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Parallel increases in grip strength in two species of *Anolis* lizards after a major hurricane on Dominica

C. M. S. Dufour[1,]* , C. M. Donihue[1,2,3], J. B. Losos[2] & A. Herrel[3]

[1] Museum of Comparative Zoology, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA
[2] Department of Biology, Washington University, St Louis, MO, USA
[3] Département 'Adaptations du vivant', UMR 7179 C.N.R.S/M.N.H.N., Paris, France

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Correspondence
Claire M. S. Dufour, Museum of Comparative Zoology. Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA.
Email: clairems.dufour@gmail.com

***Current address:** Center of Functional and Evolutionary Ecology, CNRS, University of Montpellier, IRD, EPHE, Montpellier, France

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Abstract

A recent study showed that hurricanes can act as selective agents affecting the phenotype of anole populations subjected to these extreme climatic events. Specifically, *Anolis* lizards that survived hurricanes were shown to have larger toepads than those that did not. To test whether hurricanes more generally impact populations of *Anolis* lizards, we collected data on toepad size, lamella number and grip strength for two species of *Anolis* on the island of Dominica in 2018 and compared them with data collected in 2016 before Hurricane Maria devastated the island. Our results show that populations of both species showed higher clinging forces in 2018, consistent with our predictions that lizards that are better clingers would be more likely to survive hurricanes. Unexpectedly, the increase in clinging force was not accompanied by an increase in toepad size or lamella number, suggesting that the increase in clinging strength is more likely driven by changes at the level of the setae microstructure. While the mechanism driving this pattern cannot be determined until future before/after hurricane comparisons are made, our data provide further evidence that hurricanes may be a previously overlooked driver of form and function in *Anolis* lizards.

Introduction

Extreme climate events like hurricanes, volcanoes or earthquakes have devastating effects on natural ecosystems and ecological communities (Walker *et al*., 1991; Del Moral & Grishin, 1999; Johnson & Winker, 2010; Scalley *et al*., 2010; Galassi *et al*., 2014; Fattorini *et al*., 2017). Generally, the result of such catastrophic events is substantial mortality (e.g. Willig & Camilo, 1991; Spiller, Losos & Schoener, 1998; Pavelka, McGoogan & Steffens, 2007). However, recent studies have shown that this mortality may be non-random, such that these extreme events can bring about rapid directional change in populations (Grant, 2017). For example *Anolis* lizards showed greater cold resistance associated with a shift in gene expression profiles after an extreme cold event in the southeastern United States (Campbell-Staton *et al*., 2017). A recent study further demonstrated that hurricanes can be selective agents driving the phenotype of anole populations that experience these extreme events. Specifically, *Anolis* lizards that survived hurricanes were shown to have large toepads, longer forelimbs but shorter hindlimbs than those that did not (Donihue *et al*., 2018).

Toepads are an important evolutionary innovation that evolved independently in geckoes, scincids and *Anolis* lizards (Irschick *et al*., 1996) and that allow these animals to adhere to smooth substrates. Studies have shown that, especially in Caribbean *Anolis* lizards, species that perch higher in the canopy have larger toepads, with larger toepads conferring greater clinging ability (Elstrott & Irschick, 2004). Beyond toepads, clinging also appears to be related to limb length with longer limbed *Anolis* being better clingers as it allows them to wrap their arms across perches, thus providing a better grip (Kolbe, 2015). Although the exact mechanisms remain unclear, it has been suggested that larger toepads provide an advantage to arboreal *Anolis* lizards when clinging in high winds (Donihue *et al*., 2018). If so, then survivors of extreme hurricanes are likely to show greater clinging strength and larger toepads than those that did not.

Here we test for the generality of this idea by comparing data on clinging strength and toepad morphology in two species of *Anolis* lizards (*A. oculatus* and *A. cristatellus*) from Dominica. In 2017 Dominica was hit by a category five hurricane (Maria), resulting in massive damage to the forest and agricultural areas all over the island (Fig. 1). In 2016 we had

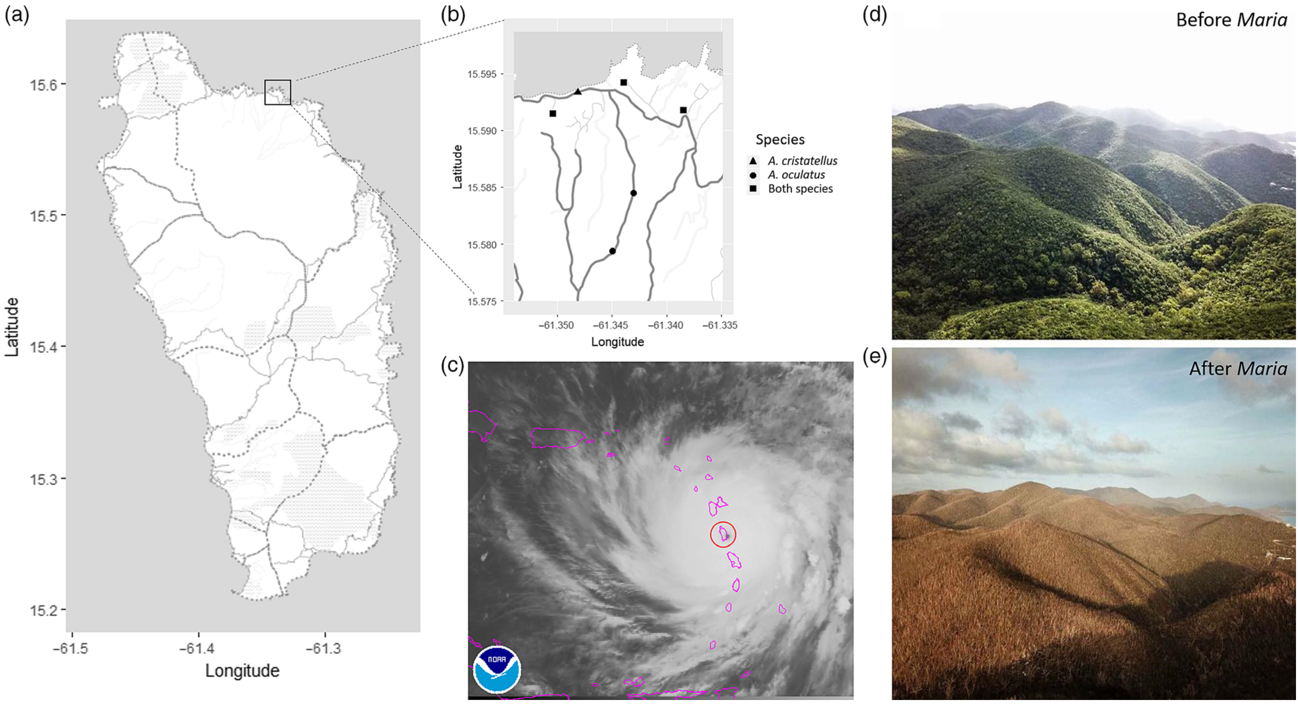

Figure 1 Location of Dominica (a) the gray and white areas represent the sea and land, map credit: Stamen Design, under a Creative Commons Attribution (CC BY 3.0) license) and zoom on the sampled sites (different shapes indicate species sampled) in Calibishie (b). On September 19, 2017 the category five Hurricane Maria hit the island of Dominica directly (red circle, c) as illustrated on the water vapor satellite map (from NOAA, www.goes.noaa.gov). The hurricane-caused massive habitat destruction as illustrated in these photos (d and e).

collected data on clinging strength and toepad size and lamella number for individuals of both species. We returned in 2018 and measured clinging strength, toepad size and lamella number in lizards that had survived the hurricane. Our predictions were that adult individuals alive after the hurricane would show greater clinging strength and larger toepads, on average, compared to individuals from populations sampled before the hurricane.

Materials and methods

Species and sites

The single native anole species on Dominica, *Anolis oculatus,* is an intermediate-sized species usually found perched on tree trunks (Dufour, Herrel & Losos, 2018). Two decades ago, an invasive anole species, *Anolis cristatellus,* appeared at the southern end of the island (Eales, Thorpe & Malhotra, 2010) and rapidly colonized the island, reaching the North-eastern region of Calibishie in 2014 (Dufour *et al*., 2018). *Anolis cristatellus*, native to Puerto Rico, is ecologically and morphologically similar to the native *A. oculatus* (Dufour *et al*., 2018). From May 1st 2016 to June 9th 2016 six sites were sampled in Calibishie. These sites were resampled during the second survey, post-hurricane, from September 9–22, 2018 (Fig. 1). Lizards were captured by noose or hand, measured and returned to the exact same spot within 10 h after capture. Because we did not anticipate the occurrence of the hurricane and, more generally, were not planning to measure survival, individuals were not permanently marked. Consequently, the survival rate (between 2016 and 2018) cannot be estimated in our study.

Toepad morphology

We took pictures of the right fore- and hind foot of each lizard (Panasonic Lumix DMC-GX8, Olympus lens 12–40 mm f/2.8 M. Zuiko EDPro focal CMOS 20.3 Mpx, 4/3, distance 20 cm). The toepad was positioned flat against a glass slide (on which a 1 cm scale was placed) to assure that all the lamellae were in contact with the surface (same observer, glass and scale for 2016 and 2018 samples). Based on these pictures, the area of the sub-digital pad of the fourth (longest and largest toe, measured and used in most morphological and functional studies) forelimb and hindlimb toe was measured with the *ImageJ* software (Rasband (1997–2018)) following the protocol of Crandell *et al*. (2014). The number of lamellae under the fourth toe was also recorded (and these are correlated with the number of lamellae of other toepads; Glossip & Losos, 1997).

Clinging performance

Clinging performance measurements were taken with a Vernier Dual Range Force Sensor DFS-BTA with an acetate transparency as a gripping surface (Crandell *et al*., 2014). The right fore-foot of the lizard was gently pressed downward on the slide and pulled across the surface by the same observer (C.MS.D) with a constant speed for one minute (average of 10 clinging force measurements per minute, Crandell *et al*., 2014). To ensure maximum clinging performance, the experiment took place right after the lizard was removed from the transport bag. The maximum force exerted was extracted using the *Logger Lite* (1.9.4) software.

Statistical analysis

Continuous morphological variables (body size – snout-to-vent length, toepad surface area) and performance traits (clinging capacity) were Log_{10}-transformed before analyses. We calculated lamella density per unit area of toepad surface by extracting the residuals of the linear regression of lamella scale counts and toepad surface area.

First, we used an analysis of variance (ANOVA) to assess differences in body size (snout-to-vent length) between the sexes and years (as factors).

Second, we used analyses of covariance (ANCOVAs) to assess the relationship between the clinging performance and the absolute toepad morphology (forelimb toepad area, number of forelimb lamellae and lamella density), with the sex and year as factors.

Then, we used ANCOVAs to assess differences in toepad morphology (toepad area, lamella number and density) and clinging performance with sex and year as factors and body size as covariate. Differences in the number of lamella scales were assessed using a Poisson distribution appropriate for count data.

Finally, we used ANCOVAs to assess the relationship between the clinging performance and the toepad morphology (forelimb toepad area, number of forelimb lamellae and lamella density), with the body size as covariate and the sex and year as factors.

For all models we initially tested interactions and removed them if they were not statistically significant (Table S1). All analyses were conducted in R 3.5.1 (R Development Core Team, 2018).

Results

Body size difference before and after the hurricane

Body size of *A. oculatus* in 2018 was significantly larger than body size of the lizards measured in 2016 (ANOVA, $P = 0.016$; Table 1, Table S2). The same pattern was observed for *A. cristatellus*, although the difference in body size was not significant between the two time periods (ANOVA, $P = 0.065$; Table 1, Table S2). Furthermore, we did not detect an interaction between sex and body size for either species between the two time points (ANOVA, *A. oculatus*, $P = 0.773$; *A. cristatellus*, $P = 0.566$).

Relationship between clinging performance and absolute toepad morphology

We then asked whether forelimb toepad morphology correlated with clinging performance for these species (Table 1, Tables S1 and S2).

We did not find a relationship in *A. oculatus* between absolute (not size-corrected) forelimb toepad area and clinging capacity (ANCOVA, $P = 0.139$; Fig. 2b) nor between forelimb lamella number and clinging capacity (ANCOVA, $P = 0.636$, Table S2). However, in *A. cristatellus* we did detect a positive

Table 1 *Anolis cristatellus* and *A. oculatus* main trait changes between before (2016) and after (2018) the populations were hit by Hurricane Maria (mean ± SE; *sample size*)

	Anolis cristatellus				*Anolis oculatus*			
	Males		Females		Males		Females	
Snout-to-vent length								
2016	60.90 ± 0.54	36	42.23 ± 0.33	29	67.86 ± 0.51	119	54.01 ± 0.39	54
2018	61.73 ± 0.57	48	43.27 ± 0.45	28	69.61 ± 0.97	38	55.74 ± 0.56	21
Max clinging force								
2016	0.11 ± 0.02	22	0.03 ± 0.01	10	0.10 ± 0.01	52	0.05 ± 0.01	13
2018	0.95 ± 0.09	43	0.35 ± 0.04	23	1.39 ± 0.16	32	0.83 ± 0.11	19
Forelimb lamella number								
2016	12.47 ± 0.12	36	9 ± 0.14	26	15.13 ± 0.1	119	12.44 ± 0.15	54
2018	12.9 ± 0.14	48	9.26 ± 0.16	27	15.5 ± 0.16	38	12.24 ± 0.19	21
Forelimb toe pad area								
2016	2.75 ± 0.08	36	0.83 ± 0.02	26	3.11 ± 0.07	116	1.59 ± 0.04	52
2018	2.71 ± 0.1	48	0.91 ± 0.02	27	3.15 ± 0.12	38	1.52 ± 0.04	21
Hind limb lamella number								
2016	21.89 ± 0.16	35	17.85 ± 0.2	27	24.4 ± 0.12	117	21.62 ± 0.18	53
2018	21.83 ± 0.19	48	18.04 ± 0.23	27	25.11 ± 0.22	38	22 ± 0.25	21
Hind limb toe pad area								
2016	6.1 ± 0.15	35	2.16 ± 0.06	27	6.46 ± 0.12	114	3.49 ± 0.06	51
2018	5.9 ± 0.16	48	2.21 ± 0.05	27	6.62 ± 0.23	38	3.6 ± 0.08	21

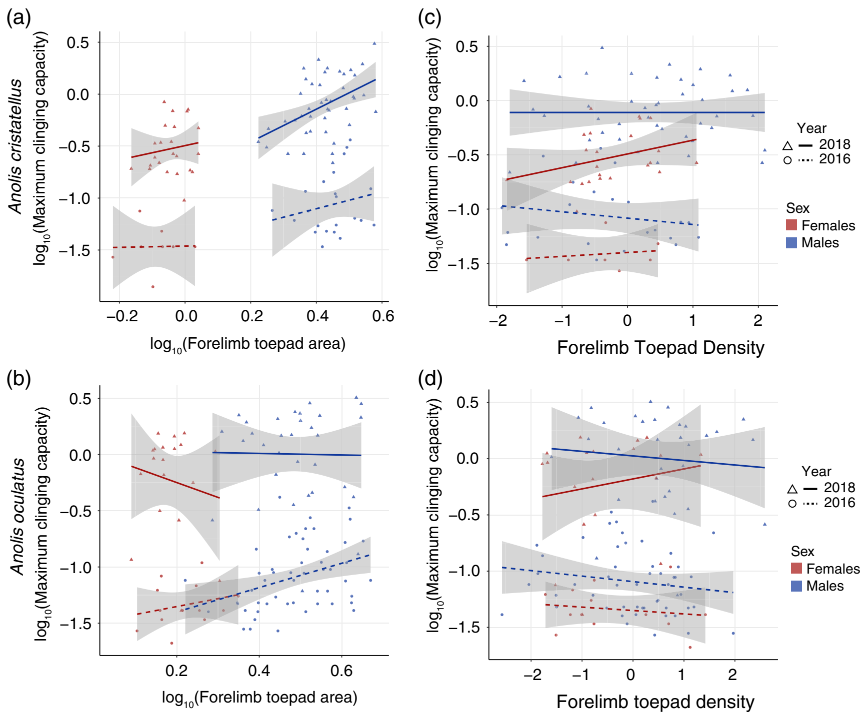

Figure 2 The relationship between forelimb toepad area and clinging capacity was generally positive for both (a) *Anolis cristatellus* and (b) *A. oculatus*, however, the slope of the relationship did not significantly vary between the 2 years. Lamella density was not a strong predictor of clinging capacity (c, d). The gray-shaded areas correspond to 95% confidence intervals.

relationship between absolute forelimb toepad area and clinging capacity (ANCOVA, $P = 0.002$; Fig. 2a), and the number of forelimb lamellae also had a significant positive relationship with clinging capacity (ANCOVA, $P = 0.009$, Table S2). The relationship between toepad area and clinging performance was parallel for both species in both years, (ANCOVA, the area-by-year interaction was non-significant: *A. oculatus*: $P = 0.243$; *A. cristatellus:* $P = 0.301$).

Furthermore, we found that in our dataset, lamella density was not a significant predictor of clinging capacity in either species (ANCOVA, *A. oculatus:* $P = 0.465$; *A. cristatellus:* $P = 0.904$; Fig. 2c,d Table S2). We also found that there was not a significant interaction in the relationship between lamella density and clinging capacity between the survey years (ANCOVA, *A. oculatus*: $P = 0.519$; *A. cristatellus:* $P = 0.327$, Table S1).

Relative clinging force and relative toepad morphology differences before and after the hurricane

In 2018, after controlling for body size, both the *A. oculatus* and *A. cristatellus* populations on Dominica exhibited significantly stronger clinging capacity than they had 2 years previously during the 2016 lizard survey (ANCOVA, *A. oculatus* $P < 0.001$; *A. cristatellus* $P < 0.001$; Fig. 3a,b, Table 1, Tables S1 and S2). This result was consistent between sexes (ANCOVA, no significant interaction between year and sex for *A. oculatus*: $P = 0.880$; and *A. cristatellus*: $P = 0.930$, Table S1).

Despite the significant increase in clinging capacity, and in contrast to our predictions, we found that the relative (i.e. body size-corrected) toepad area did not increase in both species (Table S2). The surface area of the *A. oculatus* forelimb toepads (ANCOVA, $P < 0.001$; Fig. 3d), and hindlimb toepads (ANCOVA, $P = 0.039$; Fig. 3f, Table S2) were significantly smaller in 2018 relative to 2016. We did not detect a difference in the relative number of lamellae on the *A. oculatus* forelimb toepad or hindlimb toepad (Table S2) between the time periods before and after hurricane Maria hit Dominica. The same general pattern was found in *A. cristatellus*, though relative forelimb toepad surface areas also did not differ between the survey periods (ANCOVA, forelimb toepad surface area: $P = 0.680$; Fig. 3c; hindlimb toepad area: $P = 0.004$; Fig. 3e; forelimb lamella number: $P = 0.554$; hindlimb toe lamella number: $P = 0.981$, Table S2).

Relationship between clinging performance and toepad morphology relative to body size

Anolis oculatus lizards with relatively large forelimb toepads (corrected for body size) did not cling better (ANCOVA, $P = 0.263$; Fig. S1B). In *A. cristatellus*, the positive relationship observed previously between absolute forelimb toepad area and clinging capacity was predominately explained by body size; when forelimb toepad area was corrected for body size, it was not a significant predictor of clinging capacity (ANCOVA, $P = 0.188$; Fig. S1A). Finally, there was a

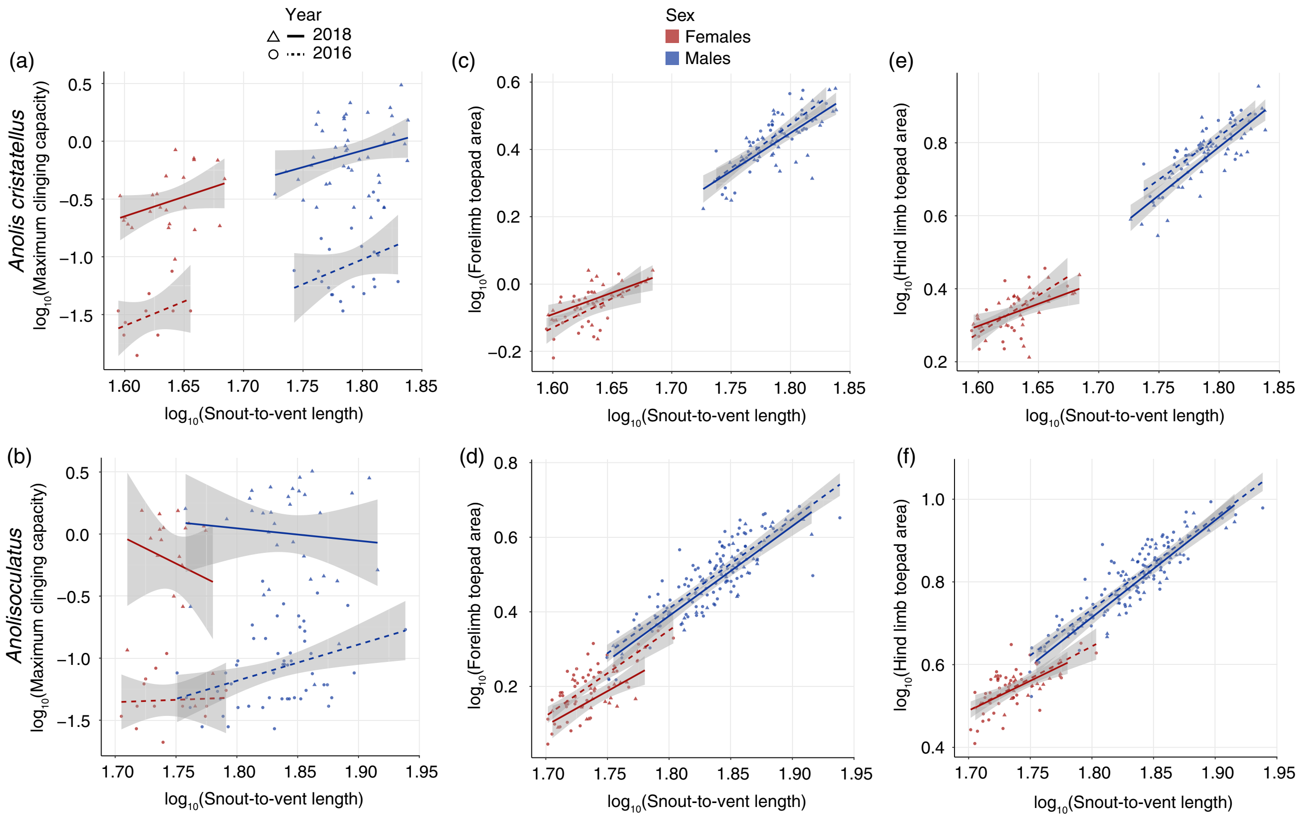

Figure 3 Significant increases in clinging capacity between survey years were detected for both (a) *Anolis cristatellus* and (b) *A. oculatus*. However, relative size of the forelimb (c, d) or hind limb (e, f) toepad did not increase. The gray-shaded areas correspond to 95% confidence intervals.

significant difference in the relative lamella density between the study years: in 2018, larger individuals from both species had relatively higher lamella densities (ANCOVA, *A. oculatus*: $P = 0.014$; *A. cristatellus:* $P = 0.002$).

As a whole, *A. oculatus* and *A. cristatellus* clinging capacity significantly increased between the 2016 and 2018 surveys; however, shifts in the number of lamella scales or toepad surface area do not explain this pattern.

Discussion

Our results show that both species of *Anolis* had higher clinging forces (absolute and relative to body size) after the passage of Hurricane Maria than they had before. Although we did not measure forces immediately before and after the hurricane, it seems most probable that the observed differences are related to the passage of Hurricane Maria. Indeed, not only are the changes in clinging force in the predicted direction (increase), but they are parallel in both species. Moreover, given that the same observer measured animals before and after, and used the same equipment, measurement error is extremely unlikely. The observed increase in clinging capacity after Hurricane Maria in *A. cristatellus* and *A. oculatus* suggests that hurricane-induced selection can act on performance traits. Whether this change occurred during the hurricane itself or in the subsequent 12 months remains unknown; nonetheless, these findings raise the question of the macroevolutionary importance of these infrequent but extreme climatic events (Grant, 2017).

Contrary to our expectations, however, we did not detect an increase in either relative forelimb or hindlimb toepad area (body size controlled) nor relative lamella number before and after the passage of Hurricane Maria that would explain this change in relative clinging force. This suggests that the changes in relative clinging force are not driven by changes in overall toepad morphology. This raises the question of what may be driving the observed changes. One possibility is that changes are cumulative across all toes and not reflected by the single toe measured here. Clinging forces are measured for the entire hand and thus represent the sum of the force generated by every single toepad. As such, small but incremental changes in the morphology of a single pad may not reflect the overall changes in force. This could also explain the relatively poor correlations between toepad characteristics and clinging force observed here (Glossip & Losos, 1997).

However, clinging force is not only dependent on the area and the number of lamellae of the sub-digital pad. Indeed, each lamella contains microscopic hair-like structures called setae (Ruibal & Ernst, 1965). Microscopic spatulae at the tips of the setae interact with the surface and produce adhesive force through van der Waals interactions (Autumn *et al.*, 2000, 2002; Autumn & Peattie, 2002). Models of van der Waals interactions suggest that the geometry of the setae and the spatulae is critical in determining the amount of frictional adhesion that can be produced (Hagey *et al*., 2014). Previous studies have demonstrated that spatula shape, setal density and setal length are all important in the production of frictional adhesion in geckos (Peattie, 2007; Hagey *et al*., 2014). Modeling studies have further suggested that longer setae may have lower stiffness and may be able to adhere at lower angles thus increasing the shear force (Hagey *et al*., 2014). Setal length is known to be variable in anoles (Crandell, Autumn & Herrel, 2010) and may thus provide a possible mechanism explaining the increase in clinging force after the passage of Hurricane Maria. Future studies investigating the microstructure of the setae in populations before and after Maria are needed to better understand the observed increase in clinging force.

Alternatively, claw morphology was recently showed to play a role in clinging performance in anoles (Yuan, Wake & Wang, 2019). In our study, claw morphology was not quantified and could not affect clinging force because the claw was not able to penetrate the acetate surface used to record clinging force. Thus, the role, if any, that hurricane-caused selection on claw length led to changes in clinging capability remains an open question.

Finally, the body size of both species increased in 2018 compared to 2016. The underlying mechanisms remain unknown, but strong directional selection that favors individuals able to hold tight during hurricane-force winds is a likely explanation for the parallel shifts in clinging performance and body size we observed. Alternatively, bigger lizards might survive better in hurricanes, independently to the clinging capability, as they would be better able to endure food shortages or other environmental changes after the hurricane.

To conclude, irrespective of the mechanism resulting in the observed increase in clinging force, our data do show that hurricanes may be important drivers of form and function in *Anolis* lizards.

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Authors' contributions

C.MS.D, A.H and J.B.L conceived the study; C.MS.D and A.H conducted fieldwork; C.MS.D and C.M.D conducted the analyses; C.MS.D, A.H, J.B.L and C.M.D wrote the manuscript.

Competing of interests

The authors declare no competing interests.

Ethical statement

This study was performed under the research permits from the Ministry of Agriculture and Fisheries, Forestry, Wildlife and Parks division of Dominica and with all the IACUC authorizations from Harvard University (26-11).

Data accessibility

The data will be available in HAL.

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Supporting Information

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

Figure S1. The correlation between the relative (body size corrected) forelimb toepad area and clinging capacity was non-significant for both (A) *Anolis cristatellus* and (B) *A. oculatus* (males in blue, females in red) in both years (circles and dashed lines in 2016; triangles and solid lines in 2018). Nonetheless, clinging performance significantly increased in 2018 as illustrated by the upward shift in intercept. The delimited areas correspond to 95% confidence intervals.
Table S1. Statistical results from the comparison of the linear models analyzing the maximum clinging performance (log transformed). The full models (models 1) considered all the variables and their interactions. The best-fitting models are highlighted in bold and were selected based on the Akaike Information Criterion (ΔAICc and weight). When $\Delta AICc<2$, the simplest model was selected. **Table S2.** Statistical results from the best-fitted linear models analyzing SVL, maximum clinging performance, forelimb and hind limb toepad area and lamella number as well as forelimb toe lamella density.

Graphical Abstract

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Extreme climate events like hurricanes, volcanoes or earthquakes have devastating effects on natural ecosystems and ecological communities. To test whether hurricanes impact populations of *Anolis* lizards, we collected data on toepad size, lamella number and grip strength for two species of *Anolis* on the island of Dominica in 2018 and compared them with data collected in 2016 before Hurricane Maria devastated the island. Our results indicate that the populations of both species showed higher clinging forces in 2018, consistent with our predictions that lizards that are better clingers would be more likely to survive hurricanes. Unexpectedly, the increase in clinging force was not accompanied by an increase in toepad size or lamella number, suggesting that the increase in clinging strength is more likely driven by changes at the level of the setae microstructure. While the mechanism driving this pattern cannot be determined until future before/after hurricane comparisons are made, our data provide further evidence that hurricanes may be a previously overlooked driver of form and function in *Anolis* lizards.