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SHORT COMMUNICATION

Tokay geckos (Gekkonidae: *Gekko gecko*) preferentially use substrates that elicit maximal adhesive performance

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ABSTRACT

Gecko substrate use is likely influenced by adhesive performance, yet few studies have demonstrated this empirically. Herein, we examined the substrate use, adhesive performance and vertical clinging behaviour of *Gekko gecko* in captivity to investigate whether adhesive performance influences patterns of substrate use. We found that geckos were observed significantly more often on the substrate (glass) that elicited maximal adhesive performance relative to its availability within our experimental enclosures, indicating that geckos preferentially use substrates on which their adhesive performance is maximal. Our work here provides additional, yet crucial data establishing connections between adhesive performance and patterns of substrate use in captivity, suggesting the hypothesis that substrate preferences of free-ranging geckos should be correlated with adhesive performance. Clearly, further experimental and field research is necessary to test this hypothesis and identify other parameters that individually and/or collectively influence the habitat use of free-ranging geckos.

KEY WORDS: Behaviour, Fibrillar adhesion, Habitat use, Substrate preference, Surface roughness

INTRODUCTION

There is a general lack of habitat use and other ecological data on geckos (Higham et al., 2019; Niewiarowski et al., 2016), particularly when compared with other groups of lizards that bear adhesive subdigital pads (e.g. *Anolis*) (Garner et al., 2019). Higham et al. (2019) noted that most data of gecko habitat use concern species that are diurnal, largely because of the difficulty in documenting habitat use for nocturnal species. Collins et al. (2015), for example, examined the habitat use, escape behaviour and adhesive system morphology of the diurnal Namib day gecko (*Rhoptropus afer*) and found that this species uses the available habitat in non-random ways. During escape manoeuvres, *R. afer* most often uses homogeneous terrain with lower slopes, likely because of the speed reduction incurred upon running on inclined substrates with subdigital adhesive pads (Collins et al., 2015; Russell and Higham, 2009).

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A number of studies have examined gecko adhesive performance in relation to substrate characteristics, and it is clear that maximal adhesive performance varies considerably depending upon substrate and surface properties (e.g. surface roughness, wettability, hardness: Gillies et al., 2014; Huber et al., 2007; Klittich et al., 2017; Pugno and Lepore, 2008; Stark et al., 2013). Thus, geckos may use substrates non-randomly in relation to variation in their adhesive capabilities (Higham et al., 2019), but this has received little attention. Field studies on a small Corsican island noted that two species of gecko on the island (*Tarentola mauritanica* and *Euleptes europaea*) used substrates non-randomly and that this was related to each species' ability to cling to available substrates; *T. mauritanica* was not able to maintain attachment to the friable rock that inundates the island because its subdigital pads would become disabled from rock particulate matter, forcing them to use only concrete walls. *Euleptes europaea*, in contrast, possessed a variant of subdigital morphology that permitted attachment to the friable rock prominent on the island (Delaugerre et al., 2015; Russell and Delaugerre, 2017). Although at least one example of free-ranging geckos using substrates non-randomly in relation to their adhesive capabilities exists, consideration of the multitude of other factors that could be individually or interactively influencing habitat use can make establishing such connections difficult (Higham et al., 2019).

Observations of habitat use using enclosures containing simulated habitat are one possible way to facilitate the collection of such data for nocturnal species and are accompanied by the benefit of implementing precise control over habitat variables (e.g. substrate type, perch diameters, shading) (Higham et al., 2019). Thus, the use of experimental enclosures offers the opportunity to identify the individual factors that influence gecko habitat use (e.g. adhesive performance). Recent work examined the substrate use of three species of *Oedura* geckos in the laboratory using experimental enclosures and found that they used the substrate that elicited maximal adhesive performance (a coarse sandpaper) more often than the other substrate (a fine sandpaper), which elicited lower maximal adhesive performance (Pillai et al., 2020). The genus *Oedura* is a member of the gecko family Diplodactylidae and very little is known about the adhesive performance and properties of this gekkotan family (Russell and Garner, 2021). Indeed, most of our knowledge of the mechanics and properties of gecko subdigital adhesive pads has come from a single species, the Tokay gecko (*Gekko gecko*). Thus, it is interesting to consider the generality of the results of Pillai et al. (2020) with those for members of other gekkotan families.

Herein, we examined the substrate use, adhesive performance and vertical clinging behaviour of the Tokay gecko (Gekkonidae: *Gekko gecko*) in the laboratory on three substrates that vary considerably in surface roughness to investigate whether adhesive performance influences patterns of substrate use in captivity. We hypothesized that geckos would use substrates non-randomly with a bias towards

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those that elicit maximal adhesive performance. The findings of this study will not only provide additional, yet crucial data to the study of the connections between habitat use and adhesive performance in geckos but will also guide the design of future laboratory and field investigations examining this topic.

MATERIALS AND METHODS

Animals

A total of *n*=19 adult Tokay geckos, *Gekko gecko* (Linnaeus 1758), were used in this study. When not undergoing trials, geckos were housed and cared for *sensu* Niewiarowski et al. (2008). All protocols involving animals were approved by the University of Akron IACUC Protocol 19-07-13-NGC.

Substrate use

Gekko gecko (*n*=18) substrate use was documented while they were individually inhabiting nine ∼38 liter glass terraria with walls that were composed of three different substrates: two grits of sandpaper (1000-grit: 3M Wet and Dry, St Paul, MN, USA; 80-grit: Black Diamond Griptape, TGM Skateboards, Mount Clemens, MI, USA) and glass. The walls of each terrarium were divided into six equally sized panels and the two grits of sandpaper were attached to four of the panels (two of each grit). One of the short sides of each terrarium was always unmodified glass (to allow for observation), while the final panel of each terrarium was glass with black construction paper secured to the outside of the terrarium to reduce large differences in colour (Fig. 1A). The placement of the substrates was randomized in each of the nine terraria (with the exception of the front pane of glass). The top and bottom of each terrarium were not modified nor included in substrate use observations.

Substrate use was monitored via web cameras (YoLuke A860, YoLuke-Tech, Shenzhen, Guangdong, China) programmed to capture still images of the terraria approximately every 30 s for 24 h. Geckos were kept on a 12 h:12 h day:night cycle. During their inactive period (day cycle), geckos were placed on the bottom of their terrarium in a random orientation every 3 h to encourage them to make independent substrate choices. During their active period (night cycle), red LED lights illuminated the terraria without disturbing the geckos. Each of 18 geckos were observed for three 24 h periods, each time in a randomly selected terrarium. Geckos were given 24 h of rest in between observations. Observations were conducted in a temperature- and humidity-controlled room. The substrates were cleaned with ethanol followed by water and then dried after each 24 h observation period.

Previous work examining the substrate use of other lizards in experimental enclosures has often employed single observations of substrate use at set intervals (e.g. every 30 min for 7–9 h; Cooper and Sherbrooke, 2012; Monasterio et al., 2010; Vanhooydonck et al., 2000). Other studies have continuously observed substrate use over set periods of time (e.g. 20 min: Marshall et al., 2016; 90 min: Pillai et al., 2020). We used this latter approach and randomly selected 4 h of images from each 24 h period (two from the inactive period and two from the active period) to document substrate use. The 2 h selected from each inactive period were the first hour immediately succeeding two separate replacements of the gecko on the bottom of the terrarium, as we considered this the best indication of independent substrate choices. Data are presented as the proportion of observations on our three substrates.

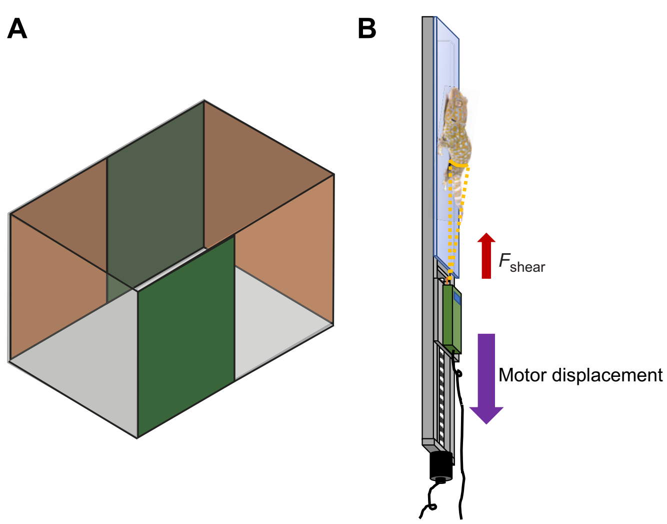

Fig. 1. Experimental enclosures and measurement of adhesive performance. (A) Schematic diagram of the terraria, the walls of which were modified with two samples of each of three substrates (glass, 1000-grit sandpaper and 80-grit sandpaper). Nine terraria were used in total and the position of the substrates was randomized in each (with the exception of the front panel of glass). (B) Schematic diagram of the motorized apparatus used to measure maximum shear adhesive force (F_{shear}) of *Gekko gecko*. Modified from Niewiarowski et al. (2019; with permission from the Society for Integrative and Comparative Biology).

Adhesive performance

Maximum shear adhesive force of *G. gecko* (*n*=4) on the three substrates was measured *sensu* Niewiarowski et al. (2008) using a vertically oriented custom-built force rig (Fig. 1B). Trials were halted if shear force reached 20 N to prevent injury to the gecko (Garner et al., 2020; Stark et al., 2014). The impact of claw use on shear force was investigated by partially clipping claws *sensu* Garner et al. (2017) after first measuring adhesion with fully intact claws. Adhesion was assayed 3 times per individual per claw state (intact or clipped) on each of the three substrates. Details of surface roughness can be found in Fig. S1 and Table S1.

Vertical clinging

Gekko gecko (*n*=5) were placed on our vertically oriented substrates and observed undisturbed for 5 min, a time frame similar to observations of lizard behaviour in past studies (e.g. Diaz, 1991; Huyghe et al., 2007; Schall and Sarni, 1987), or until they left the substrate. The total time the gecko spent on the substrate was recorded. We also recorded whether macroscale slipping of the autopodia occurred and the number of times autopodia were repositioned. A slip was defined as the visible displacement of an autopodium along the substrate's surface and a repositioning was defined as the removal and replacement of an autopodium from the substrate. The number of repositionings was divided by the total time each gecko spent on the substrate.

Statistical analysis

To examine whether geckos were using substrates non-randomly, the average proportion of observations on each substrate was compared with its relative availability within the enclosure (0.33) via binomial test (*sensu* MacLeod et al., 2019). Data from the inactive and active period were analysed separately, and alpha values were corrected for multiple comparisons via the sequential Bonferroni method (Holm, 1979). Although five of six test substrates were randomly oriented in the terraria, the front pane of glass was always unmodified to permit video monitoring of substrate use. To investigate whether geckos used the front pane of glass or the other, randomly distributed, externally darkened pane

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of glass in a non-random fashion, we used binomial tests to compare the average proportion of time geckos spent on each pane of glass with their relative availability within the enclosure (0.5). We also reanalysed the original dataset after excluding observations of geckos on the front panel of unmodified glass. We adjusted the relative availability for the remainder of the substrates accordingly (i.e. 0.4 for each of the two sandpaper substrates and 0.2 for the remaining pane of glass).

Maximum shear force was compared as a function of substrate, claw state and their interaction using a mixed model analysis of variance (ANOVA) with individual gecko modelled as a random effect (*sensu* Garner et al., 2020). Pairwise comparisons of significant effects were made with Tukey's HSD. We used two-sample *z*-tests to examine whether there were differences between substrates in the proportion of geckos that slipped or left the substrates during vertical clinging trials (Zar, 2010a). Alpha values were corrected for multiple comparisons via the traditional Bonferroni method. Wilcoxon rank-sum tests were used to examine differences in the time geckos spent on the substrates and the number of repositionings per minute during vertical clinging trials because their residuals were not normally distributed (Zar, 2010b).

Binomial tests and two-sample *z*-tests were performed using online web tools (binomial tests: https://measuringu.com/onep/; two-sample *z*-tests: https://www.socscistatistics.com/tests/ztest/). The remainder of the statistical analyses were completed in JMP Pro 14 (SAS Institute, Inc., Cary, NC, USA).

RESULTS AND DISCUSSION

During their inactive and active period, geckos were observed on glass more often (inactive: P=0.009, Bonferroni α=0.017; active: P<0.0001, Bonferroni α=0.01) and 1000-grit sandpaper less often (inactive: P=0.0006, Bonferroni α=0.012; active: P<0.0001, Bonferroni α=0.008; Fig. 2A) than their relative availability within the enclosures. Geckos were observed on 80-grit sandpaper as would be expected by its relative availability within the enclosures during both their inactive (P=0.34, Bonferroni α=0.025) and active periods (P=0.73, Bonferroni α=0.05; Fig. 2A).

During their inactive and active period, geckos used the two panes of glass (front transparent pane and randomly placed dark pane) as would be expected by their relative availability within the enclosure (inactive period – front: P=0.014, Bonferroni α=0.012; dark: P=0.043, Bonferroni α=0.017; active period – front: P=0.21, Bonferroni α=0.025; dark: P=0.21, Bonferroni α=0.05). Results with the front pane of glass included or excluded were qualitatively similar (Table S2). The findings of these analyses suggest that the non-random placement of this one substrate does not affect our overall interpretations.

Maximum shear force varied significantly as a function of substrate ($F_{2,15}$=27.7, P<0.0001), but neither claw state ($F_{1,15}$=0.68, P=0.42) nor the claw state–substrate interaction ($F_{2,15}$=1.86, P=0.19) had a significant effect on maximum shear force (Fig. 2B). Maximum shear force on glass was significantly greater than that on 80-grit and 1000-grit sandpaper (glass versus 80-grit: P<0.0001; glass versus 1000-grit: P=0.02) and was significantly greater on 1000-grit sandpaper than on 80-grit sandpaper (P=0.002).

During observations of vertical clinging, substrates did not differ significantly in the total time geckos spent on each (d.f.=2, χ^2=1.63, P=0.44; Fig. S2), the number of repositionings per minute (d.f.=2, χ^2=5.27, P=0.07; Fig. S2) or the proportion of geckos that left the

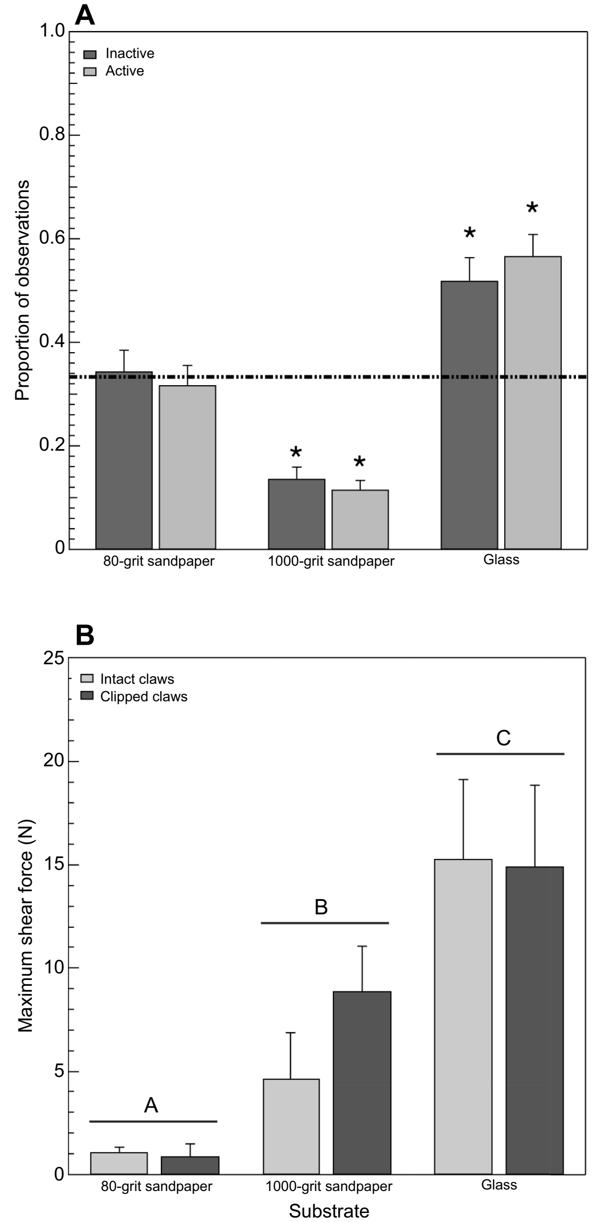

Fig. 2. Substrate choice and maximum shear force. (A) Mean proportion of observations of Tokay geckos (n=18) as a function of substrate and activity period (inactive or active). Binomial tests revealed that, regardless of activity period, glass was used significantly more often (inactive: P=0.009, Bonferroni α=0.017; active: P<0.0001, Bonferroni α=0.01) and 1000-grit sandpaper was used significantly less often (inactive: P=0.0006, Bonferroni α=0.012; active: P<0.0001, Bonferroni α=0.008) than would be expected based upon their relative availability within the enclosures. The 80-grit sandpaper was used as would be expected based on its relative availability within the enclosures, regardless of activity period (inactive: P=0.34, Bonferroni α=0.025; active: P=0.73, Bonferroni α=0.05). Asterisks indicate a significant difference in the proportion expected based on relative availability within the enclosures (0.33, indicated by the horizontal line). (B) Mean maximum shear force of Tokay geckos (n=4) as a function of substrate and claw state (intact or partially clipped claws). A mixed model ANOVA revealed that maximum shear force was significantly greater on glass compared with both 1000-grit and 80-grit sandpaper (glass versus 80-grit: P<0.0001; glass versus 1000-grit: P=0.02). Maximum shear force was significantly greater on 1000-grit sandpaper than on 80-grit sandpaper (P=0.002). Claw state had no significant influence on maximum shear force ($F_{1,15}$=0.68, P=0.42). Error bars are ±1 s.e.m.

substrate (all $P>0.05$; Fig. S3). The proportion of trials in which slipping occurred was significantly greater on 80-grit sandpaper than on glass ($z=-2.58$, $P=0.01$) but did not differ significantly between 1000-grit sandpaper and glass ($z=-1.58$, $P=0.11$) or 1000-grit sandpaper and 80-grit sandpaper ($z=1.30$, $P=0.20$; Fig. S3).

Regardless of activity period, geckos were observed significantly more often on glass than its relative availability within the enclosures, suggesting that *G. gecko* uses glass preferentially when compared with the available alternatives. As expected, shear adhesion was maximal and behaviours associated with difficulty in maintaining static clinging were minimal on glass. These data are consistent with the hypothesis that *G. gecko* preferentially uses substrates on which adhesive performance is maximal, at least in highly controlled laboratory conditions. Although we did not expect geckos to discriminate between sandpapers, they avoided using 1000-grit sandpaper and seemed indifferent to 80-grit sandpaper. Maximum shear adhesion was lowest on 80-grit sandpaper compared with that on all other substrates and slipping occurred much more often on 80-grit sandpaper than on glass. Additionally, maximum shear adhesion on 1000-grit sandpaper was intermediate between that on the other two substrates examined and there were no obvious differences in vertical clinging behaviour between 1000-grit sandpaper and glass. Thus, if we anticipated any substrate to be avoided preferentially, we would have expected that to be 80-grit sandpaper.

There are a number of possible explanations as to why geckos avoided the 1000-grit sandpaper. One hypothesis is that they were unable to effectively use their claws to interlock with surface asperities (Crandell et al., 2014; Dai et al., 2002; Garner et al., 2017; Naylor and Higham, 2019; Zani, 2000). The presence of claws, however, had no significant impact on maximum shear force production, a result that was surprising considering that recent work found that partial removal of claws reduced clinging ability of *Thecadactylus rapicauda* on rough substrates (Naylor and Higham, 2019). Another possibility is that the effectiveness of adhesive locomotion is different on the two sandpaper substrates, although we find this unlikely given the trends in maximum shear force during static clinging. Finally, all substrates were relatively dark in colour (with the exception of the front pane of glass), but 1000-grit sandpaper was noticeably lighter than 80-grit sandpaper (Fig. S4).

Our finding that geckos were observed significantly more often on substrates that elicited maximal adhesive performance is nearly identical to that of Pillai et al. (2020), who performed a similar experiment with geckos of the family Diplodactylidae. The similar findings of two studies using different species (*G. gecko* versus *Oedura* spp.) from different families (Gekkonidae versus Diplodactylidae) and different experimental setups expands the generalizability of the results of both studies and amplifies the call for future studies examining the patterns of gecko substrate use. Future experimental studies may consider implementing natural surfaces and additional factors that could influence substrate use (e.g. intraspecific and interspecific competition, resource availability, thermoregulation) to enhance our understanding of the extent to which adhesive performance impacts substrate use. Additionally, the findings of our study and those of Pillai et al. (2020) suggest the hypothesis that adhesive performance influences the substrate use patterns of free-ranging geckos. Therefore, we might expect geckos to use substrates in their natural habitat non-randomly, with substrate use patterns matching trends in maximal adhesive performance. Evidence of this has already been documented in two related studies (Delaugerre et al., 2015; Russell and Delaugerre, 2017), yet it is clear that more investigations examining the habitat use patterns of free-ranging geckos and the individual and interactive parameters that influence it are necessary.

Conclusions

Here, we examined the substrate use patterns, adhesive performance and vertical clinging behaviour of *G. gecko* on three substrates that varied in surface roughness to determine whether adhesive performance is correlated to patterns of substrate use in captivity. During both their inactive and active periods, we found that geckos were observed more often on the substrate that elicited maximal adhesive performance and minimal behaviours associated with difficulty in sustaining static clinging (i.e. glass). Substrate use of the two remaining substrates was expected to be random, but geckos preferentially avoided 1000-grit sandpaper and seemed indifferent to 80-grit sandpaper. The findings of our controlled laboratory study suggest that adhesive performance is likely one of the major drivers of substrate use patterns in free-ranging geckos, but future observations in more ecologically relevant circumstances or directly in the field are imperative to investigate this further.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: A.M.G., A.D., P.H.N.; Methodology: A.M.G., A.M.P., A.D., P.H.N.; Validation: A.M.G., A.D., P.H.N.; Formal analysis: A.M.G., A.M.P.; Investigation: A.M.G., A.M.P.; Resources: A.D., P.H.N.; Data curation: A.M.G.; Writing - original draft: A.M.G., A.M.P.; Writing - review & editing: A.M.G., A.M.P., A.D., P.H.N.; Visualization: A.M.G.; Supervision: A.M.G., A.D., P.H.N.; Project administration: A.M.G.; Funding acquisition: A.M.G., A.D., P.H.N.

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Data availability
Datasets supporting the results of this article can be found in figshare: https://doi.org/10.6084/m9.figshare.12988670

Supplementary information
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