

ORIGINAL ARTICLE

Human-induced morphological shifts in an island lizard

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Keywords*Anolis* lizards, anthropogenic change, habitat structure, island, selection.**Correspondence**

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Received: 22 July 2010

Accepted: 11 August 2010

doi:10.1111/j.1752-4571.2010.00170.x

Abstract

Understanding the evolutionary consequences of anthropogenic change is an emerging topic in evolutionary biology. While highly sensitive species may go extinct in response to anthropogenic habitat alteration, those with broader environmental tolerances may persist and adapt to the changes. Here, we use morphological data from the brown anole (*Anolis sagrei*), a lizard species that lives in both natural and human-disturbed habitats, to examine the impact of anthropogenic habitat alteration. We find populations inhabiting disturbed habitats were significantly larger in snout-vent length, hindspan, and mass and provide evidence that the observed divergence in hindspan is driven by human-induced changes in habitat structure. Populations were found to be genetically distinct among islands but are not genetically differentiated between habitat types on islands. Thus, the observed pattern of intra-island morphological differences cannot be explained by separate founding populations. Rather, our results are consistent with morphological differences between habitats having arisen *in situ* on each island. Results underscore the significant impact anthropogenic change may have on evolutionary trajectories of populations that persist in human-altered habitats.

Introduction

Two-thirds of the world's terrestrial area is now devoted directly to supporting human populations, either through agriculture, fisheries, urbanization, or infrastructure (Millennium Ecosystem Assessment 2005). Species that are able to persist in human-altered habitats are often subject to environmental conditions that are very different from those in their natural habitat. Habitat degradation can lead to shifts in community structure that in turn alter predation pressure and competitive regimes (Klein 1989; Eggleston et al. 2005; Foley et al. 2005; Laeser et al. 2005). Shifts in microclimatic conditions such as light availability and thermal characteristics are among the other effects of habitat alteration (Sumner et al. 1999). Divergent natural selection in human-altered habitats may lead to unique phenotypes not found in natural habitats (Hendry et al. 2006) and shift the evolutionary trajectories of species (Smith and Bernatchez 2008). Even if the novel traits are environmentally induced plastic responses, selection pressures acting on individuals can

alter the population's evolutionary trajectory via genetic assimilation (West-Eberhard 2003). Human-induced habitat alterations can therefore have long-term effects on populations inhabiting disturbed areas. Escalating human disturbance underscores the importance of understanding the full spectrum of evolutionary impacts that humans are having on natural populations (Smith and Bernatchez 2008; Hendry et al. 2011; Sih et al. 2011).

Anolis lizards provide an exceptional opportunity to investigate the evolutionary impacts of anthropogenic habitat alteration because of the well-documented association between morphology and habitat use in this group (Williams 1983; Losos 1990; Losos et al. 1994, 2001; Langerhans et al. 2006). The adaptive radiation of *Anolis* lizards is one of the most extraordinary vertebrate radiations known (Schluter 2000). Six distinct morphological classes, termed ecomorphs (Williams 1983), have evolved repeatedly and independently, giving rise to the nearly 150 species found in the Caribbean today (Jackman et al. 1999). Ecomorphs are characterized by divergence in body size and limb length, traits that are highly correlated

with habitat use (Losos 1990, 1994; Irschick and Losos 1998) and which are highly heritable in the species studied here (data for *A. sagrei*, body size, as indexed by snout-vent length (SVL): $h^2 = 1.02 \pm 0.29$, hindlimb length: $h^2 = 0.78 \pm 0.13$) (Calsbeek and Bonneaud 2008). Species with relatively long limbs are most often found perching on broad diameter substrates (e.g. tree trunks), whereas species with relatively shorter limbs are more often found on narrow diameter substrates (e.g. twigs). These correlations are thought to have arisen through natural selection favoring fast-moving, long-limbed lizards on broad surfaces (enhanced maximum sprint speed) and slower, more sure-footed lizards on narrow surfaces (enhanced agility) (Losos and Sinervo 1989; Losos 1990). These correlations between morphology and habitat use are considered adaptive and are thought to have played an important role in the adaptive radiation of these lizards (Losos et al. 2001). Recent work has also shown that the patterns of divergence in morphology among species are mirrored at the intraspecific level (Calsbeek et al. 2007; Marnocha 2008).

Anolis sagrei is a small (40–70 mm, SVL), semi-arboreal lizard with a broad tropical and subtropical distribution. It is a member of the trunk-ground ecomorph class and the most common anole in the Bahamas. On the islands of the Bahamas, *A. sagrei* occupies both its natural forest habitat and habitat that has been greatly altered by human activities. Here, we use morphological measurements from populations of *A. sagrei* to test the hypothesis that anthropogenic habitat alteration has led to morphological divergence between lizards living in disturbed and natural habitats. In particular, we examine whether

human-induced shifts in habitat structure have resulted in divergence in limb length, a key character in the diversification of *Anolis* lizards. Finally, we assess genetic variation among our study populations to test whether the patterns of morphological divergence are congruent with patterns of genetic divergence.

Materials and methods

Study sites

During June and July of 2003, we captured *A. sagrei* from four pairs of sites (natural and disturbed) with a pair on each of the following islands: New Providence (25°04'N, 77°22'W), Harbour Island (25°30'N, 76°38'W), Eleuthera (25°15'N, 76°18.5'W), and Great Exuma (23°30'N, 75°46'W) (Fig. 1). On each island, the natural and disturbed study sites were within 5 km of each other. Natural sites consisted of densely wooded areas (termed blackland coppice) containing a great diversity of plant species and were under little or no human influence. These areas have a dense canopy typically 30–40 feet high and are composed of broadleaf hardwood trees such as Caribbean mahogany (*Sweitenia mahagoni*) and gumbo-limbo (*Bursera simaruba*). The shady, humid understory supports numerous plant species, including bromeliads (*Tillandsia* spp.), orchids (*Spiranthes* spp. and *Habenaria* spp.), and a wide variety of shrubby plants. Disturbed habitat, by striking contrast, is highly impacted by humans and consists of largely open areas characterized by the presence of buildings and other man-made structures such as roads, sidewalks, and fences. Disturbed habitats have virtually no canopy cover and the vegetation

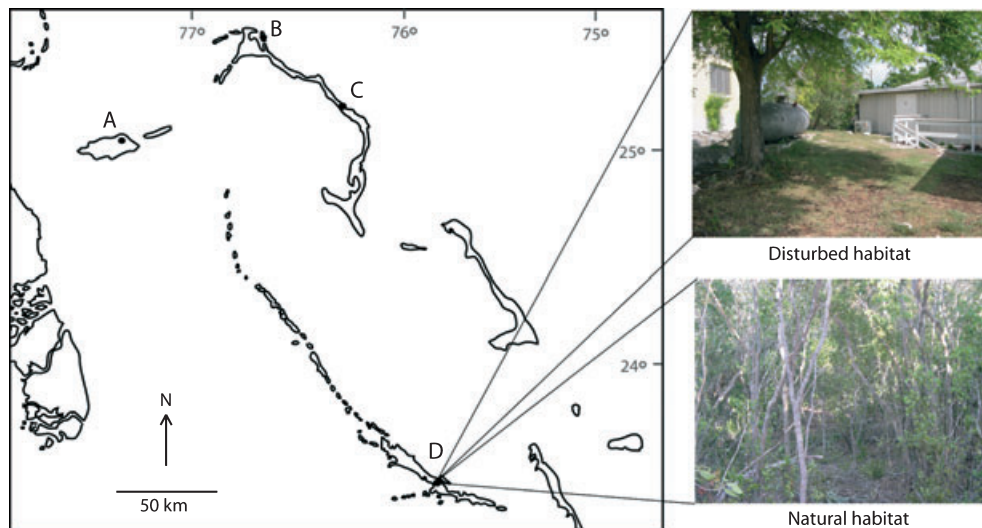


Figure 1 Map of the study islands and photographs of disturbed and natural habitat. Islands are labeled as follows: (A) New Providence; (B) Harbour Island; (C) Eleuthera; (D) Great Exuma. Points indicate location of study sites (pairs of sites on each island are within five km of each other). Photographs are of the study sites on Great Exuma.

consists primarily of palm trees (Arecaceae family), low shrubbery, and manicured lawns. Disturbed study sites are all located in towns that have been occupied by humans for at least 200–350 years (Craton 2007), the equivalent of hundreds of generations for *Anolis* lizards.

To quantitatively characterize habitat at each of our eight sites, we used satellite remote sensing data derived from the vegetation continuous field (Hansen et al. 2002) product from the MODIS satellite (https://lpdaac.usgs.gov/lpdaac/products/modis_overview) at 500-m resolution as a measure of the percentage of tree cover. We extracted the percent tree cover at our sampling sites using ArcGIS 9.3 (ESRI 2004) and visually verified the extracted data by means of optical satellite imagery. Although the environment in the Bahamas varies over small scales, the resolution of the data used is sufficiently high to provide an accurate characterization of the habitat available at each of the study sites.

Field methods

At each of the eight study sites, we captured approximately 20 adult male *A. sagrei* by hand or using a silk noose. We made the following measurements on each individual: snout-vent length (SVL; from the tip of the snout to the anterior side of the cloaca), hindspan (from one femoral–tibial joint to the other), forespan (from one humero–radio–ulnar joint to the other), gape width (width of head measured at insertion of jaw), head depth (depth of head measured at ear openings), toe pad width (across the widest part of the fourth toe of the right hindlimb), and mass (Fig. S1). SVL was measured to the nearest millimeter with a metal ruler, mass was measured to the nearest 0.1 g with a Pesola 10.0 g spring scale, and all other measurements were taken with dial calipers to the nearest 0.1 mm. A 2-mm piece of tissue from the distal tip of the tail was collected as a source of DNA for genetic analyses. Each individual was released to its original point of capture after being marked temporarily with a small spot of paint to prevent recapture. We also recorded the diameter of the structure that each individual was perched on (perch diameter) just prior to capture. As *A. sagrei* are largely sedentary and often use the same perch repeatedly (Calsbeek 2009a), perch diameter at first sighting is a relatively good estimate of habitat use. Lizards that were moving when first sighted were not scored for perch diameter.

Morphological analyses

To assess the effect of habitat type on morphological characters, we used a linear mixed model with two habitats per island (habitat crossed with island) and island as

a random effect to account for variation owing to island. Significance values were adjusted using a standard Bonferroni correction. This analysis was performed using the procedure `xtmixed` in Stata statistical software (StataCorp 2007).

To allow for visualization of size-adjusted morphological traits, we calculated residuals values from the linear regressions of the traits on SVL (all traits are highly correlated with body size in these lizards) (SAS 2006).

Analysis of perch data

Because the presence of flat perches prevented us from treating perch diameter as a continuous variable, we assigned the perch diameters to five categories. Perch diameters were categorized as follows: category 1: 0.1–2.9 cm, category 2: 3.0–5.9 cm, category 3: 6–8.9 cm, category 4: 9–40 cm, and category 5: flat surfaces. We then performed a contingency analysis to test for differences in the frequency distributions of perch diameters between natural and disturbed habitats (SAS 2006).

Analysis of genetic data

We extracted genomic DNA from tail tissue using the QIAGEN QIAamp DNA Mini. Six microsatellite loci were amplified using PCR, and length polymorphism (18–20 individuals per site) was assessed on an automated DNA sequencer (ABI 3700) using fluorescent labeling of one primer in each pair.

We tested for linkage disequilibrium among loci and for Hardy–Weinberg equilibrium using GENEPOP (Raymond and Rousset 1995). We also used GENEPOP to estimate F_{ST} values between study sites. We tested the statistical significance of pairwise F_{ST} values using the G test in the program FSTAT (Goudet 1995). To control for type I error, we applied a sequential Bonferroni correction (Rice 1989). Because relative measures of differentiation, such as estimates of F_{ST} , can be difficult to compare (Hedrick 1999), we also estimated Nei's standard genetic distance (D_S) using FSTAT. We generated a neighbor-joining network tree using the allele-sharing distance D_{AS} (Jin and Chakraborty 1993) and the program POPULATIONS v.1.2.28 (Langella 2002).

Results

Results from the linear mixed model indicate a significant difference in morphology between lizards occupying disturbed and natural habitats. Of the seven morphological traits, SVL, hindspan, and mass significantly differed between disturbed and natural habitats (Table 1). Individuals in disturbed habitats were larger in SVL, hindspan,

Table 1. Effect of habitat type on morphological traits.

Morphological trait	Coefficient of habitat/Standard error	Variance between islands	Variance within islands
Snout-vent length (SVL)	3.387* (0.581)	6.843	13.49
Hindspan	0.663* (0.176)	0.01	1.06
Forespan	0.32 (0.159)	0.384	0.853
Gape width	0.2 (0.092)	0.057	0.279
Head depth	-0.045 (0.06)	0.006	0.121
Toe pad width	0.055 (0.022)	0.002	0.017
Mass	0.817* (0.101)	0.061	0.338

Positive coefficient values indicate that individuals in disturbed habitat have larger trait values than those in natural habitat. For all traits (except for SVL), values were size adjusted using SVL as a covariate. Model formula for SVL: $SVL_t = \beta_{0i} + \beta_1 \times \text{habitat} + \epsilon_{ij}$. Model formula for all other traits: $\text{Trait} = \beta_{0i} + \beta_1 \times \text{habitat} + \beta_2 \times \text{SVL} + \epsilon_{ij}$ $\beta_{0i} = \tau_{00} + \mu_i$. d.f. = 3. *Significant at a Bonferroni-corrected α of 0.007.

and mass than individuals in natural habitats (Fig. 2, Table 1). None of the other morphological characters differed significantly between habitat types after Bonferroni correction (Table 1). Mean and variance values for each of the morphological traits are listed in Table S1.

All traits scaled linearly with SVL (linear regression, hindspan: $r^2 = 0.81$, $F_{1,159} = 676.02$, $P < 0.0001$; forespan: $r^2 = 0.82$, $F_{1,159} = 711.47$, $P < 0.0001$; gape width: $r^2 = 0.55$, $F_{1,159} = 189.83$, $P < 0.0001$; head depth: $r^2 = 0.47$, $F_{1,159} = 132.45$, $P < 0.0001$; toe pad width: $r^2 = 0.23$, $F_{1,159} = 47.61$, $P < 0.0001$; mass: $r^2 = 0.78$, $F_{1,159} = 550.54$, $P < 0.0001$). We visually inspected all linear regression plots and saw no evidence of nonlinearity. We also performed linear regressions of log-transformed traits on log-transformed SVL. *R*-square values from the log-transformed regressions were no higher than the values from the untransformed regressions, indicating that it was appropriate to calculate size-adjusted residual values from the linear regressions of trait values on SVL.

The percentage of tree cover as determined from satellite remote sensing differed between habitat types, with significantly greater cover in natural sites (*t*-test, $n = 8$, $F_{1,7} = 30.66$, $P = 0.002$). Tree cover in natural sites was much greater than disturbed sites ranging from 56% to 85% and from 2% to 38%, respectively (Fig. 3). These results mirrored observations from fieldwork on the

ground that showed relatively few trees in disturbed sites compared with natural sites. Finally, we found a significant negative relationship between percentage tree cover and hind limb length ($r = -0.79$, $P = 0.01$).

The frequency distributions of perch diameters significantly differed between habitat types (contingency analysis, $n = 160$, $\chi^2 = 35.24$, $P < 0.001$). We measured a high frequency of broad perches in disturbed habitat where

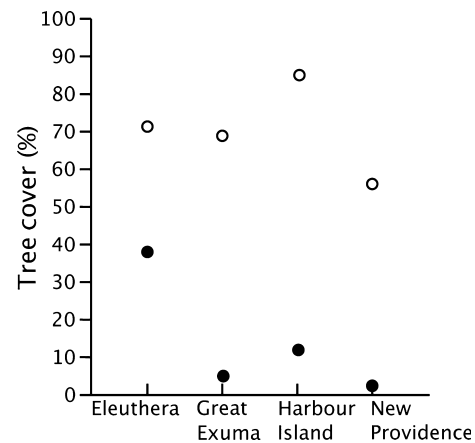


Figure 3 Percent tree cover at each of the eight study sites. Values were derived from MODIS satellite data. Closed circles indicate sites in disturbed habitat; open circles indicate sites in natural habitat.

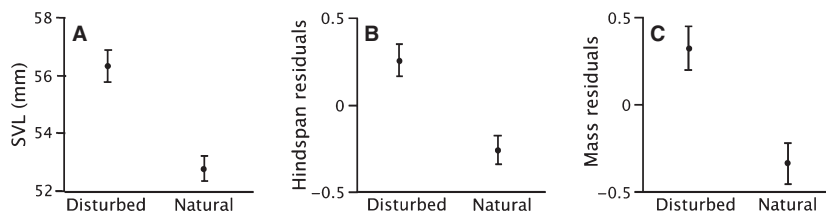


Figure 2 Mean trait values (\pm SE) for snout-vent length (SVL) (A), Hindspan residuals (B), and mass residuals (C) in each habitat type. Hindspan and mass residual values were calculated from linear regressions on SVL. Individuals in disturbed habitats were significantly larger in SVL, hindspan, and mass than individuals in natural habitats.

percentage canopy cover was lowest. By contrast, narrow perches, but not broad perches, were abundant in natural habitat (Fig. 4).

We detected no significant linkage disequilibrium between pairs of microsatellite loci and therefore consider the six loci to be independent markers. Some of the six loci were out of Hardy–Weinberg equilibrium in some of the populations. However, none of the populations were out of equilibrium at all loci, nor was any locus out of equilibrium in all populations. We therefore conclude that our results are not adversely affected by the presence of null alleles.

We detected no significant intra-island population structure between habitats, indicating that the intra-island populations are not derived from separate populations. Pairwise population comparisons of F_{ST} values were not significantly different from zero between pairs of natural and disturbed sites on each of the four islands (Table 2). We did, however, detect genetic divergence between

populations on different islands. Pairwise F_{ST} values were significantly different from zero in 18 of the 24 inter-island population comparisons (Table 2). Nei's genetic distance values indicated a similar pattern, with genetic divergence among islands (D_S range: 0.312–1.069) far exceeding genetic divergence within islands (D_S range: 0.196–0.371) (Table 2). The eight populations were strongly clustered into four island groups based on neighbor-joining analysis of allele-sharing genetic distances (Fig. 5).

Discussion

Human activities are dramatically altering ecosystems across the planet, but the evolutionary consequences of these changes remain poorly understood (Smith and Bernatchez 2008). Studies of human-driven evolutionary change have documented rapid evolution in the behavior, morphology, and life history of native insects in response to introduced host plants (Carroll and Boyd 1992;

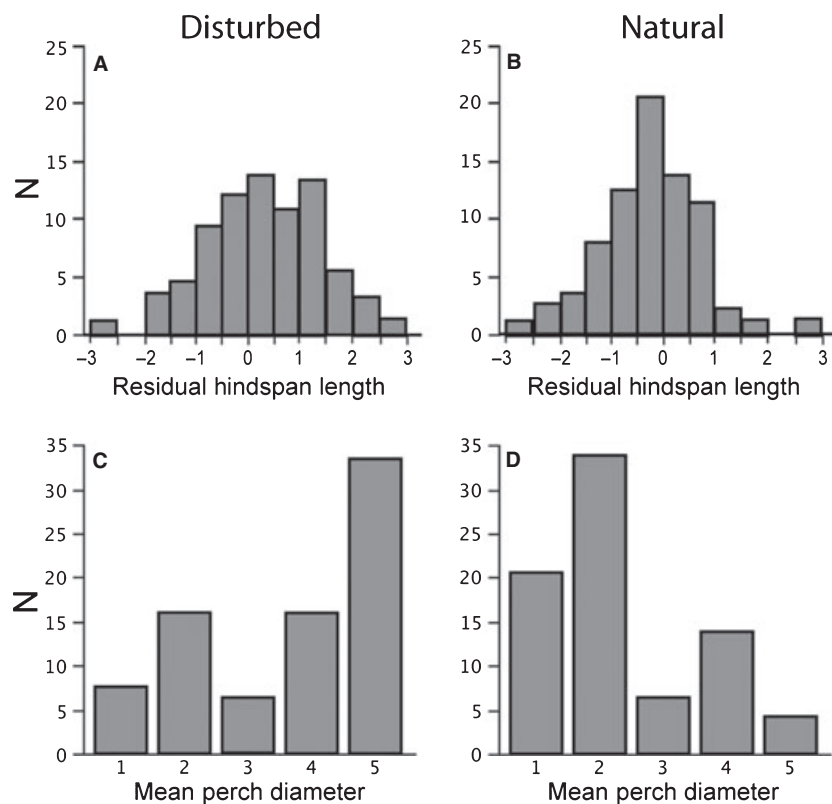


Figure 4 Frequency distributions of residual hindspan length (A and B) and mean perch diameter (C and D) in disturbed and natural habitats. The top panels show frequency distributions of residual hindspan length. Residuals were derived from the linear regression of group mean centered hindspan length on group mean centered snout-vent length. Individuals in disturbed habitats had significantly longer hindspan lengths than those in natural habitats. The bottom panels show frequency distributions of perch diameters utilized by individuals in disturbed and natural sites. Perch diameters are categorized as follows: category 1: perch diameters of 0.1–2.9 cm, category 2: 3.0–5.9 cm, category 3: 6–8.9 cm, category 4: 9–40 cm, and category 5: flat surfaces. Frequency distributions of perch diameters significantly differed between natural and disturbed sites, with a higher frequency of broad perches in disturbed habitat.

Table 2. Pairwise F_{ST} values (normal font) and Nei's distances (*italics*) between study sites. Pairs of sites on same island are indicated in bold.

	Exuma disturbed	Exuma natural	Eleuthera disturbed	Eleuthera natural	Harbour island disturbed	Harbour island natural	New providence disturbed
Exuma natural	0.031 0.247	–	–	–	–	–	–
Eleuthera disturbed	0.082 <i>0.573</i>	0.069 <i>0.312</i>	–	–	–	–	–
Eleuthera natural	0.104* <i>0.713</i>	0.094* <i>0.372</i>	0.023 0.196	–	–	–	–
Harbour island disturbed	0.119* <i>0.786</i>	0.125 <i>0.808</i>	0.151* <i>1.069</i>	0.115* <i>0.874</i>	–	–	–
Harbour island natural	0.179* <i>0.785</i>	0.224* <i>0.736</i>	0.234* <i>0.824</i>	0.182* <i>0.575</i>	0.048 0.371	–	–
New providence disturbed	0.071* <i>0.478</i>	0.079 <i>0.450</i>	0.12* <i>0.631</i>	0.107* <i>0.569</i>	0.122 <i>0.700</i>	0.191*	–
New providence natural	0.075* <i>0.513</i>	0.097* <i>0.510</i>	0.104* <i>0.547</i>	0.121* <i>0.605</i>	0.141 <i>0.898</i>	0.198*	0.021 0.262

*Significant at a Bonferroni-corrected α of 0.002.

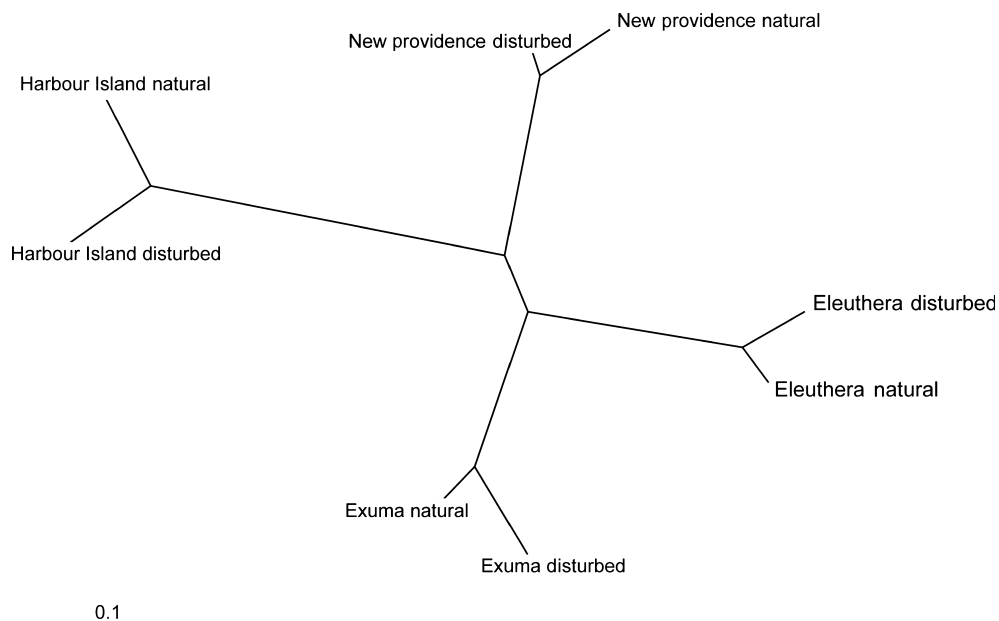


Figure 5 Neighbor-joining network based on allele-sharing distances (D_{AS}). The eight populations strongly clustered into four island groups.

Singer et al. 1993; Filchak et al. 2000). A number of studies have also shown that increased turbidity because of human activities may disrupt mate recognition in fish and thereby cause extinction through hybridization (Seehausen et al. 1997, 2008; Gow et al. 2006; Taylor et al. 2006). A recent surge in work on this topic has led to discoveries of human-induced evolutionary change in a diversity of organisms (Bradshaw and Holzapfel 2001; Parmesan 2006; Slabbekoorn and Ripmeester 2008; Smith et al. 2008; Waples et al. 2008), but much remains

unknown. Here, we contribute to this growing body of knowledge by examining anthropogenic impacts in *Anolis* lizards, a model system for studies of adaptive radiation.

Our results demonstrate morphological divergence, but not genetic divergence, between populations of *A. sagrei* inhabiting disturbed and natural habitats on four islands of the Bahamas. Lizards in disturbed habitats were significantly larger in SVL, hindspan, and mass than those in natural habitats. Our results indicate that populations are genetically distinct between each island but are not

genetically differentiated between habitat types on each island. Thus, the observed pattern of intra-island morphological differences cannot be explained by separate founding populations for each habitat nor differential immigration by distinct genetic types. Rather, our results are consistent with morphological differences between habitats having arisen *in situ* on each island.

Lizards in disturbed habitats had longer hindspans than those in natural habitats, likely reflecting differences in habitat. Estimates of percent tree cover from satellite remote sensing across islands show that disturbed habitats have roughly 30–70% less canopy cover than natural sites. Furthermore, hind limb length was negatively correlated with percentage canopy cover, consistent with the assertion that the loss of trees in human-altered habitats leads to morphological divergence. Not only are the disturbed sites more open than the natural sites, they also provide very different perches for the lizards that occupy them. The frequency distributions of perch diameters differed between habitat types, with a higher frequency of broad perches in disturbed habitats. These results are consistent with considerable evidence from previous studies that natural selection shapes the association between limb length and perch diameter in anoles (Williams 1983; Losos 1990; Calsbeek and Irschick 2007). In addition, our results suggest that anthropogenic habitat alteration can have direct impacts on the limb length of these lizards. Many of the broad perch surfaces in the disturbed habitats were novel structures such as walls, boards, and fence posts. The presence of these artificial perches appears to have altered the morphology of lizards inhabiting the disturbed sites.

Differences in habitat structure may also explain the divergence in body size between lizards occupying disturbed and natural habitats. Among ecomorphs, species that perch on large diameter surfaces tend to be larger than those that perch on smaller diameter surfaces (Williams 1972, 1983). This correlation has also been shown at the intraspecific level (Calsbeek et al. 2007). While the heritability of the traits examined here is high (Calsbeek and Bonneaud 2008), suggesting they may evolve by natural selection, the observed divergence in body size may reflect either a plastic response to environmental variation or evolutionary shifts or some combination of both. Future work will focus on common garden breeding experiments from these populations to resolve this question.

Given the differences in tree cover between habitat types, thermal environment likely differs between natural and disturbed environments. This variation in addition to differences in factors such as food availability may explain the observed differences in body size between natural and disturbed study sites. Recent results from a laboratory

study that reared lizards under varying food and temperature conditions showed that phenotypic plasticity varied greatly depending on the trait but was not apparent in hindlimb (Marnocha 2008). Hatchlings were placed in treatments that varied in temperature and food availability and were measured every 14 days until they reached adult size (defined as 196 days of age). Male SVL, as well as other indices of body size, differed between treatments in both the growth trajectories and at adult size. In contrast to overall body size, there was no evidence of plasticity in hindlimb length across the varying temperature and food conditions. Although further work is needed, these results suggest that hindlimb differences in the wild are more likely to result from selection pressures than plastic responses to food and temperature. The high heritability of this trait, the lack of evidence of plasticity in the previously described study, as well as the multitude of studies showing limb length shifts in response to natural selection (Losos et al. 2006; Calsbeek and Smith 2007; Marnocha 2008; Calsbeek 2009b) suggests that the differences in limb length found here are unlikely to be due solely to environmental effects and may have an evolutionary origin.

Our results demonstrate that anthropogenic habitat alteration may carry evolutionary consequences for species that persist in degraded habitats. We show divergence in several morphological characters between *A. sagrei* occupying natural and disturbed habitats, despite genetic evidence that the populations occupying the two habitat types are genetically undifferentiated and likely derived from the same founding population. The observed morphological shifts may be a fortuitously adaptive plastic response, the result of an adaptive norm of reaction that has evolved in response to habitat variation, or a genetic response to habitat-specific selection pressures. Future research will be needed to fully address this question. Nevertheless, the influence of human activities on morphology may have important evolutionary implications for *Anolis* lizards. The repeated evolution of ecomorphs on different islands highlights the importance of ecology in driving diversification in anoles (Losos et al. 1998; Jackman et al. 1999). Here, we show that human activities, by impacting the ecology, may also be impacting the course of evolution and the patterns of diversification in this group of lizards.

Acknowledgements

We thank T. Gillespie for assistance in the field, W. Madrid for assistance in the genetics laboratory, H. Thomassen for assistance with remote sensing data, and X. Chen and P. Ender for assistance with statistical analyses. We also thank G. Grether for his valuable

comments on previous drafts. We are grateful to the Bahamas Department of Agriculture for permission to conduct research. Funding for this study was provided by grants to EM from the United States Environmental Protection Agency, the American Museum of Natural History, and The Explorer's Club; a National Geographic Society grant and a National Science Foundation grant to TBS.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Photographs demonstrating how the following morphological characters were measured: (A) forespan, (B) snout-vent length, (C) gape width, (D) hindspan, (E) head depth, and (F) toe pad width.

Table S1. Morphological traits (raw values) in each of the habitat types. Mass is shown in grams; all other measurements are in millimeters. Statistical analyses took SVL into account as a covariate, so that all other trait values were size-adjusted.

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