COMMENTARY

Lizards, toepads, and the ghost of hurricanes past

Raymond B. Huey[a,1] and **Peter R. Grant**[b,1]

Hurricanes wreak destruction when they strike reefs, islands, and coastal regions. Forests are scrambled into giant piles of pickup sticks. Animals are killed by flooding, falling trees, and blowing debris, and some survivors later die from starvation or disease. However, some animals survive. Were they just lucky, or did they have a trait that gave them an advantage over the others? Caribbean *Anolis* lizards that survived two hurricanes in 2017 had relatively large toepads; perhaps they were better able to hold fast to arboreal perches during storms (1) (Fig. 1). In PNAS, Donihue et al. (2) now report a follow-up study and show that offspring of 2017 survivors also had large toepads, strongly suggesting a genetically based shift. Furthermore, they evaluated whether the toepad × hurricane pattern would hold for other species of *Anolis* in the Neotropics. It does, suggesting that toepad size may serve as a morphological signature of the ghost of hurricanes past.

Like many innovative studies, this one began serendipitously (1). Back in 2017, conservation biologists were planning to remove invasive rats from two small islands in the Caribbean. Colin Donihue, Anthony Herrel, and colleagues joined the group to evaluate whether rat eradication might affect the native lizard *Anolis scriptus* on two islands in the Turks and Caicos group, Water Cay and Pine Cay. They measured toepad size and limb length, traits known to affect locomotion and clinging ability (3, 4). Just 6 d after the group finished their survey and scampered home, Hurricane Irma smashed into the islands. Two weeks later, Hurricane Maria delivered a second blow.

Chance favors the prepared mind, and Donihue and colleagues (1) returned to the islands 3 wk after Maria. They replicated their prior survey and captured some of the surviving adults. They discovered that survivors had large toepads on both front and hind feet, relative to the prehurricane populations. Survivors also had relatively long forelimb bones but shorter hind limbs. Within-generation selection was directional, strong, and in some way associated with hurricanes.

Fig. 1. A composite photograph showing *Anolis carolinensis* clinging to a perch while blasted from hurricane-force winds from a leaf blower (1). When the blower was turned on, lizards did not flee but rather moved to the lee side of the perch before progressively losing their grip (usually, hind feet first). Image credit: Colin Donihue (photographer).

By returning to the islands 13 mo later and measuring lizards in exactly the same manner as before, Donihue et al. (2) discovered that the next generation of lizards had enlarged toepads, just like the hurricane survivors (1). Despite the lack of genetic data, this is strong evidence of an abrupt evolutionary change caused by selection.

To expand their perspective, the team developed two complementary ways to explore whether short-term shifts seen in *A. scriptus* are detectable in other anole species and regions, including in some that had not experienced a hurricane for several decades. Anoles are ideal for such studies, as hundreds of species are

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[a] Department of Biology, University of Washington, Seattle, WA 98195; and [b] Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544

Author contributions: R.B.H. and P.R.G. wrote the paper.

The authors declare no competing interest.

See companion article, “Hurricane effects on Neotropical lizards span geographic and phylogenetic scales,” 10.1073/pnas.2000801117.

[1] To whom correspondence may be addressed. Email: hueyrb@uw.edu or prgrant@princeton.edu.

scattered throughout much of the Caribbean and mainland Neotropics, and many are well studied (5).

First, they surveyed toepad size in 12 populations of *Anolis sagrei*, a widely distributed Caribbean species (2). After correcting for body size and phylogenetic nonindependence, they found that relative toepad size correlated positively with the number of hurricanes (zero to four) in the last 70 y, in line with their finding with *A. scriptus*.

Next, they analyzed toepad size for 188 species of anoles (2), thus broadening the geographic and phylogenetic scope of their investigation. Again, toepad size was correlated with the number of previous hurricanes. Other potential explanatory variables were unsupported.

These sets of studies (1, 2) demonstrate an association between toepad size and hurricanes and do so not only on a local, short-term scale but also on a geographic, long-term scale. Moreover, they find that this association seems to persist over decades and across the phylogeny (2).

In Search of a Mechanism

The pattern seems clear, but the mechanism is not. The anoles on Water Cay and Pine Cay perch mainly on small branches in the lower 3 m of vegetation. Donihue et al. (1, 2) propose that larger toepads enhance clinging ability and that this is adaptive in a wind storm because individuals that lose their grip might become injured or killed when landing, or even blown out to sea. Fritillary butterflies on isolated, windy islands in the Baltic have evolved enhanced grip, perhaps for similar reasons (6). Anoles do hang on tightly when challenged by the unidirectional draft of a commercial leaf blower (Fig. 1) (7), but whether they do so in wet and windy conditions—or in turbulent gusts—is unknown.

We question whether lizards cling to perches during storms, as "behavioral avoidance, not physiological adaptations, is an organism's primary response to an environmental challenge" (8). Other lizard species are hard to find in storms, probably because they leave exposed perches and head for protected retreats well before a storm intensifies. Our expectation can be tested by anyone bold enough to watch lizards during a tropical storm or able to follow their movements via electronic tracking (9).

Nevertheless, trying to hang on could be adaptive if retreats on the ground are unavailable or are subject to storm surge from the adjacent sea. Also, Caribbean anoles sleep on exposed perches (5, 10). Perhaps the ability to hold tight is adaptive if a storm arrives at night, when searching for a protected retreat might be difficult and dangerous. Alternatively, perhaps large toepads enhance locomotion through twisted debris of posthurricane vegetation (11), which might persist for years. The authors (2) discount this vegetation–structure hypothesis and favor the clinging one. They note that anole species with large toepads typically use high perches but that vegetation in hurricane-prone areas tends to be short (2). Thus, if selection on toepad size is driven by vegetation structure, then small toepads would be expected in high hurricane regions, but the opposite was found (2). Additionally, even though toepad size was relatively unchanged in two other *Anolis* species after a hurricane hit Dominica, clinging strength increased substantially (7), suggesting that clinging (whether by toepads or other mechanisms) is adaptive.

The clinging hypothesis ultimately needs biomechanical measurements to quantify the functional impact of larger toepads and limb-length shifts. Such studies should use perches with different diameters and roughness (12), dry and wet surfaces (13), and turbulent winds. Functional interactions between toepads and claws need to be addressed (2, 14).

Why toepad size seemingly remains "frozen" for decades after a hurricane is surprising and unresolved. Stasis could suggest that selection is related as much to sustained successional shifts in the vegetation as to hurricanes themselves. Otherwise, if small size was adaptive prior to the storm, why would small size not be favored again after the hurricane? Given that years or even decades may elapse between hurricanes, there is plenty of time for a reversal. However, toepad size apparently increases with each successive hurricane (2), reminiscent of a selective ratchet. Might winds of frequent subhurricane storms periodically reinforce selection for large toepad size? In any case, repeated measurements of lizards on Water Cay and Pine Cay over the next few years could show whether relatively large toepads are maintained or not and exactly if and where an adaptive advantage lies.

Elucidating the forces underlying the shift and subsequent stasis in toepads and limb length will be challenging because selective factors affecting these lizards will change over time. Initially, a hurricane is an acute "pulse" event (15), but over time it will morph into a "press" event because hurricanes disrupt vegetation structure (16) and community composition (17) for long periods. Those press changes will determine the selective matrix on other traits, as well as those altered by the hurricane itself.

Overall, Donihue et al. (2) have uncovered a surprising pattern—one that might even provide a reflection of past extreme events. Such events are often lost to the "invisible part of history" (16, 18) and are revealed only by careful detective work. In this and all such studies, only certain aspects are neat and clean. Still missing here are behavioral observations and biomechanical tests. Also needed is a complementary genetic study to estimate trait heritabilities, which enable evolution, and genetic covariances that potentially constrain it. However, as Donihue et al. (2) note, such unresolved issues can stimulate future studies that might help elucidate the generality and functional significance of hurricane-associated shifts in toepad and leg morphology.

Taking Advantage of Extreme Events

Hurricane and extreme events—natural or anthropogenic—perturb communities but can foster insights and surprises into ecological and evolutionary dynamics (19). With several colleagues, we (20) recently asked "how can we be prepared to take advantage of opportunities arising unpredictably in the future to learn about evolution caused by extreme events?" We suggested that the most informative prospects are long-term field studies that serendipitously bracket events. Of course, these "right place at the right time" examples will always be rare (2, 21–23). Inevitably, most studies of extreme events will be retrospective: they can document the aftermath but must infer the prior. Nevertheless, such studies often illustrate impacts of extreme events, although their ability to elucidate causality can be restricted (24, 25).

The challenge is how to obtain baseline data before pulse events occur. For certain extreme events (hurricanes, cold fronts, heat waves, fires), models can forecast those events days or even weeks in advance. Advance warning provides opportunities to establish quick baselines of "before" conditions. For example, if teams were assembled and organized well before specific hurricanes, they could be deployed to potential targets a few days ahead of the storm. They could quickly gather critical samples (morphology, tissues for genetics) from focal species, possibly even mark individuals for capture–recapture studies, and retreat. They could later return, gather poststorm samples, assess ecological damage, and estimate mortality and selective changes. Any site that was not hit (or hit hard) could serve as a control. A similar "call to action" has recently been proposed (26).

To our knowledge, no federal granting agency allocates funding for anticipatory planning for extreme events. However, in a world with increasing frequencies of storms, habitat destruction, pollution, and epidemics, an understanding of the impacts of such extreme events on freshwater, marine, and terrestrial environments and organisms will be enhanced if skilled teams are already in position to take advantage of impending events. The study by Donihue et al. (1, 2) brings this critical issue into sharp focus.

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