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THE EFFECT OF MORPHOLOGY, SUBSTRATE AND WIND ON THE CLINGING ABILITY OF ANOLIS LIZARDS DURING HURRICANE-FORCE WINDS

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THE EFFECT OF MORPHOLOGY, SUBSTRATE AND WIND ON THE CLINGING ABILITY OF *ANOLIS* LIZARDS DURING HURRICANE-FORCE WINDS

BY

EMMA DIPAOLO

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ABSTRACT

Extreme weather events have been identified as drivers of natural selection and evolutionary change across populations and species. A recent study showed that the high wind speeds generated by hurricanes caused selection favoring particular phenotypes for island lizards. *Anolis* lizards (or anoles) commonly live on islands and in coastal areas frequently disturbed by hurricanes. A hallmark of the *Anolis* radiation is the evolution of morphological variation among species as illustrated by the evolution of different ecomorphs, which have evolved varying limb and toe morphologies to occupy different parts of arboreal habitats. Differences in limb length and toepad size lead to clear functional differences in performance, including clinging ability, which is likely important during hurricanes. This study tests if morphological trait values affect clinging performance under different conditions. We evaluated three species in this study, each representing a different *Anolis* ecomorph (trunk-crown, trunk, and trunk-ground), which vary in limb and toepad morphology. As expected, the trunk-crown species (*Anolis carolinensis*) had the shortest limbs and most lamellae compared to the other two species in our study. The trunk ecomorph (*A. distichus*) had the longest forelimbs, intermediate hindlimb lengths, an intermediate number of forelimb lamellae, and the fewest hindlimb lamellae. Lastly, the trunk-ground species (*A. sagrei*) had intermediate forelimb lengths, the longest hindlimbs, the fewest forelimb lamellae, and an intermediate number of hindlimb lamellae. Based on morphology of these species, we hypothesized that the trunk-crown ecomorph would have the best clinging ability, followed by

the trunk ecomorph, and, lastly, the trunk-ground ecomorph. Lizards were subjected to two types of experimental trials. First, we assessed the ability of lizards to cling to substrates varying in diameter (i.e., 12 and 33 mm) and surface roughness (i.e., smooth and rough) by measuring the force needed to pull lizards off these substrates (hereafter, clinging-force trials). Second, we measured the amount of time lizards remained perched on these same substrates while experiencing hurricane-force winds (hereafter, wind-speed trials). In the clinging-force trials, for some combinations of dowel type and species, we found aspects of morphology, including increased hindlimb length, more hindlimb lamellae and body size, were related to clinging force. Our finding that more hindlimb lamellae increased clinging ability is consistent with a previous study that detected larger toepads in anole populations after hurricanes. However, our finding that longer hindlimbs increased clinging ability is not consistent with this previous study. In the wind-speed trials, we found no significant influences of morphology on clinging. These findings are not consistent with previous studies and may be due to the added behavioral aspect that the wind-speed trials included. In the clinging-force trials, with all the substrate types pooled, the trunk-crown ecomorph *A. carolinensis* had the best clinging performance, the trunk-ground ecomorph *A. sagrei* had intermediate clinging ability, and the trunk ecomorph *A. distichus* had the worst clinging ability. In contrast to the clinging force trials, we found no significant differences in clinging ability among species with substrate types pooled in the wind speed trials. We did find that *A. carolinensis* could cling longer than the other two species on the 33-mm-rough dowel. The differences between the clinging force and wind speed trials suggest that factors other than morphological variation, such as behavior, also influence clinging performance. Together, our results increase our understanding of the mechanistic basis for how substrate type and morphology influence clinging ability. Our preliminary analysis of clinging differences among *Anolis* ecomorphs also provides us with more knowledge of how anole clinging performance may be a target of natural selection during extreme weather events, such as hurricanes.

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CHAPTER 1

INTRODUCTION

Increases in the intensity and frequency of extreme weather events are among the numerous effects of recent human-mediated climate change (Trenberth 2005; Kossin et al. 2020). Weather patterns since the 1970s reveal that droughts have become more common in the subtropics and tropics and the number of hurricanes reaching categories 4 and 5 has increased (Linnenluecke et al. 2012). Along with observing these patterns, climate scientists have used models to predict the future consequences of climate change on extreme weather events. Several models show that without reducing greenhouse gases, hurricane intensities will significantly increase (Sobel et al. 2016). Other models show a non-linear, upward trend in sea surface temperatures over the past century. This upward trend, being most pronounced in the past 35 years, is associated with global warming and has been attributed to human activity (Trenberth 2005). These trends in human-influenced environmental changes are evident in regions affected by hurricanes and are expected to increase hurricane intensity and rainfall during this century and centuries to come (Trenberth 2005, Sobel et al. 2016).

Extreme weather events are destructive, transforming familiar habitats into disturbed landscapes (Little et al. 2019). For example, the high wind speeds, soil erosion, precipitation, and storm surge that accompany hurricanes can severely alter habitats for decades. These disturbances are influential ecological forces with the potential to alter radically the selective pressures that act on organisms (Little et al. 2019). As a result, organisms in the generation following a hurricane may significantly differ in their phenotypes (e.g., morphology and behavior) compared to those in generations preceding a hurricane (e.g., Donihue et al. 2018).

One possible way hurricanes can influence a population is by altering individual behavior. For example, multi-female colonies of the group-living spider (*Anelosimus studiosus*) occur along the east coasts of the United States and Mexico. These spiders exhibit either a docile or aggressive phenotype, with aggressiveness determining the speed and number of attacks towards prey (Little et al. 2019). Using a study that sampled before and after a hurricane, researchers found that more aggressive phenotypes were found in *A. studiosus* populations after the hurricane. Colonies that had more aggressive phenotypes following the hurricane produced more eggs and had more spiderlings survive into the early winter, whereas the opposite trend emerged in control sites. These results show that hurricanes (or post-hurricane environments) are potential sources of selection that may alter the phenology of populations.

Hurricanes can also alter the abundance and effects of different species in an ecosystem. In a study spanning before and after two hurricanes in the Bahamas, Spiller and Schoener (2007) showed that total rate of herbivory was 3.2 times higher in the year after the first hurricane than in the previous year, and 1.7 times higher in the year after a second hurricane. This increase in herbivory was caused by an overall reduction in predation by both lizards and arthropods. Following the first hurricane, lizard abundance was 30% lower than before the hurricane, and abundance of web spiders and hymenopteran predators was 66% and 59% lower, respectively. This shows that hurricanes can influence top-down control of ecosystems. If extreme events like hurricanes alter community composition by elevating mortality, decreasing genetic variation, or depleting environmental resources, then evolution is likely to occur (Grant et al. 2016).

Lizards belonging to the genus *Anolis* are likely influenced by Atlantic hurricanes because they inhabit areas from subtropical South America to the east coast of the United States, including most Caribbean islands (Losos 2009). The forceful winds, rains, and storm surges associated with hurricanes can impact the survival of anoles. In some studies, the hurricane exterminated all lizards on exposed islands (Spiller et al. 1998; Schoener et al. 2001). In another study, all lizards on islands lower than 3-m maximum elevation were swept away by the storm surge (Schoener et al. 2001). On islands where anoles can survive, however, hurricanes can be a source of natural selection on their morphology. For example, following Hurricanes Irma and Maria in 2017, *Anolis scriptus* populations in the Turks and Caicos had larger toepads, longer forelimbs, and shorter hindlimbs than populations observed before the hurricanes (Donihue et al. 2018; Donihue et al. 2020). Thus, morphological variation among individual lizards influences survival during high winds, showing that hurricanes are a selective force that can alter morphology.

Fitness is influenced by an organism's phenotype via ecologically relevant measures of performance (Zani 2000). Understanding how phenotypic traits function is essential to understanding organismal adaptations (Irschick et al. 1995). A classic paradigm in functional morphology suggests that morphological variation should correlate with variation in an ecologically relevant performance capacity. This, in turn, should correlate with variation in fitness of an individual (Irschick et al 2005, 2008). For arboreal lizards, such as anoles, clinging ability has profound importance. Falling from a perch several meters above ground could cause severe injury or require considerable time and energetic cost for the lizard to regain its perch within its territory (Elstrott and Irschick 2004). During a hurricane, specifically, falling to the ground might cause a lizard to be washed away by the storm surge or to be hit by falling debris. It is thus important for anoles to possess morphological attributes (i.e., longer limbs and larger toepads) that allow them to perform effectively in their environment (i.e., clinging to substrates).

Anolis lizards provide an excellent opportunity to enhance our understanding of how morphology correlates with variation in fitness-related performance because of the evolution of ecomorphs, or habitat specialists (Elstrott and Irschick 2004, Losos 2009). Ecomorphs are species that occupy the same structural habitat (i.e., similar perch heights and diameters), have similar behavior and morphology, but are not closely related phylogenetically (Losos 2009). Anoles in distinct ecomorph groups vary in both their limb lengths and toepad sizes, and therefore are likely to vary in their clinging ability (Losos 1990; Irschick 1995; Elstrott & Irschick 2004). Selective pressures favor traits that increase performance both in everyday life (i.e., sprinting, climbing, and jumping) and during hurricanes (i.e., clinging). For example, in ecomorphs that typically perch on narrow substrates and higher up in the tree (i.e., crown-giant, trunk-crown, and twig ecomorphs) selective pressures favor shorter limbs and larger toepads than in ecomorphs that perch on broad substrates that are closer to the ground (i.e., trunk, trunk-ground, and grass-bush) (Losos 2009). However, selective pressures that are caused by hurricanes might select for different traits values as compared to everyday selective pressures (Donihue et al. 2018). Because anoles in distinct ecomorph groups vary in both their limb lengths and toepad sizes, they are likely to vary in their clinging ability (Losos 1990; Irschick 1995; Elstrott & Irschick 2004). As a result, some *Anolis* ecomorphs may be better able to cling to their perches during a hurricane, increasing their chance of survival.

The ability of an anole to cling to a substrate might be essential for an individual lizard to survive extreme weather events such as hurricanes. The greater an anole's ability to cling to a substrate during hurricane-force winds, the higher likelihood that the anole will survive the storm and go on to breed in the future. The toepads of anoles consist of laterally expanded scales (i.e., lamellae) that are covered with modified hair-like scale derivates termed setae (Irschick et al. 1995). These setae enable adhesion to a surface through the establishment of intermolecular bonds between the setae and the surface. Bonds of this sort are the weakest form of intermolecular forces, known as van der Waals forces (Losos 2009). Anoles vary in toepad size, the number of lamellae composing them, and the density and distribution of setae. This morphological variation in different species of anoles leads to variation in their clinging ability. Previous studies in anoles support a positive relationship between toepad area and clinging ability (Zani 2000; Losos 1990; Irschick et al. 1995; Donihue et al. 2018) because more (or larger) lamellae increase the capacity of the toepad to mold its shape to the surface and its irregularities. This allows greater surface area contact between lamellae and the surface (Losos 1990).

Lizard limb length can also influence clinging ability (Kolbe 2015). In a study mentioned previously, *A. scriptus* populations in the Turks and Caicos sampled before and after a hurricane were found to have significantly shorter hindlimbs afterwards (Donihue et al. 2018; Donihue et al. 2020). This reduction in limb length is likely because when the anoles were exposed to high winds, longer hindlimbs presented a larger exposed surface area. Therefore, shorter hindlimbs were selected for because they reduced the amount of surface area the wind could contact and thus increased the ability of a lizard to cling to its perch. In contrast to the reduction in hindlimb length in these populations, forelimb length increased. Typically, longer limbs require more force to be removed from a substrate (Kolbe 2015, Donihue et al 2018), such that longer forelimbs should allow lizards to better hold on to branch-like substrates.

Along with clinging performance potentially influencing fitness, perch selection might also affect lizard survival during extreme events like hurricanes. According to the habitat constraint hypothesis, animals will avoid structural habitats in which their maximal performance capabilities are impaired (Irschick & Losos 1999). Because of this, lizards may specifically select perches that help them maximize performance. For example, anole species with long hindlimbs avoid using narrow perches because narrow diameter perches impair maximal sprinting speed (Irschick & Losos 1999). However, the extent to which lizards select habitats for different types of performance is unknown. Although some substrates might be preferred to others due to habitat constraints, variation in available vegetation may also influence a lizard's ability to be selective, resulting in biased or random habitat use depending on the vegetation available (Johnson et al. 2006). As a result, habitat selection that maximizes performance and the availability of vegetation types may combine to influence substrate use by anoles.

In this study, we investigated whether three species of *Anolis* lizards, each specializing in a different habitat, differed in their clinging ability. We further assessed whether clinging ability was related to morphological variation among individuals by measuring physical traits known to influence clinging performance. These include forelimb length, hindlimb length, and lamella number. Because perch characteristics are known to influence clinging and locomotor performance (Irschick & Losos 1999; Mattingly & Jayne 2004; Kolbe 2015; Kolbe et al. 2016), we conducted clinging trials using four different substrates that varied in diameter and surface texture. First, we performed clinging-force trials to evaluate the clinging ability of each lizard on the four different substrates (Kolbe 2015). Second, we performed wind-speed trials to simulate hurricane-force winds in the laboratory to assess the behavioral response and clinging ability of lizards under ecologically relevant wind speeds. For both experiments, we hypothesized that lizards would perform best on narrow and rough substrates compared to broad and smooth substrates, respectively.

For both the clinging-force trials and the wind-speed trials, we hypothesized that anoles with more lamellae will have greater clinging ability, predicting these lizards would maintain their position on a perch for a longer time while experiencing hurricane-force wind speeds and generate greater clinging force when being pulled from their perches. We also predicted that anoles with longer forelimbs will have greater clinging ability in both the clinging-force and wind-speed trials due to an increased force required to separate the lizard from the substrate (Kolbe 2015). Lastly, we predicted that anoles with longer hindlimbs will maintain their perch longer during clinging-force trials for the same reason that longer forelimbs would increase clinging. However, in the wind-speed trials, we predicted that anoles with shorter hindlimbs will maintain their perch longer during hurricane-force winds because less of their hindlimb surface area is exposed to the wind (see Donihue et al. 2018).

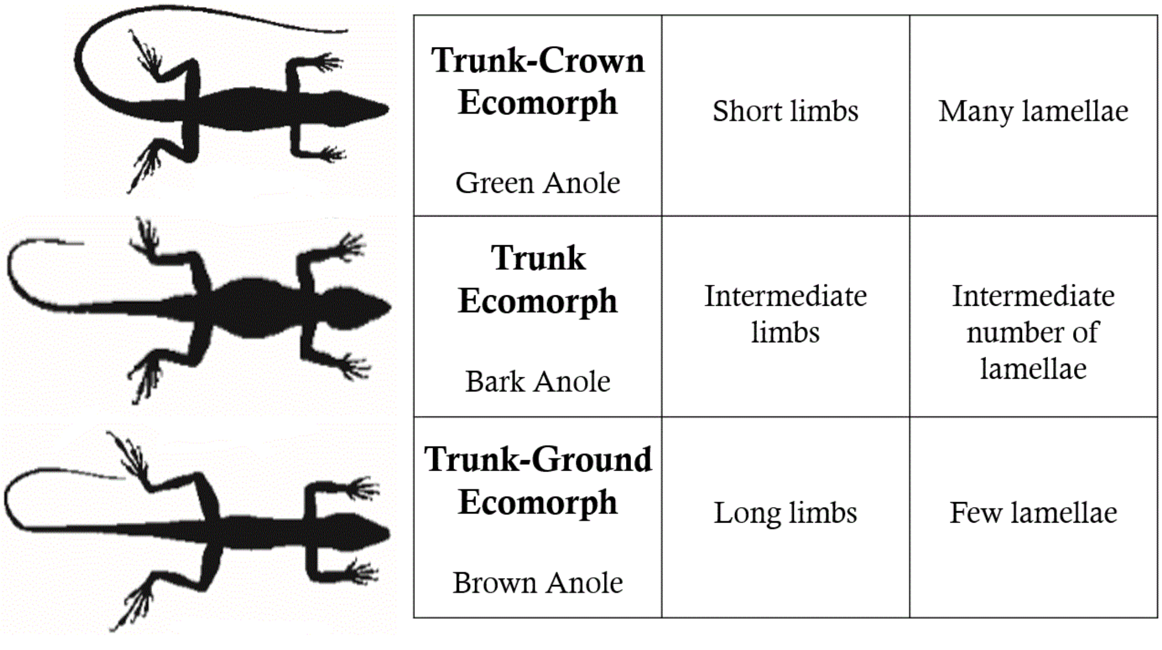
Another aim was to preliminarily assess the susceptibility of different *Anolis* ecomorphs to hurricane-force winds. Because *Anolis carolinensis* belongs to the trunk-crown ecomorph, which is characterized by short limbs and well-developed toepads (Losos 2009), we hypothesized that it would have the greatest clinging capacity among all three species. *Anolis sagrei*, belonging to the trunk-ground ecomorph with long hindlimbs and poorly developed toe pads (Losos 2009), should have the lowest clinging ability. Lastly, *Anolis distichus,* belonging to the trunk ecomorph with intermediate limb lengths and toepad size (Losos 2009), should have an intermediate clinging ability.

MATERIALS AND METHODS

Study Species

Anoles provide an excellent opportunity to enhance our understanding of how hurricanes influence survival selection because of the independent evolution of ecomorphs. Ecomorphs are named for the part of the microhabitat the species usually occupies (Losos 1990, 2009). There are six ecomorph categories: grass-bush, trunk-ground, trunk, trunk-crown, crown-giant, and twig. Anoles that occupy the same ecomorph are similar in their limb morphology and the number of subdigital lamellae, as well as their ecology, behavior, and coloration due to similarities in their perch characteristics. The anoles, therefore, have adapted to the specific part of the habitat that they inhabit (Mattingly & Jayne 2004, Losos 2009). This predicts that ecomorphs should perform optimally when they occupy the microhabitat that matches their morphology (Irschick & Losos 1999). For example, lizards with shorter limbs are more efficient at moving on narrow substrates than lizards with longer limbs; as a result, lizards with shorter limbs tend to occupy habitats with narrow substrates (Irschick & Losos 1999; Mattingly & Jayne 2004). In this experiment, we used multiple substrates with varying diameter and roughness to mimic the natural substrates that anoles use in the wild (Losos & Sinervo 1989; Losos & Irschick 1996; Irschick & Losos 1999).

Anoles of three different ecomorphs that naturally occur in Miami, Florida were used for this experiment. These anoles are relatively similar in body size but differ in their limb morphology. Each species, their ecomorph, and their respective morphologies, are shown in Figure 1 (Losos 2009).



Trunk-Crown Ecomorph Green Anole	Short limbs	Many lamellae
Trunk Ecomorph Bark Anole	Intermediate limbs	Intermediate number of lamellae
Trunk-Ground Ecomorph Brown Anole	Long limbs	Few lamellae

Figure 1. Silhouettes representing average morphologies of trunk-crown, trunk, and trunk-ground ecomorphs representing species in our study, that is *A. carolinensis, A. distichus*, and *A. sagrei*, respectively. Relative limb and toepad characteristics for each ecomorph/species are shown.

Collecting lizards

Twenty *A. sagrei* and 14 *A. distichus* were collected in South Miami, Florida in August 2020 and shipped overnight to the Kolbe lab at the University of Rhode Island. Because few *A. carolinensis* were observed in the field, we purchased 20 *A. carolinensis* from a local pet store in Rhode Island.

Considerable sexual dimorphism exists in most anole species, and interspecific differences among females are much less pronounced than among males (Losos 1990). Thus, only adult males were collected and used in our analyses.

Housing

Lizards were housed individually in the lab at the University of Rhode Island, where all experiments were performed. We provided UV light on a light:dark cycle that reflected natural conditions in South Miami. Room temperature was maintained at 27 ± 1 ^oC. 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 (*Acheta domestica*) every three days.

Clinging-force Trials

We measured the force necessary to pull a lizard off a vertically positioned dowel. Lizards were fitted with a harness around their midsection located halfway between their fore- and hindlimbs (as in Kolbe 2015). Substrates used during the clinging-force trials were 12 mm and 33 mm diameter dowels of both smooth and rough textures. 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 lizard's harness, and the gauge and lizard were pulled at a slow, constant speed 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). The highest force measurement for each dowel type was recorded using the peak force setting and used in subsequent analyses.

Morphological Measurements

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 its length from the tip of the lizard's snout to the cloaca. Following euthanasia at the end of the experiment, each lizard's forelimb and hindlimb lengths were measured in mm. Lamella numbers for the third toe of the forelimb (hereafter toe III) and the fourth toe of the hindlimb (hereafter toe IV) were counted using a dissecting microscope.

Wind-speed Trials

To determine how lizards react to hurricane-force winds, we used a Toro Leaf Blower (51619: Ultra Blower) to produce wind speeds in excess of 193 kph. We evaluated lizard behavior and clinging time 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) with 120 frames-per-second, and windspeed in kph was measured using an Inspeed pole mount 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 sheet to provide a safe landing spot to ensure lizards were unharmed after being blown off the dowel. Each lizard was placed on the dowel head up and orthogonal to the flow of wind. The leaf blower was turned on and immediately set to 72.5 kph. Over a ten second interval, the windspeed of the leaf blower was steadily increased until reaching 195 kph, the maximum windspeed produced by the leaf blower. The cone of wind created by the leaf blower encompassed the entirety of the experimental perch. If the lizard fell off before the 195-kph mark, the windspeed (in kph) at the time the lizard fell off the parch was recorded. If the lizard fell off after the 195-kph mark, then the total of time (in seconds) in which the lizard was able to hold on to the perch was recorded. Time was capped at 13 minutes.

We assessed the quality of each trial to determine if individual lizards appeared to perform maximally when clinging to the dowel. Each lizard experienced one trial per dowel unless there was evidence of submaximal performance. Trials were considered unacceptable if the lizard being tested repeatedly jumped off the perch at the start of the trial. We tested lizards up to three times to get an acceptable trial. Eight trials were considered unacceptable on the 12-mm-smooth and 33-mm-rough dowels, eleven trials were unacceptable on the 12-mm-rough dowel, and five trials were unacceptable on the 33-mm-smooth dowel.

Once the leaf blower was on, the majority of lizards immediately pivoted to the lee 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.

Statistical Analyses

To compare clinging force between species on all four substrates, we used a mixed linear effects (MLE) model with lizard identity as a random effect and tested for the effects of dowel diameter, texture, species, and interactions among these factors.

We assessed morphological variation among species using analysis of covariance models (ANCOVA), including SVL as a covariant. Models evaluating differences in morphology compared the forelimb length, hindlimb length, toe III (i.e., forelimb lamellae), and toe IV (i.e., hindlimb lamellae) for each of the three species. We used Tukey's honestly significant difference (HSD) *post-hoc* tests to evaluate differences among levels of each factor when significant. To reduce the dimensionality of the morphological data, we conducted a principal components analysis (PCA) on the correlation matrix of residuals of log-transformed forelimb and hindlimb length traits on log-SVL, toe III and toe IV lamellae, and SVL and mass. Residuals were not taken for toe III and toe IV lamellae because they were not correlated with SVL. We interpreted PC axes with eigenvalues greater than one.

We used multiple regression models to test for relationships between aspects of morphology, including limb lengths, lamella numbers, SVL, and mass, and clinging force and time (during both the clinging-force and wind-speed trials). Individual multiple regressions were run for each of the four substrate types with species pooled. Species were then separated to compare the relationship between morphological variables and clinging force within each species.

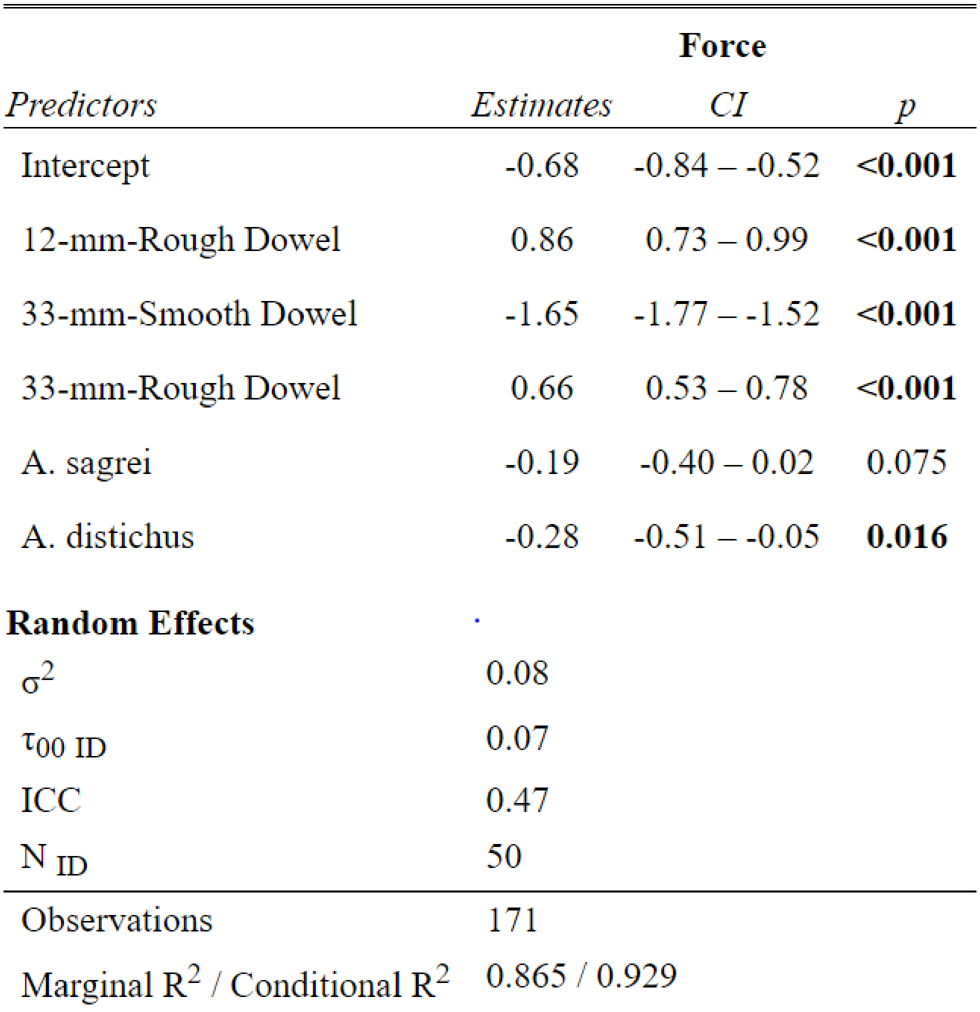
To test how species differed in time spent on each dowel during the wind-speed trials, we used a MLE model with lizard identity as a random effect and tested for the effects of dowel diameter, dowel texture, species, and interactions among these factors. All analyses were conducted in R (R Core Team, 2018).

RESULTS

Clinging Force

In the MLE model analyzing the amount of force required to remove a lizard from a substrate, the reference species is *A. carolinensis* and the reference dowel type is 12-mm-Smooth. Comparing among the three species with the four substrate types pooled, *A. carolinensis* required the greatest force to remove lizards from dowels, a result that significantly differed from *A.*

Table 1. Results from linear mixed effects model with lizard identify as a random effect testing for effects of overall dowel structure, species, and interactions among these factors on the among of force to remove a lizard from a substrate. Interactions between the overall dowel structure and species were insignificant and removed from the final model. P-values and R^2 values for the overall model are shown. Significant P-values are in bold.



	Force		
Predictors	*Estimates*	*CI*	*p*
Intercept	-0.68	-0.84 – -0.52	**<0.001**
12-mm-Rough Dowel	0.86	0.73 – 0.99	**<0.001**
33-mm-Smooth Dowel	-1.65	-1.77 – -1.52	**<0.001**
33-mm-Rough Dowel	0.66	0.53 – 0.78	**<0.001**
A. sagrei	-0.19	-0.40 – 0.02	0.075
A. distichus	-0.28	-0.51 – -0.05	**0.016**
Random Effects			
σ^2	0.08		
$\tau_{00\ ID}$	0.07		
ICC	0.47		
N_{ID}	50		
Observations	171		
Marginal R^2 / Conditional R^2	0.865 / 0.929		

distichus and was nearly significantly different from *A. sagrei* (Table 1). Across all dowels, *A. carolinensis* had a

17.2% and 14.7% greater clinging force than *A. distichus* and *A. sagrei*, respectively (Figure S1).

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 to broad and smooth dowels, respectively (Figure 2). The rank order of clinging force across the four substrates was the same for each species with the 12-mm-rough dowel requiring the greatest force, followed by the 33-mm-rough, 12-mm-smooth, and lastly the 33-mm-smooth dowels (Figure 2). Interactions between substrate type and species were not significant and, therefore, removed from the final model.

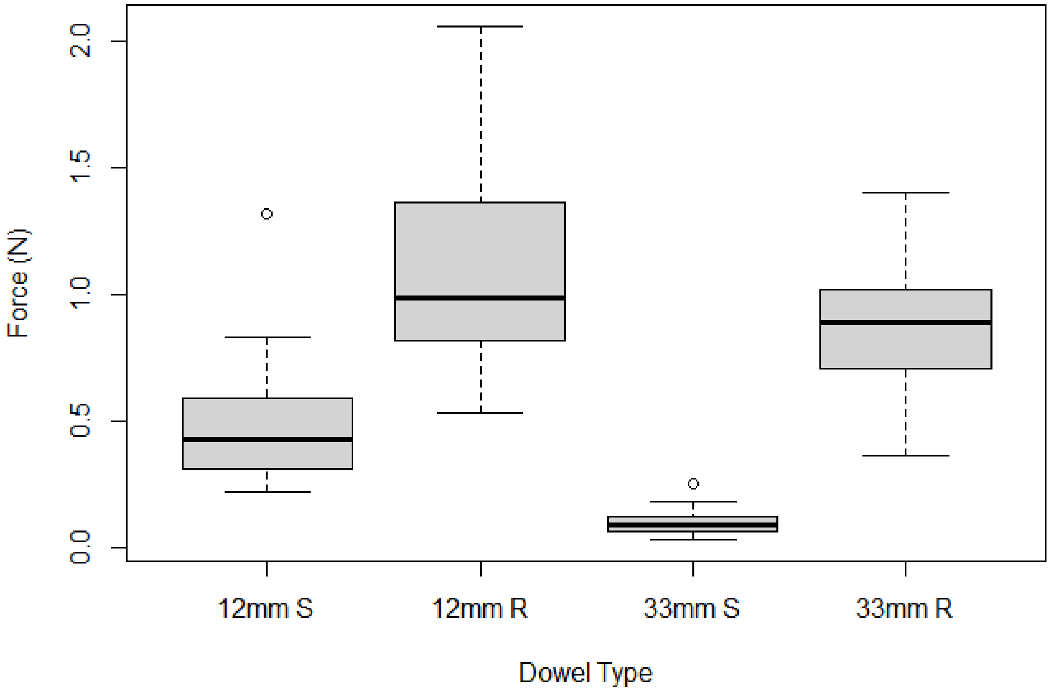


Figure 2. Mean force required to remove lizards from four different substrates varying in diameter and surface texture (species pooled).

The MLE model with dowel diameter and texture as factors showed that levels for both the two diameters (i.e., 12 and 33-mm) and two textures (i.e., smooth and rough) differed significantly in the force required to remove lizards. In this model the reference species is *A. carolinensis*, the reference dowel diameter is broad, and the reference dowel texture is rough. The 12-mm dowels required 43.6% more force than the 33-mm dowels, and the rough dowels required 112% more force than the smooth dowels. The interaction between diameter and texture was significant (Table 2), indicating that different combinations of diameter and texture influence the force required to

Table 2. Results from linear mixed effects model with lizard identity as a random effect testing for effects of diameter, texture, species, and interactions among these factors on the amount of force to remove a lizard from a substrate. Interactions between the overall dowel structure and species were found to be insignificant in previous models and were removed from this model. *P*-values and R^2 values for the overall model are shown. Significant *P*-values are in bold.

	Force		
Predictors	*Estimates*	*CI*	*p*
Intercept	-0.02	-0.18 – 0.14	0.772
Narrow Diameter	0.20	0.07 – 0.33	**0.002**
Smooth Texture	-2.30	-2.42 – -2.18	**<0.001**
A. sagrei	-0.19	-0.40 – 0.02	0.075
A. distichus	-0.28	-0.51 – -0.05	**0.016**
Narrow Diameter*Smooth Texture	1.45	1.27 – 1.62	**<0.001**
Random Effects			
σ^2	0.08		
$\tau_{00\ ID}$	0.07		
ICC	0.47		
N_{ID}	50		
Observations	171		
Marginal R^2 / Conditional R^2	0.865 / 0.929		

remove a lizard from the substrate. Specifically, narrow diameters and rough textures together resulted in the greatest clinging performance, whereas broad diameters and smooth textures together had the worst clinging performance.

Morphology

We used ANCOVA models to compare forelimb length, hindlimb length, toe III lamellae, and toe IV lamellae among all three species, with *A. carolinensis* being the reference species (Table 3). After accounting for SVL, *A. carolinensis* significantly differed from *A. sagrei* and *A. distichus* in all morphological traits. *Anolis sagrei* and *A. distichus* differed significantly in hindlimb length and toe III lamellae, but not in forelimb length and toe IV lamellae (Table S1). Although some morphological traits did not differ significantly between *A. sagrei* and *A. distichus*, the pattern of morphological differences among the three species matched descriptions in the literature (Losos 2009). *Anolis carolinensis* had the shortest forelimbs and hindlimbs, and the most lamellae on their toepads (both toe III and toe IV). *Anolis sagrei*

Table 3. Results from ANCOVAS with log-SVL as a covariate comparing log- (a) forelimb length, (b) hindlimb length, (c) toe III lamella number, and (d) toe IV lamella number between all three species. *P*-values and R^2 values of the overall models are shown. Significant *P*-values are in bold.

	Forelimb Length			**Hindlimb Length**			**Toe III Lamella Number**			**Toe IV Lamella Number**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept	0.35	-0.35 – 1.05	0.322	1.31	0.70 – 1.93	**<0.001**	3.29	2.09 – 4.50	**<0.001**	2.96	1.92 – 4.00	**<0.001**
A. sagrei	0.14	0.11 – 0.18	**<0.001**	0.19	0.16 – 0.22	**<0.001**	-0.40	-0.46 – -0.34	**<0.001**	-0.27	-0.32 – -0.22	**<0.001**
A. distichus	0.15	0.11 – 0.20	**<0.001**	0.06	0.02 – 0.10	**0.004**	-0.30	-0.38 – -0.22	**<0.001**	-0.32	-0.39 – -0.25	**<0.001**
SVL	0.69	0.52 – 0.86	**<0.001**	0.57	0.42 – 0.72	**<0.001**	-0.09	-0.38 – 0.21	0.557	0.06	-0.20 – 0.31	0.654
Observations	52			52			52			52		
R^2 / R^2 adjusted	0.637 / 0.614			0.832 / 0.822			0.857 / 0.848			0.852 / 0.843		

had intermediate forelimbs, the longest hindlimbs, the fewest number of toe III lamellae, and an intermediate number of toe IV lamellae. Lastly, *A. distichus* had the longest forelimbs, intermediate length hindlimbs, an intermediate number of toe III lamellae, and the fewest toe IV lamellae (Figure 3). According to the literature, *A. carolinensis* typically have the shortest limbs and largest toepads, *A. sagrei* typically has the longest limbs and smallest

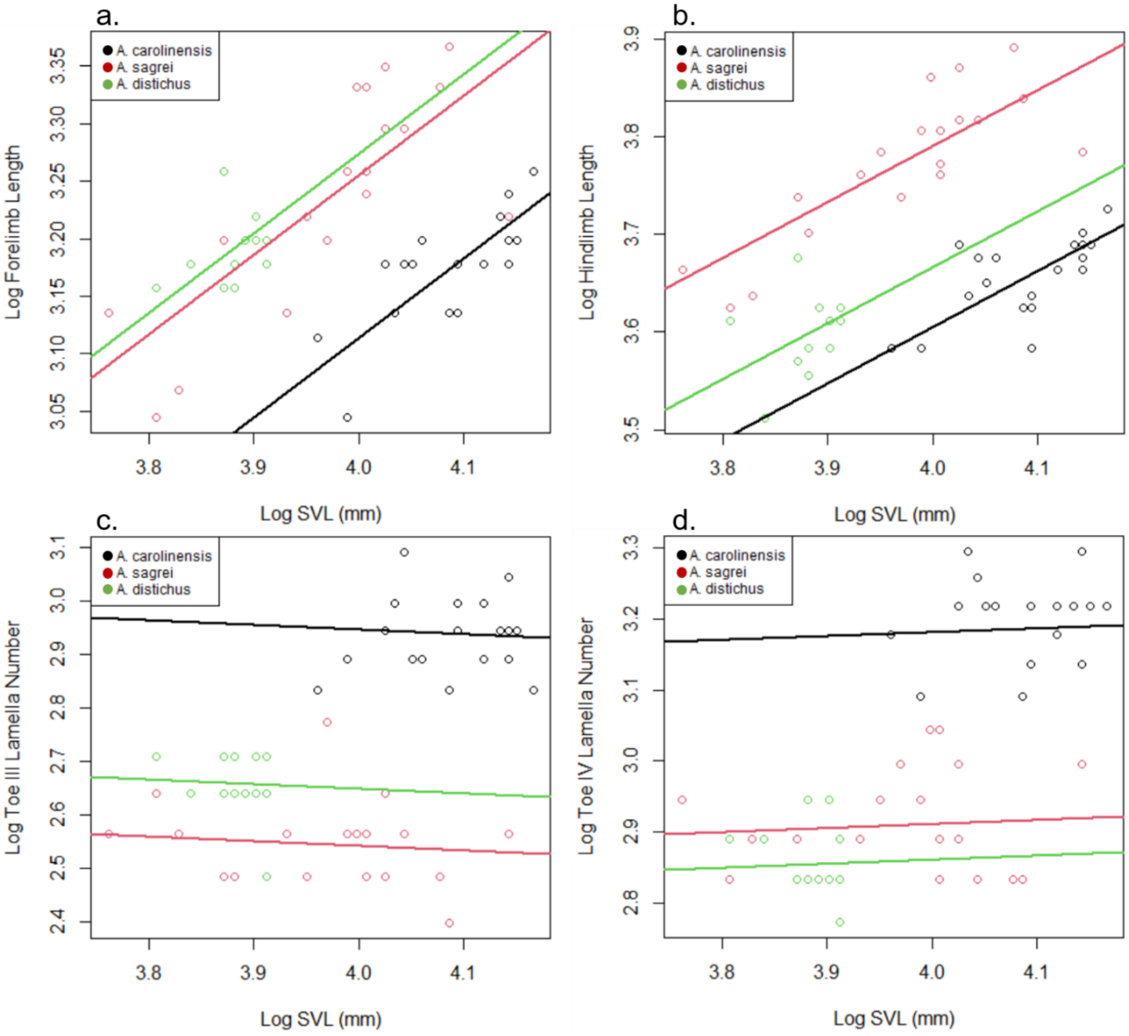


Figure 3. ANCOVA model results for the log-(a) forelimb length, (b) hindlimb length, (c) toe III lamella number, and (d) toe IV lamella number for each species with log- SVL as a covariate.

toepads, and *A. distichus* typically has intermediate limb lengths and toepad sizes (Losos 2009).

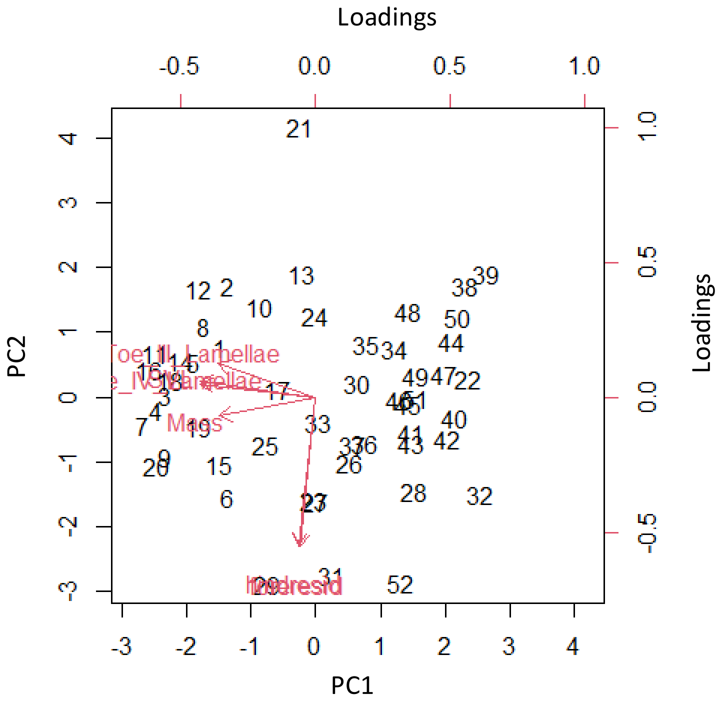


Figure 4. PCA plot showing the multivariate variation among six morphological traits. Vectors indicate the direction and strength of each morphological variable to the overall distribution. The first two principal axes explained 76% of the variance.

We performed a principal components analysis (PCA) on the correlation matrix of the morphological variables to reduce

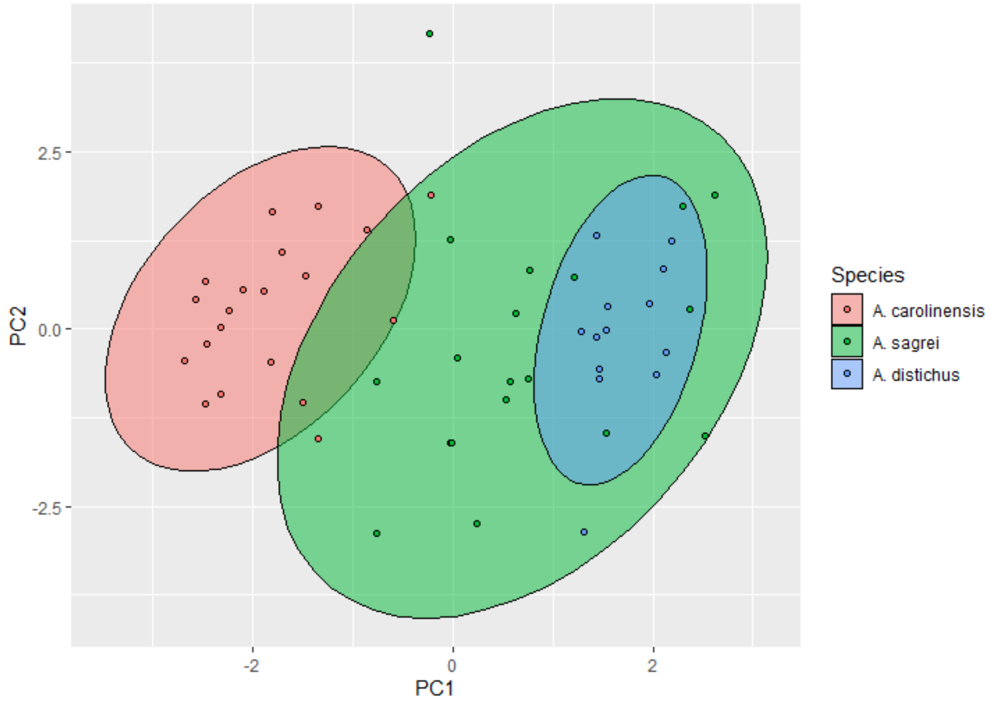


Figure 5. The 95% CI ellipses for morphological variation as represented by PC1 and PC2 for the three species.

dimensionality. The first principal component explained 47% of the total variance, while the second principal component explained 29% of the total variance. Positive values of PC1 represent lizards with fewer lamellae and smaller body size (i.e., shorter SVL and lower mass), whereas positive values of PC2 represent shorter limbs, both fore- and hindlimbs.

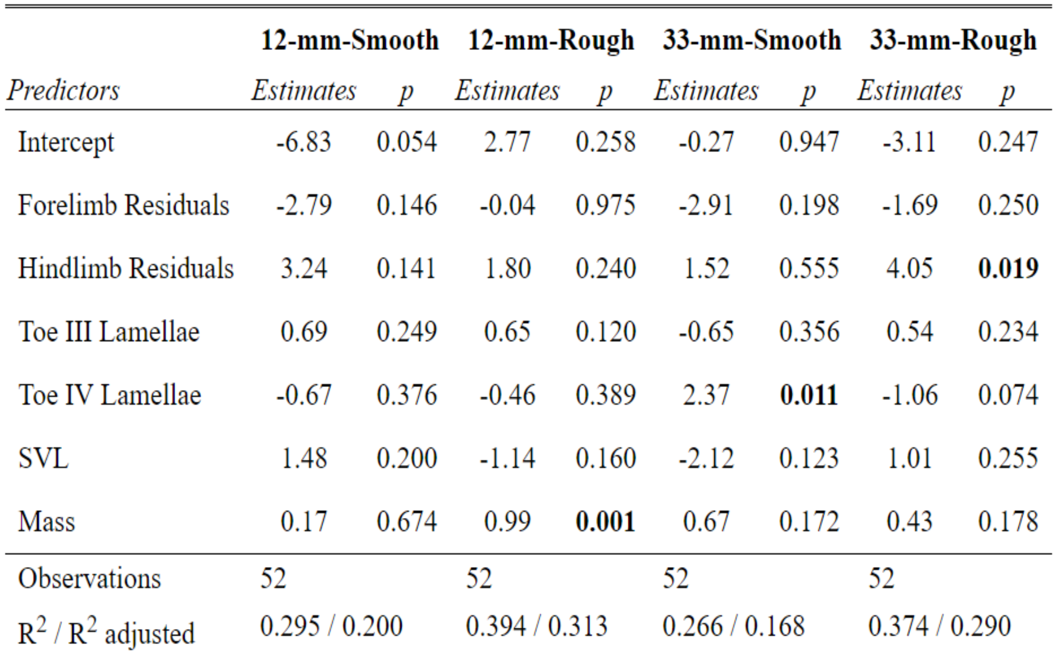
Table 4. Results from principal components analysis of morphological variables. Eigenvalues greater than 1 and substantial loadings (>0.45) are in bold.

Variable	PC1	PC2
Standard deviation	1.68	1.32
Proportion of variance	0.47	0.29
Cumulative variance	0.47	0.76
Eigen values	**2.83**	**1.75**
Forelimb loadings	-0.08	**-0.69**
Hindlimb loadings	-0.09	**-0.69**
Toe III loadings	**-0.46**	0.17
Toe IV loadings	**-0.54**	0.07
SVL loadings	**-0.54**	-0.08
Mass loadings	**-0.45**	-0.09

Clinging Force and Morphology

For the clinging-force trials, we used multiple regression models to test for relationships between morphological variables and clinging force. First, species were combined to compare the relationship between morphology and clinging force on each of the four substrates separately. Mass was the only significant morphological variable related to clinging force on the 12-mm-rough substrate, toe IV lamellae influenced clinging force on the 33-mm-smooth substrate, and hindlimb length was the only significant morphological variable related to clinging force on the 33-mm-rough substrate. No morphological variables were significantly related to clinging ability on the 12-mm-smooth substrate (Table 5).

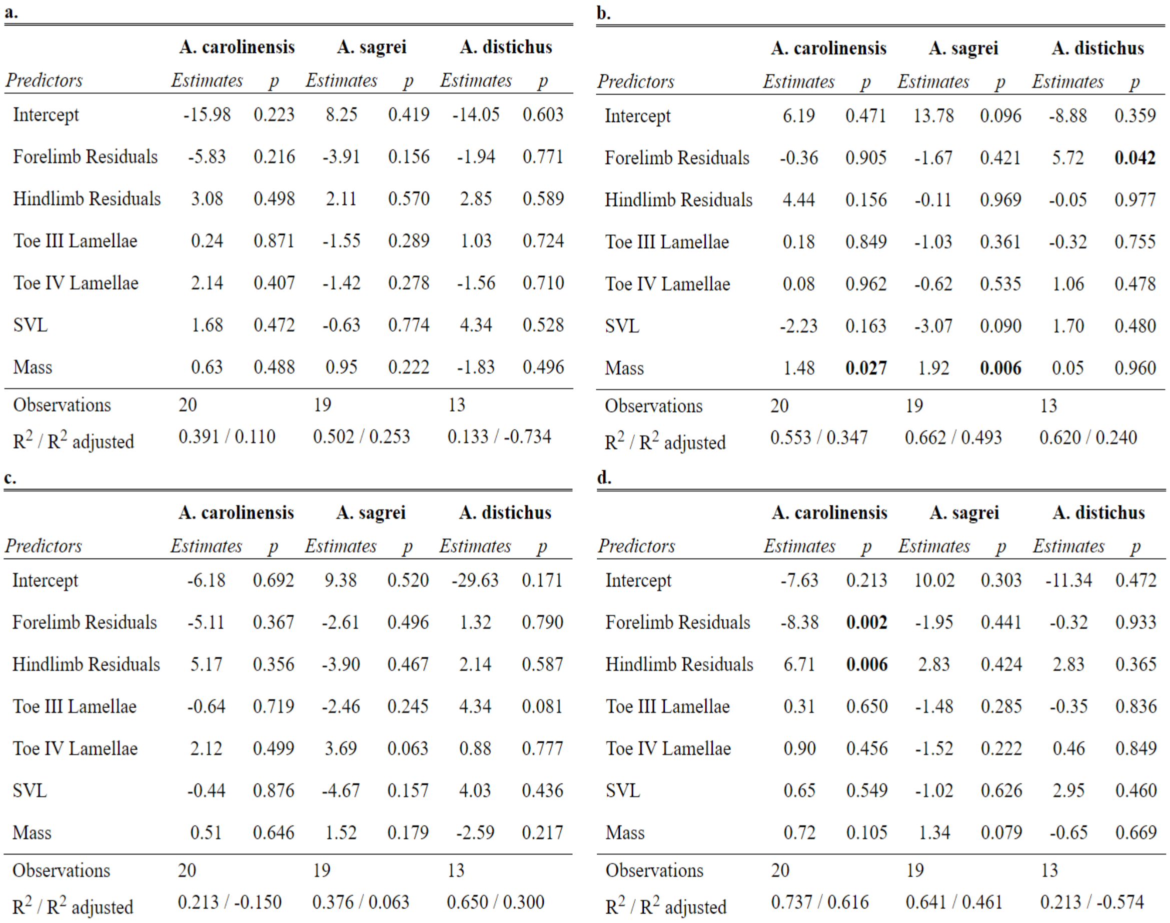
Table 5. Results from multiple regression testing for effects of the six morphological traits on the amount of force to remove a lizard from all four substrates with species type pooled. *P*-values and R^2 values for the overall model are shown. Significant *P*-values are in bold.



	12-mm-Smooth		**12-mm-Rough**		**33-mm-Smooth**		**33-mm-Rough**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
Intercept	-6.83	0.054	2.77	0.258	-0.27	0.947	-3.11	0.247
Forelimb Residuals	-2.79	0.146	-0.04	0.975	-2.91	0.198	-1.69	0.250
Hindlimb Residuals	3.24	0.141	1.80	0.240	1.52	0.555	4.05	**0.019**
Toe III Lamellae	0.69	0.249	0.65	0.120	-0.65	0.356	0.54	0.234
Toe IV Lamellae	-0.67	0.376	-0.46	0.389	2.37	**0.011**	-1.06	0.074
SVL	1.48	0.200	-1.14	0.160	-2.12	0.123	1.01	0.255
Mass	0.17	0.674	0.99	**0.001**	0.67	0.172	0.43	0.178
Observations	52		52		52		52	
R^2 / R^2 adjusted	0.295 / 0.200		0.394 / 0.313		0.266 / 0.168		0.374 / 0.290	

Species were then separated to compare the relationship between morphology and clinging force within each species. When *Anolis distichus* was clinging to the 12-mm-rough substrate, longer forelimbs increased clinging ability (Table 6b). Also on the 12-mm-rough substrate, higher mass increased clinging ability for both *A. carolinensis* and *A. sagrei* (Table 6b). *Anolis carolinensis* was the only species to have a significant result for the 33-mm-rough substrate: shorter forelimbs and longer hindlimbs increased clinging ability (Table 6d). No morphological variables were significant for any species for the 12-mm-smooth or 33-mm-smooth substrates (Tables 6a & 6c).

Table 6. Results from multiple regression testing for effects of the six morphological traits on the amount of force to remove a lizard from (a) 12-mm-smooth, (b) 12-mm-rough, (c) 33-mm-smooth, and (d) 33-mm-rough substrates with species separated. *P*-values and R^2 values for the overall model are shown. Significant *P*-values are in bold.



a.

	A. carolinensis		**A. sagrei**		**A. distichus**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
Intercept	-15.98	0.223	8.25	0.419	-14.05	0.603
Forelimb Residuals	-5.83	0.216	-3.91	0.156	-1.94	0.771
Hindlimb Residuals	3.08	0.498	2.11	0.570	2.85	0.589
Toe III Lamellae	0.24	0.871	-1.55	0.289	1.03	0.724
Toe IV Lamellae	2.14	0.407	-1.42	0.278	-1.56	0.710
SVL	1.68	0.472	-0.63	0.774	4.34	0.528
Mass	0.63	0.488	0.95	0.222	-1.83	0.496
Observations	20		19		13	
R^2 / R^2 adjusted	0.391 / 0.110		0.502 / 0.253		0.133 / -0.734	

b.

	A. carolinensis		**A. sagrei**		**A. distichus**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
Intercept	6.19	0.471	13.78	0.096	-8.88	0.359
Forelimb Residuals	-0.36	0.905	-1.67	0.421	5.72	**0.042**
Hindlimb Residuals	4.44	0.156	-0.11	0.969	-0.05	0.977
Toe III Lamellae	0.18	0.849	-1.03	0.361	-0.32	0.755
Toe IV Lamellae	0.08	0.962	-0.62	0.535	1.06	0.478
SVL	-2.23	0.163	-3.07	0.090	1.70	0.480
Mass	1.48	**0.027**	1.92	**0.006**	0.05	0.960
Observations	20		19		13	
R^2 / R^2 adjusted	0.553 / 0.347		0.662 / 0.493		0.620 / 0.240	

c.

	A. carolinensis		**A. sagrei**		**A. distichus**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
Intercept	-6.18	0.692	9.38	0.520	-29.63	0.171
Forelimb Residuals	-5.11	0.367	-2.61	0.496	1.32	0.790
Hindlimb Residuals	5.17	0.356	-3.90	0.467	2.14	0.587
Toe III Lamellae	-0.64	0.719	-2.46	0.245	4.34	0.081
Toe IV Lamellae	2.12	0.499	3.69	0.063	0.88	0.777
SVL	-0.44	0.876	-4.67	0.157	4.03	0.436
Mass	0.51	0.646	1.52	0.179	-2.59	0.217
Observations	20		19		13	
R^2 / R^2 adjusted	0.213 / -0.150		0.376 / 0.063		0.650 / 0.300	

d.

	A. carolinensis		**A. sagrei**		**A. distichus**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
Intercept	-7.63	0.213	10.02	0.303	-11.34	0.472
Forelimb Residuals	-8.38	**0.002**	-1.95	0.441	-0.32	0.933
Hindlimb Residuals	6.71	**0.006**	2.83	0.424	2.83	0.365
Toe III Lamellae	0.31	0.650	-1.48	0.285	-0.35	0.836
Toe IV Lamellae	0.90	0.456	-1.52	0.222	0.46	0.849
SVL	0.65	0.549	-1.02	0.626	2.95	0.460
Mass	0.72	0.105	1.34	0.079	-0.65	0.669
Observations	20		19		13	
R^2 / R^2 adjusted	0.737 / 0.616		0.641 / 0.461		0.213 / -0.574	

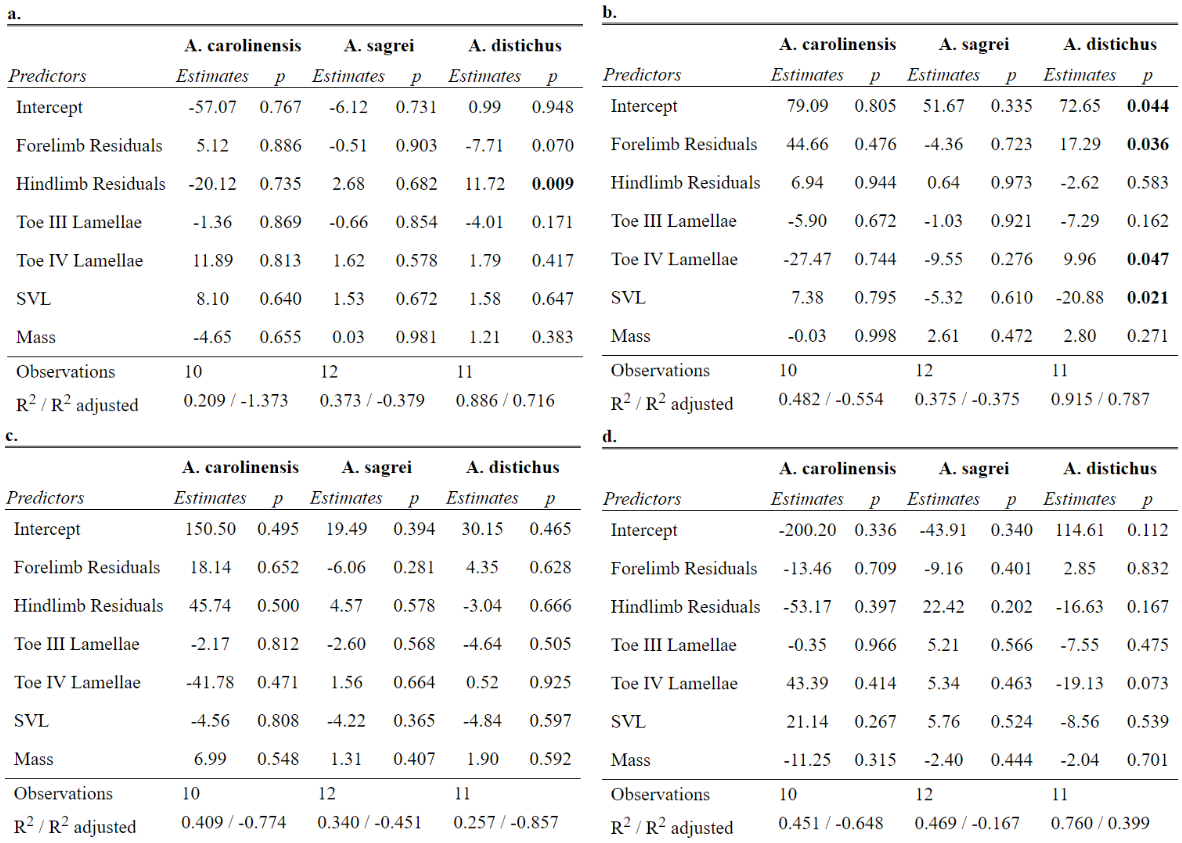
Clinging Time and Morphology

For the windspeed-trials, we used multiple regression models to test for the relationships between morphological variables and clinging time. With species pooled, there were no significant relationships between morphology and clinging time on any of the four substrate types (Table 7). With species separated, *A. distichus* had a significant relationship between an aspect of morphology and clinging time for the 12-mm-smooth substrate, longer hindlimbs increased clinging for this species (Table 8a). *Anolis distichus* also had significant relationships between some morphological variables and clinging time on the 12-mm-rough substrate. Longer forelimbs, more hindlimb lamellae, and a longer SVL increased clinging time in this species (Table 8b). No morphological variables were significant for any species for the 33-mm-smooth or the 33-mm-rough substrates (Table 8c & 8d).

Table 7. Results from multiple regression testing for effects of the six morphological traits on the amount of time to remove a lizard from all four substrates with species type pooled. *P*-values and R^2 values for the overall model are shown. Significant *P*-values are in bold.

	12-mm-Smooth		**12-mm-Rough**		**33-mm-Smooth**		**33-mm-Rough**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
Intercept	-4.54	0.512	-14.62	0.379	-3.52	0.703	-21.06	0.147
Forelimb Residuals	-2.03	0.524	4.71	0.535	-1.91	0.653	1.22	0.852
Hindlimb Residuals	6.72	0.119	-1.82	0.856	-0.06	0.991	-3.54	0.684
Toe III Lamellae	-1.03	0.346	-0.52	0.842	-0.24	0.868	2.54	0.264
Toe IV Lamellae	-0.09	0.952	1.17	0.744	1.04	0.601	3.17	0.308
SVL	2.85	0.202	4.76	0.370	1.01	0.731	2.70	0.553
Mass	-0.60	0.478	-1.80	0.371	-0.20	0.860	-0.88	0.610
Observations	33		33		33		33	
R^2 / R^2 adjusted	0.165 / -0.028		0.076 / -0.137		0.084 / -0.127		0.480 / 0.360	

Table 8. Results from multiple regression testing for effects of the six morphological traits on the amount of time to remove a lizard from (a) 12-mm-smooth, (b) 12-mm-rough, (c) 33-mm-smooth, and (d) 33-mm-rough substrates with species separated. *P*-values and R^2 values for the overall model are shown. Significant *P*-values are in bold.



a.

	A. carolinensis		**A. sagrei**		**A. distichus**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
Intercept	-57.07	0.767	-6.12	0.731	0.99	0.948
Forelimb Residuals	5.12	0.886	-0.51	0.903	-7.71	0.070
Hindlimb Residuals	-20.12	0.735	2.68	0.682	11.72	**0.009**
Toe III Lamellae	-1.36	0.869	-0.66	0.854	-4.01	0.171
Toe IV Lamellae	11.89	0.813	1.62	0.578	1.79	0.417
SVL	8.10	0.640	1.53	0.672	1.58	0.647
Mass	-4.65	0.655	0.03	0.981	1.21	0.383
Observations	10		12		11	
R^2 / R^2 adjusted	0.209 / -1.373		0.373 / -0.379		0.886 / 0.716	

b.

	A. carolinensis		**A. sagrei**		**A. distichus**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
Intercept	79.09	0.805	51.67	0.335	72.65	**0.044**
Forelimb Residuals	44.66	0.476	-4.36	0.723	17.29	**0.036**
Hindlimb Residuals	6.94	0.944	0.64	0.973	-2.62	0.583
Toe III Lamellae	-5.90	0.672	-1.03	0.921	-7.29	0.162
Toe IV Lamellae	-27.47	0.744	-9.55	0.276	9.96	**0.047**
SVL	7.38	0.795	-5.32	0.610	-20.88	**0.021**
Mass	-0.03	0.998	2.61	0.472	2.80	0.271
Observations	10		12		11	
R^2 / R^2 adjusted	0.482 / -0.554		0.375 / -0.375		0.915 / 0.787	

c.

	A. carolinensis		**A. sagrei**		**A. distichus**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
Intercept	150.50	0.495	19.49	0.394	30.15	0.465
Forelimb Residuals	18.14	0.652	-6.06	0.281	4.35	0.628
Hindlimb Residuals	45.74	0.500	4.57	0.578	-3.04	0.666
Toe III Lamellae	-2.17	0.812	-2.60	0.568	-4.64	0.505
Toe IV Lamellae	-41.78	0.471	1.56	0.664	0.52	0.925
SVL	-4.56	0.808	-4.22	0.365	-4.84	0.597
Mass	6.99	0.548	1.31	0.407	1.90	0.592
Observations	10		12		11	
R^2 / R^2 adjusted	0.409 / -0.774		0.340 / -0.451		0.257 / -0.857	

d.

	A. carolinensis		**A. sagrei**		**A. distichus**	
Predictors	*Estimates*	*p*	*Estimates*	*p*	*Estimates*	*p*
Intercept	-200.20	0.336	-43.91	0.340	114.61	0.112
Forelimb Residuals	-13.46	0.709	-9.16	0.401	2.85	0.832
Hindlimb Residuals	-53.17	0.397	22.42	0.202	-16.63	0.167
Toe III Lamellae	-0.35	0.966	5.21	0.566	-7.55	0.475
Toe IV Lamellae	43.39	0.414	5.34	0.463	-19.13	0.073
SVL	21.14	0.267	5.76	0.524	-8.56	0.539
Mass	-11.25	0.315	-2.40	0.444	-2.04	0.701
Observations	10		12		11	
R^2 / R^2 adjusted	0.451 / -0.648		0.469 / -0.167		0.760 / 0.399	

Clinging Ability During Hurricane-Force Winds

We measured the time lizards spent clinging to the dowel while experiencing high winds and the wind speed for which lizards could maintain their grip. The maximum windspeed that the leaf blower could produce was 195 kph. Most lizards reached this maximum windspeed during trials, so we did not analyze wind speed as a response variable.

Based on MLE models and Tukey's HSD *post-hoc* tests, we found no significant differences in the clinging time on any of the dowels except for the 33-mm-rough one (Table 9). In these models, the reference species is *A. carolinensis*, the reference dowel diameter is broad, and the reference dowel texture is rough. We found that *A. carolinensis* could cling significantly longer than *A. sagrei* and *A. distichus* on the 33-mm-rough dowel. For all three species, lizards stayed on the 33-mm-rough dowel the longest, followed by the 12-mm-rough, the 12-mm-smooth, and, lastly, the 33-mm-smooth dowel (Figure 6). On smooth dowels, most lizards (57%) had their hindlimbs detach from the dowel first, whereas on rough dowels most lizards (73%) had their forelimbs detach from the dowel first.

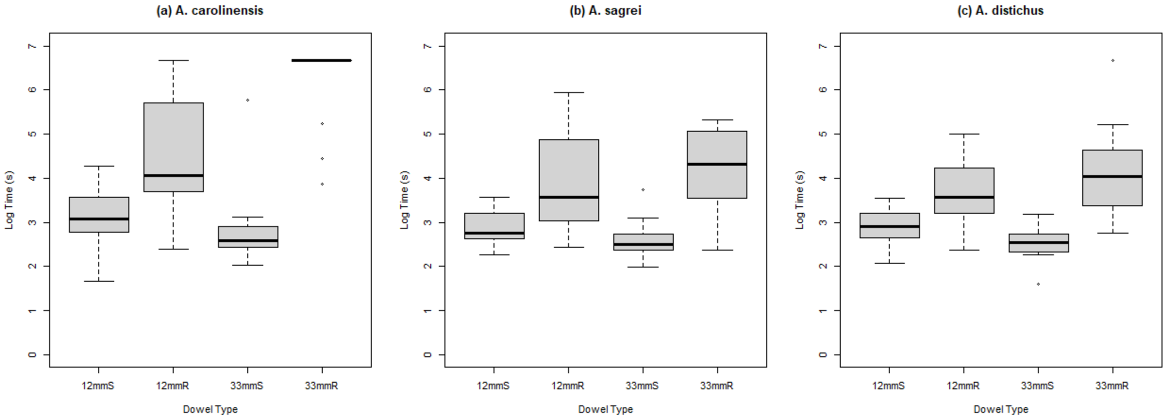
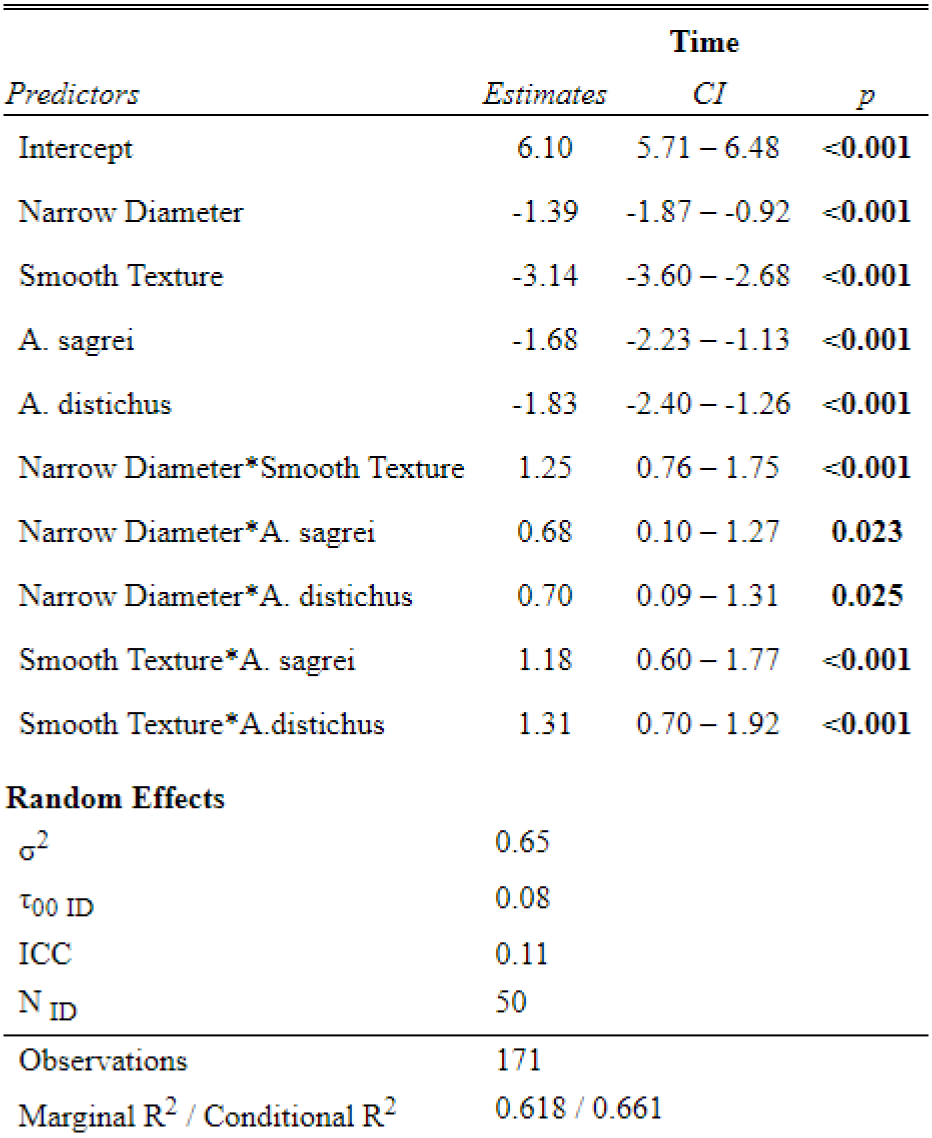


Figure 6. Mean time spent clinging during hurricane-force winds for (a) *A. carolinensis*, (b*) A. sagrei*, and (c) *A. distichus* on four different substrates varying in diameter and surface texture.

Table 9. Mixed linear effects model results with lizard identity as a random effect testing for the effects of overall dowel structure, species, and interactions among these factors. *P*-values and R^2 values for the overall model are shown. Significant *P*-values are in bold.



	Time		
Predictors	*Estimates*	*CI*	*p*
Intercept	6.10	5.71 – 6.48	**<0.001**
Narrow Diameter	-1.39	-1.87 – -0.92	**<0.001**
Smooth Texture	-3.14	-3.60 – -2.68	**<0.001**
A. sagrei	-1.68	-2.23 – -1.13	**<0.001**
A. distichus	-1.83	-2.40 – -1.26	**<0.001**
Narrow Diameter*Smooth Texture	1.25	0.76 – 1.75	**<0.001**
Narrow Diameter*A. sagrei	0.68	0.10 – 1.27	**0.023**
Narrow Diameter*A. distichus	0.70	0.09 – 1.31	**0.025**
Smooth Texture*A. sagrei	1.18	0.60 – 1.77	**<0.001**
Smooth Texture*A.distichus	1.31	0.70 – 1.92	**<0.001**
Random Effects			
σ^2	0.65		
τ_{00} ID	0.08		
ICC	0.11		
N_{ID}	50		
Observations	171		
Marginal R^2 / Conditional R^2	0.618 / 0.661		

DISCUSSION

Our experimental assessment of clinging ability in three species of *Anolis* lizards revealed several key findings. First, the diameter and texture of substrates influenced clinging performance: narrow and rough substrates increased clinging ability during clinging-force trials, while broad and rough substrates increased clinging time during wind-speed trials. Second, species differed consistently in clinging performance among the four substrates in the clinging-force trials, but only differ on the broad and rough substrate in the wind-speed trials. Third, morphological traits such as limb length, lamella number, mass, and SVL, influenced clinging ability, but the relationship varied depending on the trial type, substrate diameter and texture, and species. Taken together, these results provide us with insight into how species and individuals might perform during high-speed winds associated with hurricanes.

We found that surface diameter and roughness significantly affected anole clinging performance. However, the effect of substrate type on clinging performance differed between the clinging-force trials, which isolated the physical ability of lizards to grasp the substrate, and the wind-speed trials, which allowed for some behavioral response as well as clinging ability. In the clinging-force trials, narrower dowels likely increase clinging because the ability of lizards to wrap their limbs around a substrate increases with narrower substrates (Kolbe 2015). As a result, lizards can form a more secure grip around narrow substrates that directly opposes the pulling direction (Kolbe 2015). Lizards that are unable wrap their limbs around broad substrates would have to rely more on toepads and claws to resist being pulled from the substrate (Kolbe 2015). In the wind-speed trials, broad dowels might increase clinging time because they may have provided some protection for lizards against the wind. In both the clinging-force and wind-speed trials, lizards were intentionally placed so that all limbs and toes were fully attached to the substrate. In the wind-speed trials, however, lizards pivoted to the leeside of the dowel after the wind started, apparently to avoid the wind. This movement may have disrupted the placement of limbs and toes and inhibited the ability of the lizard to wrap its limbs around the substrate to form a strong grip, which may have been more challenging on the narrow substrates due to greater exposure to the wind during this process. Because of this, in the wind-speed trials, protection from the wind might have been more influential for clinging time than wrapping limbs around the dowel to form a stronger grip. Surface roughness increased clinging performance in anoles in both the clinging-force and wind-speed trials. Rough dowels likely increase clinging ability because claws can interlock with the substrate, increasing resistance against pulling or wind (Zani 2000). Claw measurements were not recorded in this study, but future studies should consider measuring variation in claw length and curvature to determine whether variation in this trait affects clinging performance. Detailed examination of the functional relationship between claws and clinging force is needed to answer questions surrounding the benefits of rough substrates to clinging performance (Zani 2000).

Understanding how substrate type affects lizard clinging performance can provide insight into what substrates lizards might prefer in nature. Some evidence exists that animals avoid structural habitats in which their maximal performance capabilities are impaired and will select perches that maximize performance (Irschick & Losos 1999). The results from our study suggest that lizards should select broad and rough substrates during hurricanes to enhance clinging ability, and therefore their chance of survival. However, if preferred vegetation is not available, it will hinder a lizard's ability to be selective and might force them to use substrates that they would avoid otherwise (Johnson et al. 2006). Our wind-speed trials suggest that if a variety of perch textures are available during hurricanes, broad diameters will be favored over narrow ones. If only smooth substrates are available, diameter will not matter, as lizards perform equally (poorly) on narrow and broad diameters on smooth substrates (Table S2). However, in habitats like small islands where only narrow substrates may be available, results from the clinging-force trials might be more applicable for predicting anole performance. Based on the clinging-force trials, if only narrow diameters are available, rough substrates will be favored (Table S3). Together, the clinging-force trials and the wind-speed trials help us to understand how different substrates influence anole clinging performance and may provide insights into how lizards might select perches in nature during hurricane-force winds.

Our three anole species we studied are ecomorphs that differ in morphology and thus may vary in their clinging ability. We confirmed our hypothesis that *A. carolinensis* would have the best clinging ability but rejected our hypothesis that *A. distichus* would be intermediate and *A. sagrei* would be the poorest performer. In the wind-speed trials, there were no significant relationships between morphological variables and clinging time. However, we did find that, in the clinging-force trials, larger masses, more hindlimb lamellae, and longer hindlimbs increase clinging ability on specific types of dowels, the 12-mm-rough, 33-mm-smooth, and 33-mm-rough substrates, respectively. Previous studies found that body mass was not correlated with clinging ability (Irschick et al. 1995) and that large lizards have lower ratios of clinging ability to mass than small lizards (Elstrott & Irschick 2004). Muscle size positively scales with body size (Zimmerman & Lowery 1999), and the force a muscle can produce is largely proportional to its size (Biewener 2003). Because of this, large lizards have large muscles and, therefore, might require more force to be pulled from a substrate. However, the body size ranges in these previous studies were an order of magnitude greater than ours, which might explain the discrepancy in body mass effects between the studies. More lamellae likely increase clinging ability on the 33-mm-smooth substrate because the broad and smooth surface might provide the lizards an ability to better position their limbs and flatten their toes in order to more effectively bond the lizard to its substrate (Losos 2009). Lastly, longer hindlimbs might increase clinging ability on the 33-mm-rough substrate because longer hindlimbs might require more force for lizards to be removed from their substrate (Kolbe 2015).

The wind-speed trials showed a significant result between species on the 33-mm-rough dowel, with *A. carolinensis* being able to maintain its position on this substrate significantly longer than *A. sagrei* and *A. distichus*. This might have to do with the way *A. carolinensis* was able to position itself on the dowel. Compared to *A. sagrei* and *A. distichus*, *A. carolinensis* tended to move quicker to the lee side of the dowel, likely allowing *A. carolinensis* to better protect itself from the wind. On average, *A. carolinensis* took 3.7 seconds to move to the lee side of the dowel while *A. sagrei* and *A. distichus* took 10.4 and 12.3 seconds, respectively. Other factors not included in our study, such as claw morphology or other behavior, might also be influencing lizard performance during these trials. Future studies should include these factors to see how they influence clinging performance in both wind-speed trials and clinging-force trials.

Previous studies comparing morphology of *Anolis scriptus* before and after hurricanes provided evidence that hurricanes can act as selective forces on the morphology of anoles (Donihue et al. 2018; Donihue et al. 2020). Our analyses from the clinging-force trials found that some morphological traits, including hindlimb lamella number, hindlimb length, and mass, increase clinging performance on some substrates. Our finding that more lamellae enhance clinging ability is consistent with previous findings that selection due to hurricanes favors larger toepads (Donihue et al. 2018, Donihue et al. 2020). However, our finding that increased hindlimb length enhances clinging ability does not correspond with this previous study (Donihue et al. 2018). Our analyses from the wind-speed trials found no relationship between morphological traits and clinging performance during hurricane-force winds. The lack of significant influence of morphology might be due to the behavioral aspect (i.e., jumping off the dowel or refusing it perform maximally) that was included in the wind-speed trials. Differences between our study and previous studies on the influence of morphology during hurricanes may be due to the different species involved; we also suggest that future studies consider the position of a lizard's limbs while perching during high winds. Donihue et al. (2018) noted that the hindlimbs of *A. scriptus* jutted out while they perched, such that longer hindlimbs would be selected against because they provided more surface area for the hurricane-force winds to act against. More detailed analysis of how the species in this study and other *Anolis* species hold their limbs is needed. It is also important to consider the extent to which behavior of lizards during high winds alters how selection acts on morphological traits via their clinging performance. Differences between our clinging-force and wind-speed trials suggest that behavior is important under some circumstances. Yet, although the wind-speed trials reflected conditions anoles would experience in nature more than the clinging-force trials, the wind-speed trials were still performed in a laboratory setting. The controlled laboratory setting does not include variables such as wind direction, precipitation, and substrate flexibility that could also influence anole habitat selection. Future studies should include conditions more like an actual hurricane to see if these variables influence clinging performance.

In conclusion, we found that substrate type influences clinging performance in anoles, with narrow and rough substrates increasing clinging performance during clinging-force trials but broad and rough substrates increasing clinging performance during wind-speed trials. Moreover, we found that some morphological variables increased clinging on some substrates for some species, depending on the trial (clinging-force or wind-speed). Together, our results further our understanding of how performance in anoles is affected by hurricanes, potentially acting as selective events. The role of extreme weather events in driving evolution is of pressing interest as climate change continues to increase the intensity of frequency of these events (Trenberth 2005; Grant et al. 2016; Sobel et al. 2016). More studies are needed to evaluate the contribution of other traits and environmental conditions to gain a more holistic understanding of how hurricanes might influence natural selection. Along with this, future studies should include other ecomorph types, as well as multiple species from each ecomorph, to produce a more holistic assessment of clinging differences between ecomorphs during hurricane-force winds.

SUPPLEMENTAL MATERIALS

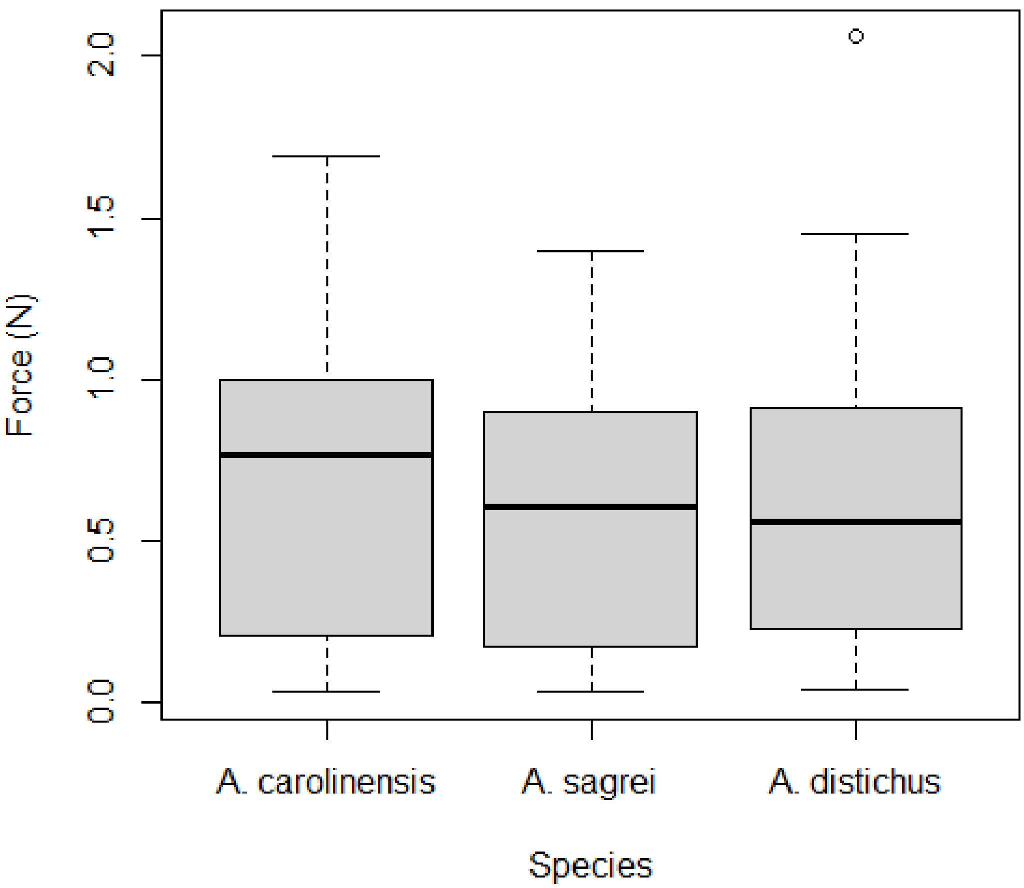


Figure S1. Mean force required to pull each species from a perch (substrate type pooled).

Table S1. Tukey HSD *post hoc* results for morphology ANCOVAS. *P*-values are shown, and significant *P*-values are in bold.

	Forelimb adj *P*-value	Hindlimb adj *P*-value	Toe III Lamella adj *P*-value	Toe IV Lamella adj *P*-value
A. sagrei – A. carolinensis	**0.02**	**<0.0001**	**<0.0001**	**<0.0001**
A. distichus – A. carolinensis	**<0.0001**	**0.02**	**<0.0001**	**<0.0001**
A. distichus – A. sagrei	0.15	**<0.0001**	**<0.0001**	**0.05**

Table S2. Tukey HSD *post hoc* results for wind-speed trial MLEs. *P*-values are shown, and significant *P*-values are in bold.

	P-value
12-mm-Smooth – 12-mm-Rough	**<0.0001**
12-mm-Smooth – 33-mm-Smooth	0.43
12-mm-Smooth – 33-mm-Rough	**<0.0001**
12-mm-Rough – 33-mm-Smooth	**<0.0001**
12-mm-Rough – 33-mm-Rough	**<0.0001**
33-mm-Smooth – 33-mm-Rough	**<0.0001**

Table S3. Tukey HSD *post hoc* results for clinging-force trial MLEs. *P*-values are shown, and significant *P*-values are in bold.

	P-value
12-mm-Smooth – 12-mm-Rough	**<0.0001**
12-mm-Smooth – 33-mm-Smooth	**<0.0001**
12-mm-Smooth – 33-mm-Rough	**<0.0001**
12-mm-Rough – 33-mm-Smooth	**<0.0001**
12-mm-Rough – 33-mm-Rough	**0.01**
33-mm-Smooth – 33-mm-Rough	**<0.0001**

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