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Stick or grip? Co-evolution of adhesive toepads and claws in Anolis lizards

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4 **1** *Stick or grip? Co-evolution of adhesive toepads and claws in Anolis lizards*

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4 23 ABSTRACT
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7 24 Exploring the relationship between phenotype and performance in an
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9 25 ecological and evolutionary context is crucial to understand the adaptive nature of
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11 26 phenotypic traits. Despite their ubiquity in vertebrates, few studies have examined
12
13 27 the functional and ecological significance of claw morphologies. Here we examine
14
15 28 the adhesive toepad and claw system of *Anolis* lizards. Claw characters are
16
17 29 significantly different between lizards classified as arboreal (perch height > 1 m)
18
19 30 and non-arboreal (perch height < 1 m). Arboreal species possess significantly higher
20
21 31 and longer claws, and show trends toward decreased claw curvature and wider claw
22
23 32 tip angles. Toepad size and claw length and height are tightly correlated with each
24
25 33 other and with perch height, suggesting that the adhesive toepad and gripping claw
26
27 34 have co-evolved to accommodate different habitats. The functional morphology and
28
29 35 evolution of claws are ripe areas for future investigation.

30
31 36 INTRODUCTION
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34 37 Studying the link between phenotype and performance is necessary for
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36 38 insight in to the adaptation of form and function (Arnold, 1983). The functional
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38 39 significance of claws is not well studied, despite their ubiquity throughout
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40 40 vertebrates. Claws are known to increase available habitat (Cartmill, 1974), yet the
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42 41 link between morphological and habitat use variation is unknown. Here, we explore
43
44 42 the claw in relation to a second structure used in attachment, the adhesive toepad,
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46 43 in *Anolis* lizards.

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48 44 Anoles are an ideal model organism with which to unravel potential
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50 45 ecological contributions of claws, as they occupy a vast array of habitats with
51
52 46 predictable evolutionary trajectories (Losos, 2009). *Anolis* lizards comprise a
53
54 47 diverse clade that has undergone adaptive radiation on the Caribbean islands of the
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56 48 Greater Antilles, producing species of similar ecology and morphology termed
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58 49 “ecomorphs” that have evolved independently on each island (Williams, 1983).
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60 50 These lizards have been the focus of many studies examining the relationships
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51 between morphology, performance, and ecology (see Losos, 2009 for a review). A
52 particularly striking feature of anoles is the adhesive toepad, which enables the
53 animal to move across smooth substrates with little difficulty. Toepads are thought
54 to be a key innovation in anoles because their evolution may have allowed these
55 lizards to occupy a larger portion of the available habitat than previously possible,
56 thus permitting their radiation and diversification (Warheit et al., 1999).

57 Toepads are effective in permitting anoles to expand their habitat use due to
58 their attachment abilities: they function best on smooth surfaces, such as leaves and
59 smooth tree bark. Microscopic hair-like structures on the ventral pad, termed setae,
60 adhere to substrates via van der Waals forces (Autumn et al., 2002; Puthoff et al.,
61 2010). Among anole species, clinging ability varies with habitat use. Species that
62 occur higher in the tree canopy possess larger toepads, and are capable of producing
63 greater shear forces (Elstrott and Irschick, 2004; Macrini et al., 2003). This variation
64 suggests that the evolution of adhesive toepads may have been critical for
65 occupation of arboreal habitats, and thus may have played a major role in the
66 diversification of Caribbean anoles into a distinct set of ecomorphs.

67 An often-neglected feature of *Anolis* relevant to clinging is their claws. Like
68 almost all other lizard species, anoles possess claws, and variation in claw
69 morphology may be related to differences in habitat use. Unfortunately, claws have
70 been overlooked not only in anoles, but also in most amniotes. Vertebrates with
71 claws can occupy larger portions of the habitat than non-clawed animals (Cartmill,
72 1974). However, the functionality of claws is less understood (see Maddin and Reisz,
73 2007 and Zani, 2000). Some aspects of claw shape are known to affect attachment
74 ability, including claw height (the distance measured from dorsal to ventral at the
75 base of the claw Zani, 2000). In animals such as beetles, claws interact with surface
76 irregularities in two ways: interlocking and friction. When surface irregularities are
77 larger than claw tip diameter, the claw mechanically interlocks with the
78 irregularities. In contrast, when surface irregularities are smaller than claw tip
79 diameter, attachment results from frictional forces. In this instance, if the tangent

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80 between the claw and the irregularity is too low, the claw slips (Dai et al., 2002). As
81 such, mechanical interlocking (accomplished with a smaller claw tip relative to
82 substrate roughness) is often times stronger than frictional attachment, with a
83 lower likelihood of failure. Thus, the ability to create a mechanical attachment,
84 rather than a friction-based attachment, is improved with smaller claw tips.
85 Decreasing the size (or effective angle) of the tip increases the likelihood of surface
86 irregularities being larger, offering more opportunity for mechanical attachment. In
87 fact, in artificial claws, decreasing the tip's effective angle significantly improves the
88 strength of attachment (Provancher et al., 2004).

89 However, understanding the broader relationship between claw morphology
90 and habitat use is not yet possible. A study linking claw morphology directly to
91 habitat use in birds indicates that ground-dwelling species have significantly less
92 curved claws than perching species, and species that climb have claws with higher
93 curvature than both ground and perch dwellers (Feduccia, 1993). Similar patterns
94 have been observed in lizards: arboreal and saxicolous species have claws with
95 higher curvature (Tulli et al., 2009). Some additional evidence for the importance of
96 claws exists in a single species, the ecologically variable *Anolis cybotes*; individuals
97 in more rocky areas appear to have more curved claws (Wollenberg et al., 2013).

98 It is reasonable to predict that the claw and adhesive toepad operate under
99 disparate conditions. The toepad functions best on relatively smooth, homogenous
100 surfaces. The attachment between microscopic hair-like structures of the ventral
101 pad and the surface is modeled to be maximal on smoother surfaces (Persson and
102 Gorb, 2003; Russell and Johnson, 2013), and performance declines with increasing
103 surface roughness (Vanhooydonck et al., 2005). In contrast, claws appear to
104 maximize functionality on very rough surfaces, where mechanical interlocking of
105 the claw is often-times stronger than friction forces on smoother surfaces (Dai et al.,
106 2002). Thus, it appears both structures are optimal in two different scenarios. This
107 observation was first put forth by Mahendra (1941), who observed following claw
108 removal, *Hemidactylus* geckos were unable to attach to rough surfaces, but

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4 109 attachment to smooth surfaces was unaffected. Further recent explorations are
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6 110 limited, but best evidenced in an analysis of performance and morphology. Zani
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8 111 (2000) found that in 85 species of lizard, toe width and lamellae number is
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10 112 correlated with attachment ability to smooth surfaces, while claw height is
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12 113 correlated with rough surface attachment.
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15 114 Examining both the adhesive toepad alongside the claw may reveal ecological
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17 115 patterns hitherto unknown, or previously overlooked and attributed to toepad
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19 116 function alone. Here, we explore the relationship between toepad clinging ability,
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21 117 claw morphology, and habitat use in *Anolis*. We test for associations between claw
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23 118 morphology and habitat use. We predict that arboreal species with higher perch
24
25 119 heights will have claw morphologies associated with improved attachment abilities:
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27 120 higher and longer (Zani, 2000), more curved (Feduccia, 1993), and sharper tips (Dai
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29 121 et al., 2002). We also test if phylogenetically corrected features of claws that are
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31 122 thought to improve attachment co-vary with toepad adhesion ability, given that
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33 123 toepads also correlate with habitat (Elstrott and Irschick, 2004). Our available
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35 124 lizards are mainland species, and as such we also confirm that mainland species
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37 125 follow the same trends as island species by testing for a positive relationship
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39 126 between toe force production and perch height (Irschick et al., 1997; Macrini et al.,
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41 127 2003).
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44 45 129 METHODS

46 47 48 130 *Study area and species*

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51 131 Fieldwork occurred at La Selva Biological Station, Playa Piro, and Palo Verde
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53 132 Biological Station in Costa Rica, and Gamboa, Panama. A total of 12 species was
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55 133 studied (see table 1). To capture animals and determine perch height, we walked
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57 134 along trails daily when lizards were active and recorded data for any individual
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59 135 sighted. Perch height was measured as distance from the ground to the individual's
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4 136 original position, and perch diameter was measured at the location the lizard was
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6 137 first observed. Lizards were captured by hand or noose and kept for no longer than
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8 138 48 hours. Lizards were kept in one-gallon plastic bags, transported to the field lab
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10 139 and returned to their original location following performance trials.

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13 140 *Adhesion performance*

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16 141 Following capture, one person (KEC) took shear-force measurements. A dual-
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18 142 range force sensor (Vernier) was attached to a vertical acetate covered glass
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20 143 microscope slide with a custom plexiglass attachment and butterfly clip. For each
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22 144 subject, the fourth (longest) digit was isolated and gently applied to the acetate
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24 145 sheet (Fig. 1). These performance measures only reflect attachment ability of the
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26 146 adhesive toepad, not the claw, because the claw was not able to penetrate the
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28 147 acetate coating. The anole was pulled by hand at an approximately constant speed,
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30 148 and the shear force was recorded at 40 Hz. Each subject underwent three repeated
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32 149 trials for left and right fourth toe.

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34 150 *Morphology*

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37 151 For all species in this study, we measured toepad and claw morphological
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39 152 characters from preserved specimens at the Museum of Comparative Zoology,
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41 153 Harvard University, and specimens from the Museum of Southwestern Biology,
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43 154 University of New Mexico (see appendix for list). A scanner (Epson Perfection 4900
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45 155 and V500) digitized images of the fourth right hind digit, with the claw flattened
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47 156 sagittally against the scanner. Measurements were taken with ImageJ (1.4g,
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49 157 Rasband). Morphological characters of the toe included toepad area, measured from
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51 158 where the pad begins to widen (i.e., where the next most distal lamellae is longer
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53 159 than the previous), and lamellae number, counted as lamellae contained within
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55 160 toepad area. Measurements of the claw included: height, length, curvature (as
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57 161 measured by Zani, 2000), and tip angle (Fig. 2).

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4 163 *Analysis*
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7 164 For all species, we determined descriptive statistics for all continuous
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9 165 characters. To meet assumptions of normality and homoscedasticity, all
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11 166 measurements except for toepad force and claw tip angle were log-10 transformed
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13 167 prior to analysis. We corrected for size in characters that significantly correlated
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15 168 with SVL. To do so, we regressed log-10 adjusted values against log-10 adjusted SVL
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17 169 and calculated residuals, which were used for subsequent regressions.
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20 170 A bivariate Pearson correlation on the log-10 transformed data was used to
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22 171 determine correlations among traits. Log-10 transformed data were then used as
23
24 172 input for an independent contrasts analysis (Felsenstein, 1985) using the GEIGER
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26 173 package in R (Harmon et al., 2008). The most complete phylogenetic tree of *Anolis*
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28 174 (Nicholson et al., 2005) served as the basis for analyses (Fig. 3). Panamanian species
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30 175 described in Castañeda and de Queiroz (2013) were added as sister taxa, and *Anolis*
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32 176 *apletophallus* was placed as sister taxon to *Anolis limifrons* (S. Poe, pers. comm.).
33
34 177 Branch lengths of the phylogeny were unknown, and were set to arbitrary lengths
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36 178 using a Grafen transformation (Grafen, 1989). The calculated residual values of
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38 179 morphological, performance, and habitat use variables were input into a linear
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40 180 regression analysis to determine correlation coefficients. An analysis of variance
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42 181 (ANOVA) tested for statistical significance for all regressions. All analyses presented
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44 182 account for phylogeny.

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46 183 We also compared claw variables between two groups of anoles classified as
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48 184 “arboreal” or “non-arboreal.” Arboreal species were defined as those with an
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50 185 average perch height greater than one meter, whereas non-arboreal were those
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52 186 found perching below one meter. Species with mean perch heights less than one
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54 187 meter are generally seen on or near the ground, whereas those above one meter are
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56 188 those that are often seen in the canopy. Claw morphologies (claw curvature, claw tip
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58 189 angle, claw height, and claw length) were first compared with a phylogenetically
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60 190 corrected MANOVA. Each character was then compared between groups with a
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62 191 phylogenetically corrected ANOVA. One-tailed tests were used in all comparisons, as
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4 192 we had a-priori predictions for claw curvature (Feduccia, 1993), claw tip angle (Dai
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6 193 et al., 2002), and claw height and length (Zani, 2000). It should be noted that Zani
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8 194 (2000) found the correlation between claw length and clinging ability on rough
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10 195 surfaces was not robust to changes in phylogenetic branch lengths in one out of four
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12 196 models. Both phylogenetic analyses used the GEIGER package in R (Harmon et al.,
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14 197 2008).

16 198 RESULTS

19 199 *Morphology and performance*

22
23 200 Table 1 lists the mean \pm SE for all morphological variables and toepad force
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25 201 production. All variables were size corrected, with analyses performed on the
26
27 202 residuals of the data regressed against body size (see methods), with the exception
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29 203 of claw tip angle ($p=0.68$, $r^2=0.02$) and claw curvature ($p=0.91$, $r^2=0.001$), because
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31 204 they were uncorrelated to overall body size. All correlations are the result of
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33 205 phylogenetically independent contrasts to account for ancestral relatedness.

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35 206 Adjusted toepad area correlates positively with the size adjusted variables
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37 207 claw height ($p<0.001$, $r^2=0.65$, d.f.=1,10), claw length ($p=0.03$, $r^2=0.35$, d.f.=1,10),
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39 208 and non-size adjusted claw curvature ($p=0.05$, $r^2=0.26$, d.f.=1,10). Pad area also
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41 209 correlates positively with toepad force production following corrections for size
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43 210 ($p<0.001$, $r^2=0.75$, d.f.=1,10). Toepad lamella number exhibits similar relationships,
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45 211 correlating positively with claw height ($p=0.02$, $r^2=0.42$, d.f.=1,10), claw length
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47 212 ($p=0.03$, $r^2=0.38$, d.f.=1,10), and toepad force production ($p<0.001$, $r^2=0.83$,
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49 213 d.f.=1,10).

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51 214 A positive correlation also occurs between toepad force production and claw
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53 215 height ($p=0.01$, $r^2=0.51$, d.f.=1,10) and claw length ($p=0.02$, $r^2=0.46$, d.f.=1,10) (Fig.
54
55 216 4). Force production and claw curvature are also related, but the relationship is not
56
57 217 statistically significant ($p=0.08$, $r^2=0.30$, d.f.=1,9). No relationship is present
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59 218 between force production and claw tip angle ($p=0.98$, $r^2<0.0001$, d.f.=1,10).

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4 219 *Habitat use*
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7 220 A positive correlation exists between perch height and toepad shear-force
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9 221 ($p=0.006$, $r^2=0.58$, $d.f.=1,9$) (Fig. 5), but no correlation occurs between adjusted
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11 222 force production and perch diameter ($p=0.22$, $r^2=0.16$, $d.f.=1,9$). Perch height does
12
13 223 not linearly correlate with claw variables, including claw height ($p=0.43$, $r^2=0.07$,
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15 224 $d.f.=1,9$), claw length ($p=0.26$, $r^2=0.14$, $d.f.=1,9$), claw curvature ($p=0.56$, $r^2=0.04$,
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17 225 $d.f.=1,9$), and claw tip angle ($p=0.90$, $r^2=0.002$, $d.f.=1,9$).
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20 226 We also compared claw variables with binomially categorized habitat by
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22 227 dividing anoles in to two classes: “arboreal,” with average perch heights of over one
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24 228 meter, and “non-arboreal,” with average perch heights below one meter. We found
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26 229 general trends in all claw morphologies between our arboreal categories
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28 230 (phylogenetic MANOVA $p=0.054$). Claw tip angle was close to statistically different
29
30 231 between categories ($p=0.054$, Fig. 6A), as was claw curvature ($p=0.054$, Fig. 6B).
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32 232 Both claw height ($p=0.007$, Fig. 6C) and claw length ($p=0.029$, Fig. 6D) were
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34 233 statistically significantly different between groups.
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39 235 DISCUSSION
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42 236 Our study is one of the first to examine toe and claw morphology in a
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44 237 vertebrate with an eye towards performance in a natural environment. We find
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46 238 support for both of our hypotheses. First, the adhesive toepad of *Anolis* species co-
47
48 239 varies with claw morphology. Secondly, all claw characters measured are associated
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50 240 with habitat use.

51 241 We found strong evidence for co-evolution between adhesive toepads and
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53 242 claws in size-corrected correlations between toepad size and claw height and length
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55 243 (Fig. 4). Adhesive toepads and claws provide clinging capability in different
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57 244 substrate conditions: smooth and rough, respectively. Arboreal animals encounter
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59 245 both types of surfaces as they move on leaves, a smooth substrate, and woody
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4 246 vegetation, a rough substrate; hence, it is not surprising that more arboreal species,
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6 247 needing greater attachment ability, should have better developed claws and toepads.
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9 248 We found strong trends and significant differences between species grouped
10 249 as arboreal (mean perch height > 1 m) and non-arboreal (mean perch height < 1 m).
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12 250 A phylogenetic MANOVA of all claw morphologies came very close to statistical
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14 251 significance at $p = 0.054$, indicating that claw characters are likely related to perch
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16 252 height. With phylogenetic ANOVAs for each character, we were able to dissect this
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18 253 trend. Claw curvature and claw tip angle were not statistically significant between
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20 254 groups, but both showed major trends in that direction, with p values very close to,
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22 255 but slightly above, 0.05. This trend does not fall in line with increased claw
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24 256 curvature in arboreal birds in comparison to ground-dwelling birds (Feduccia,
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26 257 1993). Given that claw sharpness (measured here as a smaller tip angle) improves
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28 258 attachment ability (Dai et al., 2002; Provancher et al., 2004), it is also surprising that
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30 259 arboreal species trend toward less pointed claw tips. We predict with larger sample
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32 260 sizes, a significant trend would appear. These differences suggest further studies
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34 261 examining claw function are vital. Both claw height and length were significantly
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36 262 different between the two groups (Fig. 5). Claw height improves attachment ability
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38 263 on rough surfaces (Zani, 2000). Interestingly, adhesive pad area is also correlated
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40 264 with perch height (Elstrott and Irschick, 2004). Together, differences in claw shape
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42 265 and toepad function in comparison to perch height serve as further evidence for the
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44 266 co-evolution between claws and pads.

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46 267 Despite strong differences between arboreal and non-arboreal morphologies,
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48 268 we did not find linear correlations between claw characters and perch height in this
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50 269 study. Arboreality implies a heightened need for both attachment systems, to
51
52 270 maintain attachment during motion and to avoid falling. However, the functionality
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54 271 of these systems differs in their basic attachment mechanics. In particular, the
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56 272 toepad area is continuous with an increase in surface area of the pad resulting in an
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58 273 increase in clinging ability. In contrast, claw function may not be continuous – once
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60 274 a certain threshold is reached in size or shape, an increase in size or further changes
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275 in shape may confer no more functional, and therefore selective, advantage. For
276 example, higher claws may serve no better than slightly lower ones, as both are
277 capable of mechanical interlocking with the substrate. This is in sharp contrast with
278 toepad area, where increased size confers a linear increase in force. Thus, certain
279 morphologies will be able to accommodate rough substrates, without regard to the
280 actual perch height.

281 Our study focused on the two ecological standards for anoles: perch height
282 and diameter. While we found several intriguing patterns with perch height, none
283 of our measured variables correlated with perch diameter. In a study by Macrini et
284 al. (2003), perch diameter in mainland and island anoles correlates with pad area.
285 However, we found no such relationship here. Mainland species vary in habitat use,
286 and with our relatively small sample size, such patterns may not appear due to
287 higher ecological variation of mainland anoles (Schaad and Poe, 2010). Further,
288 variation in claws may not reflect ecological differences on such a minor scale. In
289 order to stay attached to a vertical perch, the forces produced by pushing the left
290 and right limbs in to the perch must be 90 degrees or less in order to support body
291 weight. Claws are known to help reduce this effective angle (Biewener, 2003;
292 Cartmill, 1974). However, at perch diameters less than a body width, where most of
293 our species were observed, claws are not necessary as the angle between limbs is
294 much less than 90. Thus, a non-existent relationship between perch diameter and
295 claw morphologies agrees with theory.

296 Claw characters may prove important in ecological contexts not reported in
297 this study. In particular, claw height improves attachment ability on rough surfaces
298 (Zani, 2000). Thus, we predict that improved claw morphology (height, length,
299 curvature, and sharpness) is also correlated with surface roughness. This prediction
300 is opposite that which is known in adhesive toepads, which function best on smooth
301 surfaces (Vanhooydonck et al., 2005). Further, the functional interaction of claw
302 and substrate is unknown. Claws may be used to actively pierce substrates, or attach
303 solely due to passive friction. If claws are used to pierce, our results may be

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304 confounded by the wearing-down of the claw structure, as observed in artificial
305 claw systems (Provancher et al., 2004). Use of the claw is likely to vary with size and
306 morphology of the vertebrate, as well as locomotor style. For example, birds show a
307 variety of toe organizations – varying from one to two opposing toes in various
308 configurations. Alongside the differences in muscular arrangement of the flexors
309 and extensors, this variation may influence whether the claw is actively piercing or
310 passively attaching to a substrate. Body size and shape has the potential to further
311 confound claw use. For example, in four-legged vertebrates, the smaller species
312 tend to have a more sprawled posture, while larger species are more upright
313 (Biewener, 1989). The distance and angle between opposing limbs likely affects the
314 effective angle of the claw relative to the substrate – especially on substrates with a
315 limited diameter (Cartmill, 1974). Behavioral and ecological data in lizards would
316 shed light on claw use, body size, and locomotion, yet are lacking for most of the
317 species studied here. For studies outside of *Anolis*, understanding body size, posture,
318 and foot morphology will be crucial to compare claw morphologies across taxa.

319 Lastly, although not the focus of our study, we found that mainland anoles
320 studied here show similar ecological patterns to island species. In island species,
321 toepad force production positively correlates with perch height (Elstrott and
322 Irschick, 2004). This potential trend was unknown in mainland species, particularly
323 because mainland species have dramatically smaller adhesive toepads (Macrini et al.,
324 2003). Whether or not this difference in size indicates mainland species have less
325 clinging ability remains to be tested, as island studies are not comparable to our
326 data and appear more variable in sampling technique. Moreover, our study focused
327 on a single digit, while previous studies measured force production in the 10
328 forelimb digits (Irschick et al., 1996). Additionally, mainland species might
329 experience more diversity in textures and selection for claw characters might not be
330 as strong as in an island setting. Understanding potential differences and similarities
331 between clades is of particular interest, as island and mainland species appear to
332 have different patterns of morphological variation (Schaad and Poe, 2010; Velasco
333 and Herrel, 2007).

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334 Further studies exploring both mainland and island species in tandem are
335 necessary to elucidate how toepad morphologies differ between populations. Such
336 studies must use caution when collecting or comparing adhesion performance data
337 to previously published values. Our data were collected in the field and may have
338 been influenced by environmental conditions including humidity, which may reduce
339 (Niewiarowski et al., 2008; Stark et al., 2012) or increase (Chen and Gao, 2010;
340 Pesika et al., 2009; Prowse et al., 2011; Puthoff et al., 2010) clinging ability in
341 biological adhesives. In particular, high humidity environments change the
342 mechanical properties of the microscopic setae, increasing adhesion abilities
343 (Prowse et al., 2011; Puthoff et al., 2010). Similarly, increased stress of being
344 sampled in the field may impair performance. Further studies across *Anolis* with
345 standardized methods, alongside increased sample sizes, will improve our
346 understanding of relationships among pad, claw, and habitat use.

347 Here we have shown the ecological importance of claw morphology. Anoles
348 found higher in the forest have longer and higher claws, with trends toward
349 decreased claw curvature and increased claw tip angle. These results indicate the
350 importance of claws to habitat use. As almost all vertebrates have claws, this
351 character is ripe for further study. Our study also indicates that claws and adhesive
352 toepads have coevolved in *Anolis*. However, they likely serve partially differing
353 functions; a hypothesis that requires further research on the interaction between
354 the toe and natural surfaces. Understanding this interaction will entail an
355 integration of micro-scale studies of single foot-hairs (Autumn, 2006; Autumn et al.,
356 2000; Liang et al., 2000) and claw tips (Dai et al. 2002) with macro-scale studies of
357 the interaction between a variety of natural and artificial surfaces with whole claws
358 (Provancher et al. 2004) and toepads.

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Figures

Figure 1. *Anolis sagrei* hanging on a glass slide by a single toe.

Figure 2. Morphological characteristics determined for each digit. Claw height = length of line A; Claw Length = total length of segments C+D; Claw tip angle = Θ , Claw curvature = $57.296 * (2 * \arcsine(((2 * C^2 * D^2) + (2 * B^2 * D^2) + (2 * B^2 * C^2) \pm B^4 \pm C^4 \pm D^4)^{0.5} / (2 * C * D)))$ (modified from Zani, 2000)

Figure 3. Phylogenetic relationships of the 12 species in this study, modified from Nicholson et al. (2005). Branch lengths do not reflect distance.

Figure 4. Independent contrasts showing how toepad force production is correlated with claw height (A) and claw length (B), suggesting that both features have co-evolved in mainland *Anolis* lizards.

Figure 5. Independent contrasts showing that toepad force production is correlated with perch height in mainland *Anolis* lizards, illustrating that both traits have coevolved.

Figure 6. Claw morphological characters for species classified as arboreal (average perch height > 1 meter) and non-arboreal (average perch height < 1 meter). Claw curvature (a) and tip angle (b) are not statistically significantly different, but claw height (c) and length (d) are significantly different between groups.

Table 1. Morphological and performance characters measured for each species. All measurements were taken from the fourth (longest) digit of the right hind foot. Morphological measurements reflect museum specimens (supplement 1), and performance measures were taken from wild-caught individuals.

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Species	n (morphology)	n (performance)	SVL (mm)	Mass (g)	Claw height (mm)	Claw Length (mm)	Claw Curvature (degrees)	Claw Tip Angle (degrees)	Toepad Area (mm ²)	Lamellae Number	Toepad Force (N)
<i>Anolis auratus</i>	11	6	42.66	1.35	0.32 ± 0.01	0.52 ± 0.03	40.13 ± 1.57	36.34 ± 2.99	1.06 ± 0.07	10 ± 0.23	0.0084 ± 0.00081
<i>Anolis biporcatus</i>	13	3	83.18	12.88	0.79 ± 0.02	1.10 ± 0.04	32.5 ± 0.39	34.39 ± 0.91	7.23 ± 0.34	18.7 ± .3	0.012 ± 0.022
<i>Anolis capito</i>	6	2	75.86	11.22	0.70 ± 0.05	0.90 ± 0.25	35.41 ± 0.91	29.06 ± 2.14	3.60 ± 0.39	12.3 ± 0.33	0.051 ± 0.021
<i>Anolis cupreus</i>	5	4	42.66	1.62	0.32 ± 0.02	0.35 ± 0.10	36.14 ± 1.33	31.60 ± 1.37	1.20 ± 0.23	9.0 ± 0.41	0.019 ± 0.0016
<i>Anolis frenatus</i>	7	9	93.33	17.38	1.14 ± 0.04	1.69 ± 0.1	33.07 ± 0.86	34.28 ± 0.98	18.60 ± 1.90	23.38 ± 1.07	0.15 ± 0.012
<i>Anolis humilis</i>	5	5	31.62	0.91	0.34 ± 0.05	0.52 ± 0.08	34.67 ± 1.03	28.57 ± 1.13	1.32 ± 0.26	10.8 ± 1.11	0.011 ± 0.0011
<i>Anolis lemurinus</i>	5	1	51.29	2.95	0.40 ± 0.01	0.50 ± 0.13	34.24 ± 0.80	35.52 ± 1.07	3.04 ± 0.27	14.0 ± 0.41	0.034 ± 0.0013
<i>Anolis limifrons</i>	7	5	38.02	0.95	0.31 ± 0.02	0.42 ± 0.03	34.07 ± 0.85	29.13 ± 1.64	1.53 ± 0.15	11.0 ± 0.49	0.0073 ± 0.0015
<i>Anolis lionotus</i>	10	7	64.57	5.50	0.46 ± 0.05	0.73 ± 0.11	35.47 ± 0.54	29.50 ± 1.35	3.44 ± 0.52	14 ± 0.24	0.020 ± 0.0013
<i>Anolis pentaprion</i>	9	2	48.98	2.45	0.43 ± 0.03	0.51 ± 0.03	32.91 ± 0.94	36.76 ± 1.27	2.83 ± 0.24	16.9 ± 0.28	0.092 ± 0.012
<i>Anolis poecilopus</i>	6	9	61.66	5.01	0.51 ± 0.05	0.83 ± 0.09	35.67 ± 0.09	29.27 ± 0.66	4.20 ± 0.90	14.4 ± 0.68	0.032 ± 0.0014
<i>Anolis polylepis</i>	6	4	44.67	1.74	0.38 ± 0.02	0.34 ± 0.14	33.31 ± 1.59	31.89 ± 1.19	1.81 ± 0.11	11.8 ± 0.20	0.017 ± 0.0016

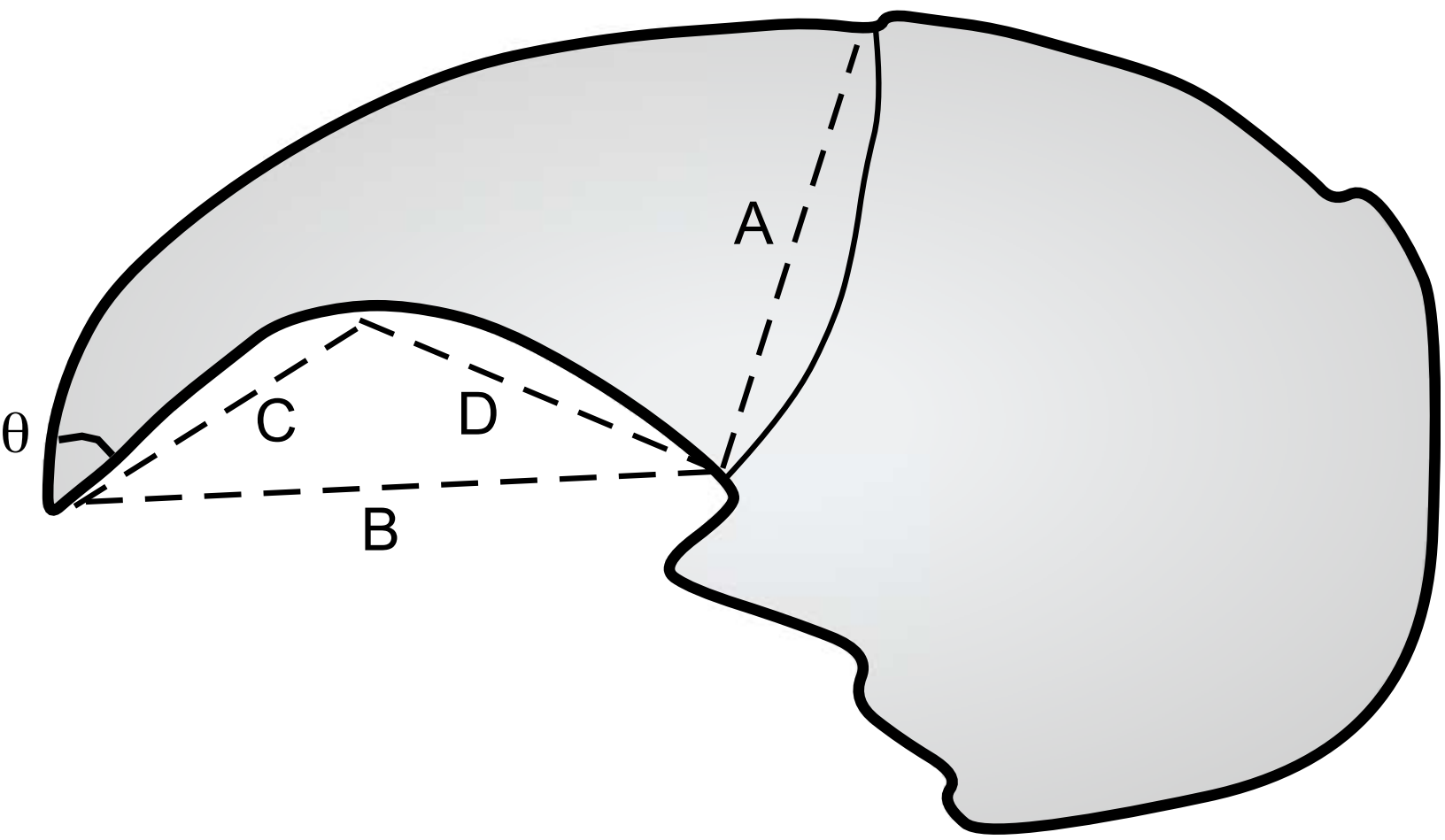
Table 1

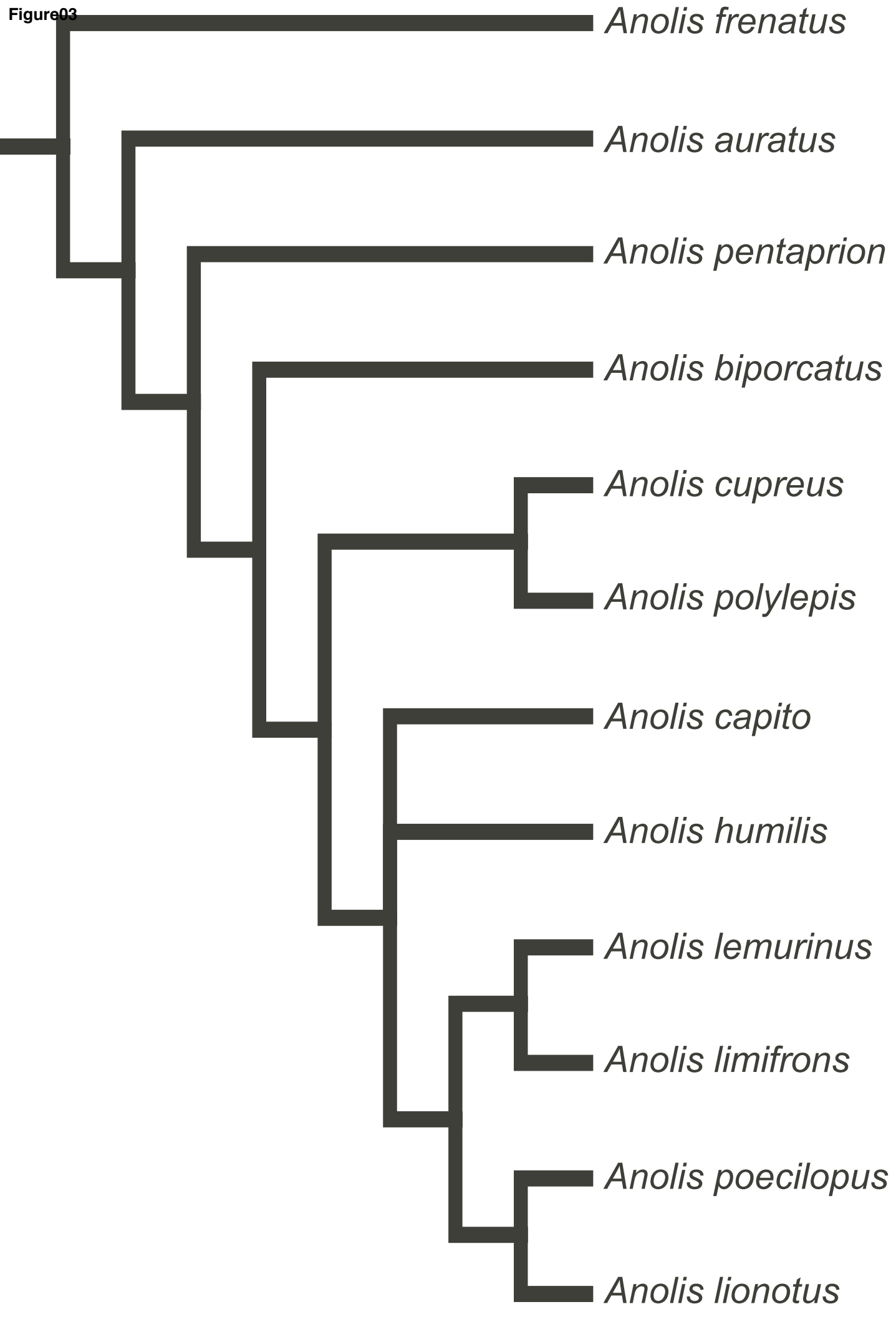
Species	n (morphology)	n (performance)	SVL (mm)	Mass (g)	Claw height (mm)	Claw Length (mm)
<i>Anolis auratus</i>	11	6	42.66	1.35	0.32 ± 0.01	0.52 ± 0.03
<i>Anolis biporcatus</i>	13	3	83.18	12.88	0.79 ± 0.02	1.1 ± 0.04
<i>Anolis capito</i>	6	2	75.86	11.22	0.70 ± 0.05	0.90 ± 0.25
<i>Anolis cupreus</i>	5	4	42.66	1.62	0.32 ± 0.02	0.35 ± 0.10
<i>Anolis frenatus</i>	7	9	93.33	17.38	1.14 ± 0.04	1.69 ± 0.1
<i>Anolis humilis</i>	5	5	31.62	0.91	0.34 ± 0.05	0.52 ± 0.08
<i>Anolis lemurinus</i>	5	1	51.29	2.95	0.40 ± 0.01	0.50 ± 0.13
<i>Anolis limifrons</i>	7	5	38.02	0.95	0.31 ± 0.02	0.42 ± 0.03
<i>Anolis lionotus</i>	10	7	64.57	5.50	0.46 ± 0.05	0.73 ± 0.11
<i>Anolis pentaprion</i>	9	2	48.98	2.45	0.43 ± 0.03	0.51 ± 0.03
<i>Anolis poecilopus</i>	6	9	61.66	5.01	0.51 ± 0.05	0.83 ± 0.09
<i>Anolis polylepis</i>	6	4	44.67	1.74	0.38 ± 0.02	0.34 ± 0.14

Figure01
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Figure02





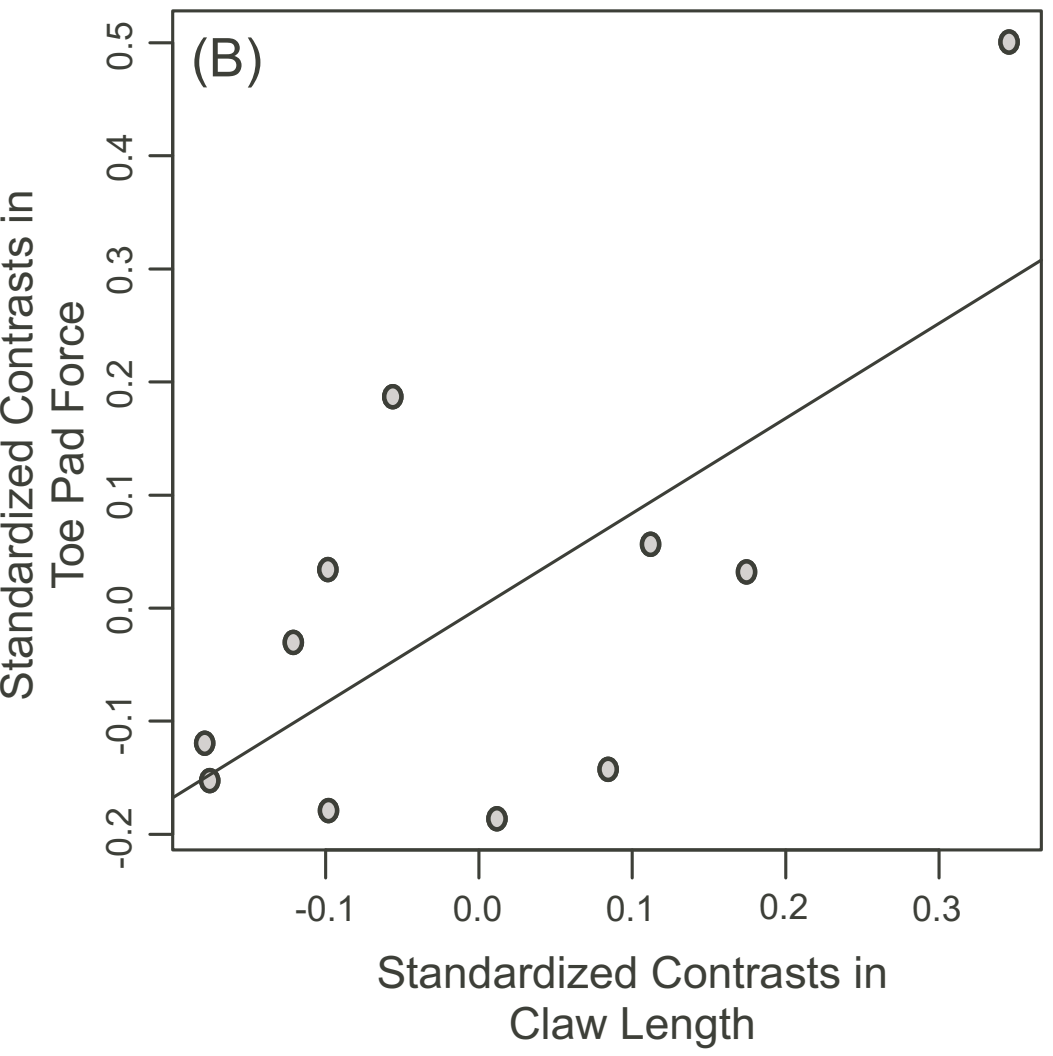
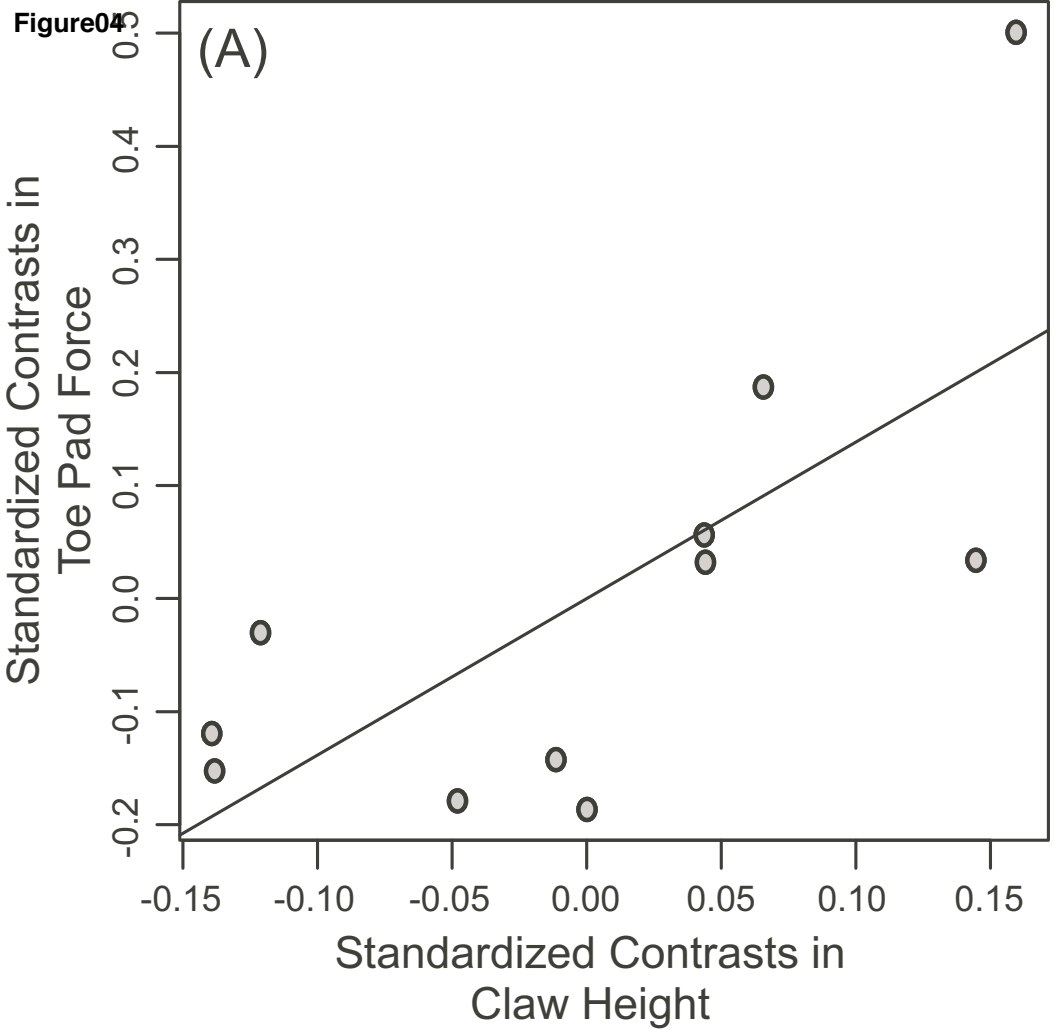


Figure05

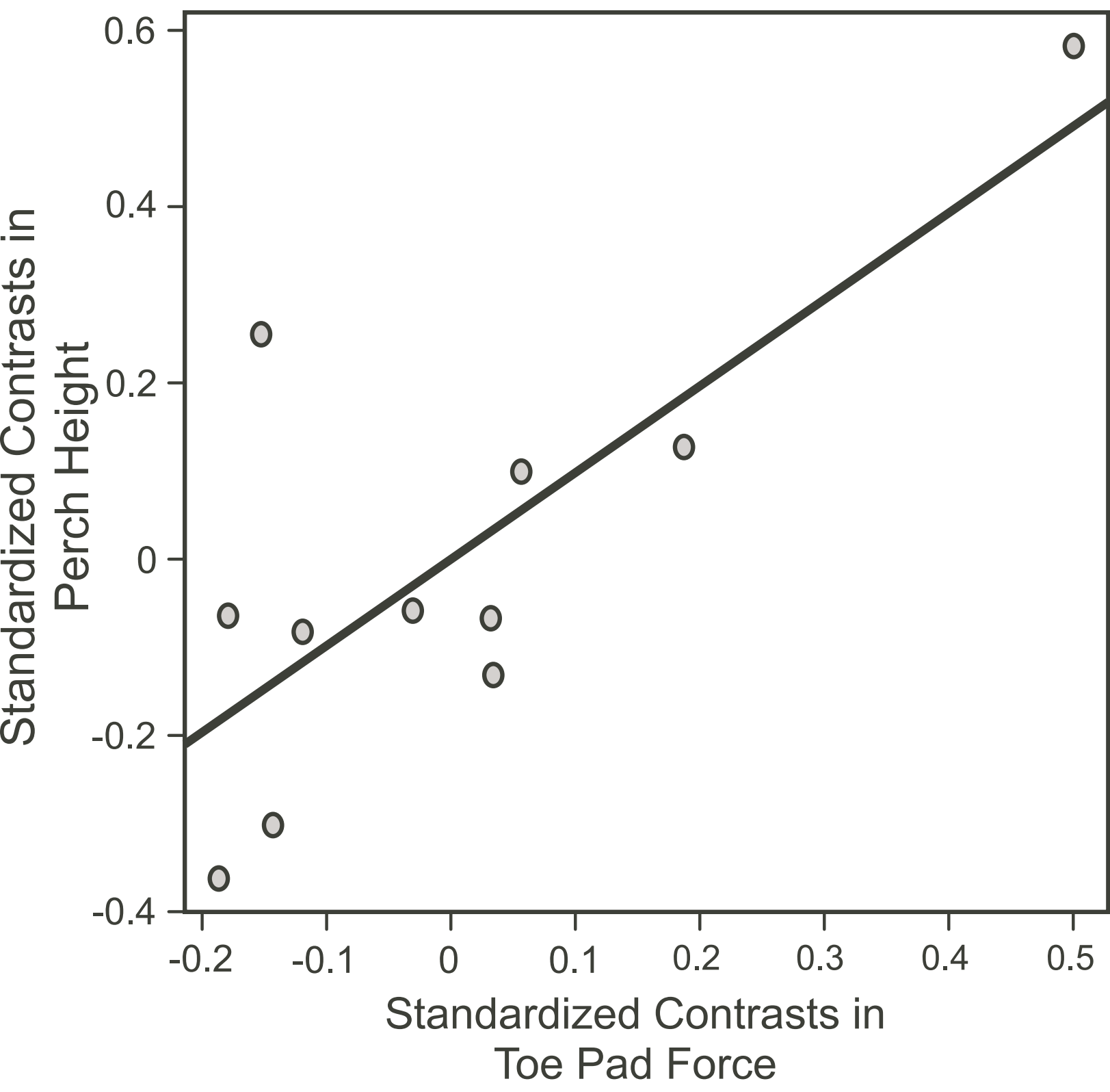
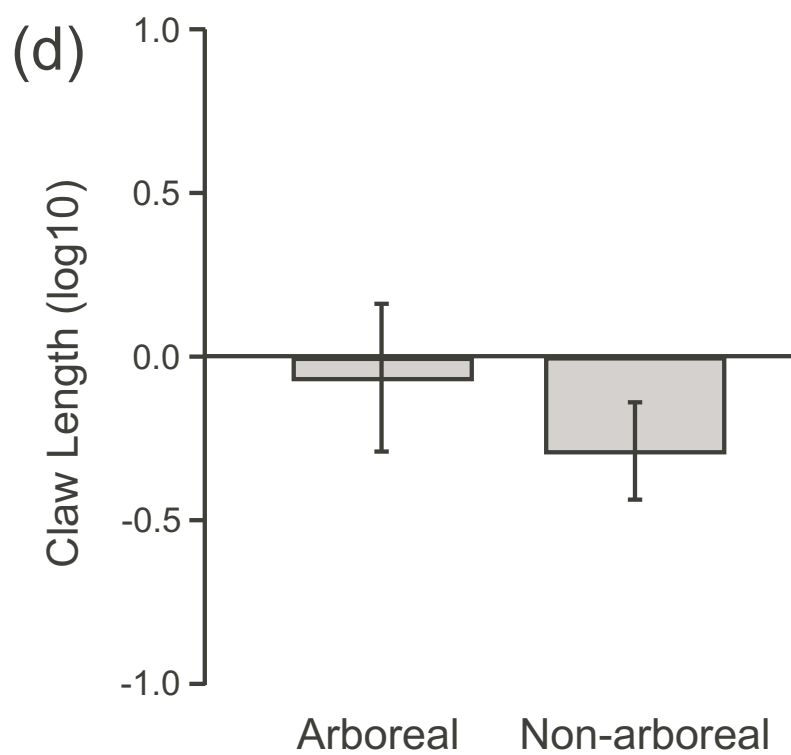
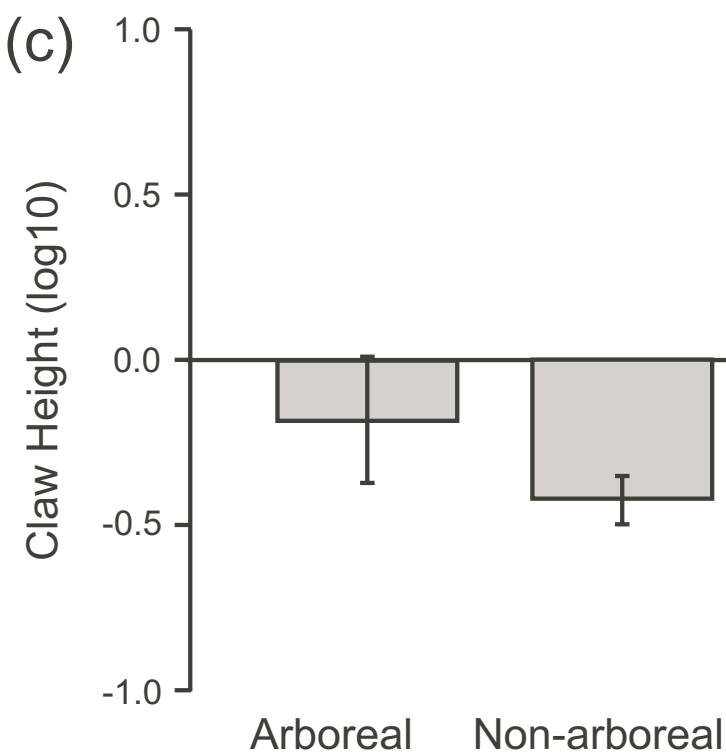
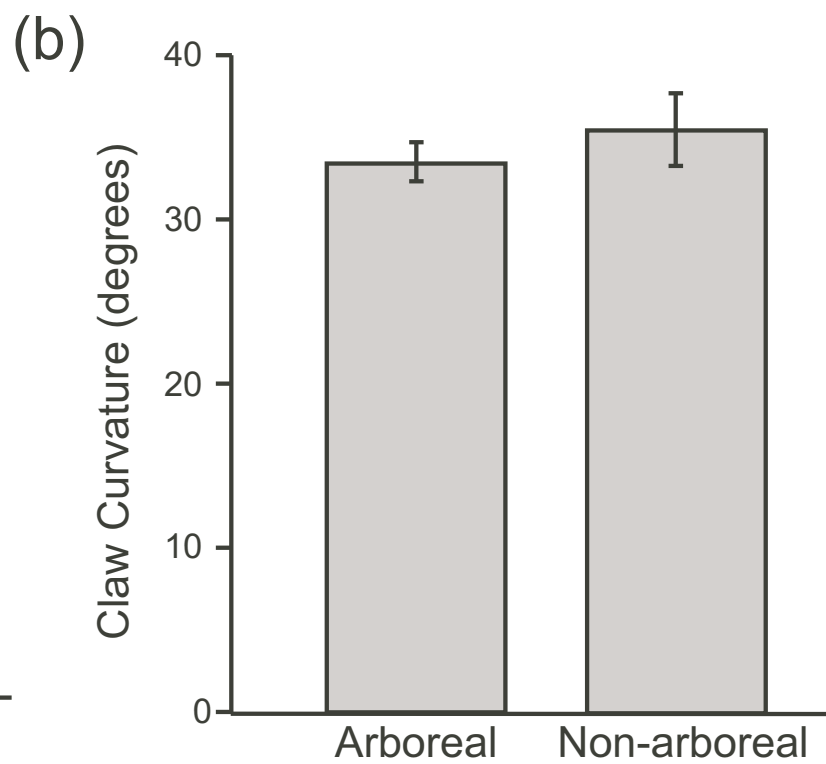
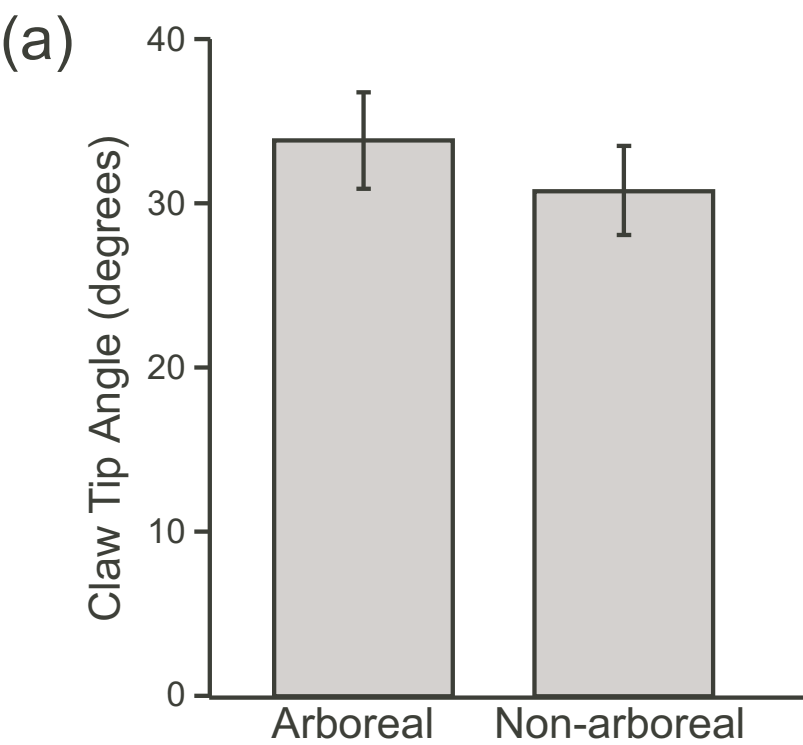


Figure06



e-component

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