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City slickers: poor performance does not deter *Anolis* lizards from using artificial substrates in human-modified habitats

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1 City slickers: poor performance does not deter *Anolis* lizards from using artificial
2 substrates in human-modified habitats

3

4 Revised for *Functional Ecology*

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10

11 **Summary**

12 1. As animals move through their environments they encounter a variety of
13 substrates, which have important effects on their locomotor performance. Habitat
14 modification can alter the types of substrates available for locomotion. In particular,
15 many types of artificial substrates have been added to urban areas, but effects of
16 these novel surfaces on animal locomotion are little-known.

17 2. In this study, we assessed locomotor performance of two *Anolis* lizard species (*A.*
18 *crisatellus* and *A. stratulus*) on substrates that varied in inclination and surface
19 roughness. Rough substrates represented the tree trunks and branches typically
20 used in natural forest habitats, whereas smooth, vertical substrates captured the
21 qualities of artificial surfaces, such as posts and walls, available in human-modified
22 habitats. We then observed habitat use to test the habitat constraint hypothesis —

23 that lizards should more frequently occupy portions of the habitat in which they
24 perform better.

25 3. Increased inclination and decreased surface roughness caused lizards to run
26 slower. Both *A. cristatellus* and *A. stratulus* ran slowest on the smooth, vertical
27 surface, and *A. cristatellus* often slipped and fell on this surface. In contrast to
28 predictions, both species frequently used smooth, vertical substrates in the wild.
29 *Anolis cristatellus* occupied artificial substrates 73% of the time in human-modified
30 habitats despite performing worse than *A. stratulus* on the smooth, vertical track.
31 We therefore rejected the habitat constraint hypothesis for anoles in these human-
32 modified habitats.

33 4. Despite overall poor performance on the smooth, vertical track, *A. cristatellus* had
34 a significant morphology-performance relationship that supports the prediction that
35 selection should favor smaller lizards with relatively longer limbs in human-
36 modified habitats. The smaller-bodied *A. stratulus* performed better than *A.*
37 *cristatellus* on smooth, vertical substrates and therefore may not be exposed to the
38 same selective pressures.

39 5. We contend that habitat modification by humans may alter morphology-
40 performance-habitat use relationships found in natural habitats. This may lead to
41 changes in selective pressures for some species, which may influence their ability to
42 occupy human-modified habitats such as cities.

43

44 **Key-words:** habitat constraint hypothesis, habitat use, locomotion, surface

45 roughness, urban environments

46

47 **Introduction**

48 Animals must successfully navigate through their local environments to
49 survive and reproduce. When animals move through terrestrial and arboreal
50 habitats they encounter a variety of substrates, which may affect locomotion
51 (Moermond 1979; Hildebrand *et al.* 1985; Biewener 2003; Mattingly & Jayne 2004).
52 Substrates vary in many ways including compliance (flexibility), diameter,
53 inclination, and surface roughness, and these characteristics affect locomotion
54 including the speed and accuracy with which animals move (Losos & Sinervo 1989;
55 Irschick & Jayne 1998; Vanhooydonck *et al.* 2005; Higham, Korchari & McBrayer
56 2011). Animals often possess morphological adaptations that increase performance
57 on frequently encountered substrates. For example, several groups of arboreal
58 lizards — anoles, geckos, and some skinks — possess subdigital pads that allow
59 them to cling to smooth substrates (Irschick *et al.* 1996; Autumn & Peattie 2002).
60 Alternatively, animals can modify their behavior to minimize the performance costs
61 associated with particular substrates in their environment on which they perform
62 poorly, such as avoiding these substrates, modulating their speed to increase
63 accuracy, or altering their mode of locomotion (Irschick & Losos 1999;
64 Vanhooydonck, Van Damme & Aerts 2002; Foster *et al.* 2015). If animals cannot
65 adjust their behavior or morphology, then they risk performing submaximally
66 during prey capture, predator escape, or social interactions and will likely incur
67 reduced fitness. Understanding how animals solve the locomotor challenges
68 presented by the various substrates they encounter is a key question in ecological

69 morphology, particularly as habitats are increasingly modified by human-mediated
70 global change (Palumbi 2001; Sih, Ferrari & Harris 2011; Robertson, Rehage & Sih
71 2013).

72 Urbanization is a dramatic form of land use change and disturbance that
73 results in a mixture of buildings, impervious surfaces, managed and unmanaged
74 vegetation, and remnant natural areas (Rebele 1994; Shochat *et al.* 2006; Marzluff *et*
75 *al.* 2008; Ramalho & Hobbs 2011; Forman 2014). Cities often produce novel
76 habitats to which animals must adjust if they are to persist. For example, the
77 increased level of low-pitched anthropogenic noise due to transportation and
78 machinery in cities disrupts avian acoustic signaling, which is key for territory
79 defense and mate attraction (Slabbekoorn & Ripmeester 2008). Great tits from the
80 Netherlands sing at higher frequencies in the city, avoiding the masking effect of
81 low-pitched traffic noise (Slabbekoorn & Peet 2003). Another way we expect
82 humans to modify habitats in cities is by adding artificial substrates, such as
83 buildings, fences, posts, roads, and walls. These novel features alter the structural
84 habitat available for locomotion. We do not yet know how animals perform on most
85 artificial substrates and the extent to which they use or avoid them compared to
86 natural substrates. Investigating how animals perform on these novel substrates
87 and the extent to which they are used will increase our understanding of whether
88 behavioral adjustments lead to persistence in human-modified habitats and if
89 evolutionary adaptation is likely to contribute to increased performance on artificial
90 substrates.

91 *Anolis* lizards (or anoles) provide an excellent model system for
92 understanding how novel substrates influence performance and habitat use.
93 Numerous studies have investigated how morphology, performance, and habitat use
94 interact in natural habitats (reviewed in Losos 2009). For example, perch diameter,
95 an important aspect of the structural microhabitat of anoles, has a strong effect on
96 sprint speed in some species. Anoles with longer limbs run faster on broad surfaces
97 (Losos & Sinervo 1989; Macrini & Irschick 1998; Spezzano & Jayne 2004); however,
98 long-legged anoles are more sensitive to changes in substrate diameter. That is,
99 sprint speed decreases more as perch diameter decreases for anoles with longer
100 limbs (Losos & Sinervo 1989). In nature, these long-legged *Anolis* species avoid
101 narrower perches on which their performance is impaired — an idea known as the
102 habitat constraint hypothesis (Irschick & Losos 1999). But do relationships like this
103 hold for *Anolis* species occupying human-modified habitats?

104 Artificial substrates, such as buildings, fences, posts, and walls, likely increase
105 the availability of smooth, vertical substrates and in some cases provide extremely
106 broad surfaces in human-modified habitats as compared to natural areas. Most
107 natural habitats, such as forests, lack substrates that combine these characteristics.
108 Smooth, vertical substrates may be challenging for lizards to move on due to the
109 lack of underlying support to counteract gravity (Cartmill 1985). Moreover, smooth
110 surfaces reduce the ability of claws to interlock (Zani 2000; Kolbe 2015), forcing
111 anoles to rely on their toepads for adhering to the substrate. Lizards must keep
112 their center of gravity close to the surface to prevent toppling when one or more
113 limbs are not in contact with the surface during locomotion. Orienting their limbs

114 more laterally will minimize the distance from the surface (Jayne & Irschick 1999;
115 Spezzano & Jayne 2004). This sprawling limb posture is more easily accomplished
116 with longer limbs and a more flattened body — morphological characteristics found
117 in some rock-dwelling lizard species (Vitt *et al.* 1997; Revell *et al.* 2007; Goodman,
118 Miles & Schwarzkopf 2008).

119 Strong morphology-substrate relationships are also found within species of
120 anoles. Comparisons among populations of *Anolis sagrei* reveal a positive
121 relationship between hindlimb length and perch diameter use (Losos, Irschick &
122 Schoener 1994), which is supported by performance studies (Losos & Sinervo 1989;
123 Spezzano & Jayne 2004). Furthermore, when anoles experience changes in the
124 diameters of available perches, populations show rapid adaptive change in limb
125 length as predicted by this relationship (Losos, Warheit & Schoener 1997; Kolbe *et*
126 *al.* 2012). Intriguingly, Marnocha, Pollinger & Smith (2011) found a pattern of
127 longer hindlimbs for lizards using broader-diameter perches, including buildings
128 and fences, in human-modified habitats for *A. sagrei* in the Bahamas. Nonetheless, it
129 remains unknown whether performance is altered on the smooth, vertical surfaces
130 common in human-modified areas and if the morphology-performance-habitat use
131 relationships found in natural habitats hold when artificial substrates are available
132 to lizards. Furthermore, if performance is impaired, do lizards avoid substrates on
133 which they perform poorly?

134 In this study, we test the habitat constraint hypothesis for anoles in human-
135 modified habitats by assessing their performance on artificial substrates in the
136 laboratory and the extent to which they use these novel substrates when available

137 in the field. We studied two tropical lizard species, *Anolis cristatellus* and *Anolis*
138 *stratulus*, which are both common in natural and human-modified habitats
139 throughout their distributions (Perry *et al.* 2008). These species differ in body size,
140 limb proportions, and toepad size, which might result in performance variation
141 relevant for understanding responses to human-modified habitats. For example,
142 larger lizards are expected to perform worse on smooth, vertical substrates due to
143 the greater force needed to maintain substrate attachment using their toepads. We
144 have also observed both species running upward on natural and artificial substrates,
145 both in response to disturbance and unprovoked (J. Kolbe, pers. obs.). Our first
146 objective was to quantify differences in locomotor performance on substrates
147 varying in inclination (37° and 90°) and roughness (rough and smooth), which are
148 properties thought to vary between natural and artificial substrates. We measured
149 including maximum velocity as well as pauses, slips, and falls by lizards during
150 performance trials (Higham *et al.* 2001). Second, we examined differences in habitat
151 use of lizards in natural and human-modified habitats, focusing on whether lizards
152 used artificial substrates when they were available and evaluating how artificial and
153 natural substrates differed in ways that might affect performance, such as
154 roughness and inclination. Finally, we quantified morphological variation to
155 determine its relationship with performance on different substrates.

156 Previous studies of ecologically similar *Anolis* species in natural habitats
157 support the habitat constraint hypothesis such that lizards more frequently occupy
158 portions of the habitat in which they perform better (Irschick & Losos 1999). When
159 applying this hypothesis to performance on and use of artificial substrates in

160 human-modified habitats, we make three predictions. First, locomotor performance
161 will be sensitive to changes in inclination and roughness with lizards performing
162 worse on steeper and smoother tracks. This decrease in performance will be in part
163 due to the ineffectiveness of lizard claws on smooth surfaces, forcing lizards to rely
164 solely on toepad adhesion. Second, lizards will avoid using vertical and smooth
165 perches due to their decreased performance on these substrates. This will occur
166 despite the increased availability of artificial substrates in human-modified areas.
167 Third, we predict that larger lizards will be more sensitive to changes in inclination
168 and roughness, and a positive relationship between limb length and locomotor
169 performance will exist for the 90°- smooth track. This prediction is based on
170 previous studies of limb kinematics in *A. sagrei* (Spezzano & Jayne 2004), limb
171 divergence between natural and human-disturbed habitats in anoles (Marnocha *et*
172 *al.* 2011), and comparative studies of morphology in some rock-dwelling lizard
173 species (Vitt *et al.* 1997; Revell *et al.* 2007; Goodman *et al.* 2008).

174

175 **Materials and methods**

176 In order to test the habitat constraint hypothesis for lizards in human-
177 modified habitats, we needed to assess locomotor sensitivity across substrates and
178 evaluate habitat use in natural and human-modified habitats. We collected lizards
179 and habitat use data for this study on four islands in the British Virgin Islands in
180 October of 2013 and 2014 (sample sizes in Tables 1 and 2). George Dog and Little
181 Camanoe are uninhabited islands, and Guana and Virgin Gorda islands have both
182 natural and human-modified habitats. We captured lizards by hand or with a noose.

183 Both species are diurnal, insectivorous, and sexually dimorphic species. *Anolis*
184 *crystalinus* typically perches up to 2 m high on tree trunks and also uses the ground,
185 and *A. stratulus* perches higher on trunks and branches compared to *A. crystalinus*
186 and is less likely to use the ground (Losos 2009). *Anolis crystalinus* is larger than *A.*
187 *stratulus*, has relatively longer limbs, and has relatively smaller toepads (Losos
188 1990).

189

190 *Laboratory Performance Trials*

191 Lizards were housed at ambient temperature prior to trials, typically 29-
192 31°C. Immediately before each performance trial, we measured lizard body
193 temperature as sprint speed varies with temperature (Bennett 1980). Locomotor
194 performance was measured on racetracks that varied in inclination and surface
195 roughness. Tracks were 1.5 m long and 10 cm wide with 10 cm-high vertical,
196 cardboard walls to prevent lizards from jumping off of the track. We used a track
197 angled upward at 37° because anoles tend to hop rather than run when on tracks at
198 lower angles (Losos & Irschick 1996). To simulate when lizards move on vertical
199 surfaces, we used tracks angled at 90°. We used fiberglass window screening (1-mm
200 mesh screen) to simulate rough substrates, which provides good traction and a
201 uniform surface for claws to interlock. For a smooth substrate, we used unpainted
202 wood. We have observed lizards using this substrate and it is similar in roughness
203 to some leaves as well as artificial substrates like metal posts. We compared
204 locomotor performance of lizards on three different tracks: 37°-rough, 90°-rough,
205 and 90°-smooth. The comparison between trials on the 37°-rough and 90°-rough

206 tracks isolated the effect of inclination, whereas the comparison between the 90°-
207 rough and 90°-smooth treatments focused on the effect of surface roughness for
208 vertical substrates.

209 To calculate maximum velocity and to quantify pauses, slips, and falls during
210 runs, lizards were filmed running on tracks in dorsal view. We placed each lizard at
211 the start of the track and encouraged it to run by tapping its tail, multiple times if
212 needed. Lizard performance trials were recorded using a Canon EOS Rebel T3i
213 DSLR camera at 60 frames-per-second. We arranged the camera on a tripod such
214 that the lens and racetrack were in parallel planes to allow for accurate velocity
215 analysis from the videos. We ran each lizard 2-3 times on each racetrack using the
216 maximum velocity for analyses, randomized the order of different tracks for groups
217 of lizards, and allowed at least 12 hours between performance trials on the different
218 tracks. All lizards attempted to move on each track suggesting a willingness to
219 perform; we therefore included all individuals in the analyses.

220 We analyzed videos of lizards sprinting on the different tracks using ImageJ
221 (Rasband 2014). We digitized the starting and final positions of the lizards for each
222 trial, calculated the distance between these points, and used the number of frames
223 between these points to calculate time. We analyzed the maximum velocity over 4-5
224 cm of steady movement. We used this relatively short distance over which to
225 measure velocity in order to obtain comparable measures across tracks. We
226 determined the number of pauses over the total run distance (distance from the
227 start of the run up to 20 cm before the end of the track). A pause was scored as any
228 instance where a lizard remained in the same position for more than 1 frame, but

229 the hindlimbs did not slide backward. Slips were scored when a lizard stopped and
230 the hindlimbs slid backward. A fall was scored when a lizard initiated forward
231 movement, but instead fell completely off the track. This was easily distinguished
232 from instances where lizards jumped off the track.

233

234 *Field Habitat Use*

235 Field habitat use data were collected in natural habitats on all islands and
236 human-modified habitats on Guana and Virgin Gorda. Natural habitats were at least
237 100 m from built structures and lacked artificial substrates. Therefore, we did not
238 assess structural habitat availability, but instead focused on whether lizards used
239 artificial substrates when they are available in human-modified areas. We took
240 habitat use data for lizards in natural habitats, and two conditions in human-
241 modified habitats, when lizards were < 1 m and < 4 m from built structures or
242 artificial substrates. This allowed us to assess the habitat use of lizards when both
243 artificial and natural substrates were easily accessible (< 1 m) or when substrates
244 were likely within the home range of the lizard (< 4 m) (Fitch, Henderson &
245 Guarisco 1989; Losos 2009). We could then assess whether lizards used artificial
246 substrates similarly when access to them varied, which could indicate active
247 selection of substrates by the lizard. For all undisturbed lizards, we recorded the
248 type of substrate, inclination of the perch in degrees, and perch diameter and height
249 in cm. To account for lizards using substrates for which diameter cannot be
250 measured (ground, rocks, and walls), we calculated the percentage of flat perch use
251 by lizards within each habitat. Because the roughness of the substrate may influence

252 lizard locomotion, we assessed the surface roughness of each perch substrate on a
253 scale from 1 to 5, described as follows: 1–very smooth, usually painted surface, such
254 as a wooden wall or post, or some plant structures, such as the leaf sheath of a palm
255 tree; 2–smooth, usually not painted, such as concrete, or leaves of some trees; 3–
256 coarse, such as unpainted stucco or tree bark with texture; 4–rough, such as
257 furrowed tree bark; 5–very rough, such as deeply furrowed tree bark or a metal
258 grate.

259

260 *Morphology*

261 We measured mass (g) and snout-vent length (SVL, mm) shortly after
262 capture. We used a portable digital x-ray system (X-Ray Associates East, LLC) to
263 capture skeletal images from lizards, which were euthanized for a separate study.
264 Following the x-ray, we used a flatbed scanner (Epson V500 Photo) to capture
265 images of the toepads on the fore- and hindfoot. Using the ObjectJ plug-in for
266 ImageJ, we measured lengths of the following skeletal elements: femur, tibia, 4th-toe
267 metatarsal, 4th-toe phalanges, humerus, ulna, 3rd-toe metacarpal + phalanges, head
268 length, head width, perctoral width, and pelvis width. Our goal was to capture
269 variation in relative body proportions that could influence locomotor performance
270 (Brickman 1980; Losos & Sinervo 1989; Irschick *et al.* 1996; Goodman *et al.* 2008;
271 Abdala *et al.* 2014). Toepad area was calculated from scanned images of 3rd-toe of
272 the forefoot and the 4th-toe of the hindfoot for all lizards. One person (AB)
273 performed all measurements for consistency.

274

275 *Data analysis*

276 Our assessment of locomotor performance included both the speed and
277 accuracy with which lizards moved on substrates varying in inclination and
278 roughness. We tested for a relationship between body temperature and maximum
279 velocity for all trials. We used mixed model analysis of covariance (ANCOVA) with
280 lizard identity as a random effect and tested for effects of track, species, sex, mass
281 (covariate), and interactions among these factors. We conducted separate analyses
282 with the same model structure for maximum velocity, distance to the 1st pause, and
283 number of pauses. We used Tukey's Honestly Significant Difference (HSD) *post hoc*
284 tests to evaluate differences among levels for each significant factor. To determine if
285 lizards differed in the number of times they slipped on the different tracks and if
286 species differed, we used non-parametric Kruskal-Wallis tests. Likelihood ratio tests
287 were used to determine if species and sexes differed in the number of times they fell
288 on the 90°-smooth track. Lizards did not fall on the other two track types.

289 We compared several aspects of habitat use — perch inclination, perch
290 height, and perch diameter — in both natural and human-modified areas for each
291 species-sex group using t-tests when data were normally distributed (or log
292 transformation achieved normality) and non-parametric Wilcoxon tests otherwise.
293 To determine if the percentage of flat perch use (ground, rocks, and walls) differed
294 between natural and human-modified areas, we used likelihood ratio tests. We
295 determined if the types of substrates used by lizards differed between natural and
296 human-modified areas using likelihood ratio tests and if substrate roughness

297 differed using Wilcoxon tests for each species separately. We also tested whether
298 natural and artificial substrates differed in roughness using a t-test.

299 We used analysis of variance (ANOVA) to test for differences in body size
300 (log-SVL and log-mass) among species and sexes and Tukey's HSD *post hoc* tests to
301 determine if these groups differed significantly. To reduce the dimensionality of the
302 morphological data and evaluate size-adjusted body shape variation, we conducted
303 a principal components analysis (PCA) on the correlation matrix of residuals from
304 linear regressions of each log-transformed trait on log-SVL. We interpreted PC axes
305 with eigenvalues greater than one and used these PC axes in subsequent analyses.
306 We tested for species and sex differences in PC axes using ANOVA and Tukey's HSD
307 tests as described previously.

308 We anticipated that both species and sex would significantly influence
309 performance owing to variation in body size (SVL and mass) and body shape
310 (relative hindlimb length), which are important determinants of sprint speed in
311 lizards (Huey & Hertz 1982; Losos 1990). We therefore tested for relationships
312 between morphological variables (log-SVL, log-mass, and PC axes describing body
313 shape variation) and maximum velocity using linear regressions for species-sex
314 groups that differed in morphology and all lizards combined. In addition to the
315 effect of morphology on maximum velocity, we also explored relationships between
316 morphology and other aspects of performance — pauses, slips, and falls. We used
317 linear regressions to test for relationships between log-SVL, log-mass, and PC axes
318 and the distance to 1st pause, number of pauses, and number of slips. We used
319 logistic regression to determine if morphological variation affected the probability

320 of falling on the 90°-smooth track. We used the same morphological groups as in
321 previous analyses.

322

323 **Results**

324 *Maximum velocity*

325 Lizard body temperatures ranged from 28.5-33.3°C (mean±SE = 30.2±1.0°C).

326 Relationships between body temperature and maximum velocity were non-
327 significant for comparisons in both species. Moreover, sprint speed for *A.*
328 *cratatellus* varies little over the range of temperatures recorded in this study
329 (Gunderson & Leal 2012); therefore we did not include body temperature in the
330 analyses. Maximum velocity across all trials ranged from 0.1- 4.6 m/s. Low
331 velocities were typically recorded prior to lizards slipping or falling, thus reflecting
332 poor performance. Tracks differed in maximum velocity, but this pattern was
333 different for each species (Fig. 1, Table 3). Tukey's HSD tests showed significant
334 differences among tracks; lizards were fastest on the 37°-rough track and slowest
335 on the 90°-smooth track. Moreover, a significant track by species interaction
336 revealed that although *A. cratatellus* and *A. stratulus* did not differ significantly in
337 velocity on the 37°-rough and 90°-rough tracks, *A. cratatellus* was significantly
338 slower on the 90°-smooth track (Fig. 1).

339

340 *Pauses, slips, and falls*

341 Lizards tended to pause for the first time after a shorter distance on the 90°-
342 smooth track as compared to the 37°-rough track (Tables 3 and 4). In particular, *A.*

343 *cratatellus* paused at a shorter distance when on the 90°-smooth track as compared
344 to the other two tracks (Tukey's HSD tests $P < 0.05$). In contrast, the distance to first
345 pause for *A. stratulus* did not differ among tracks. In addition to pausing after a
346 shorter distance, lizards on the 90°-smooth track paused significantly more often
347 compared to when moving on the 90°-rough track (Tukey's HSD tests $P < 0.05$),
348 particularly *A. cratatellus* (Tables 3 and 4). Furthermore, larger lizards had a slight
349 tendency to pause more often than smaller ones (Table 3). Lizards slipped
350 significantly more often on the 90°-smooth track compared to the other two tracks
351 ($H = 88.3$, $df = 2$, $P < 0.0001$; Table 4), which was driven by *A. cratatellus* slipping
352 more often than *A. stratulus* on the 90°-smooth track ($H = 25.4$, $df = 3$, $P < 0.0001$).
353 No lizards fell when running on the rough tracks (Table 4). In contrast, *A.*
354 *cratatellus* fell on the 90°-smooth track in 26% of trials, significantly more often
355 than *A. stratulus*, which never fell ($\chi^2 = 14.6$, $df = 1$, $p < 0.0001$). Male *A. cratatellus*
356 fell twice as often as females (Table 4); however, this difference was not significant
357 ($\chi^2 = 2.1$, $df = 1$, $P = 0.14$).

358 In summary, maximum velocity decreased for both species when increasing
359 the inclination of the track. The smooth substrate also decreased velocity,
360 particularly for *A. cratatellus* (Fig. 1). In contrast to the sure-footedness of *A.*
361 *stratulus*, *A. cratatellus* showed an increased propensity to slip and fall on the 90°-
362 smooth track. These results suggest lizards should avoid smooth, vertical substrates
363 due to their decreased performance and this effect should be stronger for *A.*
364 *cratatellus* than for *A. stratulus*.

365

366 *Habitat use*

367 When comparing each species-sex group separately, lizards did not differ
368 between natural and human-modified sites for many aspects of habitat use (Table
369 1). Lizards did not differ in log-perch height ($P > 0.14$ for all), perch diameter ($P >$
370 0.22 for all), or perch inclination ($P > 0.08$ for all), for which lizards used vertical
371 (90°) perches 57% of the time. In contrast, lizards used flat perches more often in
372 human-modified areas, which were nearly always walls ($P < 0.02$ for all), and the
373 type of substrate occupied by lizards differed between sites ($P < 0.03$ for all). In
374 natural habitats, *A. stratulus* occupied branches and trunks exclusively (Fig. 2a),
375 whereas *A. cristatellus* occupied trunks over 80% of the time, but also used
376 branches, rocks, and the ground (Fig. 2b). In human-modified habitats, *A.*
377 *cristatellus* used artificial substrates (posts and walls) most of the time, whereas *A.*
378 *stratulus* continued to use trunks most often while also using posts and walls.
379 Although we did not evaluate the availability of substrate types in each habitat,
380 lizards of both species used artificial substrates when available, especially *A.*
381 *cristatellus*. Substrates used by lizards were significantly smoother in human-
382 modified habitats as compared to natural areas for each species-sex comparison
383 (Fig. 3; $P < 0.002$ for all). In human-modified habitats, lizards used artificial
384 substrates (posts and walls), which were significantly smoother than natural
385 substrates ($t = 11.98$, $df = 342$, $P < 0.0001$). Although most aspects of habitat use did
386 not change when lizards occupied human-modified sites, lizards frequently used
387 artificial substrates, which were smoother compared to the branches and trunks of

388 trees used almost exclusively in natural sites. Differences between sites were more
389 pronounced for *A. cristatellus* compared to *A. stratulus*.

390

391 *Morphology*

392 Body size differed significantly among species and sexes (ANOVA for log-SVL:
393 $F_{3,91} = 104.25$, $P < 0.0001$, $R^2 = 0.77$; ANOVA for log-mass: $F_{3,91} = 129.93$, $P < 0.0001$,
394 $R^2 = 0.81$). Tukey's HSD tests for both SVL and mass showed male *A. cristatellus*
395 were largest, followed by female *A. cristatellus*, and both sexes of *A. stratulus* were
396 smallest and did not differ significantly. Table 2 shows mean values for
397 morphological variables. Principal component analysis of relative morphological
398 variables (residuals from regressions of traits on SVL) revealed eigenvalues greater
399 than one for the first three PC axes (Table 5). PC1 had positive loadings for limb
400 elements, head width, and pectoral width. *Anolis cristatellus* had significantly
401 greater values of PC1 compared to *A. stratulus* (ANOVA: $F_{3,91} = 8.77$, $P < 0.0001$, $R^2 =$
402 0.22 ; Tukey's HSD test for species difference at $P < 0.05$), but sexes within species
403 did not differ. In contrast, male *A. stratulus* had significantly greater values of PC2
404 compared to female *A. stratulus* and both sexes of *A. cristatellus* (ANOVA: $F_{3,91} =$
405 45.46 , $P < 0.0001$, $R^2 = 0.60$; Tukey's HSD test for group differences at $P < 0.05$).
406 Larger values of PC2 correspond to a relatively longer heads, larger toepads, and
407 narrower pelvises (Table 5). PC3 loaded positively on humerus and ulna, but did
408 not differ among groups (ANOVA: $F_{3,91} = 1.20$, $P = 0.31$, $R^2 = 0.04$).

409

410 *Morphology and Locomotor Performance on Different Substrates*

411 For all lizards combined, larger lizards in terms of both SVL and mass ran
412 faster on the 37° and 90°-rough tracks, but smaller lizards ran faster on the 90°-
413 smooth track (Table 6). Slopes for the relationship between SVL and maximum
414 velocity were consistently positive for groups on the 37°-rough track, and for *A.*
415 *stratulus* across the three tracks (although all were non-significant). For male *A.*
416 *cratatellus* (the largest lizards in terms of body size), larger individuals ran faster on
417 the 37°-rough track, but not the 90°-rough and 90°-smooth tracks. Moreover, male
418 *A. cratatellus* showed strong negative relationships between body size (SVL or
419 mass) and maximum velocity on the 90°-smooth track (Table 6). On the 37°-rough
420 track, *A. stratulus* with relatively long limbs, wide heads, and broad pectoral regions
421 (PC1) ran faster, whereas *A. cratatellus* with lower PC1 values ran faster. For *A.*
422 *cratatellus* on the 90°-smooth track, lizards with relatively long limbs, wide heads,
423 and broad pectoral regions (PC1) moved faster (Fig. 4 and Table 6). No
424 relationships were found between maximum velocity and PC2 ($P > 0.06$ for all) and
425 PC3 ($P > 0.30$ for all) for any group.

426 When assessing aspects of locomotor performance other than maximum
427 velocity, only a few morphology-performance regressions were significant. Larger
428 male *A. cratatellus* paused less often on the 37°-rough track (log-SVL: slope = -6.63,
429 $R^2 = 0.27$, $P < 0.01$, log-mass: slope = -2.00, $R^2 = 0.26$, $P < 0.01$) and larger female *A.*
430 *cratatellus* also paused less often (log-SVL: slope = -10.72, $R^2 = 0.22$, $P = 0.01$).
431 Larger male *A. cratatellus* had a higher probability of falling on the 90°-smooth
432 track (log-SVL: $X^2 = 5.44$, $df = 1$, $P = 0.02$, log-mass: $X^2 = 4.34$, $df = 1$, $P = 0.04$). Male
433 *A. cratatellus* with relatively short limbs, narrow heads, and narrow pectoral

434 regions (lower PC1 values) also had a higher probability of falling on the 90°-
435 smooth track ($\chi^2 = 4.54$, $df = 1$, $P = 0.03$).

436

437 **Discussion**

438 We found that inclination and surface roughness had significant effects on
439 locomotor performance in anoles. Sprint speeds were slowest on the 90°-smooth
440 track, especially for the larger *A. cristatellus*, which paused, slipped, and fell more
441 often compared to when running on lower inclines and rougher surfaces.
442 Based on the habitat constraint hypothesis, both species should avoid using smooth,
443 vertical substrates and *A. cristatellus* should show stronger avoidance. In stark
444 contrast to these predictions, the relatively poor performance of both species on
445 smooth, vertical substrates did not deter lizards from using these perch sites when
446 available in human-modified habitats. We therefore rejected the habitat constraint
447 hypothesis for these *Anolis* species in human-modified habitats because they did not
448 avoid perches on which their performance capabilities were impaired. We also
449 found that *A. cristatellus* with relatively long limbs and broad pectoral regions (PC1)
450 ran faster on the 90°-smooth track and had a lower probability of falling from this
451 track. This suggests that selection should favor lizards with these traits in human-
452 modified areas, such as cities. We discuss these performance, habitat use, and
453 morphology-performance results in the context of urbanization, a key aspect of
454 human-mediated global change.

455 Anoles need to move quickly and accurately in nature for a variety of reasons
456 including capturing prey, escaping predators, and fighting with rival lizards (Losos

457 2009; Foster *et al.* 2015). The substrates on which lizards perch have an important
458 impact on their locomotor performance (Losos & Sinervo 1989; Gilman & Irschick
459 2013). We assessed the effects of inclination and roughness on performance
460 because of the higher frequency of smooth, vertical substrates, such as buildings,
461 fences, and walls, in urban areas. Several previous studies have looked at how
462 increasing inclination affects velocity (Irschick & Jayne 1998; Jayne & Irschick
463 2000). Huey and Hertz (1982) found that for an agamid lizard species that varies in
464 body size, maximum speed was independent of inclination up to 60° for small
465 lizards running on a rough substrate with good traction. However, few studies have
466 assessed how lizards run on vertical surfaces. For *Sceloporus woodi* running up a
467 tree limb in the laboratory, Higham *et al.* (2011) found a modest decrease in velocity
468 on vertical compared to level surfaces, and lizards paused after shorter distances
469 and more often on the vertical surface.

470 The two *Anolis* species in our study showed a similar decrease in velocity
471 (Fig. 1) when inclination was increased from the 37° to 90°; however, lizards did not
472 pause sooner or more often. Because these anoles rarely slipped and never fell when
473 on the 90°-rough track (Table 4), it is unlikely that pausing was related to
474 maintaining their attachment to the vertical substrate (Higham *et al.* 2011). The
475 rough (1-mm mesh window screen) substrate presumably provided an excellent
476 attachment surface for their claws. This 90°-rough track represents well the rough,
477 vertical surfaces, such as tree trunks and branches, primarily used by these mostly
478 arboreal species (Fig. 3). In fact, both species used trunks over 80% of the time in
479 natural habitats (Fig. 2).

480 Previous studies of the effects of substrate on locomotor performance in
481 lizards have focused primarily on variation in substrate inclination and diameter
482 (Huey & Hertz 1982; Losos & Sinervo 1989; Spezzano & Jayne 2004), but fewer
483 studies have assessed the effects of substrate texture or roughness (but see Tulli,
484 Abdala & Cruz 2012; Brandt, Galvani & Kohlsdorf 2015; Vanhooydonck *et al.* 2015).
485 Using a lizard habitat generalist, *Tropidurus torquatus*, Brandt *et al.* (2015) found a
486 positive relationship between grip strength and maximum sprint speed across
487 seven different types of substrate on a level track. They argue that friction
488 coefficients resulting from the interaction between a lizard's foot and substrates of
489 varying roughness are an important determinant of sprint speed (Alexander 2003),
490 not to mention critical for maintaining a secure grip on vertical surfaces to prevent
491 slipping and falling. On the 90° tracks, the change from rough to smooth substrate
492 decreased maximum velocity 29-31% for *A. stratulus* and 59-70% for *A. cristatellus*
493 (Fig. 1). Moreover, *A. cristatellus* paused twice as soon and twice as often on the
494 90°-smooth track as well as slipping and falling on this substrate (Table 4). In
495 contrast to inclination, surface roughness caused a greater reduction in locomotor
496 performance in our study.

497 The wood surface of our 90°-smooth track provided little opportunity for
498 lizards to use their claws, thus anoles were primarily using their toepads to attach to
499 the surface by means of adhesion (Irschick *et al.* 1996). Increased pausing on the
500 90°-smooth track may be needed to maintain attachment of toepads on this surface,
501 but could be also related to energetics and uncertainty of movement (Higham *et al.*
502 2011). *Anolis stratulus* rarely slipped and never fell on the 90°-smooth track,

503 whereas *A. cristatellus* ran slower and fell often (Tables 4 and 6). The greater
504 stability of *A. stratulus* is likely due to its lower mass relative to its toepad area
505 (0.94-1.17 g/mm²) compared to *A. cristatellus* (1.32-1.57 g/mm²), and *A. stratulus*
506 being substantially shorter and weighing less than *A. cristatellus* (Table 2).
507 Furthermore, lizards have a propensity to rear up when accelerating at the start of a
508 run (Higham *et al.* 2011). When falling, *A. cristatellus* would often lose contact
509 between its forelimbs and the substrate, toppling over backwards while maintaining
510 contact with its larger hindlimb toepads (Table 2). This may be further complicated
511 on vertical surfaces if anoles accelerate faster compared to when on level surfaces as
512 occurs in *Sceloporus* lizards (Higham *et al.* 2011). Vertical surfaces reduce
513 locomotor performance in both species, but smooth surfaces have substantially
514 greater negative affect on *A. cristatellus* performance compared to *A. stratulus* (Fig.
515 1).

516 A critical component of testing the habitat constraint hypothesis is assessing
517 whether individuals avoid substrates on which they perform submaximally
518 (Irschick & Losos 1999). In striking contrast to predictions based on their poor
519 locomotor performance on the 90°-smooth track, *A. cristatellus* used artificial
520 substrates 73% of the time and *A. stratulus* used these substrates 27% of the time in
521 human-modified areas (Fig. 2). Furthermore, these substrates were much smoother
522 compared to ones in natural areas (Fig. 3). How might anoles reduce the negative
523 effects of frequently occupying substrates on which they perform poorly? Perhaps
524 potential predators also perform poorly on artificial substrates, an important
525 direction for future studies. Alternatively, anoles may avoid sprinting up when they

526 occupy smooth, vertical substrates. For instance, they may restrict movement to
527 sprinting down or jumping instead of sprinting (Losos & Irschick 1996). This would
528 be especially true for *A. cristatellus*, which often slipped and fell on the 90°-smooth
529 track. In contrast, *A. stratulus* rarely slipped and never fell on the 90°-smooth track,
530 this despite having relatively shorter limbs compared to *A. cristatellus*. This is likely
531 explained by *A. stratulus* being on average 40-75% lighter than *A. cristatellus* (Table
532 2), thus *A. stratulus* is not subject to the same magnitude of force acting against
533 upward movement.

534 Previous studies have found that habitat characteristics influenced
535 locomotor behavior in green anoles: despite using perches with a range of
536 compliances, green anoles selectively jumped from less compliant (less flexible)
537 perches (Gilman & Irschick 2013). Other research shows anoles tend to jump less
538 often from broad surfaces (Pounds 1988; Losos & Irschick 1996) and when nearby
539 perches are lacking (Moermond 1979; Avilés-Rodríguez 2015). Thus, anoles possess
540 the capacity to adjust their mode of locomotion to the substrate they occupy and
541 their surrounding habitat. If moving up is still the best option, then anoles could
542 modulate their speed to decrease the risk of slipping or falling. Irschick *et al.* (2005)
543 found a mismatch between maximum sprint speed measured in the laboratory and
544 escape speed measured in the field, such that faster lizards used a lower percentage
545 of their maximum speed, termed locomotor compensation. This finding suggests
546 that anoles have the ability to modulate their speed. *Anolis cristatellus* slipping and
547 falling on the 90°-smooth track may be capable of reducing their speed to increase
548 accuracy in circumstances that do not require maximum performance. Speed-

549 accuracy tradeoffs are known in a variety of decision-making and locomotor
550 scenarios (Chittka, Shorupski & Raine 2009). Whether anoles modulate their speed,
551 use alternative modes of locomotion, or otherwise behaviorally adjust to avoid
552 performing poorly on smooth, vertical surfaces is unknown.

553 If anoles commonly move on smooth, vertical substrates in human-modified
554 environments, how might selection act on morphology of these anoles? Larger
555 lizards tended to run faster on the rough tracks (Table 6), which represent the type
556 of substrates more often used by lizards in natural habitats (Table 1, Figs. 2 and 3).
557 This pattern was reversed for *A. cristatellus* on the 90°-smooth track, the properties
558 of which represent artificial substrates that lizards often use in human-modified
559 areas. Here larger *A. cristatellus* ran slower. This tradeoff between body size and
560 running speed was most strongly observed for male *A. cristatellus* (Table 6). Larger
561 lizards ran faster on lower inclines due at least in part to their longer stride lengths
562 (Navas, James & Wilson 2006). In contrast, larger lizards on the vertical, smooth
563 surface, which relied solely on toepad adhesion for surface attachment, required
564 greater force to counteract the gravitational forces directly opposing their
565 movement. Slower running speed on the smooth, vertical surface, perhaps due to
566 shorter stride lengths, was compounded for large, male *A. cristatellus* by having a
567 higher probability of falling. Despite this generally poor performance (falling 26%
568 of the time), when able to perform *A. cristatellus* with relatively longer limbs and
569 broader pectoral regions (PC1) ran faster on the 90°-smooth track. This may be due
570 to their greater ability to attain a sprawling limb posture that maintains their center
571 of gravity close to the surface. These conditions — overall poor performance but a

572 significant trait-performance correlation — should promote strong natural
573 selection. Thus, in human-modified areas where *A. cristatellus* frequently uses
574 artificial substrates that are smooth and vertical, such as posts and walls, we predict
575 selection should favor smaller-bodied lizards with relatively longer limbs, and
576 selection should be particularly strong for males. Despite the importance of toepads
577 for adhering to the smooth, vertical track, we found no evidence for a relationship
578 between toepad area (PC2) and locomotor performance for these species.

579 Consistent with this performance-based prediction (also see Spezzano &
580 Jayne 2004 for biomechanical support), two studies have found anole populations
581 with relatively long limbs where they often use artificial substrates in human-
582 disturbed (*A. sagrei*; Marnocha *et al.* 2011) and urban habitats (*A. cristatellus* in
583 Puerto Rico; Winchell *et al., pers. comm.*). In contrast to our prediction, *A. sagrei* in
584 human-disturbed habitats in the Bahamas had larger body sizes compared to
585 natural areas (Marnocha *et al.* 2011). This suggests conflicting selection pressures
586 on body size, perhaps due to sexual selection, or a weaker relationship between
587 body size and performance on artificial substrates for *A. sagrei*, which is somewhat
588 smaller than *A. cristatellus*. A body size-performance relationship was not observed
589 for the smaller *A. stratulus*, which did not suffer as great of a reduction in
590 performance on the smooth, vertical track as *A. cristatellus*.

591 In conclusion, we found that anoles in human-modified habitats do not
592 conform to the habitat constraint hypothesis supported for ecologically similar
593 species in natural environments (Irschick & Losos 1999). Lizards frequently use
594 smooth, vertical artificial substrates, despite performing poorly on these substrates.

595 Predictions for selection favoring relatively longer limbs for lizards using artificial
596 substrates in human-modified areas are supported by phenotypic patterns
597 (Marnocha *et al.* 2011; Winchell *et al.*, *pers. comm.*). Future studies should evaluate
598 how lizards move their limbs on artificial substrates and the extent to which lizards
599 modulate their speed or use other modes of locomotion to minimize the costs of
600 poor sprinting ability on these substrates. This study highlights the difficulty of
601 extrapolating functional and ecological relationships detected in populations from
602 natural settings to those in human-modified environments (Robertson *et al.* 2013).
603 The current rapid pace of change due to human activities may be fundamentally
604 altering the morphology-performance relationships under which populations have
605 evolved. Species persistence in human-modified areas may be related to the
606 behavioural flexibility of individuals and the speed with which populations can
607 evolutionarily adapt to these changing conditions.

608

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Table 1. Sample size, mean \pm SE, and range in parentheses for habitat use by lizards in natural and human-modified habitats. No significant differences existed between habitats in perch inclination, height or diameter. In contrast, natural and human-modified habitats differed the percentage of flat perch use, which consisted primarily walls but also the ground and rocks (see Figs. 2 & 3).

Species	Sex	N	Perch Inclination (°)	Perch Height (cm)	Perch Diameter (cm)	Flat Perch Use (%)
<i>A. cristatellus</i>	Male	81	76 \pm 3.1 (0-90)	125 \pm 8.0 (0-310)	11.7 \pm 1.1 (1.5-32)	Natural-7% Modified-53%
<i>A. cristatellus</i>	Female	137	66 \pm 3.0 (0-90)	68 \pm 4.6 (0-250)	9.8 \pm 1.6 (1-150)	Natural-16% Modified-33%
<i>A. stratulus</i>	Male	66	76 \pm 3.0 (0-90)	139 \pm 7.2 (10-350)	12.5 \pm 1.2 (1.5-35)	Natural-0% Modified-18%
<i>A. stratulus</i>	Female	59	78 \pm 3.0 (0-90)	119 \pm 8.2 (5-300)	8.5 \pm 1.0 (0.5-32)	Natural-0% Modified-21%

Table 2. Mean \pm SE for morphological measurements for both species and sexes separately. All measurements in mm except for mass (g), toepad area (mm²), and PCs.

Variable	<i>A. cristatellus</i>	<i>A. cristatellus</i>	<i>A. stratulus</i>	<i>A. stratulus</i>
	Male	Female	Male	Female
N	35	29	25	6
SVL	63.4 \pm 1.09	46.7 \pm 0.61	43.3 \pm 0.85	40.5 \pm 1.11
Mass	6.9 \pm 0.34	2.5 \pm 0.10	1.5 \pm 0.09	1.4 \pm 0.23
Femur	15.5 \pm 0.28	11.0 \pm 0.13	9.2 \pm 0.17	8.3 \pm 0.23
Tibia	13.3 \pm 0.23	9.3 \pm 0.11	8.0 \pm 0.17	7.3 \pm 0.19
4 th -toe metatarsal	8.0 \pm 0.12	5.8 \pm 0.07	4.5 \pm 0.11	4.4 \pm 0.15
4 th -toe phalanges	9.5 \pm 0.19	6.6 \pm 0.08	5.7 \pm 0.10	5.2 \pm 0.17
Humerus	11.2 \pm 0.21	8.1 \pm 0.12	7.5 \pm 0.15	6.7 \pm 0.20
Ulna	9.3 \pm 0.17	6.7 \pm 0.10	6.2 \pm 0.15	5.7 \pm 0.24
3 rd -toe metcarpal + phalanges	7.1 \pm 0.13	4.8 \pm 0.06	4.5 \pm 0.12	4.1 \pm 0.17
Head length	16.3 \pm 0.28	12.1 \pm 0.14	12.1 \pm 0.21	10.8 \pm 0.27
Head width	11.3 \pm 0.22	7.8 \pm 0.08	6.8 \pm 0.12	6.0 \pm 0.11
Pectoral	7.8 \pm 0.14	5.3 \pm 0.06	4.9 \pm 0.09	4.2 \pm 0.14
Pelvis	6.6 \pm 0.14	5.0 \pm 0.09	4.0 \pm 0.11	4.0 \pm 0.21
Tail	91.2 \pm 4.76	73.4 \pm 2.55	62.3 \pm 2.00	58.1 \pm 4.78
3 rd -toe Forefoot Toepad	2.9 \pm 0.13	1.1 \pm 0.04	1.0 \pm 0.05	0.8 \pm 0.06
4 th -toe Hindfoot Toepad	4.4 \pm 0.18	1.9 \pm 0.06	1.6 \pm 0.08	1.2 \pm 0.06
PC1	0.60 \pm 0.32	0.85 \pm 0.42	-1.25 \pm 0.38	-2.36 \pm 0.52
PC2	0.24 \pm 0.17	-1.56 \pm 0.22	1.56 \pm 0.15	-0.36 \pm 0.20
PC3	-0.26 \pm 0.16	0.06 \pm 0.25	0.30 \pm 0.21	0.00 \pm 0.63

Table 3. Results from mixed model ANCOVAs with lizard identity as a random effect testing for effects of track, species, sex, mass (covariate), and interactions among these factors on maximum velocity, distance to the 1st pause, and number of pauses. Interactions between main effects and the mass covariate were non-significant and removed from the final models. P-values and R² values for the overall model are shown along with the percentage of the variation explained by the random effect lizard identity. Significant p-values are bold.

	Track	Species	Sex	Track x Species	Track x Sex	Species x Sex	Track x Species x Sex	Mass (covariate)	Overall Model	Model R ²	Lizard Identity
Maximum velocity (m/s)	F _{2,179} =168.1 P < 0.0001	F _{1,90} =0.6 P=0.45	F _{1,90} =4.3 P=0.04	F _{2,179} =22.7 P < 0.0001	F _{2,179} =2.2 P=0.11	F _{1,89} =0.7 P=0.40	F _{1,179} =0.6 P=0.57	F _{1,91} =0.0 P=0.99	P < 0.0001	0.82	34%
Distance to 1 st pause (cm)	F _{2,163} =6.1 P=0.003	F _{1,82} =0.6 P=0.45	F _{1,82} =0.1 P=0.82	F _{2,163} =3.5 P=0.03	F _{2,163} =0.2 P=0.86	F _{1,80} =0.7 P=0.41	F _{1,163} =0.7 P=0.52	F _{1,87} =2.8 P=0.10	P < 0.0001	0.10	0%
Number of pauses	F _{2,178} =4.5 P=0.01	F _{1,90} =1.0 P=0.33	F _{1,90} =1.0 P=0.32	F _{2,178} =1.2 P=0.31	F _{2,178} =0.8 P=0.45	F _{1,88} =4.6 P=0.03	F _{1,178} =0.1 P=0.86	F _{1,91} =5.8 P=0.02	P < 0.0001	0.25	8%

Table 4. Mean \pm SE for maximum velocity, distance to the 1st pause, pauses and slips during performance trials on the three different tracks, and the percentage of lizards falling during trials on each track.

Species	Sex	Maximum velocity (m/s)			Distance to the 1 st pause (cm)			Number of pauses/m		
		37° - Rough	90° - Rough	90° - Smooth	37° - Rough	90° - Rough	90° - Smooth	37° - Rough	90° - Rough	90° - Smooth
<i>A. cristatellus</i>	Male	3.1 \pm 0.1	2.4 \pm 0.1	0.7 \pm 0.1	25.7 \pm 3.2	25.8 \pm 2.9	12.3 \pm 2.0	2.7 \pm 0.3	2.2 \pm 0.3	4.8 \pm 0.7
<i>A. cristatellus</i>	Female	2.8 \pm 0.1	2.1 \pm 0.1	0.9 \pm 0.1	21.5 \pm 3.1	22.9 \pm 3.3	11.9 \pm 1.8	3.4 \pm 0.4	2.6 \pm 0.3	6.0 \pm 0.8
<i>A. stratulus</i>	Male	2.7 \pm 0.1	2.1 \pm 0.1	1.5 \pm 0.1	21.1 \pm 2.4	13.3 \pm 2.0	16.9 \pm 2.3	2.9 \pm 0.2	2.9 \pm 0.4	3.1 \pm 0.5
<i>A. stratulus</i>	Female	2.1 \pm 0.3	1.7 \pm 0.2	1.2 \pm 0.2	18.9 \pm 4.8	15.6 \pm 4.5	10.9 \pm 2.0	4.4 \pm 0.8	3.8 \pm 0.9	6.1 \pm 1.9

Species	Sex	Number of slips/m			Percentage falling		
		37° - Rough	90° - Rough	90° - Smooth	37° - Rough	90° - Rough	90° - Smooth
<i>A. cristatellus</i>	Male	0	0	4.2 \pm 1.4	0%	0%	33%
<i>A. cristatellus</i>	Female	0.1 \pm 0.1	0	5.5 \pm 2.3	0%	0%	17%
<i>A. stratulus</i>	Male	0	0.1 \pm 0.1	0.1 \pm 0.1	0%	0%	0%
<i>A. stratulus</i>	Female	0	0.2 \pm 0.2	0.6 \pm 0.4	0%	0%	0%

Table 5. Results from a principal components analysis of morphological variables. Substantial loadings (> 0.50) are in bold.

Variable	PC 1	PC 2	PC 3
Femur	0.85	-0.31	-0.03
Tibia	0.91	-0.14	0.06
4 th -toe metatarsal	0.77	-0.45	-0.09
4 th -toe phalanges	0.74	-0.11	-0.25
Humerus	0.53	0.23	0.65
Ulna	0.47	0.28	0.68
3 rd -toe metacarpal + phalanges	0.50	0.35	-0.07
Head length	-0.03	0.81	0.14
Head width	0.81	-0.05	-0.25
Pectoral width	0.69	0.16	-0.16
Pelvic width	0.35	-0.52	0.32
Forefoot Toepad	0.38	0.67	-0.27
Hindfoot Toepad	0.44	0.62	-0.22
Eigenvalues	5.02	2.37	1.30
% variance	38.6	18.2	10.0

Table 6. Results of linear regression analyses for the relationship between morphology and maximum velocity on the three different tracks. We tested two aspects of body size (SVL and mass) and the first three PC axes for groups that differed significantly for the morphological traits (see Morphology section in Results) and for all individuals combined. No groups had significant relationships between maximum velocity and PC2 or PC3 ($P > 0.05$ for all).

Group	N	37°- Rough			90°- Rough			90°- Smooth		
		Slope	R ²	P	Slope	R ²	P	Slope	R ²	P
log SVL										
<i>A. cristatellus</i> - Male	35	2.02	0.09	0.09	-0.56	0.01	0.57	-2.24	0.18	0.01
<i>A. cristatellus</i> -Female	29	1.28	0.02	0.50	0.20	0.00	0.90	-1.88	0.08	0.13
<i>A. stratulus</i>	31	1.19	0.03	0.35	0.96	0.03	0.37	0.49	0.01	0.59
Combined	95	1.50	0.16	<0.0001	0.87	0.08	<0.01	-1.38	0.21	<0.0001
log Mass										
<i>A. cristatellus</i> - Male	35	0.56	0.07	0.13	-0.20	0.01	0.51	-0.69	0.18	0.01
<i>A. cristatellus</i> -Female	29	-0.23	0.01	0.73	0.20	0.01	0.68	-0.13	0.00	0.76
<i>A. stratulus</i>	31	0.29	0.02	0.41	0.17	0.01	0.57	0.12	0.01	0.63
Combined	95	0.39	0.14	<0.001	0.24	0.08	<0.01	-0.39	0.22	<0.0001
PC1										
<i>A. cristatellus</i>	64	-0.09	0.06	0.05	-0.01	0.00	0.83	0.09	0.11	<0.01
<i>A. stratulus</i>	31	0.16	0.19	0.02	-0.02	0.01	0.66	-0.02	0.01	0.68
Combined	95	0.03	0.01	0.43	0.02	0.00	0.53	-0.02	0.00	0.56

Fig. 1. Mean (\pm SE) of maximum velocity for anoles on three different tracks varying in inclination and surface roughness. Sample sizes are in Table 2.

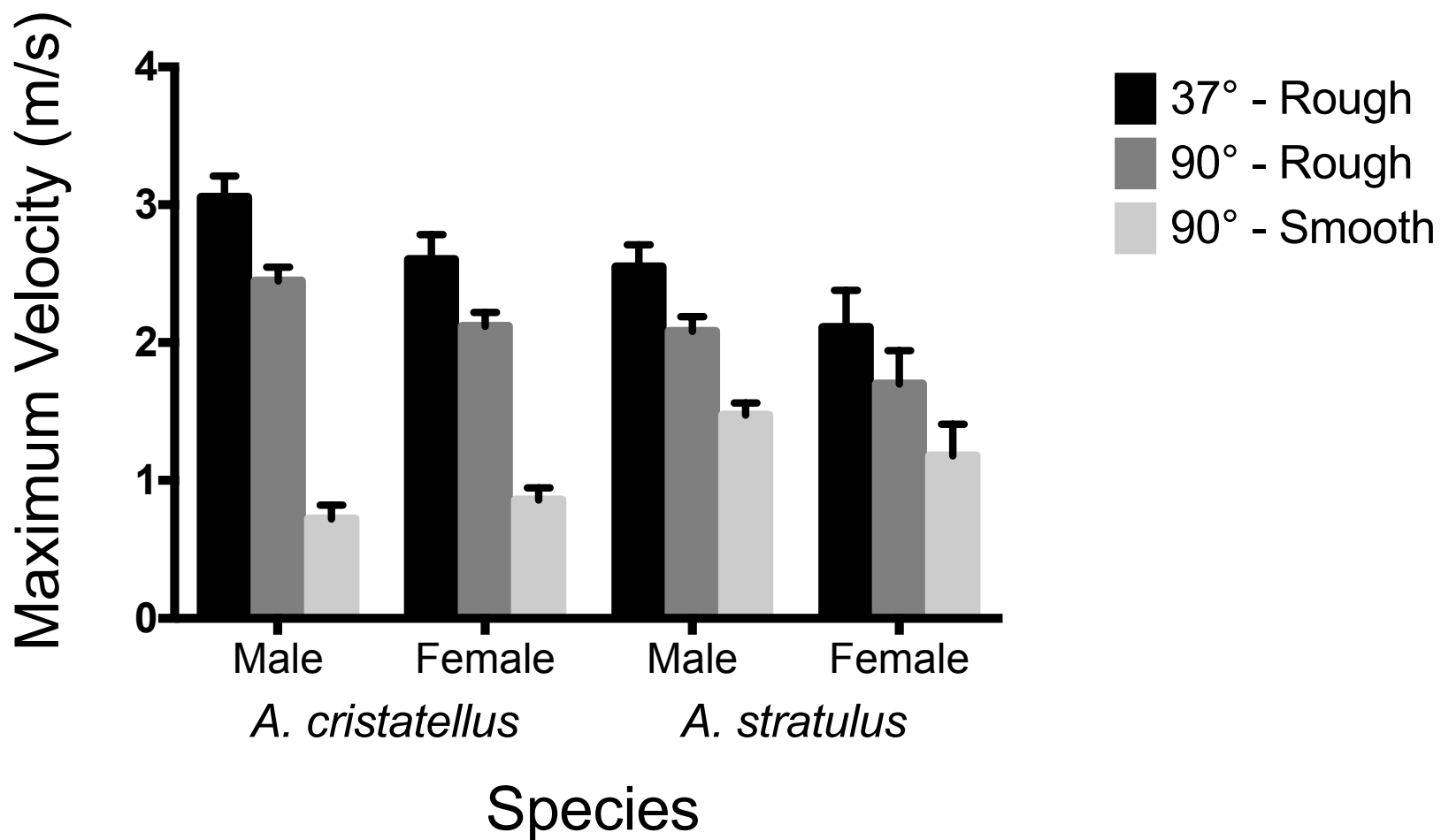
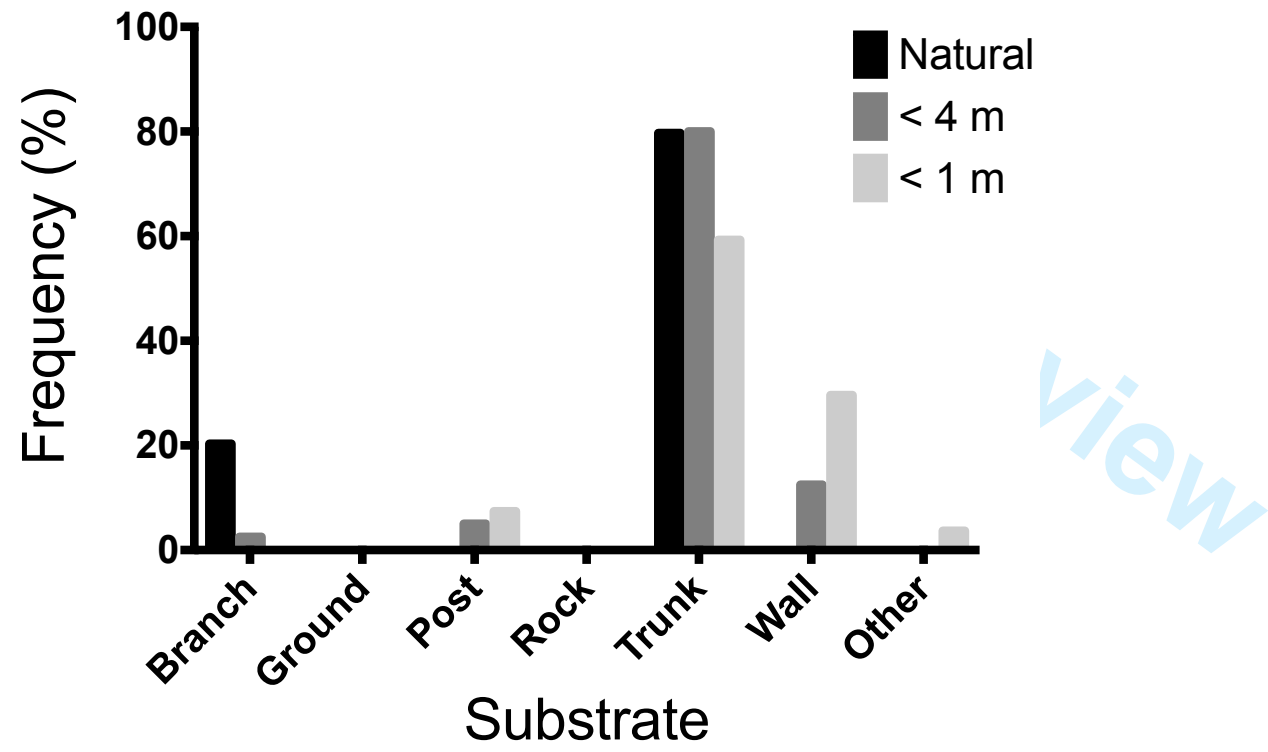


Fig. 2. Frequency distributions of substrate types for (a) *A. stratulus* and (b) *A. cristatellus* in natural habitats and human-modified habitats when lizards were < 4 m and < 1 m of built structures or artificial substrates.

a)

A. stratulus



b)

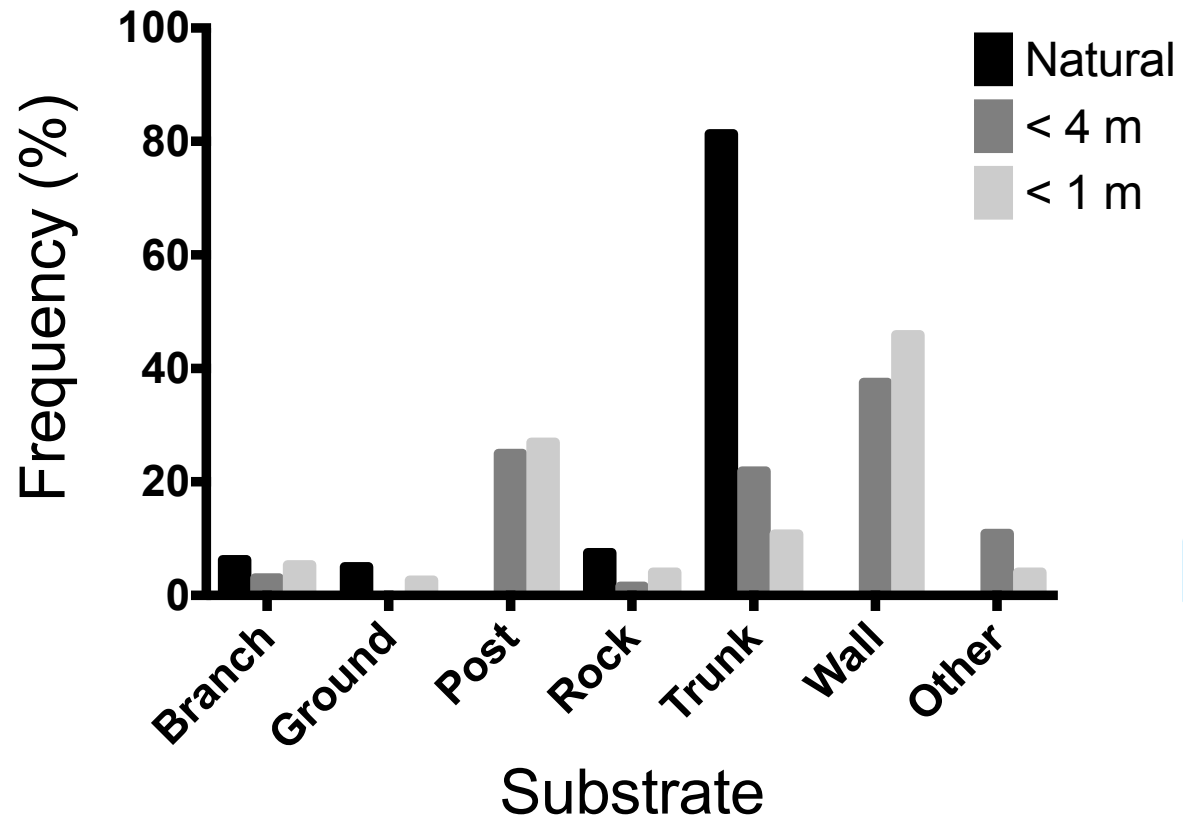
A. cristatellus

Fig. 3. Frequency distribution for surface roughness categories in natural habitats and human-modified habitats when lizards were < 4 m and < 1 m of built structures or artificial substrates.

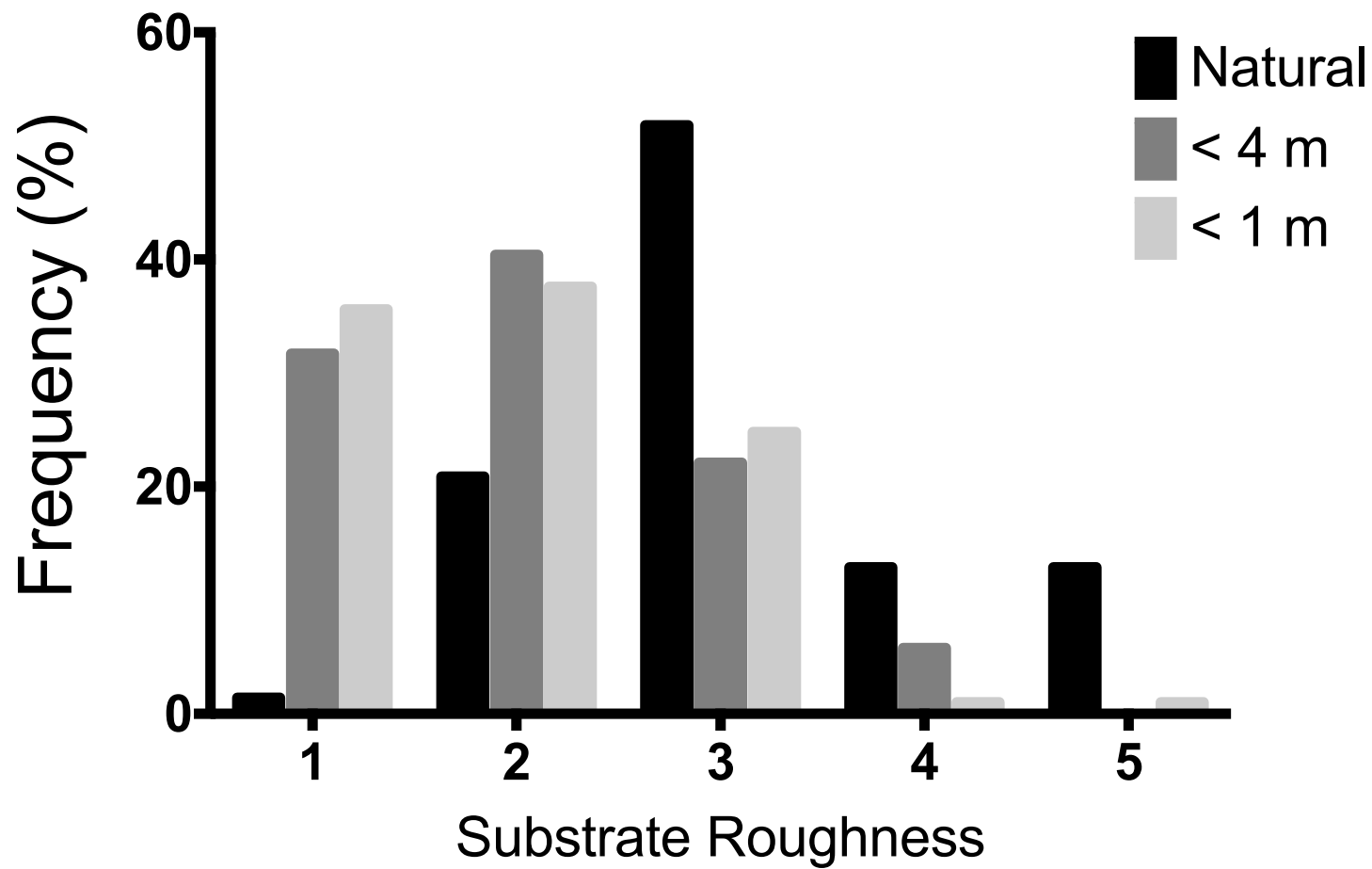


Fig. 4. Relationship between maximum velocity and PC1 on the 90°-smooth track for *A. cristatellus* (solid circles for males and open circles for females). This significant positive relationship shows that lizards with relatively long limbs, wide heads, and wide pectoral regions (PC1) run faster on smooth, vertical surfaces.

