

RESEARCH ARTICLE

Clinging performance on natural substrates predicts habitat use in anoles and geckos

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Handling Editor: Anthony Herrel

Abstract

1. For arboreal lizards, the ability to cling or adhere to the substrate is critical for locomotion during prey capture, predator escape, thermoregulation and social interactions. Thus, selection on traits related to clinging is likely strong.
2. Correlations between morphology, performance and habitat use have been documented in arboreal lizards, providing a framework for using functional traits to predict habitat use in the field.
3. We tested the hypothesis that clinging performance predicts habitat use in an actively assembling community of introduced lizards in Hawai'i comprised of anoles (*Anolis carolinensis*, *A. sagrei*) and day geckos (*Phelsuma laticauda*).
4. We measured morphological traits (toepad area and lamellae number) and tested clinging performance on two artificial and eight natural substrates in the laboratory. We measured habitat use in 10 m × 10 m outdoor enclosures where habitat availability was controlled and the lizard species assemblage was manipulated to reflect all species combinations. The enclosure experiment generated more than 9,000 habitat use observations from 360 lizards.
5. Morphological traits that predict performance in *Anolis* were not predictive in *Phelsuma*, indicating that direct measures of performance are necessary for comparisons between the genera.
6. Measuring clinging performance on multiple substrates provided key insights into patterns of habitat use. While all three species performed best on an artificial smooth substrate (acrylic), performance on natural substrates predicted which texture (rough vs. smooth) was most often used by each species.
7. Performance predicted perch height use: species with the greatest clinging performance (*A. carolinensis* and *P. laticauda*) across substrates perched twice as high as *A. sagrei*.
8. We did not observe habitat shifts in the height or texture of perches used by any species in response to experimental manipulation of the lizard species assemblage.
9. Our results highlight the inextricable link between ecology, morphology and performance, the importance of measuring functional traits in ecologically relevant ways, and the potential for resource partitioning to be influenced by differences in the ability to attach to different substrates.

KEYWORDS

adhesion, community ecology, functional morphology, lizard, resource partitioning

1 | INTRODUCTION

Arboreal animals must cope with complex three-dimensional environments with a wide range of substrates, from smooth leaves to rough bark, each with its own physical properties that affect locomotor performance. As a result of eco-evolutionary feedbacks, microhabitat use in arboreal lizards is often correlated with morphology and/or performance metrics such as clinging ability or sprint speed (e.g. Collins et al., 2015; Goodman et al., 2008; Losos, 1990; Melville & Swain, 2000). Establishing and testing such linkages between morphology, performance and ecology can provide mechanisms for species differences in resource use. In principle, we can use traits to predict potential overlap in resource use and therefore the likelihood and strength of different species interactions. Increasing such predictive power is important for anticipating community dynamics in novel assemblages, which are increasing due to global changes such as biological invasions and climate change (Williams & Jackson, 2007). The ecologically convergent anoles (*Anolis*) and day geckos (*Phelsuma*) do not naturally co-occur, but have been introduced to Hawai'i, a place with no similar native lizards. Here we aim to test how well functional traits predict performance and habitat use in this young and novel assemblage.

Geckos and anoles are model systems for studying adhesion and ecomorphology (Autumn & Peattie, 2002; Irschick et al., 1996; Russell, 1975; Zani, 2000). These clades have independently evolved frictional adhesive systems in which subdigital microscopic setae interact with a surface via Van der Waals and shear frictional forces at numerous points of contact (Autumn et al., 2000; Autumn & Peattie, 2002). As a greater number of contact points with a surface confer greater frictional adhesive force production (Arzt et al., 2003), both morphology and substrate properties determine a lizard's clinging ability (Gillies et al., 2014; Higham et al., 2019; Naylor & Higham, 2019; Song et al., 2021). Pad-bearing geckos exhibit highly branched setae, while anoles have unbranched setae that are relatively shorter, thinner and more densely packed than geckos (Garner et al., 2021; Peattie & Full, 2007; Ruibal & Ernst, 1965). In addition, *Anolis* have claws, which are important for attachment on rough and soft surfaces (Dai et al., 2002; Naylor & Higham, 2019; Zani, 2000). Day geckos (*Phelsuma*) have lost their claws (Russell & Gamble, 2019), raising the question of whether attachment mechanisms have the potential to drive structural habitat selection.

Contemporary introductions to Hawai'i provide the opportunity to test whether pre-existing differences in morphology and performance translate into differences in habitat use that could influence species interactions. In *Anolis*, the height and diameter

of perches used is one of the major axes structuring communities in the Greater Antilles (reviewed in Losos, 2009). Species differences in toepad area, lamellae number, claw morphology, as well as actual clinging performance, have been shown to correlate with perch use, and traits can rapidly evolve in the presence of congeners (e.g. Elstrott & Irschick, 2004; Glossip & Losos, 1997; Irschick et al., 2005; Stuart et al., 2014; Yuan et al., 2019). Linkages between morphology, performance and habitat use in the field are not well studied in arboreal geckos, but there is evidence of perch height partitioning in multi-species *Phelsuma* communities (Harmon et al., 2007). While their native ranges do not overlap, representative taxa from these genera are now well established on the island of O'ahu, Hawai'i due to species introductions. *Anolis carolinensis* was introduced in the late 1940s, and was widespread prior to the introduction of the other two species in the 1970s to 1980s (Kraus, 2009). While a handful of other arboreal species have also been introduced, we focused on *Anolis carolinensis*, *A. sagrei* and *P. laticauda* because they are by far the most abundant and widespread diurnal species.

In addition to taking advantage of species introductions to test whether the *Anolis* resource partitioning framework generalizes to interactions with a novel player (*Phelsuma*), we build on the vast literature on the morphology–performance–ecology spectrum in arboreal lizards in several key ways. We not only measured traits associated with clinging performance, but also measured clinging performance directly, as proxies that work in one group may not translate to another given the evolution of different solutions to the same problem (i.e. many-to-one mapping). In addition, most studies of clinging ability use artificial substrates such as acetate or acrylic to measure maximum performance in the laboratory. We included eight natural substrates (both rough and smooth) that the lizards commonly use in Hawai'i in our measures of clinging performance. Our measure of habitat use is also noteworthy because we collected thousands of observations of known, marked individuals, and we observed habitat use in semi-natural enclosures with controlled habitat availability. Thus, any differences we see in perch use among species are due to preferences, and not spatial variation in perch availability. Finally, we manipulated lizard species assemblages to see whether lizards shifted their habitat use depending on the presence of other species, which would be consistent with competitive interactions.

Based on extensive previous work outside of Hawai'i (e.g. Campbell, 2000; Elstrott & Irschick, 2004; Irschick et al., 1996; Lister, 1976; Schoener, 1975; Stuart et al., 2014), we expect that *A. carolinensis* will have larger toepads, more lamellae, greater clinging ability and use higher perches than *A. sagrei*, and that *A. carolinensis* will shift to use higher perches in the presence of *A. sagrei*. Given that geckos tend to have superior adhesive capabilities compared to

anoles, *Phelsuma laticauda* may outperform *Anolis* on smooth substrates, but anoles may outperform *Phelsuma* on rough substrates because they have claws. If so, *Phelsuma* is expected to utilize smoother natural surfaces than either species of *Anolis*.

2 | MATERIALS AND METHODS

We used three different datasets to determine species differences in morphological traits, performance, and ecology. The individuals used to measure morphological traits did not overlap with the other datasets, as toepads were measured on 87 museum specimens previously collected in Hawai'i. The individuals used to measure clinging performance ($n = 58$) and habitat use ($n = 360$) were all collected from the same two source populations. There was some overlap between these datasets: 37 individuals were used to measure both clinging performance and habitat use.

2.1 | Morphological traits

We measured toepad area and lamellae number on Hawai'i specimens from the Bernice Pauahi Bishop Museum vertebrate collection. Sample sizes and specimen collection dates were as follows: *A. carolinensis* $n = 41$ (20F, 21M, 1961–2008); *A. sagrei* $n = 26$ (11F, 15M, 1993–2005); and *P. laticauda* $n = 20$ (7F, 13M, 2000–2005). For each specimen we determined sex, measured snout–vent length (SVL) and scanned each foot at 2,400 dpi using a flatbed scanner. We counted lamellae number and measured toepad area on the fourth toe of each hindlimb (e.g. Irschick et al., 1997; Johnson & Russell, 2009; Macrini et al., 2003; Russell & Johnson, 2007; Stuart et al., 2014). We included all expanded and undivided scales in our measurements. How researchers count lamellae in anoles is variable (Stroud, 2014). On anoles, the first phalanx is within the claw and the second occurs between the claw and the toepad; thus, we included the third, fourth and fifth phalanges in our measurements. Some anole studies only include the third and fourth phalanges (Glossip & Losos, 1997; Irschick et al., 1997), but the breaks between phalanges were difficult to determine on our scans. As a result, our approach may include some non-setae-bearing lamellae in anoles. Area was measured by tracing around the toepad using ImageJ (Schneider et al., 2012). Values for each foot were averaged to generate one value per trait per individual.

To test for differences among the species while accounting for sex and size differences, we fit linear models with log-transformed toepad area in mm^2 or log-transformed lamellae number as the response, and log-transformed SVL and a species by sex interaction as predictors. Visualization of quantile–quantile plots, residual versus fitted effects and boxplots of residuals among species all indicated compliance with model assumptions. Hypothesis tests were conducted using analysis of variance in the *CAR* package, and fitted effects were estimated using the *EFFECTS* package in R version 3.4.1 (R Core Team, 2017).

2.2 | Clinging performance

We measured clinging performance on 15–25 individuals per species using 10 substrates during two sampling periods (Figure 1; complete sample sizes in Table S1). In 2016, lizards were from the University of Hawai'i at Mānoa campus (UHM), and in 2019 lizards were from UHM and Waimea Valley. In 2016, we measured clinging performance (described below) using five substrates: acrylic, banana trunk smooth *Musa* sp., Mcarthur palm trunk *Ptychosperma macarthurii*, Mcarthur palm leaf and ti trunk *Cordyline fruticosa*. In 2019, we included five additional substrates: 60-grit sandpaper, Manila palm trunk *Adonidia merrillii*, banana trunk rough *Musa* sp., snake plant *Sansevieria trifasciata* and banana leaf *Musa* sp.

The claws of padded lizards are capable of contributing significant attachment forces on penetrable surfaces and/or those with asperities, and so 'clinging ability' in our study refers to the maximum peak tension force (Newtons) generated by claws, pads or both (Naylor & Higham, 2019). As in previous studies (e.g. Higham et al., 2017), individuals freely placed the manus onto a test surface attached to a portable force gauge (MARK-10 Series M5-10, $\pm 0.1\%$ full scale) and were pulled in parallel opposition until displaced. A single maximum force from multiple trials per individual per surface was recorded to accurately estimate maximum effort (Losos et al., 2002). Preliminary visualization of the relationship between maximum clinging force and body mass showed a similar relationship among the three species (Figure S1). We divided the maximum clinging force (N) by individual body mass (kilograms) as the metric of clinging ability (i.e. maximum force per mass) in our analyses; this response variable was log transformed to meet assumptions of normality.

We fit two different mixed models with log-transformed maximum force per mass as the response ($\log(\text{N/kg})$). The first model included as fixed effects a substrate by species interaction (to test whether the species differed in performance on the 10 substrates), a species by sex interaction and a random effect for individual (to account for repeated measurements of individuals). For the second model, we focused on performance on natural substrates only, and qualitatively categorized each as rough or smooth (e.g. leaves are smooth and bark is rough; Figure 1). Quantitative measurement of clinging surface topography on a subset of our substrates (described below) supported our broad categorizations. Rough substrates were ti trunk, Manila palm trunk and banana trunk rough (dead outer sheaths), and smooth substrates were Mcarthur palm trunk, Mcarthur palm leaf, banana leaf, banana trunk smooth (live green tissue) and snake plant. Mcarthur palm trunk texture is variable; our test sample was of young green trunk (Figure 1). The second model included as fixed effects a species by texture (rough vs. smooth) interaction and a species by sex interaction. Individual and substrate were included as random effects. Hypothesis tests were conducted using the Satterthwaite approximation for degrees of freedom as implemented by the package *LMERTEST* (Kuznetsova et al., 2017). For the second model, we also compared performance on rough versus smooth substrates within species using contrasts as implemented



FIGURE 1 Natural substrates used to assess clinging performance and/or habitat use. Rough substrates: (a) ti trunk, (b) Manila palm trunk and (c) banana trunk rough. Smooth substrates: (d) Mearthur palm trunk, (e) Manila palm leaf, (f) banana trunk smooth, (g) snake plant and (h) banana leaf. Lizards: *Anolis carolinensis*: b, d, e; *Anolis sagrei*: c, h; *Phelsuma laticauda*: a, f, g. All photos were taken in the experimental enclosures except panel d which was taken on the University of Hawai'i at Mānoa campus. Photos f & g by L. Gerhart-Barley; other photos by A. Wright

by EMMEANS (Lenth, 2019). Raw individual performance data are in Figure S4.

2.3 | Clinging surface topography

To determine the roughness of some of the surfaces used in our study, we quantified the area root mean square height (Sq), a metric of 3D roughness, for acrylic, 60-grit sandpaper, banana trunk smooth, banana leaf, snake plant and Manila palm trunk. To do this, we used a confocal laser scanning microscope (LEXT OLS4000, Olympus Corporation) and 3D topographical reconstructions in MountainsMap Premium 7.2 software (Digital Surf). Unlike 2D metrics of roughness derived from a single transect through the sample, such as mean roughness (Ra) and root mean square, our area roughness values were derived from numerous surface transects (see Higham et al., 2019 for further details). As expected, acrylic was perfectly smooth (Sq = 0 μm). Banana leaf (upper surface)

followed with a Sq of 1.41. The remaining, in order of increasing roughness, were snake plant (Sq = 1.67 μm), banana trunk smooth (Sq = 16.1 μm), Manila palm trunk (Sq = 74.8 μm) and 60-grit sandpaper (Sq = 105.2 μm). Thus, a large gap in roughness separates our smooth (acrylic, banana leaf, snake plant and banana trunk smooth) and rough substrates (Manila palm trunk and 60-grit sandpaper) and supports our qualitative scoring of substrates into smooth versus rough categories.

2.4 | Habitat use

We conducted an enclosure experiment to test whether species differed in perch use and whether lizards shifted perch use in response to the presence of other species. Each enclosure was 10 m \times 10 m in size, mesh-sided and open-topped to provide ambient prey, rainfall, and thermal conditions (Wright, 2019). Key for the current study, enclosures were planted identically and all of the natural substrates

used to test clinging performance were available except for the Macarthur palm (Manila palm is similar in growth form). Prior to introducing lizards to enclosures, following Schoener (1974, 1975), we estimated the surface area of all rough and smooth trunks, stems and branches (hereafter perches) in the enclosures. The availability of smooth and rough perches was similar: $55\% \pm 5\%$ of perch surface area was smooth (mean \pm SD, range 49%–62%; Appendix S1). Pairwise differences in the composition of perch heights and diameters available among enclosures ranged from 5% to 33% (Curtis–Bray dissimilarity; Tables S2 and S3). Both smooth and rough perches were available at the heights used most often by lizards (Figure S2). Thus, microhabitat availability was very similar across enclosures, and lizards had access to a wide range of perch heights and substrates.

To test for habitat shifts, we used seven lizard species assemblage treatments to capture all species combinations: (a) *A. carolinensis*, (b) *A. sagrei*, (c) *P. laticauda*, (d) *A. carolinensis* + *A. sagrei*, (e) *A. carolinensis* + *P. laticauda*, (f) *A. sagrei* + *P. laticauda* and (g) *A. carolinensis* + *A. sagrei* + *P. laticauda*. We used a substitutive design to address species coexistence questions that are the focus of a broader study: single species treatments had six females (F) and three males (M) (9 total); paired treatments had 2F, 2M per species (8 total); the treatment with all three species had 2F, 1M per species (9 total). Our stocking densities were 0.25–0.29 lizards per square meter of vegetated area, which based on data from outside Hawai'i is relatively high for *A. carolinensis* and relatively low for *A. sagrei* (Okuchi et al., 2006; Schoener & Schoener, 1980). We are unaware of reported field densities for *P. laticauda*. Due to high year-round maintenance requirements, it was not logistically possible to maintain enclosures large enough to keep sex ratio and density exactly the same across treatments. This could make interpreting treatment effects on habitat use difficult, though ultimately there were none (described below; Appendices S3 and S4).

We replicated the treatments six times between June 2017 and March 2019; treatments were randomly assigned to enclosures and new lizards were used for each replicate. Replicates ran for 1–2 months each and required 20 adults of each species; thus, 120 lizards per species and 360 lizards in total were used over the entire experiment. Lizards for the first four replicates were captured on the UHM campus. For the last two replicates, we collected lizards from Waimea Valley because *A. carolinensis* became rare on campus. To reduce possible size-based competitive hierarchies (Tokarz, 1985), within each replicate we selected individuals to not differ by more than 10% in SVL within sexes and species. Lizards were randomly assigned to treatments and were uniquely marked with visible implant elastomer (VIE, Northwest Technologies) and non-toxic paint marks (Figure 1). *Phelsuma laticauda* were also uniquely identifiable by their red dorsal coloration.

Habitat use was measured using standardized scans and opportunistic observations. On scans, observers walked slowly around the outside of each enclosure to look for lizards. We aimed to spend similar search effort on each enclosure during each scan but

did not use a standardized time because lizard activity is highly weather dependent. We randomized which enclosure was scanned first. Every lizard spotted was identified to individual using paint marks, and we recorded the height, diameter and substrate the lizard was perching on for all lizards that were not moving when first sighted (Schoener & Schoener, 1971, Table S4). The same data were recorded when lizards were spotted outside of scans (opportunistic observations). Half of the observations were collected during standardized scans (4,932) and half during opportunistic observations (4,849). The distribution of perch heights and substrate textures used was similar for the two types of observations (Table S5; Figure S3), and the different lizard species were seen with similar frequency regardless of view type (Table S6); thus, both view types were used in analyses.

We recorded 11,038 observations of lizard perch use, and 9,781 of those observations were of uniquely identifiable individuals. Unidentifiable cases occurred when animals shed their skin; we captured and re-marked animals based on VIE throughout the study. Similar numbers of observations of uniquely identifiable lizards were obtained for the three species: 2,916 *A. carolinensis*; 3,681 *A. sagrei* and 3,184 *P. laticauda*. Analyses were conducted on data from the 9,781 observations of uniquely identifiable lizards only so that repeated measurements of individuals could be statistically accounted for (described below). Individual lizards were re-sighted 28 ± 27 times (mean \pm SD; range 1–181 sightings per individual).

To test whether perch use changed in response to which lizard species were present, we fit separate mixed models for each species because the treatments were by definition unbalanced (e.g. *A. sagrei* does not occur in all lizard species assemblages). We modelled two responses: perch height and substrate texture. As we found no treatment effects on either response for any of the three species (i.e. lizards did not change their perch use depending on lizard species assemblage; Appendices S3 and S4), we fit a single model for each response using data pooled from all treatments. For the perch height model, we used square-root-transformed perch height as the response instead of a log transformation because perch heights of zero were possible (i.e. lizards on the ground). We included species, sex and their interaction as fixed effects, and the following random effects to account for the experimental design: a factor for the combined enclosure by replicate (e.g. enclosure 1 during replicate 1) as this is the experimental unit of replication, enclosure (to account for differences among enclosures) and lizard ID (to account for repeated measurements on the same individual). The model for substrate texture had the same fixed and random factors, the only difference being that we used a binomial distribution. In 370 cases (~4% of observations), perch substrates could not be assigned to a texture category (Table S3), and these observations were excluded from the substrate texture model. Both models were fit using the `lme4` package (Bates et al., 2015). For hypothesis tests, we used `IMTEST` for the perch height model (Kuznetsova et al., 2017), and likelihood ratio tests for the substrate texture model. We also used `EMMEANS` (Lenth, 2019) for comparisons among species.

2.5 | Data visualizations

For all responses (toepad area, lamellae number, clinging performance, perch height, perch texture), we visualized differences among species by plotting the species effect as calculated by the EMMEANS package for each of the statistical models described above (Lenth, 2019). This approach is common when evaluating relationships using mixed models (Gelman & Hill, 2007). We hereafter refer to these fitted effects as modelled species means, which are also known as estimated marginal means or least-square means (Searle et al., 1980), and can be interpreted as the species means when adjusting for all other model predictors.

3 | RESULTS

3.1 | Toepad morphology

Toepad area differed among the species, with *A. carolinensis* having the largest toepads relative to snout-vent length, followed by *A. sagrei* then *P. laticauda* (species $F_{2,80} = 34.5, p < 0.0001$; Figure 2a,b). *Anolis carolinensis* toepads were estimated to be 48% larger than *P. laticauda* toepads for lizards of similar size (Figure 2a,b). The difference in species means was even greater for lamellae number, with anoles having 80%–100% more lamellae on average than *Phelsuma* of similar size (species $F_{2,80} = 1,135.6, p < 0.0001$; Figure 2c,d). Larger lizards had larger toepads and more lamellae (SVL area: $F_{1,80} = 723.7, p < 0.0001$; SVL lamellae: $F_{1,80} = 8.6, p < 0.01$; Figure 2a,c). The effect of snout-vent length on toepad area was much more pronounced than the effect of snout-vent length on lamellae number (slope estimate \pm SE: area 2 ± 0.04 ; lamellae 0.11 ± 0.04 ; Figure 2a,c). Females and males had similar toepad areas relative to body size (sex area: $F_{1,80} = 0.14, p = 0.71$; species*sex area: $F_{2,80} = 0.03, p = 0.97$). There were trends towards males having more lamellae than females, particularly in the anoles, but the magnitude of these effects were small—a difference of approximately

1 lamella (sex lamellae: $F_{1,80} = 3.3, p = 0.07$; species*sex lamellae: $F_{2,80} = 2.4, p = 0.10$).

3.2 | Clinging performance

For the mixed model considering performance on all substrates, there was a species by substrate interaction, indicating that species differences in clinging ability depended on which substrate was being evaluated (species*substrate $F_{18,382.4} = 6.1, p < 0.0001$; Figure 3a). In other words, the ranking of which species performs best varied from substrate to substrate. Species showed substantial overlap in performance on most of the rough substrates (60-grit sandpaper, ti trunk, Manila palm trunk and banana trunk rough; Figure 3a; Figure S4). For the remaining substrates, *P. laticauda* tended to have the highest performance. *Anolis carolinensis*' clinging performance was more similar to *A. sagrei* on the roughest of the smooth substrates, but tended to be more similar to *P. laticauda* on smoother substrates (Figure 3a). As a result, overall *P. laticauda* had the highest performance on average across substrates, followed by *A. carolinensis* then *A. sagrei* (species $F_{2,44.6} = 16.3, p < 0.0001$; Figure 3b). Averaging across substrates, the clinging ability of *P. laticauda* is five times greater than *A. sagrei* and two times greater than *A. carolinensis*, respectively (Figure 3b). For all species, the highest clinging ability was observed on acrylic, with performance on this substrate 2–5 times higher than each species' next best substrate (second best substrates were ti trunk for *A. sagrei*, banana trunk smooth for the other species; Figure 3a). *Anolis carolinensis* performance was indistinguishable from *P. laticauda* on acrylic (Figure 3a, Appendix S2). There were no effects of sex on clinging performance, nor was there a species by sex interaction ($p > 0.4$).

In the model where natural substrates were categorized by texture (rough vs. smooth), there was a species by texture interaction, whereby the three species performed similarly on rough substrates, but on smooth substrates the pattern was similar as to the overall species effect in Figure 3b, with *P. laticauda* performing

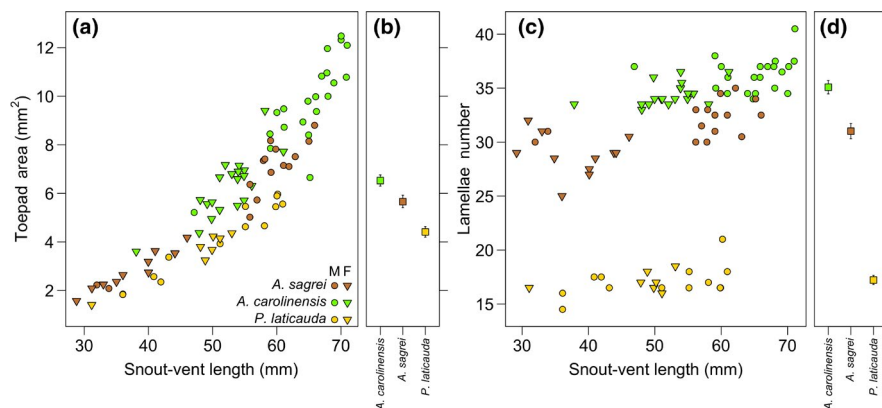


FIGURE 2 Toepad morphology. Panels (a and c) show raw data, where each symbol represents the trait value for a single individual plotted against snout-vent length. Panels (b and d) show the species means ($\pm 95\%$ confidence intervals) for toepad area and lamellae number, respectively. Species means were estimated from the statistical model described in the text, and are the modelled species means once accounting for sex and size. Panels a and b share the same y-axis, and panels c and d share the same y-axis

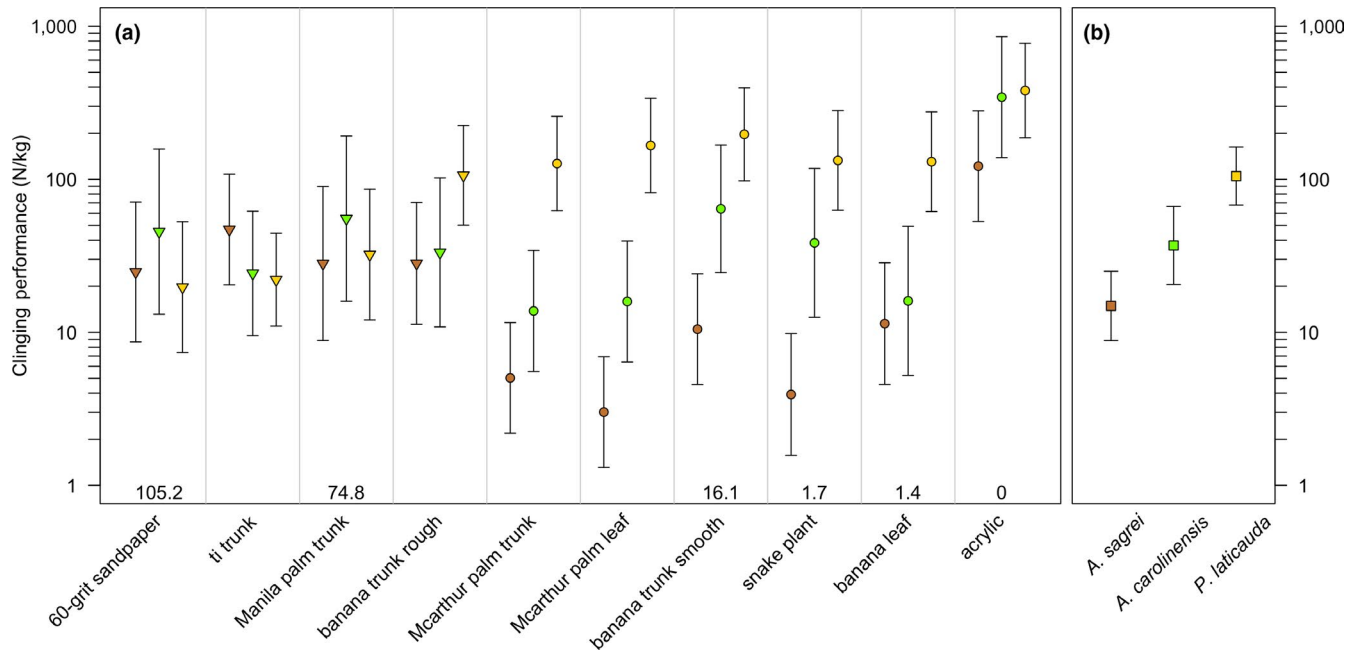


FIGURE 3 Clinging performance. (a) Mean clinging performance ($\pm 95\%$ CI) for each species on 10 different substrates. Clinging performance is the maximum force in Newtons required to dislodge a lizard from a substrate divided by lizard mass (N/kg). Means are modelled species means on each substrate derived from the mixed model described in the text. Rough substrates are shown by triangles, and smooth substrates are shown by circles; substrates are ordered from roughest on the left to smoothest on the right. Substrates with quantitative measures of 3D surface roughness are labelled with area root mean square height in μm on the x-axis. (b) Mean clinging performance ($\pm 95\%$ CI) for each species. Plotted is the modelled species mean overall (i.e. across substrates as well as all other variables included in the model) estimated from the mixed model described in the text. Colours refer to species: brown = *Anolis sagrei*, green = *Anolis carolinensis*, gold = *P. laticauda*

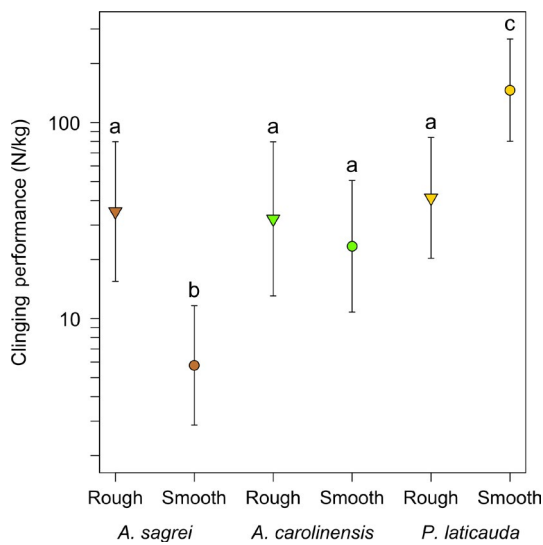


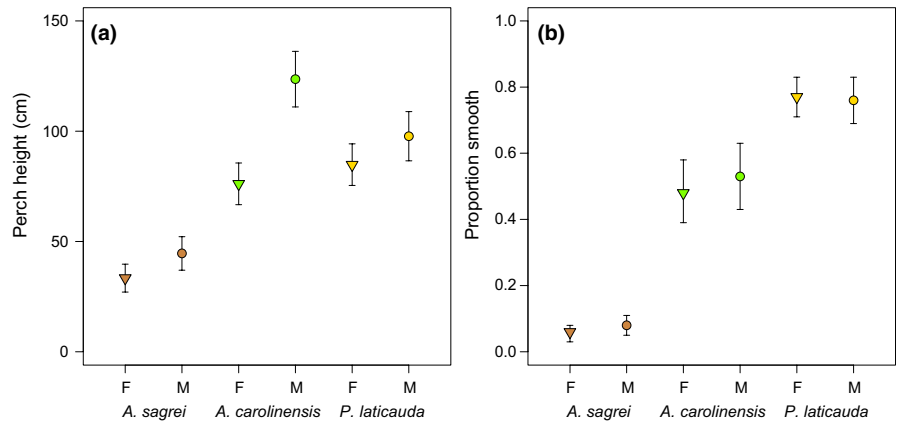
FIGURE 4 Mean ($\pm 95\%$ CI) clinging performance on rough versus smooth natural substrates. Clinging performance is the maximum force in Newtons required to dislodge a lizard from a substrate divided by lizard mass (N/kg). Means are modelled species means on each texture derived from the mixed model described in the text. Colours refer to species: brown = *Anolis sagrei*, green = *Anolis carolinensis*, gold = *Phelsuma laticauda*, and symbols refer to substrate texture: triangle = rough, circle = smooth. Letters represent similarity based on Tukey's test

best, followed by *A. carolinensis*, then *A. sagrei* ($species \times texture F_{2,313.1} = 28.7, p < 0.0001$; Figure 4). Comparing performance on natural substrates within species, *A. sagrei* had $\sim 3\times$ higher clinging performance on rough than smooth substrates (Tukey $p < 0.0001$; Figure 4a). Conversely, *P. laticauda* had $\sim 2\times$ higher performance on natural smooth substrates compared to natural rough substrates (Tukey $p < 0.0001$; Figure 4a). *Anolis carolinensis* performed similarly on smooth and rough natural substrates (Tukey $p = 0.44$; Figure 4a).

3.3 | Habitat use

Anolis sagrei used perch heights approximately half as high as the other two species ($species F_{2,265.7} = 100.9, p < 0.0001$; Figure 5a; Figure S5). Females overall perched lower than males ($sex F_{1,270.1} = 49.6, p < 0.0001$), but this effect was only large for *A. carolinensis* (~ 50 cm difference compared to ~ 12 cm difference between sexes for the other species; $species \times sex F_{2,270.7} = 8.9, p < 0.001$; Figure 5a). The three species differed in the proportion of observations occurring on rough versus smooth substrates ($species \chi^2 = 252.6, p < 0.0001$): *A. sagrei* rarely used smooth perches (7% of observations), *A. carolinensis* used smooth perches half the time (51%) and *P. laticauda* used smooth perches most of the time (76%; Figure 5b). There were no effects of sex on substrate texture use.

FIGURE 5 Perch use in enclosures. Mean ($\pm 95\%$ CI) (a) perch heights and (b) proportion of perches used that were smooth. Means are modelled species means derived from the mixed models described in the text. Colours refer to species: brown = *Anolis sagrei*, green = *Anolis carolinensis*, gold = *Phelsuma laticauda*. Symbols refer to sex: triangle = female, circle = male



4 | DISCUSSION

4.1 | Clinging performance among species

Anoles and geckos exhibit different solutions for generating adhesion (Irschick et al., 2006), and this was reflected in differences in clinging performance across the various substrates tested. Toepad morphology was not a good indicator of clinging performance in our study. Based on morphology–performance relationships in anoles, we would expect *P. laticauda* to have the poorest clinging performance because it had the smallest toepads and the fewest lamellae. Contrary to this prediction, *P. laticauda* had the highest clinging performance overall when averaging across all substrates considered. However, *P. laticauda* did not have the highest performance on every individual substrate. On acrylic, a perfectly smooth artificial substrate, performance in *P. laticauda* was indistinguishable from performance in *A. carolinensis*. Other studies have similarly found that, depending on species, anoles can generate similar forces to geckos on artificially smooth substrates (Higham et al., 2017; Irschick et al., 1996). Garner et al. (2021) found that extensive setal branching in *Gekko gecko* compared to greater setal density in *Anolis equestris* resulted in similar adhesive force production. In our study, *A. carolinensis* had larger toepads than *P. laticauda*, perhaps allowing them to close the performance gap on acrylic.

In contrast to artificially smooth surfaces, *P. laticauda* showed higher clinging ability than *A. carolinensis* on natural smooth surfaces. This may be explained by the characteristic contact splitting of gecko setae (particularly so in day geckos), which is thought to cope better with irregularities of real-world surfaces that limit setal contact (Peressadko & Gorb, 2004; Yao & Gao, 2007). Moreover, geckos exhibit multiple integrated anatomical specializations that allow their toe pads to conform to heterogeneous substrates and subsequently enhance setal contact, many of which anoles lack (Russell, 2002, 2017). Interestingly, the three species performed similarly on rough substrates overall. There is a noticeable increase in anole performance at the cut-off between our smooth and rough categorizations, indicating that the contribution of the claws becomes increasingly significant on rough substrates, even for the relatively terrestrial *A. sagrei*, such that performance is comparable to that of *P. laticauda*.

Toepad performance in the clawless *P. laticauda* decreased as substrate roughness increased. Similar performance patterns have been observed previously for *Phelsuma* (Higham et al., 2019), as well as other study systems where contributions from toepads and claws were isolated (Betz, 2002; Naylor & Higham, 2019).

4.2 | Clinging performance and habitat use

Clinging performance on natural substrates predicted which types of substrates were used in enclosures. Within species, *A. sagrei* showed their highest clinging ability on rough natural substrates, and they accordingly used rough perches almost exclusively. At the other end of the spectrum, *P. laticauda* performed best on smooth natural substrates, and despite performing as well on rough substrates as the anoles, were observed on smooth substrates three-quarters of the time. *Anolis carolinensis* performed similarly on smooth and rough natural substrates and used both types equally. Recall that *A. carolinensis* and *P. laticauda* had similar performance on acrylic, and these data alone would lead to an incorrect prediction of similarly high use of smooth substrates for both species. *Anolis sagrei* had higher clinging performance on acrylic than 60-grit sandpaper, which would also lead to incorrectly predicting higher use of smooth than rough substrates in the field. These results are noteworthy given that historically most studies have measured performance on a single artificial substrate, usually acrylic (but see Vanhooydonck et al., 2005, Zani, 2000, Kohlsdorf et al., 2001, Naylor & Higham, 2019, Higham et al., 2019).

While *P. laticauda* had higher clinging performance averaged across substrates, there was substantial overlap with *A. carolinensis*' overall performance, likely contributing to these species using the same distribution of perch heights. Both species perched higher than *A. sagrei*, the species with the lowest clinging ability overall. This supports the general pattern of higher-perching lizards exhibiting greater clinging ability, which is hypothesized to be driven by a need for greater insurance from falling (Elstrott & Irschick, 2004). Despite there being no sex differences in clinging ability, male *A. carolinensis* used higher perches on average than females, likely due to behavioural differences between the sexes driven by different

selection pressures. Male *A. carolinensis* had much larger home ranges and spent more time displaying and patrolling enclosures than females (Kennedy-Gold, 2019; Wright et al. unpubl. data). The use of higher perches may thus be associated with different demands on visual display fields and detection of rivals in male versus female *A. carolinensis*.

4.3 | Species interactions

Several comparative and experimental studies have documented that *A. carolinensis* and *A. sagrei* differ in perch height as we found here, and that the former shifts higher in the vegetation in the presence of the latter (e.g. Lister, 1976; Schoener, 1975; Stuart et al., 2014). These patterns have been interpreted as evidence for interspecific competition leading to resource partitioning. In our study, we did not see habitat shifts by any species in any community context—lizards used the same perches regardless of the presence of heterospecifics. One explanation for this result is that the species were already different enough in their functional traits (i.e. clinging performance) that they did not need to change their habitat use. To put this more generally, our results suggest that these three species can partition structural habitat to minimize interspecific overlap as long as a variety of perch heights and textures are available. This is because *A. sagrei* prefers low, rough perches, *A. carolinensis* prefers high perches of either texture and *P. laticauda* prefers high smooth perches. Gerber and Echternacht (2000) similarly noted that the abundance of *A. carolinensis* in Florida (where it is native) following the introduction of non-native *A. sagrei* is greatest in areas with high structural complexity. Alternative, non-mutually exclusive explanations for the lack of habitat shift include the short-term nature of the study, as many habitat shift studies in anoles are multi-generational, and the possibility that the lizard densities used were too low to elicit competitively induced habitat shifts.

If minimizing overlap in habitat use is important for species coexistence in this system, our results suggest that in less diverse habitats the opportunity for resource partitioning would be diminished, and who 'wins' will be highly dependent on habitat availability. For example, in a more homogeneously smooth environment, we hypothesize *A. sagrei* would be the inferior competitor, as it had the poorest performance on smooth substrates compared to the other two species. In contrast, in a habitat of predominantly rough perches, all three species have essentially the same trait value, and thus the interaction is predicted to be neutral. Additionally, because *A. carolinensis* overlaps in clinging performance with either or both of the other species on every substrate evaluated, and is intermediate between the other two species in overall performance, it faces potential competitors on both substrate textures. Thus, we predict that *A. carolinensis* would be more likely to coexist with either species alone but would have less competitor-free habitat in the presence of both. These ideas are consistent with the observation that *A. carolinensis* was widespread and abundant prior to the introduction and spread of the other two species on O'ahu.

5 | CONCLUSIONS

Our highly integrative study incorporating habitat use, morphology and ecologically relevant measures of performance revealed key mechanisms underlying differences in resource use in anoles and day geckos. The toepad morphology results underscore the importance of confirming trait–performance relationships before applying proxies to new species. This is especially key when comparing distantly related taxa as we do here, because many-to-one mapping can yield traits that are predictive of performance in one group but not another. Furthermore, we found that measuring performance on a wide range of substrates was crucial because species preferentially used microhabitats that reflected maximum performance on natural, but not artificial, substrates. While perch dimensions have long been the focus of resource partitioning studies in *Anolis*, our study supports the increasing recognition of perch texture in driving natural selection in arboreal lizards. Future studies should continue to include a wide range of real-world substrates, and some prior studies limited to acrylic may warrant revisiting. Despite day geckos having the best clinging performance overall, we found that the ecologically relevant answer to the question, 'which species has the highest clinging performance?' depends on which substrates are available in a given habitat. This 'ecomechanical' approach is critical for making predictions about species interactions, survival and ultimately fitness (Higham et al., 2021).

ACKNOWLEDGEMENTS

We thank the many students, technicians, postdocs, friends and family of the Wright and Thomson labs at UH Mānoa who since 2015 have helped in construction and maintenance of the enclosures as well as with collecting lizards, particularly Anthony Barley, Laci Gerhart-Barley and Bob Thomson. We also thank the College of Tropical Agriculture and Human Resources and Waimea Valley (Hi'ipaka LLC) for providing field access, and the staff at Waimanalo Research Station for supporting this work. Kyle Edwards provided invaluable statistical advice on the design and analysis of this project. This is publication #143 from the School of Life Sciences, University of Hawai'i at Mānoa.

CONFLICT OF INTEREST

The authors declare no conflicting interests. T.E.H. is an Associate Editor of Functional Ecology, but took no part in the peer review and decision-making processes for this paper.

AUTHORS' CONTRIBUTIONS

A.N.W. and T.E.H. conceived the ideas and designed the methods; all authors collected the data; A.N.W. analysed the data, A.N.W. and T.E.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.66t1g1k2v> (Wright et al., 2021).

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How to cite this article: Wright, A. N., Kennedy-Gold, S. R., Naylor, E. R., Screen, R. M., Piantoni, C., & Higham, T. E. (2021). Clinging performance on natural substrates predicts habitat use in anoles and geckos. *Functional Ecology*, 35, 2472–2482. <https://doi.org/10.1111/1365-2435.13919>