181 43.00115

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.08027031

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev: 2.24712e-06 0.08087247

Fixed effects: BPA ~ Vstride + SVL + T2_L2
                 Value Std.Error DF    t-value p-value
(Intercept)  0.9430441 1.1937914 20  0.7899572  0.4388
Vstride      0.1967584 0.1410621 20  1.3948348  0.1784
SVL         -0.1231445 0.7501094  6 -0.1641687  0.8750
T2_L21      -0.0750483 0.0249811 20 -3.0042079  0.0070
 Correlation:
        (Intr) Vstrid SVL
Vstride -0.013
SVL     -0.969 -0.232
T2_L21  -0.011  0.043 -0.010

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.96797850 -0.53887492 -0.03397502  0.68285889  1.85992160

Number of Observations: 46
Number of Groups:
           geckoID trial %in% geckoID
                 8                 24
> VarCorr(T2L2BPA)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 6.443322e-03 8.027031e-02
trial =     pdLogChol(1)
(Intercept) 5.049548e-12 2.247120e-06
Residual    6.540356e-03 8.087247e-02

> CPs(T2L2BPA, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.       upper
(Intercept) -1.43642937  0.94304410  3.32251757
Vstride     -0.08440767  0.19675836  0.47792439
SVL         -1.87697921 -0.12314446  1.63069029
T2_L21      -0.12484071 -0.07504829 -0.02525587
attr(,"label")
[1] "Fixed effects:"
> anova(T2L2BPA, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    20 0.624032  0.4388
Vstride         1    20 1.945564  0.1784
SVL             1     6 0.026951  0.8750
T2_L2           1    20 9.025265  0.0070
> #estimated marginal means (least squares)
> emmls = emmeans(T2L2BPA, pairwise ~ T2_L2+ Vstride + SVL, mode="containment")
> summary(emmls)
$emmeans
 T2_L2 Vstride  SVL emmean     SE df lower.CL upper.CL
 0        2.11 1.62   1.16 0.0361  6    1.070     1.25
 1        2.11 1.62   1.08 0.0361  6    0.995     1.17

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                                                         estimate    SE df t.ratio p.value
 0 2.1113725475 1.6220296866087 - 1 2.1113725475 1.6220296866087     0.075 0.025 20 3.004   0.0070

Degrees-of-freedom method: containment



> T2L2BPA2 = lme(BPA ~ SVL + T2_L2, random = ~1|geckoID/trial,
+                T2, method="ML")
> summary(T2L2BPA2)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
```

```
        AIC       BIC   logLik
  -71.93076 -60.95891 41.96538

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.08452347

 Formula: ~1 | trial %in% geckoID
         (Intercept)   Residual
StdDev: 2.268735e-06 0.08230229

Fixed effects: BPA ~ SVL + T2_L2
                 Value Std.Error DF    t-value p-value
(Intercept)  0.9599245 1.2366621 21  0.7762222  0.4463
SVL          0.1228623 0.7557892  6  0.1625616  0.8762
T2_L21      -0.0765520 0.0251020 21 -3.0496429  0.0061
 Correlation:
       (Intr) SVL
SVL    -1.00
T2_L21 -0.01   0.00

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.02128581 -0.62839873 -0.06786668  0.64847299  1.97559611

Number of Observations: 46
Number of Groups:
           geckoID trial %in% geckoID
                 8                 24
> VarCorr(T2L2BPA2)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 7.144218e-03 8.452347e-02
trial =     pdLogChol(1)
(Intercept) 5.147157e-12 2.268735e-06
Residual    6.773666e-03 8.230229e-02

> CPs(T1L1BPA2, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.      upper
(Intercept) -1.97055771 -0.29498821 1.38058128
SVL         -0.30119102  0.83993672 1.98106446
T1_L11      -0.02181413  0.03627542 0.09436496
attr(,"label")
[1] "Fixed effects:"
> anova(T2L2BPA2, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    21 0.602521  0.4463
SVL             1     6 0.026426  0.8762
T2_L2           1    21 9.300322  0.0061
> #estimated marginal means (least squares)
> emmls = emmeans(T2L2BPA2, pairwise ~ T2_L2+ SVL, mode="containment")
> summary(emmls)
$emmeans
 T2_L2  SVL emmean     SE df lower.CL upper.CL
 0     1.62   1.16 0.0373  6    1.068     1.25
 1     1.62   1.08 0.0373  6    0.991     1.17

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                             estimate     SE df t.ratio p.value
 0 1.6220296866087 - 1 1.6220296866087   0.0766 0.0251 21 3.050   0.0061

Degrees-of-freedom method: containment


> T2L2BPA3 = lme(BPA ~ Vstride  + T2_L2, random = ~1|geckoID/trial,
+               T2, method="ML")
> summary(T2L2BPA3)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
      AIC       BIC  logLik
  -73.973 -63.00116 42.9865

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:   0.0806148

 Formula: ~1 | trial %in% geckoID
        (Intercept)   Residual
StdDev: 2.16611e-06 0.08084356
```

```
Fixed effects: BPA ~ Vstride + T2_L2
                 Value  Std.Error DF   t-value p-value
(Intercept)  0.7531623 0.29117572 20  2.586625  0.0176
Vstride      0.1913554 0.13571400 20  1.409990  0.1739
T2_L21      -0.0750896 0.02467886 20 -3.042668  0.0064
 Correlation:
        (Intr) Vstrid
Vstride -0.993
T2_L21  -0.084  0.042

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.96261611 -0.54715730 -0.03997224  0.68413535  1.86386556

Number of Observations: 46
Number of Groups:
           geckoID trial %in% geckoID
                 8                 24
> VarCorr(T2L2BPA3)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 6.498746e-03 8.061480e-02
trial =     pdLogChol(1)
(Intercept) 4.692032e-12 2.166110e-06
Residual    6.535681e-03 8.084356e-02

> CPs(T2L2BPA3, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                  lower        est.       upper
(Intercept)  0.16592019  0.75316226  1.34040433
Vstride     -0.08235213  0.19135535  0.46506284
T2_L21      -0.12486181 -0.07508958 -0.02531735
attr(,"label")
[1] "Fixed effects:"
> anova(T2L2BPA3, type="marginal")
            numDF denDF  F-value p-value
(Intercept)     1    20 6.690627  0.0176
Vstride         1    20 1.988071  0.1739
T2_L2           1    20 9.257830  0.0064
> #estimated marginal means (least squares)
> emmls = emmeans(T2L2BPA3, pairwise ~ T2_L2+ Vstride , mode="containment")
> summary(emmls)
$emmeans
 T2_L2 Vstride emmean     SE df lower.CL upper.CL
 0        2.11   1.16 0.0346  7     1.08     1.24
 1        2.11   1.08 0.0345  7     1.00     1.16

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast                        estimate     SE df t.ratio p.value
 0 2.1113725475 - 1 2.1113725475   0.0751 0.0247 20 3.043   0.0064

Degrees-of-freedom method: containment



> T2L2BPA4 = lme(BPA ~ T2_L2, random = ~1|geckoID/trial,
+                T2, method="ML")
> summary(T2L2BPA4)
Linear mixed-effects model fit by maximum likelihood
 Data: T2
       AIC       BIC   logLik
  -73.9025 -64.75929 41.95125

Random effects:
 Formula: ~1 | geckoID
        (Intercept)
StdDev:  0.08455983

 Formula: ~1 | trial %in% geckoID
         (Intercept)   Residual
StdDev: 2.268052e-06 0.08232583

Fixed effects: BPA ~ T2_L2
                Value  Std.Error DF  t-value p-value
(Intercept)  1.160874 0.03547527 21 32.72347  0.0000
T2_L21      -0.076552 0.02482217 21 -3.08402  0.0056
 Correlation:
       (Intr)
T2_L21 -0.35
```

```
Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.02899421 -0.62966242 -0.07262291  0.65820892  1.96472105

Number of Observations: 46
Number of Groups:
           geckoID trial %in% geckoID
                 8                 24
> CPs(T2L2BPA4, level=0.95, which=c("fixed"))
Approximate 95% confidence CPs

 Fixed effects:
                 lower        est.       upper
(Intercept)  1.0887207  1.16087391  1.23302714
T2_L21      -0.1270379 -0.07655202 -0.02606615
attr(,"label")
[1] "Fixed effects:"
> anova(T2L2BPA4, type="marginal")
            numDF denDF   F-value p-value
(Intercept)     1    21 1070.8257  <.0001
T2_L2           1    21    9.5112  0.0056
> #estimated marginal means (least squares)
> emmls = emmeans(T2L2BPA4, pairwise ~ T2_L2, mode="containment")
> summary(emmls)
$emmeans
 T2_L2 emmean     SE df lower.CL upper.CL
 0       1.16 0.0355  7     1.08     1.24
 1       1.08 0.0355  7     1.00     1.17

Degrees-of-freedom method: containment
Confidence level used: 0.95

$contrasts
 contrast estimate     SE df t.ratio p.value
 0 - 1      0.0766 0.0248 21 3.084   0.0056

Degrees-of-freedom method: containment

> VarCorr(T2L2BPA4)
            Variance     StdDev
geckoID =   pdLogChol(1)
(Intercept) 7.150364e-03 8.455983e-02
trial =     pdLogChol(1)
(Intercept) 5.144059e-12 2.268052e-06
Residual    6.777542e-03 8.232583e-02
```

APPENDICES

Chapter 2

S2.1. Individual maximum clinging force for the right manus (newtons) with ambient conditions for all test surfaces before and after partial claw removal.

Claws intact

Indiv. No.	AC	SL	WD	SP2	RL	SP1	A.T. (˚C)	R.H. (%)
1	1.97	1.25	0.64	0.44	0.07	0.54	23.78	96.9
2	3.27	2.41	0.93	0.57	0.09	0.88	23.72	92.9
3		2.60	1.56	0.70	0.14	0.75	22.83	97.5
4		2.50	1.76	0.83	0.11	1.32	22.83	97.5
5	2.43	1.97	0.28	0.71	0.36	1.10	25.67	90.6
6	3.83	1.67	0.18		0.50	0.53	25.39	89.6
7		2.68	1.82	1.83	0.32	1.60	22.83	97.5
8	1.05	0.74	0.48		0.16	0.57	24.72	93.3
9	1.83	1.88	0.12	0.26	0.16	0.51	25.39	89.6
10	1.78	1.34	0.56	0.81	0.22	1.00	24.17	95.9
11	2.95	3.02	1.37	1.06	0.18	0.87	23.00	95.1
12	2.69	2.52	1.61	1.05	0.22	1.75	23.72	92.9
13	3.05	2.57	1.08	0.88	0.19	1.18	23.72	92.9
14	1.65	2.42	1.17	1.01	0.10	1.29	22.83	97.5

Claws removed

Indiv. No.	AC	SL	WD	SP2	RL	SP1	A.T. (˚C)	R.H. (%)
1		1.05	0.68	0.06	0.00	0.49	22.83	97.5
2		2.15	1.10	0.34	0.27	0.41	22.83	97.5
3		1.11	0.31	0.17	0.01	0.19	26.50	92.3
4		1.31	0.95	0.43	0.07	0.46	26.50	92.3
5	3.41	1.39	0.67	0.25	0.03	0.09	24.50	91.1
6	1.98	1.33	0.37	0.28	0.00	0.31	24.50	91.1
7		2.28	0.96	0.77	0.06	0.65	26.50	92.3
8	0.99	1.19	0.10	0.05	0.00	0.02	25.28	90.7
9	1.18	0.94	0.22	0.00	0.00	0.00	24.78	94.0
10	1.34	1.05	0.32	0.05	0.04	0.00	24.44	91.2
11	3.10		0.47	0.25	0.06	0.42	23.00	95.1
12	2.44	0.57	0.21	0.11	0.03	0.14	27.72	80.9
13		1.57	0.27	0.28	0.02	0.24	22.83	97.5
14	1.91	2.04	1.05	0.22	0.03	0.60	26.50	92.3

Abbreviations: AC (acrylic), SL (smooth leaf), WD (wood), SP2 (60-grit sandpaper 2), RL (rough leaf), SP1 (60-grit sandpaper 1), A.T. (ambient temperature), R.H. (relative humidity)

S2.2. Individual maximum fall angle (degrees) with ambient conditions before and after partial claw removal.

Claws intact

Indiv. No.	Test surface AC	SP2	A.T. (˚C)	R.H. (%)
1	140.45	127.59	24.56	90.1
2	148.63	139.91	24.56	90.1
3	113.34	119.52	28.11	76.8
4	117.04	138.21	28.11	76.8
7	128.95	140.88	28.11	76.8

Claws removed

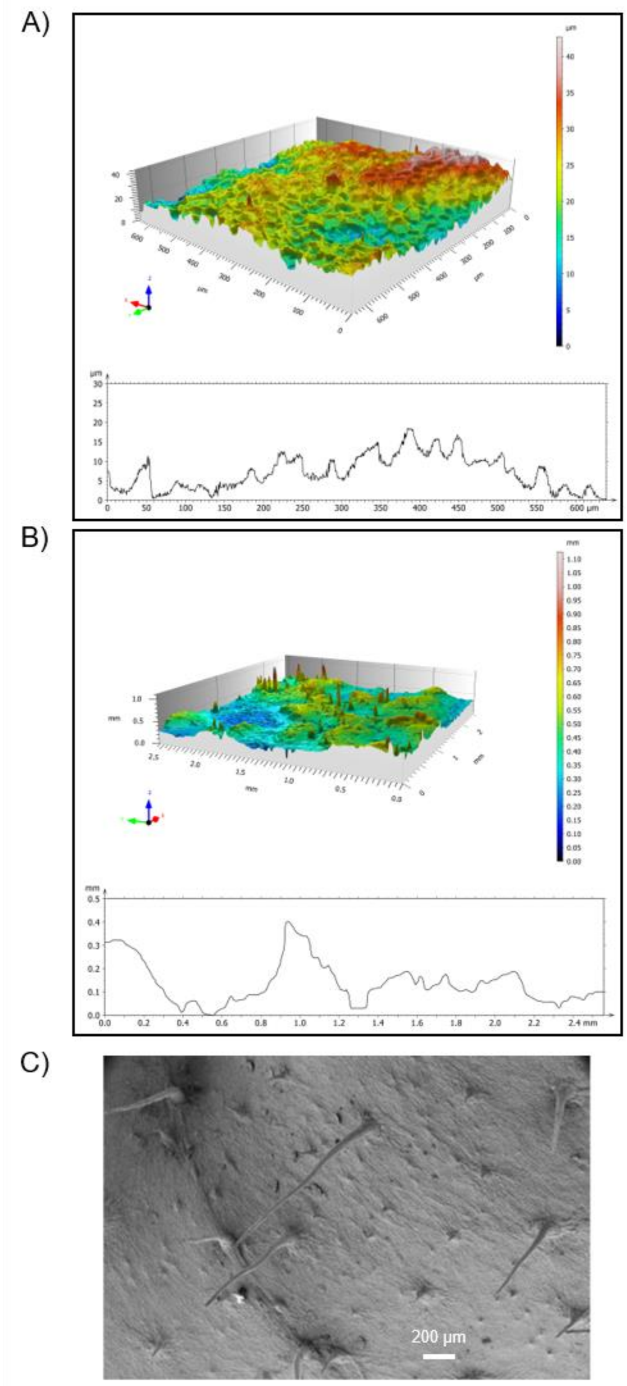
Indiv. No.	Test surface AC	SP2	A.T. (˚C)	R.H. (%)
1	105.61	109.95	28.17	77.2
2	124.43	110.36	28.17	77.2
3	110.01	124.23	26.00	91.3
4	128.32	111.41	26.00	91.3
7	112.44	116.76	26.00	91.3

Abbreviations: AC (acrylic), SP2 (60-grit sandpaper 2), A.T. (ambient temperature), R.H. (relative humidity)

S2.3. Locomotor variables defined

Locomotor Variable	**Definition**	**Unit(s)**
stride duration	time from footfall to subsequent footfall of the same limb	s
step duration	duration of stance within a stride	s
duty factor	proportion of contact time within a stride (step duration/stride duration)	
time to toe unfurling	time from onset of stance to onset of distal toe unfurling	s
duration of distal toe contact	duration of toes contacting surface in flexed posture until onset of toe hyperextension (within stance)	s
time to toe hyperextension	time from onset of stance to onset of toe hyperextension	s
duration of toe hyperextension	duration of toes in hyperextended posture until the end of stance	s
body pitch angle	angle between the substrate and a straight line connecting the pectoral (i.e., shoulder) and pelvic (i.e., hip) girdles	rad
effective hindlimb length	straight-line distance between the hip and ankle (lateral view) during stance	cm
effective forelimb length	straight-line distance between shoulder & wrist (lateral view) during stance	cm
femur depression	vertical position of the knee relative to the hip; positive values indicate knee is below hip	cm
humerus depression	vertical position of the elbow relative to the shoulder; positive values indicate elbow is below shoulder	cm
femur retraction	position of the knee relative to the hip along the x-axis; positive values indicate knee is cranial to hip	cm
humerus retraction	position of the elbow relative to the shoulder along the x-axis: positive values indicate elbow is cranial to shoulder	cm
stride length	body displacement during stride	cm
step length	body displacement during stance	cm
forefoot/hindfoot slippage	maximum rearward wrist/ankle displacement during stance	cm
velocity	body displacement over time (instantaneous and average)	cm/s
initial acceleration	change in average velocity during first 100 milliseconds of movement from a stationary position	cm/s^2

S2.4. Images of selected test surfaces. A) Smooth leaf (SL) and B) 60-grit sandpaper 2 (SP2) three-dimensional topographical reconstructions with heat map and profiles from single line transects down the center of the samples. D) Dorsal-oblique scanning electron micrograph of the rough leaf (RL) showing long trichomes.



S2.5. Linear mixed-effects (LME) model output summaries for: A) clinging force, B) station-holding capacity, locomotor variables for C) forelimb and D) hindlimb strides, and E) initial acceleration.

a) clinging force

	Original Models							Final Models						
Test Surface	**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***		**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***	
AC	(Int.)	2.875	2.050	12.2	1.40	1.86E-01		(Int.)	0.165	0.418	11.3	0.40	7.00E-01	
	A.T.	-0.036	0.030	11.7	-1.17	2.66E-01								
	R.H.	-0.016	0.012	11.0	-1.35	2.05E-01								
	Mass	0.084	0.382	15.0	0.22	8.29E-01		Mass	0.344	0.360	11.1	0.96	3.60E-01	
	Claw	-0.054	0.036	7.5	-1.51	1.73E-01		Claw	-0.042	0.031	9.2	-1.35	2.11E-01	
SL	(Int.)	0.024	1.111	26.9	0.02	9.83E-01		(Int.)	0.354	0.232	13.9	1.53	1.49E-01	
	A.T.	-0.015	0.019	23.0	-0.80	4.31E-01								
	R.H.	0.006	0.007	27.0	0.82	4.21E-01								
	Mass	0.285	0.171	13.3	1.67	1.19E-01		Mass	0.202	0.190	12.9	1.06	3.08E-01	
	Claw	-0.083	0.030	13.2	-2.75	1.62E-02	*	**Claw**	-0.112	0.030	13.0	-3.75	2.40E-03	**
WD	(Int.)	-1.222	1.185	28.0	-1.03	3.11E-01		(Int.)	-0.019	0.278	15.1	-0.07	9.46E-01	
	A.T.	-0.014	0.020	25.4	-0.69	4.95E-01								
	R.H.	0.014	0.008	28.0	1.78	8.61E-02								
	Mass	0.459	0.187	14.4	2.45	2.75E-02	*	Mass	0.324	0.228	14.0	1.42	1.76E-01	
	Claw	-0.056	0.031	14.5	-1.82	9.03E-02		**Claw**	-0.094	0.036	14.0	-2.63	2.00E-02	*
SP2	(Int.)	-1.391	0.591	19.9	-2.35	2.91E-02	*	(Int.)	-0.747	0.301	25.1	-2.49	2.00E-02	*
	A.T.	0.011	0.009	15.8	1.25	2.30E-01								
	R.H.	0.012	0.004	17.6	3.11	6.23E-03	**	R.H.	0.008	0.002	15.7	3.53	2.84E-03	**
	Mass	0.317	0.154	14.0	2.06	5.89E-02		Mass	0.327	0.152	14.0	2.16	4.88E-02	*
	Claw	-0.158	0.013	12.7	-12.37	1.94E-08	***	**Claw**	-0.153	0.013	12.7	-11.90	2.87E-08	***
RL	(Int.)	0.166	0.444	28.0	0.37	7.11E-01		(Int.)	0.078	0.075	28.0	1.04	3.08E-01	
	A.T.	0.000	0.008	28.0	0.02	9.85E-01								
	R.H.	-0.001	0.003	28.0	-0.30	7.69E-01								
	Mass	0.044	0.062	28.0	0.71	4.84E-01		Mass	0.050	0.061	28.0	0.83	4.14E-01	
	Claw	-0.061	0.013	28.0	-4.59	8.43E-05	***	**Claw**	-0.060	0.012	28.0	-4.80	4.79E-05	***
SP1	(Int.)	-1.191	0.922	27.7	-1.29	2.07E-01		(Int.)	-0.673	0.421	27.9	-1.60	1.21E-01	
	A.T.	0.010	0.015	24.4	0.63	5.36E-01								
	R.H.	0.012	0.006	27.9	1.98	5.76E-02		R.H.	0.009	0.004	25.9	2.50	1.93E-02	*
	Mass	0.222	0.154	14.5	1.45	1.70E-01		Mass	0.232	0.152	14.4	1.52	1.49E-01	
	Claw	-0.176	0.023	14.6	-7.73	1.56E-06	***	**Claw**	-0.172	0.022	14.8	-7.77	1.37E-06	***

Abbreviations: AC (acrylic), SL (smooth leaf), WD (wood), SP2 (60-grit sandpaper sample 2), RL (rough leaf), SP1 (60-grit sandpaper sample 1); Est. (estimate), S.E. (standard error), Int. (intercept), A.T. (ambient temperature), R.H. (relative humidity), Mass (body mass), Claw (claw status; bolded when predictor variable of significant for a given model).

b) station-holding capacity

	Original Models								Final Models						
Test Surface	**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***		**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***	
AC	(Int.)	6.972	1.317	10	5.29	3.51E-04	***							
	A.T.	-0.126	0.033	10	-3.84	3.25E-03	**							
	R.H.	-0.023	0.007	10	-3.34	7.51E-03	**							
	Mass	0.302	0.111	10	2.72	2.17E-02	*							
	Claw	0.057	0.033	10	1.74	1.13E-01								
SP2	(Int.)	2.780	1.207	10	2.30	4.40E-02	*	(Int.)	2.018	0.080	10	25.36	2.08E-10	***
	A.T.	-0.022	0.030	10	-0.71	4.96E-01								
	R.H.	-0.003	0.006	10	-0.52	6.13E-01								
	Mass	0.150	0.112	10	1.34	2.11E-01		Mass	0.085	0.063	10	1.34	2.09E-01	
	Claw	-0.051	0.029	10	-1.75	1.10E-01		**Claw**	-0.065	0.014	10	-4.61	9.62E-04	***

Abbreviations: AC (acrylic), SP2 (60-grit sandpaper sample 2); Est. (estimate), S.E. (standard error), Int. (intercept), A.T. (ambient temperature), R.H. (relative humidity), Mass (body mass), Claw (claw status; bolded when predictor variable of significant for a given model).

c) forelimb strides

Locomotor Variable	Inclined Sandpaper							Level Sandpaper						
	Factor	**Est.**	**S.E.**	**df**	***t***	***p***		**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***	
stride duration*	(Int.)	6.90	6.31	27.0	1.09	2.84E-01		(Int.)	19.80	23.93	6.7	0.828	4.36E-01	
	B.T.	-0.80	1.02	27.0	-0.78	4.42E-01		B.T.	-2.32	2.44	17.7	-0.954	3.53E-01	
	A.T.	-2.43	1.95	27.0	-1.25	2.24E-01		A.T.	-4.21	8.41	4.2	-0.501	6.41E-01	
	R.H.	-1.35	2.23	27.0	-0.61	5.50E-01		R.H.	-5.50	6.16	7.1	-0.893	4.01E-01	
	Mass	0.25	0.13	27.0	1.94	6.24E-02		Mass	0.05	0.29	2.2	0.186	8.68E-01	
	Claw	-0.02	0.03	27.0	-0.63	5.31E-01		Claw	0.04	0.05	23.2	0.757	4.57E-01	
step duration*	(Int.)	1.14	7.00	27.0	0.16	8.72E-01		(Int.)	46.01	32.94	9.3	1.397	1.95E-01	
	B.T.	0.07	1.13	27.0	0.06	9.50E-01		B.T.	-1.15	3.17	22.2	-0.363	7.20E-01	
	A.T.	-2.60	2.16	27.0	-1.20	2.40E-01		A.T.	-14.28	11.91	6.4	-1.199	2.73E-01	
	R.H.	1.02	2.47	27.0	0.41	6.82E-01		R.H.	-12.61	8.46	9.7	-1.49	1.68E-01	
	Mass	0.35	0.14	27.0	2.44	2.17E-02	*	Mass	0.15	0.43	4.0	0.337	7.53E-01	
	Claw	-0.04	0.04	27.0	-1.05	3.01E-01		Claw	0.09	0.06	21.9	1.494	1.49E-01	
duty factor*	(Int.)	-5.76	4.12	27.0	-1.40	1.74E-01		(Int.)	32.17	11.95	12.4	2.693	1.91E-02	*
	B.T.	0.87	0.67	27.0	1.30	2.04E-01		B.T.	0.32	0.95	24.0	0.339	7.37E-01	
	A.T.	-0.17	1.27	27.0	-0.14	8.93E-01		A.T.	-11.39	4.57	10.2	-2.493	3.14E-02	*
	R.H.	2.37	1.46	27.0	1.63	1.14E-01		R.H.	-8.62	3.05	12.6	-2.824	1.48E-02	*
	Mass	0.10	0.09	27.0	1.16	2.55E-01		Mass	0.15	0.18	6.4	0.803	4.51E-01	
	Claw	-0.02	0.02	27.0	-0.82	4.20E-01		Claw	0.05	0.02	19.3	2.543	1.97E-02	*
time to toe unfurling	(Int.)	57.68	28.48	12.8	2.03	6.41E-02		(Int.)	-47.20	16.97	24.0	-2.782	1.04E-02	*
	B.T.	0.38	3.49	24.6	0.11	9.15E-01		B.T.	4.68	1.84	24.0	2.544	1.78E-02	*
	A.T.	-21.58	9.02	14.8	-2.39	3.06E-02	*	A.T.	11.98	5.62	24.0	2.131	4.36E-02	*
	R.H.	-15.26	9.70	12.9	-1.57	1.40E-01		R.H.	10.91	4.40	24.0	2.477	2.07E-02	*
	Mass	0.12	0.61	12.6	0.19	8.52E-01		Mass	0.39	0.17	24.0	2.322	2.90E-02	*
	Claw	-0.31	0.14	13.3	-2.21	4.50E-02	*	Claw	0.03	0.04	24.0	0.828	4.16E-01	
duration of distal toe contact	(Int.)	15.17	21.29	26.0	0.71	4.83E-01		(Int.)	-10.54	94.42	9.5	-0.112	9.13E-01	
	B.T.	-3.20	3.67	26.0	-0.87	3.92E-01		B.T.	6.63	8.65	6.4	0.766	4.71E-01	
	A.T.	-2.90	6.73	26.0	-0.43	6.70E-01		A.T.	-0.26	34.17	8.1	-0.008	9.94E-01	
	R.H.	-3.81	7.52	26.0	-0.51	6.17E-01		R.H.	0.27	24.30	9.7	0.011	9.91E-01	
	Mass	0.84	0.44	26.0	1.91	6.75E-02		Mass	0.54	1.26	5.3	0.428	6.85E-01	
	Claw	0.04	0.12	26.0	0.31	7.59E-01		Claw	0.25	0.17	8.6	1.476	1.76E-01	
time to toe hyperextension*	(Int.)	2.80	14.17	27.0	0.20	8.45E-01		(Int.)	45.32	47.74	9.0	0.949	3.67E-01	
	B.T.	-2.41	2.29	27.0	-1.05	3.03E-01		B.T.	2.07	4.37	23.1	0.474	6.40E-01	
	A.T.	-1.59	4.38	27.0	-0.36	7.19E-01		A.T.	-16.53	17.57	6.4	-0.941	3.81E-01	
	R.H.	1.03	5.00	27.0	0.21	8.38E-01		R.H.	-13.39	12.24	9.3	-1.094	3.02E-01	
	Mass	0.71	0.29	27.0	2.44	2.15E-02	*	Mass	0.73	0.65	4.1	1.113	3.27E-01	
	Claw	-0.03	0.08	27.0	-0.39	6.98E-01		Claw	0.21	0.08	20.3	2.534	1.96E-02	*
duration of toe hyperextension*	(Int.)	-1.60	9.49	27.0	-0.17	8.67E-01		(Int.)	31.79	40.74	8.4	0.78	4.57E-01	
	B.T.	1.21	1.54	27.0	0.79	4.37E-01		B.T.	-4.72	3.69	23.2	-1.279	2.13E-01	
	A.T.	0.01	2.93	27.0	0.01	9.96E-01		A.T.	-6.40	15.05	6.0	-0.425	6.86E-01	
	R.H.	0.01	3.35	27.0	0.00	9.98E-01		R.H.	-7.98	10.44	8.7	-0.765	4.65E-01	
	Mass	-0.09	0.20	27.0	-0.47	6.43E-01		Mass	-0.47	0.56	3.8	-0.833	4.55E-01	
	Claw	-0.08	0.05	27.0	-1.59	1.24E-01		Claw	-0.03	0.07	19.6	-0.454	6.55E-01	

Locomotor Variable	Inclined Sandpaper							Level Sandpaper						
	Factor	**Est.**	**S.E.**	**df**	***t***	***p***		**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***	
maximum body pitch angle*	(Int.)	3.21	2.14	12.7	1.50	1.58E-01		(Int.)	1.13	5.44	13.1	0.208	8.39E-01	
	B.T.	-0.58	0.30	17.7	-1.94	6.87E-02		B.T.	-1.12	0.60	10.6	-1.859	9.10E-02	.
	A.T.	-0.93	0.69	12.9	-1.35	2.02E-01		A.T.	0.94	1.80	13.1	0.524	6.09E-01	
	R.H.	-0.53	0.73	12.9	-0.73	4.80E-01		R.H.	-0.34	1.41	13.0	-0.242	8.12E-01	
	Mass	-0.04	0.05	12.2	-0.91	3.78E-01		Mass	-0.16	0.06	9.3	-2.916	1.66E-02	*
	Claw	-0.01	0.01	13.9	-0.76	4.62E-01		Claw	0.00	0.01	12.4	-0.168	8.69E-01	
maximum effective forelimb length	(Int.)	14.71	18.07	27.0	0.81	4.23E-01		(Int.)	2.43	50.56	11.6	0.048	9.62E-01	
	B.T.	-1.33	2.90	27.0	-0.46	6.50E-01		B.T.	3.97	6.02	11.2	0.659	5.23E-01	
	A.T.	-3.14	5.55	27.0	-0.57	5.76E-01		A.T.	-4.45	16.91	11.8	-0.263	7.97E-01	
	R.H.	-4.68	6.39	27.0	-0.73	4.71E-01		R.H.	-1.03	13.11	11.6	-0.079	9.39E-01	
	FL	2.31	0.88	27.0	2.62	1.42E-02	*	FL	0.59	1.34	10.7	0.442	6.67E-01	
	Claw	0.05	0.10	27.0	0.55	5.85E-01		Claw	-0.03	0.12	11.6	-0.266	7.95E-01	
maximum extent of humerus depression	(Int.)	9.61	12.29	11.9	0.78	4.49E-01		(Int.)	15.44	20.58	6.5	0.750	4.79E-01	
	B.T.	-1.30	1.65	19.3	-0.79	4.41E-01		B.T.	0.76	2.28	15.7	0.336	7.41E-01	
	A.T.	-2.73	3.96	12.9	-0.69	5.03E-01		A.T.	-6.63	7.12	3.9	-0.931	4.05E-01	
	R.H.	-1.98	4.19	12.0	-0.47	6.45E-01		R.H.	-3.65	5.28	7.0	-0.692	5.11E-01	
	Hum.	-0.70	0.73	11.0	-0.95	3.63E-01		Hum.	-1.40	0.67	1.7	-2.094	1.95E-01	
	Claw	-0.06	0.06	12.7	-0.97	3.51E-01		Claw	0.01	0.04	24.0	0.307	7.62E-01	
maximum extent of humerus retraction*	(Int.)	-7.48	9.29	26.3	-0.81	4.28E-01		(Int.)	29.33	16.03	24.0	1.830	7.97E-02	
	B.T.	3.67	1.68	27.0	2.19	3.74E-02	*	B.T.	6.82	1.85	24.0	3.687	1.16E-03	**
	A.T.	-2.75	2.38	21.4	-1.16	2.61E-01		A.T.	-16.45	5.29	24.0	-3.110	4.78E-03	**
	R.H.	3.06	3.29	26.2	0.93	3.61E-01		R.H.	-8.17	4.14	24.0	-1.974	6.00E-02	
	Hum.	0.25	1.15	5.8	0.22	8.36E-01		Hum.	1.11	0.43	24.0	2.551	1.75E-02	*
	Claw	0.23	0.04	22.0	5.62	1.20E-05	***	Claw	0.03	0.04	24.0	0.860	3.98E-01	
step length	(Int.)	-0.96	6.88	27.0	-0.14	8.90E-01		(Int.)	59.33	38.39	7.9	1.545	1.61E-01	
	B.T.	1.03	1.08	27.0	0.95	3.52E-01		B.T.	0.82	3.42	20.2	0.240	8.13E-01	
	A.T.	-3.25	2.10	27.0	-1.55	1.34E-01		A.T.	-21.13	14.50	5.5	-1.457	1.99E-01	
	R.H.	1.35	2.39	27.0	0.56	5.77E-01		R.H.	-16.42	10.16	7.9	-1.616	1.45E-01	
	SVL	2.11	0.73	27.0	2.87	7.81E-03	**	SVL	1.77	2.62	3.6	0.676	5.40E-01	
	Claw	-0.04	0.04	27.0	-1.19	2.46E-01		Claw	0.09	0.07	20.0	1.277	2.16E-01	
stride length*	(Int.)	0.19	6.59	27.0	0.03	9.78E-01		(Int.)	29.30	25.53	24.0	1.148	2.62E-01	
	B.T.	-0.24	1.04	27.0	-0.24	8.16E-01		B.T.	-1.25	2.58	24.0	-0.483	6.33E-01	
	A.T.	-1.56	2.02	27.0	-0.78	4.45E-01		A.T.	-8.68	8.96	24.0	-0.969	3.42E-01	
	R.H.	0.24	2.29	27.0	0.10	9.18E-01		R.H.	-8.32	6.76	24.0	-1.231	2.30E-01	
	SVL	1.96	0.70	27.0	2.79	9.52E-03	**	SVL	0.88	1.42	24.0	0.621	5.40E-01	
	Claw	-0.01	0.04	27.0	-0.20	8.44E-01		Claw	0.02	0.06	24.0	0.335	7.41E-01	
forefoot slippage*	(Int.)	0.24	1.56	27.0	0.15	8.80E-01		(Int.)	-0.22	1.13	24.0	-0.197	8.45E-01	
	B.T.	0.37	0.25	27.0	1.50	1.46E-01		B.T.	0.15	0.11	24.0	1.333	1.95E-01	
	A.T.	-0.56	0.48	27.0	-1.17	2.54E-01		A.T.	-0.11	0.40	24.0	-0.286	7.78E-01	
	R.H.	-0.13	0.54	27.0	-0.24	8.16E-01		R.H.	-0.01	0.30	24.0	-0.048	9.62E-01	
	SVL	0.27	0.17	27.0	1.65	1.10E-01		SVL	0.20	0.06	24.0	3.254	3.37E-03	**
	Claw	0.00	0.01	27.0	0.58	5.65E-01		Claw	0.00	0.00	24.0	-1.067	2.97E-01	

Locomotor Variable	Inclined Acrylic							Level Acrylic						
	Factor	**Est.**	**S.E.**	**df**	***t***	***p***		**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***	
stride duration*	(Int.)	9.21	8.72	23.0	1.056	3.02E-01		(Int.)	-3.53	5.41	29.0	-0.652	5.19E-01	
	B.T.	0.86	2.28	23.0	0.378	7.09E-01		B.T.	-2.86	1.84	29.0	-1.558	1.30E-01	
	A.T.	-3.77	3.96	23.0	-0.952	3.51E-01		A.T.	3.44	1.27	29.0	2.712	1.11E-02	*
	R.H.	-3.16	2.30	23.0	-1.370	1.84E-01		R.H.	1.18	1.14	29.0	1.039	3.08E-01	
	Mass	0.87	0.31	23.0	2.795	1.03E-02	*	Mass	0.40	0.15	29.0	2.760	9.92E-03	**
	Claw	-0.02	0.06	23.0	-0.350	7.30E-01		Claw	0.05	0.03	29.0	1.465	1.54E-01	
step duration*	(Int.)	9.38	10.94	23.0	0.858	4.00E-01		(Int.)	-3.01	6.35	29.0	-0.474	6.39E-01	
	B.T.	1.16	2.86	23.0	0.406	6.88E-01		B.T.	-2.83	2.15	29.0	-1.316	1.99E-01	
	A.T.	-5.48	4.97	23.0	-1.101	2.82E-01		A.T.	3.38	1.49	29.0	2.273	3.06E-02	*
	R.H.	-1.99	2.89	23.0	-0.691	4.97E-01		R.H.	1.04	1.33	29.0	0.781	4.41E-01	
	Mass	0.45	0.39	23.0	1.148	2.63E-01		Mass	0.24	0.17	29.0	1.429	1.64E-01	
	Claw	0.00	0.08	23.0	0.025	9.80E-01		Claw	0.04	0.04	29.0	0.983	3.34E-01	
duty factor*	(Int.)	0.18	4.53	23.0	0.039	9.69E-01		(Int.)	0.65	3.10	26.9	0.208	8.37E-01	
	B.T.	0.30	1.18	23.0	0.253	8.02E-01		B.T.	0.13	1.35	15.0	0.097	9.24E-01	
	A.T.	-1.70	2.06	23.0	-0.827	4.17E-01		A.T.	-0.05	0.85	25.3	-0.055	9.56E-01	
	R.H.	1.16	1.20	23.0	0.971	3.42E-01		R.H.	-0.31	0.64	24.4	-0.490	6.28E-01	
	Mass	-0.42	0.16	23.0	-2.612	1.56E-02	*	Mass	-0.11	0.15	5.4	-0.726	4.98E-01	
	Claw	0.02	0.03	23.0	0.734	4.71E-01		Claw	-0.03	0.02	26.0	-1.329	1.96E-01	
time to toe unfurling	(Int.)	-8.26	6.42	23.0	-1.287	2.11E-01		(Int.)	9.34	7.89	29.0	1.184	2.46E-01	
	B.T.	-0.74	1.68	23.0	-0.439	6.65E-01		B.T.	-9.61	2.67	29.0	-3.593	1.19E-03	**
	A.T.	3.15	2.92	23.0	1.081	2.91E-01		A.T.	3.54	1.85	29.0	1.918	6.50E-02	
	R.H.	1.55	1.69	23.0	0.915	3.70E-01		R.H.	-1.65	1.65	29.0	-1.001	3.25E-01	
	Mass	-0.03	0.23	23.0	-0.150	8.82E-01		Mass	0.57	0.21	29.0	2.684	1.19E-02	*
	Claw	-0.06	0.05	23.0	-1.275	2.15E-01		Claw	0.11	0.05	29.0	2.258	3.17E-02	*
duration of distal toe contact	(Int.)	39.11	25.07	21.0	1.560	1.34E-01		(Int.)	11.77	16.64	25.7	0.708	4.86E-01	
	B.T.	-2.99	6.58	21.0	-0.454	6.54E-01		B.T.	-10.64	8.66	20.7	-1.228	2.33E-01	
	A.T.	-13.06	10.94	21.0	-1.195	2.46E-01		A.T.	4.29	4.97	26.6	0.864	3.95E-01	
	R.H.	-9.01	6.54	21.0	-1.377	1.83E-01		R.H.	-1.93	3.31	22.8	-0.584	5.65E-01	
	Mass	1.02	1.08	21.0	0.948	3.54E-01		Mass	0.87	1.15	6.6	0.760	4.73E-01	
	Claw	-0.20	0.18	21.0	-1.101	2.83E-01		Claw	0.10	0.13	26.5	0.788	4.38E-01	
time to toe hyperextension*	(Int.)	21.62	16.98	23.0	1.273	2.16E-01		(Int.)	-2.41	11.94	14.3	-0.202	8.43E-01	
	B.T.	-0.24	4.44	23.0	-0.053	9.58E-01		B.T.	-4.61	3.85	19.8	-1.198	2.45E-01	
	A.T.	-9.65	7.72	23.0	-1.250	2.24E-01		A.T.	4.92	2.98	9.2	1.653	1.32E-01	
	R.H.	-4.32	4.48	23.0	-0.964	3.45E-01		R.H.	0.65	2.55	12.6	0.256	8.02E-01	
	Mass	0.65	0.61	23.0	1.061	3.00E-01		Mass	0.66	0.35	8.9	1.893	9.11E-02	.
	Claw	-0.10	0.12	23.0	-0.786	4.40E-01		Claw	0.10	0.08	10.3	1.339	2.10E-01	
duration of toe hyperextension*	(Int.)	-3.63	6.78	23.0	-0.536	5.97E-01		(Int.)	-8.01	9.49	17.0	-0.844	4.10E-01	
	B.T.	2.45	1.77	23.0	1.381	1.81E-01		B.T.	-2.21	3.15	21.7	-0.703	4.90E-01	
	A.T.	-1.27	3.08	23.0	-0.411	6.85E-01		A.T.	4.57	2.28	12.2	2.004	6.78E-02	
	R.H.	0.79	1.79	23.0	0.439	6.65E-01		R.H.	2.77	2.00	15.5	1.384	1.86E-01	
	Mass	0.29	0.24	23.0	1.183	2.49E-01		Mass	-0.55	0.27	11.0	-2.079	6.19E-02	
	Claw	0.09	0.05	23.0	1.918	6.76E-02		Claw	0.06	0.06	13.7	1.075	3.01E-01	

Locomotor Variable	Inclined Acrylic							Level Acrylic						
	Factor	**Est.**	**S.E.**	**df**	***t***	***p***		**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***	
maximum body pitch angle*	(Int.)	1.87	1.72	22.4	1.088	2.88E-01		(Int.)	0.44	1.12	27.8	0.394	6.97E-01	
	B.T.	-0.49	0.52	11.9	-0.931	3.70E-01		B.T.	-0.56	0.63	26.2	-0.887	3.83E-01	
	A.T.	0.30	0.75	22.9	0.398	6.94E-01		A.T.	0.41	0.35	29.0	1.166	2.53E-01	
	R.H.	-0.80	0.45	22.6	-1.799	8.54E-02	.	R.H.	-0.05	0.22	25.1	-0.207	8.37E-01	
	Mass	-0.02	0.07	12.5	-0.273	7.89E-01		Mass	-0.12	0.10	6.9	-1.286	2.40E-01	
	Claw	-0.01	0.01	21.6	-1.053	3.04E-01		Claw	0.03	0.01	29.0	2.887	7.28E-03	**
maximum effective forelimb length	(Int.)	1.35	12.52	12.9	0.108	9.16E-01		(Int.)	-15.70	10.98	15.6	-1.430	1.72E-01	
	B.T.	1.54	3.63	10.9	0.423	6.81E-01		B.T.	4.27	3.36	23.8	1.272	2.16E-01	
	A.T.	-2.81	5.83	15.9	-0.482	6.36E-01		A.T.	2.09	2.90	9.5	0.719	4.89E-01	
	R.H.	0.28	3.15	21.4	0.089	9.30E-01		R.H.	3.54	2.37	13.7	1.493	1.58E-01	
	FL	-0.35	1.14	11.7	-0.305	7.66E-01		FL	-0.62	0.77	9.2	-0.795	4.47E-01	
	Claw	0.00	0.10	7.4	-0.039	9.70E-01		Claw	0.06	0.07	10.2	0.811	4.36E-01	
maximum extent of humerus depression	(Int.)	-1.04	6.31	23.0	-0.165	8.70E-01		(Int.)	-8.77	4.27	29.0	-2.055	4.90E-02	*
	B.T.	2.28	1.76	23.0	1.297	2.08E-01		B.T.	4.05	1.45	29.0	2.790	9.22E-03	**
	A.T.	-2.17	3.08	23.0	-0.706	4.87E-01		A.T.	-0.24	0.98	29.0	-0.239	8.13E-01	
	R.H.	0.46	1.68	23.0	0.273	7.87E-01		R.H.	1.73	0.89	29.0	1.942	6.19E-02	
	Hum.	-1.25	0.63	23.0	-1.976	6.02E-02		Hum.	-0.54	0.28	29.0	-1.922	6.45E-02	
	Claw	0.02	0.05	23.0	0.486	6.31E-01		Claw	0.05	0.03	29.0	1.779	8.57E-02	
maximum extent of humerus retraction*	(Int.)	-3.81	6.42	19.2	-0.594	5.60E-01		(Int.)	-9.80	6.79	29.0	-1.443	1.60E-01	
	B.T.	0.29	1.80	16.2	0.161	8.74E-01		B.T.	1.04	2.31	29.0	0.450	6.56E-01	
	A.T.	-0.31	3.09	20.4	-0.100	9.21E-01		A.T.	1.40	1.56	29.0	0.893	3.79E-01	
	R.H.	1.99	1.67	22.6	1.190	2.46E-01		R.H.	3.16	1.42	29.0	2.233	3.34E-02	*
	Hum.	0.28	0.65	16.4	0.436	6.68E-01		Hum.	4.40	0.45	29.0	9.832	9.69E-11	***
	Claw	-0.06	0.05	12.3	-1.269	2.28E-01		Claw	-0.09	0.04	29.0	-2.156	3.95E-02	*
step length	(Int.)	8.83	11.24	23.0	0.785	4.40E-01		(Int.)	-6.51	5.65	29.0	-1.152	2.59E-01	
	B.T.	1.80	3.54	23.0	0.508	6.17E-01		B.T.	-2.11	1.91	29.0	-1.100	2.80E-01	
	A.T.	-6.18	5.15	23.0	-1.201	2.42E-01		A.T.	3.62	1.31	29.0	2.755	1.00E-02	*
	R.H.	-2.14	2.83	23.0	-0.756	4.58E-01		R.H.	1.74	1.17	29.0	1.482	1.49E-01	
	SVL	2.13	2.38	23.0	0.898	3.78E-01		SVL	1.71	0.76	29.0	2.264	3.12E-02	*
	Claw	-0.03	0.08	23.0	-0.343	7.34E-01		Claw	0.06	0.03	29.0	1.634	1.13E-01	
stride length*	(Int.)	3.73	8.72	23.0	0.428	6.73E-01		(Int.)	-3.40	6.72	29.0	-0.505	6.17E-01	
	B.T.	2.39	2.74	23.0	0.870	3.93E-01		B.T.	-3.47	2.28	29.0	-1.522	1.39E-01	
	A.T.	-4.73	3.99	23.0	-1.185	2.48E-01		A.T.	3.26	1.56	29.0	2.084	4.61E-02	*
	R.H.	-2.51	2.19	23.0	-1.143	2.65E-01		R.H.	1.02	1.40	29.0	0.731	4.70E-01	
	SVL	4.61	1.84	23.0	2.503	1.99E-02	*	SVL	1.88	0.90	29.0	2.086	4.59E-02	*
	Claw	-0.03	0.06	23.0	-0.488	6.30E-01		Claw	0.04	0.04	29.0	0.852	4.01E-01	
forefoot slippage*	(Int.)	1.77	0.89	12.5	1.995	6.83E-02		(Int.)	-0.84	0.32	13.8	-2.621	2.03E-02	*
	B.T.	0.53	0.24	13.2	2.200	4.62E-02	*	B.T.	0.04	0.09	28.2	0.404	6.89E-01	
	A.T.	-1.07	0.32	14.7	-3.344	4.56E-03	**	A.T.	0.12	0.09	7.0	1.308	2.32E-01	
	R.H.	-0.61	0.19	14.4	-3.212	6.08E-03	**	R.H.	0.16	0.07	10.9	2.225	4.81E-02	*
	SVL	0.18	0.15	13.8	1.157	2.67E-01		SVL	0.32	0.05	7.2	6.102	4.32E-04	***
	Claw	0.00	0.01	12.3	-0.694	5.00E-01		Claw	0.00	0.00	7.8	0.834	4.29E-01	

*residuals used in analyses

Abbreviations: Est. (estimate), S.E. (standard error), Int. (intercept), A.T. (ambient temperature), R.H. (relative humidity), Mass (body mass), SVL (snout-vent-length), FL (forelimb length), Hum. (humerus length), Claw (claw status). Boxes are drawn around the predictor variable of claw status when significant for a given model.

d) hindlimb strides

Locomotor Variable	Inclined Sandpaper							Level Sandpaper						
	Factor	**Est.**	**S.E.**	**df**	***t***	***p***		**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***	
stride duration*	(Int.)	11.54	11.05	33.0	1.04	3.04E-01		(Int.)	12.44	16.06	26.0	0.77	4.46E-01	
	B.T.	2.09	1.82	33.0	1.15	2.60E-01		B.T.	-1.17	1.76	26.0	-0.67	5.10E-01	
	Mass	0.60	0.25	33.0	2.42	2.11E-02	*	Mass	0.00	0.16	26.0	-0.02	9.84E-01	
	A.T.	-6.93	3.63	33.0	-1.91	6.47E-02		A.T.	-2.63	5.27	26.0	-0.50	6.21E-01	
	R.H.	-2.83	3.87	33.0	-0.73	4.70E-01		R.H.	-3.66	4.16	26.0	-0.88	3.88E-01	
	Claw	0.05	0.06	33.0	0.85	4.03E-01		Claw	-0.01	0.04	26.0	-0.25	8.01E-01	
step duration*	(Int.)	9.40	13.21	33.0	0.71	4.82E-01		(Int.)	25.47	17.04	26.0	1.50	1.47E-01	
	B.T.	2.71	2.18	33.0	1.24	2.22E-01		B.T.	0.15	1.87	26.0	0.08	9.36E-01	
	Mass	0.49	0.30	33.0	1.65	1.08E-01		Mass	-0.15	0.17	26.0	-0.87	3.94E-01	
	A.T.	-7.60	4.34	33.0	-1.75	8.91E-02		A.T.	-8.41	5.59	26.0	-1.51	1.44E-01	
	R.H.	-1.65	4.63	33.0	-0.36	7.23E-01		R.H.	-7.05	4.42	26.0	-1.60	1.23E-01	
	Claw	0.07	0.07	33.0	0.94	3.53E-01		Claw	0.01	0.04	26.0	0.25	8.03E-01	
duty factor*	(Int.)	-0.18	3.30	25.2	-0.05	9.57E-01		(Int.)	13.04	6.09	26.0	2.14	4.18E-02	*
	B.T.	0.47	0.56	25.1	0.84	4.08E-01		B.T.	1.33	0.67	26.0	1.99	5.74E-02	
	A.T.	-0.66	0.95	31.8	-0.70	4.89E-01		A.T.	-5.78	2.00	26.0	-2.89	7.61E-03	**
	R.H.	0.31	1.16	25.7	0.27	7.92E-01		R.H.	-3.39	1.58	26.0	-2.15	4.10E-02	*
	Mass	-0.15	0.10	3.6	-1.45	2.29E-01		Mass	-0.15	0.06	26.0	-2.37	2.53E-02	*
	Claw	0.02	0.01	27.6	1.60	1.22E-01		Claw	0.02	0.01	26.0	1.38	1.81E-01	
time to toe unfurling	(Int.)	15.25	12.83	33.0	1.19	2.43E-01		(Int.)	14.80	26.26	26.0	0.56	5.78E-01	
	B.T.	2.96	2.11	33.0	1.40	1.70E-01		B.T.	0.04	2.87	26.0	0.01	9.90E-01	
	A.T.	-9.05	4.21	33.0	-2.15	3.92E-02	*	A.T.	-5.84	8.61	26.0	-0.68	5.03E-01	
	R.H.	-3.61	4.50	33.0	-0.80	4.28E-01		R.H.	-3.52	6.80	26.0	-0.52	6.09E-01	
	Mass	0.18	0.29	33.0	0.62	5.42E-01		Mass	0.21	0.26	26.0	0.80	4.32E-01	
	Claw	0.04	0.07	33.0	0.60	5.55E-01		Claw	-0.03	0.06	26.0	-0.55	5.88E-01	
duration of distal toe contact	(Int.)	14.35	23.06	18.6	0.62	5.41E-01		(Int.)	3.36	66.12	14.7	0.05	9.60E-01	
	B.T.	1.84	3.87	17.5	0.47	6.41E-01		B.T.	7.18	6.98	22.5	1.03	3.14E-01	
	A.T.	-7.55	6.88	32.7	-1.10	2.81E-01		A.T.	-5.30	23.28	9.9	-0.23	8.24E-01	
	R.H.	-3.51	8.08	18.9	-0.43	6.69E-01		R.H.	-3.79	16.98	15.4	-0.22	8.27E-01	
	Mass	0.42	0.65	2.7	0.64	5.71E-01		Mass	0.81	0.82	5.1	0.99	3.66E-01	
	Claw	0.18	0.11	27.5	1.67	1.07E-01		Claw	0.28	0.13	25.9	2.17	3.98E-02	*
time to toe hyperextension*	(Int.)	24.40	16.35	8.1	1.49	1.73E-01		(Int.)	44.45	30.13	26.0	1.48	1.52E-01	
	B.T.	3.20	2.74	6.6	1.17	2.83E-01		B.T.	2.40	3.30	26.0	0.73	4.74E-01	
	A.T.	-11.58	5.05	33.0	-2.29	2.84E-02	*	A.T.	-17.07	9.88	26.0	-1.73	9.58E-02	
	R.H.	-6.74	5.73	8.2	-1.18	2.73E-01		R.H.	-12.60	7.81	26.0	-1.61	1.19E-01	
	Mass	0.36	0.42	0.9	0.85	5.59E-01		Mass	0.44	0.30	26.0	1.46	1.57E-01	
	Claw	0.15	0.08	22.3	1.78	8.89E-02		Claw	0.18	0.07	26.0	2.63	1.41E-02	*
duration of toe hyperextension*	(Int.)	-3.91	14.45	14.4	-0.27	7.91E-01		(Int.)	-10.87	35.18	26.0	-0.31	7.60E-01	
	B.T.	0.75	2.40	10.9	0.31	7.62E-01		B.T.	-4.81	3.85	26.0	-1.25	2.23E-01	
	A.T.	-1.83	4.62	32.7	-0.40	6.94E-01		A.T.	9.01	11.54	26.0	0.78	4.42E-01	
	R.H.	2.43	5.07	14.2	0.48	6.39E-01		R.H.	2.97	9.12	26.0	0.33	7.48E-01	
	Mass	0.52	0.35	2.4	1.50	2.54E-01		Mass	-0.57	0.35	26.0	-1.61	1.20E-01	
	Claw	-0.02	0.08	28.8	-0.33	7.45E-01		Claw	-0.22	0.08	26.0	-2.70	1.22E-02	*

Locomotor Variable	**Inclined Sandpaper**							**Level Sandpaper**						
	Factor	**Est.**	**S.E.**	**df**	***t***	***p***		**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***	
maximum body pitch angle	(Int.)	3.89	1.66	6.7	2.34	5.35E-02		(Int.)	5.21	5.85	12.8	0.89	3.89E-01	
	B.T.	-0.07	0.25	17.3	-0.28	7.85E-01		B.T.	-1.81	0.66	12.3	-2.76	1.70E-02	*
	A.T.	-1.30	0.50	2.4	-2.62	9.92E-02		A.T.	0.13	1.90	13.1	0.07	9.48E-01	
	R.H.	-0.95	0.58	6.8	-1.65	1.44E-01		R.H.	-1.35	1.51	12.8	-0.89	3.89E-01	
	Mass	-0.09	0.05	1.9	-1.96	1.93E-01		Mass	-0.14	0.06	12.5	-2.39	3.36E-02	*
	Claw	0.00	0.01	1.6	0.57	6.38E-01		Claw	-0.01	0.01	13.5	-1.12	2.82E-01	
maximum effective hindlimb length	(Int.)	-28.82	10.47	33.0	-2.75	9.55E-03	**	(Int.)	-18.41	23.84	26.0	-0.77	4.47E-01	
	B.T.	-7.28	1.72	33.0	-4.24	1.67E-04	***	B.T.	1.82	2.82	26.0	0.65	5.23E-01	
	A.T.	18.68	3.50	33.0	5.33	6.88E-06	***	A.T.	3.25	7.51	26.0	0.43	6.68E-01	
	R.H.	7.00	3.65	33.0	1.92	6.39E-02		R.H.	5.70	6.18	26.0	0.92	3.65E-01	
	HL	-1.70	1.13	33.0	-1.50	1.44E-01		HL	0.47	1.09	26.0	0.44	6.67E-01	
	Claw	0.08	0.06	33.0	1.32	1.98E-01		Claw	0.02	0.05	26.0	0.46	6.48E-01	
maximum extent of femur depression	(Int.)	-10.90	9.41	10.4	-1.16	2.73E-01		(Int.)	15.12	6.14	26.0	2.46	2.07E-02	*
	B.T.	1.59	1.31	21.2	1.21	2.41E-01		B.T.	-0.40	0.68	26.0	-0.60	5.56E-01	
	A.T.	-0.78	2.99	9.2	-0.26	7.99E-01		A.T.	-5.40	1.98	26.0	-2.73	1.14E-02	*
	R.H.	4.95	3.26	10.4	1.52	1.59E-01		R.H.	-3.59	1.59	26.0	-2.26	3.24E-02	*
	Fem.	1.43	1.01	5.2	1.42	2.13E-01		Fem.	1.85	0.27	26.0	6.96	2.19E-07	***
	Claw	0.00	0.05	4.7	0.08	9.38E-01		Claw	0.04	0.01	26.0	3.01	5.81E-03	**
maximum extent of femur retraction*	(Int.)	1.95	13.08	33.0	0.15	8.82E-01		(Int.)	81.19	33.59	26.0	2.42	2.30E-02	*
	B.T.	10.63	2.15	33.0	4.94	2.23E-05	***	B.T.	2.74	3.71	26.0	0.74	4.67E-01	
	A.T.	-17.53	4.29	33.0	-4.09	2.60E-04	***	A.T.	-30.51	10.85	26.0	-2.81	9.24E-03	**
	R.H.	3.69	4.56	33.0	0.81	4.25E-01		R.H.	-21.67	8.69	26.0	-2.49	1.93E-02	*
	Fem.	3.07	1.35	33.0	2.28	2.95E-02	*	Fem.	1.58	1.46	26.0	1.08	2.88E-01	
	Claw	0.04	0.07	33.0	0.57	5.75E-01		Claw	0.06	0.08	26.0	0.84	4.10E-01	
step length*	(Int.)	-13.09	14.99	9.2	-0.87	4.05E-01		(Int.)	-18.03	37.05	26.0	-0.49	6.31E-01	
	B.T.	1.46	2.38	15.3	0.61	5.50E-01		B.T.	-5.37	3.86	26.0	-1.39	1.76E-01	
	A.T.	-0.87	4.81	9.9	-0.18	8.60E-01		A.T.	13.14	12.74	26.0	1.03	3.12E-01	
	R.H.	5.12	5.10	10.3	1.00	3.39E-01		R.H.	5.33	9.75	26.0	0.55	5.89E-01	
	SVL	2.26	1.64	9.3	1.38	2.01E-01		SVL	-3.28	2.11	26.0	-1.55	1.33E-01	
	Claw	-0.03	0.08	12.2	-0.34	7.40E-01		Claw	-0.23	0.08	26.0	-2.80	9.54E-03	**
stride length*	(Int.)	-5.66	8.39	33.0	-0.68	5.05E-01		(Int.)	44.27	19.51	26.0	2.27	3.18E-02	*
	B.T.	1.06	1.35	33.0	0.79	4.38E-01		B.T.	-1.35	2.03	26.0	-0.66	5.14E-01	
	A.T.	-1.88	2.70	33.0	-0.70	4.90E-01		A.T.	-13.45	6.71	26.0	-2.01	5.54E-02	
	R.H.	2.36	2.86	33.0	0.83	4.15E-01		R.H.	-12.16	5.13	26.0	-2.37	2.55E-02	*
	SVL	2.23	0.92	33.0	2.42	2.12E-02	*	SVL	0.25	1.11	26.0	0.23	8.22E-01	
	Claw	-0.01	0.04	33.0	-0.14	8.89E-01		Claw	0.01	0.04	26.0	0.25	8.06E-01	
hindfoot slippage*	(Int.)	-1.04	1.41	33.0	-0.73	4.68E-01		(Int.)	1.48	1.73	9.8	0.86	4.12E-01	
	B.T.	0.37	0.23	33.0	1.64	1.11E-01		B.T.	-0.19	0.18	6.3	-1.08	3.18E-01	
	A.T.	-0.39	0.45	33.0	-0.86	3.97E-01		A.T.	-0.38	0.62	3.1	-0.61	5.83E-01	
	R.H.	0.29	0.48	33.0	0.59	5.58E-01		R.H.	-0.39	0.45	9.8	-0.87	4.05E-01	
	SVL	0.51	0.15	33.0	3.30	2.32E-03	**	SVL	0.10	0.12	1.0	0.86	5.43E-01	
	Claw	-0.01	0.01	33.0	-1.70	9.78E-02		Claw	0.00	0.00	3.0	-0.26	8.12E-01	

Locomotor Variable	Inclined Acrylic							Level Acrylic						
	Factor	**Est.**	**S.E.**	**df**	***t***	***p***		**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***	
stride duration*	(Int.)	-3.91	6.30	14.6	-0.62	5.44E-01		(Int.)	-3.91	6.30	14.6	-0.62	5.44E-01	
	B.T.	-3.05	1.88	20.5	-1.62	1.21E-01		B.T.	-3.05	1.88	20.5	-1.62	1.21E-01	
	Mass	0.56	0.19	12.3	2.98	1.11E-02	*	Mass	0.56	0.19	12.3	2.98	1.11E-02	*
	A.T.	3.49	1.75	12.0	1.99	6.97E-02		A.T.	3.49	1.75	12.0	1.99	6.97E-02	
	R.H.	1.39	1.40	13.5	0.99	3.39E-01		R.H.	1.39	1.40	13.5	0.99	3.39E-01	
	Claw	-0.01	0.04	15.3	-0.26	8.01E-01		Claw	-0.01	0.04	15.3	-0.26	8.01E-01	
step duration*	(Int.)	10.71	11.19	24.0	0.96	3.48E-01		(Int.)	-7.76	5.58	26.0	-1.39	1.76E-01	
	B.T.	-0.60	2.57	24.0	-0.23	8.17E-01		B.T.	-1.58	1.81	26.0	-0.87	3.90E-01	
	Mass	-0.12	0.44	24.0	-0.28	7.80E-01		Mass	0.33	0.16	26.0	2.08	4.78E-02	*
	A.T.	-1.50	3.93	24.0	-0.38	7.07E-01		A.T.	3.71	1.49	26.0	2.48	1.98E-02	*
	R.H.	-3.89	2.67	24.0	-1.46	1.59E-01		R.H.	2.26	1.22	26.0	1.86	7.46E-02	
	Claw	0.08	0.08	24.0	1.03	3.14E-01		Claw	0.01	0.04	26.0	0.29	7.71E-01	
duty factor*	(Int.)	-1.83	3.73	24.0	-0.49	6.27E-01		(Int.)	6.83	2.21	8.4	3.08	1.43E-02	*
	B.T.	1.13	0.86	24.0	1.32	1.99E-01		B.T.	-5.78	0.88	17.7	-6.54	4.17E-06	***
	A.T.	-0.33	1.31	24.0	-0.25	8.03E-01		A.T.	2.53	0.76	6.0	3.33	1.58E-02	*
	R.H.	0.24	0.89	24.0	0.27	7.88E-01		R.H.	-0.95	0.48	5.9	-1.98	9.60E-02	
	Mass	0.14	0.15	24.0	0.94	3.56E-01		Mass	-0.26	0.30	5.4	-0.89	4.14E-01	
	Claw	0.06	0.03	24.0	2.44	2.24E-02	*	Claw	0.08	0.02	7.9	4.82	1.39E-03	**
time to toe unfurling	(Int.)	-10.38	10.31	24.0	-1.01	3.24E-01		(Int.)	-12.44	8.49	26.0	-1.47	1.55E-01	
	B.T.	7.71	2.37	24.0	3.26	3.36E-03	**	B.T.	4.20	2.75	26.0	1.53	1.39E-01	
	A.T.	-5.58	3.62	24.0	-1.54	1.36E-01		A.T.	-0.89	2.27	26.0	-0.39	7.00E-01	
	R.H.	3.00	2.46	24.0	1.22	2.34E-01		R.H.	3.49	1.85	26.0	1.89	7.03E-02	
	Mass	1.04	0.41	24.0	2.57	1.68E-02	*	Mass	0.79	0.24	26.0	3.27	3.06E-03	**
	Claw	0.15	0.07	24.0	2.06	5.01E-02		Claw	0.06	0.06	26.0	1.01	3.24E-01	
duration of distal toe contact	(Int.)	-15.89	41.39	21.9	-0.38	7.05E-01		(Int.)	-17.33	28.14	25.5	-0.62	5.44E-01	
	B.T.	-2.68	9.69	20.5	-0.28	7.85E-01		B.T.	-5.81	10.91	15.3	-0.53	6.02E-01	
	A.T.	9.17	11.51	21.7	0.80	4.34E-01		A.T.	11.96	7.87	25.9	1.52	1.41E-01	
	R.H.	3.51	9.91	22.1	0.35	7.27E-01		R.H.	3.81	6.09	24.7	0.63	5.37E-01	
	Mass	-0.09	1.85	12.4	-0.05	9.61E-01		Mass	0.96	1.16	6.7	0.83	4.36E-01	
	Claw	0.12	0.26	23.5	0.49	6.31E-01		Claw	0.08	0.19	25.8	0.41	6.82E-01	
time to toe hyperextension*	(Int.)	15.83	19.43	13.9	0.82	4.29E-01		(Int.)	-5.01	8.88	25.6	-0.56	5.78E-01	
	B.T.	2.52	4.44	16.8	0.57	5.77E-01		B.T.	-4.77	2.90	12.2	-1.65	1.25E-01	
	A.T.	-6.27	6.53	11.9	-0.96	3.56E-01		A.T.	5.42	2.38	24.7	2.28	3.19E-02	*
	R.H.	-5.60	4.65	14.4	-1.21	2.48E-01		R.H.	1.72	1.94	25.7	0.89	3.84E-01	
	Mass	0.26	0.77	14.6	0.34	7.37E-01		Mass	0.66	0.26	3.2	2.56	7.92E-02	
	Claw	0.08	0.13	10.6	0.62	5.51E-01		Claw	0.10	0.06	24.3	1.64	1.14E-01	
duration of toe hyperextension*	(Int.)	5.74	12.08	24.0	0.48	6.39E-01		(Int.)	-6.54	6.08	14.3	-1.08	3.00E-01	
	B.T.	-4.30	2.78	24.0	-1.55	1.34E-01		B.T.	0.86	1.94	20.6	0.45	6.61E-01	
	A.T.	3.77	4.24	24.0	0.89	3.84E-01		A.T.	1.36	1.64	12.0	0.83	4.23E-01	
	R.H.	-2.14	2.88	24.0	-0.74	4.65E-01		R.H.	1.89	1.33	13.1	1.42	1.78E-01	
	Mass	-0.58	0.47	24.0	-1.23	2.31E-01		Mass	-0.16	0.18	12.4	-0.94	3.66E-01	
	Claw	0.05	0.08	24.0	0.54	5.93E-01		Claw	-0.10	0.04	17.5	-2.52	2.20E-02	*

Locomotor Variable	Inclined Acrylic							Level Acrylic						
	Factor	**Est.**	**S.E.**	**df**	***t***	***p***		**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***	
maximum body pitch angle	(Int.)	1.14	3.32	21.5	0.34	7.34E-01		(Int.)	2.66	2.17	15.8	1.22	2.39E-01	
	B.T.	-0.09	0.78	20.1	-0.11	9.13E-01		B.T.	-0.19	0.58	25.2	-0.34	7.38E-01	
	A.T.	-0.09	0.94	22.3	-0.10	9.21E-01		A.T.	-0.56	0.65	11.0	-0.86	4.06E-01	
	R.H.	-0.46	0.80	21.6	-0.58	5.67E-01		R.H.	-0.74	0.49	14.2	-1.51	1.54E-01	
	Mass	0.02	0.15	13.1	0.10	9.19E-01		Mass	-0.11	0.07	11.5	-1.64	1.27E-01	
	Claw	-0.01	0.02	23.4	-0.35	7.27E-01		Claw	-0.02	0.01	12.2	-1.50	1.58E-01	
maximum effective hindlimb length	(Int.)	-2.29	16.14	18.6	-0.14	8.89E-01		(Int.)	-1.84	11.87	14.1	-0.16	8.79E-01	
	B.T.	-0.29	2.45	6.2	-0.12	9.10E-01		B.T.	2.82	3.34	20.0	0.84	4.09E-01	
	A.T.	0.14	6.44	23.7	0.02	9.83E-01		A.T.	-2.49	3.47	11.9	-0.72	4.87E-01	
	R.H.	0.88	3.93	18.7	0.22	8.26E-01		R.H.	0.42	2.69	13.3	0.16	8.79E-01	
	HL	2.22	2.04	8.2	1.09	3.06E-01		HL	1.44	1.47	14.1	0.98	3.44E-01	
	Claw	-0.06	0.10	24.0	-0.63	5.37E-01		Claw	-0.01	0.08	15.5	-0.12	9.07E-01	
maximum extent of femur depression	(Int.)	1.00	4.34	21.4	0.23	8.20E-01		(Int.)	6.00	4.26	26.0	1.41	1.71E-01	
	B.T.	-0.26	0.98	17.1	-0.26	7.97E-01		B.T.	-2.65	1.35	26.0	-1.97	5.98E-02	
	A.T.	0.37	1.35	22.3	0.28	7.85E-01		A.T.	-0.42	1.11	26.0	-0.38	7.09E-01	
	R.H.	-0.58	1.07	21.5	-0.54	5.93E-01		R.H.	-0.84	0.92	26.0	-0.92	3.68E-01	
	Fem.	0.89	0.81	12.2	1.09	2.95E-01		Fem.	1.79	0.51	26.0	3.54	1.54E-03	**
	Claw	0.00	0.03	22.9	-0.09	9.31E-01		Claw	-0.02	0.03	26.0	-0.72	4.81E-01	
maximum extent of femur retraction*	(Int.)	-0.90	15.09	12.3	-0.06	9.53E-01		(Int.)	-0.53	8.77	6.3	-0.06	9.53E-01	
	B.T.	-0.55	3.13	8.3	-0.18	8.65E-01		B.T.	-1.81	2.93	16.2	-0.62	5.47E-01	
	A.T.	1.12	5.57	23.5	0.20	8.43E-01		A.T.	1.37	2.35	6.0	0.58	5.81E-01	
	R.H.	0.19	3.70	11.6	0.05	9.60E-01		R.H.	0.50	1.90	5.5	0.26	8.03E-01	
	Fem.	-0.80	2.47	7.5	-0.32	7.56E-01		Fem.	4.97	1.22	6.4	4.07	5.81E-03	**
	Claw	-0.06	0.10	23.5	-0.59	5.62E-01		Claw	-0.12	0.06	9.0	-2.17	5.79E-02	
step length*	(Int.)	25.55	15.46	24.0	1.65	1.11E-01		(Int.)	-5.26	5.81	13.3	-0.91	3.82E-01	
	B.T.	-9.41	3.76	24.0	-2.50	1.96E-02	*	B.T.	0.65	1.89	20.2	0.34	7.36E-01	
	A.T.	4.14	3.96	24.0	1.05	3.06E-01		A.T.	1.29	1.62	10.9	0.80	4.44E-01	
	R.H.	-5.61	3.27	24.0	-1.72	9.90E-02		R.H.	1.70	1.27	12.0	1.33	2.08E-01	
	SVL	-7.15	3.13	24.0	-2.29	3.13E-02	*	SVL	-0.71	0.88	12.6	-0.81	4.32E-01	
	Claw	-0.07	0.10	24.0	-0.70	4.92E-01		Claw	-0.11	0.04	16.2	-2.58	1.99E-02	*
stride length*	(Int.)	0.59	14.54	24.0	0.04	9.68E-01		(Int.)	-11.93	4.16	26.0	-2.87	8.14E-03	**
	B.T.	4.85	3.54	24.0	1.37	1.84E-01		B.T.	1.04	1.37	26.0	0.76	4.56E-01	
	A.T.	-6.03	3.73	24.0	-1.62	1.19E-01		A.T.	2.61	1.15	26.0	2.27	3.21E-02	*
	R.H.	-1.72	3.07	24.0	-0.56	5.82E-01		R.H.	2.78	0.91	26.0	3.05	5.23E-03	**
	SVL	4.44	2.94	24.0	1.51	1.44E-01		SVL	1.42	0.63	26.0	2.26	3.22E-02	*
	Claw	0.10	0.09	24.0	1.11	2.79E-01		Claw	0.02	0.03	26.0	0.57	5.74E-01	
hindfoot slippage*	(Int.)	-1.50	1.04	20.8	-1.45	1.61E-01		(Int.)	-3.68	0.51	14.5	-7.17	4.00E-06	***
	B.T.	0.45	0.22	18.7	2.06	5.39E-02		B.T.	2.06	0.12	15.2	16.68	3.63E-11	***
	A.T.	-0.19	0.20	16.7	-0.96	3.51E-01		A.T.	-0.57	0.12	5.9	-4.85	2.97E-03	**
	R.H.	0.25	0.21	18.7	1.16	2.62E-01		R.H.	0.60	0.07	6.1	8.18	1.71E-04	***
	SVL	0.68	0.31	10.0	2.22	5.04E-02		SVL	0.40	0.42	6.6	0.97	3.67E-01	
	Claw	0.01	0.01	18.1	1.47	1.58E-01		Claw	-0.01	0.00	7.5	-5.52	6.95E-04	***

*residuals used in analyses

Abbreviations: Est. (estimate), S.E. (standard error), Int. (intercept), A.T. (ambient temperature), R.H. (relative humidity), Mass (body mass), SVL (snout-vent-length), HL (forelimb length), Fem. (femur length), Claw (claw status). Boxes are drawn around the predictor variable of claw status when significant for a given model.

e) initial acceleration

Inclined Sandpaper							Level Sandpaper						
Factor	**Est.**	**S.E.**	**df**	***t***	***p***		**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***	
(Int.)	49.05	22.87	24.0	2.15	4.23E-02	*	(Int.)	49.05	22.87	24.0	2.145	4.23E-02	*
B.T.	-3.33	3.56	24.0	-0.94	3.59E-01		B.T.	-3.33	3.56	24.0	-0.935	3.59E-01	
A.T.	-8.10	7.27	24.0	-1.12	2.76E-01		A.T.	-8.10	7.27	24.0	-1.115	2.76E-01	
R.H.	-14.83	7.97	24.0	-1.86	7.50E-02		R.H.	-14.83	7.97	24.0	-1.861	7.50E-02	
SVL	-1.22	0.51	24.0	-2.40	2.43E-02	*	SVL	-1.22	0.51	24.0	-2.403	2.43E-02	*
Claw	-0.05	0.14	24.0	-0.36	7.23E-01		Claw	-0.05	0.14	24.0	-0.359	7.23E-01	

Inclined Acrylic							Level Acrylic						
Factor	**Est.**	**S.E.**	**df**	***t***	***p***		**Factor**	**Est.**	**S.E.**	**df**	***t***	***p***	
(Int.)	49.05	22.87	24.0	2.145	4.23E-02	*	(Int.)	49.05	22.87	24.0	2.145	4.23E-02	*
B.T.	-3.33	3.56	24.0	-0.935	3.59E-01		B.T.	-3.33	3.56	24.0	-0.935	3.59E-01	
A.T.	-8.10	7.27	24.0	-1.115	2.76E-01		A.T.	-8.10	7.27	24.0	-1.115	2.76E-01	
R.H.	-14.83	7.97	24.0	-1.861	7.50E-02		R.H.	-14.83	7.97	24.0	-1.861	7.50E-02	
SVL	-1.22	0.51	24.0	-2.403	2.43E-02	*	SVL	-1.22	0.51	24.0	-2.403	2.43E-02	*
Claw	-0.05	0.14	24.0	-0.359	7.23E-01		Claw	-0.05	0.14	24.0	-0.359	7.23E-01	

Abbreviations: Est. (estimate), S.E. (standard error), Int. (intercept), A.T. (ambient temperature), R.H. (relative humidity), SVL (snout-vent-length), Claw (claw status).

S2.6. Frequency of partial toe hyperextension throughout a stride from all analyzed forelimb and hindlimb strides for all substrate treatments before and after partial claw removal

Forelimb

Substrate Treatment	Claw Status	Hyper. Strides	Total Strides	Percentage
level (0˚) acrylic	Intact	12	15	80.0%
	Removed	7	14	50.0%
inclined (30˚) acrylic	Intact	9	10	90.0%
	Removed	3	13	23.1%
level (0˚) sandpaper	Intact	7	9	77.8%
	Removed	6	15	40.0%
inclined (30˚) sandpaper	Intact	7	13	53.8%
	Removed	3	14	21.4%
All Treatments		54	103	52.4%

Hindlimb

Substrate Treatment	Claw Status	Hyper. Strides	Total Strides	Percentage
level (0˚) acrylic	Intact	7	13	53.8%
	Removed	3	13	23.1%
inclined (30˚) acrylic	Intact	8	12	66.7%
	Removed	3	12	25.0%
level (0˚) sandpaper	Intact	4	11	36.4%
	Removed	1	15	6.7%
inclined (30˚) sandpaper	Intact	0	15	0.0%
	Removed	1	18	5.6%
All Treatments		27	109	24.8%

APPENDICES

Chapter 3

S3.1. Specimen institutional information and raw measurements; ZFMK (Zoological Research Museum Alexander Koenig), HLC (Higham Lab Collection), Pad type (B=Basal, F=Fan-toed, L=Leaf-toed, N=No pad), Claw condition (F=Full, R=Reduction, N=No claw), Variable abbreviations (SVL=snout-vent-length, MSL=maximum setal length, ASAR=average setal aspect ratio, SD=setal density, TPA=total pad area, PAR=pad aspect ratio, CL=claw length, ICC=inner claw curvature, * (data taken from literature), x (species not included in analyses)

Taxon	Specimen ID	Pad	Claw	SVL (mm)	MSL (µm)	ASAR	SD (mm^-1)	TPA (mm^2)	PAR	CL (mm)	ICC (deg)
Afrogecko porphyreus	ZFMK 21922	L	F	31.34	68.228	32.288		0.414	1.363	0.459	126.088
Agamura persica	ZFMK 94368	N	F	65.25						1.437	149.007
Ailuronyx seychellensis	ZFMK 94649	B	F	109.54	90.634	26.803	9.E+03	18.816	6.574	2.243	93.830
Alsophylax pipiens	ZFMK 31827	N	F	33.62						0.525	160.717
Anolis carolinensis	x HLC KF01	B	F	65.50	19.916	25.765	2.E+06	7.812	2.249	0.903	136.586
Anolis carolinensis	x HLC KF03	B	F	62.00	20.313	25.487	2.E+06	7.319	2.506	0.920	128.988
Aristelliger lar	ZFMK 52324	B	F	106.53	73.652	32.191	3.E+04	3.665	5.825	1.661	104.577
Aristelliger praesignis	ZFMK 21534	B	F	60.98	40.132	26.232	5.E+04	3.014	1.981	0.908	109.541
Asaccus caudivolvulus	ZFMK 64860	L	F	60.04	184.100	36.816	9.E+03	3.085	1.689	1.255	113.278
Asaccus elisae	ZFMK 75814	L	F	52.54	145.102	37.120	2.E+04	2.250	1.396	1.107	121.820
Aspidoscelis sexlineata	x HLC JL01	N	F	68.50						3.094	162.975
Aspidoscelis sexlineata	x HLC JL021	N	F	61.00						2.706	156.716
Blaesodactylus boivini	ZFMK 17661	B	R	127.20	119.014	24.439	9.E+03	17.629	4.957	2.873	125.746
Blaesodactylus sakalava	ZFMK 47229	B	R	96.92	116.716	25.431	9.E+03	14.293	4.737	2.029	114.217
Blaesodactylus sakalava	ZFMK 24644	B	R	99.70	130.871	32.063	9.E+03	10.945	4.203	2.067	107.668
Bunopus tuberculatus	ZFMK 87212	N	F	51.69						1.182	152.398
Calodactylodes aureus	ZFMK 998665	L	F	82.66	120.435	34.130	3.E+04	3.974	1.243	1.341	136.048
Chondrodactylus angulifer	x ZFMK 6200	N	N	102.03							
Chondrodactylus turneri	ZFMK 32888	B	N	82.23	103.588	30.195	4.E+04	6.297	2.897		
Christinus marmoratus	ZFMK 49475	L	F	42.23	107.553	52.269	6.E+04	0.835	0.869	0.674	120.932
Cnemaspis africana	ZFMK 77301	B	F	48.23	27.414	18.082	3.E+04	0.758	1.277	0.976	133.387
Cnemaspis indica	ZFMK 41798	N	F	29.82						0.509	142.418
Cnemaspis kendallii	ZFMK 84887	N	F	55.89						1.259	163.933
Cnemaspis nigridia	ZFMK 32351	N	F	79.30						1.705	127.201
Cnemaspis spinicollis	ZFMK 19933	B	F	45.45				0.373	0.986	0.896	143.575
Coleonyx variegatus	HLC EN01	N	F	58.50						1.335	154.551
Coleonyx variegatus	HLC EN02	N	F	60.75						1.242	151.100
Colopus wahlbergii	ZFMK 62637	B	N	51.27	20.497	14.728	1.E+05	0.625	1.350		
Crossobamon eversmanni	ZFMK 35253	N	F	52.50						1.621	146.148
Cyrtodactylus cattienensis	ZFMK 88096	N	F	36.31						0.784	148.913
Cyrtodactylus consobrinus	ZFMK 86724	N	F	121.29						3.013	134.377
Cyrtodactylus intermedius	ZFMK 90309	N	F	84.37						1.722	161.819

Taxon	Specimen ID	Pad	Claw	SVL (mm)	MSL (µm)	ASAR	SD (mm^-1)	TPA (mm^2)	PAR	CL (mm)	ICC (deg)
Cyrtodactylus peguensis	ZFMK 43836	N	F	67.13						1.594	164.716
Cyrtodactylus pulchellus	ZFMK 33294	N	F	107.83						2.702	149.706
Cyrtopodion gastropholis	ZFMK 91831	N	F	48.06						0.979	137.832
Cyrtopodion scabrum	ZFMK 94331	N	F	45.49						1.001	155.539
Dipsosaurus dorsalis	x HLC EN05	N	F	104.00						5.779	154.082
Dixonius siamensis	ZFMK 90313	L	F	52.60	58.134	40.244	1.E+05	0.303	0.440	1.019	108.127
Dixonius vietnamensis	ZFMK 87272	L	F	44.61				0.222	1.250	0.836	105.465
Eublepharis macularius	HLC TEH01	N	F	89.00						1.987	128.701
Euleptes europaea	ZFMK 2450	L	F	40.39				0.652	0.646		
Euleptes europaea	ZFMK 27566	L	F	34.91	66.885	32.196		0.580	0.952	0.554	124.001
Geckolepis maculata	ZFMK 51814	B	F	67.75	75.325	19.252	9.E+03	3.381	1.940	0.996	114.087
Geckolepis typica	ZFMK 14678	B	R	44.39	106.817	27.187	2.E+04	1.001	1.313	0.702	103.649
Gehyra georgpotthasti	ZFMK 84310	B	R	114.66	99.831	28.820	9.E+03	23.953	5.823	2.409	123.721
Gehyra mutilata	ZFMK 34503	B	R	54.39	83.510	31.673	4.E+04	3.533	2.358	0.642	143.695
Gehyra variegata	ZFMK 49413	B	R	50.47	95.880	36.771	6.E+04	3.331	2.059	0.689	130.961
Gekko badenii	ZFMK 92083	B	R	84.10	84.809	20.774	9.E+03	9.009	4.776	1.271	123.038
Gekko monarchus	ZFMK 20621	B	R	82.45	81.737	29.942	2.E+04	7.636	4.469	2.057	133.376
Gekko palmatus	ZFMK 86434	B	R	67.94	89.771	32.911	2.E+04	6.536	3.981	1.130	120.611
Gekko scientiadventura	ZFMK 83670	B	R	71.68	108.858	32.855	9.E+03	6.625	4.575	1.131	136.849
Gekko vittatus	ZFMK 51820	B	R	121.02	98.003	35.408	3.E+04	32.084	8.411	1.521	111.701
Goggia lineata	ZFMK 21917	L	F	25.01	66.383	32.054	4.E+04	0.208	0.387		
Goggia lineata	ZFMK 21918	L	F	24.68	54.923	24.054		0.161	1.811	0.376	121.417
Gonatodes albogularis	ZFMK 84754	N	F	36.52						0.796	149.414
Gonatodes humeralis	ZFMK 74361	N	F	33.57						0.655	144.071
Gonatodes vittatus	ZFMK 41362	N	F	30.35						0.691	150.842
Hemidactylus ansorgii	ZFMK 77075	B	F	47.61	70.892	48.020	8.E+04	2.546	3.331		
Hemidactylus fasciatus	ZFMK 69603	B	F	73.68	59.571	21.844	4.E+04	3.966	3.040	1.441	113.722
Hemidactylus frenatus	ZFMK 90319	B	F	49.14	89.648	32.754	4.E+04	3.309	2.907	0.787	117.224
Hemidactylus mabouia	ZFMK 94696	B	F	56.67	116.181	45.285	4.E+04	3.909	2.982	0.805	136.239
Hemidactylus maculatus	ZFMK 46941	B	F	115.82	133.641	57.212	4.E+04	20.982	6.674	2.702	129.431
Hemidactylus persicus	ZFMK 53517	B	F	79.60				9.569	4.958	1.264	128.613
Hemidactylus robustus	ZFMK 92723	B	F	45.95	106.028	42.468	4.E+04	2.310	2.435	0.887	123.460

Taxon	Specimen ID	Pad	Claw	SVL (mm)	MSL (μm)	ASAR	SD (mm^-1)	TPA (mm^2)	PAR	CL (mm)	ICC (deg)
Hemidactylus turcicus	ZFMK 2427	B	F	53.37	105.508	39.181	4.E+04	3.888	4.147	0.959	127.511
Hemidactylus yerburii	ZFMK 43385	B	R	73.50	156.525	65.172	4.E+04	8.935	5.213	1.184	121.327
Hemiphyllodactylus typus	ZFMK 25350	B	R	40.27	54.520	20.697	4.E+04	1.293	1.252	0.393	119.571
Heteronotia binoei	ZFMK 49406	N	F	44.13						0.755	151.154
Homonota horrida	ZFMK 37271	N	F	54.21						1.101	129.897
Homopholis walbergii	ZFMK 86717	B	R	108.41	123.776	30.630	2.E+04	16.367	5.565	1.929	108.566
Lepidoblepharis conolepis	ZFMK 46381	N	F	32.24						0.651	127.106
Lepidodactylus euaensis	ZFMK 42046	B	R	43.23	55.904	27.452	3.E+04	2.491	2.187	0.841	118.820
Lepidodactylus lugubris	ZFMK 42052	B	R	37.42				1.497	1.436	0.555	111.132
Lygodactylus chobiensis	ZFMK 88610	B	R	36.52				1.847	2.414	0.538	157.714
Lygodactylus guibei	ZFMK 61534	B	R	33.33	94.455	38.522	8.E+04	1.946	2.728	0.711	116.194
Lygodactylus madagascariensis	ZFMK 47244	B	R	34.18				0.998	0.951	0.551	136.552
Lygodactylus ocellatus	ZFMK 74916	B	R	32.74	60.298	52.534	1.E+05	0.883	0.943	0.391	131.064
Lygodactylus picturatus	ZFMK 82084	B	R	36.27	89.800	45.151	8.E+04	1.530	1.428	0.405	125.985
Mediodactylus heterocercus	ZFMK 75864	N	F	48.04						0.933	157.501
Mediodactylus kotschyi	ZFMK 98534	N	F	42.62						1.004	142.589
Meroles cuneirostris	x HLC NAM10	N	F	48.00						2.870	159.690
Nactus pelagicus	ZFMK 80502	N	F	49.13						0.901	144.055
Pachydactylus rangei	x*	N	N	70.00							
Pachydactylus rugosus	ZFMK 72903	B	N	57.87	83.562	36.248	6.E+04	2.335	1.601		
Pachydactylus vansoni	ZFMK 31470	B	N	45.59	68.770	25.976	6.E+04	1.345	1.214		
Paroedura androyensis	ZFMK 83414	L	F	40.48	63.398	21.582	4.E+04	0.450	0.545	0.595	141.547
Paroedura stumpffi	ZFMK 50619	L	F	61.44	65.566	21.978	4.E+04	0.819	0.722	0.947	121.021
Phelsuma barbouri	ZFMK 51483	B	N	47.50	67.882	35.239	3.E+04	4.368	3.130		
Phelsuma cepediana	ZFMK 48499	B	N	56.25	69.805	36.685	3.E+04	6.078	3.276		
Phelsuma modesta	ZFMK 54977	B	N	45.02	74.853	32.354	3.E+04	2.965	2.535		
Phelsuma quadriocellata	ZFMK 82144	B	N	36.03	52.520	22.540	4.E+04	1.494	1.648		
Phelsuma standingi	ZFMK 21809	B	N	106.80	102.660	33.373	4.E+04	26.367	7.397		
Phelsuma sundbergi	ZFMK 73555	B	N	87.40	89.822	29.698	5.E+04	13.773	5.598		
Phyllodactylus interandinus	ZFMK 88749	L	F	45.89	76.989	24.608	4.E+04	0.679	0.787	0.695	131.740
Phyllodactylus magister	ZFMK 90883	L	F	53.00	128.855	33.968	4.E+04	1.638	1.147	1.039	113.171

Taxon	Specimen ID	Pad	Claw	SVL (mm)	MSL (µm)	ASAR	SD (mm^-1)	TPA (mm^2)	PAR	CL (mm)	ICC (deg)
Phyllodactylus reissii	ZFMK 98709	L	F	57.68	132.735	37.162	4.E+04	1.624	1.097	1.169	129.149
Phyllodactylus thompsoni	ZFMK 90917	L	F	41.71				0.601	0.727	0.720	111.737
Phyllopezus maranjonensis	ZFMK 90870	B	F	102.41	169.003	31.013	2.E+04	19.560	6.598	1.422	134.333
Phyllopezus pollicaris	ZFMK 101238	B	F	70.47	152.358	31.963	9.E+03	5.759	3.103	1.018	141.919
Pristurus sokotranus	ZFMK 82460	N	F	38.35						0.722	146.845
Pseudogekko smaragdinus	ZFMK 76368	B	R	55.66	51.444	26.823	4.E+04	5.190	4.135	0.627	123.683
Ptenopus garrulus	ZFMK 32723	N	F	50.60						1.414	167.167
Ptychozoon lionotum	ZFMK 45377	B	R	78.14	119.251	33.787	9.E+03	8.682	3.618		
Ptyodactylus guttatus	ZFMK 46340	F	F	57.33	120.172	25.606	2.E+04	2.800	1.705	1.052	114.130
Ptyodactylus oudrii	ZFMK 49678	F	F	60.41				7.744	1.836	0.931	117.608
Quedenfeldtia trachyblepharus	ZFMK 50750	N	F	45.00						0.730	142.634
Rhoptropus afer	HLC CEC06	B	N	37.50	59.775			1.159			
Rhoptropus afer	HLC CEC07	B	N	31.50	64.590			1.315			
Rhoptropus afer	HLC CEC08	B	N	40.00	62.236			1.103			
Rhoptropus afer	HLC CEC09	B	N	46.00	61.321			1.553			
Rhoptropus afer	HLC CEC10	B	N	52.00	64.024			2.228			
Rhoptropus biporosus	*	B	N	42.55	99.190		2.E+04	0.890			
Saurodactylus brosseti	ZFMK 73007	N	F	30.28						0.430	148.109
Sphaerodactylus parkeri	ZFMK 50825	L	F	36.83	77.290	28.335				0.516	123.594
Stenodactylus arabicus	ZFMK 92751	N	F	35.89						1.210	156.730
Stenodactylus petrii	ZFMK 79630	N	F	62.10						1.504	149.784
Tarentola ephippiata	ZFMK 79526	B	R	82.64	143.456	47.711	2.E+04	9.011	3.342	1.735	113.902
Tarentola parvicarinata	ZFMK 57188	B	R	94.84	159.127	27.607	4.E+04	15.392	5.813	1.747	131.622
Tenuidactylus caspius	ZFMK 95153	N	F	59.14						1.360	152.602
Tenuidactylus turcmenicus	ZFMK 94237	N	F	60.91						1.421	131.633
Teratoscincus keyserlingii	ZFMK 26328	N	F	73.22						1.281	141.715
Teratoscincus microlepis	ZFMK 50437	N	F	103.16						1.660	154.957
Teratoscincus scincus	ZFMK 25546	N	F	79.51						1.721	145.383
Thecadactylus rapicauda	ZFMK 85463	B	F	89.88	109.554	18.320	2.E+04	11.199	3.591	1.060	109.981
Tropiocolotes steudneri	ZFMK 33851	N	F	31.67						0.657	166.010
Uroplatus henkeli	ZFMK 61858	F	F	148.22	82.329	27.248	3.E+04	15.931		2.584	89.561
Uroplatus lineatus	ZFMK 73592	F	F	152.15				15.875		1.789	120.765

Taxon	Specimen ID	Pad	Claw	SVL (mm)	MSL (µm)	ASAR	SD (mm^-1)	TPA (mm^2)	PAR	CL (mm)	ICC (deg)
Uroplatus phantasticus	ZFMK 60516	F	F	57.45	52.381	27.759	5.E+04	2.229		0.969	110.258

S3.2. Species habitat data and citations, along with citations for phylogenetic placement (see **S3.6** for full citations); * (citation from the International Union for Conservation of Nature (IUCN) Red List), x (species not included in analyses)

Taxon	Species Author(s)	Habitat Use	Habitat Use Citations	Phylogenetic Placement Citations
Afrogecko porphyreus	Daudin 1802	M	Branch 1998; Jacobsen and Randall 2013	
Agamura persica	Duméril 1856	G	Anderson 1999; Mohammadi & Naderi 2012	
Ailuronyx seychellensis	Duméril & Bibron 1836	A	Roberts 2009; Rocha et al. 2016	
Alsophylax pipiens	Pallas 1827	T	Ananjeva & Orlov 1995; Anajeva et al. 2019*	
Anolis carolinensis x	Voight, 1832	A	Schoener 1968; Irschick et al. 2005b	
Aristelliger lar	Cope 1861	M	Schwartz 1980; Schwartz and Henderson 1991; Landestoy et al. 2016*	
Aristelliger praesignis	Hallowell 1856	M	Schwartz & Henderson 1991	
Asaccus caudivolvulus	Arnold & Gardner 1994	S	Arnold & Gardner 1994	Papenfuss et al. 2010
Asaccus elisae	Werner 1895	S	Parsa et al. 2009	Papenfuss et al. 2010
Aspidoscelis sexlineata x	Linneaus 1766	T	Stebbins 2003	
Blaesodactylus boivini	Duméril 1856	A	Metcalf et al. 2007; Glaw & Vences 2007	
Blaesodactylus sakalava	Grandidier 1867	A	Glaw & Vences 2007	
Bunopus tuberculatus	Blanford 1874	T	Arnold 1980; Fathnia et al. 2009	
Calodactylodes aureus	Beddome 1870	S	Daniel et al. 1986	
Chondrodactylus angulifer x	Peters 1870	T	Branch 1998; Bauer & Branch 2001	
Chondrodactylus turneri	Gray 1864	G	Bauer & Branch 2001; Eifler et al. 2017; Hedman et al. 2014	
Christinus marmoratus	Gray 1845	G	Kearney & Prevadec 2000; Wilson & Swan 2013; Taylor et al. 2015	
Cnemaspis africana	Werner 1896	G	Spawls et al. 2002; Spawls et al. 2018	
Cnemaspis indica	Gray 1846	S	Bauer et al. 2007; Srinivasulu & Srinivasulu 2013*	Russell & Gamble 2019
Cnemaspis kendallii	Gray 1845	M	Werner & Chou 2002; Grismer et al. 2014	
Cnemaspis nigridia	Smith 1925	S	Grismer et al. 2014; Das 2015	Grismer et al. 2014
Cnemaspis spinicollis	Müller 1907	G	Joger 1981; Sura 1987; Gonwouo et al. 2007	Gamble et al. 2012
Coleonyx variegatus	Baird 1858	T	Parker 1972; Stebbins 2003	

Taxon	Species Author(s)	Habitat Use	Habitat Use Citations	Phylogenetic Placement Citations
Colopus wahlbergii	Peters 1869	T	Fitzsimmons & Brain 1958; Schmidt 2002	
Crossobamon eversmanni	Wiegmann 1834	T	Clark 1990; Anderson 1999	Bauer et al. 2013
Cyrtodactylus cattienensis	Geissler, Nazarov, Orlov, Böhme, Phung, Nguyen, & Ziegler 2009	A	Geissler et al. 2009	Brennan et al. 2017
Cyrtodactylus consobrinus	Peters 1871	S	Onn et al. 2010	Brennan et al. 2017
Cyrtodactylus intermedius	Smith 1917	S	Geissler et al. 2019	
Cyrtodactylus peguensis	Boulenger 1893	S	Grismer et al. 2018a, b	
Cyrtodactylus pulchellus	Gray 1827	M	Grismer et al. 2012	
Cyrtopodion gastropholis	Werner 1917	S	Anderson 1999; Anderson 2009*	Červenka et al. 2010
Cyrtopodion scabrum	Heyden 1827	S	Anderson 1999; Fathnia et al. 2009	
Dipsosaurus dorsalis x	Baird & Girard 1852	G	Stebbins 2003	
Dixonius siamensis	Boulenger 1899	T	Geissler et al. 2019	
Dixonius vietnamensis	Das 2004	G	Das 2004; Stuart et al. 2006; Geissler et al. 2011	
Eublepharis macularius	Blyth 1854	T	Khan 1999; Khan 2006	
Euleptes europaea	Gené 1839	S	Renet et al. 2013; Delaugerre et al. 2014; Russell & Delaugerre 2017	
Geckolepis maculata	Peters 1880	A	Lehtinen 2002; Glaw & Vences 2007	
Geckolepis typica	Grandidier 1867	A	Glaw & Vences 2007	
Gehyra georgpotthasti	Flecks, Schmitz, Böhme, Henkel & Ineich 2012	A	Flecks et al. 2012	Flecks et al. 2012; Oliver et al. 2016
Gehyra mutilata	Wiegmann 1834	G	Grismer et al. 2001; Rocha et al. 2009; Lagat 2011	
Gehyra variegata	Duméril & Bibron 1836	M	Bustard 1969; Hutchinson et al. 2014	
Gekko badenii	Szczerbak & Nekrasova 1994	S	Nguyen et al. 2018*	
Gekko monarchus	Schlegel 1836	M	Grismer et al. 2004	
Gekko palmatus	Boulenger 1907	M	Nguyen et al. 2018; Nguyen 2018*	Luu et al. 2015; Russell & Gamble 2019

Taxon	Species Author(s)	Habitat Use	Habitat Use Citations	Phylogenetic Placement Citations
Gekko scientiadventura	Rösler, Ziegler, Vu, Herrmann & Böhme 2004	M	Rösler et al. 2005	Luu et al. 2015
Gekko vittatus	Houttuyn 1782	A	Ineich et al. 2012	
Goggia lineata	Gray 1838	T	Bauer & Branch 2001	
Gonatodes albogularis	Duméril & Bibron 1836	G	Dominguez-Lopez et al. 2016; Carvajal-Ocampo et al. 2019	
Gonatodes humeralis	Guichenot 1855	A	Prudente et al. 2013; Higham et al. 2016	
Gonatodes vittatus	Lichtenstein & Martens 1856	G	Higham et al. 2016	
Hemidactylus ansorgii	Boulenger 1901	A	Henle & Bohme 2003; Ullenbruch et al. 2010	Carranza & Arnold 2006
Hemidactylus fasciatus	Gray 1842	M	Bauer & Pauwels 2002; Leache et al. 2006	
Hemidactylus frenatus	Schlegel in Duméril & Bibron 1836	M	Bauer & Sadlier 2000; Grismer et al. 2004; Agarwal et al. 2011	
Hemidactylus mabouia	Moreau De Jonnés 1818	A	Conradie et al. 2011; Breuil et al. 2013	
Hemidactylus maculatus	Duméril & Bibron 1836	M	Ingle 2011	
Hemidactylus persicus	Anderson 1872	S	Fathnia et al. 2009	
Hemidactylus robustus	Heyden 1827	M	Baha El Din 2005; Carranza & Arnold 2012	
Hemidactylus turcicus	Linnaeus 1758	S	Arnold 1980; Trout & Schwaner 1994	
Hemidactylus yerburii	Anderson 1895	S	Arnold 1980	
Hemiphyllodactylus typus	Bleeker 1960	G	Bauer & Sadlier 2000; Karunarathna 2015	
Heteronotia binoei	Gray 1845	G	Cogger 2000	
Homonota horrida	Burmeister 1861	T	Talbot 1978; Cacciali et al. 2017	Cacciali et al. 2017
Homopholis walbergii	Smith 1849	M	Branch 1998; Greenbaum et al. 2007	
Lepidoblepharis conolepis	Avila-Pires 2001	T	Avila-Pires 2001; Alvear & Reyes-Puig 2016	
Lepidodactylus euaensis	Gibbons & Brown 1988	A	Gibbons & Brown 1988	Stubbs et al. 2017
Lepidodactylus lugubris	Duméril & Bibron 1836	M	Bauer & Sadlier 2000; Karunarathna 2015	
Lygodactylus chobiensis	Fitzsimons 1932	A	Branch et al. 2005	
Lygodactylus guibei	Pasteur 1965	A	Puente et al. 2009	

Taxon	Species Author(s)	Habitat Use	Habitat Use Citations	Phylogenetic Placement Citations
Lygodactylus madagascariensis	Boettger 1881	A	Glaw & Vences 2007; Blumgart et al. 2017	
Lygodactylus ocellatus	Roux 1907	S	Jacobsen 1989; Branch 1998	Puente et al. 2005; Travers et al. 2014
Lygodactylus picturatus	Peters 1870	A	Spawls et al. 2002; Malonza et al. 2005	
Mediodactylus heterocercus	Blanford 1874	G	Anderson 1999; Fathnia et al. 2009	
Mediodactylus kotschyi	Steindachner 1870	M	Petrov 2007; Böhme et al. 2009*; Ajtić 2014; Urošević 2016	
Meroles cuneirostris x	Strauch 1867	T	Murray & Gareth 1987; Bauer & Branch 2001; Hedman et al. 2014;	
Nactus pelagicus	Girard 1858	G	Bauer & Sadlier 2000	
Pachydactylus rangei x	Andersson 1908	T	Branch 1998; Hedman et al. 2014	
Pachydactylus rugosus	Smith 1849	T	Fitzsimons & Brain 1958; Bauer & Branch 2002	
Pachydactylus vansoni	Fitzsimons 1933	T	Fitzsimons 1933; Rosler 1993; Heinicke et al. 2017	
Paroedura androyensis	Grandidier 1867	T	D'Cruze et al. 2009	
Paroedura stumpffi	Boettger 1879	T	Glaw & Vences 1994	
Phelsuma barbouri	Loveridge 1942	S	Vences et al. 2002; Glaw & Vences 2007	
Phelsuma cepediana	Milbert 1812	A	Raxworthy & Nussbaum 1993; Harmon et al. 2007	
Phelsuma modesta	Mertens 1970	A	Nussbaum et al. 2000; Ramanamanjato et al. 2002; Glaw & Vences 2007	
Phelsuma quadriocellata	Peters 1883	A	Lethinen et al. 2003; Glaw & Vences 2007	
Phelsuma standingi	Methuen & Hewitt 1913	A	Glaw & Vences 2007	
Phelsuma sundbergi	Rendahl 1939	A	Glaw & Vences 2007; Noble et al. 2011	
Phyllodactylus interandinus	Dixon & Huey 1970	G	Koch et al. 2018	Koch et al. 2016
Phyllodactylus magister	Noble 1924	S	Koch et al. 2016	Koch et al. 2016
Phyllodactylus reissii	Peters 1862	M	Carillo de Espinoza et al. 1990; Aurich et al. 2011	
Phyllodactylus thompsoni	Venegas, Townsend, Koch & Böhme 2008	G	Venegas et al. 2008; Aurich et al. 2011	Koch et al. 2016

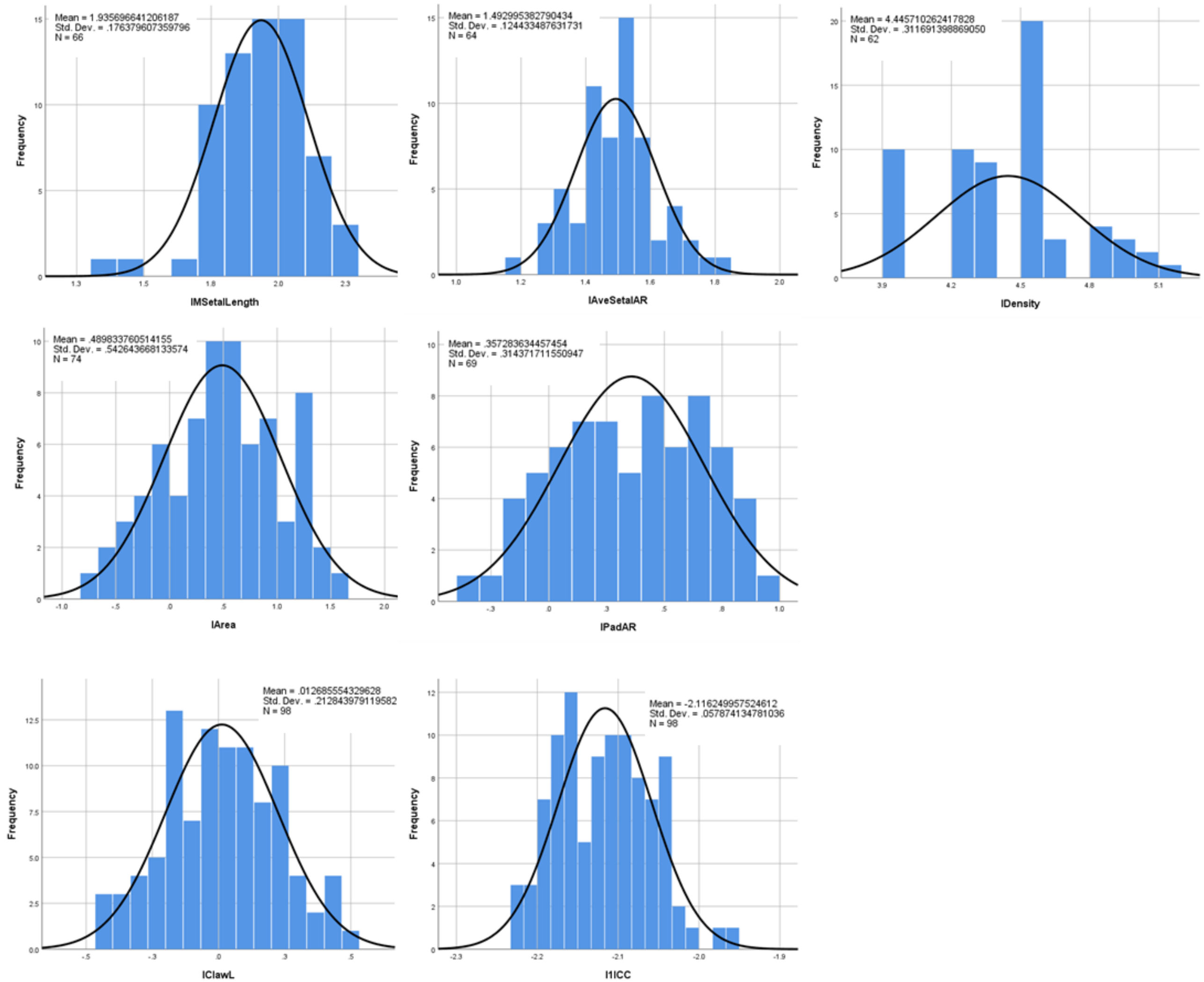
Taxon	Species Author(s)	Habitat Use	Habitat Use Citations	Phylogenetic Placement Citations
Phyllopezus maranjonensis	Koch, Venegas & Böhme 2006	S	Koch et al. 2006; Aurich et al. 2011	
Phyllopezus pollicaris	Spix 1825	S	Recoder et al. 2012; Righi et al. 2012	
Pristurus sokotranus	Parker 1938	M	Razzetti et al. 2011; Sancho et al. 2017	
Pseudogekko smaragdinus	Taylor 1922	A	Siler et al. 2014	
Ptenopus garrulus	Gray 1866	T	Bauer & Branch 2001; Schmidt 2002	
Ptychozoon lionotum	Annandale 1905	A	Pawar & Biswas 2001	
Ptyodactylus guttatus	Heyden 1827	S	Perry & Brandeis 1992; Johnston & Bouskila 2007	
Ptyodactylus oudrii	Lataste 1880	S	Mateo & Cuadrado 2012	
Quedenfeldtia trachyblepharus	Boetteger 1874	S	Schleich et al. 1995; Carretaro et al. 2005	
Rhoptropus afer	Peters 1869	T	Haacke & Odendaal 1981; Hedman et al. 2014	
Rhoptropus biporosus	Fitzsimons 1957	S	Branch 1998; Russell & Johnson 2007	
Saurodactylus brosseti	Bons & Pasteur 1957	T	Meek 2008	Harris & Rato 2008
Sphaerodactylus parkeri	Grant 1939	T	Henderson & Powell 2009	
Stenodactylus arabicus	Haas 1957	T	Arnold 1980; Fathnia & Gholamifrad 2014; Nazarov et al. 2018	
Stenodactylus petrii	Anderson 1896	T	Baha El Din 2001; Attum et al. 2006	
Tarentola ephippiata	O'shaughnessy 1875	M	Joger 1981; Spawls 2008	
Tarentola parvicarinata	Joger 1980	S	Joger 1981; Trape et al. 2012	Brójo de Melo 2016
Tenuidactylus caspius	Eichwald 1831	G	Anderson 1999; Yousefkhani 2019	
Tenuidactylus turcmenicus	Szczerbak 1978	S	Szczerbak & Golubev 1996; Anderson 1999	Bauer et al. 2013
Teratoscincus keyserlingii	Strauch 1863	T	Anderson 1999; Gholamifard et al. 2015	
Teratoscincus microlepis	Nikolsky 1900	T	Anderson 1999; Sanchooli 2018	
Teratoscincus scincus	Schlegel 1858	T	Anderson 1999; Seligmann et al. 2007	
Thecadactylus rapicauda	Houttuyn 1782	A	Vitt & Zani 1997; Russell & Bauer 2002	

Taxon	Species Author(s)	Habitat Use	Habitat Use Citations	Phylogenetic Placement Citations
Tropiocolotes steudneri	Peters 1869	T	Frakenberg 1975; Baha El Din 2001	Macey et al. 2005
Uroplatus henkeli	Böhme & Ibisch 1990	A	Andreone et al. 2003; Glaw & Vences 2007; Ratsoavina et al. 2013	
Uroplatus lineatus	Duméril & Bibron 1836	A	Glaw & Vences 2007; Ratsoavina et al. 2013	
Uroplatus phantasticus	Boulenger 1888	A	Glaw & Vences 2007; Ratsoavina et al. 2013; 2015	

S3.3. Morphometric trait definitions

Variable	Definition	Unit
Maximum Setal Length	length of longest seta within the distalmost 25% of the total pad length	µm
Average Setal Aspect Ratio	average length/width ratio of multiple setae within the distalmost 25% of the total pad length; maximum width taken 5-15µm from the setal base	
Setal Density	(maximum number of setae along a 32µm length within the distalmost 25% of the total pad length)^2 * 1000	mm^-1
Total Pad Area	total area of of the scansors	mm^2
Pad Aspect Ratio	maximum proximodistal pad length/maximum pad width perpendicular to the length segment; mean aspect ratio taken for species with multiple symmetric pad lobes	
Claw Length	hypotenuse c + hypotenuse d of the right triangles created by drawing a straight line (f) from the base of the claw to the tip and a straight line (g) from the midpoint of f to the ventral surface of the claw (hypotenuse=$\sqrt{(f^2 + g^2)}$; see Fig. 3.2)	mm
Inner Claw Curvature	angle of the apex of the triangle drawn with opposite edge f and symmetric adjacent edges c and d; arccos (c^2+d^2-f^2/2c^2 d^2) (see Fig. 3.2)	deg

S3.4. Morphometric variable histograms (log-transformed); max. setal length (MSetalLength), average setal aspect ratio (AveSetalAR), setal density (Density), total pad area (Area), pad aspect ratio (PadAR), claw length (ClawL), and inner claw curvature (1/ICC)



S3.5. R output (packages {ape}, {nlme}, {emmeans}) for phylogenetic ANCOVAs via PGLS with λ transformation; starting value for alpha was estimated in {caper}

a)

Model: *Max. Setal Length ~ Habitat + SVL*

```
BM <- gls(lSetalL ~ Hab5 + lSVL, data=data, correlation=corPagel(0.755, ptree, fixed=FALSE), method="ML")

Analysis of Deviance Table (Type III tests)
            Df  Chisq Pr(>Chisq)
(Intercept)  1 57.206  3.926e-14 ***
Hab5         4 10.185    0.03742 *
lSVL         1 17.887  2.344e-05 ***

Coefficients:
              Estimate Std. Error t value  Pr(>|t|)
(Intercept)  1.267295   0.167556  7.5634 3.311e-10 ***
Hab5bS       0.088443   0.038895  2.2739   0.02669 *
Hab5cM       0.021890   0.039754  0.5506   0.58400
Hab5dG      -0.014603   0.057048 -0.2560   0.79887
Hab5eT      -0.059399   0.055270 -1.0747   0.28696
lSVL         0.368745   0.087189  4.2293 8.429e-05 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate 95% confidence intervals
 Coefficients:
                  lower        est.      upper
(Intercept)  0.93189663  1.26729545 1.60269427
Hab5bS       0.01058649  0.08844324 0.16629999
Hab5cM      -0.05768642  0.02189025 0.10146693
Hab5dG      -0.12879686 -0.01460320 0.09959047
Hab5eT      -0.17003440 -0.05939884 0.05123671
lSVL         0.19421815  0.36874544 0.54327273

 Correlation:
       (Intr) Hab5bS Hab5cM Hab5dG Hab5eT
Hab5bS -0.291
Hab5cM -0.241  0.481
Hab5dG -0.276  0.371  0.353
Hab5eT -0.415  0.390  0.338  0.352
lSVL   -0.965  0.182  0.140  0.206  0.336

Standardized residuals:
       Min         Q1        Med         Q3        Max
-2.9181801 -0.5625672  0.2123767  0.8886592  2.1508167

Residual standard error: 0.117873

#estimated marginal means (least squares) and post-hoc
BMemm<- nlme::gls(lSetalL ~ Hab5 + lSVL, data=data, correlation=corPagel(0.755, ptree, fixed=TRUE), method="ML")
emmls = emmeans(BMemm, pairwise ~ lSetalL ~ Hab5 + lSVL, mode=c("auto"))
summary(emmls)
$emmeans
 Hab5 lSVL emmean     SE df lower.CL upper.CL
 aA   1.79   1.93 0.0442 58     1.84     2.01
 bS   1.79   2.01 0.0432 58     1.93     2.10
 cM   1.79   1.95 0.0454 58     1.86     2.04
 dG   1.79   1.91 0.0599 58     1.79     2.03
 eT   1.79   1.87 0.0555 58     1.76     1.98

Degrees-of-freedom method: df.error
Confidence level used: 0.95

$contrasts
 contrast                                      estimate     SE df t.ratio p.value
 aA 1.78552053140625 - bS 1.78552053140625   -0.0885 0.0389 58 -2.274  0.1681
 aA 1.78552053140625 - cM 1.78552053140625   -0.0219 0.0398 58 -0.551  0.9814
 aA 1.78552053140625 - dG 1.78552053140625    0.0146 0.0570 58  0.256  0.9990
 aA 1.78552053140625 - eT 1.78552053140625    0.0594 0.0553 58  1.075  0.8187
 bS 1.78552053140625 - cM 1.78552053140625    0.0666 0.0401 58  1.661  0.4658
 bS 1.78552053140625 - dG 1.78552053140625    0.1030 0.0559 58  1.844  0.3590
 bS 1.78552053140625 - eT 1.78552053140625    0.1478 0.0538 58  2.749  0.0588
 cM 1.78552053140625 - dG 1.78552053140625    0.0365 0.0569 58  0.641  0.9676
 cM 1.78552053140625 - eT 1.78552053140625    0.0813 0.0561 58  1.448  0.5995
 dG 1.78552053140625 - eT 1.78552053140625    0.0448 0.0639 58  0.701  0.9555

Degrees-of-freedom method: df.error
P value adjustment: tukey method for comparing a family of 5 estimates
```

Habitat (Hab5) categories: aA=arboreal (base group), bS=saxicolous, cM=mixed scansorial, dG=generalist, eT=terrestrial
lSVL: log-transformed snout-vent-length; response variable also log-transformed

b)

Model 1: *Ave. Setal Aspect Ratio ~ Habitat + SVL*

```
BM <- gls(lSetalAR ~ Hab5 + lSVL, data=data, correlation=corPagel(0.282, ptree, fixed=FALSE), method="
ML")

Analysis of Deviance Table (Type III tests)
            Df   Chisq Pr(>Chisq)
(Intercept)  1 86.3393     <2e-16 ***
Hab5         4  6.2661     0.1801
lSVL         1  0.6629     0.4155


Coefficients:
                 Value  Std.Error   t-value p-value
(Intercept)  1.6104325 0.17331581  9.291896  0.0000
Hab5bS       0.0514025 0.04154707  1.237210  0.2211
Hab5cM       0.0518727 0.04108786  1.262482  0.2119
Hab5dG      -0.0030140 0.05966210 -0.050518  0.9599
Hab5eT      -0.0704123 0.05424778 -1.297975  0.1995
lSVL        -0.0750231 0.09214429 -0.814191  0.4189
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1


Approximate 95% confidence intervals
Coefficients:
                  lower         est.      upper
(Intercept)  1.26337355  1.610432461 1.95749138
Hab5bS      -0.03179411  0.051402460 0.13459903
Hab5cM      -0.03040435  0.051872661 0.13414968
Hab5dG      -0.12248533 -0.003014033 0.11645727
Hab5eT      -0.17904156 -0.070412252 0.03821706
lSVL        -0.25953884 -0.075023091 0.10949266


Correlation:
       (Intr) Hab5bS Hab5cM Hab5dG Hab5eT
Hab5bS -0.226
Hab5cM -0.159  0.426
Hab5dG -0.270  0.306  0.301
Hab5eT -0.411  0.325  0.313  0.311
lSVL   -0.980  0.125  0.060  0.206  0.338


Standardized residuals:
        Min          Q1         Med          Q3         Max
-2.14560088 -0.44088184 -0.01232395  0.53358855  2.57403957

Residual standard error: 0.1135328
Degrees of freedom: 63 total; 57 residual

#estimated marginal means (least squares) and post-hoc
BMemm<- nlme::gls(lSetalAR ~ Hab5 + lSVL, data=data, correlation=corPagel(0.282, ptree, fixed=TRUE), m
ethod="ML")
emmls = emmeans(BMemm, pairwise ~ lSetalAR ~ Hab5 + lSVL, mode=c("auto"))
summary(emmls)

$emmeans
Hab5 lSVL emmean     SE df lower.CL upper.CL
 aA   1.79   1.48 0.0347 57     1.41     1.55
 bS   1.79   1.53 0.0371 57     1.45     1.60
 cM   1.79   1.53 0.0378 57     1.45     1.60
 dG   1.79   1.47 0.0567 57     1.36     1.59
 eT   1.79   1.41 0.0498 57     1.31     1.51

Degrees-of-freedom method: df.error
Confidence level used: 0.95
```

Habitat (Hab5) categories: aA=arboreal (base group), bS=saxicolous, cM=mixed scansorial, dG=generalist, eT=terrestrial
lSVL: log-transformed snout-vent-length; response variable also log-transformed

Model 2: *Ave. Setal Aspect Ratio ~ Habitat*

```
BM <- gls(lSetalAR ~ Hab5, data=data, correlation=corPagel(0.440, ptree, fixed=FALSE), method="ML")

Analysis of Deviance Table (Type III tests)
            Df     Chisq Pr(>Chisq)
(Intercept)  1 1487.5132     <2e-16 ***
Hab5         4    5.0492     0.2823

Coefficients:
                 Value  Std.Error  t-value p-value
(Intercept)  1.4708017 0.03813500 38.56829  0.0000
Hab5bS       0.0524958 0.04125884  1.27235  0.2083
Hab5cM       0.0529263 0.04105459  1.28917  0.2025
Hab5dG       0.0069310 0.05828511  0.11892  0.9058
Hab5eT      -0.0528920 0.05247815 -1.00789  0.3177


Approximate 95% confidence intervals
 Coefficients:
                  lower         est.      upper
(Intercept)  1.39446618  1.470801671 1.54713716
Hab5bS      -0.03009278  0.052495763 0.13508430
Hab5cM      -0.02925342  0.052926260 0.13510594
Hab5dG      -0.10973934  0.006930982 0.12360130
Hab5eT      -0.15793840 -0.052891973 0.05215445


 Correlation:
       (Intr) Hab5bS Hab5cM Hab5dG
Hab5bS -0.497
Hab5cM -0.472  0.435
Hab5dG -0.334  0.298  0.308
Hab5eT -0.398  0.295  0.307  0.280


Standardized residuals:
        Min          Q1         Med          Q3         Max
-2.14562282 -0.36470623 -0.05488214  0.47480532  2.49780165

Residual standard error: 0.1164066
Degrees of freedom: 63 total; 58 residual

#estimated marginal means (least squares) and post-hoc
BMemm<- nlme::gls(lSetalAR ~ Hab5, data=data, correlation=corPagel(0.440, ptree, fixed=TRUE), method="
ML")
emmls = emmeans(BMemm, pairwise ~ lSetalAR ~ Hab5, mode=c("auto"))
summary(emmls)

$emmeans
Hab5 emmean     SE df lower.CL upper.CL
 aA     1.47 0.0381 56     1.39     1.55
 bS     1.52 0.0399 56     1.44     1.60
 cM     1.52 0.0408 56     1.44     1.61
 dG     1.48 0.0580 56     1.36     1.59
 eT     1.42 0.0511 56     1.32     1.52

Degrees-of-freedom method: df.error
Confidence level used: 0.95
```

Habitat (Hab5) categories: aA=arboreal (base group), bS=saxicolous, cM=mixed scansorial, dG=generalist, eT=terrestrial
lSVL: log-transformed snout-vent-length; response variable also log-transformed

c)

Model: *Setal Density ~ Habitat + SVL*

```
BM <- gls(lDensity ~ Hab5+ lSVL, data=data, correlation=corPagel(0.761, ptree, fixed=FALSE), method="M
L")

Analysis of Deviance Table (Type III tests)
            Df    Chisq Pr(>Chisq)
(Intercept)  1 187.0418  < 2.2e-16 ***
Hab5         4   8.6624   0.070114 .
lSVL         1   7.1107   0.007663 **

Coefficients:
             Estimate Std. Error t value Pr(>|t|)
(Intercept)  5.359438   0.391877 13.6763  < 2e-16 ***
Hab5bS      -0.025660   0.087384 -0.2937  0.77013
Hab5cM       0.063376   0.090206  0.7026  0.48529
```

```
Hab5dG       0.151270   0.127862  1.1831  0.24187
Hab5eT       0.346357   0.133754  2.5895  0.01228 *
lSVL        -0.538206   0.201833 -2.6666  0.01004 *
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate 95% confidence intervals
                  lower        est.      upper
(Intercept)  4.57409829  5.35943742  6.1447766
Hab5bS      -0.20078179 -0.02566041  0.1494610
Hab5cM      -0.11740097  0.06337594  0.2441528
Hab5dG      -0.10497169  0.15126996  0.4075116
Hab5eT       0.07830841  0.34635685  0.6144053
lSVL        -0.94268872 -0.53820596 -0.1337232

Correlation:
       (Intr) Hab5bS Hab5cM Hab5dG Hab5eT
Hab5bS -0.252
Hab5cM -0.200  0.457
Hab5dG -0.295  0.360  0.319
Hab5eT -0.376  0.314  0.268  0.353
lSVL   -0.966  0.155  0.102  0.231  0.319

Standardized residuals:
        Min          Q1         Med          Q3         Max
-1.79701638 -0.77877989 -0.02600329  0.65150303  2.44711889

Residual standard error: 0.2615361

#estimated marginal means (least squares) and post-hoc
BMemm<- nlme::gls(lDensity ~ Hab5, data=data, correlation=corPagel(0.761, ptree, fixed=TRUE), method="
ML")
emmls = emmeans(BMemm, pairwise ~ lDensity ~ Hab5, mode=c("auto"))
summary(emmls)
$emmeans
Hab5 lSVL emmean    SE   df lower.CL upper.CL
 aA    1.8   4.39 0.102 22.4     4.18     4.60
 bS    1.8   4.37 0.103 26.9     4.15     4.58
 cM    1.8   4.45 0.105 27.8     4.24     4.67
 dG    1.8   4.54 0.137 44.0     4.27     4.82
 eT    1.8   4.74 0.141 30.2     4.45     5.03

Degrees-of-freedom method: satterthwaite
Confidence level used: 0.95
```

Habitat (Hab5) categories: aA=arboreal (base group), bS=saxicolous, cM=mixed scansorial, dG=generalist, eT=terrestrial
lSVL: log-transformed snout-vent-length; response variable also log-transformed

d)

Model: *Pad Area ~ Habitat + SVL*

```
BM <- gls(lArea ~ Hab5+ lSVL, data=data, correlation=corPagel(0.906, ptree, fixed=FALSE), method="ML")

Analysis of Deviance Table (Type III tests)
Response: lArea
            Df   Chisq Pr(>Chisq)
(Intercept)  1 148.530  < 2.2e-16 ***
Hab5         4  18.097   0.001181 **
lSVL         1 238.383  < 2.2e-16 ***

Coefficients:
             Estimate Std. Error  t value  Pr(>|t|)
(Intercept) -3.582872   0.293984 -12.1873 < 2.2e-16 ***
Hab5bS      -0.061077   0.067697  -0.9022 0.3701353
Hab5cM      -0.095355   0.068347  -1.3952 0.1675038
Hab5dG      -0.308125   0.086787  -3.5504 0.0007034 ***
Hab5eT      -0.355704   0.093362  -3.8100 0.0003014 ***
lSVL         2.316409   0.150030  15.4397 < 2.2e-16 ***
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate 95% confidence intervals
 Coefficients:
                 lower        est.       upper
(Intercept) -4.1695081 -3.58287174 -2.99623539
Hab5bS      -0.1961645 -0.06107653  0.07401141
Hab5cM      -0.2317386 -0.09535522  0.04102814
Hab5dG      -0.4813067 -0.30812550 -0.13494432
Hab5eT      -0.5420040 -0.35570379 -0.16940356
lSVL         2.0170296  2.31640915  2.61578874
```

```
Correlation:
       (Intr) Hab5bS Hab5cM Hab5dG Hab5eT
Hab5bS -0.304
Hab5cM -0.324  0.496
Hab5dG -0.418  0.460  0.425
Hab5eT -0.360  0.416  0.366  0.636
lSVL   -0.955  0.194  0.231  0.338  0.288

Standardized residuals:
       Min         Q1        Med         Q3        Max
-2.5829176 -0.5668103  0.5677442  1.0122609  1.8548912

Residual standard error: 0.2258724
Degrees of freedom: 74 total; 68 residual

#estimated marginal means (least squares) and post-hoc
BMemm<- nlme::gls(lArea ~ Hab5, data=data, correlation=corPagel(0.906, ptree, fixed=TRUE), method="ML"
)
emmls = emmeans(BMemm, pairwise ~ lArea ~ Hab5, mode=c("auto"))
summary(emmls)

$emmeans
Hab5 lSVL emmean     SE df lower.CL upper.CL
 aA   1.78  0.535 0.0882 68   0.3594    0.711
 bS   1.78  0.474 0.0851 68   0.3044    0.644
 cM   1.78  0.440 0.0884 68   0.2636    0.616
 dG   1.78  0.227 0.0983 68   0.0311    0.423
 eT   1.78  0.180 0.1051 68  -0.0299    0.389

Degrees-of-freedom method: df.error
Confidence level used: 0.95

$contrasts
 contrast                                  estimate     SE df t.ratio p.value
 aA 1.77785404921622 - bS 1.77785404921622   0.0611 0.0677 68 0.902   0.8950
 aA 1.77785404921622 - cM 1.77785404921622   0.0954 0.0683 68 1.395   0.6327
 aA 1.77785404921622 - dG 1.77785404921622   0.3081 0.0868 68 3.550   0.0061
 aA 1.77785404921622 - eT 1.77785404921622   0.3556 0.0933 68 3.810   0.0027
 bS 1.77785404921622 - cM 1.77785404921622   0.0343 0.0683 68 0.502   0.9869
 bS 1.77785404921622 - dG 1.77785404921622   0.2470 0.0819 68 3.016   0.0287
 bS 1.77785404921622 - eT 1.77785404921622   0.2945 0.0897 68 3.285   0.0135
 cM 1.77785404921622 - dG 1.77785404921622   0.2127 0.0846 68 2.513   0.0997
 cM 1.77785404921622 - eT 1.77785404921622   0.2602 0.0933 68 2.789   0.0517
 dG 1.77785404921622 - eT 1.77785404921622   0.0475 0.0770 68 0.617   0.9719

Degrees-of-freedom method: df.error
P value adjustment: tukey method for comparing a family of 5 estimates
```

Habitat (Hab5) categories: aA=arboreal (base group), bS=saxicolous, cM=mixed scansorial, dG=generalist, eT=terrestrial
lSVL: log-transformed snout-vent-length; response variable also log-transformed

e)

Model: *Pad Aspect Ratio ~ Habitat + SVL*

```
BM <- gls(lPadAR ~ Hab5+lSVL, data=data, correlation=corPagel(0.684, ptree, fixed=FALSE), method="ML")

Analysis of Deviance Table (Type III tests)
Response: lPadAR
            Df  Chisq Pr(>Chisq)
(Intercept)  1 50.237  1.362e-12 ***
Hab5         4 26.646  2.344e-05 ***
lSVL         1 88.712  < 2.2e-16 ***

Coefficients:
             Estimate Std. Error t value  Pr(>|t|)
(Intercept) -1.688789   0.238266 -7.0878 1.405e-09 ***
Hab5bS      -0.066654   0.055125 -1.2091    0.2311
Hab5cM      -0.050773   0.054327 -0.9346    0.3536
Hab5dG      -0.174682   0.069406 -2.5168    0.0144 *
Hab5eT      -0.411506   0.080720 -5.0979 3.373e-06 ***
lSVL         1.179221   0.125200  9.4187 1.230e-13 ***
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate 95% confidence intervals
 Coefficients:
                lower        est.       upper
(Intercept) -2.1649262 -1.68878904 -1.21265191
Hab5bS      -0.1768129 -0.06665361  0.04350564
```

```
Hab5cM      -0.1593371 -0.05077324  0.05779059
Hab5dG      -0.3133775 -0.17468154 -0.03598557
Hab5eT      -0.5728120 -0.41150591 -0.25019983
lSVL         0.9290284  1.17922054  1.42941266

Correlation:
       (Intr) Hab5bS Hab5cM Hab5dG Hab5eT
Hab5bS -0.224
Hab5cM -0.250  0.478
Hab5dG -0.373  0.404  0.407
Hab5eT -0.349  0.302  0.320  0.480
lSVL   -0.967  0.108  0.145  0.287  0.282

Standardized residuals:
       Min         Q1        Med         Q3        Max
-2.4983911 -0.4924124  0.4160796  1.0885583  2.2967772

Residual standard error: 0.164506
Degrees of freedom: 69 total; 63 residual

#estimated marginal means (least squares) and post-hoc
BMemm<- nlme::gls(lPadAR ~ Hab5 + lSVL, data=data, correlation=corPagel(0.684, ptree, fixed=TRUE), met
hod="ML")
emmls = emmeans(BMemm, pairwise ~ lPadAR ~ Hab5 +lSVL, mode=c("auto"))
summary(emmls)

$emmeans
Hab5 lSVL  emmean     SE df lower.CL upper.CL
 aA   1.77  0.3998 0.0616 63   0.2766    0.523
 bS   1.77  0.3331 0.0600 63   0.2132    0.453
 cM   1.77  0.3490 0.0615 63   0.2262    0.472
 dG   1.77  0.2251 0.0715 63   0.0822    0.368
 eT   1.77 -0.0117 0.0835 63  -0.1785    0.155

Degrees-of-freedom method: df.error
Confidence level used: 0.95

$contrasts
 contrast                                  estimate     SE df t.ratio p.value
 aA 1.77114780697101 - bS 1.77114780697101   0.0667 0.0551 63   1.209  0.7460
 aA 1.77114780697101 - cM 1.77114780697101   0.0508 0.0543 63   0.935  0.8824
 aA 1.77114780697101 - dG 1.77114780697101   0.1747 0.0694 63   2.517  0.0997
 aA 1.77114780697101 - eT 1.77114780697101   0.4115 0.0807 63   5.098  <.0001
 bS 1.77114780697101 - cM 1.77114780697101  -0.0159 0.0559 63  -0.284  0.9985
 bS 1.77114780697101 - dG 1.77114780697101   0.1080 0.0691 63   1.565  0.5253
 bS 1.77114780697101 - eT 1.77114780697101   0.3448 0.0829 63   4.161  0.0009
 cM 1.77114780697101 - dG 1.77114780697101   0.1239 0.0685 63   1.808  0.3782
 cM 1.77114780697101 - eT 1.77114780697101   0.3607 0.0816 63   4.421  0.0004
 dG 1.77114780697101 - eT 1.77114780697101   0.2368 0.0772 63   3.069  0.0254

Degrees-of-freedom method: df.error
P value adjustment: tukey method for comparing a family of 5 estimates
```

Habitat (Hab5) categories: aA=arboreal (base group), bS=saxicolous, cM=mixed scansorial, dG=generalist, eT=terrestrial
lSVL: log-transformed snout-vent-length; response variable also log-transformed

f)

Model: *Claw Length ~ Habitat + SVL*

```
BM <- gls(lClawL ~ Hab5+ lSVL, data=data, correlation=corPagel(0.872, ptree, fixed=FALSE), method="ML"
)

Analysis of Deviance Table (Type III tests)
            Df    Chisq Pr(>Chisq)
(Intercept)  1 302.0055     <2e-16 ***
Hab5         4   6.9744     0.1372
lSVL         1 381.6627     <2e-16 ***

Coefficients:
              Estimate Std. Error  t value Pr(>|t|)
(Intercept) -1.8996641  0.1093124 -17.3783  < 2e-16 ***
Hab5bS       0.0077756  0.0279455   0.2782  0.78145
Hab5cM       0.0461729  0.0281494   1.6403  0.10436
Hab5dG       0.0054128  0.0321810   0.1682  0.86680
Hab5eT       0.0576734  0.0330247   1.7464  0.08408 .
lSVL         1.0733609  0.0549422  19.5362  < 2e-16 ***
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Coefficients:
```

```
                  lower          est.        upper
(Intercept) -2.116767731 -1.899663909 -1.68256009
Hab5bS      -0.047726626  0.007775577  0.06327778
Hab5cM      -0.009734185  0.046172866  0.10207992
Hab5dG      -0.058501388  0.005412783  0.06932695
Hab5eT      -0.007916637  0.057673242  0.12326312
lSVL         0.964240921  1.073360830  1.18248074

Correlation:
       (Intr) Hab5bS Hab5cM Hab5dG Hab5eT
Hab5bS -0.177
Hab5cM -0.225  0.581
Hab5dG -0.337  0.545  0.497
Hab5eT -0.367  0.524  0.477  0.609
lSVL   -0.916  0.024  0.094  0.208  0.206

Standardized residuals:
       Min         Q1        Med         Q3        Max
-2.2712831 -0.6740238  0.1387499  0.7431620  2.4861375

Residual standard error: 0.1028415
Degrees of freedom: 98 total; 92 residual


#estimated marginal means (least squares) and post-hoc
BMemm<- nlme::gls(lClawL ~ Hab5 + lSVL, data=data, correlation=corPagel(0.872, ptree, fixed=TRUE), met
hod="ML")
emmls = emmeans(BMemm, pairwise ~ lClawL ~ Hab5 +lSVL, mode=c("auto"))
summary(emmls)

$emmeans
Hab5 lSVL   emmean     SE df lower.CL upper.CL
 aA    1.76 -0.01447 0.0441 92  -0.1021   0.0731
 bS    1.76 -0.00670 0.0421 92  -0.0904   0.0770
 cM    1.76  0.03170 0.0432 92  -0.0541   0.1175
 dG    1.76 -0.00907 0.0436 92  -0.0957   0.0776
 eT    1.76  0.04318 0.0412 92  -0.0387   0.1250

Degrees-of-freedom method: df.error
Confidence level used: 0.95
```

Habitat (Hab5) categories: aA=arboreal (base group), bS=saxicolous, cM=mixed scansorial, dG=generalist, eT=terrestrial
lSVL: log-transformed snout-vent-length; response variable also log-transformed

g)

Model 1: *Inner Claw Curvature ~ Habitat + SVL*

```
BM <- gls(lICC ~ Hab5 + lSVL, data=data, correlation=corPagel(1.00, ptree, fixed=FALSE), method="ML")

Analysis of Deviance Table (Type III tests)
            Df     Chisq Pr(>Chisq)
(Intercept)  1 1564.4982  < 2.2e-16 ***
Hab5         4   66.8865  1.03e-13 ***
lSVL         1    1.7353     0.1877

Coefficients:
                Estimate  Std. Error  t value  Pr(>|t|)
(Intercept) -2.16671047  0.05477954 -39.5533 < 2.2e-16 ***
Hab5bS      -0.00052059  0.01413414  -0.0368  0.970701
Hab5cM       0.00150904  0.01416090   0.1066  0.915372
Hab5dG      -0.02767652  0.01522613  -1.8177  0.072437 .
Hab5eT      -0.04109717  0.01494312  -2.7502  0.007198 **
lSVL         0.03635963  0.02760012   1.3174  0.191058
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate 95% confidence intervals
                  lower          est.        upper
(Intercept) -2.27553267 -2.1667050849 -2.05787750
Hab5bS      -0.02859897 -0.0005191272  0.02756072
Hab5cM      -0.02662334  0.0015096962  0.02964273
Hab5dG      -0.05792105 -0.0276732558  0.00257454
Hab5eT      -0.07078557 -0.0411018982 -0.01141822
lSVL        -0.01847448  0.0363572238  0.09118892


Correlation:
       (Intr) Hab5bS Hab5cM Hab5dG Hab5eT
```

```
Hab5bS -0.122
Hab5cM -0.203  0.593
Hab5dG -0.378  0.606  0.544
Hab5eT -0.268  0.624  0.546  0.992
lSVL   -0.893 -0.049  0.063  0.207  0.079

Standardized residuals:
       Min         Q1        Med         Q3        Max
-2.0727532 -0.6820606 -0.1718620  0.7077137  1.9899646

Residual standard error: 0.05593161
Degrees of freedom: 96 total; 90 residual


#estimated marginal means (least squares) and post-hoc
BMemm<- nlme::gls(lICC ~ Hab5 + lSVL, data=data, correlation=corPagel(1.00, ptree, fixed=FALSE),
method="ML")
emmls = emmeans(BMemm, pairwise ~ lClawL ~ Hab5 +lSVL, mode=c("auto"))
summary(emmls)

$emmeans
Hab5 lSVL emmean     SE df lower.CL upper.CL
 aA   1.75  -2.10 0.0247 88    -2.15    -2.05
 bS   1.75  -2.10 0.0235 88    -2.15    -2.06
 cM   1.75  -2.10 0.0241 88    -2.15    -2.05
 dG   1.75  -2.13 0.0227 88    -2.18    -2.09
 eT   1.75  -2.14 0.0225 88    -2.19    -2.10

Degrees-of-freedom method: df.error
Confidence level used: 0.95

$contrasts
 contrast                                      estimate      SE df t.ratio p.value
 aA 1.74906427745833 - bS 1.74906427745833  0.000519 0.01413 88   0.037  1.0000
 aA 1.74906427745833 - cM 1.74906427745833 -0.001510 0.01416 88  -0.107  1.0000
 aA 1.74906427745833 - dG 1.74906427745833  0.027673 0.01523 88   1.818  0.3701
 aA 1.74906427745833 - eT 1.74906427745833  0.041102 0.01494 88   2.751  0.0546
 bS 1.74906427745833 - cM 1.74906427745833 -0.002029 0.01277 88  -0.159  0.9999
 bS 1.74906427745833 - dG 1.74906427745833  0.027154 0.01307 88   2.078  0.2390
 bS 1.74906427745833 - eT 1.74906427745833  0.040583 0.01263 88   3.214  0.0154
 cM 1.74906427745833 - dG 1.74906427745833  0.029183 0.01406 88   2.076  0.2398
 cM 1.74906427745833 - eT 1.74906427745833  0.042612 0.01388 88   3.070  0.0232
 dG 1.74906427745833 - eT 1.74906427745833  0.013429 0.00197 88

Degrees-of-freedom method: df.error
P value adjustment: tukey method for comparing a family of 5 estimates
```

Habitat (Hab5) categories: aA=arboreal (base group), bS=saxicolous, cM=mixed scansorial, dG=generalist, eT=terrestrial
lSVL: log-transformed snout-vent-length; response variable also log-transformed

Model 2: *Inner Claw Curvature ~ Habitat*

```
BM2 <- gls(lICC ~ Hab5, data=data, correlation=corPagel(1.00, ptree, fixed=FALSE), method="ML")

Analysis of Deviance Table (Type III tests)
            Df      Chisq Pr(>Chisq)
(Intercept)  1 7.2013e+03  < 2.2e-16 ***
Hab5         4 6.3091e+08  < 2.2e-16 ***
Coefficients:
               Estimate  Std. Error  t value  Pr(>|t|)
(Intercept) -2.10227987  0.02477309 -84.8614 < 2.2e-16 ***
Hab5bS       0.00040148  0.01417373   0.0283  0.977465
Hab5cM       0.00032620  0.01418937   0.0230  0.981710
Hab5dG      -0.03183276  0.01495527  -2.1285  0.035995 *
Hab5eT      -0.04265593  0.01495576  -2.8521  0.005374 **
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate 95% confidence intervals
Coefficients:
                  lower          est.        upper
(Intercept) -2.15148870 -2.1022794834 -2.053070263
Hab5bS      -0.02775180  0.0004024870  0.028556773
Hab5cM      -0.02785872  0.0003266685  0.028512055
Hab5dG      -0.06153651 -0.0318308976 -0.002125287
Hab5eT      -0.07236366 -0.0426580526 -0.012952441

Correlation:
       (Intr) Hab5bS Hab5cM Hab5dG
Hab5bS -0.370
Hab5cM -0.326  0.598
Hab5dG -0.439  0.631  0.544
Hab5eT -0.439  0.631  0.544  1.000
```

```
Standardized residuals:
       Min         Q1        Med         Q3        Max 
-2.0340286 -0.6929637 -0.1229791  0.6731997  1.9657551 

Residual standard error: 0.05646825 
Degrees of freedom: 96 total; 91 residual

#estimated marginal means (least squares) and post-hoc
BMemm<- nlme::gls(lICC ~ Hab5 , data=data, correlation=corPagel(1.00, ptree, fixed=FALSE), method="ML"
)
emmls = emmeans(BMemm, pairwise ~ lICC ~ Hab5, mode=c("df.error"))
summary(emmls)

$emmeans
 Hab5 emmean     SE df lower.CL upper.CL
 aA    -2.10 0.0248 89    -2.15    -2.05
 bS    -2.10 0.0236 89    -2.15    -2.06
 cM    -2.10 0.0242 89    -2.15    -2.05
 dG    -2.13 0.0226 89    -2.18    -2.09
 eT    -2.14 0.0226 89    -2.19    -2.10

Degrees-of-freedom method: df.error 
Confidence level used: 0.95 

$contrasts
 contrast    estimate         SE df t.ratio   p.value
 aA - bS  -0.00040249 1.4174e-02 89    -0.028 1.0000
 aA - cM  -0.00032667 1.4189e-02 89    -0.023 1.0000
 aA - dG   0.03183090 1.4955e-02 89     2.128 0.2173
 aA - eT   0.04265805 1.4955e-02 89     2.852 0.0419
 bS - cM   0.00007582 1.2720e-02 89     0.006 1.0000
 bS - dG   0.03223338 1.2538e-02 89     2.571 0.0847
 bS - eT   0.04306054 1.2538e-02 89     3.434 0.0079
 cM - dG   0.03215757 1.3932e-02 89     2.308 0.1520
 cM - eT   0.04298472 1.3932e-02 89     3.085 0.0222
 dG - eT   0.01082715 4.3100e-07 89                 

Degrees-of-freedom method: df.error 
P value adjustment: tukey method for comparing a family of 5 estimates 
```

Habitat (Hab5) categories: aA=arboreal (base group), bS=saxicolous, cM=mixed scansorial, dG=generalist, eT=terrestrial
lSVL: log-transformed snout-vent-length; response variable also log-transformed

S3.6. References for habitat use and phylogenetic placement (see table in **S3.2**)

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