Received: 11 March 2022 | Accepted: 20 December 2022

DOI: 10.1111/1365-2435.14260

Functional Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Blowing in the wind: Experimental assessment of clinging performance and behaviour in *Anolis* lizards during hurricane-force winds

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Funding information
National Science Foundation, Grant/Award Number: IOS-1806420; University of Rhode Island

Handling Editor: Anthony Herrel

Abstract

1. Extreme weather events, such as hurricanes, can be ecologically devastating and cause widespread mortality. Recent studies in *Anolis* lizards report hurricane-induced phenotypic shifts and selection favouring morphological variation related to clinging performance. Although it is difficult to observe organismal responses during extreme events in nature, we can experimentally simulate the high-speed winds associated with hurricanes to evaluate the putative mechanism underlying observed patterns of natural selection.
2. In this study, we used two laboratory experiments to better understand the clinging performance and behaviour of *Anolis* lizards when experiencing hurricane-force winds. We assessed the physical ability of lizards when using the combined function of their claws, limbs, toepads and other traits to resist forces pulling them off a perch. We also evaluated the combination of this physical clinging ability of lizards and their behavioural responses to avoid being blown off a perch during high winds. We assessed behaviour that could decrease exposure of lizards to wind and increase their clinging ability.
3. Clinging force measurements revealed variation in performance among species and substrates not reflected in clinging times for lizards experiencing hurricane-force winds, revealing the importance of behaviour when experiencing high winds. The most arboreal species (*A. carolinensis*) had substantially longer clinging times on rough substrates compared with the other species, presumably due to its larger toepads for increased clinging as well as its shorter limbs that reduced drag.
4. Under high-speed winds, lizards commonly shifted to the more protected leeward side of dowels, especially on broad and rough substrates, presumably to reduce exposure. This reveals how behaviour can mediate factors influencing clinging ability during hurricanes and, in conjunction with ecologically relevant variation in morphology and substrate properties, contribute to clinging performance.
5. Our experiments reveal that behaviour strongly influences clinging performance during high winds beyond that predicted by physical traits alone. Thus, micro-habitat selection of perches and the position of a lizard on its perch during a

hurricane will likely have important consequences for clinging performance. This may alter how selection acts on morphological traits and influence the susceptibility of different species to these extreme weather events.

KEYWORDS
extreme weather events, hurricanes, microhabitat use and selection, substrate diameter, surface roughness

1 | INTRODUCTION

Increases in the intensity and frequency of extreme weather events are among the numerous effects of recent human-mediated climate change (Bhatia et al., 2019; Holland & Bruyère, 2013; Kossin et al., 2020; Trenberth, 2005). Past studies have revealed the devastating ecological consequences of extreme weather (e.g. Kemp et al., 2011; Spiller et al., 1998) and recent work has documented examples of evolution resulting from such events (e.g. cold snaps: Campbell-Staton et al., 2017; fires: Forsman et al., 2011; hurricanes: Donihue et al., 2018; see review by Grant et al., 2016). Because severe weather events are predicted to increase in frequency and magnitude in the coming decades (Sobel et al., 2016; Trenberth, 2005), understanding the functional responses of organisms to extreme weather is critical for predicting ecological and evolutionary dynamics, and ultimately, whether populations will persist under changing climatic conditions. One major factor limiting our ability to better understand organismal responses to extreme weather is the lack of opportunity for direct observation of organisms during these events. The response, performance and behaviour of organisms when faced with extreme weather is largely a mystery (but see Boucek et al., 2017; Strickland et al., 2019).

Hurricanes are one type of extreme weather that has increased in frequency and magnitude in recent decades (Sobel et al., 2016; Trenberth, 2005). For *Anolis* lizards (or anoles), we know hurricanes cause mortality based on studies documenting extirpation of Bahamian island populations after storms (Schoener et al., 2001; Spiller et al., 1998). Other studies show selective mortality based on morphological trait variation; for example, using comparisons of pre- and post-hurricane populations, Donihue et al. (2018) found that natural selection favoured lizards with larger toepads and longer forelimbs, trait values that enhance clinging ability in anoles (Elstrott & Irschick, 2004; Kolbe, 2015), as well as shorter hindlimbs that reduce aerodynamic drag and improve the clinging ability of lizards (Debaere et al., 2021). Several other studies have reported changes in performance, behaviour and morphology of anole populations after hurricanes (Aviles-Rodriguez et al., 2021; Dufour et al., 2019; Fokidis & Brock, 2020; Rabe et al., 2020). The limb and toepad morphology of lizards surviving hurricanes is mostly consistent with survivors having greater clinging performance (Debaere et al., 2021; Elstrott & Irschick, 2004, but see Aviles-Rodriguez et al., 2021), pointing to the likely functional relationship underlying the observed selection. The ability of lizards to cling to vegetation or rocks without being blown off by high winds or swept away by the storm surge is likely to be important for survival.

Past studies show how some aspects of morphological trait variation should influence clinging ability during a hurricane. Larger toepads (i.e. more subdigital lamellae and larger areas) produce greater adhesive force on smooth surfaces, such as leaves (Donihue et al., 2018; Elstrott & Irschick, 2004; Irschick et al., 1996), and arboreal anoles tend to have larger toepads and more lamellae (Glossip & Losos, 1997; Losos, 2009). Claws generate force when they interlock with rough surfaces. Evidence shows that higher claws increase clinging performance in New World lizards (Zani, 2000) and more arboreal anoles have higher and longer claws (Crandell et al., 2014). Limb-length variation both within and among anole species influences clinging performance; greater clinging force is associated with narrower perches and longer limbs when lizards are on cylindrical substrates (Kolbe, 2015). In contrast, longer limbs that extend further out away from the body of a lizard may result in increased drag under high winds, increasing the chance of being blown off a perch (Debaere et al., 2021; Donihue et al., 2018). Thus, variation in morphology and microhabitat use (e.g. the texture and diameter of substrates) clearly affects clinging performance, which should be relevant when lizards experience hurricane-force winds (>119 kph). What remains to be clarified is whether longer limbs are overall beneficial or detrimental to clinging performance and the context in which a functional tradeoff might exist. Moreover, whether other factors such as behaviour modify how morphology and substrate variation combine to influence the clinging performance of lizards is little known.

Lizards may be able to attenuate exposure to high winds or avoid substrates that result in poor performance through their behaviour. For example, white-tailed deer in southwestern Florida selected upland forests and avoided marshes during Hurricane Irma in 2017, likely mitigating the negative effects of the storm (Abernathy et al., 2019). Microhabitat selection is known in *Anolis* lizards; a study found that species with high variation in sprint speed on different substrates avoided using perches in nature on which their sprinting ability would be impaired ("habitat constraint hypothesis" from Irschick & Losos, 1999; also see Gilman & Irschick, 2013). Moreover, experiments reveal that some *Anolis* species prefer substrate diameters and textures that would enhance locomotor performance (Kolbe et al., 2021). Anoles are likely capable of adjusting their behaviour in ways that maximize clinging performance, but whether they reduce their exposure or susceptibility to high winds through behaviour needs to be investigated. Behavioural adjustments and modifications in microhabitat use could be the difference between surviving or perishing during an extreme weather event. Experiments provide one way to evaluate factors influencing clinging performance and behaviour relevant for selective mortality during hurricanes.

In this study, we conducted two laboratory experiments to assess the importance of factors that should influence the clinging performance of *Anolis* lizards during hurricanes. First, we measured the force needed to pull lizards from artificial perches. For these trials, we predicted lizards would show greater clinging force on narrow substrates that allow lizards to grasp farther around dowels and on rough substrates because their claws would better interlock with deviations in the surface texture. Furthermore, we predicted more arboreal species would have greater clinging ability (Losos, 2009). Second, we measured the time until lizards lost their grip from perches when experiencing simulated hurricane-force winds. In terms of substrate diameter, narrower diameters allow lizards to interlock their limbs around substrates, generating greater clinging force (Kolbe, 2015). However, depending on behaviour and posture of lizards, portions of their body and limbs exposed to wind on narrow substrates will increase drag, decreasing clinging ability (Debaere et al., 2021). On the other hand, broader diameter substrates likely obstruct the wind, which could buffer lizards from the brunt of the wind force. If the clinging ability of lizards during hurricanes is based primarily on their physical attributes (i.e. morphological variation), then clinging force values on the different substrates should predict clinging time under ecologically realistic wind speeds.

Some previous studies of *Anolis* lizards show how morphological and substrate variation influence clinging ability and how selection favours some morphological traits during hurricanes, but behavioural responses to high winds have not been previously evaluated. We explored behavioural responses to hurricane-force winds with the general prediction that lizards would behave in ways that decrease exposure to the wind and increase their clinging time. Do lizards behave in ways that make them more or less likely to maintain their grip on a substrate? Are behavioural responses context-dependent, varying with the substrate or differing among species? Because of the difficulty observing lizards during hurricanes in nature, our experiments provide an opportunity to enhance our understanding of how lizards may respond to the extreme conditions experienced during these events.

2 | MATERIALS AND METHODS

2.1 | Study system

Anolis lizards are an excellent system for studying clinging ability and how it relates to performance when lizards experience the high-speed winds associated with hurricanes. Nearly 400 species of anoles are found throughout the Neotropics; populations of anoles in coastal areas and on Caribbean islands are particularly susceptible to the multiple hurricanes occurring annually in the North Atlantic (Donihue et al., 2020). We studied three *Anolis* species that vary in their habitat use and morphology, which we predict will result in clinging performance differences. The following descriptions of species are based on Losos (2009). *Anolis carolinensis* is primarily arboreal, perching as high as the canopy and using trunks, branches, twigs and leaves. This species has the shortest limbs of the three species, but the largest toepads. *Anolis distichus* is a mostly arboreal species, perching primarily on tree trunks, and has intermediately sized limbs and toepads. Lastly, *A. sagrei* is a semi-terrestrial species, perching low on trunks and branches and often descending to the ground. This species has relatively long limbs and smaller toepads.

2.2 | Collecting and housing lizards

We acquired 20 *A. carolinensis*, 13 *A. distichus* and 18 *A. sagrei* in August 2020. The *A. carolinensis* were purchased from a local pet store in Rhode Island, and the *A. distichus* and *A. sagrei* were collected in South Miami, Florida and shipped overnight to the University of Rhode Island. All lizards were adult males and were housed individually in 40 cm (long) × 24 cm (wide) × 32 cm (high) terraria in the laboratory where all experiments were performed. We provided UV light above each cage on a light:dark cycle that reflected natural conditions in South Miami. Room temperature was maintained at 27 ± 1°C with cage temperatures being several degrees warmer due to heat from the UV light fixtures. Humidity was maintained at a minimum of 40% in the lizard room and lizard cages were misted with water twice per day to maintain higher humidity in cages. Room conditions were monitored and recorded daily, and lizards were fed three adult crickets every 3 days. Protocols for use of lizards were approved by the Institutional Animal Care and Use Committee at the University of Rhode Island (AN11-09-005).

2.3 | Morphology

Prior to the start of experimental trials, we assessed the body size of each lizard by measuring its snout-vent length (SVL) in mm and mass in grams. The SVL was recorded by measuring a lizard's length from the tip of its snout to its cloaca. At the end of the experiments, we measured forelimb and hindlimb length, each from the insertion of the limb into the body wall to the tip of the claw on the longest toe. We measured the tail length from the cloaca to the tip of the tail. Some tails showed partial regeneration. All tail measurements were included in the analyses. SVL, limb length and tail length were measured using a ruler. We also counted the number of sub-digital lamellae on the third toe of the forelimb and the fourth toe of the hindlimb using a dissecting microscope.

2.4 | Clinging-force trials

We measured the horizontal force necessary to pull a lizard off a vertically positioned dowel. Lizards were fitted with a harness made of plastic non-adhesive tape around their midsection located halfway between their fore- and hindlimbs. Substrates used during the clinging-force trials were 12-mm and 33-mm diameter dowels with both smooth and rough textures. We used these substrates to mimic the natural substrates that anoles use in the wild (Irschick & Losos, 1999; Losos & Irschick, 1996; Losos & Sinervo, 1989) but at the same time provide a uniform substrate for each lizard. Smooth dowels were made of plain, sanded wood and rough dowels were created by gluing window screen around the dowels. Harnessed lizards were placed on a dowel such that their limbs wrapped around the dowel and their toes were fully gripping the substrate. A digital force gauge (Extech Model 475040) was attached to the midpoint of the harness, and the gauge and lizard were pulled at a slow, constant speed in a perpendicular position away from the dowel until the lizard lost contact with the substrate. Each lizard was tested at least three times on each of the four substrates to determine the maximum force in Newtons (N) required to pull the lizard off the dowel. The highest force measurement for each dowel type was recorded using the peak force setting and this value was used in subsequent analyses. Lizards were allowed to rest for at least 1 h in between trials on different substrates.

2.5 | Clinging-time trials

To determine how lizards respond to hurricane-force winds, we used a Toro Leaf Blower (51619: Ultra Blower) to produce wind speeds up to 195 kph (or 121 mph, a Category 3 hurricane). We evaluated lizard clinging time and behaviour using the same four substrates as in the previously described clinging-force trials. All experiments were recorded using a slow-motion Casio digital camera (EX-ZR1000) at 120 frames-per-second, and windspeed in kph was measured using an Inspeed pole-mounted anemometer.

Vertical dowels were placed directly in front of and 30 cm from the opening of the leaf blower. This produced the strongest cone of wind hitting the dowel. On the opposite side of the dowel, we hung a cloth sheet to provide a safe landing spot to ensure lizards were unharmed after being blown off the dowel. No lizards were harmed during this experiment. Each lizard was placed on the dowel head up, all 4 feet in contact with the dowel, and orthogonal to the flow of wind, creating direct exposure to the wind on the lizard's lateral (right) side at the start of the trial. The camera view captured the dorsal view of the lizard at the start of the trial (i.e. the camera view was rotated 90° from the position of the leaf blower).

The leaf blower was turned on and immediately set to approximately 75 kph. Over a 10-s interval, the windspeed of the leaf blower was steadily increased until reaching 195 kph (a Category 3 hurricane), the maximum windspeed produced by the leaf blower. The cone of wind created by the leaf blower encompassed the entirety of the experimental perch. Clinging time was recorded as the total duration of time (in seconds) for which the lizard was able to hold on to the perch. The maximum time allotted for each trial was 780 s (i.e. 13 min).

We assessed the quality of each trial to determine if individual lizards appeared to perform maximally when clinging to the dowel (Losos et al., 2002). Each lizard experienced one trial per dowel unless there was evidence of submaximal performance. Trials were considered unacceptable if the lizard being tested jumped off the perch at any point during the trial. We tested lizards up to three times to get an acceptable trial. Once the leaf blower was turned on, most lizards quickly pivoted to the leeward side of the dowel, grasping it with their forelimbs tucked close to their bodies and their feet on the perch so that their hindlimbs jutted out to either side (see Donihue et al., 2018).

Based on our observations of lizard behaviour in response to high winds, we scored several aspects and timing of lizard movement from the videos. We assessed whether the forelimbs or hindlimbs of lizards extended out past the edges of the dowel at the start of trials. This limb positioning may provide some insight into whether the combination of lizard body size, limb length and dowel diameter can shield lizards from the wind. Unfortunately, we were unable to assess limb position when lizards were on the leeward side of the dowel because of the single camera position. We recorded whether, and if so when, lizards actively shifted from the start position to the leeward side of the dowel after the wind started and how long it took lizards to do this. If lizards lost their grip during a trial, we noted whether their forelimbs or hindlimbs detached first or both limbs simultaneously. We also scored the position of lizards at the end of each trial, varying from the start position to the leeward side of the dowel, regardless of whether lizards actively shifted or slid around the dowel under the force of the wind. We tested for differences in movement and timing among species and substrates.

2.6 | Statistical analyses

We tested for morphological differences among species using analysis of variance (ANOVA) for log SVL and analysis of covariance models (ANCOVA) for mass, limb length, tail length and number of toepad lamellae, including log SVL as a covariate. In cases where the species by log SVL interaction was non-significant, we removed it from the final model. We used Tukey's honestly significant difference (HSD) *post-hoc* tests to evaluate differences among the three species when a factor was significant.

To compare clinging force among species on the four substrates, we used a generalized linear mixed model with a Gamma distribution because the response variable was right-skewed. Lizard identity was a random effect to avoid pseudoreplication associated with multiple trials per lizard. Fixed effects were species (*A. carolinensis*, *A. distichus* and *A. sagrei*), diameter (12 and 33 mm), texture (smooth and rough), all interactions among these factors and log mass. A general linear mixed model using the same fixed and random effects was used to test clinging time differences among species and substrates when experiencing hurricane-force winds. We log-transformed clinging time to improve normality for this model. For categorical behavioural responses (i.e. whether a lizard shifted its position and which limbs detached first), we used likelihood ratio tests to evaluate associations with species and substrates. For the continuous behavioural responses of time until a lizard shifted position and the time it took to shift, we used non-parametric Kruskal–Wallis (KW) tests to assess differences among species and substrates. Sample sizes varied among analyses due to the failure of some individuals to perform on one or more substrates. Although our sample sizes were suitable for estimating mean values for species, we refrained from intraspecifc analyses for which our samples sizes were too small. All analyses were conducted in JMP 15 (JMP, 2021).

3 | RESULTS

3.1 | Morphology

Variation in body size, relative limb length, tail length and toepad lamella counts for the lizards in this study were consistent with expectations for these species (Tables 1 and 2; Losos, 2009). *Anolis carolinensis* was the longest and *A. distichus* the shortest in SVL, and both *A. distichus* and *A. sagrei* were relatively more massive than *A. carolinensis* for a given SVL. *Anolis sagrei* had the longest limbs relative to body size, whereas *A. carolinensis* had the shortest. Both *A. carolinensis* and *A. sagrei* had longer tails than *A. distichus*. In terms of toepads, *A. carolinensis* had the most lamellae and *A. sagrei* the fewest.

3.2 | Clinging force trials

When comparing the force required to pull lizards from different substrate types, greater force was required to remove lizards from both narrow and rough dowels compared with broad and smooth dowels, respectively (Table 3; Figure 1a). Surface texture resulted in a greater difference in clinging force than dowel diameter. The combination of narrow diameter and rough texture resulted in the greatest clinging performance for all three species, whereas the broad diameter and smooth texture together had the worst clinging performance. Across all dowel types, *A. carolinensis* had greater clinging ability than *A. distichus* or *A. sagrei*.

3.3 | Clinging time during hurricane-force winds

We measured the time lizards spent clinging to the dowel before losing their grip while experiencing hurricane-force winds. All lizards on the two smooth dowels performed poorly (Table 4; Figure 1b), losing their grip after an average of only 21 s. Lizards on the rough dowels performed substantially better, lasting an order of magnitude longer on average (mean = 231 s). However, this result was driven by the much better clinging performance of *A. carolinensis* on these rough dowels compared with the other two species (Figure 1b). Whereas *A. distichus* and *A. sagrei* tended toward greater clinging time on the rough substrates, *A. carolinensis* clinging times were substantially longer on the rough substrates—about four times longer on the 12 mm-rough dowel and six times longer on the 33 mm-rough dowel compared with clinging times on the smooth substrates. For trials on the two rough dowels, lizards in almost 10% of trials maintained their grip for the entire 13 min. All were *A. carolinensis* except for one *A. distichus*; 15 of these lizards were on the 33 mm-rough dowel and two were on the 12 mm-rough dowel.

3.4 | Behaviour during hurricane-force winds

Limb position at the start of trials differed markedly by dowel diameter with the forelimbs (X^2 = 142.42, df = 3, $p<0.0001$) and hindlimbs (X^2 = 159.00, df = 3, $p<0.0001$) of most lizards extending out past the 12-mm dowels but not the 33-mm ones (Figure 2). Given these differences in limb position between the two dowel diameters, we tested for species differences for each dowel diameter separately. Lizard forelimbs never extended out past the edges of the 33-mm dowels for any species, but the hindlimbs of *A. sagrei* jutted out significantly more often than the other two species on this broader substrate (20% vs. 2%, X^2 = 8.03, df = 2, p = 0.018). On the 12-mm dowels, lizard hindlimbs always extended out past the edges regardless of the species, but *A. carolinensis* forelimbs jutted out significantly less often compared with the other two species (68% vs. 96%, X^2 = 8.36, df = 2, p = 0.015). These results are consistent with *A. sagrei* having relatively longer limbs and *A. carolinensis* relatively shorter limbs (Table 1).

TABLE 1 Sample sizes and means ± SD for morphological measurements of the three *Anolis* species. Relative forelimb and hindlimb length are body size-adjusted residuals from regressions of log forelimb or log hindlimb on log snout-vent length (SVL). Tail length did not scale with body size for any of the species. Lamellae on the third toe of the forefoot and fourth toe of the hindfoot are counts

Species	*N*	SVL (mm)	Mass (g)	Relative forelimb length	Relative hindlimb length	Tail length (mm)	Toepad lamellae forefoot	Toepad lamellae hindfoot
A. carolinensis	20	60.5 ± 3.0	4.6 ± 0.7	−0.019 ± 0.018	−0.024 ± 0.017	109.3 ± 16.1	19.0 ± 1.4	24.4 ± 1.5
A. distichus	13	48.9 ± 1.9	3.0 ± 0.3	0.004 ± 0.014	−0.020 ± 0.018	58.1 ± 12.0	14.3 ± 0.9	17.5 ± 0.9
A. sagrei	18	54.2 ± 4.4	4.4 ± 1.2	0.017 ± 0.033	0.040 ± 0.025	87.6 ± 22.0	12.7 ± 1.1	18.5 ± 1.4

Response variable	F	df	p	R^2	Tukey's HSD
SVL	46.3	2, 50	**<0.0001**	0.65	Ac > As > Ad
Mass	17.4	2, 48	**<0.0001**	0.83	Ad = As > Ac
SVL	112.1	1, 48	**<0.0001**		
Forelimb length	33.1	2, 46	**<0.0001**	0.62	Ad = As > Ac
SVL	53.1	1, 46	**<0.0001**		
Hindlimb length	66.9	2, 46	**<0.0001**	0.78	As > Ad > Ac
SVL	33.8	1, 46	**<0.0001**		
Tail length	11.0	2,46	**<0.0001**	0.57	Ac = As > Ad
SVL	0.9	1,46	0.3401		
Toepad lamellae forefoot	88.2	2, 49	**<0.0001**	0.86	Ac > Ad > As
SVL	0.2	1, 49	0.6766		
Toepad lamellae hindfoot	52.3	2, 49	**<0.0001**	0.86	Ac > Ad = As
SVL	3.2	1, 49	0.0786		

TABLE 2 Results from the ANOVA for differences in snout-vent length (SVL) among species and the ANCOVAs for differences in mass, forelimb length, hindlimb length, tail length and number of forefoot and hindfoot toepad lamellae among species with SVL as a covariate. All continuous variables were log-transformed prior to analysis. All interactions between species and SVL were non-significant in ANCOVAs and, therefore, removed from the final models. Significant *p*-values are in bold. Tukey's HSD results show significant differences among species at the $p < 0.05$ level. Abbreviations are as follows: Ac = *A. carolinensis*, Ad = *A. distichus* and As = *A. sagrei*

TABLE 3 Results from a generalized linear mixed model testing for clinging force differences with fixed effects of species, diameter, texture, all interactions and log mass. The random effect of lizard identity explained 7.4% of variation. Significant *p*-values are in bold

Factor	F	df	p
Species	3.3	2, 168	**0.0386**
Diameter	244.1	1, 140	**<0.0001**
Texture	364.4	1, 140	**<0.0001**
Species by diameter	4.4	2, 140	**0.0147**
Species by texture	5.8	2, 140	**0.0037**
Diameter by texture	226.5	1, 140	**<0.0001**
Species by diameter by texture	4.3	2, 140	**0.0149**
Log mass	33.9	1, 46	**<0.0001**

Whether a lizard shifted its position at the start of a trial did not differ among species ($X^2 = 3.16$, df = 2, $p = 0.206$), but did depend on the substrate ($X^2 = 21.93$, df = 3, $p < 0.0001$). On the 12-mm-smooth substrate, lizards in only 13% of trials actively shifted their position after the wind started. In contrast, on the other three substrates, lizards actively shifted their position to the leeward side of the dowel 50%–58% of the time. Lizards that actively shifted their position (43% of lizards in total) did so quickly (1.3 ± 1.1 s, mean ± SD, range 0.2–6.2 s) and there was no difference among the three species (KW test: $X^2 = 1.27$, df = 2, $p = 0.531$). On the 33-mm-rough substrate, lizards took over twice as long to initiate movement (mean = 2.4 s) than when on any other substrate (means = 0.91–0.96 s; KW test: $X^2 = 19.65$, df = 3, $p = 0.0002$). The percentage of lizards that successfully shifted or slid to the leeward side of the dowel did not vary among species. Nearly all lizards made it to the leeward side of the 33 mm-rough dowel, half did so on the 33 mm-smooth and 12 mm-rough dowels, and few lizards managed this on the 12 mm-smooth dowel. *Anolis carolinensis* (mean = 6.3 s) moved to the leeward side of the 33 mm-rough dowel over three times faster than *A. distichus* (mean = 21.1 s) and *A. sagrei* (mean = 22.0 s), but this difference was not significant (KW test: $X^2 = 2.16$, df = 2, $p = 0.339$). Sample sizes were too small to test for differences among species on the other dowels.

For lizards that lost their grip before the end of the trial, whether their forelimbs or hindlimbs detached first, or both limbs at the same time, depended on the substrate ($X^2 = 32.91$, df = 6, $p < 0.0001$), but did not differ among species ($X^2 = 6.99$, df = 4, $p = 0.137$). On smooth dowels, the hindlimbs of most lizards (54%) detached first, whereas on rough dowels most lizards (74%) had their forelimbs detach first. Dowel diameter did not have a substantial effect on limb detachment. By the time lizards lost their grip or made it to the end of the trial, most lizards (88%) had shifted or otherwise moved to the leeward side of the dowel. Lizards not quickly shifting to the leeward side eventually rotated the 90° from the start position to the leeward side without their limbs losing contact with the substrate. These lizards appeared to slide around the dowel under the force of the wind. Lizards ended trials on the leeward side significantly less often when on the 33-mm-smooth substrate (68%), remaining in the start position or rotating only partially to the leeward side, compared with the three other substrates where lizards ended on the leeward side 88%–100% of the time ($X^2 = 28.95$, df = 3, $p < 0.0001$).

4 | DISCUSSION

Our experimental assessments of clinging ability in three species of *Anolis* lizards revealed several key findings. Although clinging performance differed consistently among species in the clinging-force trials with *A. carolinensis* performing best, and lizards on narrow and rough

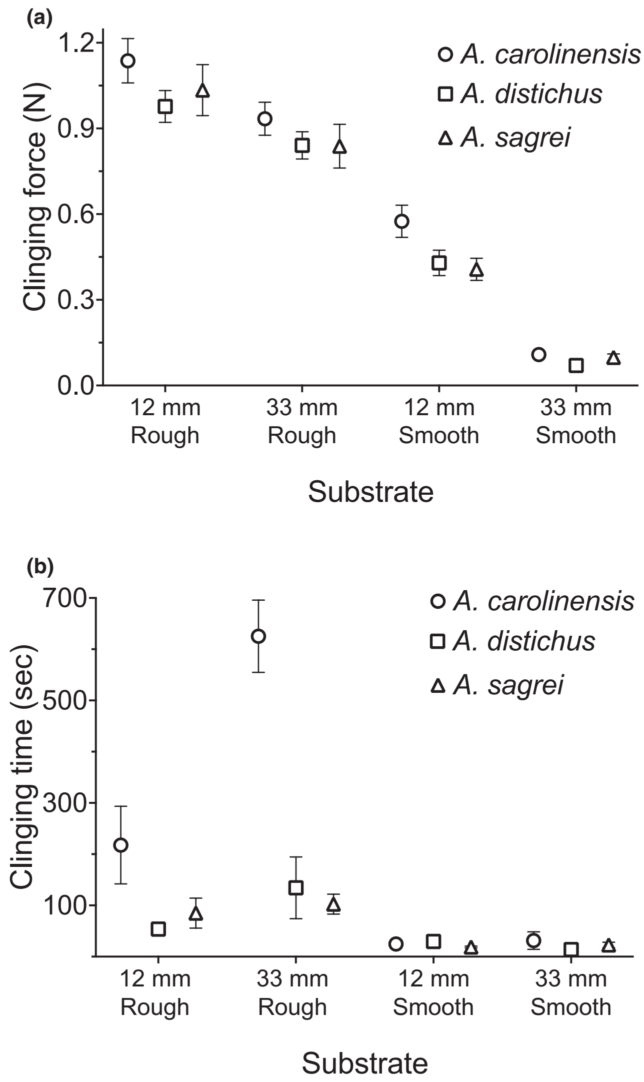

FIGURE 1 Differences in mean (± SE) clinging ability for the three *Anolis* species on four substrates varying in diameter (12 or 33 mm) and texture (rough or smooth) as measured by (a) clinging force and (b) clinging time under hurricane-force wind. See Tables 3 and 4 for statistical results.

dowels had increased clinging ability, these results did not translate to the wind-speed trials. Lizard clinging times were uniformly poor on smooth dowels, whereas clinging ability on the rough dowels varied substantially among species and was primarily driven by the significantly greater clinging performance of *A. carolinensis*. Species differences appeared to have less of an influence on behaviour when experiencing high winds compared with the substrate, which influenced whether lizards shifted to the more protected leeward side of the dowel. Taken together, these results provide ecologically relevant insights into how lizards might perform and behave while experiencing the high-speed winds associated with hurricanes.

The contrasting results between the two trials suggest that they measure different aspects of whole-animal clinging performance (Irschick et al., 2005). The clinging-force trials, which focused on the physical ability of lizards to grasp the dowel, measured the combined function of their claws, limbs, toepads and other traits for generating clinging force on the various substrates (Irschick et al., 1996; Zani, 2000). This measure of performance did not predict clinging time during high-speed wind trials, which measured clinging performance as a combination of physical clinging ability of lizards and their behavioural responses to high winds, among other potential factors. Previous research showed that anoles generated greater clinging force when they could wrap their limbs around a dowel, which is facilitated by longer limbs and narrower substrates (Kolbe, 2015). Clinging force was over four times greater on the 12 mm-smooth dowel compared with the 33 mm-smooth one for the three species, but there was little difference in the poor clinging times for these different diameter substrates. Contrasting results between the two trials suggest a potential functional trade-off: lizards that wrap their limbs around the dowel can generate greater clinging force, but this greater exposure of their limbs or body to the wind causes instability for their grasp when holding on or attempting to shift position because of increased drag (Debaere et al., 2021). Furthermore, the relatively high clinging forces recorded for lizards on rough dowels was largely not reflected in their clinging times. Because *A. carolinensis* performed much better on rough substrates than the other two species under high winds, we focus some discussion on better understanding why.

As predicted, the most arboreal species (*A. carolinensis*) generated greater clinging force than the other two species. The larger toepads of *A. carolinensis* may explain its ability to generate greater clinging force. Adaptive arguments for why arboreal anoles have larger toepads and greater clinging ability stem from the greater cost of falling from higher in the canopy, both in terms of the risk of physical injury as well as time and energy wasted regaining perches within territories (Elstrott & Irschick, 2004; Glossip & Losos, 1997; Losos, 2009). Moreover, falling to the ground during a hurricane might cause a lizard to be washed away by the storm surge or flooding or otherwise injured. Despite larger toepads, *A. carolinensis* had substantial variation among substates in clinging time, which suggests other factors are important when facing high winds. For example, is it more important for a lizard to maintain a strong grasp on the substrate in a single position or to shift its position to minimize exposure to the wind during a hurricane? The relatively shorter limbs of *A. carolinensis* likely led to decreased drag and greater stability while clinging, especially on the broad dowel. Indeed, the limb position of lizards at the start of each trial suggests that *A. carolinensis* would experience less exposure than the other two species and, therefore, minimize drag. However, drag forces (<100 mN) on anole bodies and limbs simulated using computational fluid dynamics (Debaere et al., 2021) are orders of magnitude lower than clinging forces (>1 N) generated by lizards in this study. Despite this quantitative discrepancy, lizards in our videos clearly experienced drag caused by exposure of their body, limbs and tail to wind and relatively low drag force could still be important for clinging performance on challenging substrates (e.g. 33 mm-smooth dowel) or have a significant cumulative effect over the duration of a hurricane. In future studies, a second camera capturing the limb position and posture of lizards after they move to the leeward side of the dowel would provide a better angle for assessing how limb position relates to drag during high winds.

Most lizards actively shifted to the leeward side of dowels after the start of wind-speed trials except on the 12 mm-smooth dowel, on which lizards had greater exposure and less stable footing. Movement was initiated quickly by lizards, but it was only on the 33 mm-rough dowel that they successfully rotated to the leeward side nearly every time and *A. carolinensis* tended to do this faster than the other species. Lizards on the other dowels often lost contact between one or more limbs and the substrate during movement, which frequently contributed to being blown off the dowel completely, although not necessarily immediately. Based on these results, we suggest that anoles can readily shift their position to minimize wind exposure, but they are more likely to do so on more stable (rough) substrates, and perhaps when their trait values confer greater stability during this movement. Larger toepads increase adhesion and shorter limbs reduce drag (both characteristics of *A. carolinensis*), which may aid lizards shifting in response to wind. Despite potentially compromising limb positions best suited for generating clinging force (i.e. wrapping limbs around the substrate), lizards may receive the benefits of protection against the wind if they successfully complete the movement. Therefore, the ability of lizards to make fine-scale adjustments in posture and positioning could strongly influence their exposure to wind, and potentially their ability to persist through a storm. Differences in clinging ability detected for species in this study may reflect variation in the susceptibility of lizards to hurricanes and may, therefore, influence how selection operates on the different species. Our simplified laboratory conditions revealed strong effects of substrate variation and species differences for clinging performance; however, variable wind speeds and directions during a hurricane are likely more challenging for lizards. Future experiments should endeavour to incorporate more realistic wind conditions along with precipitation, flexible substrates and other factors that could influence lizard performance in nature.

Understanding how substrates affect lizard clinging performance provides insight into what substrates lizards might select in nature. Some evidence exists that anoles avoid structural habitats in which their maximal performance capabilities are impaired and will select perches that enhance performance (Gilman & Irschick, 2013; Irschick & Losos, 1999). Results from our experiments suggest that lizards should select broad and rough substrates during hurricanes to enhance their clinging ability. In nature, the availability of preferred vegetation could influence the ability to select performance-enhancing substrates (Johnson et al., 2006). For example, selection of broad vegetation, which is preferred by some *Anolis* species (Kolbe et al., 2021), could decrease direct exposure to winds during a hurricane. However, some habitats have a limited range of vegetation, such as small islands with only narrow, scrubby vegetation (Kolbe et al., 2012). Moreover, the ability to access preferred perches during hurricanes may be risky. In our experiment, lizards often pivoted to the leeward side of the dowel after the wind started, apparently to

TABLE 4 Results from a general linear mixed model testing for clinging time differences with fixed effects of species, diameter, texture, all interactions and log mass. The random effect of lizard identity explained 12.5% of variation. Significant *p*-values are in bold

Factor	*F*	df	*p*
Species	10.0	2, 49	**0.0002**
Diameter	6.3	1, 124	**0.0137**
Texture	183.5	1, 127	**<0.0001**
Species by diameter	4.0	2, 124	**0.0207**
Species by texture	11.4	2, 127	**<0.0001**
Diameter by texture	23.7	1, 124	**<0.0001**
Species by diameter by texture	3.2	2, 124	**0.0422**
Log mass	0.0	1, 52	0.9642

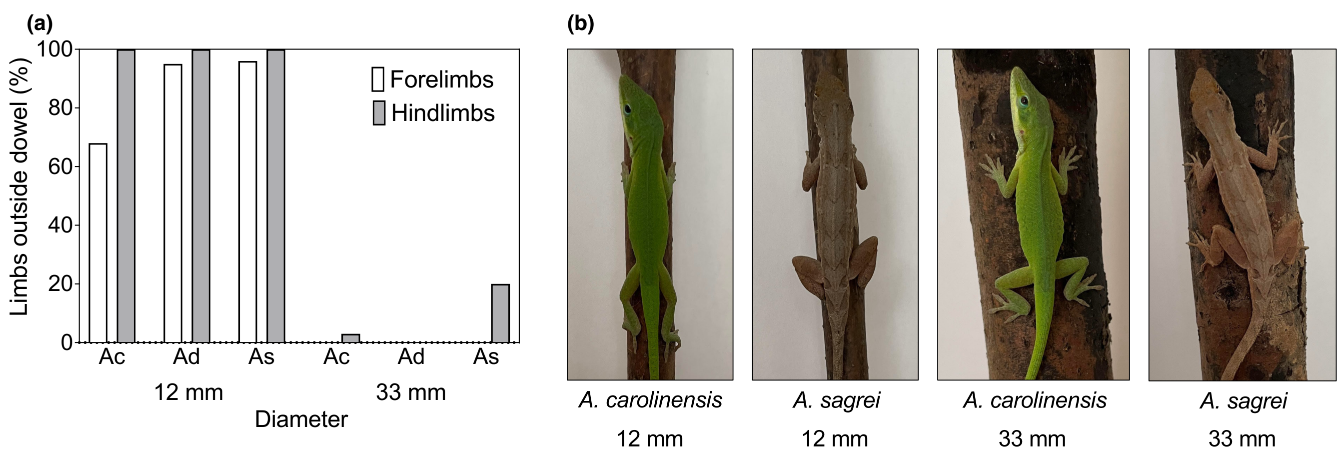

FIGURE 2 (a) Percentage of the time a lizard's forelimbs and hindlimbs extended out past the edges of the dowel (12 or 33 mm) at the start of high-speed wind trials. Abbreviations are Ac = *A. carolinensis*, Ad = *A. distichus* and As = *A. sagrei*. (b) Representative photos of *A. carolinensis* and *A. sagrei* perching on 12 and 33 mm-diameter substrates in the same head-up position as at the start of trials when limb position was scored. Note lizards in these photos are perching on natural vegetation of the same diameter as the dowels in the trials. Photos were taken by Tyler DeVos.

avoid the wind. This movement required them to move their limbs and to disengage toepads and claws, which should inhibit their ability to wrap their limbs around the substrate to form a strong grip. Movement was also more difficult on the narrow dowels due to greater exposure to the wind. These findings suggest that movement during a hurricane, especially on narrow vegetation, would increase the risk of a lizard losing its grip and being blown away. This suggests a series of behavioural decisions that could both enhance or inhibit clinging performance depending on the characteristics of the microhabitat and the timing of movement. An important question is whether lizards actively select perches that enhance clinging performance or whether they occupy perches for other reasons and then attempt to remain on these perches through the hurricane because of the risks associated with moving.

Our assessment of behaviour during the static wind conditions in our experiment suggests lizards can regulate their exposure to winds during a hurricane. Although observations of lizards during hurricanes do not exist, we can infer from studies documenting hurricane-associated mortality that such behaviour is likely important for survival. Anoles use holes and crevices in their territories to hide from predators and avoid the sun, among other reasons (Losos, 2009), and this behaviour could also reduce exposure to high winds during hurricanes. However, such behaviour could have its own risks, such as being vulnerable to drowning or being washed away by the coastal storm surge or flooding in heavy rains associated with hurricanes. Most anoles are at least semi-arboreal and commonly found in vegetation. Rotating to the leeward side of trunks or branches might be a good tactic if the movement itself does not result in slipping or losing grip on the substrate, and this movement might be dependent on the characteristics of the substrate.

5 | CONCLUSIONS

Results from recent studies of hurricane-induced selection (Donihue et al., 2018) and phenotypic shifts (Aviles-Rodriguez et al., 2021; Dufour et al., 2019; Fokidis & Brock, 2020; Rabe et al., 2020) provided the impetus for our experiments, which were designed to investigate the ecological and functional relationships that influence clinging performance as well as how behaviour might affect the ability of lizards to survive hurricanes. Our experiments showed that clinging force based on the physical ability of lizards did not predict clinging ability when experiencing the more realistic conditions of hurricane-force winds. Substrate diameter and roughness had strong influences on clinging ability in both trials, emphasizing the importance of lizard habitat use for mediating their performance. The behaviour of lizards during wind-speed trials suggests that moving to the leeward side of perches should increase clinging performance. The benefits of movement are especially true for more sure-footed lizards—those with larger toepads and shorter limbs—and lizards moving on broad and rough substrates. Together, our results further our understanding of how anoles function during hurricanes, which is important for clarifying the mechanisms underlying hurricane-induced selection. To this end, the behaviour of lizards during high winds may alter how selection acts on morphological traits via clinging performance. Both microhabitat selection of perches and the position of a lizard on its perch will likely have important consequences for clinging performance during a hurricane. The role of extreme weather events in driving evolution is of pressing interest as climate change continues to increase the intensity and frequency of these events (Bhatia et al., 2019; Grant et al., 2016; Sobel et al., 2016; Trenberth, 2005). Behaviour is widely acknowledged as the first response for coping with rapid environmental change (Sih, 2013), and our study shows that behaviour may be an important factor for clinging performance during high winds and, therefore, a relevant contributor to survival. Future studies should evaluate additional aspects of behaviour, habitat characteristics and storm conditions, which will contribute to a more holistic understanding of how hurricanes might influence natural selection.

AUTHOR CONTRIBUTIONS

Emma C. C. DiPaolo and Jason J. Kolbe developed the ideas and designed the experiments, collected and analysed the data and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

Protocols for use of lizards were approved by the University of Rhode Island Institutional Animal Care and Use Committee (AN11-09-005). This research was funded by the University of Rhode Island and a grant from the National Science Foundation (IOS-1806420). We thank C. Cox, T. DeVos and T. Fieldsend for assistance and T. DeVos, O. Lapiedra and S. Giery for helpful comments that improved the manuscript.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.bg79cnpf6 (DiPaolo & Kolbe, 2022).

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How to cite this article: DiPaolo, E. C. C., & Kolbe, J. J. (2023). Blowing in the wind: Experimental assessment of clinging performance and behaviour in *Anolis* lizards during hurricane-force winds. *Functional Ecology*, *00*, 1–10. https://doi.org/10.1111/1365-2435.14260