2015

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

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Citation/Publisher Attribution

Kolbe, J. J., Battles, A. C. and Avilés-Rodríguez, K. J. (2016), City slickers: poor performance does not deter *Anolis* lizards from using artificial substrates in human-modified habitats. Funct Ecol, 30: 1418-1429. doi: 10.1111/1365-2435.12607 Available at: https://doi.org/10.1111/1365-2435.12607

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Functional Ecology
British Ecological Society

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Journal:	*Functional Ecology*
Manuscript ID	FE-2015-00611.R1
Manuscript Type:	Standard Paper
Date Submitted by the Author:	n/a
Complete List of Authors:	Kolbe, Jason; University of Rhode Island, Battles, Andrew; University of Rhode Island, Biological Sciences Avilés-Rodríguez, Kevin; University of Rhode Island, Biological Sciences
Key-words:	habitat constraint hypothesis, habitat use, locomotion, surface roughness, urban environments

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

Revised for *Functional Ecology*

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Summary

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

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

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

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

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

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

Key-words: habitat constraint hypothesis, habitat use, locomotion, surface roughness, urban environments

Introduction

Animals must successfully navigate through their local environments to survive and reproduce. When animals move through terrestrial and arboreal habitats they encounter a variety of substrates, which may affect locomotion (Moermond 1979; Hildebrand *et al.* 1985; Biewener 2003; Mattingly & Jayne 2004). Substrates vary in many ways including compliance (flexibility), diameter, inclination, and surface roughness, and these characteristics affect locomotion including the speed and accuracy with which animals move (Losos & Sinervo 1989; Irschick & Jayne 1998; Vanhooydonck *et al.* 2005; Higham, Korchari & McBrayer 2011). Animals often possess morphological adaptations that increase performance on frequently encountered substrates. For example, several groups of arboreal lizards — anoles, geckos, and some skinks — possess subdigital pads that allow them to cling to smooth substrates (Irschick *et al.* 1996; Autumn & Peattie 2002). Alternatively, animals can modify their behavior to minimize the performance costs associated with particular substrates in their environment on which they perform poorly, such as avoiding these substrates, modulating their speed to increase accuracy, or altering their mode of locomotion (Irschick & Losos 1999; Vanhooydonck, Van Damme & Aerts 2002; Foster *et al.* 2015). If animals cannot adjust their behavior or morphology, then they risk performing submaximally during prey capture, predator escape, or social interactions and will likely incur reduced fitness. Understanding how animals solve the locomotor challenges presented by the various substrates they encounter is a key question in ecological morphology, particularly as habitats are increasingly modified by human-mediated global change (Palumbi 2001; Sih, Ferrari & Harris 2011; Robertson, Rehage & Sih 2013).

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

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

Artificial substrates, such as buildings, fences, posts, and walls, likely increase the availability of smooth, vertical substrates and in some cases provide extremely broad surfaces in human-modified habitats as compared to natural areas. Most natural habitats, such as forests, lack substrates that combine these characteristics. Smooth, vertical substrates may be challenging for lizards to move on due to the lack of underlying support to counteract gravity (Cartmill 1985). Moreover, smooth surfaces reduce the ability of claws to interlock (Zani 2000; Kolbe 2015), forcing anoles to rely on their toepads for adhering to the substrate. Lizards must keep their center of gravity close to the surface to prevent toppling when one or more limbs are not in contact with the surface during locomotion. Orienting their limbs more laterally will minimize the distance from the surface (Jayne & Irschick 1999; Spezzano & Jayne 2004). This sprawling limb posture is more easily accomplished with longer limbs and a more flattened body — morphological characteristics found in some rock-dwelling lizard species (Vitt *et al.* 1997; Revell *et al.* 2007; Goodman, Miles & Schwarzkopf 2008).

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

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

Previous studies of ecologically similar *Anolis* species in natural habitats support the habitat constraint hypothesis such that lizards more frequently occupy portions of the habitat in which they perform better (Irschick & Losos 1999). When applying this hypothesis to performance on and use of artificial substrates in human-modified habitats, we make three predictions. First, locomotor performance will be sensitive to changes in inclination and roughness with lizards performing worse on steeper and smoother tracks. This decrease in performance will be in part due to the ineffectiveness of lizard claws on smooth surfaces, forcing lizards to rely solely on toepad adhesion. Second, lizards will avoid using vertical and smooth perches due to their decreased performance on these substrates. This will occur despite the increased availability of artificial substrates in human-modified areas. Third, we predict that larger lizards will be more sensitive to changes in inclination and roughness, and a positive relationship between limb length and locomotor performance will exist for the 90°- smooth track. This prediction is based on previous studies of limb kinematics in *A. sagrei* (Spezzano & Jayne 2004), limb divergence between natural and human-disturbed habitats in anoles (Marnocha *et al.* 2011), and comparative studies of morphology in some rock-dwelling lizard species (Vitt *et al.* 1997; Revell *et al.* 2007; Goodman *et al.* 2008).

Materials and methods

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

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

Laboratory Performance Trials

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

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

We analyzed videos of lizards sprinting on the different tracks using ImageJ (Rasband 2014). We digitized the starting and final positions of the lizards for each trial, calculated the distance between these points, and used the number of frames between these points to calculate time. We analyzed the maximum velocity over 4-5 cm of steady movement. We used this relatively short distance over which to measure velocity in order to obtain comparable measures across tracks. We determined the number of pauses over the total run distance (distance from the start of the run up to 20 cm before the end of the track). A pause was scored as any instance where a lizard remained in the same position for more than 1 frame, but the hindlimbs did not slide backward. Slips were scored when a lizard stopped and the hindlimbs slid backward. A fall was scored when a lizard initiated forward movement, but instead fell completely off the track. This was easily distinguished from instances where lizards jumped off the track.

Field Habitat Use

Field habitat use data were collected in natural habitats on all islands and human-modified habitats on Guana and Virgin Gorda. Natural habitats were at least 100 m from built structures and lacked artificial substrates. Therefore, we did not assess structural habitat availability, but instead focused on whether lizards used artificial substrates when they are available in human-modified areas. We took habitat use data for lizards in natural habitats, and two conditions in human-modified habitats, when lizards were < 1 m and < 4 m from built structures or artificial substrates. This allowed us to assess the habitat use of lizards when both artificial and natural substrates were easily accessible (< 1 m) or when substrates were likely within the home range of the lizard (< 4 m) (Fitch, Henderson & Guarisco 1989; Losos 2009). We could then assess whether lizards used artificial substrates similarly when access to them varied, which could indicate active selection of substrates by the lizard. For all undisturbed lizards, we recorded the type of substrate, inclination of the perch in degrees, and perch diameter and height in cm. To account for lizards using substrates for which diameter cannot be measured (ground, rocks, and walls), we calculated the percentage of flat perch use by lizards within each habitat. Because the roughness of the substrate may influence lizard locomotion, we assessed the surface roughness of each perch substrate on a scale from 1 to 5, described as follows: 1–very smooth, usually painted surface, such as a wooden wall or post, or some plant structures, such as the leaf sheath of a palm tree; 2–smooth, usually not painted, such as concrete, or leaves of some trees; 3–coarse, such as unpainted stucco or tree bark with texture; 4–rough, such as furrowed tree bark; 5–very rough, such as deeply furrowed tree bark or a metal grate.

Morphology

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

Data analysis

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

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

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

We anticipated that both species and sex would significantly influence performance owing to variation in body size (SVL and mass) and body shape (relative hindlimb length), which are important determinants of sprint speed in lizards (Huey & Hertz 1982; Losos 1990). We therefore tested for relationships between morphological variables (log-SVL, log-mass, and PC axes describing body shape variation) and maximum velocity using linear regressions for species-sex groups that differed in morphology and all lizards combined. In addition to the effect of morphology on maximum velocity, we also explored relationships between morphology and other aspects of performance — pauses, slips, and falls. We used linear regressions to test for relationships between log-SVL, log-mass, and PC axes and the distance to 1st pause, number of pauses, and number of slips. We used logistic regression to determine if morphological variation affected the probability of falling on the 90°-smooth track. We used the same morphological groups as in previous analyses.

Results

Maximum velocity

Lizard body temperatures ranged from 28.5-33.3°C (mean±SE = 30.2±1.0°C). Relationships between body temperature and maximum velocity were non-significant for comparisons in both species. Moreover, sprint speed for *A. cristatellus* varies little over the range of temperatures recorded in this study (Gunderson & Leal 2012); therefore we did not include body temperature in the analyses. Maximum velocity across all trials ranged from 0.1- 4.6 m/s. Low velocities were typically recorded prior to lizards slipping or falling, thus reflecting poor performance. Tracks differed in maximum velocity, but this pattern was different for each species (Fig. 1, Table 3). Tukey's HSD tests showed significant differences among tracks; lizards were fastest on the 37°-rough track and slowest on the 90°-smooth track. Moreover, a significant track by species interaction revealed that although *A. cristatellus* and *A. stratulus* did not differ significantly in velocity on the 37°-rough and 90°-rough tracks, *A. cristatellus* was significantly slower on the 90°-smooth track (Fig. 1).

Pauses, slips, and falls

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

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

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

Habitat use

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

Morphology

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

Morphology and Locomotor Performance on Different Substrates

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

When assessing aspects of locomotor performance other than maximum velocity, only a few morphology-performance regressions were significant. Larger male *A. cristatellus* paused less often on the 37°-rough track (log-SVL: slope = -6.63, $R^2 = 0.27$, $P < 0.01$, log-mass: slope = -2.00, $R^2 = 0.26$, $P < 0.01$) and larger female *A. cristatellus* also paused less often (log-SVL: slope = -10.72, $R^2 = 0.22$, $P = 0.01$). Larger male *A. cristatellus* had a higher probability of falling on the 90°-smooth track (log-SVL: $X^2 = 5.44$, df = 1, $P = 0.02$, log-mass: $X^2 = 4.34$, df = 1, $P = 0.04$). Male *A. cristatellus* with relatively short limbs, narrow heads, and narrow pectoral regions (lower PC1 values) also had a higher probability of falling on the 90°-smooth track ($X^2 = 4.54$, df = 1, P = 0.03).

Discussion

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

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

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

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

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

The wood surface of our 90°-smooth track provided little opportunity for lizards to use their claws, thus anoles were primarily using their toepads to attach to the surface by means of adhesion (Irschick *et al.* 1996). Increased pausing on the 90°-smooth track may be needed to maintain attachment of toepads on this surface, but could be also related to energetics and uncertainty of movement (Higham *et al.* 2011). *Anolis stratulus* rarely slipped and never fell on the 90°-smooth track, whereas *A. cristatellus* ran slower and fell often (Tables 4 and 6). The greater stability of *A. stratulus* is likely due to its lower mass relative to its toepad area (0.94-1.17 g/mm^2) compared to *A. cristatellus* (1.32-1.57 g/mm^2), and *A. stratulus* being substantially shorter and weighing less than *A. cristatellus* (Table 2). Furthermore, lizards have a propensity to rear up when accelerating at the start of a run (Higham *et al.* 2011). When falling, *A. cristatellus* would often lose contact between its forelimbs and the substrate, toppling over backwards while maintaining contact with its larger hindlimb toepads (Table 2). This may be further complicated on vertical surfaces if anoles accelerate faster compared to when on level surfaces as occurs in *Sceloporus* lizards (Higham *et al.* 2011). Vertical surfaces reduce locomotor performance in both species, but smooth surfaces have substantially greater negative affect on *A. cristatellus* performance compared to *A. stratulus* (Fig. 1).

A critical component of testing the habitat constraint hypothesis is assessing whether individuals avoid substrates on which they perform submaximally (Irschick & Losos 1999). In striking contrast to predictions based on their poor locomotor performance on the 90°-smooth track, *A. cristatellus* used artificial substrates 73% of the time and *A. stratulus* used these substrates 27% of the time in human-modified areas (Fig. 2). Furthermore, these substrates were much smoother compared to ones in natural areas (Fig. 3). How might anoles reduce the negative effects of frequently occupying substrates on which they perform poorly? Perhaps potential predators also perform poorly on artificial substrates, an important direction for future studies. Alternatively, anoles may avoid sprinting up when they occupy smooth, vertical substrates. For instance, they may restrict movement to sprinting down or jumping instead of sprinting (Losos & Irschick 1996). This would be especially true for *A. cristatellus*, which often slipped and fell on the 90°-smooth track. In contrast, *A. stratulus* rarely slipped and never fell on the 90°-smooth track, this despite having relatively shorter limbs compared to *A. cristatellus*. This is likely explained by *A. stratulus* being on average 40-75% lighter than *A. cristatellus* (Table 2), thus *A. stratulus* is not subject to the same magnitude of force acting against upward movement.

Previous studies have found that habitat characteristics influenced locomotor behavior in green anoles: despite using perches with a range of compliances, green anoles selectively jumped from less compliant (less flexible) perches (Gilman & Irschick 2013). Other research shows anoles tend to jump less often from broad surfaces (Pounds 1988; Losos & Irschick 1996) and when nearby perches are lacking (Moermond 1979; Avilés-Rodríguez 2015). Thus, anoles possess the capacity to adjust their mode of locomotion to the substrate they occupy and their surrounding habitat. If moving up is still the best option, then anoles could modulate their speed to decrease the risk of slipping or falling. Irschick *et al.* (2005) found a mismatch between maximum sprint speed measured in the laboratory and escape speed measured in the field, such that faster lizards used a lower percentage of their maximum speed, termed locomotor compensation. This finding suggests that anoles have the ability to modulate their speed. *Anolis cristatellus* slipping and falling on the 90°-smooth track may be capable of reducing their speed to increase accuracy in circumstances that do not require maximum performance. Speed-accuracy tradeoffs are known in a variety of decision-making and locomotor scenarios (Chittka, Shorupski & Raine 2009). Whether anoles modulate their speed, use alternative modes of locomotion, or otherwise behaviorally adjust to avoid performing poorly on smooth, vertical surfaces is unknown.

If anoles commonly move on smooth, vertical substrates in human-modified environments, how might selection act on morphology of these anoles? Larger lizards tended to run faster on the rough tracks (Table 6), which represent the type of substrates more often used by lizards in natural habitats (Table 1, Figs. 2 and 3). This pattern was reversed for *A. cristatellus* on the 90°-smooth track, the properties of which represent artificial substrates that lizards often use in human-modified areas. Here larger *A. cristatellus* ran slower. This tradeoff between body size and running speed was most strongly observed for male *A. cristatellus* (Table 6). Larger lizards ran faster on lower inclines due at least in part to their longer stride lengths (Navas, James & Wilson 2006). In contrast, larger lizards on the vertical, smooth surface, which relied solely on toepad adhesion for surface attachment, required greater force to counteract the gravitational forces directly opposing their movement. Slower running speed on the smooth, vertical surface, perhaps due to shorter stride lengths, was compounded for large, male *A. cristatellus* by having a higher probability of falling. Despite this generally poor performance (falling 26% of the time), when able to perform *A. cristatellus* with relatively longer limbs and broader pectoral regions (PC1) ran faster on the 90°-smooth track. This may be due to their greater ability to attain a sprawling limb posture that maintains their center of gravity close to the surface. These conditions — overall poor performance but a significant trait-performance correlation — should promote strong natural selection. Thus, in human-modified areas where *A. cristatellus* frequently uses artificial substrates that are smooth and vertical, such as posts and walls, we predict selection should favor smaller-bodied lizards with relatively longer limbs, and selection should be particularly strong for males. Despite the importance of toepads for adhering to the smooth, vertical track, we found no evidence for a relationship between toepad area (PC2) and locomotor performance for these species.

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

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

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

Acknowledgements

We thank Gad Perry, Skip Lazell, and Lianna Jarecki for their support while working on Guana Island, British Virgin Islands. Adam Duerr helped collect and process lizards in the field. Oriol Lapiedra, Hanna Wegener, and Jonathan Losos provided helpful feedback on early drafts. This work was supported in part by the Falconwood Foundation through a grant to The Conservation Agency, funds from the University of Rhode Island, and grants from the National Geographic Society and the National Science Foundation (DEB-1354897). The University of Rhode Island

Institutional Animal Care and Use Committee approved protocols for use of live animal in this study (AN11-09-005).

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Table 1. Sample size, mean ± 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 (%)
A. cristatellus	Male	81	76 ± 3.1 (0-90)	125 ± 8.0 (0-310)	11.7 ± 1.1 (1.5-32)	Natural-7% Modified-53%
A. cristatellus	Female	137	66 ± 3.0 (0-90)	68 ± 4.6 (0-250)	9.8 ± 1.6 (1-150)	Natural-16% Modified-33%
A. stratulus	Male	66	76 ± 3.0 (0-90)	139 ± 7.2 (10-350)	12.5 ± 1.2 (1.5-35)	Natural-0% Modified-18%
A. stratulus	Female	59	78 ± 3.0 (0-90)	119 ± 8.2 (5-300)	8.5 ± 1.0 (0.5-32)	Natural-0% Modified-21%

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

Variable	*A. cristatellus* Male	*A. cristatellus* Female	*A. stratulus* Male	*A. stratulus* Female
N	35	29	25	6
SVL	63.4 ± 1.09	46.7 ± 0.61	43.3 ± 0.85	40.5 ± 1.11
Mass	6.9 ± 0.34	2.5 ± 0.10	1.5 ± 0.09	1.4 ± 0.23
Femur	15.5 ± 0.28	11.0 ± 0.13	9.2 ± 0.17	8.3 ± 0.23
Tibia	13.3 ± 0.23	9.3 ± 0.11	8.0 ± 0.17	7.3 ± 0.19
4th-toe metatarsal	8.0 ± 0.12	5.8 ± 0.07	4.5 ± 0.11	4.4 ± 0.15
4th-toe phalanges	9.5 ± 0.19	6.6 ± 0.08	5.7 ± 0.10	5.2 ± 0.17
Humerus	11.2 ± 0.21	8.1 ± 0.12	7.5 ± 0.15	6.7 ± 0.20
Ulna	9.3 ± 0.17	6.7 ± 0.10	6.2 ± 0.15	5.7 ± 0.24
3rd-toe metcarpal + phalanges	7.1 ± 0.13	4.8 ± 0.06	4.5 ± 0.12	4.1 ± 0.17
Head length	16.3 ± 0.28	12.1 ± 0.14	12.1 ± 0.21	10.8 ± 0.27
Head width	11.3 ± 0.22	7.8 ± 0.08	6.8 ± 0.12	6.0 ± 0.11
Pectoral	7.8 ± 0.14	5.3 ± 0.06	4.9 ± 0.09	4.2 ± 0.14
Pelvis	6.6 ± 0.14	5.0 ± 0.09	4.0 ± 0.11	4.0 ± 0.21
Tail	91.2 ± 4.76	73.4 ± 2.55	62.3 ± 2.00	58.1 ± 4.78
3rd-toe Forefoot Toepad	2.9 ± 0.13	1.1 ± 0.04	1.0 ± 0.05	0.8 ± 0.06
4th-toe Hindfoot Toepad	4.4 ± 0.18	1.9 ± 0.06	1.6 ± 0.08	1.2 ± 0.06
PC1	0.60 ± 0.32	0.85 ± 0.42	-1.25 ± 0.38	-2.36 ± 0.52
PC2	0.24 ± 0.17	-1.56 ± 0.22	1.56 ± 0.15	-0.36 ± 0.20
PC3	-0.26 ± 0.16	0.06 ± 0.25	0.30 ± 0.21	0.00 ± 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 R^2 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 1st 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 ± 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.

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

			Number of slips/m			Percentage falling	
Species	Sex	37° - Rough	90°- Rough	90°- Smooth	37° - Rough	90°- Rough	90°- Smooth
A. cristatellus	Male	0	0	4.2±1.4	0%	0%	33%
A. cristatellus	Female	0.1±0.1	0	5.5±2.3	0%	0%	17%
A. stratulus	Male	0	0.1 ± 0.1	0.1±0.1	0%	0%	0%
A. stratulus	Female	0	0.2 ± 0.2	0.6±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
4th-toe metatarsal	**0.77**	-0.45	-0.09
4th-toe phalanges	**0.74**	-0.11	-0.25
Humerus	**0.53**	0.23	**0.65**
Ulna	0.47	0.28	**0.68**
3rd-toe metcarpal + 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).

		37°-Rough			**90°-Rough**			**90°-Smooth**		
Group	N	Slope	R^2	P	Slope	R^2	P	Slope	R^2	P
log SVL										
A. cristatellus - Male	35	2.02	0.09	0.09	-0.56	0.01	0.57	-2.24	0.18	0.01
A. cristatellus -Female	29	1.28	0.02	0.50	0.20	0.00	0.90	-1.88	0.08	0.13
A. stratulus	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										
A. cristatellus - Male	35	0.56	0.07	0.13	-0.20	0.01	0.51	-0.69	0.18	0.01
A. cristatellus -Female	29	-0.23	0.01	0.73	0.20	0.01	0.68	-0.13	0.00	0.76
A. stratulus	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										
A. cristatellus	64	-0.09	0.06	0.05	-0.01	0.00	0.83	0.09	0.11	<0.01
A. stratulus	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 (± SE) of maximum velocity for anoles on three different tracks varying in inclination and surface roughness. Sample sizes are in Table 2.

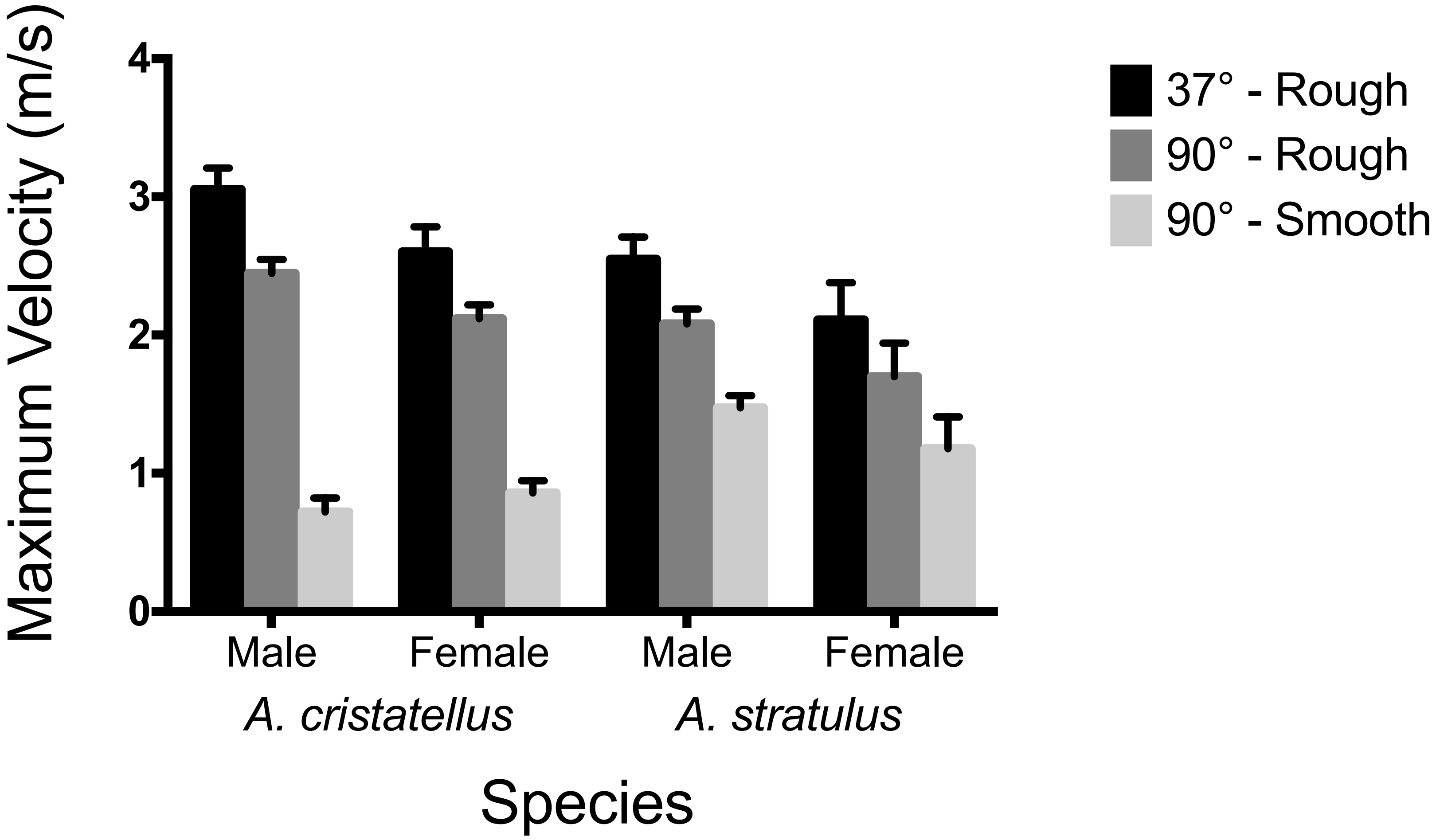
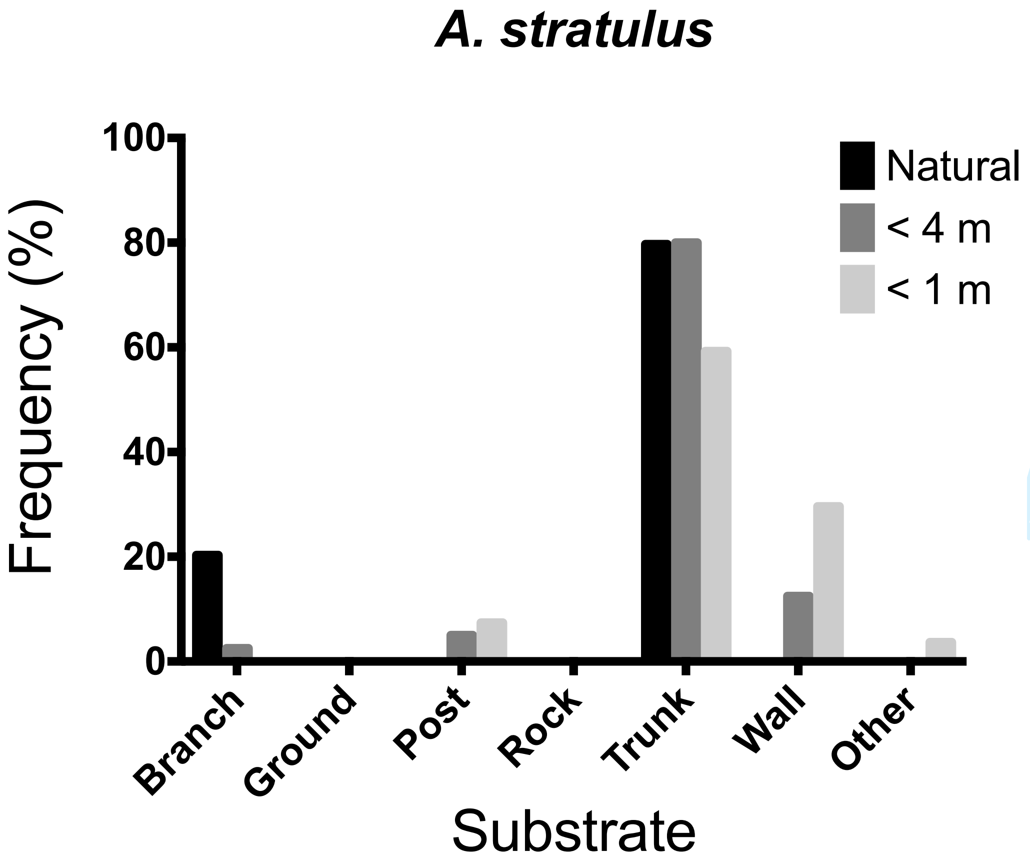


Fig. 2. Frequency distributions of substrate types for (a) *A. stratulus* and (b) *A. cristatellus* in natural habitats and human-modified habitats when lizards were < 4 m and < 1 m of built structures or artificial substrates.

a)



b)

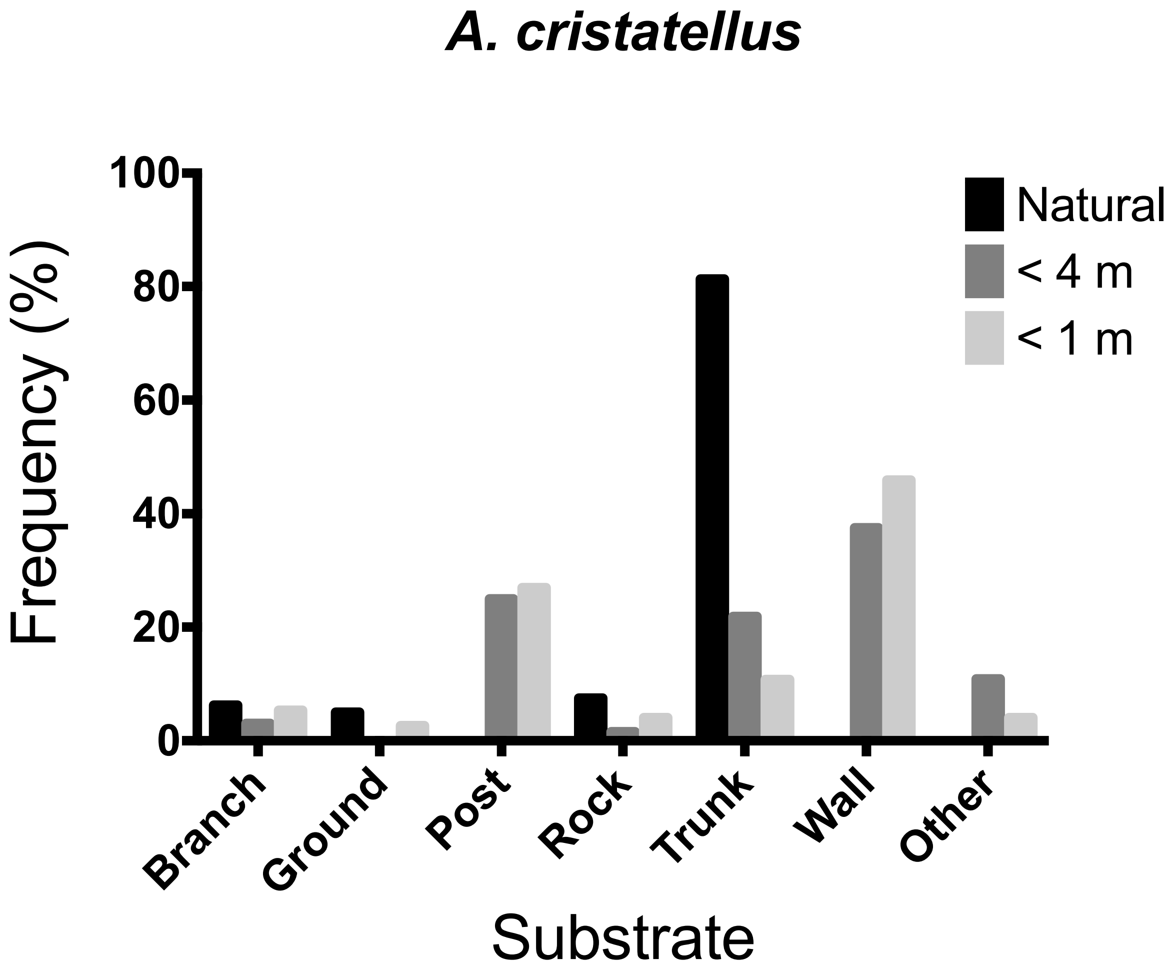

A. cristatellus
Frequency (%)
100
80
60
40
20
0
Natural
< 4 m
< 1 m
Branch
Ground
Post
Rock
Trunk
Wall
Other
Substrate

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.

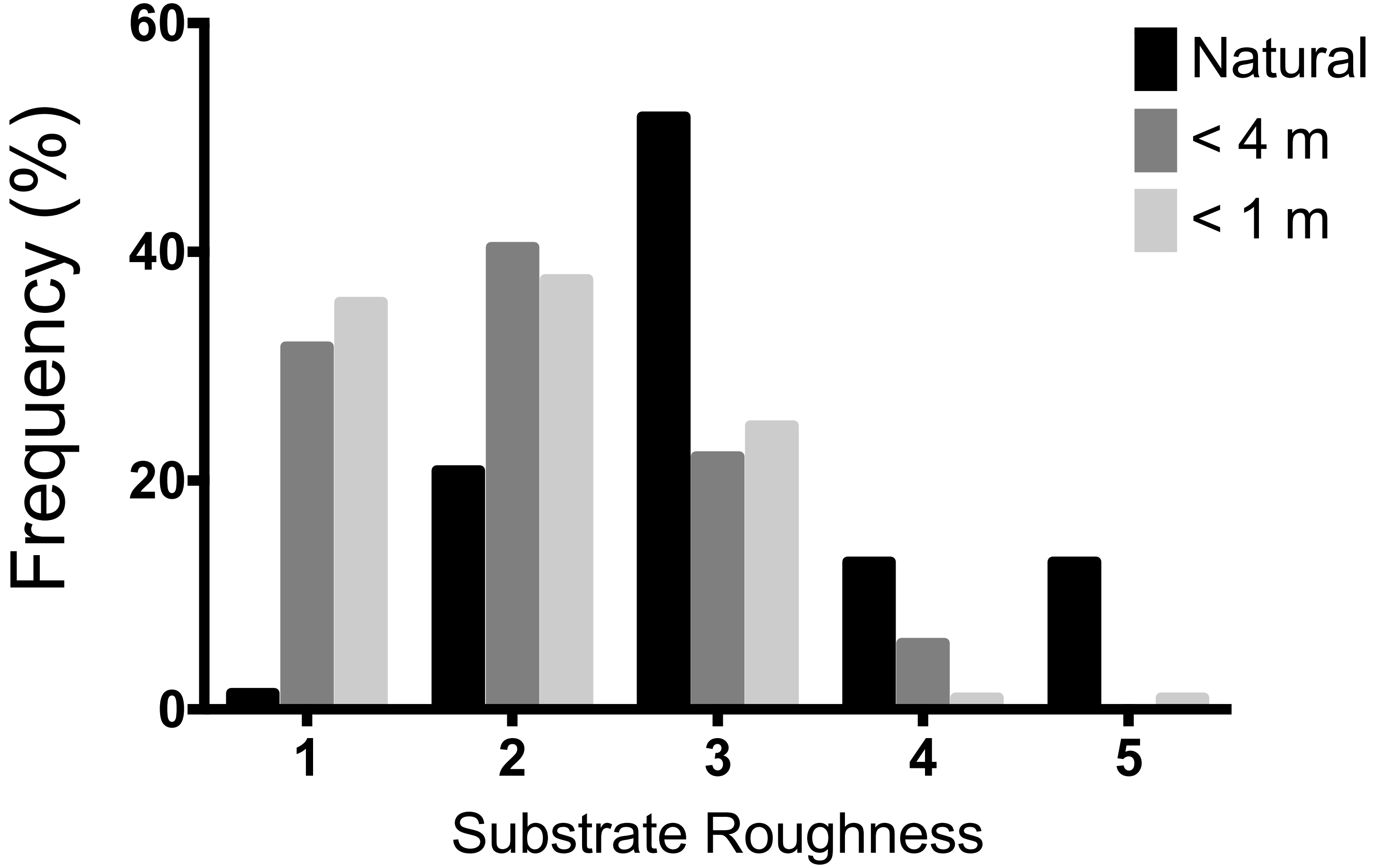


Fig. 4. Relationship between maximum velocity and PC1 on the 90°-smooth track for *A. cristatellus* (solid circles for males and open circles for females). This significant positive relationship shows that lizards with relatively long limbs, wide heads, and wide pectoral regions (PC1) run faster on smooth,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