

RESEARCH ARTICLE

There's more than one way to climb a tree: Limb length and microhabitat use in lizards with toe pads

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Abstract

Ecomorphology links microhabitat and morphology. By comparing ecomorphological associations across clades, we can investigate the extent to which evolution can produce similar solutions in response to similar challenges. While *Anolis* lizards represent a well-studied example of repeated convergent evolution, very few studies have investigated the ecomorphology of geckos. Similar to anoles, gekkonid lizards have independently evolved adhesive toe pads and many species are scansorial. We quantified gecko and anole limb length and microhabitat use, finding that geckos tend to have shorter limbs than anoles. Combining these measurements with microhabitat observations of geckos in Queensland, Australia, we observed geckos using similar microhabitats as reported for anoles, but geckos with relatively longer limbs were using narrower perches, differing from patterns observed in anoles and other lizards. We also observed arboreal geckos with relatively shorter proximal limb segments as compared to rock-dwelling and terrestrial geckos, similar to patterns observed for other lizards. We conclude that although both geckos and anoles have adhesive pads and use similar microhabitats, their locomotor systems likely complement their adhesive pads in unique ways and result in different ecomorphological patterns, reinforcing the idea that species with convergent morphologies still have idiosyncratic characteristics due to their own separate evolutionary histories.

Introduction

Ecomorphology is the study of morphology and performance in the context of ecology. Ecomorphological studies typically rely on correlations between morphology, performance, and habitat use to suggest adaptation [1–7], with lizards having been a classic system. Overall, researchers have described a wide range of patterns linking lizard locomotor morphology, performance, and microhabitat [8]. However, ecomorphological studies are typically limited to a clade of closely related species and general comparisons across distantly related groups are uncommon (but see [3]).

We investigated the extent of ecomorphological similarities between two distantly related groups of lizards, geckos and anoles. Anoles represent a well-studied example of ecomorphology, with correlated morphologies and ecologies having evolved repeatedly in Caribbean anoles. For example, anoles have repeatedly evolved shorter limbs in association with narrow perches. This correlation between relatively short limbs and narrow perches has also been observed for *Tropidurus* and *Draco* [9, 10], and is likely due to an interaction between sprint speed, balance, and limb length with perch diameter [6, 11–18]. Similar trade-offs between sprint speed and clinging ability have also been observed in chameleons [19, 20], suggesting that relatively short limbs may be a common adaptation associated with movement on narrow perches. While this ecological-morphological correlation has been observed across many groups of lizards, the repeatedly evolved Caribbean anole ecomorphs have not. Even closely related mainland anole species do not show the same ecomorphological patterns [21]. Alternatively, other studies have reported examples of distantly related ecomorphological convergence [3].

Given the ecological and morphological similarities between gecko and anole lizards, we were interested in investigating similarities in their ecomorphological traits, focusing on the relationship between limb length and microhabitat use. Geckos provide an excellent opportunity for comparison to anoles. Both geckos and anoles also exhibit fibrillar adhesive toe pads [22–29]. Although many studies have focused on the biomechanical properties of fibrillar toe pad adhesion [30–36], few have considered it in an ecological context [37–40] especially in the case of geckos (but see [25, 41–45]). Anoles are nearly all arboreal. Similarly, most pad bearing geckos are scansorial (climbing) using arboreal or saxicolous (rock dwelling) microhabitats [45–49]. Furthermore, similarities in habitat use patterns have previously been suggested between geckos and anoles [50, 51]. We hypothesized similar positive correlations between gecko limb length and arboreal perch diameter in light of the biomechanical trade-off between sprint speed and balance observed in anoles and other lizards [6, 9–20, 48, 52, 53].

Materials and methods

For this study we used two distinct datasets, a morphological dataset and a microhabitat dataset. Our morphological dataset was comprised of 38 species of geckos and 63 species of anole (Fig 1). These data were used to compare gecko and anole limb lengths (Fig 2). We also collected a dataset of observed microhabitat patterns from 13 species of geckos from Queensland, Australia and 63 species of Caribbean anoles (Fig 3). When considering morphological and microhabitat data together, we only included species for which we had morphological and microhabitat measurements (Figs 4–7, 13 species of gecko and 63 species of anole).

Morphology

We measured morphological characters from 38 species of pad-bearing geckos and retrieved equivalent measurements for 63 species of anole from the literature (S1 Table and [13, 54]). Gecko specimens included field caught, captive, and museum samples. Species were chosen to maximize taxonomic diversity. Using a ruler (SVL) or digital calipers (all other measurements), we externally measured snout-to-vent length (SVL); thigh length (from the point in which the hind limb enters the body to the apex of the knee); crus length (from the apex of the knee to the ankle joint); and foot length (from the center of ankle joint, measured on the dorsal side, to the tip of longest digit, toe four); brachium length (from the axilla to apex of the elbow joint), antebrachium length (from the apex of the elbow joint to the center of the wrist joint, on the dorsal side), and hand length (from the dorsal center of the wrist joint to the tip of longest digit, Fig 1). We summed our segmental fore- and hind limb lengths estimate total fore-

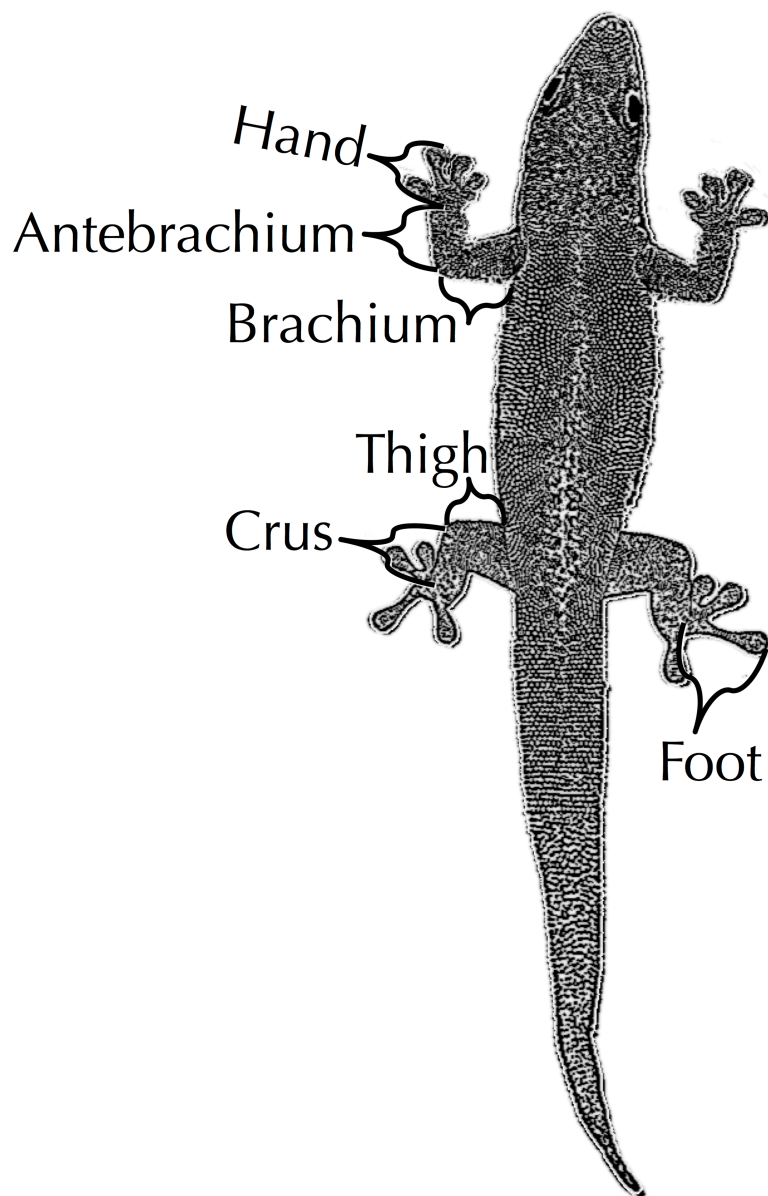


Fig 1. Limb measurements. Our limb measurements included hand length (from the center of the wrist joint to the tip of longest digit measured on the dorsal side), antebrachium length (from apex of the elbow joint to center of the wrist joint, on the dorsal side), brachium length (from the axilla to apex of the elbow joint), thigh length (from the point in which the hind limb enters the body to the apex of the knee); crus length (from the apex of the knee to the ankle joint); and foot length (from the center of ankle joint to the tip of longest digit, toe four, measured on the dorsal side).

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and hind limb lengths for each individual gecko observed (S1 Table). Investigator T. Hagey collected all gecko morphological measurements. Adjustments for the various sources of our measurements, *i.e.* wild, captive, or museum specimens or previously published data, were not made. All of our external morphological measurements were dictated by the underlying skeletal structure and not soft tissue. We feel the potential error introduced due to variation in specimen source was likely minimal compared to the differences we observed between species.

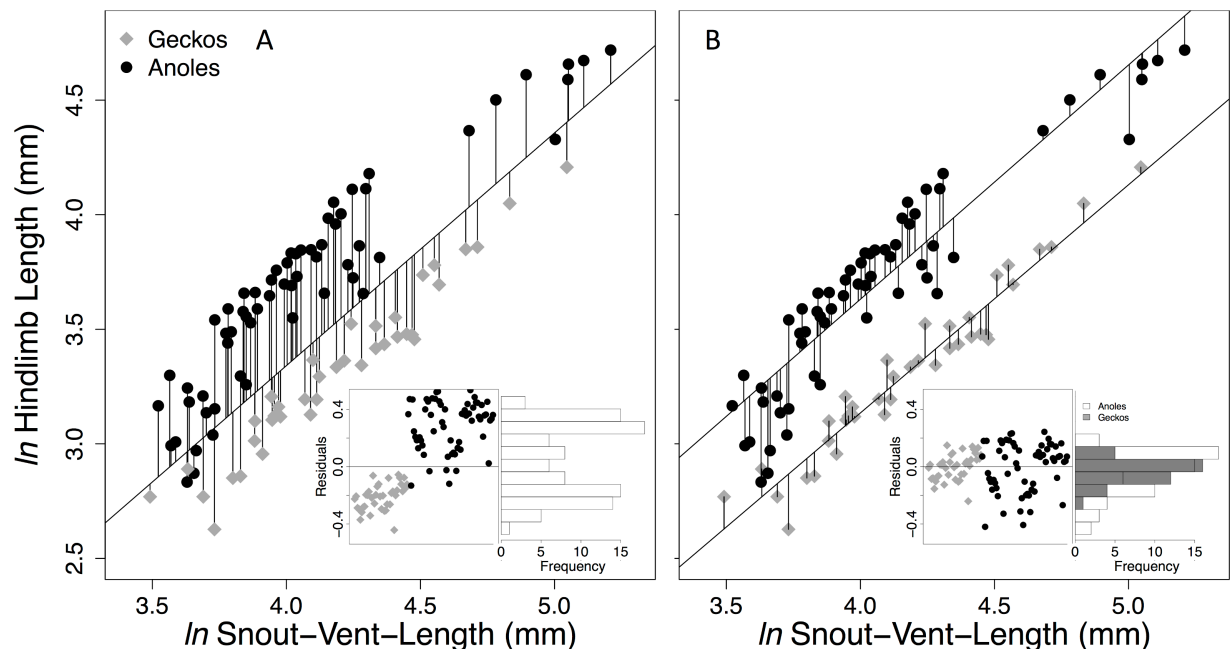


Fig 2. Body and total hind limb lengths. Pad-bearing gecko (grey) and anole (black) residuals from a single regression (A) and residuals from clade-specific regressions (B). Variation in residuals is shown in inserted scatter plots and horizontal bar graphs.

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Microhabitat use

We examined microhabitat use for 63 species of anole and 13 species (69 individuals) of pad-bearing gecko (S1 Table). Anole information came from the literature [13, 54]. To collect gecko habitat use in the field, our field techniques were approved by the University of Idaho animal care and use committee (protocol #2012–14), the James Cook University Animal Ethics committee (JCU-A1813), and the Queensland Department of Environment and Heritage Protection (scientific collection permit #WISP11483112). Geckos were observed in Queensland, Australia during September and October 2012. Observations and collections were carried out while geckos were active, between sunset and midnight. We recorded the substratum on which animals were first sighted, categorizing them as vegetation, rock, or ground. Individuals observed on rocks were on either large boulders or rock outcrops. We calculated the proportion of observations occurring on each substrate for each species. When geckos were observed on vegetation, perch height and diameter were measured at the point of initial observation. Perch angle was recorded for all perches using a digital goniometer (Johnson model #40–6060) with measurements ranging from 0° i.e., a flat surface, 90° representing a vertical surface, and beyond 90° indicating an inverted surface. Specimens were captured by hand. After we collected morphological measurements, specimens were euthanized using MS-222 (tricaine methanesulfonate; [55]), formalin-fixed, and prepared as museum specimens. Fifty preserved specimens were submitted to the Queensland Museum (S2 Table). Individuals not euthanized were released twenty-four hours after capture at their original point of capture.

Analyses

To conduct our analyses, we used the R Studio statistical software version 0.98.501 [56]. To ensure normality before statistical analyses, species mean perch diameter, perch height, limb lengths, and SVL were natural-log transformed. Our proportional perch-type observations

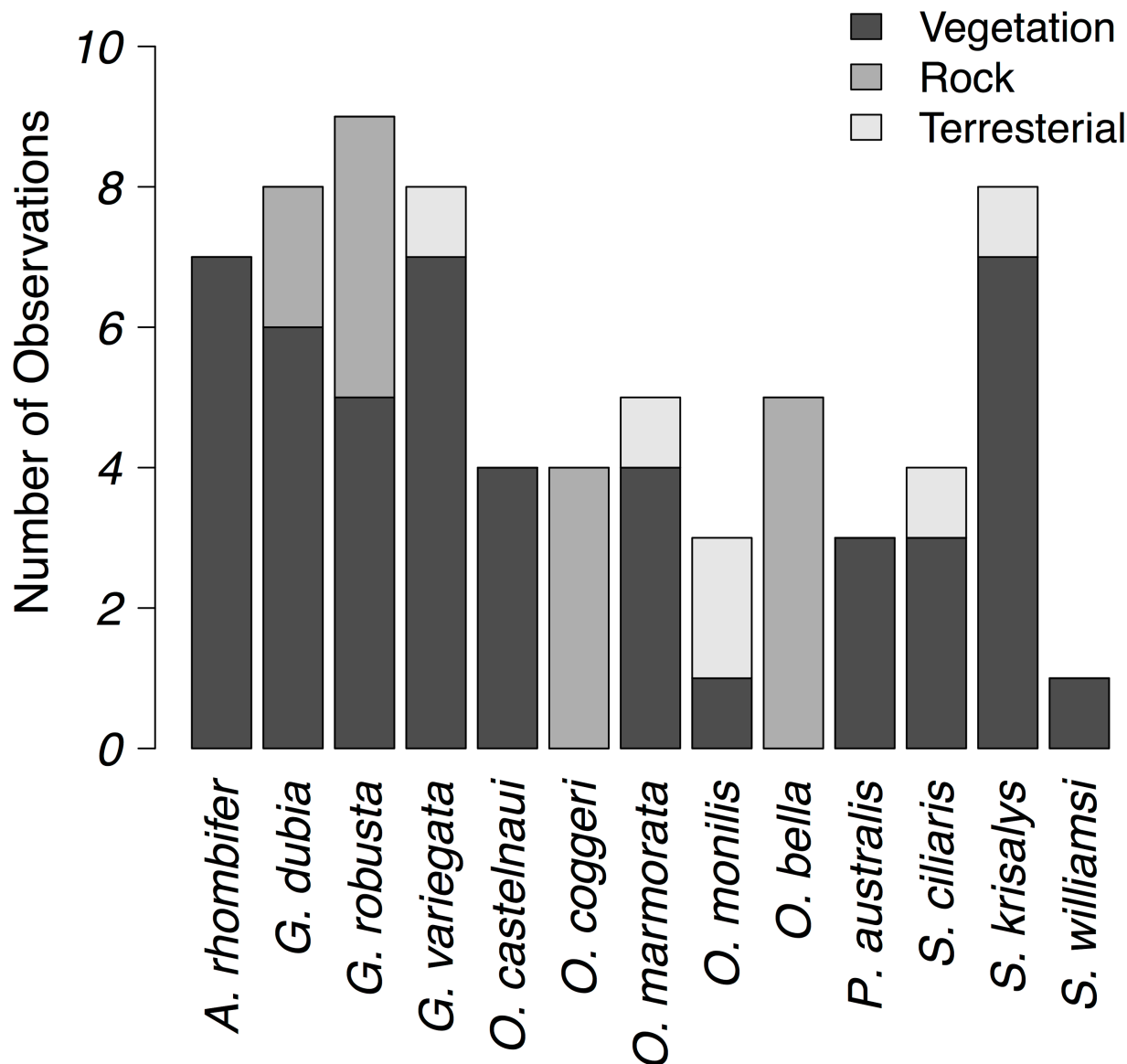


Fig 3. Perche types used by geckos observed in Queensland, Australia. The number of individual geckos observed using vegetation (dark gray), rocks (medium gray), and the ground (light gray) are shown.

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were arcsine square-root transformed. Perch angle was not transformed. After calculating and natural-log transforming our species-mean limb length measurements, we extracted residuals from SVL-limb length phylogenetic generalized least squares regressions (PGLS) using the *ape* package [57], to calculate size-independent limb measurements. We used a pruned ultrametric squamate phylogeny [58]. We calculated residual limb lengths using geckos and anoles together, as well as residuals for geckos and anoles separately (see Results). To evaluate correlations between morphology and ecology, we used PGLS via the *caper* library [57, 59, 60] and the same phylogeny [58]. This approach also estimated Pagel's λ , which is bounded between zero (phylogenetic relationship is not related to the residuals) and one (residuals evolve under Brownian motion).

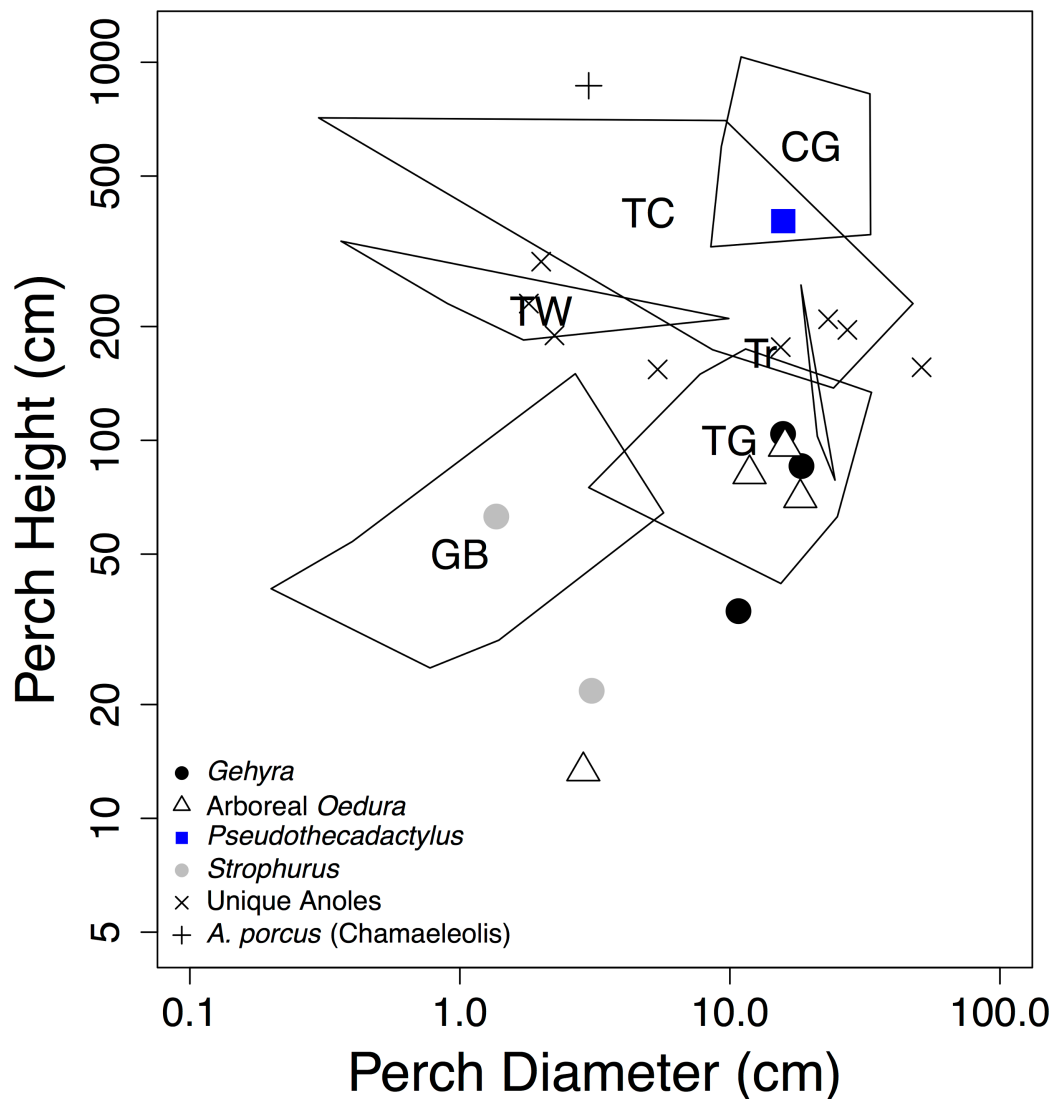


Fig 4. Perch heights and perch diameters of Caribbean anole ecomorphs and arboreal geckos from Queensland Australia. Polygons indicate ranges for anole ecomorphs [10, 13, 54]. Note that many geckos use perch heights and diameters that are similar to those used by anole ecomorphs. Symbols are: CG = crown giant, TC = trunk-crown, TW = twig, TG = trunk ground, GB = grass bush, *Gehyra* spp. (black circles), *Oedura* spp. and closely related *Amalosia rhombifer* (white triangles), *Pseudothecadactylus australis* (blue square), *Strophurus* spp. (grey circles), non-ecomorph (unique) anole species (X), and *Anolis porcus* from the subgenus *Chamaeleolis* (+).

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Due to differences between our focal species and the species included in the Pyron and Burbrink phylogeny [58], we reassigned four species in the phylogeny to correspond with observed species. These changes did not greatly affect the information present in the phylogeny. *Pseudothecadactylus lindneri* became *P. australis*, *Afroedura karroica* became *A. loveridgei*, and *Geckolepis maculata* became *Afroedura hawequensis*. In the Pyron and Burbrink phylogeny *Geckolepis* is sister to *Afroedura* [58]. As a result, the only affect of substituting *Afroedura hawequensis* into *Geckolepis*, as opposed to substituting it as another species of *Afroedura*, which was not available, is that the age of the node between *A. hawequensis* and *A. loveridgei*

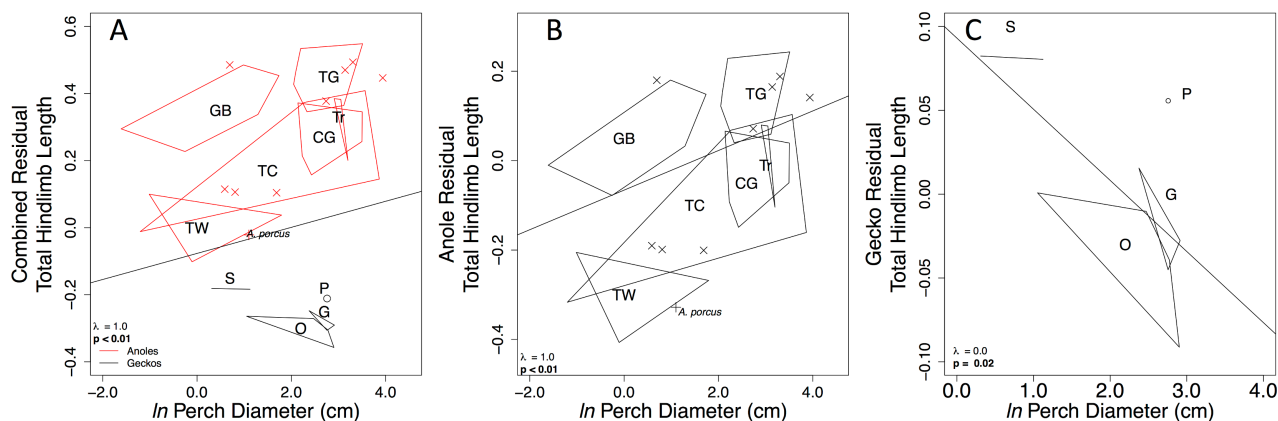


Fig 5. Relationships between relative limb length and perch diameter. Regression residuals of combined geckos and anoles (A), clade-specific regression residuals for anoles only (B), and geckos only (C). All plots display the PGLS correlation line, Pagel's λ , and slope p-values. Symbols are: CG = crown giant, TC = trunk-crown, TW = twig, TG = trunk ground, GB = grass bush, non-ecomorph (unique) anole species (X), *Anolis porcus* of the subgenus *Chamaeleolis* (+), *Gehyra* spp. = G, arboreal *Oedura* spp. and closely related *Amalosia rhombifer* = O, *Pseudothecadactylus australis* = P, *Strophurus* spp. = S. Plot A illustrates a positive correlation with anole data in red and gecko data in black. Plot B illustrates the positive correlation for anoles only. Plot C displays the negative correlation for geckos only.

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may be overestimated. We also collected data from the recently described *Oedura bella* [61]. We assumed a similar age of divergence between *Oedura marmorata* and *O. bella* as Pyron and Burbrink [58] observed between *O. marmorata* and its sister species *O. gemmata*, because Oliver et al. [61, 62] hypothesized deep divergences between *O. marmorata* and *O. bella*, similar to the distance between *O. marmorata* and *O. gemmata*. Lastly, we would like to note that the Pyron and Burbrink [58] phylogeny differed from previously published phylogenies, specifically within the genus *Strophurus* [63, 64]. We retained the topology of Pyron and Burbrink [58] and suggest additional sampling to resolve conflicts.

Results

Morphology

Overall, geckos had relatively shorter hind limbs than anoles (Fig 2). When we calculated residual total hind limb length combining geckos and anoles, the resulting residual lengths were not normally distributed (Shapiro-Wilk normality test, $p < 0.01$, see Fig 2A inserts). All gecko species had negative residual hind limb lengths and nearly all anoles had positive residuals, resulting in a bimodal distribution (Fig 2A insert). When we calculated residual limb lengths for each group separately (Fig 2B), this approach generated normally distributed residuals for geckos (Shapiro-Wilk normality test $p = 0.5$, see Fig 2B inserts), yet the anole residuals still differed significantly from normal with a negative skew (Shapiro-Wilk normality test $p < 0.01$, see Fig 2B inserts).

Microhabitat

We observed a wide variation in substratum used by geckos in Queensland. Our focal gecko species were observed using vegetation (*Amalosia rhombifer*, *Gehyra dubia*, *G. variegata*, *Oedura castelnaui*, *O. marmorata*, *Pseudothecadactylus australis*, *Strophurus ciliaris*, *S. krisalys*, and *S. williamsi*), rock (*Oedura coggeri* and *Oedura bella*), or a combination of perch types (*Gehyra robusta* and *Oedura monilis*, Fig 3).

We observed perch diameter and height values that overlapped with described anole ecomorphs (Fig 4). *Pseudothecadactylus australis* used large-diameter perches, high above the

ground, very similar perch characteristics as anole trunk-crown and crown-giant ecomorphs (Fig 4). Similarly, the habitat use of most *Gehyra* and arboreal *Oedura* species overlapped with the anole trunk-ground ecomorph, as these geckos usually used vertical tree trunks (Fig 4). Geckos of the genus *Strophurus* used narrow perches near the ground, similar to grass-bush anoles (Fig 4). In addition, *Strophurus* and grass-bush anoles both also have relatively long limbs (Fig 5B and 5C). *Oedura monilis* and *Gehyra robusta* differed in microhabitat use from that of trunk-ground anoles, both using rocks and terrestrial microhabitats, in addition to arboreal perches (Figs 3 and 4). We also observed a nearly significant relationship between gecko perch height and diameter (S1 Fig).

Considering species for which we had both morphological and ecological observations, we examined the relationship between limb length and perch diameter, using residual limb lengths calculated from geckos and anoles combined and separate (Fig 5). Residual limb lengths calculated by combining anoles and geckos were positively correlated with perch diameter (Fig 5A, $\lambda = 1.0$, $p < 0.01$), suggesting that, across all focal species, species with relatively longer limbs use wider perches. Residual limb lengths calculated for each group separately suggested different patterns. Residuals of anole limb length were significantly positively correlated with perch diameter (Fig 5B, $\lambda = 1.0$, $p < 0.01$), consistent with previously published observations. Conversely, when we examined gecko limb length versus perch diameter, limb length was significantly negatively correlated with perch diameter (Fig 5C, hind total $\lambda = 0.0$, $p < 0.02$), suggesting that gecko species with relatively longer limbs use narrower perches. Closer examination revealed geckos with relatively longer thigh, crus, brachium, and antebrachium segments used narrower perches (thigh: $\lambda = 0.0$, $p < 0.01$; crus: $\lambda = 0.0$, $p < 0.01$; foot: $\lambda = 1.0$, $p = 0.8$; brachium: $\lambda = 0.0$, $p < 0.01$; antebrachium: $\lambda = 0.0$, $p = 0.02$; hand: $\lambda = 1.0$, $p = 0.8$; fore total: $\lambda = 0.2$, $p = 0.05$).

Other Microhabitat considerations

When considering additional morphological and microhabitat relationships, including perch type and perch angle, we found that geckos we observed using vegetation had significantly shorter thigh and brachium segments and slightly longer hand segments. Hand length was weakly positively correlated with the use of vegetation (thigh: $\lambda = 1.0$, $p = 0.01$, Fig 6; crus: $\lambda = 0.0$, $p = 0.4$; foot: $\lambda = 1.0$, $p = 0.3$; hind total: $\lambda = 0.0$, $p = 0.7$; brachium: $\lambda = 1.0$, $p = 0.03$; antebrachium: $\lambda = 1.0$, $p = 0.6$; hand: $\lambda = 1.0$, $p = 0.08$; fore total: $\lambda = 1.0$, $p = 0.4$). We also observed geckos using steeper perches with relatively shorter thigh, crus, brachium, antebrachium, and total fore- and hind limb segment lengths as compared to species using more horizontal surfaces (thigh: $\lambda = 0.0$, $p = 0.01$; crus: $\lambda = 0.0$, $p = 0.04$; foot: $\lambda = 1.0$, $p = 0.8$; hind total: $\lambda = 0.0$, $p = 0.02$, Fig 7; brachium: $\lambda = 0.0$, $p = 0.03$; antebrachium: $\lambda = 0.0$, $p = 0.02$; hand: $\lambda = 1.0$, $p = 0.8$; fore total: $\lambda = 0.4$, $p = 0.03$).

Discussion

In this study, we compared limb lengths and microhabitat use of gecko and anole lizards. Our data suggest that geckos, as a group, have relatively shorter limbs than anoles, i.e. they had a lower y-intercept, or coefficient of allometry [65]. Even after adjusting for phylogenetic non-independence in our data, when geckos and anoles were analyzed together, all limb length residuals of geckos were negative, whereas residuals of nearly all anoles were positive (Fig 2A). This overall difference in limb lengths between geckos and anoles can only be observed when analyzing these groups together (Fig 2A). However, when using residuals calculated this way in secondary analyses, such as investigations of limb length and microhabitat use, interesting relationships maybe disguised as we discovered (Fig 5B and 5C). This a phenomenon should be considered when comparing distantly related groups.

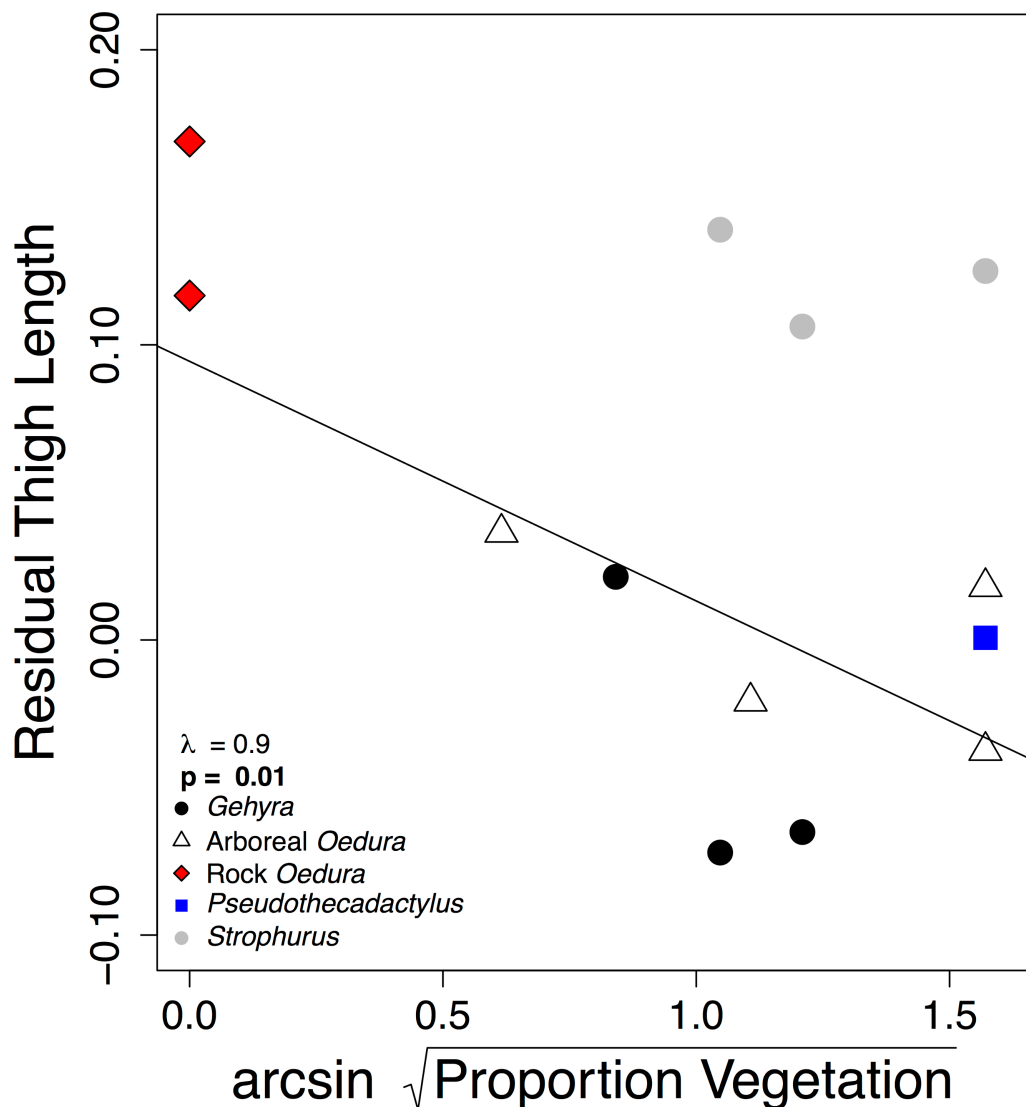


Fig 6. Negative correlation between residual thigh lengths and the proportion of vegetation use for each species. Brachium segment length showed a similar pattern. Symbols are: arboreal *Gehyra* spp. (black circles), arboreal *Oedura* spp. and closely related *Amalosia rhombifer* (white triangles), rock-dwelling *Oedura* spp. (red diamonds), arboreal *Pseudothecadactylus australis* (blue square), and arboreal *Strophurus* spp. (grey circles). Line = PGLS model with estimated Pagel's λ and slope p-values.

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We observed arboreal gecko species and Caribbean anoles using similar microhabitats (Fig 4). For example, *Strophurus* geckos are ecologically and morphologically similar to grass-bush anoles. Both groups use narrow perches low to the ground (Fig 4) and have relatively long limbs (Fig 5A and 5B). Further investigations comparing arboreal gecko habitat use to mainland anoles would prove very interesting. Mainland anoles, although also arboreal, do not exhibit repeated ecomorphs. We also predicted that shorter-limbed arboreal geckos would use narrower perches, similar patterns reported in anoles, *Draco*, and *Tropidurus* [6, 9–11, 14, 18]. However, we observed the opposite pattern: geckos using narrower perches had relatively longer, not shorter, limbs (Fig 5). Our results illustrate that although our focal geckos and anoles used very similar microhabitats, they have different morphological-ecological relationships. Previous studies have cited a trade-off between speed and balance to explain the negative limb

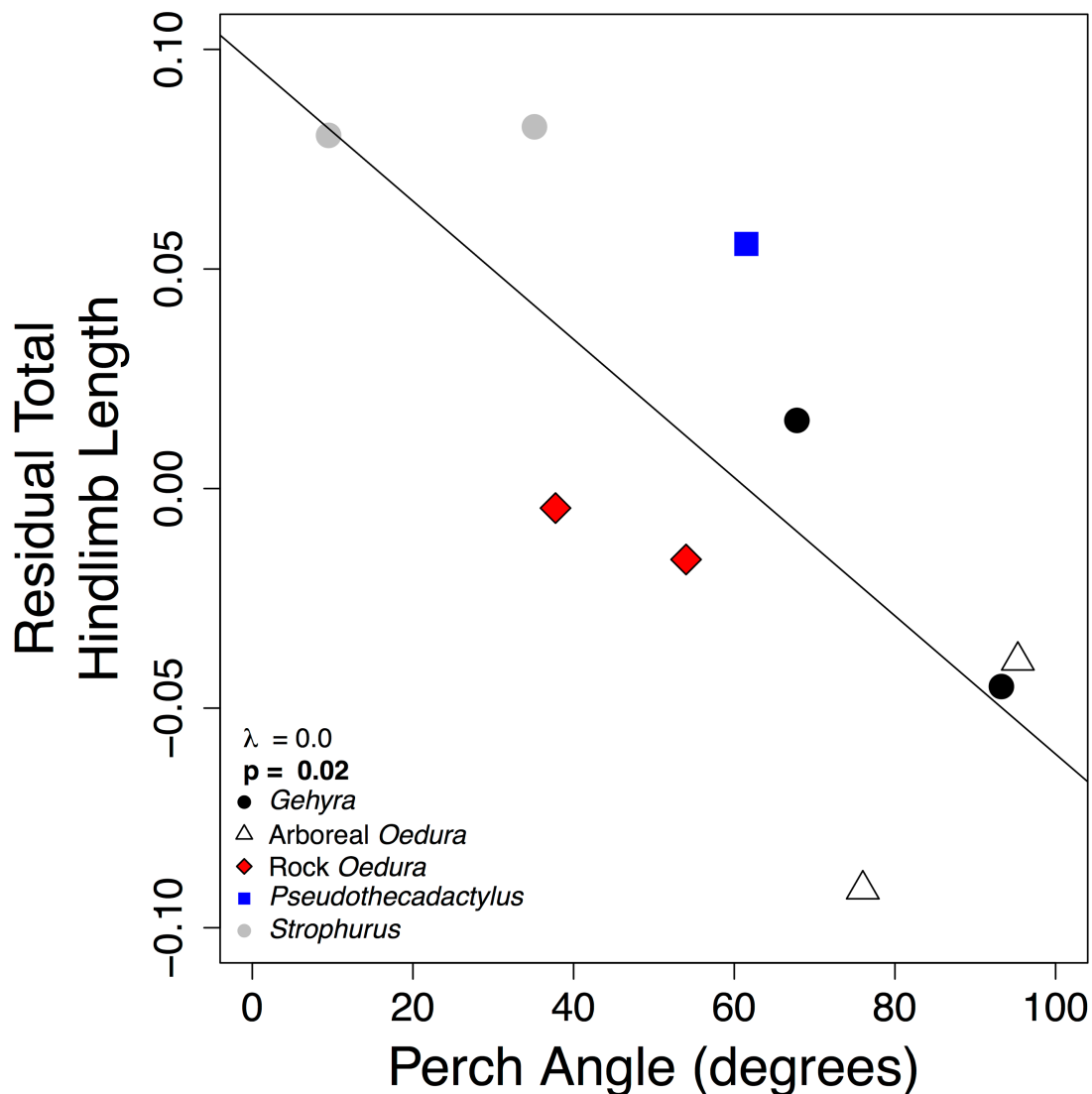


Fig 7. Negative correlation between perch angle and total hind limb length. Residual thigh, crus, brachium, antebrachium, and total fore segment lengths had a similar pattern. Symbols are: arboreal *Gehyra* spp. (black circles), arboreal *Oedura* spp. and closely related *Amalosia rhombifer* (white triangles), rock-dwelling *Oedura* spp. (red diamonds), arboreal *Pseudothecadactylus australis* (blue square), and arboreal *Strophurus* spp. (grey circles). Line = PGLS model with estimated Pagel's λ and slope p-values.

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length perch diameter relationship observed in other lizards [6, 16, 19, 66, 67]. Since the Queensland gecko species we observed did not display this same morphological-ecological relationship, perhaps geckos are not sensitive to the same speed and balance trade-off and negotiate narrow perches differently (see S2 Fig for additional analyses considering absolute hind limb length and perch diameter). In particular, while both geckos and anoles have adhesive pads (*Draco* and *Tropidurus* lack adhesive pads), geckos generally generate greater frictional and adhesive forces (negative normal forces) compared to anoles [26, 68, 69], possibly allowing geckos to resist better lateral forces and cling to narrow perches. Previous locomotor studies of arboreal pad-bearing lizards have found that lizards tend to lower their center of

mass on narrower perches [70–74]. Future studies incorporating species limb length, adhesive capabilities, and perch diameter would be very informative.

Other Microhabitat considerations

Studies of lizard functional morphology have also considered limb length in non-arboreal microhabitats [75–78]. For example, many studies have reported long-limbed species living on rocks, but this may not be a general trend [52, 53, 79, 80]. Similar to most previous studies, the geckos we observed more frequently on vegetation, as opposed to rocks, had significantly shorter thigh and brachium limb segments. In addition, perch diameter may not be the only variable influencing scansorial locomotion in lizards. Perch texture is likely an important factor influencing locomotion, especially of padded lizards. Although much theoretical work has been done considering surface texture and gecko performance [33, 35, 41, 42, 81, 82], few studies have examined shear forces and adhesion separately in regards to their relationship to texture and microhabitat use (but see [42]). We often observed arboreal Australian geckos using ironbark (*Eucalyptus* spp.) and paperbark (*Melaleuca* spp.) trees. Generating clinging forces on these surfaces would be difficult due to the bark of ironbark trees is very rough, with large valleys and ridges, greatly limiting the available surface area for adherence [42]. The bark of paperbark trees is smooth, but dusty and flaky, again limiting a species' clinging ability and likely fouling their toe pads (see [83, 84]). In addition to perch texture, perch angle also likely affects scansorial lizard locomotion. Perch angle, defined the angular incline, above the horizontal, of the support, correlates with lizard adhesive toe pad size [44, 48, 85] and affects locomotor kinematics and sprint speed in some but not all lizards [25, 66, 71, 86–88]. The focal gecko species we observed using steeper perches also had relatively shorter limbs. Lizards may also navigate arboreal habitats using different locomotor strategies; for example, chameleons and twig anoles typically move along the top of single branches and twigs, whereas lacertids have been reported to “clamber” over, under, and around branches and twigs [18, 66, 89]. This clambering style may also describe how *Strophurus* and grass-bush anoles move through arboreal microhabitats. Our results suggest that there may be subtle relationships linking limb length, perch angle, and the adhesive system [6, 25, 50, 90–92]. Shorter thigh and brachium limb lengths may bring the body closer to the surface and reduce the chance of toppling off steep perches. It might be fruitful to consider microhabitats in terms of the behavior or locomotion that is associated with them, instead of categorically by composition, to improve our understanding of the biomechanics of scansorial lizards [6, 11, 66, 67, 93–98].

In this study, we measured individual limb segment lengths in addition to total limb length. This approach allowed for a more detailed understanding of the interaction between microhabitat and the locomotor system. We found differences between pad-bearing geckos and anoline lizards suggesting that although both groups have evolved similar fibrillar adhesive systems and use similar arboreal microhabitats, their relative limb lengths differ with different morphological-microhabitat relationships. These results provide an example of how morphologically and ecologically convergent systems have aspects of historical contingency and group-specific idiosyncrasies that likely impact their ecology, evolution, and adaptation.

Supporting information

S1 Table. Species means. Over the course of this study, we collected two datasets, a microhabitat dataset and a morphological data. Our anole data were compiled with the assistance of J. Losos [13, 54]. We collected gecko habitat use measurements from Queensland, Australia. 95% confidence intervals are shown in parentheses. Microhabitat column header abbreviations are PH: perch height; ArbPD: arboreal perch diameter; PercTree: proportion of observations

on vegetation; PA: perch angle; N: number of individuals; Location: location of observations in Queensland; and anoline Ecomorphs: TG: trunk-ground, TC: trunk-crown, T: trunk, GB: grass-bush, TW: twig, CG: crown-giant, U: unique (non-ecomorph), CH: subgenus *Chamaeleolis*). Morphological column header abbreviations are N: number of individuals; SVL: snout-vent-length; FTotal: Total front limb length; Thigh; Crus; Foot; HTotal: Total hindlimb length; Brachium; Antebrachium; Hand; and FTotal: Total front limb length (see [Fig 1](#)).

(XLSX)

S2 Table. Collected specimens deposited in the Queensland Museum. We submitted 50 wild caught lizard specimens to the Queensland Museum. Please note that species names may have been changed to follow the museum's current species designations.

(XLSX)

S1 Fig. Perch height vs perch diameter. Using a phylogenetic generalized least squares approach, we compared the relationship between perch height and perch diameter, both natural log transformed, of the perches we observed geckos using in Queensland. With an estimated λ of 0.0, we observed a near significant relationship ($p = 0.07$), suggesting that the high perches we observed geckos on also tended to be thick. We do not feel this weak relationship confounded our results.

(PDF)

S2 Fig. Absolute limb length vs perch diameter. Using a phylogenetic generalized least squares approach, we considered the relationship between absolute hind limb length and perch diameter, both natural log transformed, for our observed Queensland geckos and Caribbean anoles. Note that both plots have the same axes. While we found no significant relationship within our focal geckos ($p = 0.7$), we did observe a significant relationship for anoles ($p < 0.01$). Overall, it appears that our observed geckos are using perches of similar diameter as compared to anoles (mostly tree trunks wider than 10 cm), but with shorter absolute limb lengths. This may suggest the limb length–perch diameter trade off observed in anoles is not present in geckos.

(PDF)

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Author Contributions

Conceptualization: Travis J. Hagey, Luke J. Harmon.

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References

1. Autumn K, Ryan MJ, Wake DB. Integrating historical and mechanistic biology enhances the study of adaptation. *Q Rev Biol.* 2002; 77(4):383–408. Epub 2003/02/26. PMID: [12599913](#)
2. Wainwright PC, Reilly SM. *Ecological Morphology*. Chicago IL: University of Chicago Press; 1994.
3. Melville J, Harmon LJ, Losos JB. Intercontinental community convergence of ecology and morphology in desert lizards. *P R Soc B.* 2006; 273(1586):557–63.
4. Sistrom M, Edwards DL, Donnellan S, Hutchinson M. Morphological differentiation correlates with ecological but not with genetic divergence in a *Gehyra* gecko. *J Evol Biol.* 2012; 25(4):647–60. <https://doi.org/10.1111/j.1420-9101.2012.02460.x> PMID: [22269015](#)
5. Losos JB. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. *Annual Review of Ecology and Systematics.* 1994; 25:467–93.
6. Losos JB. *Lizards in an evolutionary tree: the ecology of adaptive radiation in anoles*. Berkeley: University of California Press; 2009. 507 p.
7. Arnold SJ. Morphology, performance and fitness. *Am Zool.* 1983; 23(2):347–61.
8. Schulte JA, Losos JB, Cruz FB, Nunez H. The relationship between morphology, escape behaviour and microhabitat occupation in the lizard clade Liolaemus (Iguanidae: Tropidurinae: Liolaemini). *J Evol Biol.* 2004; 17(2):408–20. <https://doi.org/10.1046/j.1420-9101.2003.00659.x> PMID: [15009274](#)
9. Kohlsdorf T, Garland T, Navas CA. Limb and tail lengths in relation to substrate usage in *Tropidurus* lizards. *J Morphol.* 2001; 248(2):151–64. <https://doi.org/10.1002/jmor.1026> PMID: [11304746](#)
10. Ord TJ, Klomp DA. Habitat partitioning and morphological differentiation: the Southeast Asian *Draco* lizards and Caribbean *Anolis* lizards compared. *Oecologia.* 2014; 175(2):651–66. <https://doi.org/10.1007/s00442-014-2921-y> PMID: [24658764](#)
11. Losos JB, Sinervo B. The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J Exp Biol.* 1989; 145:23–30.
12. Losos JB. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution.* 1990; 44(5):1189–203. <https://doi.org/10.1111/j.1558-5646.1990.tb05225.x> PMID: [28563896](#)
13. Losos JB. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards—an evolutionary analysis. *Ecol Monogr.* 1990; 60(3):369–88.
14. Losos JB, Irschick DJ. The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory predictions and field tests. *Anim Behav.* 1996; 51:593–602.
15. Irschick DJ, Losos JB. A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution.* 1998; 52(1):219–26. <https://doi.org/10.1111/j.1558-5646.1998.tb05155.x> PMID: [28568148](#)
16. Macrini TE, Irschick DJ. An intraspecific analysis of trade-offs in sprinting performance in a West Indian lizard species (*Anolis lineatopus*). *Biol J Linn Soc.* 1998; 63(4):579–91.

17. Calsbeek R, Irschick DJ. The quick and the dead: Correlational selection on morphology, performance, and habitat use in island lizards. *Evolution*. 2007; 61(11):2493–503. <https://doi.org/10.1111/j.1558-5646.2007.00206.x> PMID: 17725626
18. Jones ZM, Jayne BC. Perch diameter and branching patterns have interactive effects on the locomotion and path choice of anole lizards. *J Exp Biol*. 2012; 215(12):2096–107.
19. Losos JB, Walton BM, Bennett AF. Trade-Offs between Sprinting and Clinging Ability in Kenyan Chameleons. *Funct Ecol*. 1993; 7(3):281–6. <https://doi.org/10.2307/2390206>
20. Fischer MS, Krause C, Lilje KE. Evolution of chameleon locomotion, or how to become arboreal as a reptile. *Zoology*. 2010; 113(2):67–74. <https://doi.org/10.1016/j.zool.2009.07.001> PMID: 19747806
21. Irschick DJ, Vitt LJ, Zani PA, Losos JB. A comparison of evolutionary radiations in mainland and Caribbean *Anolis* lizards. *Ecology*. 1997; 78(7):2191–203. [https://doi.org/10.1890/0012-9658\(1997\)078\[2191:Acoer\]2.0.Co;2](https://doi.org/10.1890/0012-9658(1997)078[2191:Acoer]2.0.Co;2)
22. Gamble T, Greenbaum E, Jackman TR, Russell AP, Bauer AM. Repeated origin and loss of adhesive toepads in geckos. *PLoS ONE*. 2012; 7(6):e39429. <https://doi.org/10.1371/journal.pone.0039429> PMID: 22761794
23. Ruibal R, Ernst V. The structure of the digital setae of lizards. *J Morphol*. 1965; 117(3):271–93. <https://doi.org/10.1002/jmor.1051170302> PMID: 5883924
24. Russell AP. Integrative Functional Morphology of the Gekkotan Adhesive System (Reptilia: Gekkota). *Integr Comp Biol*. 2002; 42(6):1154–63. <https://doi.org/10.1093/icb/42.6.1154> PMID: 21680400
25. Russell AP, Higham TE. A new angle on clinging in geckos: incline, not substrate, triggers the deployment of the adhesive system. *Proc R Soc B*. 2009; 276(1673):3705–9. <https://doi.org/10.1098/rspb.2009.0946> PMID: 19656797
26. Irschick DJ, Austin CC, Petren K, Fisher RN, Losos JB, Ellers O. A comparative analysis of clinging ability among pad-bearing lizards. *Biol J Linn Soc*. 1996; 59(1):21–35.
27. Russell AP. Parallelism and integrated design in the foot structure of gekkonine and diplodactyline geckos. *Copeia*. 1979; 1979(1):1–21.
28. Russell AP, Baskerville J, Gamble T, Higham TE. The evolution of digit form in *Gonatodes* (Gekkota: Sphaerodactylidae) and its bearing on the transition from frictional to adhesive contact in gekkotans. *J Morphol*. 2015; 276(11):1311–32. <https://doi.org/10.1002/jmor.20420> PMID: 26248497
29. Bauer A, Russell A. Alternative digital scansor design in the New Caledonian gekkonid genera *Bavayia* and *Eurydactylodes*. *Mem Qld Mus*. 1990; 29:299–310.
30. Hagey TJ, Puthoff JB, Holbrook M, Harmon LJ, Autumn K. Variation in setal micromechanics and performance of two gecko species. *Zoomorphology*. 2014; 133(2):111–26. <https://doi.org/10.1007/S00435-013-0207-2>
31. Autumn K, Dittmore A, Santos D, Spenko M, Cutkosky M. Frictional adhesion: a new angle on gecko attachment. *J Exp Biol*. 2006; 209(18):3569–79.
32. Autumn K, Majidi C, Groff RE, Dittmore A, Fearing R. Effective elastic modulus of isolated gecko setal arrays. *J Exp Biol*. 2006; 209(18):3558–68.
33. Huber G, Gorb SN, Hosoda N, Spolenak R, Arzt E. Influence of surface roughness on gecko adhesion. *Acta Biomater*. 2007; 3(4):607–10. <https://doi.org/10.1016/j.actbio.2007.01.007> PMID: 17376751
34. Pesika NS, Gravish N, Wilkinson M, Zhao B, Zeng H, Tian Y, et al. The Crowding Model as a Tool to Understand and Fabricate Gecko-Inspired Dry Adhesives. *J Adhesion*. 2009; 85(8):512–25.
35. Pugno NM, Lepore E. Observation of optimal gecko's adhesion on nanorough surfaces. *BioSystems*. 2008; 94(3):218–22. <https://doi.org/10.1016/j.biosystems.2008.06.009> PMID: 18718501
36. Yamaguchi T, Gravish N, Autumn K, Creton C. Microscopic Modeling of the Dynamics of Frictional Adhesion in the Gecko Attachment System. *J Phys Chem B*. 2009; 113(12):3622–8. PMID: 19673062
37. Elstrott J, Irschick DJ. Evolutionary correlations among morphology, habitat use and clinging performance in Caribbean *Anolis* lizards. *Biol J Linn Soc*. 2004; 83(3):389–98.
38. Macrini TE, Irschick DJ, Losos JB. Ecomorphological differences in toepad characteristics between mainland and island anoles. *J Herpetol*. 2003; 37(1):52–8.
39. Zani PA. The comparative evolution of lizard claw and toe morphology and clinging performance. *J Evol Biol*. 2000; 13(2):316–25.
40. Crandell KE, Herrel A, Sasa M, Losos JB, Autumn K. Stick or grip? Co-evolution of adhesive toepads and claws in *Anolis* lizards. *Zoology*. 2014; 117(6):363–9. <https://doi.org/10.1016/j.zool.2014.05.001> PMID: 25069967
41. Russell AP, Johnson MK. Real-world challenges to, and capabilities of, the gekkotan adhesive system: contrasting the rough and the smooth. *Can J Zool*. 2007; 85(12):1228–38.

42. Russell AP, Johnson MK. Between a rock and a soft place: microtopography of the locomotor substrate and the morphology of the setal fields of Namibian day geckos (Gekkota: Gekkonidae: *Rhoptropus*). *Acta Zool.* 2014; 95:299–318.
43. Lamb T, Bauer AM. Footprints in the sand: independent reduction of subdigital lamellae in the Namib–Kalahari burrowing geckos. *Proc R Soc B.* 2010; 273(1588):855–64.
44. Collins CE, Russell AP, Higham TE. Subdigital adhesive pad morphology varies in relation to structural habitat use in the Namib Day Gecko. *Funct Ecol.* 2015; 29:66–77. <https://doi.org/10.1111/1365-2435.12312>
45. Johnson MK, Russell AP, Bauer AM. Locomotor morphometry of the *Pachydactylus* radiation of lizards (Gekkota: Gekkonidae): a phylogenetically and ecologically informed analysis. *Can J Zool.* 2005; 83(12):1511–24.
46. Pianka ER, Huey RB. Comparative ecology, resource utilization and niche segregation among gekkonid lizards in the Southern Kalahari. *Copeia.* 1978; 1978(4):691–701.
47. Zaaf A, Herrel A, Aerts P, De Vree F. Morphology and morphometrics of the appendicular musculature in geckoes with different locomotor habits (Lepidosauria). *Zoomorphology.* 1999; 119(1):9–22.
48. Higham TE, Russell AP. Divergence in locomotor performance, ecology, and morphology between two sympatric sister species of desert-dwelling gecko. *Biol J Linn Soc.* 2010; 101(4):860–9.
49. Carillo de Espinoza N, Rothenstein D, Salas A, Werner YL. Radiation and convergence among desert geckos: *Phyllodactylus* species resembling both *Ptyodactylus* and *Stenodactylus*. *Amphibia-Reptilia.* 1990; 11(1):1–13. <https://doi.org/10.1163/156853890X00267>
50. Harmon LJ, Harmon LL, Jones CG. Competition and community structure in diurnal arboreal geckos (genus *Phelsuma*) in the Indian Ocean. *Oikos.* 2007; 116(11):1863–78.
51. Bauer AM, Jackman T, Sadlier RA, Whitaker AH. Review and phylogeny of the New Caledonian diplodactylid gekkotan genus *Eurydactylodes* Wermuth, 1965, with the description of a new species. *Mémoires du Muséum national d'histoire naturelle.* 2009; 198:13–36.
52. Vitt LJ, Caldwell JP, Zani PA, Titus TA. The role of habitat shift in the evolution of Lizard morphology: Evidence from tropical *Tropidurus*. *P Natl Acad Sci USA.* 1997; 94(8):3828–32.
53. Goodman BA, Miles DB, Schwarzkopf L. Life on the Rocks: Habitat Use Drives Morphological and Performance Evolution in Lizards. *Ecology.* 2008; 89(12):3462–71. PMID: [19137951](https://pubmed.ncbi.nlm.nih.gov/19137951/)
54. Losos JB. An Approach to the Analysis of Comparative Data When a Phylogeny Is Unavailable or Incomplete. *Syst Biol.* 1994; 43(1):117–23. <https://doi.org/10.2307/2413584>
55. Conroy CJ, Papenfuss T, Parker J, Hahn NE. Use of Tricaine Methanesulfonate (MS222) for Euthanasia of Reptiles. *J Am Assoc Lab Anim.* 2009; 48(1):28–32.
56. RStudio Team. RStudio: Integrated Development Environment for R. 0.98.501 ed. Boston, MA: RStudio, Inc; 2015.
57. Paradis E, Claude J, Strimmer K. APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics.* 2004; 20(2):289–90. <https://doi.org/10.1093/Bioinformatics/Btg412> PMID: [14734327](https://pubmed.ncbi.nlm.nih.gov/14734327/)
58. Pyron RA, Burbrink FT. Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. *Ecol Lett.* 2013; 17(1):13–21. Epub 2013/08/21. <https://doi.org/10.1111/ele.12168> PMID: [23953272](https://pubmed.ncbi.nlm.nih.gov/23953272/).
59. Orme CDL, Freckleton RP, Thomas GH, Petzoldt T, Fritz SA. caper: Comparative Analyses of Phylogenetics and Evolution in R. (<http://R-ForgeR-project.org/projects/caper/>). 2011.
60. Pagel M. Inferring the historical patterns of biological evolution. *Nature.* 1999; 401(6756):877–84. <https://doi.org/10.1038/44766> PMID: [10553904](https://pubmed.ncbi.nlm.nih.gov/10553904/)
61. Oliver PM, Doughty P. Systematic revision of the marbled velvet geckos (*Oedura marmorata* species complex, Diplodactylidae) from the Australian arid and semi-arid zones. *Zootaxa.* 2016; 4088(2):151–76. <https://doi.org/10.11646/zootaxa.4088.2.1> PMID: [27394333](https://pubmed.ncbi.nlm.nih.gov/27394333/)
62. Oliver PM, Bauer AM, Greenbaum E, Jackman T, Hobbie T. Molecular phylogenetics of the arboreal Australian gecko genus *Oedura* Gray 1842 (Gekkota: Diplodactylidae): another plesiomorphic grade? *Mol Phylogenet Evol.* 2012; 63(2):255–64. <https://doi.org/10.1016/j.ympev.2011.12.013> PMID: [22209860](https://pubmed.ncbi.nlm.nih.gov/22209860/)
63. Sadlier RA, O'Meally D, Shea GM. A new species of spiny-tailed gecko (Squamata: Diplodactylidae: *Strophurus*) from Inland Queensland. *Mem Queensl Mus.* 2005; 51(2):573–82.
64. Brown D, Wilmer JW, Macdonald S. A revision of *Strophurus taenicauda* (Squamata: Diplodactylidae) with the description of two new subspecies from central Queensland and a southerly range extension. *Zootaxa.* 2012;(3243):1–28.
65. Gould SJ. Geometric similarity in allometric growth: a contribution to the problem of scaling in evolution of size. *Am Nat.* 1971; 105(942):113–&. <https://doi.org/10.1086/282710>

66. Vanhooydonck B, Van Damme R. Evolutionary trade-offs in locomotor capacities in lacertid lizards: are splendid sprinters clumsy climbers? *J Evol Biol*. 2001; 14(1):46–54. <https://doi.org/10.1046/J.1420-9101.2001.00260.X>
67. Goodman BA, Krockenberger AK, Schwarzkopf L. Master of them all: performance specialization does not result in trade-offs in tropical lizards. *Evol Ecol Res*. 2007; 9(3):527–46.
68. Hagey TJ, Puthoff JB, Crandell KE, Autumn K, Harmon LJ. Modeling observed animal performance using the Weibull distribution. *J Exp Biol*. 2016; 219(11):1603–7. <https://doi.org/10.1242/jeb.129940> PMID: 26994180
69. Hagey TJ. Mechanics, Diversity, and Ecology of Gecko Adhesion. Moscow: University of Idaho; 2013.
70. Zhuang MNV, Higham TE. Arboreal Day Geckos (*Phelsuma madagascariensis*) Differentially Modulate Fore- and Hind Limb Kinematics in Response to Changes in Habitat Structure. *Plos One*. 2016; 11(5). <https://doi.org/10.1371/journal.pone.0153520> PMID: 27145027
71. Spezzano LC Jr., Jayne BC. The effects of surface diameter and incline on the hindlimb kinematics of an arboreal lizard (*Anolis sagrei*). *J Exp Biol*. 2004; 207(Pt 12):2115–31. Epub 2004/05/15. PMID: 15143145.
72. Foster KL, Higham TE. How forelimb and hindlimb function changes with incline and perch diameter in the green anole, *Anolis carolinensis*. *J Exp Biol*. 2012; 215(13):2288–300. <https://doi.org/10.1242/jeb.069856> PMID: 22675190
73. Birn-Jeffery AV, Higham TE. Geckos decouple fore- and hind limb kinematics in response to changes in incline. *Front Zool*. 2016; 13. <https://doi.org/10.1186/s12983-016-0144-2> PMID: 26941828
74. Clemente CJ, Withers PC, Thompson GG, Lloyd D. Lizard tricks: overcoming conflicting requirements of speed versus climbing ability by altering biomechanics of the lizard stride. *J Exp Biol*. 2013; 216(20):3854–62.
75. Thompson GG, Clemente CJ, Withers PC, Fry BG, Norman JA. Is body shape of varanid lizards linked with retreat choice? *Australian Journal of Zoology*. 2009; 56(5):351–62.
76. Thompson GG, Withers PC. The relationship between size-free body shape and choice of retreat for Western Australian Ctenophorus (Agamidae) dragon lizards. *Amphibia-Reptilia*. 2005; 26(1):65–72. <https://doi.org/10.1163/1568538053693323>
77. Clemente CJ, Thompson GG, Withers PC. Evolutionary relationships of sprint speed in Australian varanid lizards. *J Zool*. 2009; 278(4):270–80. <https://doi.org/10.1111/j.1469-7998.2009.00559.x>
78. Bauwens D, Garland T, Castilla AM, Vandamme R. Evolution of Sprint Speed in Lacertid Lizards—Morphological, Physiological, and Behavioral Covariation. *Evolution*. 1995; 49(5):848–63. <https://doi.org/10.1111/j.1558-5646.1995.tb02321.x> PMID: 28564867
79. Miles DB. Covariation between Morphology and Locomotor Performance in Sceloporine Lizards. In: Vitt LJ, Pianka ER, editors. *Lizard Ecology: Historical and Experimental Perspectives*. Princeton, NJ: Princeton University Press; 1994. p. 207–35.
80. Revell LJ, Johnson MA, Schulte JA, Kolbe JJ, Losos JB. A phylogenetic test for adaptive convergence in rock-dwelling lizards. *Evolution*. 2007; 61(12):2898–912. <https://doi.org/10.1111/j.1558-5646.2007.00225.x> PMID: 17894806
81. Vanhooydonck B, Andronescu A, Herrel A, Irschick DJ. Effects of substrate structure on speed and acceleration capacity in climbing geckos. *Biol J Linn Soc*. 2005; 85(3):385–93.
82. Persson BNJ. Biological adhesion for locomotion: basic principles. *J Adhesion Sci Technol*. 2007; 21(12–13):1145–73.
83. Cole NC, Jones CG, Harris S. The need for enemy-free space: The impact of an invasive gecko on island endemics. *Biol Conserv*. 2005; 125(4):467–74.
84. Hansen WR, Autumn K. Evidence for self-cleaning in gecko setae. *Proc Natl Acad Sci USA*. 2005; 102(2):385–9. <https://doi.org/10.1073/pnas.0408304102> PMID: 15630086
85. Bauer AM, Russell AP, Powell GL. The Evolution of Locomotor morphology in *Rhoptropus* (Squamata: Gekkonidae): Functional and Phylogenetic Considerations. *Afr J Herpetol*. 1996; 45(1):8–30.
86. Higham TE, Jayne BC. Locomotion of lizards on inclines and perches: hindlimb kinematics of an arboreal specialist and a terrestrial generalist. *J Exp Biol*. 2004; 207(Pt 2):233–48. Epub 2003/12/12. PMID: 14668308.
87. Krause C, Fischer MS. Biodynamics of climbing: effects of substrate orientation on the locomotion of a highly arboreal lizard (*Chamaeleo calyptratus*). *J Exp Biol*. 2013; 216(8):1448–57.
88. Mattingly WB, Jayne BC. Resource use in arboreal habitats: Structure affects locomotion of four ecophenotypes of *Anolis* lizards. *Ecology*. 2004; 85(4):1111–24.
89. Peterson JA. The locomotion of *Chamaeleo* (Reptilia: Sauria) with particular reference to the forelimb. *J Zool*. 1984; 202(Jan):1–42.

90. Gardner AS. The evolutionary ecology and population systematics of day geckos (*Phelsuma*) in the Seychelles: University of Aberdeen; 1984.
91. Aerts P, Van Damme R, Vanhooydonck B, Zaaf A, Herrel A. Lizard locomotion: How morphology meets ecology. *Neth J Zool.* 2000; 50(2):261–77.
92. Wang ZY, Gu WH, Wu QA, Ji AH, Dai ZD. Morphology and reaction force of toes of geckos freely moving on ceilings and walls. *Sci China Technol Sc.* 2010; 53(6):1688–93.
93. Zaaf A, Van Damme R. Limb proportions in climbing and ground-dwelling geckos (Lepidosauria, Gekkonidae): a phylogenetically informed analysis. *Zoomorphology.* 2001; 121(1):45–53.
94. Goodman BA, Hudson SC, Isaac JL, Schwarzkopf L. The Evolution of Body Shape in Response to Habitat: Is Reproductive Output Reduced in Flat Lizards? *Evolution.* 2009; 63(5):1279–91. <https://doi.org/10.1111/j.1558-5646.2009.00621.x> PMID: 19154395
95. Sinervo B, Losos JB. Walking the tight rope: arboreal sprint performance among *Sceloporus occidentalis* lizard populations. *Ecology.* 1991; 72(4):1225–33.
96. Wang ZY, Wang JT, Ji AH, Zhang YY, Dai ZD. Behavior and dynamics of gecko's locomotion: The effects of moving directions on a vertical surface. *Chinese Sci Bull.* 2011; 56(6):573–83.
97. Jusufi A, Goldman DI, Revzen S, Full RJ. Active tails enhance arboreal acrobatics in geckos. *P Natl Acad Sci USA.* 2008; 105(11):4215–9.
98. Russell AP, Bels V. Biomechanics and kinematics of limb-based locomotion in lizards: review, synthesis and prospectus. *Comp Biochem Physiol A Mol Integr Physiol.* 2001; 131(1):89–112. Epub 2001/12/06. PMID: 11733169.