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Effects of Hind-Limb Length and Perch Diameter on Clinging Performance in *Anolis* Lizards from the British Virgin Islands

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Abstract.—**Most previous studies of clinging ability in *Anolis* lizards have focused on how toepads adhere to smooth, flat surfaces; yet lizards in nature use a wide variety of substrates ranging from smooth to rough and narrow to broad. I used an ecologically relevant measure of performance to determine the effects of hind-limb length and substrate diameter on clinging ability for two species of *Anolis* lizards from the British Virgin Islands. Clinging force was greater on the 12-mm smooth, wooden dowel compared to the 33-mm one for both species. Male *Anolis cristatellus* had considerably larger hind limbs than female *A. cristatellus* and both sexes of *Anolis stratulus*, and consequently performed substantially better on both dowel diameters. Results suggest two important components of clinging ability on cylindrical substrates: first, the ability of lizards to reach around and interlock their limbs with the substrate increases with longer limbs and narrower substrates; and second, the limb strength to maintain a grip on the dowel when limbs wrap fully around and the ability to apply compressive force when limbs wrap only partially around the dowel. These abilities are likely related to muscle size (e.g., cross-sectional area) and may be correlated with limb length. Further studies to understand how multiple morphological traits and different substrates affect clinging performance will contribute to a better understanding of this morphology-performance-habitat use relationship.**

Morphology affects many aspects of performance in *Anolis* lizards (anoles) including running, jumping, biting, and clinging (Losos, 2009). For example, limb length shows a strong relationship with locomotor performance with longer-limbed species (and individuals) running faster on broad substrates (Macrini and Irschick, 1998; Losos, 2009). This relationship changes across perch diameters, with sprint speed decreasing on narrower perches for most species and longer-limbed species showing a greater decrease in sprint speed than do shorter-legged species (Losos and Sinervo, 1989; Spezzano and Jayne, 2004). Thus, variation in both morphology and substrate can interact to affect performance.

Some authors have demonstrated that *Anolis* lizards show a positive relationship between toepad size and clinging ability on smooth, flat surfaces (Irschick et al., 1996; Elstrott and Irschick, 2004). Enlarged scales on the toes (i.e., subdigital lamellae) allow anoles to climb on smooth vertical substrates because of the presence of microscopic structures (i.e., setae) that adhere to surfaces through van der Waals forces; thus, more setae imply more force of adhesion (Autumn and Peattie, 2002; Autumn et al., 2002). Irschick et al. (1996) allowed both front feet of lizards to contact a nearly vertical force platform and then pulled the lizards down parallel to the surface to measure clinging ability. This experimental design was well suited for measuring how lizards adhere to smooth, flat surfaces using their toepads. However, other specialized structures such as sharply curved claws or limbs, tendons, and toes could influence clinging performance across different substrates (Zani, 2000; Tulli et al., 2009, 2011). For example, in a diverse group of 68 species of New World lizards including some *Anolis* species, Zani (2000) found wider toes and more lamellae increased clinging performance on smooth surfaces, whereas thicker claws and shorter toes were better suited for rough substrates. Because anoles in nature use substrates that vary in roughness and diameter (e.g., broad, smooth leaves or rough, narrow twigs), how aspects of morphology other than toepads influence clinging ability warrants further study.

Measuring clinging ability on smooth, flat surfaces isolates how toepads adhere through van der Waals forces (e.g., Irschick et al., 1996). In contrast, lizards clinging onto rougher and narrower surfaces, such as tree trunks or branches, will likely employ a combination of several phenomena when clinging. In addition to toepads adhering to the substrate, the tips of claws may interlock the substrate, producing force parallel to the surface that counteracts the horizontal component of shear (Cartmill, 1985; Hildebrand and Goslow, 2001; Alexander, 2003). Even if claws cannot interlock, they may still increase frictional resistance in a manner dependent on the substrate (Cartmill, 1985). Furthermore, toes or limbs may grasp the substrate through muscular effort, creating forces normal to the surface of the support that increase frictional resistance to slipping (Cartmill, 1985; Hildebrand and Goslow, 2001; Abdala et al., 2009; for detail, see white arrows in Fig. 1). These compressive forces directed toward the object during grasping are a function of the contact area with the substrate and the muscular effort exerted by the lizard, which is likely influenced by factors such as muscle cross-sectional area. Moreover, these forces best resist forces pulling a lizard away from a perch when they are in line with the pulling direction (i.e., the applied force), such as when a lizard forms a grip by wrapping its limbs around a perch to the side opposite its body (For detail see white and black arrows for 12-mm dowels in Fig. 1).

Based on this functional argument for grasping, clinging performance should increase with the ability to wrap limbs around the perch and the muscular effort to form a firm grip. When a lizard grasps a branch, its limbs will wrap around more as the perch diameter decreases and limb length increases (Fig. 1). Therefore, clinging performance is expected to increase with longer limbs and on narrower perches, particularly when these factors combine resulting in a grip that encircles the substrate. Furthermore, lizards with longer limbs likely have larger muscles (i.e., cross-sectional areas), which should increase clinging force. A better understanding of this morphology-performance relationship is important for evaluating the functional significance of morphological variation and its ecological relevance (Losos, 1990; Wainwright, 1994; Irschick, 2003).

I measured clinging performance of two *Anolis* species using an ecologically relevant, whole-organism approach. Given the relationship between limb length and locomotor performance in *Anolis* lizards (e.g., Losos and Sinervo, 1989; Losos, 1990;

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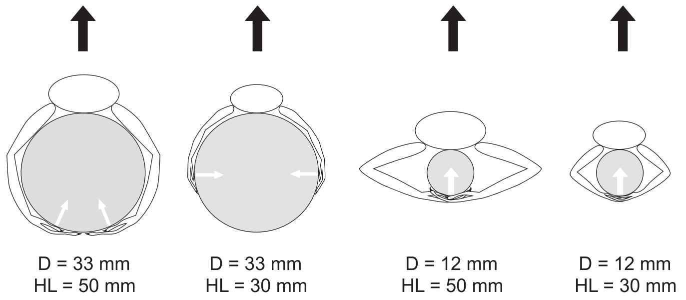

FIG. 1. Schematic diagram of limb postures for anoles during the clinging performance trials. I show hind-limb postures here but forelimbs grasped the dowel in a similar manner. Hind-limb lengths (HL) and dowel diameters (D) depicted in the figure are proportional to values in this study. A hind-limb length of 30 mm is typical of female *Anolis cristatellus* as well as male and female *Anolis stratulus*, whereas a hind-limb length of 50 mm is typical of male *A. cristatellus* (Table 1). The view is looking down from above on a vertically positioned dowel and lizard and shows the long axis of each limb segment perpendicular to the long axis of the cylindrical dowel. The black arrows indicate the direction (horizontal) the lizards were pulled to measure clinging force (i.e., the applied force). The white arrows indicate a predicted normal reference between the most distal limb segment (toes or claws) and the cylindrical surface with thin arrows for separate limbs and thick arrows for both limbs combined. Lizards best resist being pulled away from the dowel when the normal reference (white arrow) is in line with the force pulling the lizards (black arrow), as observed for lizards of both hind-limb lengths on the 12-mm dowel. Note that, for a lizard with shorter limbs on the 33-mm dowel, the limbs are too short to reach around to the side opposite the body, but a variety of limb lengths can do so on the 12-mm dowel.

Macrini and Irschick, 1998), I was interested in determining whether a similar relationship exists between limb length and clinging performance and whether this relationship differs with perch diameter. An understanding of how trait variation affects multiple measures of performance, such as the effect of limb length on both running and clinging, is essential for evaluating how morphology and performance interact to influence fitness.

MATERIALS AND METHODS

Study System.—I sampled two species of *Anolis* lizards on Guana Island, British Virgin Islands, in October 2012. Both species are distributed throughout the Greater Puerto Rican Bank from mainland Puerto Rico to the U.S. and British Virgin Islands. On Guana Island, these species occur in natural forest and disturbed areas, such as gardens, orchards, and landscaping around buildings and trails (Lazell, 2005). They are active diurnally and are mostly insectivorous. *Anolis cristatellus* is typically active on the ground and on tree trunks up to 2 m high and shows strong sexual size dimorphism with males up to 72 mm snout–vent length (SVL) and females up to 52 mm SVL (Schwartz and Henderson, 1991; Losos, 2009). *Anolis stratulus* typically perches higher on trunks than *A. cristatellus*, uses somewhat narrower perches on average compared to *A. cristatellus* (Losos, 1990), and sexual size dimorphism is weak in this species with males up to 48 mm SVL and females up to 45 mm SVL.

Habitat Use and Morphology.—Most lizards encountered during this study were perched on vegetation, although both species were observed on the ground at times. I measured perch height and perch diameter for every undisturbed adult lizard using a measuring tape or ruler.

TABLE 1. Sample sizes, means ± SD, and ranges for morphological measurements, structural habitat use, and clinging force for both *Anolis* species separated by sex.

Species	Sex	*N*	SVL (mm)	Hind-limb length (mm)	*N*	Perch height (cm)	Perch diameter (mm)	*N*	Clinging force (N) 12 mm	Clinging force (N) 33 mm
A. stratulus	Female	19	41.9 ± 1.4 (39.5–44.5)	27.1 ± 1.0 (25–29)	10	122.6 ± 79.4 (19–300)	99.1 ± 52.9 (38–190)	19	0.18 ± 0.1 (0.07–0.33)	0.10 ± 0.1 (0.05–0.21)
A. stratulus	Male	19	45.5 ± 2.5 (36.5–48)	30.3 ± 1.3 (27–32)	22	127.9 ± 59.5 (38–230)	122.2 ± 79.2 (30–300)	19	0.29 ± 0.1 (0.15–0.5)	0.16 ± 0.1 (0.07–0.24)
A. cristatellus	Female	22	46.8 ± 3.1 (41–52)	34.8 ± 2.0 (31–38)	31	65.6 ± 38.3 (3–133)	60.6 ± 56.4 (6–250)	22	0.25 ± 0.1 (0.1–0.47)	0.13 ± 0.1 (0.05–0.25)
A. cristatellus	Male	22	58.7 ± 7.0 (48–72)	46.5 ± 5.8 (38–58)	17	117.6 ± 63.7 (15–250)	110.3 ± 84.4 (15–300)	22	0.79 ± 0.3 (0.23–1.47)	0.53 ± 0.3 (0.12–1.43)

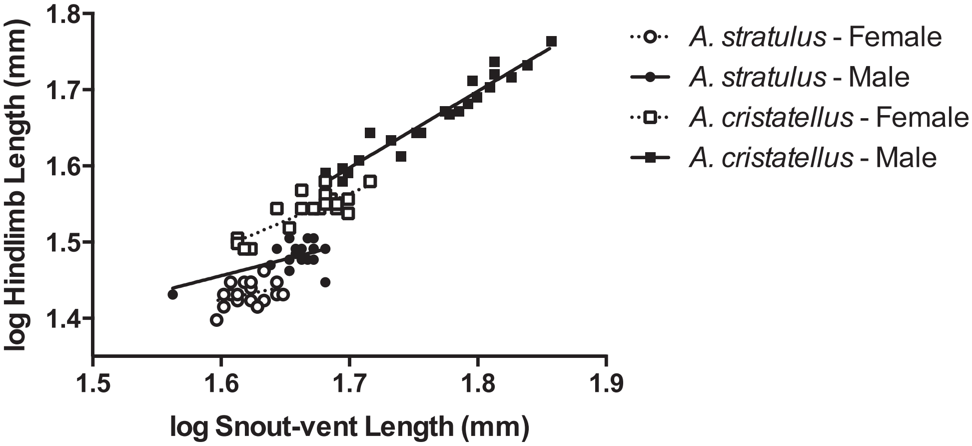

FIG. 2. The relationship between log hind-limb length and log snout–vent length for two species of *Anolis* lizards. Lines on the plot indicate linear relationships calculated separately for each species-sex combination.

For each individual used in the clinging performance trials, I recorded species and sex and measured hind-limb length and SVL with a ruler to the nearest 0.5 mm. Hind limbs were measured from the insertion of the limb into the body wall to the tip of the claw and SVL from the tip of the snout to the cloaca.

Performance.—I measured the force necessary to pull a lizard off of a vertically positioned smooth, wooden dowel. Field-caught lizards were fitted with a harness around their midsection located half way between their fore- and hind limbs. Lizards were positioned so that all four limbs wrapped around the perch rather than being held close to their body (Fig. 1). This increased maximal clinging force in practice trials and likely better replicates the posture of a lizard attempting to hold on to a perch during a storm, predation attempt, or aggressive interaction. I attached the harnessed lizard to a digital force gauge (Extech Model 475040) with an accuracy of 0.01 Newtons (N), which I set on peak force mode. I then moved the perch and lizard at a slow, constant speed away from the force gauge such that the perch and lizard were oriented vertically and perpendicular to the sensing head of the force gauge. I tested lizards on perches of two dowel diameters: 12 and 33 mm. Each lizard was tested at least three times on each diameter to determine maximal force using the 12-mm dowel first. Trials in which lizards did not attempt to hold on or clearly underperformed (i.e., when not all four limbs remained in contact with the dowel) were discarded (Losos et al., 2002). All trials were conducted by the author to maintain consistency. The highest force measurement on each of the two diameters was used in subsequent statistical analyses.

Statistical Analyses.—All variables were log-transformed prior to analyses because raw distributions were not normal. A value of 1 was added to clinging force before log transformation. Perch height and diameter use differences between species (*A. cristatellus* and *A. stratulus*), sex (male and female), and their interaction were evaluated using a two-way analysis of variance (ANOVA). I tested for a difference in hind-limb length between species, sex, and their interaction using analysis of covariance (ANCOVA) with SVL as a covariate. In cases where the interpretation of the main effect was invalidated by heterogeneous regression slopes (i.e., a significant interaction between the main effect and covariate), I used the Johnson-Neyman procedure (White, 2003). This method determined the range of covariate values (i.e., SVL) in which hind-limb length differed between groups. I used a mixed model ANOVA to test for main effects of species, sex, dowel diameter (12 and 33 mm), their pairwise interactions, log hind-limb length, and log SVL on clinging force. Because I used most individuals to measure clinging force on both the 12- and 33-mm diameter dowels, the identity of the lizard was included as a random factor to avoid pseudoreplication. The scaling relationship of clinging performance was investigated by regressing log clinging force + 1 against log hind-limb length for each species-sex combination and dowel diameter separately.

RESULTS

Consistent with previous studies of habitat use in these species (Losos 1990, 2009), *A. stratulus* perched higher than *A. cristatellus* (two-way ANOVA; $F_{1,62} = 4.36$, $P = 0.041$; Table 1), and males perched higher than females ($F_{1,62} = 4.16$, $P = 0.046$). The species by sex interaction was not significant ($F_{1,62} = 2.06$, $P = 0.156$). In contrast to expectations, *A. stratulus* perched on broader vegetation compared to *A. cristatellus* (two-way ANOVA; $F_{1,76} = 5.57$, $P = 0.021$; Table 1). Males perched on broader vegetation than did females ($F_{1,76} = 3.97$, $P = 0.050$), and the species by sex interaction was not significant ($F_{1,76} = 1.64$, $P = 0.205$). In the model testing for hind-limb length differences, the three-way interaction involving species, sex, and the SVL covariate was nonsignificant and removed from the final model. The significant interactions between the SVL covariate and the main effects of species and sex indicated that the relationship between hind-limb length and SVL varied between species and sexes (Fig. 2, Table 2). Pairwise comparisons of each species-sex combination revealed significant

TABLE 2. Results of an ANCOVA using snout–vent length (log SVL) as a covariate to explore factors affecting differences in log hind-limb length for *Anolis cristatellus* and *Anolis stratulus*. The species by sex by log SVL interaction was nonsignificant and removed from the final model.

Factor	*F*	df	*P*
Species	239.6	1, 75	<0.0001
Sex	53.4	1, 75	<0.0001
Species by sex	2.4	1, 75	0.127
log SVL	74.5	1, 75	<0.0001
Species by log SVL	16.4	1, 75	0.0001
Sex by log SVL	5.0	1, 75	0.028

TABLE 3. Results from a mixed model ANOVA with lizard ID as a random effect testing for effects of species, sex, dowel diameter, log hind-limb length, log SVL, and interactions among these factors. The random effect of lizard identity explained 44% of variation.

Factor	*F*	df	*P*
Species	7.9	1, 75	0.006
Sex	0.0	1, 75	0.976
Dowel diameter	122.8	1, 76	<0.0001
log hind-limb length	11.1	1, 74	0.001
log SVL	1.9	1, 74	0.172
Species by sex	5.1	1, 75	0.027
Species by dowel diameter	5.5	1, 76	0.022
Sex by dowel diameter	7.7	1, 76	0.007

interactions with the SVL covariate only in cases involving male *A. cristatellus*. For all other comparisons, pairwise hind-limb length differences were significant (all $P < 0.0001$), and slopes were homogeneous. The Johnson-Neyman procedure showed male *A. cristatellus* had significantly longer hind limbs when compared to female *A. stratulus* over all values of the SVL covariate, to male *A. stratulus* for SVL values greater than 38 mm, and to female *A. cristatellus* for SVL values greater than 44 mm (Fig. 2).

Clinging force differed significantly between species and dowel diameters (Table 3). Across all species-sex combinations, lizards generated greater clinging force when tested on the narrower 12-mm dowel (Fig. 3). Furthermore, male *A. cristatellus* generated substantially greater clinging force compared to female *A. cristatellus* and both sexes of *A. stratulus* (Fig. 3; Table 1). Clinging force increased with hind-limb length (Figs. 4, 5) but not SVL (Table 3). Interactions between main effects and log hind-limb length were nonsignificant and removed from the final model. Significant interactions among main factors of species, sex, and dowel diameter were detected (Table 3) and primarily driven by the large difference in morphology and clinging force between male *A. cristatellus* and the other groups (Figs. 3–5).

The scaling relationship of clinging force on hind-limb length showed significant positive allometry for all groups except male *A. stratulus* (Table 4). Slopes were greater for this scaling relationship on the 12-mm dowel as compared to the 33-mm one for all groups except male *A. cristatellus*, although 95% confidence intervals indicate slope estimates were not significantly different between dowel diameters for any group. When comparing among groups, slopes were greater for male *A. cristatellus* compared to male *A. stratulus* on the 12-mm dowel and greater for male *A. cristatellus* compared to all three groups on the 33-mm dowel (Table 4).

DISCUSSION

Clinging ability differed between dowel diameters and across hind-limb lengths for the *Anolis* lizards in this study (Table 3). Thus, similar to previous studies of sprinting ability in *Anolis* lizards (e.g., Losos and Sinervo, 1989; Marcrini and Irschick, 1998; Spezzano and Jayne, 2004), performance is influenced by characteristics of the substrate as well as morphology of the lizards. However, in contrast to sprint speed where performance decreases on narrower surfaces (Losos and Sinervo, 1989), clinging performance increased on the narrower diameter dowel in this study. A similar trade-off exists in two species of Kenyan chameleons where sprint speed decreased on narrower dowels, but clinging ability increased (Losos et al., 1993). In contrast, Liolaemini lizards do not show a trade-off between sprint speed and clinging performance, perhaps because of their relatively conserved body shape (Tulli et al., 2011, 2012).

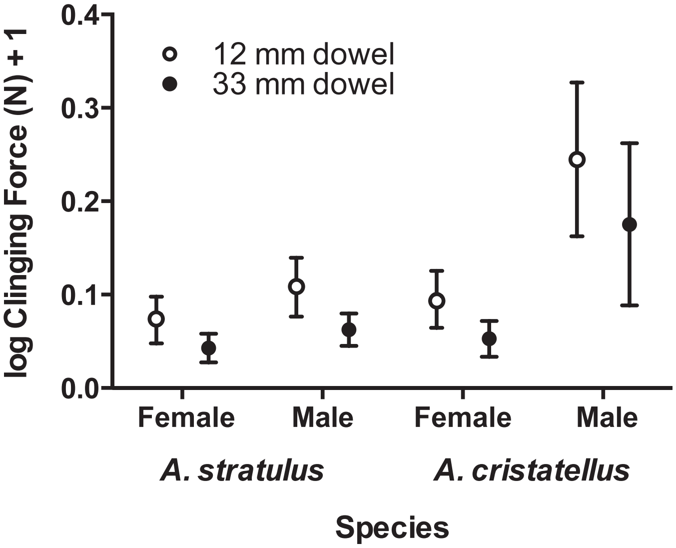

FIG. 3. Differences in mean (± SD) log (clinging force + 1) by species, sex, and dowel diameter. See Table 2 for statistical results.

Clinging force increased substantially for all groups on the 12-mm dowel compared to the 33-mm one: the average increase was 49% for male *A. cristatellus*, 92% for female *A. cristatellus*, 81% for male *A. stratulus*, and 80% for female *A. stratulus* (Fig. 3). Lizards accomplished this increase in clinging force in part because all groups of lizards could wrap their limbs completely around the 12-mm dowel, which allowed them to form a more secure grip that directly opposed the pulling direction (Fig. 1). In contrast, only the male *A. cristatellus* with the longest limbs could fully wrap around the 33-mm dowel. Limbs of most female *A. cristatellus* and both sexes of *A. stratulus* could only reach about half way around the 33-mm dowel (Fig. 1; Table 1). Therefore, individuals with relatively short limbs relied primarily on compressive force from limb adduction to generate friction to prevent slippage, whereas individuals with the longest limbs also could form a grip that encircled the 33-mm dowel, which increased clinging performance substantially. Although lizards used both fore- and hind limbs when clinging in this study, I only measured hind-limb length. Fore- and hind-limb lengths are highly correlated in anoles (Kolbe et al., 2011); yet future studies should consider evaluating the effects of fore- and hind limbs on clinging ability separately.

Forming a grip appeared to be an important component of clinging; yet variation in limb length still affected clinging performance on both dowel diameters. In general, clinging ability increased with longer hind limbs in all groups for both diameter dowels (Figs. 4–5; Table 4). However, the relationship between clinging force and hind-limb length differed between the two dowel diameters, scaling relationships were more similar among species-sex combinations on the 12-mm dowel, likely because all individuals could wrap their limbs around the dowel (Fig. 4; Table 4). In contrast, on the 33-mm dowel, clinging force remained relatively low and scaling relationships similar up to a hind-limb length of approximately 40 mm (Fig. 5; Table 4). At this point, the increase in clinging force per unit of hind-limb length increased substantially. Only male *A. cristatellus* had hind-limb lengths larger than 40 mm, which allowed them to reach farther around the dowel when grasping it (Fig.

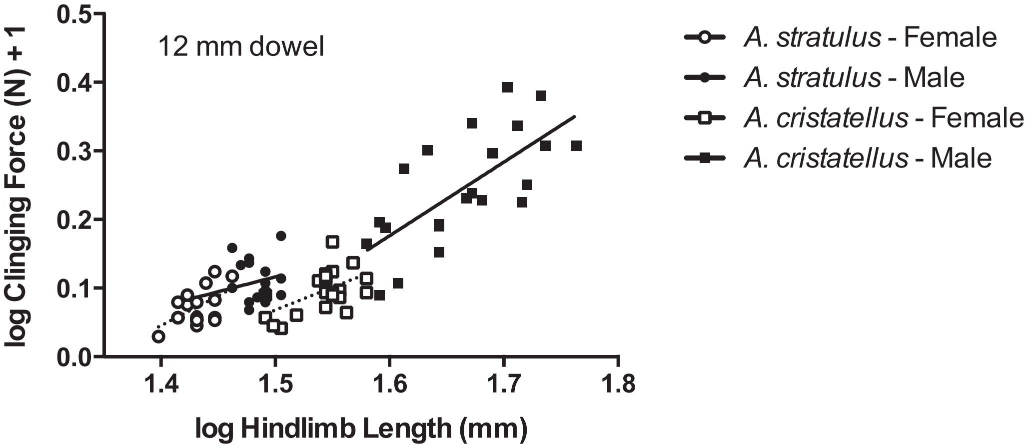

FIG. 4. The relationship between log hind-limb length and log (clinging force + 1) on the 12-mm diameter dowel. Lines on the plot indicate linear relationships calculated separately for each species-sex combination.

1), resulting in an increase in clinging force as described above. An additional consideration is that muscle cross-sectional area should scale with hind-limb length, such that the greater clinging force of lizards with longer limbs is likely attributable in part to greater muscular effort. Unfortunately, to my knowledge, no studies of intraspecific scaling of muscles with limb length (or body size) exist for anoles or any other lizards, but positive scaling of muscle cross-sectional area with body size is plausible (e.g., Zimmerman and Lowery, 1999).

These results suggest two important components of clinging to cylindrical substrates in lizards. First, the ability to reach around the substrate and form a grip with their limbs increases with limb length in general. For narrow diameter substrates, most adult lizards of the species in this study would be capable of this limb position (Fig. 1). Second, limb strength is needed to maintain a grip on the cylinder when limbs wrap around fully or to apply compressive force when limbs wrap around only partially. The force that a muscle can produce is largely proportional to its cross-sectional area (Biewener, 2003) and likely correlated with limb length.

Most individuals experienced a reduction in clinging force on the broader diameter dowel (Fig. 2). When extrapolating to diameters larger than those used here and more similar to the perches used by these species in nature (Table 1), I would expect clinging ability to decrease further. But why then do lizards occupy such broad perches when clinging performance is so poor? There are at least three explanations. First, broad perches are often trees with rough bark; thus, claws become a more important factor in clinging ability (Zani, 2000). Mahendra (1941) experimentally tested the importance of claws for climbing on rough surfaces, finding clawless geckos lose their ability to climb on such surfaces. Most previous studies of *Anolis* isolate the performance of toepad lamellae on smooth surfaces (Irschick et al., 1996; Elstrott and Irschick, 2004). The extent to which claws, and possibly lamellae, improve clinging performance on the rough substrates that *Anolis* lizards typically use has not been tested directly. Claws were unlikely to contribute substantially to clinging force on the smooth dowels used in this study because they were unable to interlock with the substrate, but larger toepads or more lamellae could contribute to performance differences by increasing adhesion. *Anolis* species and populations within species that use broader diameter perches tend to have larger toepads (Macrini et al., 2003; Irschick et al., 2005), suggesting toepads could compensate to some degree for the reduced clinging ability of lizards on broad substrates by increasing adhesion. Toepad area data are not available for *A. stratulus*, but an ecologically similar species on Puerto Rico, *Anolis evermanni*, has larger toepads and greater clinging ability compared to *A. cristatellus* (Elstrott and Irschick, 2004). In this study, *A. stratulus* had greater clinging force

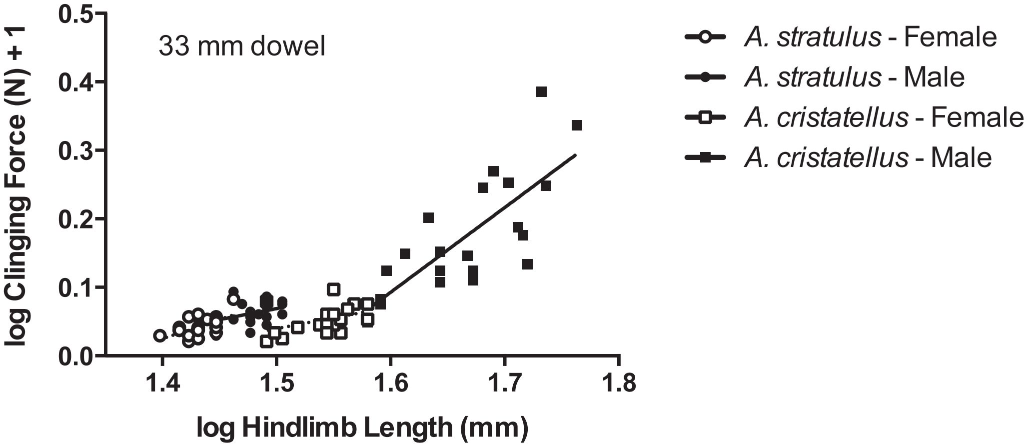

FIG. 5. The relationship between log hind-limb length and log (clinging force + 1) on the 33-mm diameter dowel. Lines on the plot indicate linear relationships calculated separately for each species-sex combination.

TABLE 4. Scaling of log hind-limb length with log clinging force for each species-sex combination separately on both the 12-mm and 33-mm diameter dowels.

Species/Sex	Dowel diameter	*N*	Intercept	Slope	*r*	*P*	95% Confidence interval
A. stratulus—Female	12	19	−1.17	0.87	0.54	0.02	0.18–1.56
	33	19	−0.76	0.56	0.57	0.01	0.15–0.97
A. stratulus—Male	12	19	−0.53	0.43	0.27	0.27	–
	33	18	−0.41	0.32	0.37	0.13	–
A. cristatellus—Female	12	22	−0.92	0.66	0.55	<0.01	0.19–1.13
	33	21	−0.43	0.32	0.43	0.05	0–0.63
A. cristatellus—Male	12	22	−1.54	1.07	0.70	<0.01	0.57–1.58
	33	21	−1.89	1.24	0.76	<0.01	0.74–1.74

compared to female *A. cristatellus* despite having relatively shorter hind limbs over a similar range of body sizes (Figs. 2–5). Future studies should evaluate the effect of multiple morphological traits on clinging performance. Indeed, Irschick et al. (1996) found approximately 50% of the variation in clinging ability on a smooth surface among diverse pad-bearing lizards remained unexplained after removing the effects of body size, suggesting multiple factors including toepad area may influence clinging ability.

Second, running or jumping performance may be more important than clinging ability when on broad perches. In contrast to clinging force, sprint speed increases with perch diameter (Losos and Sinervo, 1989; Marcrini and Irschick, 1998), and when using broad surfaces, lizards may rely on their running ability. Moreover, anoles in nature selectively jump from perches that are relatively noncompliant, which improves their performance (Gilman and Irschick 2013). Broader perches are typically less flexible and better for jumping. Whether habitat use and behavior influence the choice of performance mode in nature is an important question for future studies (Losos and Irschick, 1996; Zani, 2001).

Third, variation in clinging ability may not be important ecologically. The relatively weak clinging ability of lizards on broad substrates may be sufficient for normal activities. For example, a large male *A. cristatellus* at this site would weigh about 10 g (JJK, unpubl. data). Given the clinging forces measured in this study (Table 1), such a lizard could likely support over 100 g on both the 12-mm and 33-mm dowels (1 N is approximately 100 g). Therefore, the safety margin for normal activity appears large compared to the size of these lizards, but less common events may play a role in shaping clinging ability. The selective pressures influencing this morphology-performance-habitat use relationship are not well known (Elstrott and Irschick, 2004; Losos, 2009), clinging ability could be related to numerous factors including aggressive interactions, predation pressure, risk of falling, use of smooth surfaces, and tropical storms. Disentangling how these potential selective forces and morphological trait variation interact to influence clinging performance is a challenging task.

In conclusion, lizards showed greater clinging performance on the narrower diameter substrate, and clinging force increased with hind-limb length for both species. Studies are needed to simultaneously evaluate the contribution of toepad lamellae, toe and limb morphology, and claws to clinging performance and whether the relative importance of these morphological variables varies on different substrate types (e.g., roughness and diameter). Because traits may be subject to multiple selective forces that vary over time and space, a thorough understanding of the ways in which a trait functions in multiple ecological contexts is needed.

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