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The finer points of urban adaptation: intraspecific variation in lizard claw morphology

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Human activity drastically transforms landscapes, generating novel habitats to which species must adaptively respond. Consequently, urbanization is increasingly recognized as a driver of phenotypic change. The structural environment of urban habitats presents a replicated natural experiment to examine trait–environment relationships and phenotypic variation related to locomotion. We use geometric morphometrics to examine claw morphology of five species of *Anolis* lizards in urban and forest habitats. We find that urban lizards undergo a shift in claw shape in the same direction but varying magnitude across species. Urban claws are overall taller, less curved, less pointed and shorter in length than those of forest lizards. These differences may enable more effective attachment or reduce interference with toepad function on smooth anthropogenic substrates. We also find an increase in shape disparity, a measurement of variation, in urban populations, suggesting relaxed selection or niche expansion rather than directional selection. This study expands our understanding of the relatively understudied trait of claw morphology and adds to a growing number of studies demonstrating phenotypic changes in urban lizards. The consistency in the direction of the shape changes we observed supports the intriguing possibility that urban environments may lead to predictable convergent adaptive change.

ADDITIONAL KEYWORDS: adaptation – anole – Caribbean – claw – climbing – convergence – geometric morphometrics – urbanization.

INTRODUCTION

Anthropogenic activity transforms natural areas, altering structural habitats for species in urban environments. Urban habitats are characterized by anthropogenic structures, impervious surfaces, maintained green spaces and human presence (Forman, 2014). Recently, studies have documented phenotypic differences in urban populations in diverse taxa (Johnson & Munshi-South, 2017), including behavioural (reviewed in Lowry *et al.*, 2013), physiological (e.g. Angilletta *et al.*, 2007; Campbell-Staton *et al.*, 2020), genetic (e.g. Harris & Munshi-South, 2017) and morphological shifts (e.g. Winchell *et al.*, 2016). Among these, urban morphological shifts are relatively understudied, and few studies have explicitly considered terrestrial locomotor morphology in urban environments.

Urban species must contend with a more open environment dominated by anthropogenic structures that are structurally simplistic and relatively smooth compared to forested areas (Winchell *et al.*, 2016, 2018a, b, 2020; Avilés-Rodríguez & Kolbe, 2019). Urban vegetation differs from vegetation present prior to human modifications, with landscaped spaces composed of large mature trees, ornamental vegetation and discontinuous canopy cover (Forman, 2014). Urban environments thus represent a replicated novel structural habitat in which we can examine adaptation related to locomotion and arboreality (Winchell *et al.*, 2020). For example, urban western fence lizards (*Sceloporus occidentalis*) sprint less and more slowly, changes that are associated with shorter limbs (Putman *et al.*, 2019). In other instances, urban habitats favour enhanced locomotor or climbing performance. For example, urban anole lizards (*Anolis*

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cristatellus) sprint faster and have longer limbs compared to forest populations (Winchell *et al.*, 2016, 2018b).

Anolis lizards ('anoles') are a model system for studying evolution (Losos, 2009). Trait–environment relationships are well-studied, particularly regarding ecologically relevant and heritable traits, such as limb length and toepad morphology (Losos, 1994; Stuart *et al.*, 2014). Habitat changes in non-urban environments have been correlated with interspecific and intraspecific morphological variation and rapid phenotypic shifts (reviewed in Losos, 2009). In addition, anoles have become a key taxon for understanding urban adaptation. Phenotypic changes have been observed in urban populations of *Anolis sagrei* and *A. cristatellus* in relation to the structural habitat: in both species, urban populations have relatively longer limbs, larger toepads and more subdigital lamellae for adhesion (Marnocha *et al.*, 2011; Winchell *et al.*, 2016, 2018b). These traits appear to enhance locomotion on smooth surfaces typical of urban environments (Kolbe *et al.*, 2016; Winchell *et al.*, 2018b).

We know relatively little about another trait important to anole locomotion: claws. Although critical for climbing in species without toepads (Cartmill, 1985), claws are also important integrated components of the attachment system in pad-bearing lizards such as anoles (Yuan *et al.*, 2019). Bloch and Irschick (2005) found that claw removal in anoles results in a drastic reduction in clinging ability on smooth substrates, although removal of claws may sever tendons important to toepad function (e.g. Garner *et al.*, 2017). Even so, Zani (2000) found that claw curvature and toepad morphology were positively associated with clinging ability on smooth substrates and claw height was positively associated with clinging ability on rough substrates. This evidence supports a significant and synergistic importance of claws for climbing (Song *et al.*, 2016; Yuan *et al.*, 2019), yet trade-offs likely exist between claw shape and locomotion on different substrates and in different habitats, which could lead to intra- and interspecific variation in claw morphology. For example, Wollenberg *et al.* (2013) documented differences in claw morphology of *A. cybotes* correlated with variation in habitat by elevation, and Yuan *et al.* (2019) documented interspecific differences in claw shape across 57 species of anoles associated with habitat use.

Generally, claws of climbing species tend to be sharper, more curved and have taller bases compared to terrestrial species (Cartmill, 1985; Zani, 2000; Tulli *et al.*, 2009, 2016; Crandell *et al.*, 2014; Muñoz *et al.*, 2015; D'Amore *et al.*, 2018; Yuan *et al.*, 2019). This pattern of long, straight claws in terrestrial species and short, pointed, curved claws in arboreal species has been documented in many taxa, including: rodents (Tulli *et al.*, 2016), birds (Feduccia, 1993) and lizards (Tulli *et al.*, 2009; Birn-Jeffrey *et al.*, 2012; D'Amore *et al.*, 2018; Baeckens *et al.*, 2019). Consistent with these findings, Yuan *et al.* (2019) found that arboreal anoles had more curved claws than less-arboreal anoles and that overall claw shape varied with microhabitat use (but see Crandell *et al.*, 2014). More recently, Yuan *et al.* (2020) found that anole species without congener competitors have predictable relationships between claw morphology and habitat use, with species occupying more forested habitats possessing more strongly curved claws compared to species occupying open habitat requiring terrestrial movement.

Extensive use of smooth substrates may selectively favour claw morphologies that improve clinging ability on these substrates, such as more acute tips, increased curvature and taller base heights (discussed in Winchell *et al.*, 2020). Alternatively, claws may interfere with toepad function on these surfaces by impeding adhesive attachment (Naylor & Higham, 2019), in which case selection on toepads may be strong and selection on claw morphology may be relaxed. If claws are ineffective on anthropogenic substrates, other selective pressures may shape claw morphology in idiosyncratic ways. This might arise, for example, if claws are not sharp enough to interlock with the minute surface asperities of anthropogenic substrates. Moreover, selective pressures for climbing may be at odds with those for terrestrial locomotion. If urban anoles have increased demands for quick terrestrial locomotion as evidence suggests (Winchell *et al.*, 2018b), we would instead expect urban claw morphologies to resemble long and straight claws typical of terrestrial species. In brief, the urban environment poses multiple structural challenges that may favour different adaptive optima depending on claw effectiveness on anthropogenic substrates and habitat use.

We take advantage of the replicated natural experiment of urbanization to investigate adaptive responses in claws, a functionally relevant and biomechanically conserved trait. We examined claw morphology in paired urban and forest populations of five species of anoles representing four deeply diverged lineages in the Greater Antilles: *Anolis cristatellus*, *A. cybotes*, *A. grahami*, *A. lineatopus* and *A. sagrei*. We examined three main questions with the following predictions, each of which builds on the previous:

1. How does surface roughness in urban and forest habitats differ and do lizards discriminate perches based on this factor? We predicted that urban habitats would be characterized by smoother perches because of abundant anthropogenic substrates, and that lizards would use smoother perches in urban compared to forest habitats.
2. Does claw shape vary between urban and forest populations and, if so, in what dimensions? If urban

lizards use smoother substrates compared to forest conspecifics (question 1), then we predict that urban and forest claws would differ. Specifically, we predict based on trait–environment relationships in anoles and other taxa that urban claws would be shorter in length, taller at the base, more curved and sharply pointed.

3. Are differences in claw morphology between urban and forest populations consistent across species? If we detect clear differences between urban and forest populations (question 2), then we predict that similar selection pressures related to the biomechanical demands of climbing smooth anthropogenic substrates should lead to parallel directional shifts in claw shape.

MATERIALS AND METHODS

FIELD METHODS

We sampled five *Anolis* species from paired urban and forest sites from four island groups between June 2018 and June 2019: the Bahamas (New Providence), Dominican Republic (Santo Domingo), Jamaica (Kingston) and Puerto Rico (Arecibo) (Fig. 1, details in Supplement S1). Forest sites were mature secondary growth forests with near-continuous canopy cover and minimal human activity. Urban habitats ranged from park-like habitat with large buildings (museums), recreational green space and walking paths (Dominican Republic) to urban residential areas (Puerto Rico). Although the degree of urbanization sampled for each species differs, the sites share common characteristics relevant to locomotion: reduced and discontinuous tree canopy, extensive impervious surface cover and abundant anthropogenic structures. Ideally, we would have sampled urban sites with identical characteristics; however, logistical concerns including lizard presence and abundance, property access, researcher safety and distance from forest sites influenced our site choices.

On each island, we sampled the dominant native urban anole species: *A. sagrei* (Bahamas), *A. lineatopus* and *A. grahami* (Jamaica), *A. cybotes* (Dominican Republic) and *A. cristatellus* (Puerto Rico). Four of these species are considered 'trunk–ground' ecomorphs,

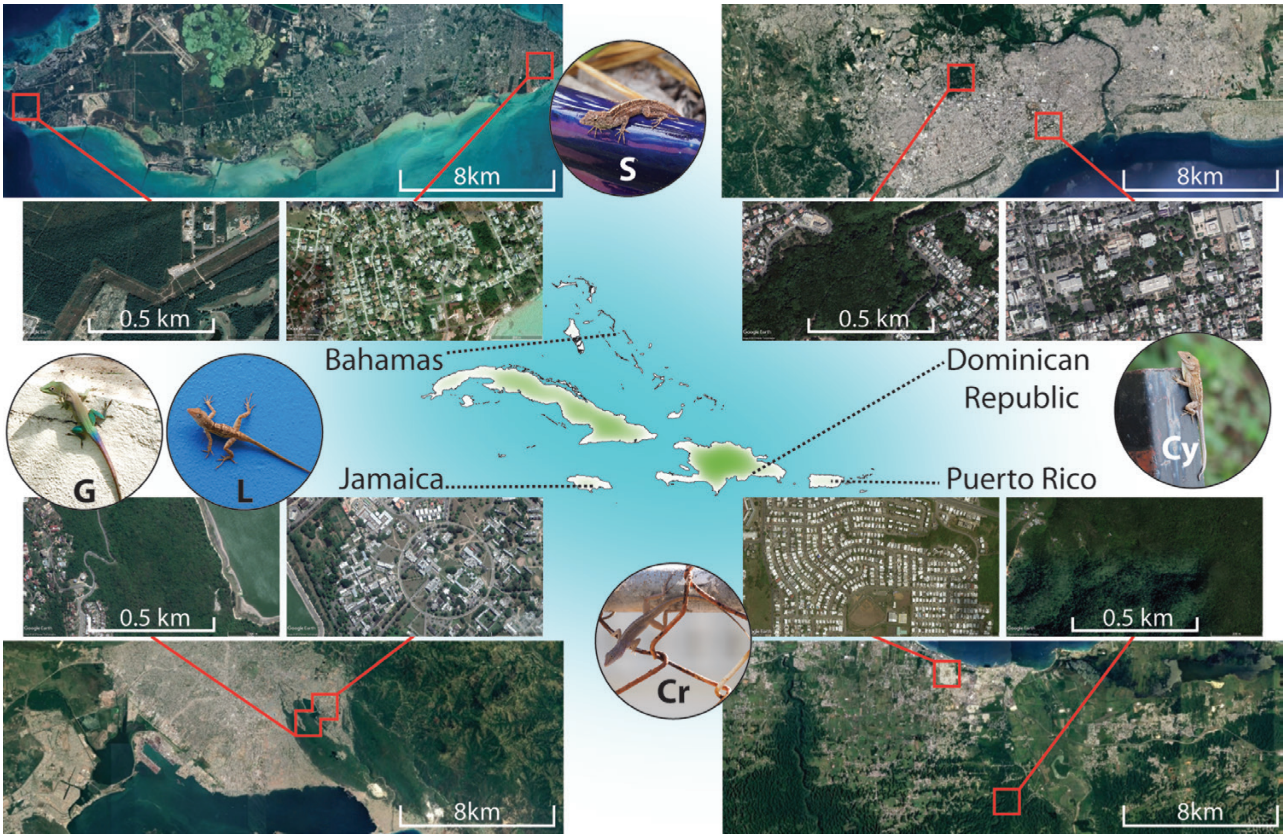

Figure 1. We sampled urban and forest habitat from Bahamas, Dominican Republic, Jamaica and Puerto Rico. Letters correspond to species: *A. sagrei* (S), *A. grahami* (G), *A. lineatopus* (L), *A. cybotes* (Cy) and *A. cristatellus* (Cr). Satellite imagery from Google Earth: CNES/Airbus (2019), Maxar Technologies (2019), TerraMetrics (2019). Lizard photos by KMW.

whereas one (*A. grahami*) is a 'trunk–crown' ecomorph (Losos, 2009). These categories describe unique ecological and morphological specializations linked to habitat specialization. We included two species from the Jamaican lineage because both were abundant in urban habitats. We sampled adult males using standard methods (floss lasso and hand capture) as encountered at each site without specifically targeting lizards on anthropogenic versus natural surfaces. We imaged the claw profile on the 3rd digit of the forefoot and 4th digit of the hindfoot (the longest digits in these species and commonly measured in anole studies) using a macro lens with a size standard (Fig. 2). To standardize the focal point and aspect of our claw images, we affixed an acrylic Petri dish to our camera lens and held each claw flat against this surface. We imaged one forefoot and one hindfoot of each animal. If claws on both sides were visibly damaged (size or appearance differed from other claws on the same foot) we did not image the digit (sample sizes in Supplement S2). We measured body size (snout–vent length, SVL) and returned lizards to their capture site following measurement.

For a random subset of lizards (sample sizes in Supplement S3), we took macro photographs with a size and colour standard of a representative section of the perch surface out of direct sunlight at the capture location ('used' perch) and a randomly selected potential perch nearby ('random' perch, as in Winchell *et al.*, 2018a). To select 'random' perches, we used a random direction generator, choosing the closest structure that could potentially be used as a perch (i.e. support an adult lizard) in the direction indicated and at the same height as the used perch.

DIGITAL DATA COLLECTION

A single researcher (KMW) reviewed images (blind to population), excluding any in which the claw was broken or the shape, tip and base of the claw were not clearly visible (e.g. out of focus or over-exposed). A single researcher (CHF) placed landmarks on claw images in TPSDig (Rohlf, 2006). We placed curves along the dorsal and ventral surface (using *draw curves* function) and landmarks at the claw base and tip (Fig. 2). We distributed 30 evenly spaced semi-landmarks along each curve using the function *resample curves*. We imported landmark files into R (v.3.6.2, R Development Core Team, 2019) using the package 'geomorph' (Collyer & Adams, 2019). Because the resample tool in TPSDig sometimes produced

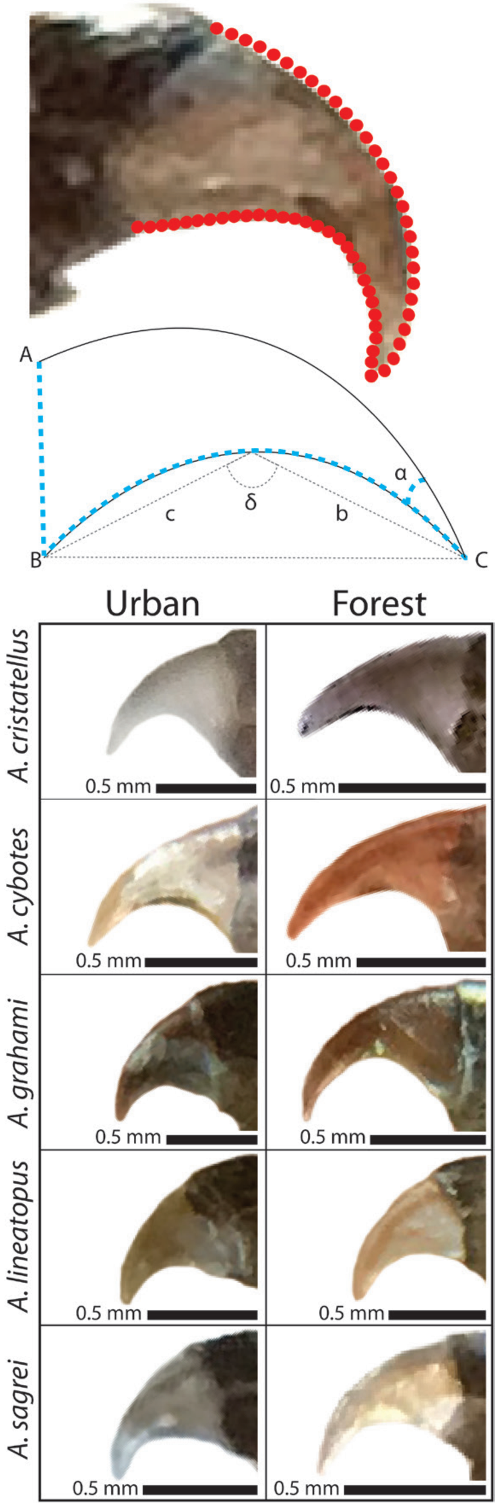

Figure 2. (Top panel) We distributed 30 semi-landmarks along the dorsal and ventral claw with two overlapping tip points. (Middle) We also measured four univariate metrics: height (distance from A to B), length (ventral arc length from B to C), tip angle (angle α at the distal tip) and curvature (as in Zani, 2000 and others), which describes the curvature of the arc at the vertex of the claw where angle δ is maximized. (Bottom panel) Example rear claw images of forest and urban lizards of each species.

aberrantly jagged lines over very short distances, we performed an additional curve smoothing step using Chaikin's corner-cutting algorithm with the R package 'smoothr' (Strimas-Mackey, 2018). We redistributed 30 equidistant points along the smoothed curve using the 'geomorph' function *digit.curves*. We then dropped the overlapping tip point for the dorsal and ventral curves and redundant semi-landmarks that overlapped with the dorsal and ventral base landmarks, resulting in a total of 56 semi-landmarks.

Additionally, we extracted the following univariate measurements from the landmarks: base height, length (ventral arc length from base to tip), curvature and tip angle (Fig. 2). We calculated curvature with the formula

$$\frac{180}{\pi}\left(2 \times arcsine\left(\frac{\sqrt{\begin{matrix}(2A^2B^2) + (2A^2C^2)\\ + (2B^2C^2) - (A^4)\\ -(B^4) - (C^4)\end{matrix}}}{(2AB)}\right)\right)$$

where A and B are distances from the claw base and tip to the ventral vertex and C is the distance from the base to the tip (Zani, 2000; Crandell *et al.*, 2014; Yuan *et al.*, 2019). This metric has been widely adopted across taxa and has been shown to reliably estimate claw curvature (Tinius & Patrick Russel, 2017).

To quantify surface roughness, we size and colour standardized our surface images, selecting a representative portion in uniform light (i.e. no direct sunlight or aberrant shadows) of at least 1 cm^2. We quantified roughness using the ImageJ plugin 'SurfCharJ' (Chinga *et al.*, 2007), which assumes light intensity corresponds to surface plane deviation (i.e. shadows are interpreted as depth). This method yields results consistent with published surface roughness values using more sophisticated methods and previous studies have found anthropogenic and vegetative surfaces consistently vary with these estimates (Winchell *et al.*, 2016, 2018b). We calculated the arithmetic mean deviation (R_a), a common measure of surface roughness, wherein larger values indicate rougher surfaces.

STATISTICAL METHODS

We performed all statistical analyses using R 3–6.2 (R Core Team, 2019). We implemented LME models with the R package 'lme4' and the function *lmer*, along with the R package 'lmerTest', which assigns significance levels to model terms using Satterwaite's approximation method and Type III ANOVA (Bates *et al.*, 2015). We provide more details for each model below.

Habitat use

We investigated how surface roughness (R_a) varied with substrate type across all perches (used and random) in all sites by first using a one-way ANOVA of R_a by perch type to establish how anthropogenic and natural (e.g. leafy and woody vegetation, rocks) substrates differ treating perch type as an objective, binary categorization. However, these categories may be overly simplistic, with their mean perch roughness values likely influenced by the types of vegetation and anthropogenic surfaces sampled. Consequently, we additionally a-priori classified perches into five categories based on substrate type and appearance: smooth anthropogenic, rough anthropogenic, smooth vegetation, rough vegetation, or rock (definitions in Supplement S4) and repeated the one-way ANOVA with this more subjective perch categorization.

We then asked if surface roughness (R_a) differed between used and random perches (i.e. discriminatory habitat use) using a linear mixed-effects model with species as a random effect and fixed effects of habitat type (urban or forest) and use with an interaction. A significant effect of 'use' would indicate discriminatory habitat use based on surface roughness. A significant effect of 'habitat' would indicate surface roughness differs by habitat type. A significant habitat–use interaction would indicate different patterns of habitat use discrimination based on surface roughness in urban and forest habitat types. Thus, the purpose of this analysis is twofold: establish how urban and forest habitats differ and determine if lizards (across all species) discriminately use perches based on roughness in each habitat type. Because this analysis does not capture species-level variation in habitat use, we also asked how surface roughness of used perches varied with species and habitat type. We used individual t-tests for each species to test if mean roughness of used perches significantly differed between urban and forest populations.

Claw morphology

Using geometric morphometrics, we analysed two-dimensional claw profile shape in R with the package 'geomorph' (Collyer & Adams, 2018, 2019; Adams *et al.*, 2019). We performed generalized Procrustes analysis (GPA) on our semi-landmarks (using function *gpagen*) across species and populations, aligning and conducting separate analyses for front and rear claws.

We performed principal components analyses (PCA) of shape variation on aligned shapes using the function *gm.prcomp* with minimized bending energy of semi-landmarks along the two curves.

We tested for differences in shape disparity between urban and forest populations across all species using the function *morphol.disparity* (in 'geomorph'). We repeated this analysis to perform pairwise comparisons within each species. Relatively low values for shape disparity are equivalent to decreased variance in the shape phenotype. We next tested if population mean aligned shape differed by species, habitat type, and their interaction (species × habitat) using Procrustes ANOVA implemented with the function *procD.lm*. We included body size (SVL) as a covariate, which we natural-log transformed to improve normality. We examined the effect of habitat for each species with functions *interaction* and *pairwise*, from the package 'RPPP' implemented in 'geomorph', which performs pairwise comparisons of least-square means. As part of the Procrustes landmark alignment process, absolute size is removed from the data set, but size-related aspects of shape remain, such as allometric changes in shape or differences in size due to changes in shape. We also considered how size-related shape may be captured in our PC axes with linear models of each of the first two principal components by centroid size across all species for front and rear claws separately.

In addition to our geometric morphometric analyses, we used a two-factor MANOVA to perform an analogous analysis on our univariate variables of claw shape with natural-log transformed SVL as a covariate, again with habitat type interacting with species, for front and rear claws separately. We natural-log transformed claw height and claw length for this analysis to meet assumptions of multivariate normality. The purpose of these analyses was to determine if claw shape differed by habitat type (urban versus forest) and if the directionality and magnitude of this variation differed across species, indicated by a significant interaction effect.

Lastly, we investigated claw damage to better understand if wear and damage contribute to shape differences. We tallied the number of broken claws in our data set, which were generally entire claw failures with detachment at the base (examples in Supplement S7). We tested if claw damage frequency differed by habitat type with a Chi-square test across all species.

RESULTS

HABITAT USE

Anthropogenic perches were smoother than natural perches (Fig. 3A; ANOVA, $F_{\mathrm{df}\,=\,1,\,694} = 130.14$, $P < 0.001$). Rocks ($N = 13$) and rough vegetation ($N = 258$) were the roughest, whereas rough anthropogenic surfaces ($N = 26$) had similar roughness as smooth vegetation ($N = 281$), and smooth anthropogenic surfaces were significantly smoother than all a-priori assigned categories ($N = 121$; Fig. 3B; Supplement S4). Urban and forest habitats differed as expected: perches were smoother in urban environments ($N = 361$ urban, $N = 338$ forest; Type III ANOVA, $\beta = -4.828 \pm 0.905$ μm,

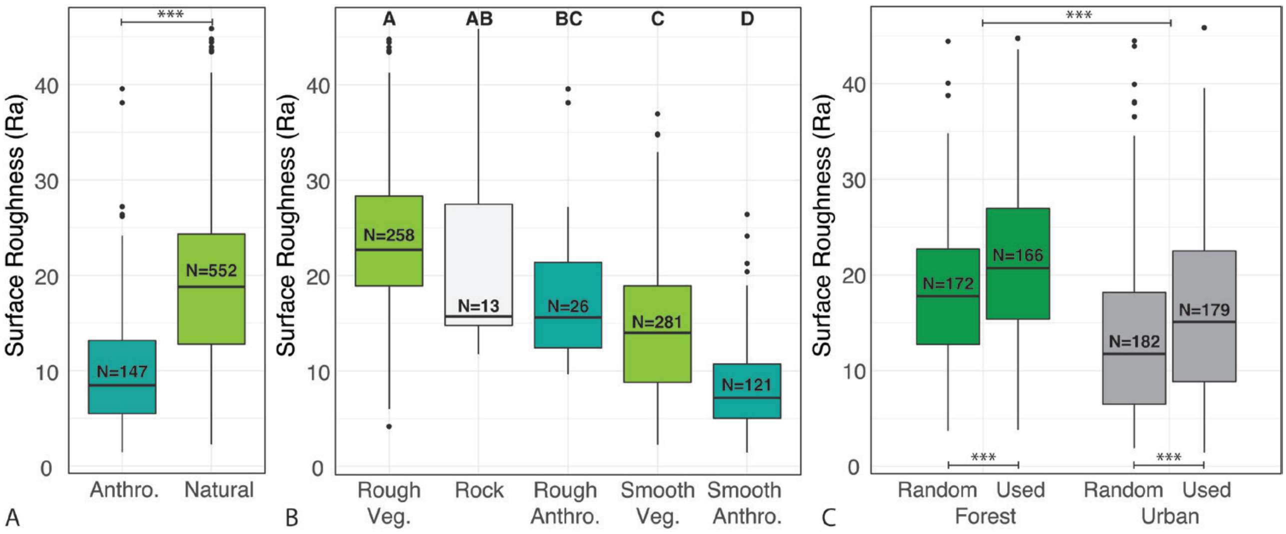

Figure 3. A, Surface roughness differs between anthropogenic and natural perch types, with smooth anthropogenic surfaces far smoother than any other. Letters represent grouped pairwise comparisons of marginal means at $P < 0.05$. B, Lizards in both urban and forest habitats used rougher perches than randomly available even though urban perches were overall smoother than forest perches.

$F_{\mathrm{df}\,=\,1,\,690}$ = 59.030, P < 0.001; Fig. 3B). In both habitats, lizards discriminately used rougher perches than were randomly available (Type III ANOVA, β = 3.234 ± 0.922 µm, $F_{\mathrm{df}\,=\,1,\,688}$ = 23.313, P < 0.001; Fig. 3C, Supplement S5). Analysis of habitat use for each species revealed that urban lizards used smoother perches compared to forest conspecifics in only two species: *A. cristatellus* (t-test, β = –10.367 ± 1.690 µm, $t_{\mathrm{df}\,=\,100}$ = –6.135, P < 0.001) and *A. sagrei* (t-test, β = –8.703 ± 2.134 µm, $t_{\mathrm{df}\,=\,76}$ = –4.079, P < 0.001), with a marginally significant trend in the same direction in *A. lineatopus* (t-test, β = –3.672 ± 1.863 µm, $t_{\mathrm{df}\,=\,56}$ = –1.971, P = 0.054). Perches used by *A. cybotes* and *A. grahami* did not differ in roughness by habitat (t-test; *A. cybotes*: β = 4.306 ± 2.473 µm, $t_{\mathrm{df}\,=\,48}$ = 1.741, P = 0.088; *A. grahami:* β = 0.0387 ± 2.36 µm, $t_{\mathrm{df}\,=\,54}$ = 0.016, P = 0.987).

CLAW SHAPE

We quantified claw shape for 396 front claws (N = 217 urban, N = 179 forest) and 454 rear claws (N = 220 urban, N = 234 forest; sample sizes by species in Supplement S2). Rear claws had 1.6 times greater variance in shape (morphological disparity) in urban versus forest populations across all species (P = 0.001), with greatest pairwise differences in *A. cristatellus* (1.6 times greater), *A. cybotes* (1.7 times greater) and *A. sagrei* (2.3 times greater). Front claws had 1.5 times greater morphological disparity in urban populations across all species (P = 0.001), ranging from 1.1 times (*A. cristatellus*) to 1.7 times greater variance (*A. sagrei*).

PCA of claw shape variation (represented by landmarks) captured 78.1% of variation in the first two principal components for front claws (PC1: 58.2%, PC2: 19.8%) and 76.3% for rear claws (PC1: 56.8%, PC2: 19.4%; Fig. 4). These principal components represent the main axes of size-independent shape variation in claw morphology. The size of the claw (represented by centroid size) significantly decreased with PC1 and increased with PC2, suggesting that these two descriptive axes are capturing some aspect of size-related shape, possibly because of size changes that result from shape differences (front claw: df = 394; PC1 t = –8.986, P < 0.001; PC2 t = 2.139, P = 0.033; rear

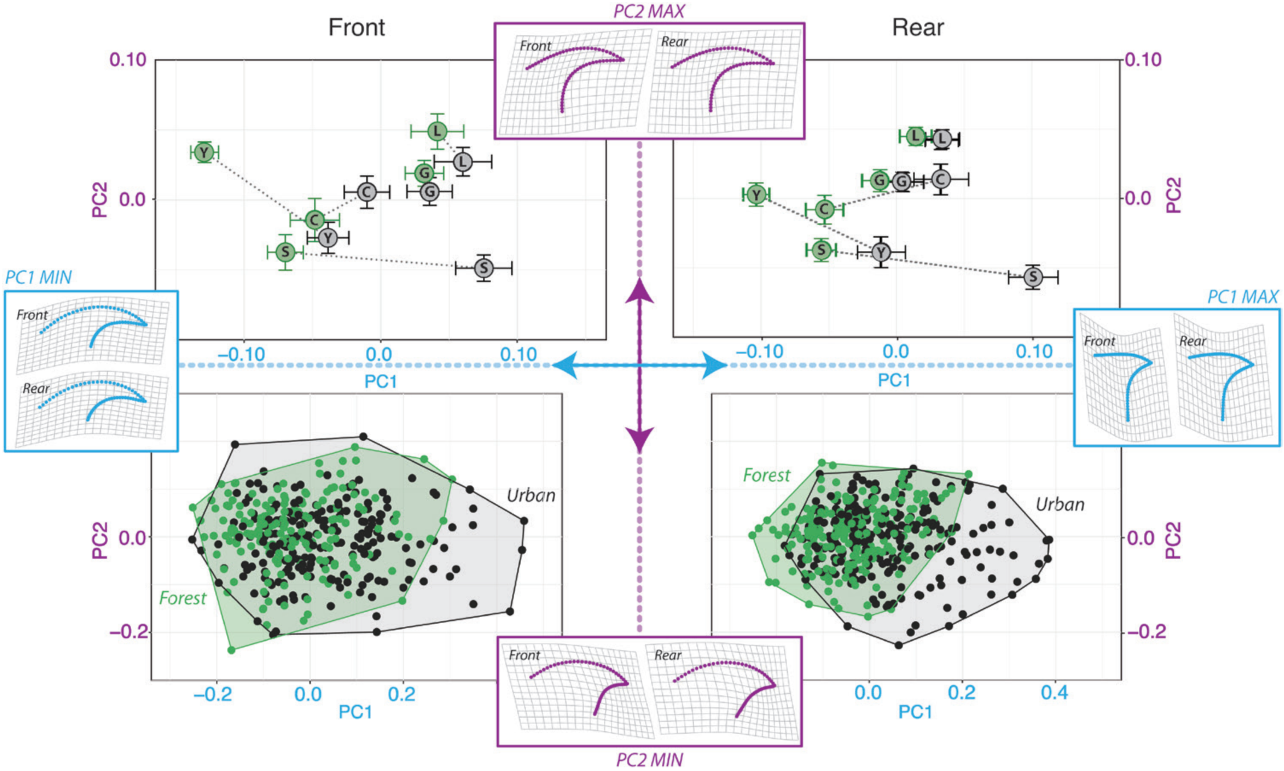

Figure 4. Principal components analysis of front (left) and rear (right) claw shape coloured by habitat type: green—forest, grey—urban. (Top row) Mean values of the first two principal components of claw shape per population are shown with standard error; dotted lines connect population pairs: 'C' *A. cristatellus*, 'Y' *A. cybotes*, 'G' *A. grahami*, 'L' *A. lineatopus*, 'S' *A. sagrei*. Mesh shapes represent minimum and maximum representative shapes for PC1 (light blue) and PC2 (purple). (Bottom row) Minimum convex polygons of PC1 and PC2 across all species.

claw: df = 452; PC1 $t = -9.189$, $P < 0.001$; PC2 $t = 2.080$, $P = 0.038$). Mean front and rear claw shapes varied between forest and urban populations in the same direction across species (Procrustes ANOVA; front: $F_{\mathrm{df}=1,\,384} = 24.348$, $P = 0.001$; rear: $F_{\mathrm{df}=1,\,441} = 36.862$, $P = 0.001$; Fig. 5). However, the magnitude of this shape change differed between species (site × species interaction, Procrustes ANOVA; front: $F_{\mathrm{df}=4,\,384} = 4.303$, $P = 0.001$; rear: $F_{\mathrm{df}=4,\,441} = 5.067$, $P = 0.001$).

Within species, front claw shape differed between forest and urban populations for *A. cybotes* (pairwise effect size: 2.193, $P = 0.017$) and *A. sagrei* (pairwise effect size: 3.162, $P = 0.003$), determined by pairwise comparison of means from the Procrustes linear model. Rear claw shape differed within species between forest and urban populations of *A. sagrei* only (pairwise comparison of Procrustes linear model, effect size: 4.127, $P = 0.001$). Both front and rear claws shifted in the same direction (but varying magnitude) along PC1 but variable directions along PC2 (Fig. 4A, Supplement S6). Overall, claws of urban lizards occupied a larger and overlapping morphospace with those of forest lizards for both front and rear claws (Fig. 4B).

In our analysis of univariate claw measurements (height, length, curvature, tip angle), we detected an overall effect of habitat type for front and rear claws (MANOVA, habitat effect; front: $F_{\mathrm{df}=4,\,381} = 10.524$, $P < 0.001$; rear: $F_{\mathrm{df}=4,\,438} = 9.115$, $P < 0.001$; Table 1). The interaction term for habitat and species was significant for both, indicating variable responses across species (MANOVA; front: $F_{\mathrm{df}=16,\,1165} = 2.058$, $P = 0.008$; rear: $F_{\mathrm{df}=16,\,1339} = 3.282$, $P < 0.001$; Fig. 6). Subsequent ANOVA revealed significant shifts across all species for length, height, curvature and tip angle (Table 2). Compared to forest lizards, urban lizards had rear claws that were shorter in length, taller in height and had less-acute tip angles. Front claws of urban lizards were similarly taller and had less-acute tip angles, but also were less curved compared to forest lizards. We detected a significant interaction term of habitat and species for front and rear claw length and rear claw height. In all three, Jamaican species were the only species inconsistent with overall trends: urban *A. lineatopus* had overall longer claws, and urban *A. grahami* claws were shorter in height.

CLAW WEAR AND DAMAGE

We found 20.2% of forest lizards had at least one broken claw (front or rear) compared to only 6.7% of urban lizards—a threefold increase in broken claw frequency (Chi-square test; $\chi^2 = 12.596$, df = 1, $P < 0.001$). This trend was driven by front claw breaks—22.2% of forest lizards had broken foreclaws versus 5.5% of urban lizards (Chi-square test; $\chi^2 = 17.300$, df = 1, $P < 0.001$). Rear claws were less likely to be broken (3.1% in forest lizards, 2.1% in urban lizards) and did not differ in break frequency between urban and forest populations (Chi-square test; $\chi^2 = 0.124$, df = 1, $P = 0.725$).

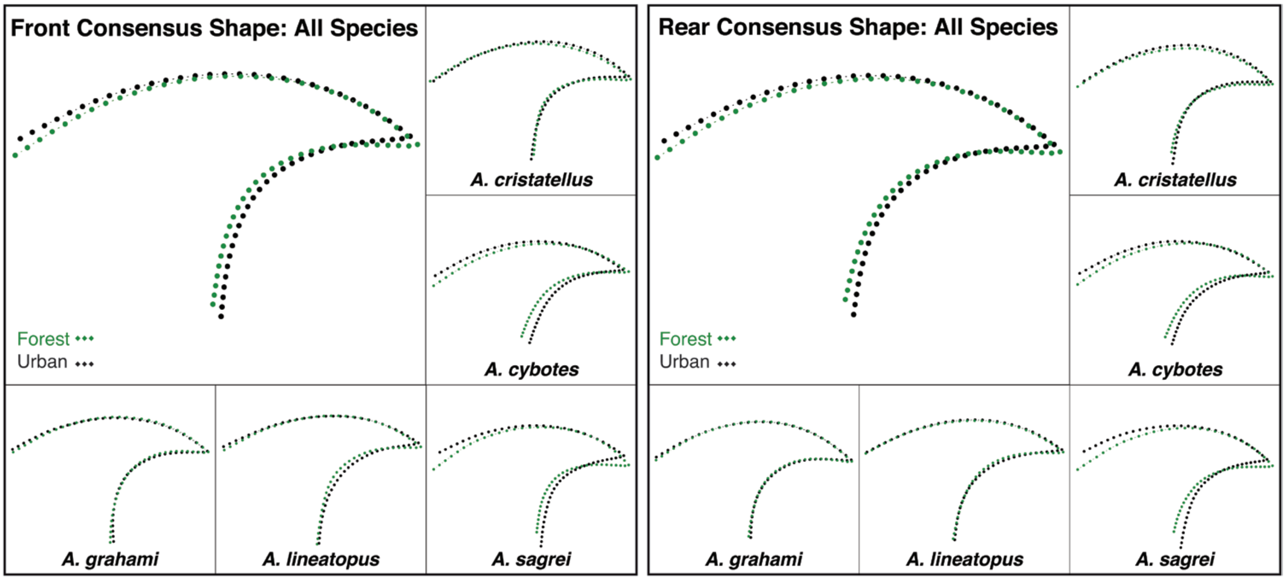

Figure 5. Mean shape variation across all species (large image) and each species separately (insets), coloured by habitat (green: forest, black: urban). Shape changes are in the same direction across all species for front and rear claws but magnitude of shape differences varies by species.

Table 1. Results from MANOVAs of univariate measures of claw shape

	Wilks' λ	*F*	*df*	*P*-value
Front Claws				
Habitat	0.901	10.524	4, 381	**< 0.001**
Species	0.331	31.719	16, 1165	**< 0.001**
ln-SVL	0.736	34.085	4, 381	**< 0.001**
Habitat × Species	0.918	2.058	16, 1165	**0.008**
Rear Claws				
Habitat	0.923	9.115	4, 438	**< 0.001**
Species	0.372	31.987	16, 1339	**< 0.001**
ln-SVL	0.692	48.649	4, 438	**< 0.001**
Habitat × Species	0.889	3.282	16, 1339	**< 0.001**

Significant effects indicated in bold. Significant interaction effect of 'habitat × species' indicates the effect of habitat on claw morphology differs by species. SVL was natural-log transformed.

DISCUSSION

Our study represents, as far as we are aware, the first examination of claw morphology with respect to urbanization. Our three main questions address (1) substrate smoothness and substrate use across habitat types, (2) intraspecific patterns of claw variation with respect to urbanization and (3) parallel responses of interspecific patterns of claw variation with respect to urbanization.

URBAN LIZARDS ENCOUNTER SMOOTHER SUBSTRATES

We found anthropogenic substrates were smoother than natural substrates, and substrates used by urban lizards were significantly smoother than those in the forest despite lizard efforts to use rougher surfaces within each habitat (Fig. 3). These differences in substrate smoothness set the stage for claw morphology divergence by habitat. Smooth substrates typical of urban habitats hinder locomotion, particularly at more vertical inclinations (Kolbe *et al.*, 2016; Winchell *et al.*, 2018b). Thus, it is unsurprising that in both habitat types, lizards use rougher perches than are randomly available. Our finding of discriminate habitat use based on surface roughness is consistent with previous work in *A. cristatellus* (Winchell *et al.*, 2018a, b). This suggests that although urban lizards are exposed to selective pressures related to the use of smooth surfaces, the strength of selection may be reduced by lizards discriminately using rougher perches when available (i.e. 'habitat constraint hypothesis', Irschick & Losos, 1999). In addition, the strength of selection related to anthropogenic substrate use is also related to locomotor performance on these substrates (Winchell *et al.*, 2018b), which may be impacted in complex ways by altered ecological and abiotic conditions of urban environments. For example, differences in predation or competition (e.g. evidenced by injury rates: Tyler *et al.*, 2016; Winchell *et al.*, 2019) could lead to shifts in habitat use or escape strategy (e.g. Aviles-Rodriguez & Kolbe, 2019).

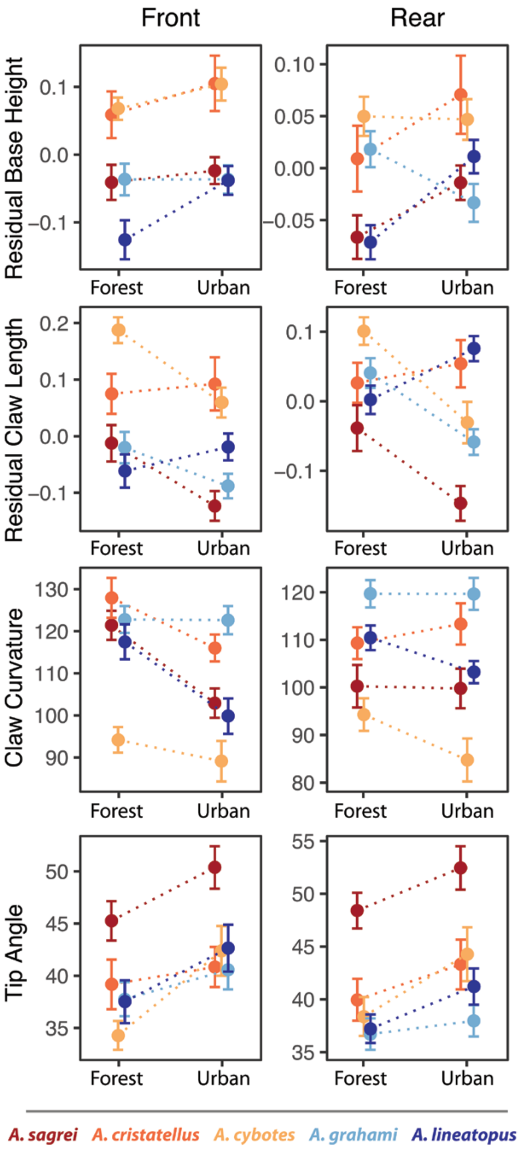

Figure 6. Mean and standard error of the four univariate claw measures by species. Colour represents species (red: *A. sagrei*, orange: *A. cristatellus*, light orange: *A. cybotes*, light blue: *A. grahami*, dark blue: *A. lineatopus*). See Table 2 for significance of habitat type and the interaction term habitat × species per variable.

URBAN CLAW MORPHOLOGY DIVERGES

We found that overall claw shape differed between urban and forest populations. Based on

Table 2. Results from ANOVAs subsequent to MANOVAs in Table 1

	Front Claws			Rear Claws		
	F	*df*	*P*-value	*F*	*df*	*P*-value
Habitat						
ln-ventral length	7.911	1, 384	**0.005**	9.073	1, 441	**0.003**
ln-base height	5.908	1, 384	**0.015**	5.085	1, 441	**0.025**
Curvature	14.537	1, 384	**< 0.001**	1.517	1, 441	0.219
Tip angle	16.119	1, 384	**< 0.001**	12.968	1, 441	**< 0.001**
Species						
ln-ventral length	105.128	4, 384	**< 0.001**	105.681	4, 441	**< 0.001**
ln-base height	72.466	4, 384	**< 0.001**	66.228	4, 441	**< 0.001**
Curvature	21.999	4, 384	**< 0.001**	20.908	4, 441	**< 0.001**
Tip angle	8.706	4, 384	**< 0.001**	15.475	4, 441	**< 0.001**
Habitat × Species						
ln-ventral length	4.181	4, 384	**0.003**	8.361	4, 441	**< 0.001**
ln-base height	0.661	4, 384	0.620	4.113	4, 441	**0.003**
Curvature	2.363	4, 384	0.053	0.240	4, 441	0.916
Tip angle	0.482	4, 384	0.749	0.286	4, 441	0.887
Body size (ln-SVL)						
ln-ventral length	111.904	1, 384	**< 0.001**	163.819	1, 441	**< 0.001**
ln-base height	98.027	1, 384	**< 0.001**	141.839	1, 441	**< 0.001**
Curvature	0.038	1, 384	0.845	8.292	1, 441	**0.004**
tip angle	1.935	1, 384	0.165	1.027	1, 441	0.311

Significant effects indicated in bold. Significant effect of 'habitat × species' indicates the effect of habitat on the trait differs by species. SVL (snout–ventral length) and base height were natural-log transformed.

trait–environment relationships across diverse terrestrial species, Winchell *et al.* (2020) proposed that claws of arboreal species in urban areas might be shorter in length, taller at the base, more curved and sharply pointed to best adhere to smooth anthropogenic surfaces. Our findings provide mixed support for this prediction. Both our geometric morphometric and univariate analyses of shape demonstrate that urban lizards had claws that were overall taller at the base, less curved, less pointed and shorter in length than forest lizards (Figs 4, 5). Prior studies primarily interpret *interspecific* variation in shape in relation to terrestriality versus arboreality. Generally, lizard species that climb have claws that are taller at the base, shorter in length and more curved (Cartmill, 1985; Zani, 2000; Tulli *et al.*, 2009, 2016; Muñoz *et al.*, 2015; D'Amore *et al.*, 2018; Yuan *et al.*, 2019). These shapes likely improve climbing ability, particularly on rough substrates (Zani, 2000). In contrast, terrestrial species tend to have longer, straighter and blunt claws compared to arboreal species.

Increased terrestriality of urban anoles seems plausible given the reduction in tree canopy cover and increased habitat openness of urban habitats (Winchell *et al.*, 2018a, 2020; Prado-Irwin *et al.* 2019). However, this idea has not been tested. If urban anoles are more terrestrial, we might expect corresponding shifts in claw shape. Tulli *et al.* (2009) determined that claw height and length were most important in distinguishing arboreal versus terrestrial lizards; however, claw curvature has often been used to describe terrestriality versus arboreality. Feduccia (1993) analysed over 500 bird species and found that terrestrial species had average claw curvatures of approximately 60°, perching species 120° and climbing species 150°. These approximations have been used to characterize dinosaur habitat use as terrestrial or arboreal based on claw morphology alone (e.g. Feduccia, 1993). Although we detect a difference in claw curvature between urban and forest populations, we do not detect intraspecific differences by habitat as drastic as the interspecific differences reported in Feduccia (1993) (although we note that interspecific variation of most traits generally exceeds intraspecific variation). We find mean claw curvatures in urban populations between 85 and 120 and in forest populations between 94 and 128 . Based on claw curvature alone, our findings do not support increased terrestriality in urban populations, but rather suggest that both urban and forest populations use scansorial 'perching' habitat. However, we note that we do not know if this property of claw shape may be reliably used to interpret habitat use of non-avian reptiles.

Consequently, we suggest that the key difference influencing *intraspecific* claw morphology in urban anoles is not the degree of terrestriality, but rather differences in the substrates on which these lizards must cling. Prior research has documented intraspecific shifts in toepad morphology and locomotor performance with increased use of anthropogenic substrates in urban habitats (Winchell *et al.*, 2016, 2018b). Claw and toepad traits are strongly correlated and form an integrated attachment system (Crandell *et al.*, 2014; Naylor & Higham, 2019; Yuan *et al.*, 2019). Studies of claw morphology in taxa using rocks and cliffs (which resemble anthropogenic structures in that they are often smooth and vertically inclined) find that these species tend to have shorter and less-curved claws compared to arboreal species (e.g. Muñoz *et al.*, 2015; D'Amore *et al.*, 2018). This claw shape may be most appropriate for engaging with vertical rock substrates while minimizing fall risk. Given the integrated nature of claws and toepads, our observed shifts in claw morphology may be attributable to selection on clinging ability in urban environments in two ways: selection for reduced claw interference, or selection for improved claw function.

The functional relationship between claws and adhesive toepads in pad-bearing lizards is an exciting yet understudied area of research. There is limited evidence that claw morphology may be shaped as a consequence of its relationship with toepad effectiveness. While there are no species of anoles exhibiting total claw loss, Yuan *et al.* (2019) found that the specialized twig anole, *Anolis occultus*, had reduced claws compared to other anole species. The authors suggest that this claw size reduction might arise because of altered biomechanical demands (e.g. claws may contribute minimally to clinging in this species) or because of interference with toepad function in its treetop habitat. Conversely, there is only one species of anole without toepads, the terrestrial *A. onca*, suggesting that anole toepads and claws are optimized to work well together across the surfaces they use. In Gekkota, there are multiple examples of claw reduction or loss, all in taxa with robust toepads (Russell & Bauer, 2008; Khannoon *et al.*, 2015). A loss or reduction of claws may arise because of functional trade-offs between claws and toepads, with reduced claws improving the accessibility of adhesive toepads (Russell & Bauer, 1990; Khannoon *et al.*, 2015). Alternatively, claws and adhesive toepads may provide animals with versatility, with claws providing traction on rough surfaces and pads working best on smooth surfaces (Naylor & Higham, 2019). Given the documented concurrent increase in toepad size and lamellae number in *A. cristatellus* (Winchell *et al.*, 2016, 2018b), it is plausible that similar antagonistic trade-offs or complementary mechanisms might be operating here. Future studies exploring functional trade-offs between claw and toepad size in anoles would prove insightful.

Alternatively, claws may improve climbing locomotion in urban habitats if they can penetrate anthropogenic surfaces or interact with the surface by friction or interlocking with surface asperities. Naylor and Higham (2019) found that claws contributed to frictional attachment, particularly at more vertical inclinations, even on very smooth surfaces (roughness of 6.4 μm, but not acrylic, which they measured as 0.0 μm). Anthropogenic surfaces, although much smoother than natural surfaces, fall within this range in which claws should still provide some attachment function (Fig. 3A). Zani (2001) demonstrated that western fence lizards (*Sceloporus occidentalis*, which lack adhesive toepads) were able to adhere to fine-grained sandpaper (R_a = 0.23 μm, 400 grit) by interlocking or frictional forces (or both) without penetrating the surface. An important factor for claw interlocking is the sharpness of the tip (Labonte & Federle, 2015). Claws become ineffective at interlocking when claw tip diameter exceeds the substrate surface roughness (R_a), at which point they generate only weaker frictional forces (Dai *et al.*, 2002; Pattrick *et al.*, 2018). We estimated the tip diameter of anole claws from a random sample in our data set at 0.09 ± 0.03 μm and 0.05 ± 0.02 μm for rear and front claws, respectively, which falls well below the surface roughness of most smooth anthropogenic substrates (Fig. 3A). Thus, although anole claws are unlikely to penetrate hard anthropogenic substrates, the claw may still interlock with small surface asperities and should provide some frictional benefit even on smoother surfaces. The urban phenotype of shorter, less-curved claws with less-acute tip angles may be optimal to engage with these types of surfaces, a hypothesis that should be tested with functional experiments.

It is also possible that claw differences between urban and forest lizards may be attributable to damage and wear. There is a trade-off between claw tip size and structural integrity: more-acute claw tips are susceptible to fractures (Asbeck *et al.*, 2005; Labonte & Federle, 2015; Pattrick *et al.*, 2018), and thicker bases may protect claws from being worn down by high-impact activities (Zhang *et al.*, 2019). Our finding of duller claw tips in urban populations could reflect breakage and wear. D'Amore *et al.* (2018) also considered wear as a mechanism for observing shorter, less-curved, more blunt claws in rock-climbing varanids, but concluded that because there was little visible wear that an adaptive explanation was more likely. Moreover, experimental tests on Western fence lizards demonstrated that repeated testing of claw attachment on sandpaper and rough stone did not result in any visible damage to claws (Zani, 2001).

We similarly observed no visible differences in wear between urban and forest animals, and found that forest lizards, not urban lizards, were more likely to experience claw breakage. One possible explanation for this pattern may be that urban claws are shaped such that they are 'out of the way', which is consistent with an explanation of toepad–claw interaction and interference. Urban claws may also be more robust and less likely to break, either as a consequence of their shape or because of selective pressures related to climbing hard anthropogenic surfaces. Admittedly, both possibilities are speculative, but we suggest that exploring patterns of claw wear and failure may be an interesting new avenue for research on claw morphology.

Claw morphology across species

We observed shifts in urban lizard claw shape in the same direction across all five species but varying in magnitude (Figs 5, 6). The overall effect of habitat was significant whether considering overall shape or univariate measurements. Most species had similar directional shifts in morphology along the dichotomy of habitat type. However, the Jamaican species (*A. lineatopus* and *A. grahami*) exhibited the smallest difference in claw shape between urban and forest populations and differed in the directionality of some univariate shape differences (urban *A. lineatopus* claws were longer and urban *A. grahami* claws were shorter in height). These two closely related species may be constrained in their adaptive responses because of shared population history (i.e. gene flow) or shared evolutionary history. Unfortunately, without population-level genetic information we cannot rule out this possibility. It is also possible that competition between *A. lineatopus* and *A. grahami* reduces the magnitude of the observed differences. Competition for microhabitat space may constrain adaptive morphological responses in urban habitats if it results in habitat partitioning. Yuan *et al.* (2020) invoked this as an explanation for a lack of relationship between vegetation and claw morphology in Lesser Antillean anoles. Future studies should explore effects of interspecific competition on morphological divergence in urban environments.

Variation among urban habitats might influence the strength of selection and degree of morphological divergence observed across species or populations. For example, the four urban areas sampled likely differ in age and intensity of urbanization, among many other unmeasured features. These habitat features could impact habitat use and the strength or nature of selection leading to non-parallel responses. In addition, ecological differences between species could explain variation in morphological shifts observed. However, four of the five species belong to the same ecomorphological group ('trunk–ground') representing similar ecological and morphological starting points. In addition, Yuan *et al.* (2019) found that claw morphology of trunk–ground and trunk–crown ecomorphs were highly similar. Unfortunately, without multiple replicate populations per species, we cannot at this time disentangle habitat-specific effects from species-level effects.

Alternatively, forest phenotypes of the Jamaican species may already be suitable for urban environments (i.e. 'preadapted'). We find some support for this assertion as the phenotypic difference was slightest for these two species. Moreover, forest populations of both species had the highest values for the principal axis of shape variation (PC1) and in the same direction as urban population shifts. If both species extensively use smooth perches in the forest and relevant habitat elements do not differ between forest and urban habitats, claw phenotypes may already be near the urban phenotypic optimum. Indeed, in the forest we observed both species extensively using smooth agave plants and surface roughness of perches used by *A. grahami* did not differ by habitat. To test this hypothesis, future studies should explore claw morphology of populations of *A. lineatopus* and *A. grahami* in habitats where smooth vegetation is not commonly used.

Urban claws are more variable

Interestingly, urban claw shapes are more variable than forest lizards, occupying a larger morphospace and exhibiting greater shape disparity. Yuan *et al.* (2020) suggested that shape disparity of claws increases on islands with relaxed competition because animals take advantage of wider niches. Urban populations may similarly expand their niche space in response to increased habitat heterogeneity (e.g. exposure to both extremely smooth and rough perches), reduced competition (urban habitats are typically dominated by only one or two *Anolis* species; personal observation), or shifts in predator pressures (evidenced by patterns of injury in urban anoles; Tyler *et al.*, 2016; Winchell *et al.*, 2019). This interpretation is consistent with previous analyses, which demonstrate an expansion of urban niche space associated with anthropogenic microhabitat use (Winchell *et al.*, 2018a; Battles *et al.*, 2019). Use of more variable niche space may decrease demand for morphological specialization and instead favour variable and generalized forms. Birn-Jeffrey *et al.* (2012) found that species of birds, lizards and dinosaurs that use or used their claws in both terrestrial and arboreal habitat have more generalized and variable claw shapes. They asserted that multifunctionality and compromise in claw shape are likely common across taxa that use a broad range of habitat types, which may pull claw morphology towards different, species-specific or even population-specific optima.

CONCLUSIONS

This study expands our understanding of a relatively understudied trait, claw morphology, through the lens of the altered biomechanical demands of urban environments. We find parallel intraspecific variation in claw morphology between urban and forest populations of varying magnitude across five species, suggesting that natural selection is shaping urban claw morphology. Urban claws tend to be shorter, more robust, and tend to break less frequently than forest claws, perhaps because the shorter claw allows for it to be out of the way of the toepad when navigating the urban environment. We suspect these differences are attributable to substantial differences in perch smoothness in urban habitats and suggest that these claw shapes may maximize claw effectiveness, reduce breakage, or reduce interference with the adhesive toepad on common anthropogenic surfaces. The differences we observe in urban populations are not characteristic of either terrestrial or arboreal species, but rather seem to be an alternate phenotypic optimum. Our findings add to a growing body of work demonstrating novel phenotypic trajectories in urban anoles and raise the intriguing possibility that urban phenotypic shifts may be repeatable across species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

S1. Table of sample site information.
S2. Table of sample sizes for morphology.
S3. Table of sample sizes for habitat use.
S4. Table of substrate types and definitions.
S5. Figure of surface roughness of used and available habitat by species.
S6. Figure of PCA measures of claw morphology by species.
S7. Examples of claw breakage and damage

SHARED DATA

All data and R code to conduct analyses are archived in the Zenodo open-access repository with DOI: 10.5281/zenodo.3905399.