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Post-hurricane shifts in the morphology of island lizards

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Hurricanes are expected to increase in both frequency and intensity as a result of climate change, but the impacts of these disturbances on the evolutionary trajectories of the species they affect are not yet well understood. In this project, we investigated population-level changes in morphology in the lizard *Anolis carolinensis* after Hurricane Irma in 2017. We found that anole populations were morphologically distinct after the hurricane, exhibiting significantly longer forelimbs and hindlimbs compared with pre-hurricane measurements. These morphological changes were consistent across two replicate islands and between males and females. The observed morphological shifts were potentially driven by positive selection from Hurricane Irma on clinging capacity. In this opportunistic study, we documented post-hurricane changes in the morphology of island lizards and suggest the potential for increasingly frequent and intense hurricanes to play an important role in natural selection and anole evolution.

ADDITIONAL KEYWORDS: *Anolis* – extreme climate events – Hurricane Irma – natural selection.

INTRODUCTION

The growing threat of climate change and the accompanying increase in the frequency and intensity of extreme climate events has led to great interest in the responses of species and communities to disturbances (Bender *et al.*, 2010; Knutson *et al.*, 2010; Lindner *et al.*, 2010; Turner, 2010; Hegerl *et al.*, 2011; Schowalter, 2012; Jones *et al.*, 2013; Ummenhofer & Meehl, 2017; Pruitt *et al.*, 2019). Natural disturbances, such as droughts, fires and hurricanes, can strongly perturb ecological systems (Sousa, 1984; Boose *et al.*, 2004; Scalley *et al.*, 2010), driving ecological changes and acting as agents of natural selection (Sousa, 1984). Although extreme climate events have the potential for important evolutionary consequences, the responses of individual species to disturbance events have received relatively little attention in research (Grant *et al.*, 2017). This deficit is attributable, in part, to the unpredictability of most extreme climate events, such that collecting the necessary predisturbance data is a matter of serendipity. Nevertheless, these disturbances provide valuable opportunities to investigate the responses of species to environmental perturbations, and such research is integral to the anticipation of future responses to extreme events (Turner, 2010). Here, we report on a serendipitous study of the effects of a hurricane on the morphology of the lizard *Anolis carolinensis*.

Anolis lizards, also called anoles, are a diverse genus of lizards that have become an invaluable tool for studying ecology and evolution (Losos, 2009). Anoles exhibit a strong relationship between morphology and habitat, characterized by particular limb proportions and specialized toepads of varying size and structure suited for the preferred microhabitat of each species. Proportional limb length is related to behaviour and microhabitat structure in a way that confers a locomotory advantage to a specific species. For example, limb length is positively correlated with increased sprint speed on broader surfaces, and species with longer relative limbs tend to prefer larger perch diameters. Conversely, anoles with shorter limbs relative to their body size are able to maintain balance on narrow perches much better than anoles with longer limbs, and these shorter-limbed anoles also tend to prefer narrower perches (Losos & Sinervo, 1989; Losos, 2009). Likewise, toepad structure varies with microhabitat. Each toepad features tightly overlapping, laterally expanded scales called lamellae that are covered in microscopic, hair-like structures

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called setae, and across species, the number of lamellae is positively correlated with average perch height (Glossip & Losos, 1997). To investigate whether these highly specialized morphological traits shift in a population after an acute disturbance, in our project we explored the effects of Hurricane Irma on the morphology of two *A. carolinensis* populations by looking at limb lengths and toepad size and structure before and after the hurricane.

We collected morphological data from two island populations of *A. carolinensis* in the summer of 2017 for an ongoing ecological study. In September 2017, Hurricane Irma struck the island. We returned the following summer (2018) to measure these populations again and thus perform a serendipitous investigation of the potential morphological consequences of the hurricane. We hypothesized that the hurricane would act as a strong selective event, such that lizards with weaker clinging capacity would be torn from their perches in the high winds and perish, whereas lizards with stronger clinging capacity would survive. Previous studies found that both toepad area (Irschick *et al.*, 1996; Elstrott & Irschick, 2004) and limb length (Kolbe, 2015) are positively correlated with clinging capacity. Furthermore, a study conducted by Schoener *et al.* (2017) reported consistent post-hurricane increases in the limb length of *Anolis sagrei* populations after four hurricanes over a period of 20 years. Considering these studies, we therefore predicted that toepad area and limb length would be larger in the post-hurricane populations.

In recent months, however, new studies on the responses of anole populations to hurricanes have shown conflicting results, complicating our understanding of how hurricanes influence anole morphology. Donihue *et al.* (2018) conducted an opportunistic study that investigated the potential selection imposed by Hurricane Irma on *Anolis scriptus* populations in Turks and Caicos. They observed morphological shifts within the populations after the hurricane, reporting an increase in toepad area and an increase in humerus length, both of which suggested that the hurricane selected for an increased clinging capacity. However, the authors also observed a decrease in femur length, which contradicted the previously documented relationship between limb length and clinging capacity (Irschick *et al.*, 1996; Elstrott & Irschick, 2004; Kolbe, 2015). In another recent study, Dufour *et al.* (2019) measured directly the clinging capacity of two anole species in Dominica, *Anolis cristatellus* and *Anolis oculatus*, before and after Hurricane Maria. They discovered in both species an increase in clinging capacity without a change in toepad size or structure. The current understanding of anole responses to hurricanes is therefore complicated; some findings fall in line with expectations from precedent, whereas others seem to contradict predictions based on previously established relationships between morphological traits and clinging capacity in anoles. All projects, however, have shown significant differences in the form or function of anole populations after a hurricane. Our project contributes new evidence to this area of research with the inclusion of a species previously unstudied in this context and suggests the capacity of hurricanes to act as potentially important factors in anole evolution.

MATERIAL AND METHODS

We performed our study on two islands, SL9 and SL10, located in the Indian River Lagoon near Fort Pierce, FL, USA (Island SL9, 27.502868°N, 80.331112°W; Island SL10, 27.50122°N, 80.330854°W). The two islands were of comparable size (~0.4 ha^2), had similar habitat structures and were separated by > 100 m of water at their closest points. The island interiors were composed of a sandy substrate and vegetation throughout, with a dense red mangrove (*Rhizophora mangle*) growth around the perimeters of the islands. Hurricane Irma hit Fort Pierce on the night of 10 September 2017, with sustained 115 km h^{-1} winds and a total of > 55 cm of rainfall between 9 and 12 September (Cangialosi *et al.*, 2018). The hurricane caused substantial changes to the habitat structure of the islands, including multiple fallen trees and broken and scattered branches (Fig. 1C, D). No other severe weather events occurred between our sampling periods.

Data collection

We collected data on lizard morphology from 11 to 19 June 2017 and from 19 June to 1 July 2018. In 2017, we captured 50 *A. carolinensis* (SL9, 17 males and eight females; SL10, 13 males and 12 females). In 2018, we captured 48 *A. carolinensis* (SL9, 18 males and six females; SL10, 16 males and eight females), following the same search and collection protocol both years. Pre-hurricane collection required 99 h of labour, whereas post-hurricane collection required 159 h of labour to capture a similar number of individuals. We surveyed each island daily, typically from 8:00 to 15:00 h, and captured lizards using an extendable pole with a slipknot. We used digital callipers to measure lengths of the humerus, ulna, femur and tibia and digital scales to measure the body mass of each individual. We used a ruler to measure the body size [snout–vent length (SVL)]. Using a flatbed document scanner, we scanned images of the lizard toepads for future quantification using image analysis

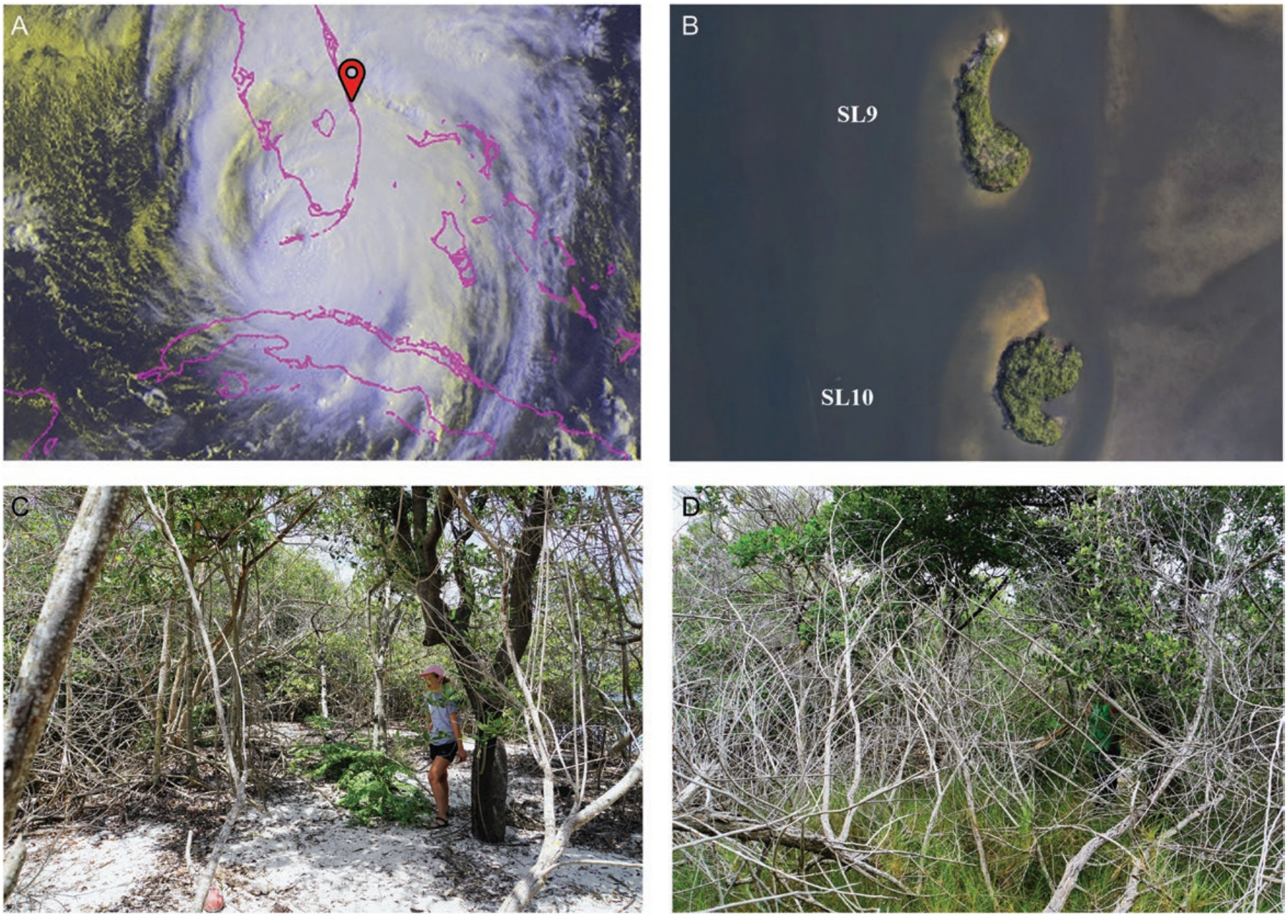

Figure 1. Images of the study islands. A, Hurricane Irma struck the study islands (location denoted by place marker) in September 2017 (image courtesy National Oceanic and Atmospheric Administration, www.goes.NOAA.gov). B, the islands are of similar shape, size and structure (imagery: © 2019 Maxar Technologies, U.S. Geological Survey; map data © 2019 Google). C, D, the hurricane caused substantial changes to habitat structure on the islands, visible in comparison between the images taken from the same location on SL9 in July 2017 (C) and in July 2018 (D) (images courtesy N.C.H.).

software. Before release, we marked each lizard with a permanent marker to prevent recapture.

Data analysis

We used the software program FIJI (Schindelin *et al.*, 2012; Rueden *et al.*, 2017) with the plugin ObjectJ (Visher & Nastase, 2014) to measure the toepad area and the number of adhesive scales (lamellae) on the medial toe on the forelimb and the fourth toe on the hindlimb, with lamellae being counted from the tip of the toe to where the second and third phalanx join. For consistency, the same researcher quantified all mass, limb and SVL measurements (N.C.H.) and toepad measurements (A.M.R.).

We used R v.3.5.2 for all data analysis (R Core Team, 2019). To begin our analysis, we $\log_{10}$-transformed the raw data to attain normality. Owing to sexual dimorphism (Supporting Information, Fig. S1), we conducted our analyses separately for each sex. Given the the small sample size of the female *A. carolinensis* populations, we included these analyses in the Supporting Information only. We also conducted analyses separately for each island. We treated the islands as replicates, because they represented distinct populations that underwent the same environmental perturbation. In our analysis between populations, we recognized that our sample sizes were relatively small. However, natural disasters are difficult to study owing to their frequency and unpredictability, and we therefore found this opportunistic study valuable nonetheless.

To gain a visual representation of the distribution of morphological traits in *A. carolinensis* populations, we used principal components analyses (PCAs). To investigate changes in SVL and the number of lamellae between years, we conducted Welch's two-sample *t*-tests on the $\log_{10}$-transformed values. The remaining

Table 1. Differences in morphological traits of male *Anolis carolinensis* between pre- and post-hurricane populations

Parameter	SL10			SL9		
	Mean pre-hurricane	Mean post-hurricane	Percentage difference	Mean pre-hurricane	Mean post-hurricane	Percentage difference
Humerus (mm)	8.13	9.36	**+15.13**	8.18	9.34	**+14.18**
Ulna (mm)	6.85	7.37	**+7.59**	7.03	7.84	**+11.52**
Femur (mm)	10.46	11.04	**+5.54**	10.74	11.83	**+10.15**
Tibia (mm)	9.37	9.90	**+5.66**	9.55	10.60	**+10.99**
Front toepad area (mm^2)	2.32	2.39	+3.02	2.70	2.86	+5.93
Hind toepad area (mm^2)	3.62	3.88	+7.18	4.21	4.46	+5.94
Front number of lamellae	17.46	17.06	−2.29	17.69	18.33	+3.62
Hind number of lamellae	23.00	23.13	+0.57	24.25	24.94	+2.85

Mean lengths of the humerus, ulna, femur and tibia were all longer in the post-hurricane populations of both islands, SL10 and SL9. Percentage changes reflect raw values. Differences determined to be significant ($P < 0.05$) by ANCOVA tests are shown in bold. Females exhibited the same trends (Supporting Information, Table S3).

morphological traits (limb lengths and toepad area) are continuous variables typically correlated with SVL in anoles (Losos, 2009). For these SVL-correlated traits, we performed analysis of covariance (ANCOVA) tests for both islands and sexes using $\log_{10}$-transformed trait values. We first tested for heterogeneity of slopes of trait–SVL regressions between the pre- and post-hurricane treatments using the lm() command in R, with year as a predictor and SVL as an interaction term for each morphological trait. If the slopes were not significantly different between the pre- and post-hurricane measurements, we tested for heterogeneity of intercepts using the lm() command in R, with year as a predictor and SVL as a covariate for each morphological trait. We visualized these changes in pre- and post-hurricane morphological traits by plotting the linear regressions of the $\log_{10}$-transformed values against $\log_{10}$-transformed SVL.

RESULTS

Pre- and post-hurricane SVL did not differ on either island or for either sex (males on SL10, $t_{20} = -1.90$, $P = 0.07$; males on SL9, $t_{25} = -1.87$, $P = 0.07$; females on SL10, $t_{16} = -1.79$, $P = 0.09$; females on SL,9 $t_{12} = -0.73$, $P = 0.48$). The numbers of forelimb and hindlimb toepad lamellae likewise did not differ between pre- and post-hurricane measurements (forelimb lamellae: males on SL10, $t_{23} = 0.84$, $P = 0.41$; males on SL9, $t_{28} = -1.64$, $P = 0.11$; females on SL10, $t_{17} = 0.47$, $P = 0.64$; females on SL9, $t_7 = 0.67$, $P = 0.52$; and hindlimb lamellae: males on SL10, $t_{27} = -0.28$, $P = 0.78$; males on SL9, $t_{29} = -1.44$, $P = 0.16$; females on SL10, $t_{18} = -1.77$, $P = 0.09$; females on SL9, $t_{10} = 0.56$, $P = 0.58$).

For males on SL10, principal component 1 (PC1) was loaded primarily for SVL (0.87) and principal component 2 (PC2) was loaded primarily for humerus length (0.75), femur length (0.39) and SVL (0.344). Likewise, PC1 for males on SL9 was loaded primarily with SVL (0.86), wereas PC2 was loaded primarily for humerus length (0.56), femur length (0.51) and tibia length (0.47) (Supporting Information, Table S1). Principal component analyses showed that *A. carolinensis* populations from both islands were morphologically distinct post-hurricane for both males (Fig. 2A, B) and females (Supporting Information, Fig. S2). For both islands, the pre- and post-hurricane measurements appeared to be divided primarily along the PC2 axes (Supporting Information, Table S1).

Using ANCOVAs, we detected significantly longer post-hurricane lengths of the humerus, ulna, femur and tibia in the populations. We found significant heterogeneity of slopes for SL9 male humerus, femur and tibia length measurements ($P < 0.05$), such that the relationships between these traits and SVL changed in the populations after the hurricane. All other limb measurements, for both islands and both sexes, showed non-significant differences between slopes ($P > 0.05$) and significant heterogeneity of intercepts ($P < 0.05$), indicating that for these traits, the relationship between limb length and SVL did not differ after the hurricane (Supporting Information, Table S2).

For all limb measurements (humerus, ulna, femur and tibia lengths) of males and females on SL10 and females on SL9, and for ulna length of males on SL9, ANCOVA results showed that the size-corrected limb lengths were significantly longer post-hurricane (Table 1; Supporting Information, Tables S2 and S3). For males on SL9, the slopes of the relationships

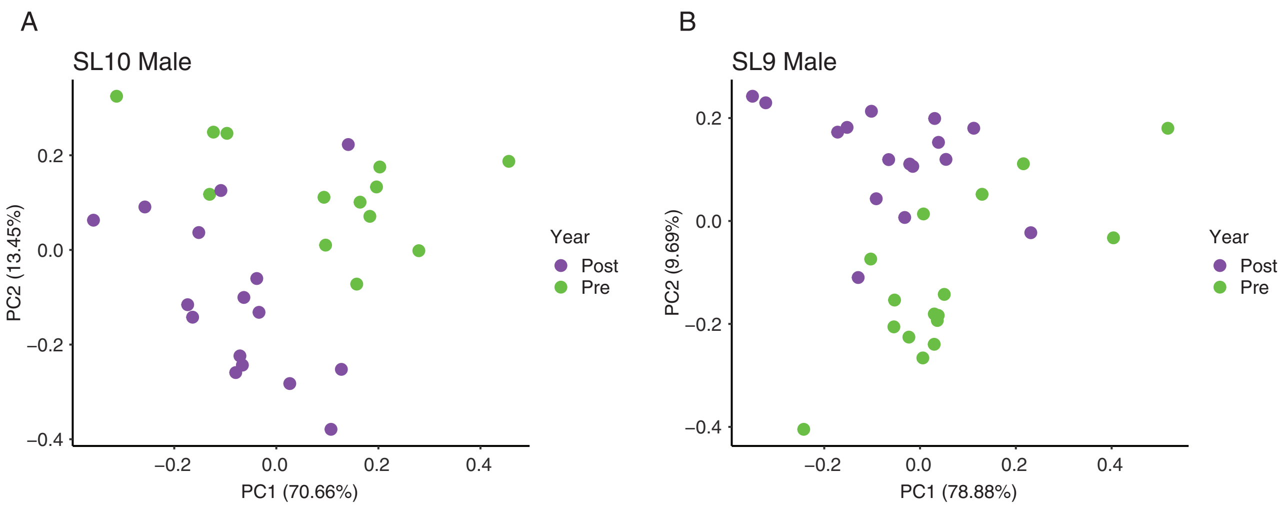

Figure 2. Male post-hurricane *Anolis carolinensis* populations appeared morphologically distinct on both islands, SL10 (A) and SL9 (B). We included all recorded morphological traits in the principal components analyses (PCAs) and conducted separate PCAs for each island. Loadings suggested that measurements of snout–vent length (SVL), humerus, ulna, femur and tibia were generally responsible for the differences between the pre- and post-hurricane population groupings for both islands (Supporting Information, Table S1). Females exhibited the same trends (Supporting Information, Fig. S2).

between SVL and humerus, femur and tibia lengths were all unequal between the pre- and post-hurricane measurements. This heterogeneity of slopes invalidated estimates of the intercept in an ANCOVA, preventing direct statistical comparison of these three size-corrected limb traits (SL9 humerus, femur and tibia lengths). However, although the slopes were not equal, it is clear from inspection of the linear regressions (Fig. 3A–D; Supporting Information, Fig. S3) that post-hurricane trait measurements were generally much greater than pre-hurricane measurements for any given SVL in the observed range. The populations had total average increases in limb length of 8.22% (SL10 males), 11.58% (SL9 males), 9.25% (SL10 females) and 10.17% (SL9 females) after the hurricane. ANCOVAs also showed that both forelimb and hindlimb size-corrected toepad areas were not significantly different post-hurricane for either island or sex (Supporting Information, Table S2).

DISCUSSION

Extreme climate events can impose substantial selection pressures on organisms, driving rapid, non-random responses in the populations they affect (Grant *et al.*, 2017). Although the evolutionary consequences of natural disasters can be severe, investigations of the responses to disturbance are particularly difficult given the rarity of extreme events and the required serendipitous collection of pre-disturbance data (Grant *et al.*, 2017). This topic is nevertheless increasing in urgency, because hurricanes, in particular, are projected to increase in frequency and intensity as a result of climate change (Bender *et al.*, 2010; Knutson *et al.*, 2010). Our project thus provides novel insight into an under-researched topic of growing importance and contributes to our knowledge of responses to disturbance. In our study, we observed significant, parallel morphological shifts in two populations of *A. carolinensis* lizards after Hurricane Irma. Here, we explore the potential causes of the post-hurricane increases in population-level limb length, namely selection on clinging capacity and potential post-hurricane hatchling plasticity. Furthermore, we suggest that hurricanes have the potential to act as intermittent yet severe agents of selection, which may have importance in anole evolution.

Although our study did not assess the clinging ability of lizards explicitly, we suggest that the hurricane might have selected for increased clinging capacity in our populations. Limb length in anoles is positively correlated with clinging capacity (Kolbe, 2015), and we reported significant, parallel increases in all limb trait lengths for both populations and both sexes. Likewise, Dufour *et al.* (2019), who measured clinging capacity directly, reported significant increases in the clinging capacity of two anole species (*A. oculatus* and *A. cristatellus*) after a hurricane. Surprisingly, neither relative toepad area nor the number of lamellae, traits typically correlated with clinging capacity in anoles (Irschick *et al.*, 1996; Zani, 2000; Elstrott & Irschick, 2004), was significantly different post-hurricane. Interactions between wind speeds and rainfall may

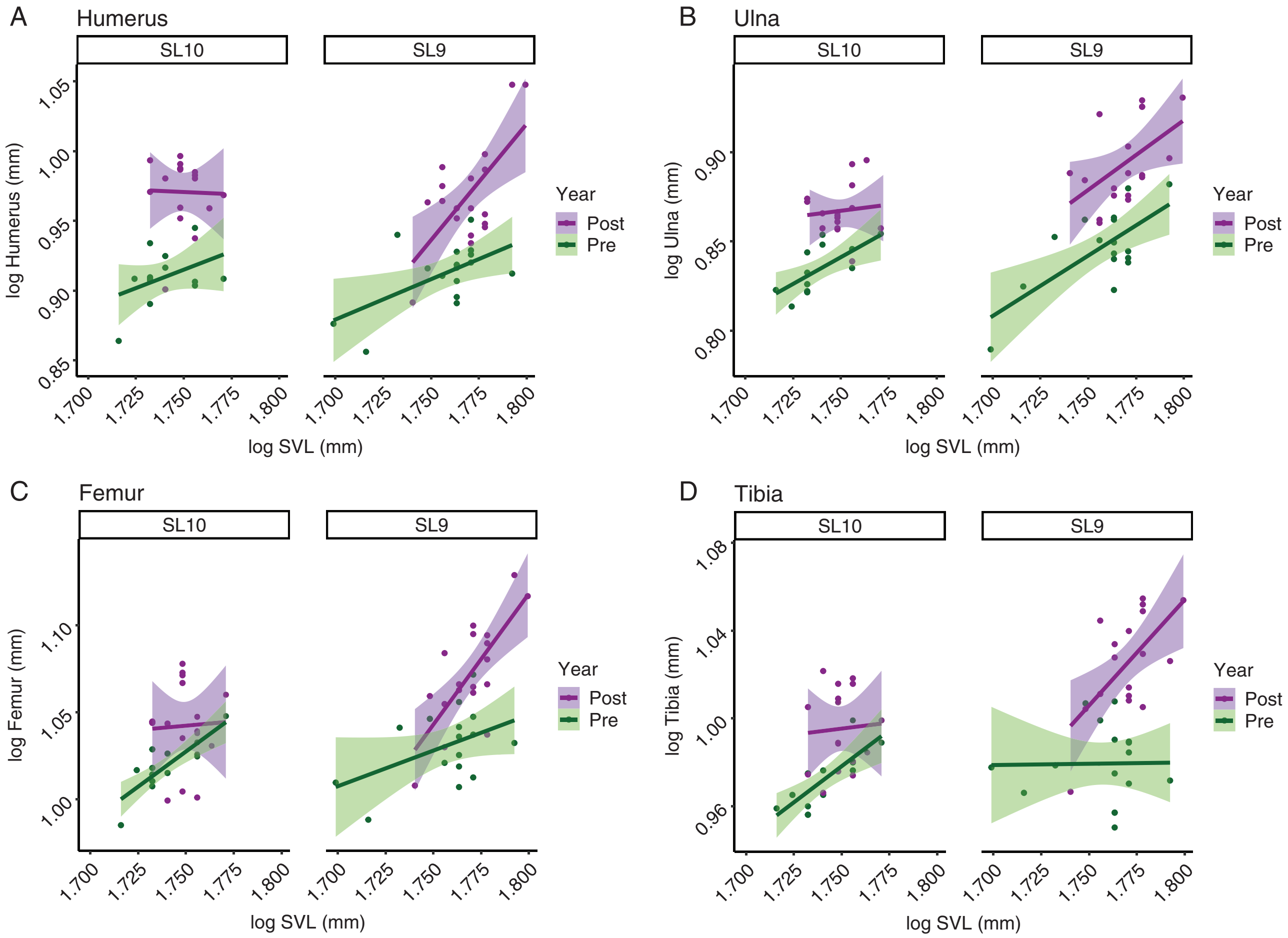

Figure 3. Linear regressions of traits against snout–vent length (SVL) showed that all male *Anolis carolinensis* limb measurements were longer in post-hurricane populations on both islands. The humerus (A), ulna (B), femur (C) and tibia (D) showed upward shifts in lengths. Both front and hind toepad areas were unchanged. Females exhibited the same trends (Supporting Information, Fig. S3).

explain inconsistent changes documented in anole toepad traits following hurricanes. Our study islands experienced 55 cm of rainfall during Hurricane Irma. Although the influence of torrential downpours on anole toepad clinging ability is not well understood, research conducted on geckos, whose toepads use lamellae and setae similar to those of anoles (Losos, 2009), found that toepads have significantly reduced clinging ability when wet (Stark *et al.*, 2012). A lack of change in toepad area or the number of lamellae between pre- and post-hurricane measurements in both this study and Dufour *et al.* (2019) might reflect this decreased function in clinging capacity of toepads during hurricane conditions. However, the increase in toepad area documented after another hurricane with extreme rainfall (Donihue *et al.*, 2018) suggests that overall, evidence for the clinging effectiveness of large anole toepads in hurricane conditions is conflicting.

The observed parallel increases in limb length point to Hurricane Irma as the likely driving factor behind the morphological shifts in our *A. carolinensis* populations. When replicate populations experience similar selection pressures, the populations tend to respond with parallel adaptations (Hendry & Kinnison, 2001). The morphological shifts we reported in *A. carolinensis* limb lengths were indeed parallel, consistent across the independent replicate islands and between sexes, suggesting Hurricane Irma was likely to be the cause. In addition, the observed increases in limb length appeared consistent with directional selection (Supporting Information, Fig. S4), in which the mean of a trait shifts towards an extreme within a generation (Phillips & Arnold, 1989). Other studies have also shown that severe climate events can be particularly effective at imposing directional selection (Brown & Brown, 1998). Directional selection is a major driver of adaptation and evolution (Hoekstra *et al.*, 2001). As such, short-term but extreme events that impose directional selection could potentially have an impact on the evolutionary trajectory of a population. Indeed, extreme events in general have the capacity to effect drastic evolutionary change across both contemporary and geological scales (Grant *et al.*, 2017). The potential hurricane-driven directional selection reported in our study thus suggests the possibility that hurricanes might be important factors in anole evolution.

Thus far, we have suggested that hurricane-driven selection on clinging capacity might be responsible for the morphological shifts we observed following a hurricane. However, plasticity of hatchlings in the post-hurricane environment could also explain the reported patterns. The prevalence and evolutionary importance of phenotypic plasticity in anole limb morphology is relatively unknown, but previous laboratory experiments have shown substantial intra-individual limb length plasticity in response to environment in two anole species: *A. sagrei* (Losos *et al.*, 2000; Langford *et al.*, 2014) and *A. carolinensis* (Kolbe & Losos, 2005). Each study reported that hatchlings exposed only to broad perches developed relatively longer hindlimbs than hatchlings raised in environments with only narrow surfaces. Given that hurricanes can drastically alter the structure of an environment, phenotypic plasticity in young anoles might drive a morphological response. Although we do not have data on the available perch diameters in the immediate aftermath of Hurricane Irma, images of the islands suggest that the interior vegetation and habitat structure of the islands were severely altered by the hurricane (Fig. 1C, D). In *A. carolinensis*, hatching peaks in August but can range from July to November, and individuals can reach adult SVL (> 40 mm for females and > 45 mm for males) within a year (Michael, 1972). As a result, phenotypic plasticity in individuals born either shortly before or immediately after the hurricane could potentially have contributed to the morphological shifts we observed in the adult anole populations. Observed changes in post-hurricane morphology as a result of limb length plasticity would nevertheless still be an effect of hurricane-induced changes to habitat structure. In total, our data suggest that Hurricane Irma might have contributed to population-level morphological shifts in *A. carolinensis* through both immediate (through initial selection) and prolonged (through developmental phenotypic plasticity of hatchlings) influences.

The parallel, directional shifts in limb length we observed are likely to be a result of hurricane-induced selection on clinging capacity and, potentially, hatchling phenotypic plasticity, but alternative explanations are possible. In particular, migration of individuals from the mainland to the islands or between islands might also have influenced the study populations, leading to the different trait distributions before and after the hurricane. Yet this explanation is unlikely to be wholly responsible for the observed morphological shifts given the large distances both between the islands and to the mainland. In addition, the consistent direction in the morphological shifts between the two study islands makes it unlikely that migration played a large role in observed differences, because this would have required non-random migration with respect to morphology.

Although the present study adds to the growing field of hurricane impacts on anole populations, our understanding of the effect of hurricanes on anole morphology is incomplete. In the past several years, contrasting patterns have emerged, which suggest that morphological responses to hurricanes might differ between anole species. For example, limb length responses varied by species, such that studies of *A. carolinensis* (the present study) and *A. sagrei* (Schoener *et al.*, 2017) reported increases in limb length after hurricanes, whereas a study of *A. scriptus* (Donihue *et al.*, 2018) reported an increase in forelimb length and a decrease in hindlimb length. Likewise, toepad area responses are varied. The absence of a significant change in the relative toepad area of our A. *carolinensis* populations was mirrored in *A. oculatus* and A. cristatellus populations observed by Dufour *et al.* (2019), but contrasts with populations of *A. scriptus* which showed significant post-hurricane increases in relative toepad area (Donihue *et al.*, 2018). It is worth noting, however, that although we did not report statistically significant differences in toepad area following the hurricane, we did observe post-hurricane increases in mean front and hind toepad area across both islands. The consistency of these shifts across our populations is similar to those shifts reported in *A. scriptus*. Considering that selection was likely responsible for the similar increases documented in *A. scriptus* populations, it is possible that selection acted similarly in *A. carolinensis* populations but happened to not lead to statistically significant differences, perhaps because of our relatively smaller sample size. Altogether, the varied results among these studies suggest that different anole species may respond to hurricanes in different ways, leading to inconsistent morphological outcomes after these extreme events. As such, additional work is needed to understand the overarching patterns of anole toepad responses and determine the consequences of selection pressures from hurricanes on population morphology.

Through this study, we contribute to the understudied and increasingly urgent topic of responses to natural disaster by furthering our understanding of how severe climate events can act as selective agents and influence contemporary evolution. We report significant morphological shifts in populations of *A. carolinensis* after a hurricane disturbance and suggest that the parallel changes in post-hurricane morphology might have been driven by hurricane-induced directional selection on clinging capacity and, potentially, phenotypic plasticity. Considering these reported morphological shifts and the parallel, directional nature of the trends, we suggest that hurricanes and the selection pressures they impose are potentially important factors in anole evolution.

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SUPPORTING INFORMATION

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

Figure S1. Morphological differences between male and female *Anolis carolinensis*. We examined the morphological differences between males and females by comparing the mass and snout–vent length (SVL) of each sex on both islands for both pre- and post-hurricane populations. Welch's two-sample *t*-tests showed that differences between sexes within a year were significant ($P < 0.05$) for both mass (A) and SVL (B). As a result of distinct morphology, we conducted all subsequent analyses separately for each sex.

Figure S2. Principal components analyses (PCAs) of female *Anolis carolinensis* morphology. Female *A. carolinensis* pre- and post-hurricane populations appeared morphologically distinct on PCAs for both islands, SL10 (A) and SL9 (B). We included all recorded morphological traits in the PCAs. The pre- and post-hurricane groupings appeared divided along the principal component 2 (PC2) axis, which was loaded primarily with humerus, femur and tibia for the female populations from both islands.

Figure S3. Linear regressions of traits against snout–vent length (SVL) for both islands of female *Anolis carolinensis* showed that post-hurricane populations had longer limbs than pre-hurricane populations. The humerus (A), ulna (B), femur (C) and tibia (D) showed upward shifts in lengths. ANCOVAs of the female populations from both islands reported significant increases for each limb measurement (Supporting Information, Table S2C, D). Fore and hind toepad areas were not different for either island between pre- and post-hurricane populations.

Figure S4. Trends in density plots potentially reflect directional selection. The population-level shift in recorded morphology, specifically limb length relative to snout–vent length (SVL), shows a post-hurricane shift towards longer limbs. This trend matches with directional selection, in which extreme forms on a phenotypic distribution have a fitness advantage compared with intermediate forms (Phillips & Arnold, 1989). Owing to our small sample size, we cannot determine rigorously whether directional selection is indeed present; however, the data appear to be consistent with directional selection.

Table S1. Loadings of the male and female morphology principal component analyses (PCAs) for both islands. We calculated the loadings for each individual PCA in order to determine the variables driving differences within each island and sex. For ease of comparison, loadings reflect absolute values. Loadings > 0.3 are shown in bold. Pre- and post-hurricane populations from both islands and both sexes appeared to be divided along the principal component 2 (PC2) axis in each PCA.

Table S2. ANCOVA results for heterogeneity of slopes and intercepts for both islands and sexes. Significant *P*-values (< 0.05) are shown in bold. We did not conduct ANCOVAs for male SL9 humerus, femur or tibia because these traits had significant heterogeneity of slope, disallowing accurate analysis for heterogeneity of intercept. All other values, however, had non-significant heterogeneity of slope and significant heterogeneity of intercept, indicating a significant change between pre- and post-hurricane populations for each of these traits.

Table S3. Differences in female *Anolis carolinensis* morphological traits between pre- and post-hurricane populations. Mean humerus, ulna, femur and tibia lengths were longer in the post-hurricane populations of both SL10 and SL9. Percentage changes reflect raw values. Results determined significant ($P < 0.05$) by ANCOVA tests are shown in bold.