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Digital hyperextension has no influence on the active self-drying of gecko adhesive subdigital pads

Austin M. Garner[1,2,3] | Carrie Buo[2,3] | Jennifer M. Piechowski[2,3] | Alexandra M. Pamfilie[1,2] | Sharon R. Stefanovic[2,3] | Ali Dhinojwala[1,3,4] | Peter H. Niewiarowski[1,2,3]

[1]Gecko Adhesion Research Group, The University of Akron, Akron, Ohio
[2]Department of Biology, The University of Akron, Akron, Ohio
[3]Integrated Bioscience Program, The University of Akron, Akron, Ohio
[4]Department of Polymer Science, The University of Akron, Akron, Ohio

Correspondence
Austin M. Garner, Gecko Adhesion Research Group, Integrated Bioscience Program, Department of Biology, The University of Akron, Akron, OH.
Email: amg149@zips.uakron.edu

Present address
Sharon R. Stefanovic, Cuyahoga Community College, Health Careers and Science Division, Metropolitan Campus, Cleveland, OH.

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Abstract
The remarkable properties of the gecko adhesive system have been intensively studied. Although many gecko-inspired synthetic adhesives have been designed and fabricated, few manage to capture the multifunctionality of the natural system. Analogous to previously documented self-cleaning, recent work demonstrated that gecko toe pads dry when geckos take steps on dry substrates (i.e., self-drying). Whether digital hyperextension (DH), the distal to proximal peeling of gecko toe pads, is involved in the self-drying process, had not been determined. Here, the effect of DH on self-drying was isolated by preventing DH from occurring during normal walking locomotion of *Gekko gecko* after toe pads were wetted. Our initial analysis revealed low statistical power, so we increased our sample size to determine the robustness of our result. We found that neither DH nor the DH–substrate interaction had a significant effect on the maximum shear adhesive force after self-drying. These results suggest that DH is not necessary for self-drying to occur. Interestingly, however, we discovered that shear adhesion is higher on a surface tending hydrophobic compared to a hydrophilic surface, demonstrating that gecko adhesion is sensitive to substrate wettability during the subdigital pad drying process. Furthermore, we also observed frequent damage to the adhesive system during shear adhesion testing post-drying, indicating that water may compromise the structural integrity of the adhesive structures. Our results not only have behavioral and ecological implications for free-ranging geckos but also have the potential to influence the design and fabrication of gecko-inspired synthetic adhesives that can regain adhesion after fouling with water.

KEYWORDS
adhesion, *Gekko gecko*, Gekkonidae, van der Waals, wetting

1 | INTRODUCTION

The remarkable adhesive capabilities of geckos have gained considerable interest over the past few decades, particularly after the discovery that the van der Waals intermolecular forces are responsible (Autumn et al., 2002). The gecko adhesive system is composed of arrays of broadened subdigital scales (scansors/lamellae) that contain hierarchical, as yet uncharacterized, β-keratin and phospholipid fibrils (setae; Alibardi, 2003; Alibardi et al., 2011; Hsu et al., 2012). Setae further branch into nanoscale contact points (spatulae), that allow for the intimate contact needed to generate the van der Waals interactions (Autumn et al., 2002; Maderson, 1964; Ruibal & Ernst, 1965; Russell, 1975). The van der Waals intermolecular forces are inherently weak, but they can generate forces strong enough to support many times a gecko's body weight when multiplied by the millions of setae found on gecko toes (Autumn et al., 2000, 2002). While much of gecko adhesion research has been carried out under controlled laboratory conditions, efforts investigating gecko adhesion and adhesive locomotion under less than ideal environmental conditions are increasing.

Through experiments utilizing both whole animals and isolated lamellae, the gecko adhesive system has been shown to be a reusable, self-cleaning, dry adhesive that can maintain its adhesion in unfavorable conditions (e.g., certain rough surfaces, under vacuum, and underwater; Autumn, 2006; Autumn et al., 2000; Hansen & Autumn, 2005; Huber, Gorb, Hosoda, Spolenak, & Arzt, 2007; Stark et al., 2013). While substantial advancement has been made in the fabrication of gecko-inspired synthetic adhesives, with some of these generating higher shear adhesive forces than a single gecko is capable of producing, there are few that can match the multifunctionality observed in the natural system (Autumn, Niewiarowski, & Puthoff, 2014; Garner, Wilson, Russell, Dhinojwala, & Niewiarowski, 2019; Niewiarowski, Stark, & Dhinojwala, 2016). For example, most synthetic adhesives are subject to an apparent trade-off between adhesive performance and their ability to regain adhesion after fouling. In general, adhesives that sustain higher adhesive forces have a decreased ability to recover adhesion after fouling (Sethi, Ge, Ci, Ajayan, & Dhinojwala, 2008). Geckos, however, have the ability to both generate high adhesive forces on clean substrates and regain adhesion after fouling with either dirt particles or water (Autumn & Hansen, 2006; Hansen & Autumn, 2005; Hu, Lopez, Niewiarowski, & Xia, 2012; Stark, Wucinich, Paoloni, Niewiarowski, & Dhinojwala, 2014). Thus, further investigation into how geckos recover adhesion after fouling may provide critical information for those designing gecko-inspired synthetic adhesives capable of maintaining operation under a wide array of environmental conditions.

Stepping on clean, dry surfaces restores the adhesive performance of gecko toe pads experimentally debilitated with silica microspheres (Hansen & Autumn, 2005). It was suggested that this phenomenon was a result of the substrate having higher adhesion energy relative to the spatulae, causing particles to be more attracted to the substrate than the spatulae. As a follow-up, Hu et al. (2012) proposed an active self-cleaning mechanism, a process known as digital hyperextension (DH; the distal to proximal peeling of gecko adhesive toe pads; Figure 1a; Movie S1). Similar to Hansen and Autumn (2005), live gecko toe pads were debilitated with silica microspheres and geckos were prompted to walk, inducing self-cleaning. To separate the effect of DH on gecko self-cleaning, Hu et al. (2012) prevented DH from occurring in half of their experimental trials and found that DH largely increases the rate of self-cleaning. Although the mechanism has yet to be determined empirically, they proposed that setae store elastic energy during detachment via DH, which, when released, results in the effective

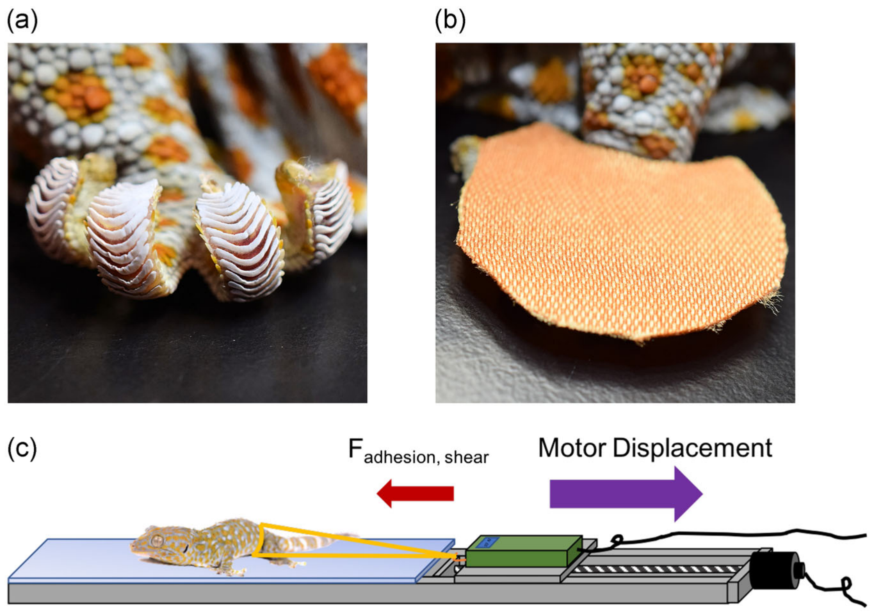

FIGURE 1 Digital hyperextension (DH; the distal to proximal peeling of gecko toe pads), the present study's means of preventing DH, and the force measurement system. (a) Digital hyperextension of *Gekko gecko*. (b) "Shoes" fashioned from the ends of adhesive bandages and acetate transparency sheets prevented DH from occurring. When DH was disabled, geckos peeled their toes in a proximal-to-distal direction instead. (c) Diagram of the force measurement system utilized in the experiment, as described in Niewiarowski et al. (2008). A force sensor (green box; Shimpo FGV-10×; Shimpo Instruments, Glendale Heights, IL) was displaced parallel to the substrate via motor and measured shear adhesive force ($F_{adhesion, shear}$). Harnesses attached to the gecko's pelvis (yellow lines) applied a constant shear load. Modified from Niewiarowski, P.H., A. Dhinojwala, and A.M. Garner. 2019. Adapting a thermal physical model approach to estimate gecko adhesion performance opportunity and constraint: How rough could it be? Integrative and Comparative Biology 59(1): 203–213, by permission of the Society for Integrative and Comparative Biology [Color figure can be viewed at wileyonlinelibrary.com]

propulsion of dirt particles from the setal array during setal disengagement from the substrate (setal jump-off). When DH was prevented, geckos peeled their toe pads in a proximal-to-distal direction and this was suggested to prevent or substantially lower elastic energy storage during setal jump-off (Hu et al., 2012).

While free-ranging geckos likely encounter dirty surfaces on a regular basis, geckos likely encounter wet surfaces as well. Several studies have investigated gecko adhesion under wet conditions, and substrate wettability (hydrophobicity) appears to be a significant factor in gecko adhesion underwater (Badge, Stark, Paoloni, Niewiarowski, & Dhinojwala, 2014; Stark et al., 2013; Stark, Sullivan, & Niewiarowski, 2012). Stark et al. (2013) recorded live gecko adhesive force production on wet and dry substrates that varied in hydrophobicity. Interestingly, gecko adhesion was significantly lower on wet hydrophilic substrates but was similar on wet and dry substrates that tended hydrophobic. Gecko toe pads are naturally superhydrophobic (i.e., water repellant), but this state has been shown to be metastable (Badge et al., 2014; Stark et al., 2012). By forcing water into gecko toe pads, they undergo a transition from a nonwetting state (superhydrophobic) to a wetting state (hydrophilic). In this latter state, geckos have significantly lower shear adhesion on clean, dry substrates (Stark et al., 2012). Stark et al. (2014) discovered that geckos with soaked toe pads can regain their adhesive capacity by stepping on clean, dry substrates. Geckos that took steps were able to regain maximum shear adhesion at a faster rate than those prohibited from taking steps. It was also reported by Stark et al. (2014) that soaked toe pads can dry without stepping, but a longer time is required. Thus, gecko toe pads appear to not only be self-cleaning but also self-drying. Substrate wettability was hypothesized to be important in the self-drying process because, theoretically, hydrophilic substrates should attract water more strongly than hydrophobic substrates and increase self-drying efficacy. Surprisingly, Stark et al. (2014) found that gecko toe pads self-dried at similar rates regardless of substrate wettability.

Although Stark et al. (2014) showed that maximum shear adhesion is regained after successive steps and hypothesized that DH may be involved, the potential role of DH had not been tested. Hu et al. (2012) demonstrated that DH of gecko toes leads to active self-cleaning of gecko toe pads. Following Hu et al. (2012), we tested the hypothesis that DH would also enhance the self-drying of gecko adhesive toe pads. DH may actively expel water from gecko toe pads during self-drying, similar to dirt particles in the model proposed by Hu et al. (2012), or perhaps increase evaporation rates. To test this hypothesis, we fully soaked the toe pads of *Gekko gecko* and prevented DH from occurring while they were walking on a glass or polymethylmethacrylate (PMMA) surface to vary substrate wettability. After a 15-min drying period, we measured maximum shear adhesive force production on the same substrate on which the geckos walked. We predicted that DH would increase the efficacy of self-drying, as it does in the self-cleaning of dirt particles. Although Stark et al. (2014) found that substrate wettability does not affect self-drying, DH may have masked any effect of substrate wettability on the self-drying process. The prevention of DH affects how geckos engage and disengage their adhesive toe pads (Hu et al., 2012), thus it is plausible that the self-drying process is impacted by substrate wettability under these circumstances. We predicted that glass would result in higher efficacy of self-drying when DH is prevented because of its hydrophilic nature. The results of this study will provide a greater understanding of how geckos recover adhesion after encountering water in their natural environments and also serve to influence the design of synthetic adhesives based on the gecko adhesive system.

2 | MATERIALS AND METHODS

2.1 | Animals

Twelve adult *G. gecko* (Linnaeus, 1758), purchased from California Zoological Supply, were used in this experiment ($n = 12$) and housed in 10-gallon glass terraria. Geckos were provided water via misting two times per day and fed cockroaches or crickets three times per week (Niewiarowski, Lopez, Ge, Hagan, & Dhinojwala, 2008). The average gecko mass was 72.1 ± 3.7 g.

2.2 | Experimental procedures

To test the effect of DH on the self-drying of gecko toe pads, geckos were fitted with restrictive "shoes", functioning similarly to those described by Hu et al. (2012), to prevent DH. Shoes were constructed of an acetate transparency sheet sandwiched between the adhesive ends of fabric bandages cut to match the dimensions of the geckos' feet (Figure 1b). The top of the shoe was the nonadhesive side of the fabric bandage and the bottom of the shoe was the adhesive side that could be easily attached to the tops of gecko feet, preventing DH. A notch was cut out of the shoes to allow for the natural articulation of the feet and limbs. Geckos not able to perform DH peel their toes in a proximal-to-distal motion, as opposed to a distal-to-proximal motion as observed during DH (Hu et al., 2012). No damage to the underlying gecko epidermis was observed after shoe removal. For half of the trials, geckos wore these shoes and for the rest of the trials, geckos were allowed to walk unrestricted and perform DH.

All trials were completed in an environmental chamber maintained at a temperature of 24.5 ± 0.14°C and relative humidity of 41.6 ± 0.50%. Geckos were acclimated to the environmental conditions for 10 min. Following that period, geckos underwent an extensive wetting procedure, similar to the protocol described in Stark et al. (2014). Gecko toe pads were agitated with a wet cloth for 10 min to induce the wetting transition. Geckos were placed in small plastic containers with ~0.5 cm of room temperature reverse osmosis (RO) water and allowed to soak for 20 min. The holding containers were small enough to restrict excessive movement. The bodies of geckos and the tops of geckos' feet were towel dried. Gecko toe pads were not touched during this time but were permitted to drip dry until water droplets no longer fell from their adhesive pads (Stark et al., 2014).

Geckos with soaked toe pads were induced to walk about 10 steps with their front feet and back feet, for a minimum of about 20 steps total, on either dry glass or dry PMMA at an incline of 40°. This substrate angle was chosen for two reasons: (a) geckos engage their subdigital adhesive system via DH at angles greater than 30° (Russell &

Higham, 2009), and (b) geckos were unable to climb on substrates inclined at greater substrate angles because their adhesive system was debilitated with water. We chose glass and PMMA to test whether a potential interaction exists between substrate wettability and DH during self-drying. Glass is a hydrophilic surface where water is strongly attracted to its surface (water contact angle ~50°; Stark et al., 2013). PMMA is an intermediately wetting surface; that is, it is neither hydrophobic nor hydrophilic (water contact angle ~85°; Stark et al., 2013). The stepping process was recorded via DSLR camera (Nikon D3300; Nikon Inc., Melville) and the number of steps taken was recorded post hoc. After stepping, geckos were returned to dry holding containers for 15 min. The previous work by Stark et al. (2014) demonstrated geckos with soaked toe pads that took steps on clean, dry surfaces regained adhesion at a faster rate than those that were not. Shear adhesion was measured at intervals of 15 min, and the geckos that took steps required at least an average of 15 min for maximum shear adhesion to be regained (Stark et al., 2014). Thus, self-drying reduces the time to regain maximum adhesion and does not result in dry toe pads by the end of the bout of stepping. Geckos have significantly reduced adhesion when toe pads are soaked with water (Stark et al., 2012), thus we waited for 15 min to permit some drying to occur so we could then examine differences between our treatment groups. If geckos were wearing shoes, they were removed before containment to control for potential differences in drying associated with wearing shoes.

Immediately following the 15-min drying period, maximum shear adhesion was determined for each gecko using a custom force rig (Niewiarowski et al., 2008). The force rig is composed of a force sensor (Shimpo FGV-10×; Shimpo Instruments, Glendale Heights, IL) that can be displaced parallel to a substrate via motor (Figure 1c). Small dorsal and ventral harnesses were placed around each gecko's pelvis. Geckos were placed on horizontally oriented substrates that were of the same material as the substrates on which they took steps (i.e., glass or PMMA). Geckos were encouraged to naturally place their steps with each foot. Once the gecko placed its feet, harnesses were attached to the force sensor, which measured the maximum shear adhesion the gecko could produce. Maximum shear adhesion was defined as the point when all four feet were noticeably slipping on the substrate. An upper shear adhesion threshold of 20 Newtons (N) was utilized, as this value is consistent with reported maximum shear adhesion values for *G. gecko* with fully dry feet (Stark et al., 2014). Shear adhesion values higher than 20 N can result in damage to the subdigital adhesive pads. Due to this possibility of damage, trials were halted if a shear adhesion force of 20 N was achieved. During trials, some geckos lost strips of setae (lamellae). When this occurred, trials were immediately stopped and geckos were returned to their enclosures to rest. Geckos with more than two lamellae missing per toe were not tested again until their lamellae were regenerated after the next shed cycle.

Six geckos were subjected to four different treatments: two control treatments (DH permitted, on both glass and PMMA) and two experimental treatments (no DH permitted, on both glass and PMMA). An additional six geckos were subjected to the control treatment and experimental treatment on PMMA because the statistical analysis of our original data exhibited relatively low statistical power, particularly when analyzing the potential difference between the DH groups on the PMMA substrate. Thus, we doubled the sample size of our PMMA treatments ($n = 12$) to examine the robustness of our original result. In the rest of the manuscript, we report and discuss the results obtained with sample sizes of $n = 6$ for the glass treatments and $n = 12$ for the PMMA treatments. All results were in qualitative agreement. A discussion and qualitative comparison between all of our results can be found in the Supporting Information Data. All measurements outlined in this procedure were carried out three times for each gecko tested. Individual geckos were not tested more than once per trial day. Geckos were given at least one day of rest between trial days to ensure the geckos were well-rested and possessed fully dry toe pads at the start of each trial. Between each bout of stepping and adhesion testing, substrates were first cleaned with a 70% ethanol solution, followed by RO water. Substrates were dried with lint-free tissue paper after the application of each cleaning liquid. Gecko mass was recorded at the end of each experimental trial. The order of individuals and their respective treatment groups were randomly selected before experimentation. All experimental procedures were consistent with The University of Akron IACUC Protocol 16-08-14-NGC and with guidelines created by the Society for the Study of Amphibians and Reptiles (Beaupre, 2004).

2.3 | Statistical analyses

The mean maximum shear adhesion observed for each individual gecko per treatment was obtained by taking the mean of maximum shear adhesion values for each gecko's three trials per treatment. To determine the effect of DH on the self-drying of gecko toe pads, we used a mixed model analysis of variance (ANOVA) to compare maximum shear adhesion as a function of whether DH was permitted (DH or no DH), substrate (glass or PMMA), and their interaction. Another mixed model ANOVA was completed comparing total number of steps taken by geckos as a function of the treatment group. Individual gecko was modeled as a random effect in all analyses.

The residuals in all analyses were normally distributed as determined by Shapiro–Wilks' normality test ($p > .05$), the variance between treatment groups was determined to be homogeneous via Hartley's F_{max} test ($p > .05$), and a repeated-measures approach was utilized to control for the nonindependence of multiple measurements from the same individual. Therefore, data conformed to the assumptions of ANOVA. All statistical analyses were performed using JMP Pro 14 (SAS Institute, Inc., Cary, NC).

3 | RESULTS

After a 15-min drying period, geckos that utilized DH attained a mean maximum shear adhesive force of 6.95 ± 1.58 N on glass and 10.73 ± 1.54 N on PMMA. Geckos prevented from using DH

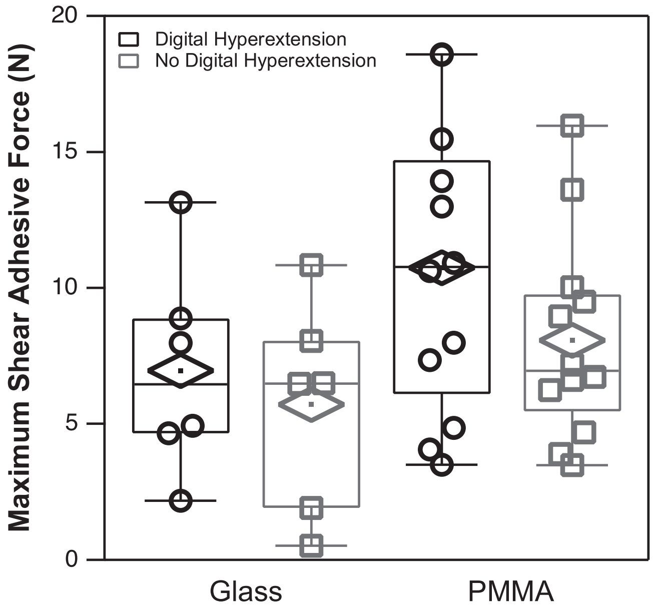

FIGURE 2 Box plots of maximum shear adhesive force of *Gekko gecko* ($n = 6$ for glass; $n = 12$ for polymethylmethacrylate [PMMA]) as a function of the substrate and whether or not digital hyperextension was permitted. A mixed model analysis of variance (ANOVA) revealed that neither digital hyperextension ($F_{1,22.1} = 1.32$; $p = .26$) nor the interaction between digital hyperextension and substrate ($F_{1,22.1} = 0.17$; $p = .68$) had a significant effect on the maximum shear force of *G. gecko*. The substrate, however, significantly impacted the maximum shear adhesion of *G. gecko* after a 15-min drying period ($F_{1,31.2} = 4.38$; $p = .04$). After *G. gecko* subdigital adhesive pads underwent a 15-min drying period, the maximum shear adhesive force was higher on PMMA compared to glass. Diamonds represent mean maximum shear adhesive force, circles represent maximum shear force per individual gecko utilizing digital hyperextension, and squares represent maximum shear force per individual gecko not utilizing digital hyperextension

generated, on average, 5.71 ± 1.57 N on glass and 8.07 ± 1.09 N on PMMA. On average, geckos took a total of 36 ± 1 steps. Geckos that used DH took, on average, 37 ± 3 steps on glass and 37 ± 1 steps on PMMA. Geckos that did not utilize DH took, on average, 36 ± 2 steps on glass and 36 ± 1 steps on PMMA.

The mixed model ANOVA revealed no significant effect of DH ($F_{1,22.1} = 1.32$; $p = .26$) or the interaction between DH and substrate ($F_{1,22.1} = 0.17$; $p = .68$) on mean maximum shear force (Figure 2). Interestingly, substrate had a significant effect on the mean maximum force ($F_{1,31.2} = 4.38$; $p = .04$). Shear adhesion tests on PMMA resulted in significantly higher shear adhesive force compared to glass. The mixed model ANOVA for the total number of steps showed no significant effect of treatment ($F_{3,22.1} = 0.70$; $p = .56$).

4 | DISCUSSION

We hypothesized that the use of DH enhances the self-drying of gecko toe pads after wetting. We tested the adhesion of geckos on glass and PMMA substrates after saturating their toe pads with water and allowing them to walk with and without DH, on clean, dry substrates. Our initial analysis exhibited low statistical power, likely as a result of our relatively low sample size ($n = 6$) and high variance. We assessed the robustness of our original result by increasing our sample size in the PMMA treatment groups ($n = 12$). The increase in sample size revealed that our initial results were robust, as all analyses were in qualitative agreement (see Supporting Information Data). Overall, we found that DH appears to have no effect on maximum shear force after a 15-min drying period, suggesting that DH is of minimal importance in the ability of geckos to self-dry their toe pads. The principal mechanism is that they are able to take steps on a clean, dry substrate. Interestingly, our findings are in contrast to what has been observed with the ability of geckos to self-clean their toe pads after fouling with "dirt" particles. Hu et al. (2012) found that geckos using DH regained adhesion at a faster rate than those that did not. It was suggested that during DH, setae were able to generate enough inertial force during adhesive locomotion to effectively "flick" dirt particles from the setal array. Although this explanation has yet to be verified empirically, we hypothesized that the same principle might also accelerate the drying of toe pads. Surprisingly, we found no significant effect of DH on the maximum shear adhesive force of *G. gecko* after allowing self-drying to occur.

Stark et al. (2014) expected self-drying to be dependent on substrate wettability, with hydrophilic substrates allowing for enhanced self-drying compared to hydrophobic substrates. Instead, Stark et al. (2014) found that substrate wettability had no significant impact on the time to regain maximum shear adhesion after soaking gecko toe pads with water. Although not significant, Stark et al. (2014) noted that the time to regain maximum adhesion on PMMA was, on average, shorter than that on the glass. Interestingly, we found that maximum shear force significantly increased on PMMA compared to glass after self-drying, primarily driven by an increase in maximum shear force in the PMMA no DH group. While this finding may suggest that the extent of self-drying is dependent on substrate wettability, there is no clear theoretical explanation as to why a surface tending hydrophobic would increase the efficacy of self-drying (Stark et al., 2014). Therefore, we argue that this trend may instead be a consequence of how self-drying is empirically quantified. The recovery ability of gecko subdigital adhesive pads in the presence of particulate or liquid contaminants has historically been quantified by examining how adhesive force capacity changes after contact is made with the surface (Hansen & Autumn, 2005; Hu et al., 2012; Stark et al., 2014), as opposed to measuring the amount of contaminant present on the subdigital pad surface. Thus, our finding likely demonstrates that adhesive force production of drying gecko subdigital pads is higher on more hydrophobic surfaces, rather than the notion that surfaces tending hydrophobic increase the extent of the self-drying process. Previous work by Stark et al. (2013) observed no significant differences in the maximum shear force of *G. gecko* on surfaces of varying wettability in dry conditions. Under wet conditions, however, maximum shear force decreased on a hydrophilic surface (glass), while remaining relatively unchanged on surfaces tending hydrophobic (PMMA and octadecyltrichlorosilane self-assembled monolayer). Purportedly, this differential performance is observed because water becomes trapped in the interface between the superhydrophobic gecko toe pad and hydrophilic surface, reducing the van der Waals component of gecko adhesion. On hydrophobic surfaces, however, gecko adhesive pads are capable of expelling water from the interface allowing for relatively dry contact (Stark et al., 2013). Although we could not observe water being excluded from the interface, it is possible that small amounts of water were being repelled by gecko subdigital pads while they were drying and recovering their superhydrophobic state, resulting in significantly higher adhesion on PMMA compared to glass. Thus, it may be that the impact of substrate wettability on self-drying is only a consequence of how self-drying is quantified in this study and by Stark et al. (2014). Future studies could identify methods for quantifying the volume of water in gecko toe pads as a function of time to examine whether substrate wettability improves the efficacy of active self-drying. Additionally, the amount of water present at the interface between a drying gecko subdigital pad and surfaces of varying wettability could be investigated.

In addition to determining that DH had no significant effect on self-drying, we also observed the frequent loss of lamellae during shear adhesion testing after soaked toe pads were allowed to dry. Approximately 18% of trials across all treatments resulted in some loss of lamellae during testing, and, of these trials, 53% of them were from the DH group, and 47% of them were from the no DH group. This observation leads one to question whether the wetting of toe pads can lead to the destruction of the adhesive system once adhesion starts to be regained. To our knowledge, this is the first observation that water may actually cause the structural integrity of the gecko adhesive system to be compromised, although this condition and the resulting damage appears to be temporary. Gecko setae can absorb water and this results in a change in their mechanical and chemical properties (Pesika et al., 2009; Prowse, Wilkinson, Puthoff, Mayer, & Autumn, 2011; Puthoff, Prowse, Wilkinson, & Autumn, 2010). Markedly, the elastic modulus of a single seta decreases after absorbing water, resulting in setal softening (Prowse et al., 2011; Puthoff et al., 2010). As such, if the contact interface of a single seta is dry and the setal stalk has been softened by water, cohesive failure of the seta could occur if adhesion is strong. If this is the case, this may prove to be a significant challenge for geckos in their natural habitat. Although it is unlikely that free-ranging geckos would remain stationary in surface water for timespans similar to those used in this study, this scenario could have significant consequences for geckos in their natural environment, particularly geckos that are highly arboreal. If a gecko's toe pads were to become soaked with water in its natural habitat, it is possible that the adhesive system could be damaged during an event where a gecko is under high shear forces. Recent work has shown that the adhesive system of geckos performing aerial escape maneuvers may be subjected to remarkably high shear force, potentially approaching the adhesive force capacity of the system under such conditions (Higham, Russell, & Niklas, 2017). As such, if water compromises the structural integrity of the gecko adhesive system and a gecko undergoes such an escape maneuver with recently soaked toe pads, damage to the adhesive system may occur. While it is unclear how or if the temporary loss of adhesive capability has any effect on the survivability of geckos, our results demonstrate that a common environmental condition (i.e., surface water) may result in a temporary reduction in structural integrity.

Clearly, the cumulative work on the self-drying of gecko adhesive toe pads is relevant to the ecology of free-ranging geckos and raises important questions regarding how the gecko adhesive system is exploited in nature. For example, if gecko toe pads soaked with water have significantly reduced shear adhesive force (Stark et al., 2012), what would a free-ranging gecko do if its toe pads have been soaked by water? Stark et al. (2014) demonstrated that geckos can dry their toes at a faster rate by walking on clean, dry substrates. While it may seem unlikely that a gecko would have soaked toe pads in a dry environment, little has been documented on conditions of the substrates utilized by free-ranging geckos, not to mention their ecology and behavior (Niewiarowski et al., 2016). Nevertheless, it is unlikely that the natural habitat of *G. gecko* is homogeneously wet after rainfall. For example, there may be patches of the environment that are protected from rainfall, and those substrates may remain relatively dry. Furthermore, at least one species of gecko has been known to travel distances over 10 m and adjust habitat use depending on environmental conditions (Collins, Russell, & Higham, 2015). Therefore, self-drying could be a behavior exhibited by free-ranging geckos, although most geckos are classified as sit-and-wait foragers (Pianka, 1973) and may not travel large distances. Clearly, this gap of information demonstrates the need for comprehensive studies documenting the substrates utilized by free-ranging geckos, the conditions of such substrates, and generally how geckos exploit their adhesive system in natural circumstances (Garner et al., 2019; Niewiarowski et al., 2016; Niewiarowski, Stark, & Dhinojwala, 2017). Furthermore, the self-drying property of gecko adhesive toe pads is relevant to the design and fabrication of gecko-inspired synthetic adhesives. This ability would likely be a marketable property for gecko-inspired synthetic adhesives because self-drying synthetic adhesives could be dried and reused simply by repeatedly pressing them to dry surfaces. Even so, this property has not been heavily studied in gecko-inspired synthetic adhesives, indicating the need for future experiments to determine if synthetic adhesives exhibit similar self-drying behavior and if this process is dependent on the method of peeling.

Our study further investigated the mechanism of self-drying in *G. gecko* and found that DH had no significant effect on the extent of self-drying of adhesive toe pads. This suggests that stepping, regardless of the method of peeling, is sufficient to permit the self-drying of the gecko adhesive system. In addition, we found that maximum shear adhesive force is higher on a surface tending hydrophobic compared to a hydrophilic surface during the self-drying process, indicating that surface wettability is not only important under wet conditions but also after gecko toe pads have been soaked with water. Finally, we found that gecko toe pads recently soaked with water appear to be more susceptible to adhesive pad damage, although further investigation is needed. While our work here has implications for both the ecology of free-ranging geckos and the development of gecko-inspired synthetic adhesives, future studies should investigate the self-drying property of gecko toes in more ecological and evolutionary contexts, as well as determine whether this property is present in gecko-inspired synthetic adhesives and other fibrillar adhesive systems. Clearly, self-drying is one of several remarkable properties of the gecko adhesive system that warrants further investigation by materials scientists and biologists alike.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

ORCID

Austin M. Garner http://orcid.org/0000-0003-1053-9168

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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