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Author(s): Austin M. Garner, Alyssa Y. Stark, Scott A. Thomas, and Peter H. Niewiarowski
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Geckos go the Distance: Water's Effect on the Speed of Adhesive Locomotion in Geckos

Austin M. Garner,[1] Alyssa Y. Stark,[2] Scott A. Thomas, and Peter H. Niewiarowski

Department of Biology, Program in Integrated Bioscience, University of Akron, Akron, Ohio USA

Abstract.—The gecko adhesive system has been subject to widespread investigation for many decades, but relatively few studies explore environmentally relevant conditions that geckos likely face in their natural habitat. Recent evidence suggests that after *Gekko gecko* take more than three steps on wet glass, their shear adhesion is significantly lower than adhesion on dry substrates. Such an observation is intriguing because many species of geckos are indigenous to the tropics and must commonly navigate wet substrates. Here we report the locomotor performance of two gecko species, *G. gecko* and *Chondrodactylus bibronii*, measured on wet vertical glass and acrylic substrates over a distance of 2 m. We found that neither water nor substrate type had a significant effect on the mean sprint velocity of either species. Mean sprint velocity was unaffected despite variation in frequencies of slipping between species, where *C. bibronii* slipped significantly more than did *G. gecko*. Interestingly, the substrate effect on the frequency of slipping was nonsignificant, but misted glass showed a general trend of producing more slips than did misted acrylic. Our results suggest that geckos can sustain adhesive locomotion for at least 2 m on wet substrates.

The gecko adhesive system has been subjected to widespread investigation over the past few decades, but much is still unknown about how geckos use adhesive locomotion in their natural habitat (Ruibal and Ernst, 1965; Irschick et al., 1996; Autumn et al., 2000; Autumn, 2006). So far, geckos are known to adhere exceptionally well to a variety of substrates, particularly those that are smooth and free of debris (Hansen and Autumn, 2005; Hu et al., 2012; Stark et al., 2012, 2013). Although the gecko adhesive system performs well under these fairly uniform and controlled conditions, natural substrates are likely highly variable (Russell and Johnson, 2007) and may pose as a significant challenge for free-ranging geckos.

Despite considerable work on the effect of substrate on both gecko adhesion and adhesive locomotion, substrate effects appear to be more complex than previously thought (Hiller, 1968; Vanhooydonck et al., 2005; Huber et al., 2007; Russell and Johnson, 2007; Russell and Higham, 2009; Stark et al., 2013). In particular, the effect of surface water on gecko adhesion is dependent on substrate wettability (Stark et al., 2013; Badge et al., 2014). For instance, shear adhesion is significantly reduced on wet hydrophilic substrates but not on wet hydrophobic substrates, which is likely related to the superhydrophobicity (strong water-repelling property) of the gecko toe pad and its interaction with the substrate (Autumn and Hansen, 2006; Stark et al., 2013, 2014a; Badge et al., 2014). Although the gecko adhesive system appears to be insensitive to water on hydrophobic substrates, theory and some data suggest that water could be a significant environmental challenge to geckos in other contexts (i.e., hydrophilic substrates, adhesive toe pads soaked by water), implying that geckos may possess means to avoid or overcome the effects of water on a regular basis (Stark et al., 2012, 2013, 2014b).

Geckos in natural environments likely use their adhesive system more dynamically, such as during a walk or run, and the effects of water on static and dynamic adhesion appears to be considerably different. When geckos walked (up to four steps) on a glass surface misted with water droplets, shear adhesion was significantly reduced to the point where geckos could not support their body weight vertically (Stark et al., 2012). Surprisingly, *G. gecko* were able to maintain similar sprint velocities on both wet and dry substrates over a distance of 1 m, which took more than four steps to complete. This suggests that dynamic adhesion was not affected by water over 1 m (Stark et al., 2015). Such observations beg the questions: why does static and dynamic adhesion differ on wet substrates, and is there a limit to the improved dynamic performance in this context?

Considering that some lizards can sprint long distances to avoid predators (Jayne and Ellis, 1998; Irschick and Jayne, 1999; Higham and Russell, 2010), and that at least one nocturnal gecko species (*Gonatodes antillensis*) appears to sprint from potential predators when discovered at its daytime retreat (Bennett and Gorman, 1979), some geckos may be forced to run on wet substrates for >1 m. Although Stark et al. (2015) determined that geckos sprint equally fast on wet and dry substrates over 1 m, how far that can be maintained before the response seen in the static adhesion experiments is observed (i.e., total loss of adhesion) is not clear. In this context, a substantial reduction in sprint velocity would occur. Although there is a lack of literature detailing the typical distance traveled by free-ranging geckos, investigating the resiliency of the gecko adhesive system over longer distances is also relevant beyond general gecko ecology. The gecko adhesive system is a popular biomimetic model with hundreds of synthetic adhesives designed around its structure and performance (Boesel et al., 2010); however, these bio-inspired adhesives have yet to match the resiliency and efficiency that the gecko adhesive system expresses when encountering difficult substrates or conditions. Further investigation of the gecko adhesive system under natural conditions may be critical in designing gecko-inspired synthetic adhesives that can adapt in a wide variety of environmental situations (Autumn et al., 2014; Niewiarowski et al., 2016).

In this study, we tested the locomotor performance of two species of geckos on wet and dry substrates when sprinting a distance of 2 m. We chose this distance because it is within the locomotor repertoire of at least one gecko species (Higham and Russell, 2010), is a well-represented racetrack length among lizard locomotion studies (Van Damme and Vanhooydonck, 2001), and is twice as long as the sprinting distance tested in previous work (Stark et al., 2015). Geckos were sprinted on both vertical glass and acrylic to test the effect of substrate wettability

[2]Present address: Department of Biology, University of Louisville, Louisville, Kentucky USA

[1]Corresponding Author. E-mail: amg149@zips.uakron.edu
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on mean sprint velocity (SV). In addition to SV, we also recorded the frequency of three observations associated with sprinting on wet substrates (slipping, stopping, and total number of wet toes).

We hypothesized that mean sprint velocity would be negatively affected by water during a 2-m sprint. We also expected previously reported species-level differences to be magnified over this increased distance (Stark et al., 2015). The goal of this study was to increase our understanding of how resilient dynamic gecko adhesive locomotion is under wet conditions, which better represent the environmental variation in substrate quality and gecko behavior (i.e., predator escape on wet substrates).

Materials and Methods

Animals.—Five *Gekko gecko* and four *Chondrodactylus bibronii* were individually housed in glass terraria, fed a diet of cockroaches three times a week, and misted with water twice daily (Niewiarowski et al., 2008).

Experimental Procedure.—The experiment was performed in an environmental chamber kept at a temperature of 25.4 ± 0.14°C and a relative humidity of 60.5 ± 0.29%. Geckos were acclimated to test conditions for at least 1 h before sprinting. Because both species are nocturnal, trials were performed at night during their active period and in the dark using only red headlamps for illumination (Stark et al., 2015). We coerced geckos to sprint up a 2-m vertical racetrack by pursuing the geckos with our hands. The racetrack was equipped with seven light sensors that reported six split time measurements of velocity (cm/sec) (Huey et al., 1989). Geckos were tested in each of these four treatments: dry acrylic, acrylic misted with water to produce an even distribution of water droplets on the surface, dry glass, and glass misted with water in the same fashion as the acrylic substrate. We chose acrylic and glass because glass is hydrophilic, where water remains attracted to its surface more so than with acrylic, which is intermediately wetting (Stark et al., 2013). Before each trial, the substrate was cleaned with ethyl alcohol followed by water and then dried. For the misted trials, the substrates were sprayed evenly with water from a fine-misting spray bottle before each trial.

Geckos were limited to three trials per day, with at least an hour break in between each trial. All geckos were tested three times per treatment. When a gecko was sprinted on a misted substrate, the individual was not tested the rest of the day so that their toe pads could dry, ensuring that geckos began every trial with dry toes. Geckos and treatment were randomly selected prior to each trial.

Three observations associated with sprinting on wet surfaces were recorded: the frequency of slips, stops, and wet toes. Observations were made during live trials. One researcher was responsible for pursuing the gecko up the racetrack with their hands while another researcher was solely responsible for recording the above observations. A slip was recorded when there was an obvious loss in traction from at least one foot, and a stop was recorded when all four feet stopped. The above protocol for recording slips and stops makes the assumption that all of the above observations are drastic events that likely impact sprint velocity. Small stopping and slipping events, particularly slipping at microscopic scales, also may occur during dynamic adhesive locomotion and these would not be observable without a microscope (Gravish et al., 2010). Wet toes were counted at the end of each misted trial; a wet toe was determined by color of the toe (white color indicates a dry toe and grey color indicates a wet toe) and further confirmed to be wet when the toe felt moist to the touch (Stark et al., 2012, 2015).

Statistical Analyses.—We calculated mean SV for each gecko as the mean of all split time measurements for each treatment. We analyzed mean velocity, rather than maximum burst performance, because we were interested in overall performance across the 2-m track. To facilitate species comparisons, we calculated the difference between SV on wet and dry substrates by subtracting each gecko's SV on wet substrates from their SV on dry substrates (SV_{D-M} in cm/s). We tested the effect of water using a repeated measures multivariate analysis of variance (MANOVA). Alternative approaches to analyses (univariate and mixed model) gave qualitatively similar results. SV_{D-M} on glass and acrylic substrates were the dependent variables and species was the independent variable (Irschick and Losos, 1999). We used JMP (v.12; SAS Institute Inc., Cary, North Carolina, USA) for all statistical analyses and refer interested readers to statistical details on analyzing repeated measures analyses with a multivariate, adjusted univariate, or mixed model approach in the JMP documentation library.

We also used repeated measures MANOVAs to test the effect of species and substrate on slips and wet toes. Specifically, species was the independent variable and either the total number of slips or the total number of wet toes per substrate type were the dependent variable. Substrate wetness was not included in the MANOVA of slips and wet toes because these observations never occurred on dry substrates. Finally, we used a repeated measures MANOVA to test the effects of water, substrate, and species on the frequency of stops. Species was modeled as the independent variable and the total number of stops on each substrate type and substrate treatment (i.e., wetness) were the dependent variables.

Results

The MANOVA to test the effect of water on sprint velocity (SV_{D-M}) revealed that neither species ($F_{1,7} = 1.4925$, $P = 0.2614$), substrate type ($F_{1,7} = 0.9165$, $P = 0.3703$), nor their interaction ($F_{1,7} = 0.8707$, $P = 0.3818$) had significant effects on the difference in running velocity on dry and misted substrates (SV_{D-M}) (Fig. 1). Specifically, the 95% confidence intervals of SV_{D-M} included 0 cm/s, indicating no difference in SV on dry and misted substrates. Mean sprint velocities for both species of geckos in each treatment are reported in Table 1.

The MANOVA testing the effect of substrate and species on the total number of slips showed a significant difference in the total number of slips between species ($F_{1,7} = 7.2977$, $P = 0.0306$) but not substrate or the species by substrate interaction ($F_{1,7} = 5$, $P = 0.0604$ and $F_{1,7} = 2.222$, $P = 0.1797$ respectively). In general, *Chondrodactylus bibronii* slipped significantly more than did *G. gecko* (Fig. 2), and glass showed a trend toward more slips than did acrylic, but the difference was not statistically significant ($P = 0.0604$; Fig. 3). Variation in the frequency of wet toes was not significantly explained by substrate type (MANOVA; $F_{1,7} = 0.7633$, $P = 0.4113$) or species (MANOVA; $F_{1,7} = 0.9136$, $P = 0.3710$). The frequency of stopping was not significantly affected by substrate type (MANOVA; $F_{1,7} = 1.5109$, $P = 0.2587$), substrate wetness ($F_{1,7} = 0.3078$, $P = 0.5963$), or the three-way interaction (species * substrate type * substrate wetness; $F_{1,7} = 0.0427$, $P = 0.8421$).

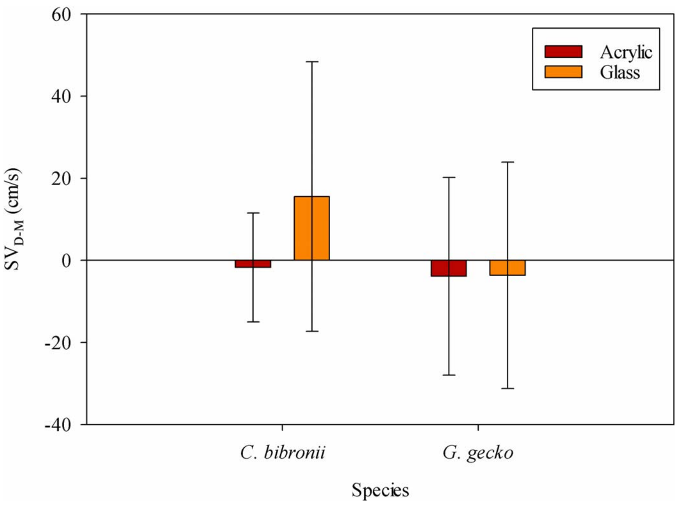

FIG. 1. Mean (±95% C.I.) SV on misted substrates subtracted from mean SV on dry substrates (SV_{D-M} in cm/s) are represented on the y-axis. Mean SV_{D-M} values on both glass and acrylic for *Chondrodactylus bibronii* and *Gekko gecko* are displayed. Positive values indicate the mean SV was lower on the misted susbstrate compared to the dry substrate. Negative values indicate the mean SV was higher on the misted substrate compared to the dry substrate. Neither species ($F_{1,7} = 1.4925$, $P = 0.2614$), substrate type ($F_{1,7} = 0.9165$, $P = 0.3703$), nor their interaction ($F_{1,7} = 0.8707$, $P = 0.3818$) had a significant effect on SV_{D-M}.

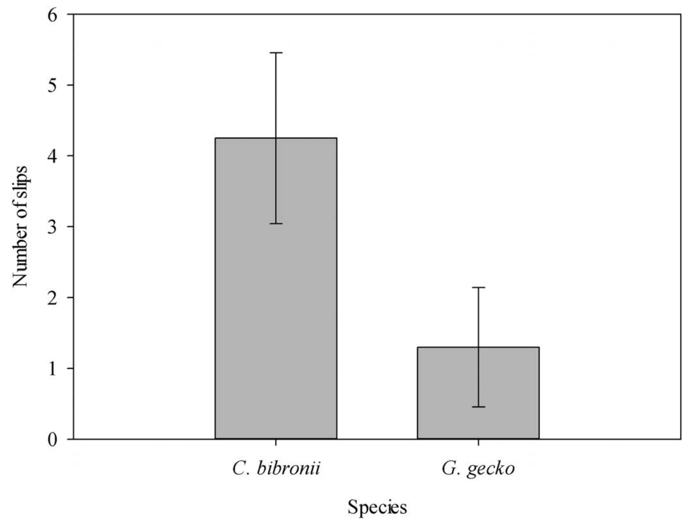

FIG. 2. Mean (±SE) frequency of slips for *Chondrodactylus bibronii* and *Gekko gecko* on all substrates. *Chondrodactylus bibronii* slipped significantly more compared to *G. gecko* ($F_{1,7} = 7.2977$, $P = 0.0306$).

DISCUSSION

In this study, we investigated how water affects the sprint velocity of two species of geckos over 2 m and hypothesized that water would have a significant effect on the sprint velocity of both species. Furthermore, we expected the species-level differences in behavior, as noted by Stark et al. (2015), would be amplified over the increased distance. Surprisingly, substrate wetness had no effect on sprint velocity over our 2-m track across all tested combinations of species and substrate (Fig. 1), despite increased slipping by *C. bibronii* (Fig. 2). Although contrasts between the native environments of these two species are dramatic (*G. gecko* inhabits tropical Southeast Asia and *C. bibronii* inhabits arid South Africa), our experimental design lacks replication within 'environment' and cannot, without further work, definitely ascribe species differences to habitat of origin. Furthermore, our study does not appropriately sample across the gecko phylogeny, so making evolutionary and/or ecological inferences based on our results (Garland and Adolph, 1994) would be problematic. Nonetheless, our results suggest that wet substrates do not dramatically affect the speed of adhesive locomotion in two species of geckos over distances up to 2 m.

Our results suggest that the negative effects of water seen in static adhesion experiments do not directly translate into a performance decrement over 2 m. The nonsignificant effect of water on sprint velocity suggests there are components of sprinting that aid in the resiliency of the toe pad to water. For example, arboreal geckos generally increase the frequency of their strides to achieve higher velocities (Zaaf et al., 2001). Although this would result in toe pads contacting the substrate more frequently, this may decrease the total time toe pads are in contact with the surface (i.e., duty cycle). Therefore, toe pads may be preserved in their dry, superhydrophobic state, suggesting the hypothesis of a negative correlation between duty cycle and stride frequency when geckos run on wet surfaces compared to dry surfaces. Furthermore, the normal forces exhibited by toe pads during attachment may assist in pressing the water out of the setal array, creating dry contact (Stark et al., 2013, 2014a). Given these hypotheses, we are uncertain how much further geckos can maintain this resiliency and remain unaffected by water because of physiological and morphological constraints related to sprinting and adhesion. We encourage future work to focus on investigating the micromechanics of the gecko adhesive system during locomotion and the kinematic differences between walking and sprinting on both wet and dry substrates.

In addition to SV, we also analyzed the effects of substrate type and species on the frequency of three recorded observations: slips, stops, and wet toes. Similar to the previous study by Stark et al. (2015), the frequency of slips was significantly affected by species. *Chondrodactylus bibronii* experienced significantly more slips on misted substrates than did *G. gecko* (Fig. 2) without suffering from a significant reduction in sprint velocity. We predicted that an increase in frequency of slipping behavior would result in a reduction of sprint velocity, especially over 2 m. Hence, our results suggest that *C. bibronii* likely is engaging in compensatory locomotor behaviors to adjust for the loss of traction. Because species and substrate were not significant in the analysis of wet toes, an increased frequency of wet toes could not explain the slipping behavior observed in *C. bibronii*. Clearly, further research will help explain the relationship

TABLE 1. Mean (±SE) SV (cm/s) of both *Chondrodactylus bibronii* and *Gekko gecko* for each treatment (DA = dry acrylic; MA = misted acrylic; DG = dry glass; MG = misted glass) along with other detailed information about the geckos tested.

Species	*n*	Mass (g)	DA (cm/s)	MA (cm/s)	DG (cm/s)	MG (cm/s)
C. bibronii	4	31.5 ± 1.6	43.4 ± 7.0	45.1 ± 5.5	56.4 ± 13.5	40.8 ± 4.2
G. gecko	5	68.7 ± 2.2	70.7 ± 14.7	74.6 ± 19.7	75.4 ± 17.4	79.0 ± 17.2

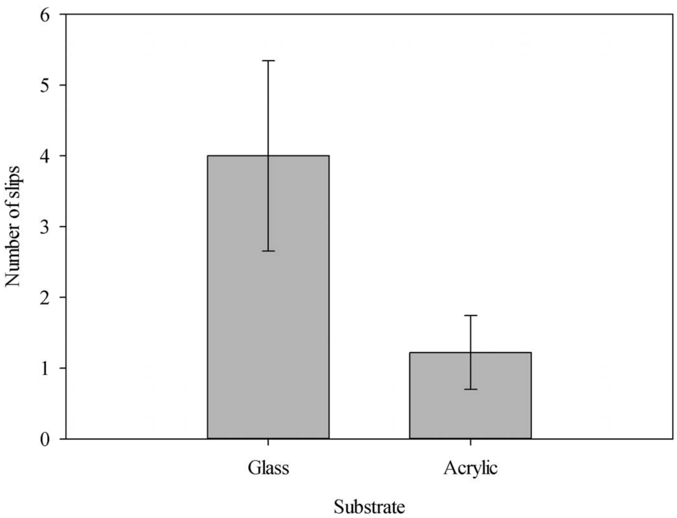

FIG. 3. Mean (± SE) frequency of slips on either glass or acrylic for all geckos are displayed. The effect of substrate type on the frequency of slips was not significant ($F_{1,7} = 5$, $P = 0.0604$) but showed a general trend wherein misted glass produced more slips than did acrylic.

between locomotion and slipping on wet substrates, but our study demonstrates that slipping does not necessarily translate into a reduction in velocity.

The effect of substrate on the frequency of slips was marginally not significant; however, larger sample sizes may lead to a significant effect. A general trend of misted glass producing more slips than did misted acrylic was apparent (Fig. 3). As suggested by Stark et al. (2013), this may be because water is acting as a lubricating layer between the hydrophilic glass surface and the gecko toe pad, resulting in the slipping we observed during experimental trials. Additionally, Pesika et al. (2009) and Hsu et al. (2012) determined that water can alter the chemical properties of the gecko setae themselves, and we have yet to discover the impacts of this on static and dynamic adhesion. Therefore, we cannot ignore the possibility of structural, mechanical, or chemical alterations that could be responsible for the observance of this slipping behavior. Such interactions are beyond the scope of our study; however, observing setal behavior during locomotion on wet substrates to determine the origin of these types of behaviors (Stark et al., 2012) would be interesting.

Although the present study and Stark et al. (2015) are similar in their design and results, this study more rigorously tested the effect of water on gecko adhesive locomotion, and our results suggest that it is far more resilient to water than predicted from static adhesive performance. Our study calls for the design of future investigations that can appropriately examine differences between species that inhabit distinct environments. Furthermore, this information may be useful in the design of gecko-inspired synthetic adhesives that can function under difficult environmental conditions. Clearly, more research is needed regarding water's effect on gecko locomotion. Overall, our work not only reveals further complexity associated with the gecko adhesive system but also reveals more of its remarkable efficiency and resiliency that make it such a popular biomimetic model.

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