

Hurricane-induced selection on the morphology of an island lizard

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Hurricanes are catastrophically destructive. Beyond their toll on human life and livelihoods, hurricanes have tremendous and often long-lasting effects on ecological systems^{1,2}. Despite many examples of mass mortality events following hurricanes^{3–5}, hurricane-induced natural selection has not previously been demonstrated. Immediately after we finished a survey of *Anolis scriptus*—a common, small-bodied lizard found throughout the Turks and Caicos archipelago—our study populations were battered by Hurricanes Irma and Maria. Shortly thereafter, we revisited the populations to determine whether morphological traits related to clinging capacity had shifted in the intervening six weeks and found that populations of surviving lizards differed in body size, relative limb length and toepad size from those present before the storm. Our serendipitous study, which to our knowledge is the first to use an immediately before and after comparison⁶ to investigate selection caused by hurricanes, demonstrates that hurricanes can induce phenotypic change in a population and strongly implicates natural selection as the cause. In the decades ahead, as extreme climate events are predicted to become more intense and prevalent^{7,8}, our understanding of evolutionary dynamics needs to incorporate the effects of these potentially severe selective episodes^{9–11}.

Hurricanes bring death and destruction to the ecosystems in their path. Their effects are myriad—decimating populations^{3,4}, reshuffling plant and animal communities^{1,2,5,12}, and fundamentally altering ecosystem cycles^{2,13}. Long-term demography studies have provided numerous examples of substantial mortality events in plants¹⁴, sponges¹⁵, land snails⁴, stick insects⁴, lizards¹⁶, birds⁵ and monkeys³ due to hurricanes. It remains an open question, however, whether hurricanes cause selective mortality on the basis of phenotypic traits or are instead so indiscriminately destructive that survival is random with regard to phenotype.

The fall of 2017 was an extraordinary season for Atlantic storms with three record-breaking events: Hurricanes Harvey, Irma and Maria. Four days before Hurricane Irma made landfall in the Turks and Caicos Islands, we finished surveying the morphology of *A. scriptus* on two small islands (Pine Cay and Water Cay) in the archipelago (Fig. 1). Hurricane Irma hit the islands with sustained 265-kph winds and, two weeks later, Hurricane Maria followed with sustained 200-kph winds.

Six weeks after our initial survey and three weeks after Hurricane Maria, we returned to Pine Cay and Water Cay, resurveyed the same transects on both islands, caught a sample of the surviving lizards and measured their morphology (Methods). Decades of previous research on *Anolis* species have demonstrated that the size of their toepads and the length of their limbs are related to habitat use and locomotor performance. We therefore tested whether the mean toepad surface area¹⁷ and limb lengths¹⁸ of the surviving lizards were larger than those of the lizards in the populations that we initially surveyed, as these increases are predicted to improve clinging ability^{17,18}.

We found parallel shifts in limb and toepad morphology between the pre- and post-hurricane populations on both islands (see Supplementary Information for complete results and model output). A multivariate analysis of covariance on all limb components revealed that the morphology of the post-hurricane lizard populations differed significantly from the pre-hurricane lizard populations ($F_{146} = 18.278$, $P < 0.0001$), and that the post-hurricane shifts were parallel on both islands—there was no hurricane \times island interaction; $F_{146} = 1.377$, $P = 0.1833$. The multivariate analysis of covariance structure coefficients indicate relative femur length most significantly distinguished the pre- and post-hurricane populations (see Supplementary Information).

Post hoc analyses examining traits individually indicate that the surviving populations of both islands had proportionately longer humeri (relative humerus length: $\beta \pm$ s.e.: 0.03 ± 0.008 ; $t_{159} = 3.64$; $P = 0.0004$; Fig. 2)—the average humerus length increased by 1.8%, despite a significant 1.4% decrease in mean body size (snout-to-vent length (SVL): $\beta \pm$ s.e.: 1.20 ± 0.484 ; $t_{159} = -2.483$; $P = 0.0141$). By contrast, we observed a significant 6% decrease in relative femur length across both populations after the hurricane ($\beta \pm$ s.e.: -0.05 ± 0.009 ; $t_{159} = -5.92$; $P < 0.0001$; Fig. 2) and a decrease of 4.6% in the length of the longest toe (relative longest toe length: $\beta \pm$ s.e.: -0.03 ± 0.009 ; $t_{159} = -3.75$; $P = 0.0002$; Supplementary Information).

On average, the post-hurricane lizards of both islands had larger toepads on both their forelimbs and hindlimbs (relative forelimb toepad area: $\beta \pm$ s.e.: 0.13 ± 0.017 ; $t_{158} = 7.93$; $P < 0.0001$; relative hindlimb toepad area: $\beta \pm$ s.e.: 0.10 ± 0.015 ; $t_{158} = 6.819$; $P < 0.0001$; Fig. 2), which correspond to increases in population means of 9.2% and 6.1% for forelimb and hindlimb toepad area, respectively. We also found a parallel sex \times hurricane interaction in body size ($\beta \pm$ s.e.: 2.87 ± 0.949 ; $t_{159} = 3.027$; $P = 0.003$)—on average, male SVL decreased by 4.3% whereas female SVL increased by 0.9%.

Despite the overall trend for parallel shifts, which was evident in both the multivariate analysis of covariance and many of the morphological traits, we found that forelimb toe length showed a differing response between the two islands (hurricane \times island interaction: $\beta \pm$ s.e.: -0.05 ± 0.025 ; $t_{159} = -2.11$; $P = 0.036$), decreasing by 3.9% on Pine Cay and increasing by 2.2% on Water Cay. In addition to the parallel and non-parallel changes detected for many traits, we did not detect a difference between pre- and post-hurricane populations in the length of any other segments of the limbs, nor in the number of lamellar scales on the forelimb or hindlimb toepads (Supplementary Information).

We next considered what might be responsible for the parallel shifts in phenotypes in the two populations. Two lines of evidence suggest that natural selection favoured individuals able to survive the hurricanes. First, if the hurricanes caused directional selection, then the survivors should exhibit reduced trait variation after the hurricanes⁶. We tested this prediction by calculating the variance in each of the measurements that showed a significant shift in their mean after the

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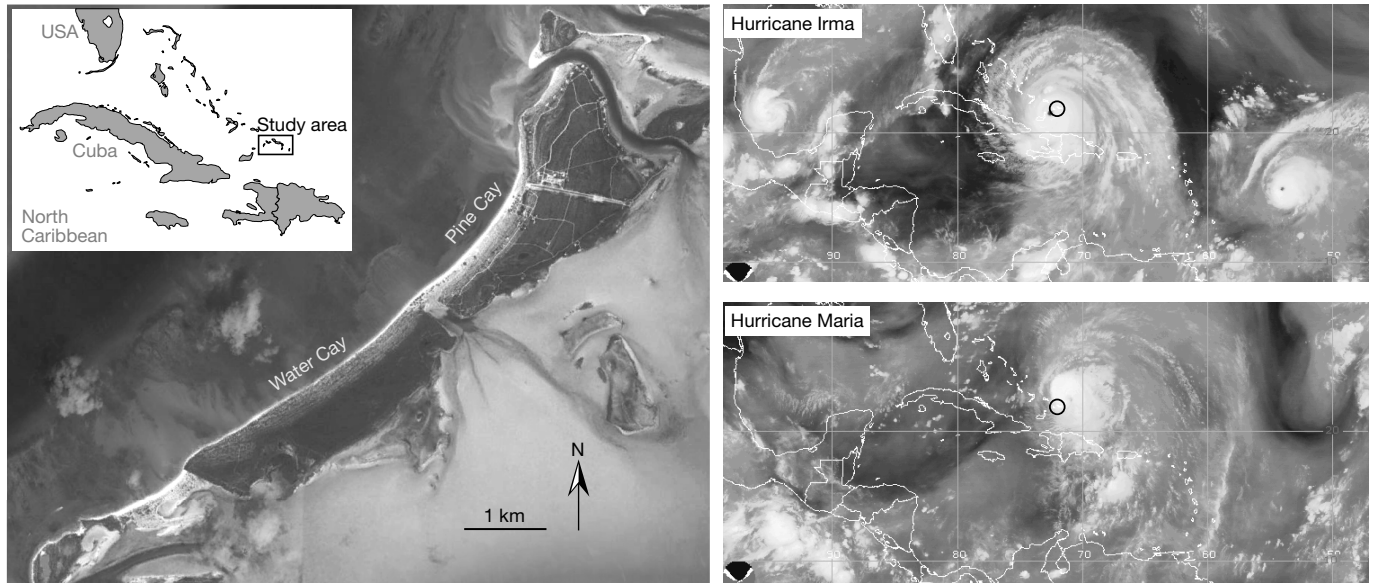


Fig. 1 | Location of Pine Cay and Water Cay with respect to Hurricanes Irma and Maria. Pine Cay and Water Cay are located in the Turks and Caicos Islands in the West Indies. They are home to the endemic Turks and Caicos anole, *Anolis scriptus*. On 8 September 2017, Hurricane Irma

directly hit Turks and Caicos (black circle), shown in the water vapour satellite maps (from NOAA, www.goes.noaa.gov). Two weeks later, on 22 September 2017, Hurricane Maria struck Turks and Caicos. Map data: Google, © 2018 DigitalGlobe.

hurricanes. The variance in all six of these traits decreased among the surviving *A. scriptus* on Pine Cay, and decreased in four of the six on Water Cay (Supplementary Information), a result that is unlikely to have occurred by chance ($P=0.019$ using the binomial test; analyses on principal component axes gave similar results, see Supplementary Information).

Second, survivors had traits associated with greater clinging ability. The positive relationship between toepad size and clinging capacity among anoles is well-established^{17,19}; we confirmed this relationship

for *A. scriptus* ($\beta \pm \text{s.e.}: 0.031 \pm 0.01$; $t_{86} = 3.26$; $P = 0.0016$; Methods). The larger toepads of surviving lizards support the hypothesis that natural selection favoured individuals with greater clinging capacity, which were able to withstand high winds. The observed shifts in limb length may have a similar functional explanation. Previous work has demonstrated that more force is needed to pull long-limbed anoles off a perch¹⁸. The longer forelimbs of surviving *A. scriptus* may have been beneficial during the hurricanes for this reason. However, the parallel decrease in femur and hind toe length was contrary to our predictions.

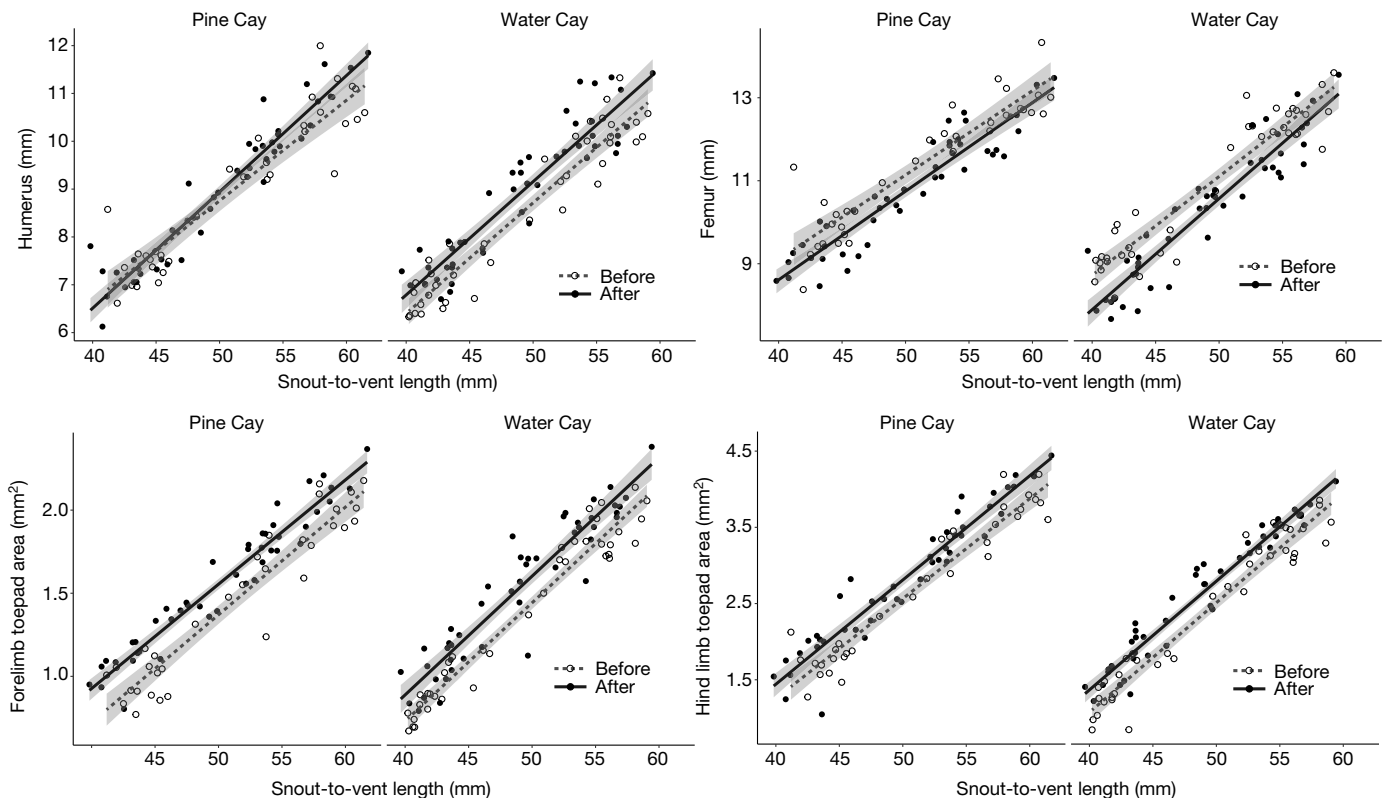


Fig. 2 | Parallel shifts in body-size-corrected humerus and femur length and surface area of the forelimb and hindlimb toepads for lizards on both Pine Cay and Water Cay. Dashed lines are the linear best fit of lizards

measured before the hurricane ($n = 71$), which are represented by open circles. Filled circles are lizards from after the hurricane ($n = 93$) with solid lines of best fit. The grey-shaded areas correspond to 95% confidence intervals.

Table 1 | Variance-standardized selection differentials

| | Pine Cay | Water Cay |
|-----------------------------|----------|-----------|
| Snout-to-vent length | −0.17 | −0.05 |
| Humerus | 0.40 | 0.8 |
| Femur | −0.67 | −0.89 |
| Hindlimb longest toe | −0.67 | −0.39 |
| Forelimb toepad | 1.18 | 1.04 |
| Hindlimb toepad | 0.88 | 1.08 |

See Methods for details. Variance-standardized selection differentials for humerus length, femur length, hindlimb longest toe length and toepad surface areas were calculated using body-size-corrected residuals.

Preliminary experimental trials (Supplementary Information) suggest one potential explanation: because of the posture *A. scriptus* adopts when exposed to high winds, longer hindlimbs could present a larger exposed surface area—which would increase the likelihood that a lizard would be blown off its perch.

Strong directional selection that favoured individuals able to hold tight during hurricane-force winds is a likely explanation for the parallel shifts in phenotype we observed. Of course, other explanations are possible: the hurricanes wrought environmental changes that affected vegetation structure, thermal microclimates and—most probably—food availability (though if lizards were starving, body condition would decrease, which on average it did not; $\beta \pm \text{s.e.}: 0.017 \pm 0.019$; $t_{161} = -0.867$; $P = 0.3874$; Supplementary Information). Although we cannot rule out these potential selective pressures, the fact that traits associated with clinging ability changed in ways that should increase survival in high winds lends credence to our hypothesis that the storms, and not their aftermath, drove these changes. Whatever the selective force was, selection must have been strong. For context, we calculated selection differentials for body size and the size-corrected morphological components that demonstrated a significant shift in their mean (Table 1), and found that they exceeded the majority of published selection differentials^{20–22} and were of comparable magnitude to the selection experienced by Darwin's finches in two famously harsh periods²³.

Evolutionary processes other than natural selection could conceivably have produced these patterns, though we consider them implausible. We cannot rule out that lizard dispersal from elsewhere—unsampled microhabitats, other parts of the islands or other islands altogether—caused the observed phenotypic shifts. However, both Pine Cay and Water Cay are small islands with homogenous vegetation structure and all available microhabitats were thoroughly sampled. The appearance of morphologically different migrants would have increased rather than decreased trait variation in the recipient populations and would have had to occur in parallel on both islands (see Methods for additional sampling descriptions). We therefore discount this alternative explanation.

Attention to the evolutionary importance of phenotypic plasticity has increased in recent years, and adaptive phenotypic plasticity is more prevalent than previously realized²⁴. We considered whether hurricane-induced phenotypic plasticity, either during the storms or as a result of post-hurricane conditions, could be responsible for the phenotypic shifts that we documented. In lizards, adult limb length can be affected by perch use during ontogeny^{25,26}, and bone shrinkage has been documented in starving marine iguanas²⁷. By contrast, plasticity in toepad size has not been reported²⁸. All of these studies, however, documented responses that occurred over long exposure periods or during ontogeny; our comparison spanned six weeks and was restricted to adults. Lastly, plastic decreases in skeletal elements have only previously been observed in response to food stress^{27,29}; if food stress were the cause here—and our body condition data suggest this was not the case—it would have decreased the length of all skeletal elements. For these reasons, we consider phenotypic plasticity to be an unlikely explanation for the observed phenotypic shifts.

The role of extreme climate events in driving evolution is of pressing interest, and although some examples due to prolonged heat, cold or drought have been documented (reviewed in Grant et al.¹¹), additional studies are needed in our era of rapidly changing and intensifying climate extremes^{7,9}. Previous studies^{9,11,30} have only alluded to the evolutionary ramifications of hurricanes. A 20-year study of a smaller lizard species, *Anolis sagrei*, on much smaller islands in the Bahamas—which are more vulnerable to hurricane-induced storm surges¹⁶ than the islands in this study—showed that after the populations were hit by hurricanes, in the next sampling period mean tibia length had increased³⁰. Whether these shifts were the result of natural selection and, if so, whether the selection had occurred during the hurricane itself or in the subsequent 8–48 months before the population was resampled remains unknown.

The long-term evolutionary consequences of these hurricanes on *A. scriptus* remain to be seen. Despite the extensive work on *Anolis* lizards, the biology of *A. scriptus* is little known. Indeed, our initial survey was conducted to gather baseline data on the natural history of the species in anticipation of a conservation project. That survey provided a serendipitous baseline from which to measure this selection event; future work is needed to determine whether the within-generational selection that we documented translates into evolutionary change across generations.

The macroevolutionary importance of infrequent but severe selective events such as these is an open question¹¹. On the one hand, if such events are rare then natural selection in intervening periods might be expected to erase the signature of infrequent bouts of extreme selection. On the other hand, if hurricanes occur frequently enough—or if the selection is strong enough—then present-day populations may bear the mark of such events, in which case selection during normal years would not be able to fully explain current phenotypic distributions. In this light, it is notable that *Anolis* species occupying Caribbean islands have substantially larger toepads relative to their body size and habitat use than do congeners on mainland Central and South America³¹. Why this difference exists has long been questioned, but our findings suggest the possibility that hurricane-induced selection, a much more common occurrence on islands than on the mainland, may be responsible for this macroevolutionary pattern.

Online content

Any Methods, including any statements of data availability and Nature Research reporting summaries, along with any additional references and Source Data files, are available in the online version of the paper at <https://doi.org/10.1038/s41586-018-0352-3>.

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Additional information

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METHODS

No statistical methods were used to predetermine sample size.

Pine Cay and Water Cay are islands in the Turks and Caicos archipelago. Pine Cay, the larger of the two, is approximately 350 ha, sparsely inhabited by approximately 20 private residences, and covered with low vegetation (1–3 m in height). Water Cay (250 ha) was a separate island until the mid-1990s, when Water and Pine Cays were connected by a sand bridge deposited by a hurricane storm surge. Although some patches of vegetation grow between the islands, the narrow sand bar probably strongly inhibits the movement of lizards between the two islands; no lizards were observed on our trips crossing it.

A. scriptus, the Turks and Caicos anole, is a small (adult SVL 40–70 mm) and largely insectivorous lizard. It is abundant on Pine and Water Cays, readily detectable and typically found perched on vegetation at or below 3 m in height³². Our initial pre-hurricane survey of the anoles of these cays for an ongoing conservation project started on 28 August 2017 and lasted until 4 September 2017. As we did not anticipate investigating hurricane-induced selection, none of the captured lizards were permanently marked. Hurricane Irma hit Turks and Caicos on 8 September 2017, followed by Hurricane Maria on 22 September 2017. Our post-hurricane visit spanned from 16 October 2017 to 20 October 2017. To sample the lizard populations, C.M.D., A.-C.F. and A.H. walked a transect approximately 2-km long on each island, catching lizards whenever sighted with a noose and pole. These transect paths were repeated by C.M.D. and A.H. in the post-hurricane revisit. In total, we caught 71 adult lizards in the initial survey and 93 during the revisit. The increased number of lizards in the second visit reflects an increase in sampling time; care was taken to sample in all of the same microhabitats before and after the hurricane.

Both Pine Cay and Water Cay are small islands with homogeneous vegetation structure; consequently, microgeographic morphological variation within each island is likely to be minimal and we attempted to survey what variation does exist within our 2-km-long transects. We therefore think it unlikely that dispersal of individuals from elsewhere on the island into our sampling area would shift the population mean. Further, if migrants were morphologically different from the initial study population, it is unlikely that migration from outside the study site would shift phenotypic distributions in the same way on both islands. Moreover, if migrants arrived from one or more phenotypically distinct populations, the result would be more likely to increase than decrease the variation within the recipient population, in contrast to our findings. This last point also applies to the possibility that lizards were blown in from another island (the closest point given the direction of storm being North Caicos Island, 7 km away), an explanation that we consider to be even less likely.

An additional consideration inextricably linked to capturing samples of animal populations is that during our pre-hurricane surveys we failed to detect morphologically distinct lizards occupying unique microhabitats (for example, tree canopies). If those lizards became more apparent after the hurricanes, they could change the sample trait means, and spuriously suggest population-wide trait shifts. This possibility seems unlikely for several reasons: we thoroughly sampled all available microhabitats along the capture transects; *A. scriptus* individuals are rarely found above 3 m³² and spend the majority of their time within 1.5 m of the ground where they are particularly easy to spot. More generally, previous studies have found no evidence to indicate that, within anole populations, individuals that use different microhabitats differ in limb or toepad characteristics^{33,34}. The proportion of individuals with extreme values for the morphological traits in the post-hurricane samples suggests that mortality was probably very high; however, because we did not estimate population size or individually mark lizards, change in population size could not be estimated.

During both surveys, A.H. measured the morphology (snout-to-vent length, and length of the humerus, radius, metacarpal, longest forelimb toe, femur, tibia, metatarsal and longest hindlimb toe³⁵) of each individual using digital calipers

(Mitutoyo 500-752). In addition, a photograph was taken of the right fore and hind feet of each lizard, unless a digit was missing—in which case the left was photographed. All photographs were captured with an iPhone 7 using a Moment Macro Lens attachment. Using ImageJ (v.1.51a., W. Rasband, National Institute of Health, Bethesda), C.M.D. measured the toepad area of the longest toe three times for each forelimb and hindlimb. The repeated measurements were highly consistent and the average was used for analyses (intraclass correlation coefficient for forelimb toepad area was 98.9% (95% confidence interval (CI): 98.6–99.2%) and for hindlimb toepad area was 99.6% (95% CI: 99.5–99.7%). C.M.D. also counted the number of lamellae on the toepad of the longest toe on the right forelimb and hindlimb.

Lizard clinging performance measurements were taken using a Vernier Dual Range Force Sensor DFS-BTA with an acetate transparency as a gripping surface¹⁷. Following standard protocols¹⁷, the right forelimb of each lizard was pulled down the surface by C.M.D. and the maximum force exerted by the forelimb toepads was recorded and analysed by A.-C.F. Methods for the wind speed behavioural study are presented in the Supplementary Information. All procedures were approved by Harvard IACUC (26-11) and all lizards were released unharmed after the experiment to their point of capture.

Analyses. All analyses were conducted in R³⁶ on adult lizards (female SVL >40 mm, male SVL >45 mm). We used a multivariate analysis of covariance to evaluate whether limb morphology varied between lizards on both islands before and after the hurricane. To do so, we log-transformed all morphometric measurements and used sex as a fixed effect and body size (SVL) as a covariate. The fixed effects of interest were island of origin (Water Cay or Pine Cay), hurricane treatment (pre-/post-) and their interaction. We did not detect a three-way interaction with sex. Following the multivariate analysis of covariance, we conducted post hoc general linear models on individual limb traits and SVL. An interaction of hurricane and island of origin was tested in the linear model and removed if the interaction was not significant. For all models, sex was included as a fixed effect. For all relative morphometric analyses (that is, comparisons taking into account differences in body size) we used SVL as a covariate. We used the 'lsmeans' and 'effects' packages in R to test for significance in the model estimates (see Supplementary Information for additional analysis details).

To calculate selection differentials, we transformed SVL as well as the body-size-corrected humerus, femur and toepad areas to have a zero mean and unit variance. The post-hurricane population means were then subtracted from the pre-hurricane population means to calculate the differential³⁷. We compared these differentials to other published studies^{20–22}, most of which, however, were calculated over longer periods. We calculated body condition as residual of a linear regression between body mass and snout-to-vent length.

Reporting summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this paper.

Data availability. All morphological and performance data collected for this study are available on Dryad, <https://doi.org/10.5061/dryad.2t41r64>.

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► Experimental design

1. Sample size

Describe how sample size was determined.

A total of 164 adult lizards (M SVL < 45 mm, F SVL < 40mm) were captured from the field as part of this study. Before the hurricanes 33 lizards were sampled from Pine Cay and 38 from Water Cay. After the hurricanes, 46 were sampled from Pine Cay and 47 were measured from Water Cay. Only the post-hurricane lizards were measured for performance capacity.

2. Data exclusions

Describe any data exclusions.

Two individuals from Pine Cay after the hurricanes (IDs 568 and 588) were excluded from analyses of toepad area because during processing it was found that a toe was missing (568) and due to a clerical mistake toe pad pictures were not captured in the field (588).

3. Replication

Describe the measures taken to verify the reproducibility of the experimental findings.

Due to the unpredictability of hurricanes, complete replication in time of this experiment was impossible. However, we have attempted to inform the generality of our findings by conducting the before-after comparison on two islands (Pine Cay and Water Cay). Furthermore, to ensure the reproducibility of our data capture the same researcher (AH) took all body and limb dimension measurements and (CD) captured all toepad area and cling force measurements. Before capturing data these trials were repeated and found to be highly consistent (as described in the methods).

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

All lizards used in this study were captured as they were seen along a random transect on each island. Their group and treatment was determined based upon the island they were captured on and whether they were caught before or after the hurricanes had hit Turks and Caicos.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

Due to the nature of the treatment - before and after the hurricanes - the researchers were not blinded to the group allocation during data collection and analysis.

Note: all in vivo studies must report how sample size was determined and whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

- n/a Confirmed
- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
 - A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
 - A statement indicating how many times each experiment was replicated
 - The statistical test(s) used and whether they are one- or two-sided
Only common tests should be described solely by name; describe more complex techniques in the Methods section.
 - A description of any assumptions or corrections, such as an adjustment for multiple comparisons
 - Test values indicating whether an effect is present
Provide confidence intervals or give results of significance tests (e.g. P values) as exact values whenever appropriate and with effect sizes noted.
 - A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
 - Clearly defined error bars in all relevant figure captions (with explicit mention of central tendency and variation)

See the web collection on [statistics for biologists](#) for further resources and guidance.

► Software

Policy information about [availability of computer code](#)

7. Software

Describe the software used to analyze the data in this study.

All analyses were conducted using R (2017) and the packages LME4 and Effects as described in the methods.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). [Nature Methods guidance for providing algorithms and software for publication](#) provides further information on this topic.

► Materials and reagents

Policy information about [availability of materials](#)

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a third party.

No restrictions

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

Not applicable

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

Not applicable

b. Describe the method of cell line authentication used.

Not applicable

c. Report whether the cell lines were tested for mycoplasma contamination.

Not applicable

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

Not applicable

► Animals and human research participants

Policy information about [studies involving animals](#); when reporting animal research, follow the [ARRIVE guidelines](#)

11. Description of research animals

Provide all relevant details on animals and/or animal-derived materials used in the study.

This experiment used wild-caught *Anolis scriptus* lizards. These lizards are ubiquitous throughout the Turks and Caicos Islands. They are relatively small (SVL 40 - 70 mm), insectivorous, and sexually dimorphic. The animals were captured with a handheld noose, measured in a controlled setting (a hotel room) and released to their point of capture. All animals used in this experiment were released unharmed.

Policy information about [studies involving human research participants](#)

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

Not applicable