Tails of the City: Caudal Autotomy in the Tropical Lizard, *Anolis cristatellus*, in Urban and Natural Areas of Puerto Rico

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Abstract.—Urbanization creates drastic changes in habitat and presents considerable challenges and new sources of predation to urban-dwelling herpetofauna. Research on lizards has documented increased rates of mortality in urban areas due to generalist predators such as raccoons, feral cats, and domestic animals. Caudal autotomy (self-amputation of the tail) is a defense mechanism used to escape predation in a wide range and large number of lizard species. The tail is autotomized to evade capture, and in most species with autotomy, the tail is regenerated partially or completely. Caudal autotomy can be used as an indirect measure of predation environment; however, few prior studies have used lizard caudal autotomy to measure the predation environment of urban areas. We compared caudal autotomy rates in the Puerto Rican crested anole, *Anolis cristatellus*, between urban and natural sites in four Puerto Rican municipalities. Across all municipalities, we found the frequency of caudal autotomy and regeneration to be consistently, significantly higher in urban than in natural areas. Our findings suggest that differences exist in the predation regime experienced by lizards in urban and natural habitats across the island of Puerto Rico. At this time, however, we are not able to identify the specific nature of the difference in predation regime between sites. The difference in autotomy rate that we found may be driven by higher predation pressure in urban areas, differences in the predator assemblage between sites, or simply lower predator efficiency in urban habitats.

Urban development is rapidly increasing throughout the world, and presently more than half of the global human population lives in urban areas. Furthermore, this fraction is projected to rise to two-thirds by the year 2050, leading to increasingly extensive urbanization in coming decades (United Nations, 2014). Typical urban habitats are extremely fragmented and highly modified with dramatically restructured vegetation and species composition (Koenig et al., 2002; McKinney, 2002). Degradation of natural habitat has many negative direct and indirect impacts on native wildlife including limited access to refuges, food, and mates (Andren, 1994; Shine et al., 1998; Bateman and Fleming, 2012).

Most species decline in abundance or are absent in urban environments; however, some plant and animal species may exhibit altered behavior or life-history strategies in urban areas and thrive (Ditchkoff, 2006; Sol et al., 2013). Most species that succeed in urban environments are synanthropic generalists: species with broad preferences that tend to be ecologically associated with anthropogenically modified environments (McKinney, 2002). Alpha diversity declines with increasing urbanization, yet abundance of these synanthropic species can be very high (Shochat et al., 2006). This results in the general bio-homogenization of urban and suburban faunas throughout the world (Miller and Hobbs, 2002; McKinney, 2002, 2006).

Inhabitants of urban areas are under novel stresses relative to rural conspecifics (Ditchkoff, 2006). Mortality rates of urban-dwelling species may be elevated because of altered predator communities composed of introduced generalist predators (e.g., dogs, cats, or raccoons; Koenig et al., 2002) and automobile incidents (e.g., Fahrig et al., 1995; Bonnet et al., 1999). Predation pressures and trophic dynamics in urban areas are complex. Most evidence shows that predator numbers are elevated in urban habitats; however, mortality rates are typically lower than in natural areas, suggesting decreased predation pressure (Fischer et al., 2012). Apex predators are mostly nonexistent in urban areas, allowing for increased populations of mesopredators, which can reach very high densities (McKinney, 2006;

Prugh et al., 2009). To date, the majority of studies on predatory survival in urban habitats have focused on birds; consequently, we know relatively little about predation on other taxa (Fischer et al., 2012). However, it seems likely that habitats experiencing drastic anthropogenic change are more likely to harbor generalist, inefficient predators, and this could have implications for defensive prey behaviors (Ditchkoff, 2006).

The morphology, behavior, and habitat use of anoles (lizards in the diverse Neotropical genus, *Anolis*) have been thoroughly studied (Williams, 1983; Losos, 1990, 2009; Losos et al., 1994, 2001; Langerhans et al., 2006). They therefore present a great opportunity to investigate the effects of human-induced habitat change on predation pressure of an urban fauna. Puerto Rican Crested Anoles, *Anolis cristatellus*, are relatively small (male snout–vent length, SVL, of 50–75mm), arboreal lizards native to Puerto Rico where they are widely distributed. *Anolis cristatellus* is common in urban and natural settings throughout the island (Rivero, 1998).

Studies on anoles have found significant evidence for behavioral and phenotypic shifts in response to urbanization. For instance, K. Winchell, G. Reynolds, S. Prado-Irwin, A. Puente, and L. Revell (unpubl. data; henceforward, Winchell et al., unpubl. data) found that *A. cristatellus* in Puerto Rico use habitat differently in urban areas by perching on broader, smoother, artificial substrates such as concrete walls and metal fences, rather than on the trunks of trees found in natural areas. Studies have revealed phenotypic differences in this and other anole species found inhabiting highly disturbed and urban habitats such as longer limbs and more toepad lamellae (expanded subdigital scales used for clinging; Winchell et al., unpubl. data) as well as larger SVL, hind-limb lengths, and mass (Marnocha et al., 2011). These studies offer evidence that anthropogenic changes in habitat structure can drive the divergence of physical attributes in anoles.

Autotomy is a highly specialized morphological defense mechanism used to avoid predation by voluntarily shedding a body part (Etheridge, 1967; Arnold, 1984; Bellairs and Bryant, 1985; Russell and Bauer, 1992). Tail autotomy is common in lizards, being found in a wide range and large number of lizard
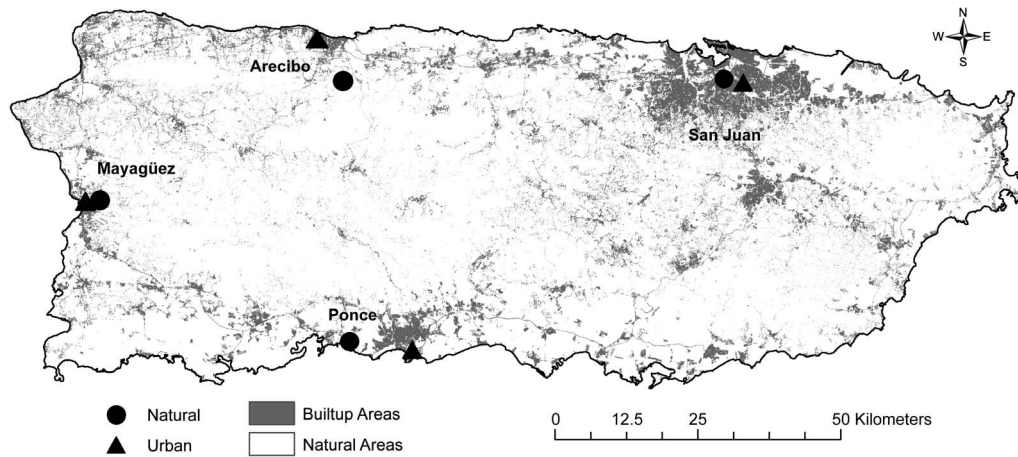
FIG. 1. Map of Puerto Rico showing paired study sites as well as built-up areas (in gray) as quantified in Gould et al. (2008). Although we actually used samples from two natural and two urban sites in the municipality of Mayagüez (only one each is shown), these sites were each so geographically close that the marker pins would directly overlap on a map of this scale.

species (13 of 20 previously recognized lizard families; Dial and Fitzpatrick, 1983; McConnachie and Whiting, 2003; Clause and Capaldi, 2006). Anoles exhibit intravertebral autotomy in which postpygal caudal vertebrae have fracture planes that allow intravertebral separation when sufficient, usually abrupt, pressure is applied to break the tail. Following separation of a vertebra at the fracture plane, regeneration of the tail usually occurs over the next few weeks. The caudal vertebrae are replaced with a rod of calcified cartilage, and the dermis and epidermis redevelop covering this rod (Etheridge, 1967). Although tail autotomy significantly increases survival from a predator confrontation (Daniels et al., 1986), it comes with notable costs. Tail loss in anoles is associated with costs to locomotion, increased vulnerability to predation, the energetic expense of regenerating the tail, as well as negative social impacts, all of which contribute to decreased fitness of the animal (e.g., Vitt et al., 1977; Irschick and Losos, 1998; Naya et al., 2007; Kuo et al., 2012).

The relative frequency of lizards with autotomized and regenerated tails may differ between different environments due to both differences in predator density and in predator efficiency. Numerous studies have found that with increased presence of inefficient predators, the incidence of autotomized tails is greater (Bateman and Fleming, 2011). Efficient predation tends to lead to lower observed rates of caudal autotomy, because most predation attempts lead to consumption, rather than tail autotomy, leaving relatively few lizards in the population with autotomized and regenerated tails (Schoener, 1979). Predator efficiency and its effect on caudal autotomy in lizards has been the focus of many studies (such as Medel et al., 1988; Chapple and Swain, 2004a,b; Bateman and Fleming, 2009, 2011).

Generally, predation in urban areas is understudied, and although caudal autotomy can be used to measure predation, few studies have explicitly compared caudal autotomy of lizards in urban areas to conspecifics in natural habitats (for a counterexample, see Chapple and Swain, 2004b; and for a related study comparing autotomy in areas with and without domestic or feral cats, see Fleming and Bateman, 2011). In this study, we compared the frequency and pattern (number of caudal vertebrae remaining) of caudal autotomy in A. cristatellus between urban and natural areas within four different Puerto Rican municipalities. Due to the complex relationship between

predation rate, predator efficiency, and caudal autotomy, we could not predict a priori whether caudal autotomy would be higher or lower in urban areas; however, we hypothesized that autotomy rates would be more similar between urban areas in different municipalities than to natural areas in the same municipality attributable to similarities in the (presumably anthropogenically modified) predator regime, or in different factors, such as habitat structure, that might influence predator efficiency in different urban sites across the island.

MATERIALS AND METHODS

Over three years (2012–14), we sampled A. cristatellus from paired natural and urban sites in four Puerto Rican municipalities: Mayagüez, Ponce, San Juan, and Arecibo (Fig. 1). Mayagüez is a midsized city on the west coast of the island (201.13 km², population: 89,080, metro population: 106,330, founded in 1760). We sampled lizards from four locations in this municipality (two urban, two natural). The first natural area (18.2162°N, 67.1242°W) was located east of the Mayagüez Zoo, near the Miradero neighborhood, and consists of secondary forest (abandoned plantation land). The second natural site was located in a large, privately owned secondary forest in a mountainous area 2.5 km east of the first site (18.2328°N, 67.1080°W). The urban sites in Mayagüez were the Mayagüez Terrace residential neighborhood west of the University of Puerto Rico, Mayagüez (18.2149°N, 67.1475°W), and an un-named residential neighborhood 2 km north of Mayagüez Terrace (18.2344°N, 67.1521°W). Because of the geographic proximity and physiognomic similarities of both our natural and our urban sites in Mayagüez, we henceforward treat (and refer to) each pair of sites as our Mayagüez urban site and our Mayagüez natural site, respectively (thus pooling the data for Mayagüez within site type). Ponce, on the south coast of the island, is the second largest municipality outside the San Juan metropolitan area (297.23 km²; population: 166,327; metro: 350,480; founded in 1692). In Ponce, we sampled lizards from a single urban site located in the Villa del Carmen residential neighborhood (17.9835°N, 66.6096°W) and from a single natural site located ~11 km west of the city in a tropical dry forest (17.9940°N, 66.7113°W). San Juan has the largest population of any municipality on the island (123.93 km²; population: 395,326; metro: 2,350,126; founded in 1509) and is the capital of Puerto
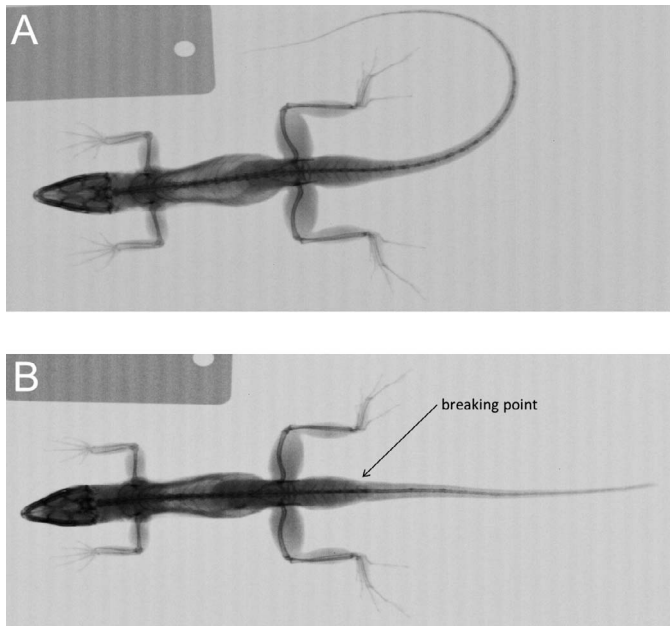
FIG. 2. Digital x-ray images of anesthetized *Anolis cristatellus* showing (A) a lizard with a fully original intact tail and (B) a lizard with an autotomized and regenerated tail. Although the original tail is supported by caudal vertebrae throughout its entire length, the regenerated tail (although it can resemble the original tail in length and outward appearance) is supported by a rod of cartilage and is easily identified from radiographs.

Rico (U.S. Census Bureau, 2012). Here, our natural sampling site was a small (30 ha) forest called Bosque Urbano San Patricio (18.4087°N, 66.0931°W) that is surrounded by urbanization. Our San Juan urban site was the University Gardens residential area adjacent to the University of Puerto Rico at Río Piedras (18.4041°N, 66.0625°W). Finally, our fourth municipality, Arecibo, is the largest municipality in Puerto Rico by land area (326 km^2; population: 96,440; metro: 199,471; founded in 1616). It is located in the mesic northwestern karst region of Puerto Rico where difficult terrain has led to relatively less deforestation than in other areas of Puerto Rico. Our urban site in Arecibo is the campus of a small private university: Universidad Interamericana de Puerto Rico, Recinto de Arecibo (18.4754°N, 66.7587°W). Our natural site in this municipality is a nearby biological field station, the Mata de Plátano Nature Reserve (18.4144°N, 66.7255°W), operated by the Universidad Interamericana de Puerto Rico, Recinto de Bayamón. Habitat at this site consists of young secondary forest that was used for agriculture until approximately 25 years ago.

All urban sites were high-density residential areas dominated by impervious surfaces, sparse tree cover, and an abundance of anthropogenic substrates such as metal fences and concrete walls. Our natural sites in San Juan, Mayagüez, and Arecibo consisted of subtropical moist forest and receive approximately 1,800 mm, 2,100 mm, and 1,400 mm of rain per year, respectively. By contrast, our natural site in Ponce consists of tropical dry forest and receives total annual precipitation less than 1,000 mm (National Weather Service, 2010). All four natural sites harbored many native and nonnative plant species. These locations and their populations were selected for this study based on the availability of relatively high-quality natural forests (which can be scarce around some urban areas of Puerto Rico) as well as accessibility and personal safety of investigators. In some ways, our "natural" site in San Juan (Bosque San Patricio) differed from our other natural areas in consisting of an isolated forest remnant surrounded by urbanization, a feature that did not characterize our other natural sampling areas (although our natural site in Ponce was directly adjacent to a small area of urbanization). Nonetheless, we feel that it is, from the perspective of an anole, much more similar to our other natural sites than to any urban locality. For instance, the forest, although small, consists of unmanaged tropical mesic forest vegetation—secondary forest, but forest that has been undergoing natural regeneration for several decades if not longer. The predator fauna, although unquantified by us, includes species such as the colubrid Puerto Rican Racer, *Borikenophis portoricensis* (quite common in this forest), and the Puerto Rican Boa, *Chilabothrus inornatus*, both of which tend to be extremely scarce or absent from urban sites. In addition, at least one congener, the Emerald Anole (*Anolis evermanni*), which is considered by us to be an "urban avoider" (sensu McKinney, 2002) and is not found in any of our urban sites, is in fact found in Bosque San Patricio. Some introduced predators common to urban areas, such as domestic cats, also might be found in Bosque San Patricio; however, we suspect the importance of these predators is mitigated by the abundant natural substrates and hides available to anoles in the forest that are not present in urban habitats. Anecdotally, we did not observed cats in Bosque San Patricio, whereas domestic cats were common in all urban areas. Finally, no natural area exists in Puerto Rico untouched by human interference—therefore, from one perspective, all natural and urban sites fall on a gradient of human disturbance. Our assessment of the gross physiognomic characteristics of this forest, its faunal constituents, habitat structure, and appearance suggest that it falls much closer to other natural sites of this study than to any of our urban research areas. In accordance with our observations, Suárez et al. (2005) report that both structurally and with respect to physiognomy the regenerated forest in Bosque San Patricio is highly similar to a small, untouched area at the same site. (This part of the forest was unavailable for our use in this study because of restrictions on access to that area.) Tree species composition differed, however, with a greater abundance of invasive trees in the canopy of regenerated areas (although recruitment was dominated by native tree species).

We captured subadult and adult male *A. cristatellus* (> 45 mm SVL) at each site by noosing. Lizards were transported to the field lab in each municipality where we used aerial isoflurane to temporarily immobilize each animal to obtain high-resolution digital x-ray images using a custom designed Kodex portable digital x-ray system. We also measured the mass of each lizard, total size (SVL), and head height. We marked all lizards with semipermanent, nontoxic ink (to prevent recapture) and returned them to their point of capture within 24 hours. We processed all digital x-rays using the software "tpsDIG2" (Rohlf, 2013).

We scored digital radiographs for caudal autotomy and the number of remaining tail vertebrae. We manually counted the number of vertebrae in the tail of each individual and noted whether the tail was autotomized. Autotomized tails are identifiable and measurable in x-rays because they lack caudal vertebrae in the regenerated portion (Fig. 2). We elected to count caudal vertebrae (rather than just scoring autonomy) because, since caudal vertebrae can only be lost and never regained, the number of caudal vertebrae in the tail tends to decrease with multiple autotomy events, and thus may provide additional information about autotomy inducing events in the population
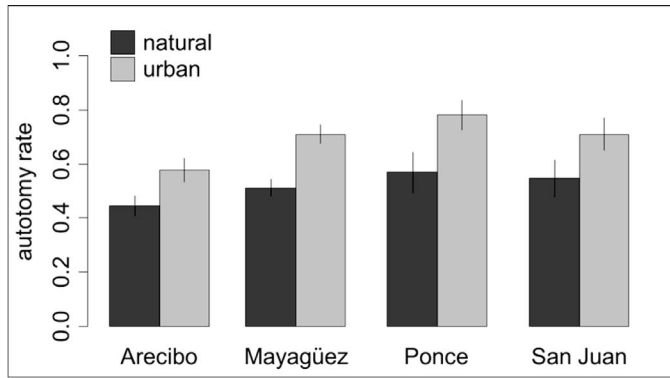
FIG. 3. More lizards from urban areas tended to have autotomized and regenerated tails than did animals from nearby natural sites. Bars show the proportion of lizards with autotomized and regenerated tails for each site, with whiskers showing ± SE of each proportion.

beyond the autotomy rate alone (e.g., Lovely et al., 2010; Cromie and Chapple, 2013). All measures of autotomy and caudal vertebrae counts were scored by a single investigator (RKT).

To test for an effect of urbanization on caudal autotomy, we compared our data for autotomy between sites. We fit a logistic regression model with municipality (San Juan, Mayagüez, Ponce, Arecibo) and site type (urban, natural) as model factors and body size as a covariate. Using data only from lizards with autotomized and regenerated tails, we also fit a Poisson regression model for vertebrae number with municipality, site type, and body size as explanatory factors. The logic of including body size as a covariate in all analyses is that, given a constant autotomy risk, both body size and the probability of autotomy should increase through life. Therefore, overall body size also was used as an imperfect proxy variable for age, which we did not measure directly in this study. We performed all statistical analyses using R 3-2.0 (R Core Team, 2015).

RESULTS

We captured 948 lizards in total. In 2012, we captured adult male lizards from San Juan ($N = 55$ natural, $N = 55$ urban), Mayagüez ($N = 55$ natural, $N = 55$ urban), and Ponce ($N = 44$ natural, $N = 55$ urban). In 2013, we captured 320 lizards from two additional sites in Mayagüez ($N = 201$ natural, $N = 119$ urban). In 2014 we captured 308 lizards from two sites in Arecibo ($N = 185$ natural, $N = 123$ urban). We found that frequency of caudal autotomy differed between urban and natural sites (Fig. 3). Across all municipalities, controlling for municipality and overall body size, we found more lizards with autotomized tails in urban areas than in nearby natural sites ($P < 0.001$; Table 1). Averaging over all sites, we found that 67.9% (277/408) of lizards in urban sites had autotomized and

TABLE 1. Coefficients, z-scores, and P-values from the fitted logistic regression model of autotomy as a function of site type (urban vs. natural), body size (SVL), and municipality ($N = 947$, df = 946, 941).

Model variable	Coefficient (SE)	z-value	P-value
Intercept	5.47 (3.32)	1.65	0.099
Site type (urban)	0.823 (0.148)	5.57	<0.001
Municipality (Mayagüez)	0.478 (0.160)	2.98	0.003
Municipality (Ponce)	0.811 (0.256)	3.17	0.002
Municipality (San Juan)	0.694 (0.265)	2.62	0.009
log(SVL) (mm)	−1.44 (0.825)	−1.74	0.082

TABLE 2. Model coefficients, z-scores, and P-values from a fitted Poisson regression model of the number of remaining caudal vertebrae as a function of site type (urban vs. natural), body size (SVL), and municipality ($N = 548$, df = 544, 539). OLS multivariable regression with log-vertebrae number yielded highly qualitatively similar results.

Model variable	Coefficient (SE)	z-value	P-value
Intercept	3.36 (0.473)	7.09	<0.001
Site type (urban)	0.003 (0.021)	0.129	0.897
Municipality (Mayagüez)	−0.020 (0.024)	−0.825	0.410
Municipality (Ponce)	−0.078 (0.035)	−2.20	0.028
Municipality (San Juan)	0.064 (0.036)	1.76	0.079
log(SVL) (mm)	−0.099 (0.118)	−0.838	0.402

partially or fully regenerated tails. In natural sites, 49.6% (268/540) of lizards had autotomized and regenerated tails.

Among only lizards with autotomized and regenerated tails, we did not find any effect of site type, municipality, or overall body size on the number of caudal vertebrae remaining in the tail (with the exception of the municipality of Ponce, in which lizards had marginally fewer caudal vertebrae than expected by chance; Table 2). We used a Poisson regression because it is more appropriate for count data; however an ordinary least-squares multivariate regression model with the logarithm of vertebrae number as the response variable yielded highly similar results (although different coefficients and P-values). In addition to this analysis, we also compared the distribution of caudal vertebrae between urban and natural sites, pooling across all municipalities (Fig. 4). Aside from the higher frequency of lizards with original tails found in natural sites (Fig. 4B), we did not find any difference in the relative frequency of different caudal vertebrae numbers between urban and natural areas (goodness-of-fit test $\chi^2 = 22.5$, df = 52, $P = 0.999$). In the goodness-of-fit test, we excluded categories of vertebrae number greater than 32 because these were very infrequent among autotomized and regenerated tails in our data.

DISCUSSION

Urbanization can generate drastic changes in community structure and population dynamics, as well as in the behavior and morphology of species that inhabit human-dominated areas (Shochat et al., 2006). Predation pressure in general in these environments is understudied but may be important for understanding how human changes to the environment affect ecological and evolutionary processes in urban areas as well as in other human-modified habitats. In this project, we considered a relatively novel approach to urban ecology: using reptilian caudal autotomy to draw inferences about the differences in predation pressure and efficiency between natural and urban areas (but for another example of this approach see Chapple and Swain, 2004b).

In general, we found a higher rate of autotomy in urban populations compared to natural ones, a pattern that was highly similar across urban areas. Although our analysis uncovered a relatively strong effect of urban areas on the probability of autotomy, we saw no evidence for an effect of site type, municipality, or body size on the total number of caudal vertebrae remaining in lizards with autotomized and regenerated tails.

Our a priori hypothesis that autotomy frequencies in urban areas would be more similar to each other than to nearby natural sites was supported. We did not have a specific a priori
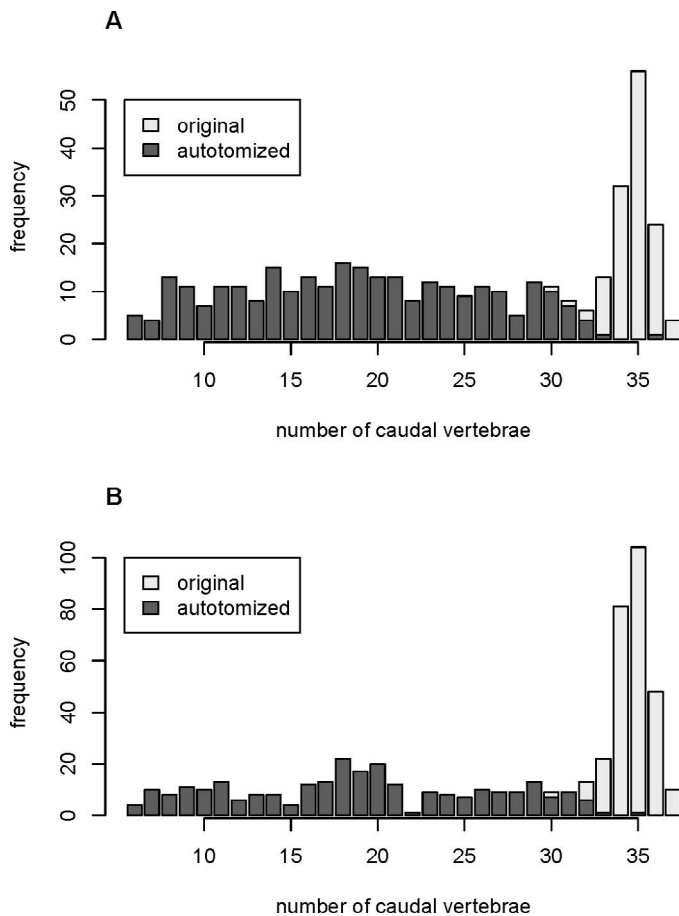
A

B

Fɪɢ. 4. Distribution of caudal vertebrae number in autotomized and regenerated tails, integrating across all urban (A) and natural (B) sites in this study.

hypothesis regarding the direction of these differences (i.e., whether urban or natural sites would have increased autotomy relative to the other). The increased rate of caudal autotomy that we found in urban areas could reflect any of a variety of factors, including (but not restricted to) inefficient predators in urban areas or an increase in predator density, a shortage of refuges offering protection from predators, or genetic adaptation.

Autotomy frequency may differ between habitats due to differences in predator density and efficiency (Bateman and Fleming, 2011). Urban areas are commonly characterized by altered trophic dynamics, and there may be an increased number of potential predators inhabiting urban environments (Fischer et al., 2012). Although it is possible that anoles may autotomize more often in urban areas due to increased predation attempts resulting from a higher density of predators, we hesitate to link autotomy rate directly to predation intensity. In a seminal paper on lizard tail autotomy, Schoener (1979) demonstrated theoretically that increased predation intensity should not cause a higher frequency of autotomized lizard tails in the population, but rather that predator efficiency was the most influential factor. Specifically, inefficient predators (that is, predators for whom predation attempts more often result in caudal autotomy than capture) tend to leave behind more lizards with broken and regenerated tails (Schoener, 1979). Bateman and Fleming (2011) found that autotomy frequency of Brown Anoles (Anolis sagrei) almost doubled in areas of central Florida with house cats (inefficient predators) compared to areas

with feral cats (efficient predators). This suggests that efficient predators successfully capture their prey, possibly resulting in a higher mortality rate and lower autotomy rate in natural areas; while in urban areas inhabited by inefficient predators, the autotomy rate is higher and mortality rate from predator encounters, lower. In the present study, we did not measure predator abundance or diversity; however, we can report some anecdotal observations with regard to the potential anole predators present in our study sites. We commonly observed the endemic specialist lizard predator Coccyzus vieilloti (Puerto Rican Lizard Cuckoo) in at least two of the natural areas (Mayagüez and Arecibo) but saw none in urban sites. We commonly saw domestic/feral cats and dogs at all urban sites but never during our surveys of natural areas (although feral cats are known for at least one of our natural areas and are probably found at least occasionally in all of them). We frequently observed the lizard predating colubrid snake species B. portoricensis (Puerto Rican Racer) at three of the four natural sites (Arecibo, Mayagüez, and San Juan), but this species was not observed in any of the urban sites. Greater Antillean Grackles (Quiscalus niger), a generalist avian predator known to at least occasionally predate even relatively large anoles (Graves, 2006), were extremely abundant in all urban areas but were seldom (if ever) observed at natural sites.

In addition to the possibility that predators differ characteristically between urban and natural areas, a second possible explanation for the elevated autotomy rates in urban sites is that lizards living in urban areas use the habitat in ways that place them at greater risk for predation or attempted predation. The lack of natural substrates and the increase of anthropogenic structures result in a shortage of potential refuges. Also, urban habitats tend to be more fragmented and open. Average canopy cover at three of our urban study sites was negligible (mean 1.15%), whereas natural sites had more complete canopy cover (mean 64.67%; Winchell et al., unpubl. data). Additionally, distance to the nearest perch in urban areas can be extremely large. In urban areas, we have observed lizards using habitat as far as 18 m from the nearest perch, whereas the greatest distance from the nearest perch we measured in natural habitats was < 2 m (Winchell et al., unpubl. data). Blamires (1999) found that, when fleeing a potential predator, the lizard's perch had the greatest impact on flight distance. Lizards perched on trees fled shorter distances, generally to the opposite side of the tree trunk (a behavior called "squirreling"), whereas lizards on the ground fled to the nearest refuge (Blamires, 1999). The openness of urban habitats may increase the exposure of urban lizards if there are not abundant suitable refuges, and the structure of the habitat (e.g., walls instead of trees) may prevent typical perch squirreling behavior. Moreover, lizards in urban areas may become less sensitive to the presence of potential predators, increasing their predation risk. Recently, Avilés-Rodríguez (2015) found that urban A. cristatellus have shorter flight initiation distances (how close a simulated predator can get before the lizard flees) compared to lizards in natural areas. Their escape behavior seems to be related to the openness of habitat as Avilés-Rodríguez (2015) also discovered that urban lizards are more likely to squirrel around a perch to avoid a predator whereas natural lizards will jump to the nearest vegetation. The openness of the urban habitat likely constrains the escape modes available to urban lizards and may increase their overall exposure to visual predators.

A third somewhat speculative, but nonetheless interesting, possibility is that lizards in urban areas may be adapting to

autotomize more easily in response to increased predation pressures or altered locomotory demands. Human activities can influence the evolution of populations (e.g., Hendry et al., 2000; Coltman et al., 2003; Stockwell et al., 2003; Olsen et al., 2004), and other species of *Anolis* have evolved rapidly in response to changes in habitat availability or the presence of an introduced predator (reviewed in Losos, 2009). With respect to urbanization, Marnocha et al. (2011) found that *A. sagrei* in disturbed habitats were significantly larger in SVL, hind span, and mass than those in natural habitats. Similarly, Winchell et al. (unpubl. data) found morphological shifts in urban populations of *A. cristatellus* for limb length and lamellae number and showed that at least some of this change is likely to have a genetic basis. It thus also seems possible that altered urban selection pressures may have influenced the patterns in autotomy uncovered in this study. Fox et al. (1994) compared lizard species living in environments with different predation regimes and found that the force required to generate autotomy was quite evolutionarily labile among species. Generally, species in environments with high predation required less force to induce caudal autotomy than did species from areas with relatively low predation (Fox et al., 1994).

Alternatively, the cost of caudal autotomy may differ between urban and natural sites and could similarly influence evolution of the propensity to autotomize. For instance, a recent study on the Green Anole, *Anolis carolinensis*, found that neither jump distance nor jump velocity were negatively impacted by tail loss, but in-air stability during jumping was detrimentally affected (Gillis et al., 2009). In urban areas, where perch substrates often are broad, lizards may jump less overall, or may jump less often to narrow substrates, relaxing selection on the ability to maintain in-air stability during jumping. If this were the case, then we could imagine that relaxed selection against tail loss (rather than increased selection by predators to autotomize the tail during predator encounters) could be responsible for an evolved difference in the propensity to autotomize.

To date, we have not measured selection on tail loss in urban areas nor have we directly measured behaviors relevant to tail loss (for instance, the number of jumps). It is nonetheless intriguing to consider the possibility that the difference in autotomy rate we have observed may be due, in part, to evolved differences in autotomy behavior or caudal anatomy between sites—either due to selection by predators for increased autotomy, or by way of relaxed selection against tail loss due to altered locomotory demands of urban habitats.

Although we show strong evidence of a change in the rate of caudal autotomy in urban areas of Puerto Rico in *A. cristatellus*, we do not yet have data on the mechanism that might underlie this intriguing difference. We hypothesize that differences in autotomy rate in urban areas are due to differences in the efficiency of predators found in those areas, such as domestic cats versus native avian specialist predators, or due to differences in habitat structure, which may cause different exposure to attempted predation in different areas, including differential natural selection between habitats. Future study using field models or direct observations could help us quantify the predation pressure of different areas and therefore clarify the underlying basis for the intriguing differences that we present herein.

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