

The perils of city life: patterns of injury and fluctuating asymmetry in urban lizards

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Animals that live in cities face a number of challenges particular to the urban environment that may impact on overall health and survival. Nevertheless, relatively few studies have investigated injury and health in urban species. We measured body condition, injury rate and fluctuating asymmetry in urban and forest populations of the tropical lizard *Anolis cristatellus*. We found that although there were strong differences in body condition between urban and forest populations, the direction of this difference varied between municipalities. We also found that injury rates (amputated digits and bone fractures) were slightly, but significantly, more common in urban populations; this phenomenon may be due to changes in intraspecific interactions or predation pressure in urban sites. Contrary to our expectations, we found that fluctuating asymmetry was greater in forest compared to urban populations. Because our data were collected from adults, this may be a sign of stronger natural selection on the symmetry of functional traits in urban than in forest environments. Finally, we found no persuasive evidence that city living is inherently detrimental to individuals of this species despite a slightly higher rate of injury. Being able to overcome the challenges of city life may be integral to urban persistence and a step along the path to urban adaptation.

ADDITIONAL KEYWORDS: Anole – *Anolis cristatellus* – bone fracture – digit amputation – intraspecific aggression – predation – Puerto Rico – urbanization.

INTRODUCTION

Cities pose unique ecological challenges to urban animals. Drastic environmental changes associated with urbanization result in structural habitat and resource distributions that differ from those encountered in more pristine environments (Forman, 2014). In addition, urban animals face threats from humans, habitat fragmentation, elevated temperatures, shifts in predator communities and exposure to pollutants (Ditchkoff *et al.*, 2006; Shochat *et al.*, 2006; Forman, 2014). Consequently, populations in urban environments may exhibit differing patterns of injury rate, body condition and overall health compared to those in more natural habitats nearby.

Many animals exploit novel food resources of urban settings. For instance, urban red foxes (*Vulpes*

vulpes) forage at waste piles and scavenge meat, fruit and crops (Contesse *et al.*, 2004). Similarly, urban red squirrels (*Sciurus vulgaris*) adjust their home-ranges when resources are scarce to incorporate anthropogenic foods, with heavier animals being found closer to these resources (Reher *et al.*, 2016). In addition to consuming food waste, many insectivorous taxa, including bats, birds, spiders and herpetofauna, feed on arthropods attracted to artificial lights and waste in urban areas (Heiling, 1999; Henderson & Powell, 2001; Jung & Kalko, 2010; Russ *et al.*, 2015). Urban lizards, including members of the genus *Anolis*, are also known to consume anthropogenic foods as well as insects attracted to anthropogenic lights and waste (Henderson & Powell, 2001; Perry *et al.*, 2008).

Use of anthropogenic food resources can have unpredictable impacts, particularly if resources are patchily distributed (Newsome & Rodger, 2008). Across taxa, the effect of urbanization on body condition (mass controlling for overall size) varies widely. In some species, urban animals exhibit higher body condition

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compared to their non-urban counterparts (e.g. [Auman et al., 2008](#)), while in other species the opposite pattern has been observed (e.g. [Liker et al., 2008](#)). Indeed, even among anoles findings are mixed: [Battles et al. \(2013\)](#) showed that lizards from undisturbed environments had better body condition, while [Hall & Warner \(2017\)](#) found better body condition in lizards from urban environments. The magnitude and direction of the effect of urbanization on body condition may be influenced by resource distribution, as well as by ecological factors related to foraging. For instance, even if food is locally more abundant at urban sites, higher competitor densities or altered predation pressures may influence an individual's willingness and success in exploiting food resources in lizards ([Drakeley et al., 2015](#)). In some species, this could result in greater hesitancy to feed on novel items in an urban setting ([Chejanovski et al., 2017](#)).

The distribution and abundance of urban resources in turn impacts on the density and distribution of wildlife. Lizards frequently occupy a subset of the urban habitat, often restricted to small patches or specific environmental features (e.g. vegetation; [Winchell et al., 2018a](#)). This habitat discrimination may be driven by uneven resource distribution combined with ecological factors, such as preference for specific microclimatic or structural habitat, and constraint due to performance limitations ([Shochat et al., 2006](#); [Winchell et al., 2018a, b](#)). By contrast, forest habitats tend to be more spatially homogeneous with more evenly distributed resources.

These environmental factors can lead to locally elevated densities of conspecifics in urban environments, which can in turn increase competition and the rate of intraspecific encounters ([Wiens, 1976](#); [Shochat et al., 2006](#)). An increase in intraspecific aggressive encounters may lead to elevated injury rates. [Vervust et al. \(2009\)](#) found higher rates of digit amputation in denser populations of Italian wall lizards (*Podarcis sicula*), and attributed this to aggressive intraspecific interactions. Aggressive encounters could also lead to an increased rate of bone fractures, although so far as we know no previous study has investigated bone fractures in urban wildlife.

Urban lizards face other potential sources of injury specifically related to their use of the urban habitat. The majority of structures in urban areas are anthropogenic, which tend to have smoother surfaces and are usually much less compliant than natural materials. This could lead to increased slipping and falling by urban species that locomote on anthropogenic structures ([Winchell et al., 2018b](#)). Consequently, increased strain energy must be repeatedly absorbed by limb bones and these forces could exceed the limb safety factor as lizards land and move about ([Biewener, 2005](#)). In addition, urban

lizards can be injured or killed intentionally or unintentionally by humans.

Changes in the abundance and type of predators in urban areas may also contribute to sub-lethal injury rates. Urban habitats can exhibit an increase in meso- and domestic predators compared to forests, in some cases leading to elevated mortality of urban prey species ([Koenig et al., 2002](#); [Gillies & Clout, 2003](#); [Lepczyk et al., 2004](#)). However, the relationship between injury rate and predation pressure is not straightforward (see [Schoener, 1979](#); [Bateman & Fleming, 2009](#); [Lovely et al., 2010](#); [Tyler et al., 2016](#)). For instance, a low injury rate might either indicate low predation pressure or high predator efficiency. Similarly, a high injury rate suggests low predator efficiency, regardless of overall predation rate ([Schoener, 1979](#)). Thus, more frequent healed injuries in urban animals could indicate a shift in the predator community towards less efficient generalist predators, rather than an overall increase in predation.

While traumatic injuries such as bone fractures and missing digits provide a snapshot of health, other metrics may provide insight into the long-term effects of urban living. The measurement of fluctuating asymmetry (FA), or the small non-directional deviations from perfect bilateral symmetry ([van Valen, 1962](#)), provides a subtle assessment of long-term organismal and population health. FA is thought to be linked to developmental instability, and in particular the balance between developmental noise, which produces asymmetry, and developmental stability, which suppresses it ([Palmer, 1994](#)). Previous research suggests that greater environmental stress as well as genetic conditions induced by inbreeding or hybridization can lead to higher levels of FA ([Palmer & Strobeck, 1992](#)). In addition, differences in FA between habitats have in some cases been linked to differences in performance and fitness ([Møller, 1997](#)).

Although many studies of FA consider anthropogenically impacted or degraded habitats, few have focused specifically on urban areas. In wall lizards (*Podarcis muralis*), [Lazić et al. \(2013\)](#) found increased FA in multiple traits in urban compared to rural populations. In carabid beetles, [Weller & Ganzhorn \(2004\)](#) also found a positive correlation between asymmetry and urbanization in three species, but in the species most tolerant of urbanization they detected no correlation. In general, we expect that the stress of the urban environment, including genetic effects of population isolation and environmental stressors such as pollution, should elevate developmental instability and lead to a pattern of increased FA in urban populations. Based on previous studies, we expect the degree of FA to vary depending on the susceptibility of the organism to these stresses (e.g. [Weller & Ganzhorn, 2004](#)), and on the functional importance of the trait ([van Dongen, 2006](#)).

We examined a 4-year dataset of the Puerto Rican crested anole (*Anolis cristatellus*) for evidence of short- and long-term differences in our proxy measures for organismal health (condition, digit loss, bone fractures and FA) between urban and forest habitats. *Anolis cristatellus* is a medium-sized arboreal lizard [adult males *c.* 50–70 mm snout–vent length (SVL)], native to Puerto Rico and the Virgin Islands, that is abundant in urban and forest sites across its range. We explored three hypotheses with specific predictions. (1) We predicted that injury rates would be higher in urban than in forest populations, which might occur if populations are subject to different rates or types of traumatic events. (2) We predicted that urban lizards would have higher body condition than lizards in forest habitats, which should occur if supplemental food resources in urban habitats are abundant and commonly consumed. (3) Lastly, we predicted that urban lizards might have higher levels of FA than forest lizards, which is expected if urban lizards experience elevated developmental stress.

The field of urban ecology, and more specifically urban evolution, is young but rapidly growing (Rivkin *et al.*, 2018). Understanding how eco-evolutionary dynamics are impacted by urbanization provides insight into fundamental evolutionary questions and has conservation implications (Donihue & Lambert, 2015; Rivkin *et al.*, 2018). We believe that studying traumatic injury and health in urban populations should lead to a better understanding of the ecological and evolutionary dynamics of urban habitats (e.g. natural selection), and help us to better predict the long-term persistence of urban-tolerant species.

MATERIAL AND METHODS

Between 2012 and 2016 we sampled 1169 lizards from urban and forest sites in five municipalities in Puerto Rico (Fig. 1). Sampling was conducted between April and August for all sites except one (UPR Arcibo, sampled in November). We sampled 13 sites in total and all lizards were tagged with semi-permanent marker to prevent inadvertent recapture during a sampling period (Supporting Information, Table S1). We sampled six sites in multiple years. Three of these sites were sampled in 2012 and 2016, and few if any animals are likely to have survived this 4-year period as all individuals were adults when initially captured. The other three sites were sampled in 2013/2014 and again in 2016, and all lizards from these sites were given permanent injected alphanumeric tags and elastomers. None of the lizards captured in 2016 was tagged and so we are confident that no double-sampling occurred at any of our sites.



Figure 1. Satellite imagery of each site and surrounding area at 600-m² scale. Note that we did not sample the entire area shown. In particular, at forest sites with encroaching urbanization we sampled in the core of the forest. Map data: Google, Digital Globe (2018).

We measured the degree of urbanization at each site using ArcMap (ArcGIS 10.5.1, ESRI) and the 2011 National Land Cover Database impervious surface and canopy cover layers (Xian *et al.*, 2011; Homer *et al.*, 2015). Urban sites were high-density residential areas or university campuses, which were characterized by very little tree cover (0.3–10%) and high amounts of impervious surface (asphalt, concrete, buildings; 36–62%; Fig. 2). Universities have higher foot traffic than residential areas, which have higher levels of car traffic, but the two habitats were otherwise very similar. Forest habitats were characterized by high percentages of canopy cover (18–78%) and low percentages of impervious surface (0–39%). Sites included young secondary growth (~30 years) with dense understorey and remnant crop plants (e.g. coffee), mature secondary growth with open understorey and closed canopy, and tropical dry forest with patchy canopy. One forest site had paved footpaths and receives light foot traffic while the others had unpaved trails with minimal foot traffic.

We sampled adult male *A. cristatellus* (minimum SVL 40 mm) by noosing as we encountered them at each site. All lizards over the 4-year period were captured by a team led by the same researcher (KMW), with no bias towards capturing animals observed on

man-made (e.g. buildings and fences) or natural (e.g. trees) substrates. We transported lizards to a field laboratory where we anaesthetized them with aerial isoflurane, weighed them, and obtained digital X-ray images (Kodex portable digital X-ray system) and high-resolution scans of toepads (2100 d.p.i., Epson V300). We returned lizards to their site of capture the following morning.

We quantified three variables: body condition, injury rate (missing digits and bone fractures) and FA. The same researcher collected all measurements (KMW), and injury rates were independently tallied for the entire dataset by two researchers (KMW, DB). From the toepad scans we counted missing digits on both front and rear limbs. From X-rays we counted the number of fractured bones, including healed breaks. We measured body size skeletally (internally measured SVL) in ImageJ (Rashband, 1997), measuring from the tip of the snout to the base of the pelvis. This measurement was highly repeatable (intraclass correlation coefficient: 0.963 on 128 individuals measured three times). We measured the lengths of eight pairs (left and right) of bones: humerus, radius, ulna, 3rd metacarpal, femur, tibia, fibula, 4th metatarsal and digit (to the first joint). We did not measure any bones that had evidence of a fracture, even if it had subsequently healed, so measures of skeletal asymmetry exclude these individuals. We quantified repeatability by taking three repeat measurements of each skeletal trait from a subset of the dataset ($N = 128$) and then computing the intraclass correlation coefficient (ICC) implemented in the R package 'ICC' (Wolak *et al.*, 2012). We also re-measured three times any trait in an individual for which $|\log(R) - \log(L)|$ exceeded 0.1 to verify that larger asymmetry measurements were accurate.

We analysed body condition with a linear mixed effects model of log-transformed mass by log-transformed body size with interacting fixed effects of context (forest or urban) and municipality, and with month nested within year as a random factor. We included municipality and context as interacting fixed factors in this model to test for the possibility that differences in body condition between urban and forest sites vary between different regions of the island, and we included month and year to account for seasonal and yearly variation. We investigated regional variation in the difference between urban and forest populations with a Tukey's post-hoc test of least-squares means for the context by municipality interaction. We also investigated if log-transformed body condition index (mass divided by SVL) was correlated with any of the other metrics (missing digits, bone fractures and FA) with a linear mixed effects model of similar form: condition index by asymmetry (combined metric, described below), presence/absence of breaks and

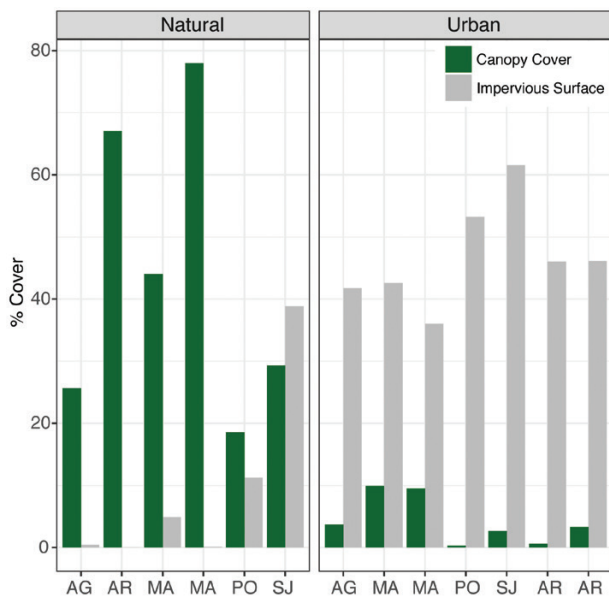


Figure 2. Percentages of canopy cover and impervious surface for each site sampled, estimated from National Land Cover Database (NLCD) GIS data in ArcMap (ArcGIS 10.5.1, ESRI). Urban sites were characterized by high percentages of impervious surface and low percentages of canopy cover, while forest sites have the opposite pattern. Sites are labelled by municipality: AG, Aguadilla; AR, Arecibo; MA, Mayagüez; PO, Ponce; SJ, San Juan.

missing digits, and the interaction of context and municipality as fixed effects and month nested within year as a random effect.

We analysed missing digits and bone fractures as binary variables (presence/absence of at least one missing digit) in separate generalized linear mixed effect models with binomial error distributions. We included context and municipality as fixed effects, and, as with the body condition model, month nested within year as a random effect to account for seasonal and yearly variation. The interaction term of municipality and context was not significant in either model (likelihood ratio test) and was dropped from the final models. In addition, we tested if frequency of front vs. rear digit loss and frequency of healed vs. fresh fractures differed between urban and forest populations overall using a χ^2 contingency test. We did not include samples from 2016 in the injury analyses because lizards with visible injuries were intentionally avoided for that sampling period. A digit was scored as 'missing' if at least part of the digit past the base of the claw was lost; this did not include loss of claws only, or digits that were damaged but intact. Both healed and new fractures were considered in our analysis.

We followed the protocol outlined by Palmer (1994) to test for and quantify FA. We first tested for directional asymmetry (DA) across all populations with ANOVA of each log-transformed trait value by side, where a significant effect of side would indicate a consistent directional difference between right and left measurements across individuals. We next calculated absolute FA for each bone as the unsigned difference between log-transformed right and left values for each pair [i.e. $|\log(R) - \log(L)|$; 'FA1' in Palmer (1994)]. We tested for the presence of FA in each population and across all populations by investigating if the mean absolute FA deviated from 0 for each trait using *t*-tests. We also tested for the presence of FA after accounting for measurement error (in our subset of 128 individuals measured three times) with a two-way ANOVA for replicate measures of each trait (log-transformed) with side (right or left) interacting with individual. A significant interaction of side by individual indicates the presence of FA after taking into account measurement variation. Finally, we tested for an effect of body size on FA by regressing the log-transformed absolute difference between right and left measurements by log-transformed body size (SVL) for each trait [i.e. $\log(|R - L|) \sim \log(\text{SVL})$].

We summed FA values of all bones measured per individual to calculate a composite metric of skeletal FA ('FA11' in Palmer, 1994). Composite metrics are considered more reliable and have greater power to detect FA (Palmer, 1994; Leung *et al.*, 2000). We investigated if the degree of skeletal FA (summed

across all traits) differed by context with a two-way ANOVA including site. We then tested if skeletal asymmetry is organism-wide with a two-way ANOVA of absolute FA by trait location (forelimb or hindlimb) and context (urban or forest) interacting. We investigated significant interactions of bone location (i.e. if the bone is a forelimb or hindlimb element) by context with post-hoc Tukey's honest significant difference (HSD) test. Lastly, we tested the relationship between skeletal FA and body size (as a proxy for age) with ANCOVA including site as a covariate.

We performed all statistical analyses using R 3–4.2 (R Core Team, 2017). We used the R package 'lme4' for linear mixed model analyses with the functions *lmer* and *glmer* (Bates *et al.*, 2015). We estimated the significance of fixed effects with the package 'lmerTest' (Kuznetsova *et al.*, 2017), which estimates degrees of freedom, *t*-statistic and *P*-value for *lme* objects using type III ANOVAs with Satterthwaite's approximation. We performed Tukey's post-hoc tests of least-square means using the R package 'lsmeans' (Lenth, 2016). All linear mixed-effects model formulas and likelihood ratio tests for context by municipality interactions are summarized in the Supporting Information (Table S3).

RESULTS

Relative mass (body condition) differed significantly by context (urban vs. forest) but the effect was not consistent across municipalities (Fig. 3). In Aguadilla, Mayagüez and San Juan, urban animals were heavier than their forest counterparts when controlling for overall size (Aguadilla: $13.4 \pm 3.8\%$, $t = -3.574$, $P < 0.001$; Mayagüez: $3.1 \pm 1.1\%$, $t = -2.866$, $P = 0.004$; San Juan: $8.3 \pm 1.8\%$, $t = -4.505$, $P < 0.001$). In the two remaining populations, Arecibo and Ponce, urban lizards were lighter than those at forested sites nearby (Arecibo: $-6.8 \pm 1.2\%$, $t = 5.486$, $P < 0.001$; Ponce: $-13.8 \pm 2.2\%$, $t = 6.181$, $P < 0.001$). Body condition index (log-transformed mass/body size) was negatively correlated with FA (-0.9 ± 0.1 , $\chi^2 = 47.599$, $P < 0.001$), but uncorrelated with the number of missing digits and the number of bone fractures (digits: $\chi^2 = 0.150$, $P = 0.699$; fractures: $\chi^2 = 0.308$, $P = 0.579$).

The percentage of individuals with at least one lost digit ranged from 1.8 to 10.9% per population. The maximum number of digits lost per individual was four, and most lizards with amputations were missing only one digit. The frequency of missing digits was higher in urban populations compared to forest populations overall, although in both contexts this was a relatively rare occurrence (7.2% across all urban populations vs. 3.9% across all forest populations; $z = 2.196$, $P = 0.028$; Fig. 4A). This pattern trended in the opposite direction in San Juan, but the difference between urban and

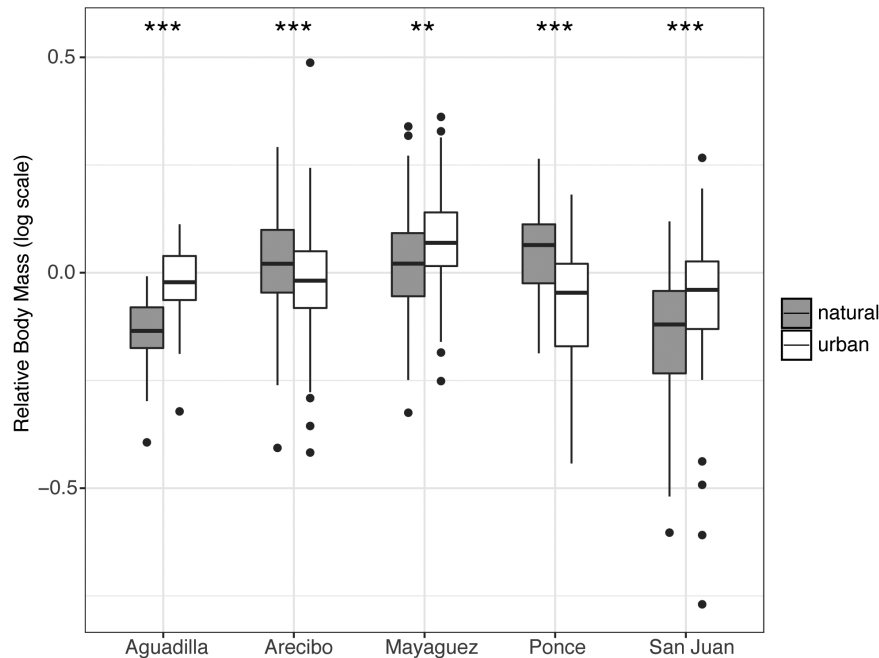


Figure 3. Body condition (residuals of mass relative to body size, log scale) was significantly different between urban and forest populations in all municipalities, although the directionality of this relationship differed. Whiskers represent the first and third quartiles (with maximum 1.5 times the interquartile range) and closed circles represent outliers. Significance levels: $**P < 0.01$, $***P < 0.001$.

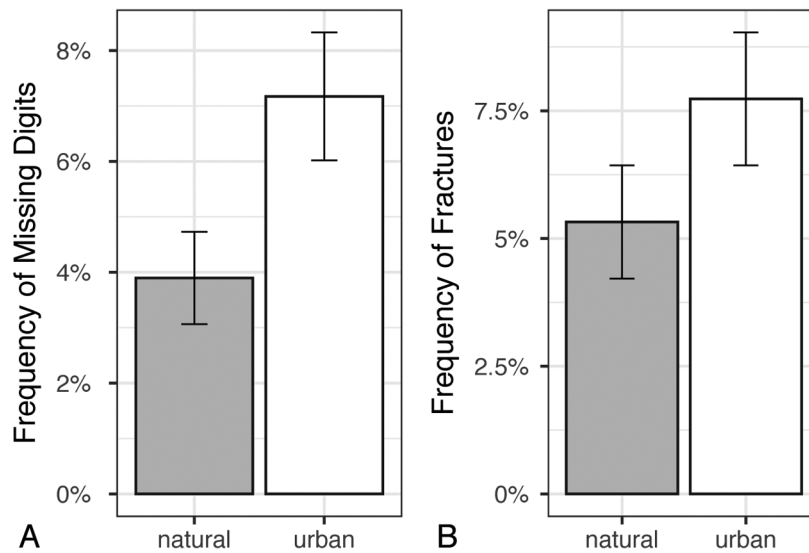


Figure 4. More lizards have missing digits and bone fractures in urban compared to forest populations across all sites. Height of bars represents the percentage of individuals with at least one missing digit (A) or bone fracture (B) in each group (across all urban and natural populations) and whiskers represent \pm standard error of each percentage.

forest frequencies in this case was not statistically significant ($z = -1.401$, $P = 0.161$). Loss of rear and front digits was equally common across all lizards and the frequency of front vs. rear digit loss did not differ between urban and forest environments ($\chi^2 = 0.013$, d.f. = 1, $P = 0.909$).

Bone fractures were similarly rare occurrences. The percentage of individuals with at least one bone fracture ranged from 2.8 to 10.5% per population. No lizard had more than two fractured bones, and multiple breaks were most commonly radius/ulna and tibia/fibula combinations. Healed breaks were more

common across all populations and the proportion of unhealed vs. healed breaks did not differ by context ($\chi^2 = 1.819$, d.f. = 1, $P = 0.177$). In urban lizards, the most common fractures were in the radius ($N = 9$) followed by ulna ($N = 8$). In forest lizards, the most common fractures were in the fibula ($N = 12$) followed by the radius ($N = 6$). A slightly higher percentage of urban lizards had bone fractures than forest lizards (6.5% of urban lizards and 4.2% of forest lizards; $z = 2.231$, $P = 0.026$; Fig. 4B).

We did not detect significant DA across all our sites for any trait (ANOVA; Table 1). We detected no significant effect of body size for all traits within each site and across all sites (within sites: Supporting Information, Table S3; across sites: Table 1). Measurement error was not a significant issue in our dataset. For our subset ($N = 128$) of repeatedly measured individuals, we found very high repeatability for all traits across all sites (Table 1). For all traits, intraclass correlation coefficients were greater than 0.98 and the among-individual variance far exceeded within-individual variance. In addition, the side-by-individual effects in our two-way ANOVAs were significant for all traits, indicating the detection of FA after accounting for individual variation (Table 1).

Unsigned FA was normally distributed for all traits (Table 2). Mean absolute FA ($|R - L|$) differed significantly from 0 at the population level (t -test, $P < 0.001$ for all; Supporting Information, Table S3) and across all populations (t -test, $P < 0.001$ for all; Table 2), indicating the presence of FA for all traits in and across all populations. Mean FA ranged from around 1% (tibia and fibula) to 4.6% (metacarpal) across all populations.

We found a consistent pattern of elevated FA in forest compared to urban populations in each municipality (Fig. 5). Forest populations across all municipalities had on average 4.7% greater asymmetry compared to urban populations (ANOVA; forest: $4.698 \pm 0.908\%$, $t = 5.174$, $P < 0.001$). Although we used a composite metric, this pattern was consistent for all bones measured (Fig. 5A). The magnitude of the difference varied by bone location (i.e. whether the bone was a forelimb or hindlimb element) and type. In particular, hindlimb elements had significantly lower asymmetry than forelimb elements (ANOVA; hindlimb: $-1.142 \pm 0.062\%$, $t = -18.349$, $P < 0.001$), with a nearly significant interaction of body location by context ($t = -1.893$, $P = 0.058$). Tukey's post-hoc analysis revealed no difference in asymmetry in forelimbs between urban and forest lizards, but a highly significant difference in hindlimb asymmetry with forest lizards exhibiting greater asymmetry (forest: 0.217% , $P < 0.001$). Finally, we found a negative correlation of FA with body size across all sites, suggesting that younger animals exhibit greater asymmetry in skeletal traits (estimate for body size: -0.166 ± 0.020 , $t = -8.182$, $P < 0.001$).

DISCUSSION

Our results paint a mixed picture of how urbanization impacts on the well-being of urban animals. Body condition differed inconsistently but highly significantly between our urban and forest sites, but was not correlated with missing digits or bone fractures. In addition, urban lizards consistently had slightly higher injury rates than their forest counterparts,

Table 1. Descriptors of traits analysed for asymmetry across all sites for the eight traits examined (see Supporting Information for site-level summaries).

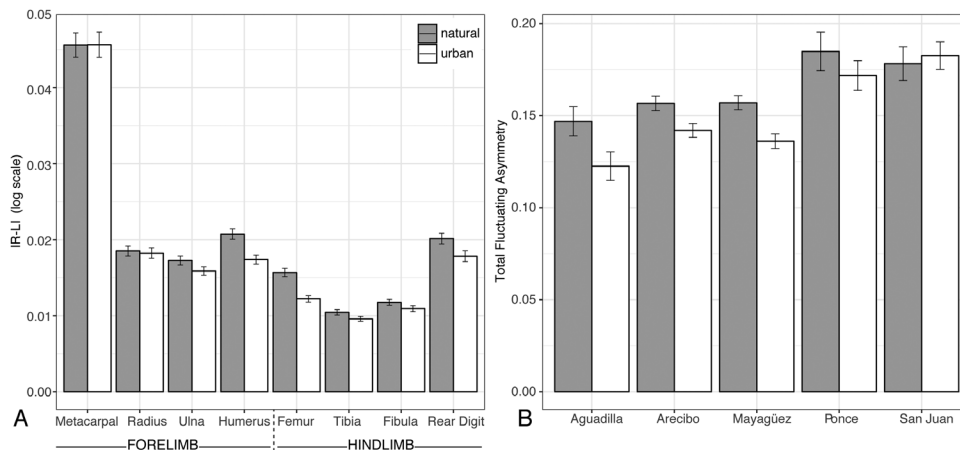
Trait	N	^A (R+L)/2	^B Body size	^C DA-test	ICC	^D Repeat measures
		Trait mean \pm SE	Slope \pm SE	Trait-side		Side \times individual
Metacarpal	1152	3.472 \pm 0.011	-0.002 \pm 0.012	$F_{1,2307} = 0.275$, $P = 0.600$	0.981	$F_{254,510} = 24.934$, $P < 0.001$
Radius	1138	8.853 \pm 0.025	0.0003 \pm 0.005	$F_{1,2293} = 0.072$, $P = 0.789$	0.997	$F_{252,506} = 24.558$, $P < 0.001$
Ulna	1140	9.440 \pm 0.027	-0.005 \pm 0.004	$F_{1,2295} = 0.255$, $P = 0.614$	0.997	$F_{254,510} = 19.731$, $P < 0.001$
Humerus	1149	11.746 \pm 0.033	-0.0004 \pm 0.005	$F_{1,2304} = 3.339$, $P = 0.068$	0.998	$F_{254,510} = 50.066$, $P < 0.001$
Femur	1154	15.586 \pm 0.044	-0.019 \pm 0.003	$F_{1,2309} = 0.747$, $P = 0.387$	0.999	$F_{255,512} = 49.370$, $P < 0.001$
Tibia	1150	13.228 \pm 0.038	-0.010 \pm 0.002	$F_{1,2305} = 0.060$, $P = 0.807$	0.998	$F_{254,510} = 9.897$, $P < 0.001$
Fibula	1138	13.275 \pm 0.037	-0.010 \pm 0.003	$F_{1,2293} = 0.338$, $P = 0.561$	0.998	$F_{245,492} = 14.411$, $P < 0.001$
Rear digit	1137	13.209 \pm 0.034	-0.015 \pm 0.005	$F_{1,2292} < 0.001$, $P = 0.995$	0.995	$F_{253,508} = 10.267$, $P < 0.001$

Rear digit is the metatarsal and first phalanx of the fourth digit. A, mean raw trait value (R+L)/2 and standard error. B, the relationship of each trait to body size with the slope and standard error of the regression: $\log(|R - L|) \sim \log(\text{SVL})$, where SVL is snout-vent length, a measure of body size. C, ANOVA of trait by side (right or left) to test for the presence of directional asymmetry. D, measurement error estimated for the subset of repeatedly measured lizards ($N = 128$). Intraclass correlation coefficient (ICC) describes repeatability and the two-way ANOVA of trait by side \times individual indicates the detection of fluctuating asymmetry after accounting for individual measurement variation.

Table 2. Descriptors of trait asymmetry across all sites for the eight traits examined (see Supporting Information for site-level summaries).

trait	^A $\log(R) - \log(L) = FA$			^B $ FA \neq 0$	^C $ FA $
	Mean \pm SE	Skew	Kurtosis	<i>t</i> -test	Mean \pm SE
Metacarpal	-0.009 ± 0.006	-0.007	4.105	$t = 39.714$, d.f. = 1151, $P < 0.001$	0.046 ± 0.001
Radius	-0.004 ± 0.006	0.576	7.330	$t = 38.382$, d.f. = 1137, $P < 0.001$	0.018 ± 0.001
Ulna	0.018 ± 0.006	0.290	3.540	$t = 41.258$, d.f. = 1139, $P < 0.001$	0.017 ± 0.0004
Humerus	0.093 ± 0.008	-0.003	3.317	$t = 41.814$, d.f. = 1148, $P < 0.001$	0.019 ± 0.001
Femur	-0.051 ± 0.008	-0.100	5.104	$t = 39.924$, d.f. = 1153, $P < 0.001$	0.014 ± 0.0004
Tibia	0.014 ± 0.005	0.131	3.635	$t = 41.673$, d.f. = 1149, $P < 0.001$	0.010 ± 0.0002
Fibula	0.032 ± 0.006	-0.072	3.644	$t = 41.391$, d.f. = 1137, $P < 0.001$	0.011 ± 0.0003
Rear digit	-0.001 ± 0.010	0.393	7.121	$t = 37.954$, d.f. = 1136, $P < 0.001$	0.019 ± 0.001

Rear digit is the metatarsal and first phalanx of the fourth digit. A, descriptors of normality for the signed asymmetry of log-transformed trait values, summarized by the mean, standard error, and skew and kurtosis of the distribution. B, test for mean $|FA| \neq 0$ with *t*-test, with significant values indicating the presence of fluctuating asymmetry for a trait. C, mean and standard error of $|\log(R) - \log(L)|$, a measure of absolute fluctuating asymmetry.

**Figure 5.** Mean and standard error of fluctuating asymmetry (FA) for urban and forest populations across all sites sampled show elevated FA in forest compared to urban populations, mainly in hindlimb elements. A, FA for each bone; B, composite FA ($\Sigma |R - L|$) per individual across all populations within a municipality.

suggesting that they face elevated risks from some combination of accidents, predator encounters and intraspecific aggression. Lastly, we found consistently higher FA in forest populations compared to urban populations, contrary to our a priori prediction, and found that higher FA was associated with lower body condition and smaller overall size.

Within municipalities, lizards in urban and forest sites invariably differed significantly in body condition, but in different directions. In some municipalities (Aguadilla, Mayagüez, San Juan) urban lizards had higher body condition than their forest counterparts, but in others (Arecibo, Ponce) the opposite was true (Fig. 3). This makes it impossible to link differences in body condition to any consistent effect of urbanization across our five municipalities. The differences in

body condition may have resulted from characteristic differences between forested and urbanized habitat in each municipality, or they could merely be the product of unknown idiosyncratic factors that also happen to vary among our study sites.

The effect of urbanization on body condition has been understudied with no general consensus. Indeed, it is even debatable how well correlated body condition is with individual survivorship and reproductive success. For instance, Dananay *et al.* (2015) found that increased road salt pollution led to frogs with greater body mass but lower overall adult survival. Consequently, we present the results as we found them, but refrain from interpreting higher or lower conditions as indicative of greater or lesser average health. The prevailing thought on body condition is that relative body mass is

related to access to high-quality food, even if this does not translate into higher individual fitness or survival. In birds, a diet dominated by anthropogenic foods has been shown to lead to reduced fitness, smaller body size and skeletal abnormalities, presumably because of nutritional deficiencies (Richner, 1989; Pierotti & Annett, 2001). However, it is not clear if urban lizards regularly include anthropogenic foods in their diet, nor how body condition relates to fitness in urban environments.

We observed higher rates of digit loss and bone fractures in urban populations, although these injuries are relatively rare occurrences overall. Digit loss in lizards has been previously associated with aggressive intraspecific interactions, which are more common when animal densities are higher (Zweifel & Lowe, 1966; Gvozdik, 2000; Vervust *et al.*, 2009). Predation attempts can also result in digit loss in lizards (Schoener & Schoener, 1980; Hudson, 1996). Schoener & Schoener (1980) suggested that a higher proportion of rear digit and/or tail loss implies predation as the cause of injury, whereas a higher proportion of front digit loss may indicate intraspecific encounters. We found front and rear digit loss to be equally common in urban and forest populations, suggesting both predation and intraspecific aggression contribute to these patterns. We hope that our findings will help stimulate further investigation into the relationship between injuries, predation and intraspecific aggression in urban lizards.

Even less is known about the causes and prevalence of bone fractures in wild animals. As with missing digits, fractures may be attributable to predation and/or intraspecific aggressive encounters. In addition, there are plausible reasons to suspect that falls in urban habitats may both occur more frequently and be more likely to result in serious injury. Previous research has shown that urban *A. cristatellus* predominantly perch on anthropogenic structures (Winchell *et al.*, 2016, 2018a, b), yet lizards commonly lose traction when running on these smooth surfaces (Winchell *et al.*, 2018b). This may result in increased falls in an environment with relatively little structural complexity (e.g. branches) to break the velocity of a fall. This would in turn result in more frequent impacts on the hard impervious surfaces, such as concrete, that dominate urban spaces. Bone fractures resulting from falls or jumps are common in domestic animals, most often resulting in fractures to the radius, ulna, humeral condyle and tibia (Phillips, 1979; Harasen, 2003). In forest environments, jumping behaviour tends to originate from rigid perches and terminate on more compliant substrates, which absorb excess forces and prevent injury (Gilman & Irschick, 2013). In urban environments, by contrast, lizards must frequently land on non-compliant anthropogenic substrates,

increasing the risk of injury. In addition, repeated high-stress loading on limb bones experienced when running and landing on non-compliant substrates exposes urban lizards to higher bone stresses. This can lead to the accumulation of fatigue damage, causing bone failure at much lower stresses than would be expected otherwise (Biewener, 2005).

Bones of urban lizards may also be weakened for reasons other than repeated bone stress. Musculoskeletal pathologies leading to weakened bones and increased fractures have been linked to poor nutrition in reptiles, and diets heavily reliant on human food sources may lead to bone development abnormalities (McWilliams & Leeson, 2001; Pierotti & Annett, 2001; Reavill, 2014). In amphibians, decreased bone density can result from urban pollution, increasing the risk of fractures and disrupting the processes of healing (Kaczmarski *et al.*, 2016).

A significant issue with virtually all injury studies in wild populations is that they only detect sub-lethal injuries. If the probability of surviving an injurious event differs between environments, then patterns of injury could simply reflect more sub-lethal compared to lethal injury events in urban populations. Some evidence suggests this may be the case, at least if predation is the cause. Lizard populations exposed to inefficient predators (e.g. cats) have higher frequencies of autotomized tails (Bateman & Fleming, 2011), and we have previously documented higher rates of tail autotomy in urban compared to forest lizard populations (Tyler *et al.*, 2016). In addition, injuries may carry different consequences for survival in different sites. If the same injury results in higher mortality in forest than in urban environments, the number of lizards with healed injuries would be higher in the latter site type than in the former. However, we found similar rates of healed and fresh bone fractures in the two contexts. Unfortunately, we are unable to fully explore these various intriguing explanations for our observed patterns, and instead recommend further research on how injuries relate to survival in urban environments.

We found greater FA in forest compared to urban lizards, contrary to our a priori expectation. Interestingly, this difference is driven by FA in hindlimbs and not forelimbs. Hindlimb length is an important functional trait in anoles and is strongly correlated with locomotor performance and fitness (Losos, 1990; Calsbeek & Irschick, 2007; Winchell *et al.*, 2018b). Functionally important traits such as limb length may be more effectively buffered against high levels of asymmetry (van Dongen, 2006). For example, Karvonen *et al.* (2003) found that traits important for flight exhibited lower levels of FA in greenfinches (*Carduelis chloris*) compared to non-flight-linked traits. Similarly, Garland & Freeman (2005) found

that mice with greater running endurance had lower levels of hindlimb asymmetry. In lizards, higher levels of asymmetry in hindlimb bones are correlated with decreased sprinting performance and survival (e.g. López & Martín, 2002).

Asymmetry may be suppressed more strongly in hindlimb elements than in forelimb elements because of the relative importance for locomotion (even if the same genetic mechanisms underlie developmental stability in both). Our results support this conclusion: across all sites, we found the lowest levels of asymmetry in hindlimb bones and the highest levels in forelimb bones. However, even when considering functionally important traits, we might still expect elevated FA in disturbed habitats if these environments indeed generate greater developmental instability (or at most the effect should be buffered and no difference would be detected; Palmer & Strobeck, 1992). Therefore, either our forest habitats actually represent more stressful environments leading to greater developmental instability, or another factor is mediating this effect.

One possibility is that asymmetry itself may be a target of natural selection resulting in reduced asymmetry in populations after selection (e.g. Brown & Brown, 1998). Regardless of whether developmental noise is higher or lower in urban environments, if the cost of asymmetry is high then we might expect reduced FA in adults due to stronger natural selection against asymmetric individuals. Although we measured only adults, we found that FA decreased with body size regardless of context. Because body size tends to be correlated with age (Ellstrand, 1983), this suggests that older individuals exhibit lower levels of asymmetry than younger individuals. An intriguing alternative hypothesis is that FA may be reduced with age because of compensatory growth. Lazić *et al.* (2016) found that FA of head shape decreased ontogenetically in urban lizards (*Podarcis muralis*), but remained constant throughout development in forest environments. We are unable to rule out the possibility that urban lizards in our study may also experience compensatory growth, leading to the observed patterns and body size correlation.

An important distinction, however, between the Lazić *et al.* (2016) study and this one is that the traits examined here have an established functional relevance and are probably subject to differential natural selection between environments related to locomotor performance. Winchell *et al.* (2016, 2018b) documented repeated shifts of increased limb length in urban compared to forest populations of *A. cristatellus* and found that these differences have functional consequences relevant to habitat use. If hindlimb length is subject to stronger selective forces in urban

populations, then the effects of increased FA may be exceptionally disadvantageous. In other words, if fast sprinting is important for fitness in urban habitats and is impeded by higher levels of asymmetry, then natural selection may act on asymmetry in hindlimb elements, explaining the lower level of hindlimb asymmetry found in adult lizards in urban populations in this study.

In conclusion, the effect of urbanization on the well-being of animals varies depending on the trait and the relationship of that trait to fitness. Using traditional metrics of health, we did not find strong evidence that urban lizards were in poorer health than their forest counterparts. Although we found slightly higher injury rates in urban populations, body condition was not consistently depressed in urban habitats and skeletal asymmetry in urban populations was actually significantly lower than in forested areas nearby. These results raise intriguing questions about the relationships between body condition, injury, FA of functional traits and fitness. Finally, we emphasize that our results do not suggest that urban habitats are of higher quality or that urbanization does not have strong negative impacts on urban animals. Urbanization undoubtedly has negative impacts at the population and community levels. However, at the individual level, city life may be perilous, but is not necessarily detrimental to health. Overcoming the challenges of life in the urban environment may be integral to colonization or persistence in urban habitats and a key step in urban adaptation.

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REFERENCES

- Auman HJ, Meathrel CE, Richardson A. 2008.** Supersize me: does anthropogenic food change the body condition of silver gulls? A comparison between urbanized and remote, non-urbanized areas. *Waterbirds* **31**: 122–126.
- Bateman PW, Fleming PA. 2009.** To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years. *Journal of Zoology* **277**: 1–4.
- Bateman PW, Fleming PA. 2011.** Frequency of tail loss reflects variation in predation levels, predator efficiency, and the behaviour of three populations of brown anoles. *Biological Journal of the Linnean Society* **103**: 648–656.
- Bates D, Maechler M, Bolker B, Walker S. 2015.** Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**: 1–48.
- Battles AC, Whittle TK, Stehle CM, Johnson MA. 2013.** Effects of human land use on prey availability and body condition in the green anole lizard, *Anolis carolinensis*. *Herpetological Conservation and Biology* **8**: 16–26.
- Biewener AA. 2005.** Biomechanical consequences of scaling. *The Journal of Experimental Biology* **208**: 1665–1676.
- Brown CR, Brown MB. 1998.** Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. *Evolution* **52**: 1461–1475.
- Calsbeek R, Irschick DJ. 2007.** The quick and the dead: correlational selection on morphology, performance, and habitat use in island lizards. *Evolution* **61**: 2493–2503.
- Chejanovski ZA, Avilés-Rodríguez KJ, Lapiedra O, Preisser EL, Kolbe JJ. 2017.** An experimental evaluation of foraging decisions in urban and natural forest populations of *Anolis* lizards. *Urban Ecosystems* **20**: 1–8.
- Contesse R, Hegglin D, Gloor S, Bontadina F, Deplazes P. 2004.** The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mammalian Biology* **69**: 81–95.
- Dananay KL, Krynak KL, Krynak TJ, Benard MF. 2015.** Legacy of road salt: apparent positive larval effects counteracted by negative postmetamorphic effects in wood frogs. *Environmental Toxicology and Chemistry* **34**: 2417–2424.
- Ditchkoff SS, Saalfeld ST, Gibson CJ. 2006.** Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosystems* **9**: 5–12.
- van Dongen S. 2006.** Fluctuating asymmetry and developmental instability in evolutionary biology: past, present and future. *Journal of Evolutionary Biology* **19**: 1727–1743.
- Donihue CM, Lambert MR. 2015.** Adaptive evolution in urban ecosystems. *Ambio* **44**: 194–203.
- Drakeley M, Lapiedra O, Kolbe JJ. 2015.** Predation risk perception, food density and conspecific cues shape foraging decisions in a tropical lizard. *PLoS One* **10**: e0138016.
- Ellstrand NC. 1983.** Why are juveniles smaller than their parents? *Evolution* **37**: 1091–1094.
- Forman RT. 2014.** *Urban ecology: science of cities*. Cambridge: Cambridge University Press.
- Garland T Jr, Freeman PW. 2005.** Selective breeding for high endurance running increases hindlimb symmetry. *Evolution* **59**: 1851–1854.
- Gillies C, Clout M. 2003.** The prey of domestic cats (*Felis catus*) in two suburbs of Auckland City, New Zealand. *Journal of Zoology* **259**: 309–315.
- Gilman CA, Irschick DJ. 2013.** Foils of flexion: the effects of perch compliance on lizard locomotion and perch choice in the wild. *Functional Ecology* **27**: 374–381.
- Gvozdik L. 2000.** Intrapopulation variation in injury frequencies in the sand lizard, *Lacerta agilis* (Squamata, Lacertidae). *Biologia-Bratislava* **55**: 557–562.
- Hall JM, Warner DA. 2017.** Body size and reproduction of a non-native lizard are enhanced in an urban environment. *Biological Journal of the Linnean Society* **122**: 860–871.
- Harasen G. 2003.** Common long bone fracture in small animal practice—part 2. *The Canadian Veterinary Journal* **44**: 503–504.
- Heiling AM. 1999.** Why do nocturnal orb-web spiders (*Araneidae*) search for light?. *Behavioral Ecology and Sociobiology* **46**: 43–49.
- Henderson RW, Powell RO. 2001.** Responses by the West Indian herpetofauna to human-influenced resources. *Caribbean Journal of Science* **37**: 41–54.
- Homer CG, Dewitz JA, Yang L, Jin S, Danielson P, Xian G, Coulston J, Herold ND, Wickham JD, Megown K. 2015.** Completion of the 2011 National Land Cover Database for the conterminous United States – Representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing* **81**: 345–354.
- Hudson S. 1996.** Natural toe loss in southeastern Australian skinks: implications for marking lizards by toe-clipping. *Journal of Herpetology* **30**: 106–110.
- Jung K, Kalko EKV. 2010.** Where forest meets urbanization: foraging plasticity of aerial insectivorous bats in an anthropogenically altered environment. *Journal of Mammalogy* **91**: 144–153.
- Kaczmarek M, Kolenda K, Rozenblut-Kościsty B, Sońnicka W. 2016.** Phalangeal bone anomalies in the European common toad *Bufo bufo* from polluted environments. *Environmental Science and Pollution Research International* **23**: 21940–21946.
- Karvonen E, Merilä J, Rintamäki PT, van Dongen S. 2003.** Geography of fluctuating asymmetry in the greenfinch, *Carduelis chloris*. *Oikos* **100**: 507–516.
- Koenig J, Shine R, Shea G. 2002.** The dangers of life in the city: patterns of activity, injury and mortality in suburban lizards (*Tiliqua scincoides*). *Journal of Herpetology* **36**: 62–68.
- Kuznetsova A, Brockhoff PB, Christensen RH. 2017.** lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* **82**: 1–26.
- Lazić MM, Carretero MA, Crnobrnja-Isailović J, Kaliontzopoulou A. 2016.** Postnatal dynamics of developmental stability and canalization of lizard head shape under different environmental conditions. *Evolutionary Biology* **43**: 368–379.
- Lazić MM, Kaliontzopoulou A, Carretero MA, Crnobrnja-Isailović J. 2013.** Lizards from urban areas are more asymmetric: using fluctuating asymmetry to evaluate environmental disturbance. *PLoS One* **8**: e84190.

- Lenth RV. 2016.** Least-squares means: the R package lsmeans. *Journal of Statistical Software* **69**: 1–33.
- Lepczyk CA, Mertig AG, Liu J. 2004.** Landowners and cat predation across rural-to-urban landscapes. *Biological Conservation* **115**: 191–201.
- Leung B, Forbes MR, Houle D. 2000.** Fluctuating asymmetry as a bioindicator of stress: comparing efficacy of analyses involving multiple traits. *The American Naturalist* **155**: 101–115.
- Liker A, Papp Z, Bókony V, Lendvai AZ. 2008.** Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. *The Journal of Animal Ecology* **77**: 789–795.
- López P, Martín J. 2002.** Locomotor capacity and dominance in male lizards *Lacerta monticola*: a trade-off between survival and reproductive success?. *Biological Journal of the Linnean Society* **77**: 201–209.
- Losos JB. 1990.** The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* **44**: 1189–1203.
- Lovely KR, Mahler DL, Revell LJ. 2010.** The rate and pattern of tail autotomy in five species of Puerto Rican anoles. *Evolutionary Ecology Research* **12**: 67–88.
- McWilliams DA, Leeson S. 2001.** Metabolic bone disease in lizards: prevalence and potential for monitoring bone health. *Nutrition Advisory Group* **19**: 120.
- Møller AP. 1997.** Developmental stability and fitness: a review. *The American Naturalist* **149**: 916–932.
- Newsome D, Rodger K. 2008.** *To feed or not to feed: a contentious issues in wildlife tourism*. Mosman: Royal Zoological Society of New South Wales.
- Palmer AR. 1994.** Fluctuating asymmetry analyses: a primer. In: Markow TA, ed. *Developmental instability: its origins and evolutionary implications*. Dordrecht: Springer, 335–364.
- Palmer AR, Strobeck C. 1992.** Fluctuating asymmetry as a measure of developmental stability: implications of non-normal distributions and power of statistical tests. *Acta Zoologica Fennica* **191**: 57–72.
- Perry G, Buchanan BW, Fisher RN, Salmon M, Wise SE. 2008.** Effects of artificial night lighting on amphibians and reptiles in urban environments. In: Mitchell JC, Jung Brown RE, Bartholomew B, eds. *Urban herpetology*. Society for the Study of Amphibians and Reptiles, 239–256.
- Phillips IR. 1979.** A survey of bone fractures in the dog and cat. *The Journal of Small Animal Practice* **20**: 661–674.
- Pierotti R, Annett C. 2001.** The ecology of Western Gulls in habitats varying in degree of urban influence. In: Marzluff J, Bowman R, Donnelly R, eds. *Avian ecology and conservation in an urbanizing world*. Berlin: Springer, 307–29.
- R Core Team. 2017.** *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: <https://www.R-project.org>.
- Rashband WS. 1997.** *Imagej*. Bethesda: U.S. National Institutes of Health. Available at: <http://imagej.nih.gov/ij/>.
- Reavill DR. 2014.** Review of musculoskeletal pathology in reptiles. *Proceedings Association of Reptilian and Amphibian Veterinarians* **2014**: 86–96.
- Reher S, Dausmann KH, Warnecke L, Turner JM. 2016.** Food availability affects habitat use of Eurasian red squirrels (*Sciurus vulgaris*) in a semi-urban environment. *Journal of Mammalogy* **97**: 1543–1554.
- Richner H. 1989.** Habitat-specific growth and fitness in carrion crows (*Corvus corone corone*). *The Journal of Animal Ecology* **58**: 427–440.
- Rivkin LR, Santangelo JS, Alberti M, Aronson MF, de Keyzer CW, Diamond SE, Fortin M, Frazee LJ, Gorton AJ, Hendry AP, Liu Y, Losos JB, MacIvor JS, Martin RA, McDonnell M, Miles LS, Munshi-South J, Ness R, Newman AE, Stothart MR, Theodorou P, Thompson KA, Verrelli BC, Whitehead A, Winchell KM, Johnson MT. 2018.** A roadmap for urban evolutionary ecology. *Evolutionary Applications*. doi:10.1111/eva.12734
- Russ A, Rüger A, Klenke R. 2015.** Seize the night: European Blackbirds (*Turdus merula*) extend their foraging activity under artificial illumination. *Journal of Ornithology* **156**: 123–131.
- Schoener TW. 1979.** Inferring the properties of predation and other injury-producing agents from injury frequencies. *Ecology* **60**: 1110–1115.
- Schoener TW, Schoener A. 1980.** Ecological and demographic correlates of injury rates in some Bahamian *Anolis* lizards. *Copeia* **5**: 839–850.
- Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D. 2006.** From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution* **21**: 186–191.
- Tyler RK, Winchell KM, Revell LJ. 2016.** Tails of the city: caudal autotomy in the tropical lizard, *Anolis cristatellus*, in urban and natural areas of Puerto Rico. *Journal of Herpetology* **50**: 435–41.
- van Valen LV. 1962.** A study of fluctuating asymmetry. *Evolution* **16**: 125–142.
- Vervust B, van Dongen S, Grbac I, van Damme R. 2009.** The mystery of the missing toes: extreme levels of natural mutilation in island lizard populations. *Functional Ecology* **23**: 996–1003.
- Weller B, Ganzhorn JU. 2004.** Carabid beetle community composition, body size, and fluctuating asymmetry along an urban–rural gradient. *Basic and Applied Ecology* **5**: 193–201.
- Wiens JA. 1976.** Population responses to patchy environments. *Annual Review of Ecology and Systematics* **7**: 81–120.
- Winchell KM, Carlen EJ, Puente-Rolón AR, Revell LJ. 2018a.** Divergent habitat use of two urban lizard species. *Ecology and Evolution* **8**: 25–35.
- Winchell KM, Maayan I, Fredette JR, Revell LJ. 2018b.** Linking locomotor performance to morphological shifts in urban lizards. *Proceedings of the Royal Society B: Biological Sciences* **285**: 20180229.
- Winchell KM, Reynolds RG, Prado-Irwin SR, Puente-Rolón AR, Revell LJ. 2016.** Phenotypic shifts in urban areas in the tropical lizard *Anolis cristatellus*. *Evolution* **70**: 1009–1022.

- Wolak ME, Fairbairn DJ, Paulsen YR. 2012.** Guidelines for estimating repeatability. *Methods in Ecology and Evolution* **3**: 129–137.
- Xian G, Homer C, Dewitz J, Fry J, Hossain N, Wickham J. 2011.** The change of impervious surface area between 2001 and 2006 in the conterminous United States. *Photogrammetric Engineering and Remote Sensing* **77**: 758–762.
- Zweifel RG, Lowe CH. 1966.** The ecology of a population of *Xantusia vigilis*, the desert night lizard. *American Museum Novitates* **2247**: 1–57.

SUPPORTING INFORMATION

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

Table S1. Details on forest type, dates sampled, marking method, sample size and land cover for each site. Muni., Municipality: AG, Aguadilla; AR, Arecibo; MA, Mayagüez; PO, Ponce; SJ, San Juan. Dates sampled are in M/YYYY format, or M-M/YYYY when two consecutive months were sampled. Imp% and Can% are impervious surface and canopy cover percentages estimated from NLCD 2011 layers in ArcMAP (ArcGIS 10.5.1, ESRI).

Table S2. Formulas for all linear mixed-model analyses. SVL is body size, 'snout–vent length', measured from X-ray images. The significance of the interaction term context × municipality in each was tested with a likelihood ratio test of the full model (with interaction term) and the reduced model (with terms additive). LL, log likelihood.

Table S3. Summary information for fluctuating asymmetry analyses by population and trait. Sites are identified by municipality (AG, Aguadilla; AR, Arecibo; MA, Mayagüez; PO, Ponce; SJ, San Juan) and context (F, forest; U, urban). (a) Descriptors of traits analysed for asymmetry in each population for the eight traits examined. Rear digit is the metatarsal and first phalanx of the fourth digit. A, the mean raw trait value $(R+L)/2$ and standard error. B, the relationship of each trait to body size with the slope and standard error of the regression: $\log[|R - L| \sim \log(\text{SVL})]$, where SVL is snout–vent length, a measure of body size. C, ANOVA of trait by side (right or left) to test for the presence of directional asymmetry. (b) Descriptors of trait asymmetry across all sites for the eight traits. Rear digit is the metatarsal and first phalanx of the fourth digit. A, descriptors of normality for the signed asymmetry of log-transformed trait values, summarized by the mean, standard error, and skew and kurtosis of the distribution. B, test for mean $|FA| \neq 0$ with *t*-test, with significant values indicating the presence of FA for a trait. C, mean and standard error of $|\log(R) - \log(L)|$, a measure of absolute fluctuating asymmetry.