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RESEARCH ARTICLE

Gecko toe and lamellar shear adhesion on macroscopic, engineered rough surfaces

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ABSTRACT

The role in adhesion of the toes and lamellae – intermediate-sized structures – found on the gecko foot remains unclear. Insight into the function of these structures can lead to a more general understanding of the hierarchical nature of the gecko adhesive system, but in particular how environmental topology may relate to gecko foot morphology. We sought to discern the mechanics of the toes and lamellae by examining gecko adhesion on controlled, macroscopically rough surfaces. We used live Tokay geckos, *Gekko gecko*, to observe the maximum shear force a gecko foot can attain on an engineered substrate constructed with sinusoidal patterns of varying amplitudes and wavelengths in sizes similar to the dimensions of the toes and lamellae structures (0.5 to 6 mm). We found shear adhesion was significantly decreased on surfaces that had amplitudes and wavelengths approaching the lamella length and inter-lamella spacing, losing 95% of shear adhesion over the range tested. We discovered that the toes are capable of adhering to surfaces with amplitudes much larger than their dimensions even without engaging claws, maintaining 60% of shear adhesion on surfaces with amplitudes of 3 mm. Gecko adhesion can be predicted by the ratio of the lamella dimensions to surface feature dimensions. In addition to setae, remarkable macroscopic-scale features of gecko toes and lamellae that include compliance and passive conformation are necessary to maintain contact, and consequently, generate shear adhesion on macroscopically rough surfaces. Findings on the larger scale structures in the hierarchy of gecko foot function could provide the biological inspiration to drive the design of more effective and versatile synthetic fibrillar adhesives.

KEY WORDS: Gecko, Adhesion, Friction, Tribology, Contact mechanics, Synthetic gecko adhesive

INTRODUCTION

The exceptional climbing ability of the gecko has been attributed primarily to the fibrillar structures found on the toe pads (Autumn et al., 2000; Autumn et al., 2006a; Tian et al., 2006; Bhushan, 2007; Autumn and Gravish, 2008). Toe pads are in-folded to form rows that hold modified keratinized scales called lamellae. These lamellae are composed of hundreds of tiny hairs called setae, which are then further subdivided into hundreds of nanoscale-sized spatulae (Russell, 1981; Russell, 1986). These spatulae individually adhere to surfaces using intermolecular van der Waals forces (Autumn et al., 2000; Autumn et al., 2002). This hierarchical system, along with claws (Zani, 2000; Bloch and Irschick, 2005) that are used for mechanical interlock, allows the gecko to attach to a wide variety of surfaces ranging from smooth glass and plants to the roughest tree bark.

Although the majority of research on the gecko adhesive system has focused on the nanoscale features, the lamellae, the tendons, blood vessels and muscles of the foot are known to play an important role (Russell, 1975; Peattie, 2009; Tian et al., 2013). Russell (Russell, 1981; Russell, 1986; Russell, 2002) proposed that the intermediate structures are used to cushion the foot against the surface, and to allow the flexible lamellae to conform more closely to the surface to which they are adhering. Another theory on the function of the intermediate structures is that the size, shape and angle of the larger hierarchical structures aid in rapid detachment of the foot (Gao et al., 2005; Cheng et al., 2012). Other investigators have also shown analytically that the hierarchical structures uniformly distribute the adhesive force across the attachment pads, resulting in stronger and more robust adhesion on rough surfaces (Kim and Bhushan, 2007; Chen et al., 2008). Investigators have also identified a range of surface roughness that is too rough for the setae alone to adhere to, but is also too smooth for the claws to form a mechanical interlock on, indicating that the intermediate-sized structures may be critical in allowing the hierarchical system to adhere across a wide range of length scales (Vanhooydonck et al., 2005; Bhushan, 2007). Vanhooydonck et al. (Vanhooydonck et al., 2005) found that the acceleration of the geckos, and thus the effective force they were able to produce, decreased when running vertically on mesh and cloth compared with fine-grained wood, although the final running speed was the same. However, this study was not conclusive because (1) acceleration of the center of mass is not limited by peak adhesive force of the foot for these surfaces; there is no reason to expect peak single leg forces to approach even the static adhesive or shear capacity unless the number of attached spatulae could be reduced by one to two orders of magnitude, and (2) peak body accelerations estimated by twice differentiating position digitized from a 250 frames s^{-1} video do not provide a good estimate of the instantaneous forces acting at the interface between setae and substrate. A recent study by Russell and Johnson compared surface topology on a wide range of irregular surfaces including sandstone, glass, acetate, sandpaper, cinderblock and oak, focusing primarily on the available contact area of each surface (Russell and Johnson, 2007; Johnson et al., 2009), and later found that deployment of the gecko adhesion system is based on the surface incline, and not on roughness (Russell and Higham, 2009). These studies indicate that the gecko is able to adhere to rough surfaces at some reduced level of adhesion. However, it is still unclear how adhesion to rough surfaces is accomplished, and to what degree surfaces of varying roughness compromise total foot clinging

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ability. Furthermore, the randomly rough nature of the surfaces used in studies thus far limits the ability to compare models of lamellar contact mechanics, as well as data from other studies and among diverse species.

We attempt to better understand toes and lamellar function by measuring how geckos adhere to surface features that are too rough for the setae alone to adhere to, but are too smooth for the claws to form a mechanical interlock (Bhushan, 2007; Vanhooydonck et al., 2005), and to identify any possible limitations of the hierarchical structure, as it is known analytically that roughness will dramatically decrease adhesion between smooth surfaces (Peressadko et al., 2005; Sriwijaya et al., 2007). We studied whole-foot gecko adhesion on extruded sinusoidal patterns of varying amplitudes and wavelengths similar to the dimensions of the lamella and toe structures. By observing the maximum shear force a gecko foot can attain on a variety of controlled surfaces, we propose to quantify the role of these macroscopic structures in shear adhesion. We hypothesize that surface amplitudes greater than lamellae depth will cause a decrease in shear adhesive force, and that increasing surface wavelength will increase shear adhesion.

Our data will be useful for validation of models attempting to explain contact mechanics of the lamellar structures due to the computable nature of the sinusoidal surfaces used to test shear adhesion. In addition, this information can be used to explain how evolutionary forces shaped lamellar traits by allowing a more rigorous comparison between surface features found in the species' environment and the dimensions and fidelity of the toe structures found on various lizards' feet. Insights from this study can provide biological inspiration for the design of hierarchical synthetic adhesives and further improve their adhesive capability on rough surfaces.

RESULTS

Shear adhesive force as a function of time

As we loaded the gecko's foot, normal force increased to our target preload of 1–2 N (Fig. 1). Shear adhesive force increased rapidly to a steady state, while normal force remained near zero (Fig. 1). Shear adhesive force steady state was maintained for more than 5 s, allowing estimation of the maximum value for the given trial. The force traces were not filtered. Data were collected at 1000 Hz. Maximum shear adhesive forces ranged from 0.21 to 14 N.

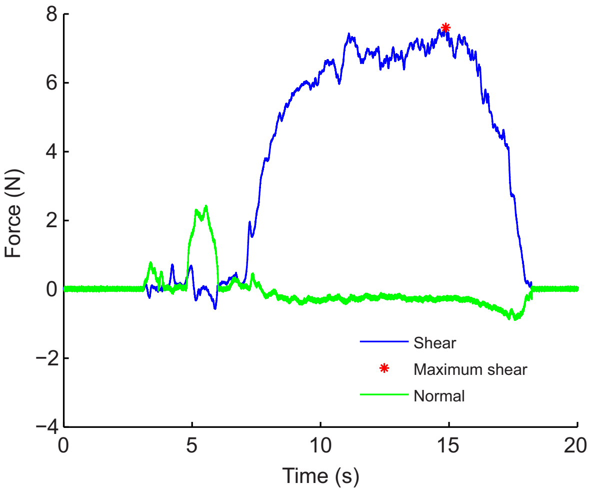

Fig. 1. Shear (blue line) and normal (green line) adhesion data from a single load-drag-pull step of a Tokay gecko (*Gekko gecko*) on a sinusoidal surface with an amplitude of 2 mm and a wavelength of 3 mm.

Effect of surface amplitude and wavelength

To determine the effect of surface features, we plotted the per cent relative maximum shear in relation to a flat polyurethane (PU) control surface as a function of the surface wavelength and amplitude (Fig. 2). Multi-factor ANOVA results showed no significant effect of individual (P=0.06). As amplitude increased, maximum shear adhesion decreased significantly for each wavelength tested (ANOVA, $F_{4,213}$=74.3; P<0.001; Fig. 2A,B). As wavelength increased, maximum shear adhesion increased significantly at each amplitude tested (ANOVA, $F_{6,213}$=88.6; P<0.001; Fig. 2C,D). The condition with surface amplitude of 1 mm and wavelength of 6 mm showed no significant difference in adhesion from a flat control surface made from the same material (one-sample t-test, P=0.076). Video evidence shows that the surface feature dimensions that caused this decrease in adhesion correspond approximately to the dimensions of the gecko toe and lamella features (supplementary material Movie 1).

Conformation of toes and lamella to engineered rough surface

Video footage of trials revealed a wide range of toe and lamella conforming behavior, from the entire toe and lamella contacting sinusoids, to lamella and toes not conforming at all to the surface (Fig. 3). At wavelengths below the lamella dimensions (Fig. 3A,B), the toes and lamella were not conforming to the surface and instead are only resting on the peaks of the engineered surface. It is on these surfaces that we measured the most significant reduction in shear adhesion. The intermediate surface dimensions (Fig. 3C,D) approximately correspond to the point at which lamella can slightly conform, but the toes cannot, reducing the number of contacting lamella. Toes are seen slightly curling around the surface features, but not enough to bring all the lamella into contact. We observed lamella extending from the bottom of the toes, but not being long enough to reach the deepest parts of the surface. At the largest surface dimensions (Fig. 3E,F), the lamella and toes conform to the surface, and they appear to make complete contact. There is no significant loss in adhesion on these surfaces from a flat control surface of the same material [surface: amplitude (A)=1, wavelength (λ)=6, one-sample t-test, P=0.076].

DISCUSSION

The interactions between the gecko lamella and surface features that allow the gecko to adhere with such large forces remain a complex phenomenon. Previous studies of whole body forces have given some indication of how roughness may decrease adhesive forces, but the randomly rough nature of these surfaces and lack of data have made making conclusions about toe and lamellar contact mechanics difficult (Vanhooydonck et al., 2005; Johnson et al., 2009; Pugno and Lepore, 2008). The systematic approach taken by this study is the first to shed light on how varying both surface amplitude and wavelength effect adhesion at the whole foot level. Specifically, the data suggest that the ratio of lamella to surface feature size plays a large role in whole foot clinging ability, as indicated by both force measurements, and video data that show lamellar features interdigitating to various levels depending on the amplitude and wavelength of the surface as shown in Fig. 4.

Russell and Johnson (Russell and Johnson, 2013) suggested that setae or lamella features would be able to make contact with the uppermost portion of the surface corresponding to the length of the lamella. They go on to predict that this potential area of available contact could be used to predict adhesive forces. However, our data show that just using the available area of contact only poorly predicts adhesive forces. Fig. 4 shows the measured shear adhesive

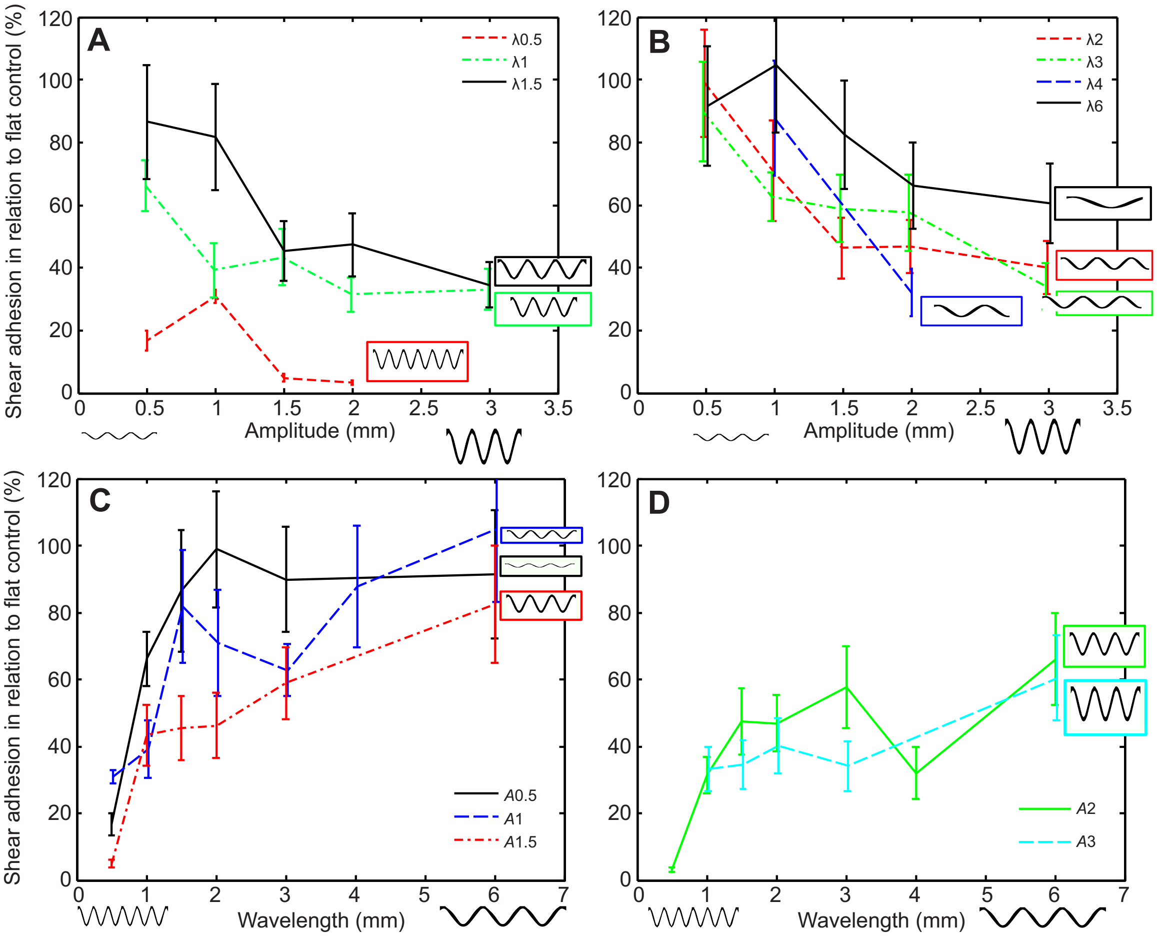

Fig. 2. Percent shear adhesion across surfaces that vary in amplitude (*A*) and wavelength (λ) relative to a flat control surface. (A,B) Percent shear adhesion as a function of amplitude with wavelength held constant across low (A) and high (B) wavelengths shown in inset. (C,D) Percent shear adhesion as a function of wavelength with amplitude held constant across low (C) and high (D) amplitudes shown in inset. Adhesion decreased significantly with increasing amplitudes and decreasing wavelengths (ANOVA, $P<0.001$; error bars represent one standard error).

force as a function of the projected area available for contact for the top 0.87 mm of the conditions tested (as this depth is the measured lamella length for the *Gekko gecko* individuals we used in this study). As can be seen, no clear trend exists between the available area for contact and the shear adhesion. The data suggest that the available area of contact is a weak predictor of shear adhesive capabilities (r^2=0.29), and as Russell and Johnson contend, more exploration is needed surrounding the relationship between toe pad geometry, surface features and adhesive capability across a wider variety of species.

It may be that beyond certain amplitudes and below certain wavelengths the lamella can no longer adapt to the surface, and adhesion is lost due to geometric constraints (e.g. the lamella cannot fit between the surface features to make contact with the surface). Interestingly, Huber et al. reported that for spatular attachment, a roughness on the same size scale as the feature size created a decrease in the adhesive force (Huber et al., 2007). This is strikingly similar to the trend we have found at the lamellar size scale, and may suggest that the smaller size scale structures are behaving similarly to the larger size scale structures, and again supports the hypothesis that it is the relationship between the anatomical feature size and the surface feature size that best predicts adhesive capability. [We did not directly measure foot area of the geckos used in this study, as we were using each individual as its own control by comparing with the flat control surface. However, Irschick (Irschick, 1996) found the combined pad area of the two front feet of *Gekko gecko* to be 227 mm^2. Making an approximation, a single rear gecko foot pad area would be 114 mm^2.]

It is also possible that the local angle of the surface features determines clinging ability, and this has been demonstrated at the setal size scale (Autumn et al., 2000; Gravish et al., 2008; Hill et al., 2011). During contact, the lamella can be seen bending to an angle in order to conform to the surface, and this angle may be determined by the ratio of lamella to surface feature size. However, further modeling would be required to conclusively say how local lamellar angle effects whole foot adhesion. It is our hope that data from this study could be used to verify such a model.

The significant drop in adhesive forces on surfaces with higher amplitude and shorter wavelengths suggests that the lamellae and toe structures have evolved to conform to only a certain range of rough surfaces. There has been some speculation that there may be a positive relationship between lamellae number and clinging ability (Irschick et al., 2006); however, our data suggest that clinging ability on rough surfaces may also be linked to lamellae dimensions. It is still difficult to make these conclusions, as data from other species do not yet exist. These results do indicate that surface roughness plays an important role in explaining the disproportionately high

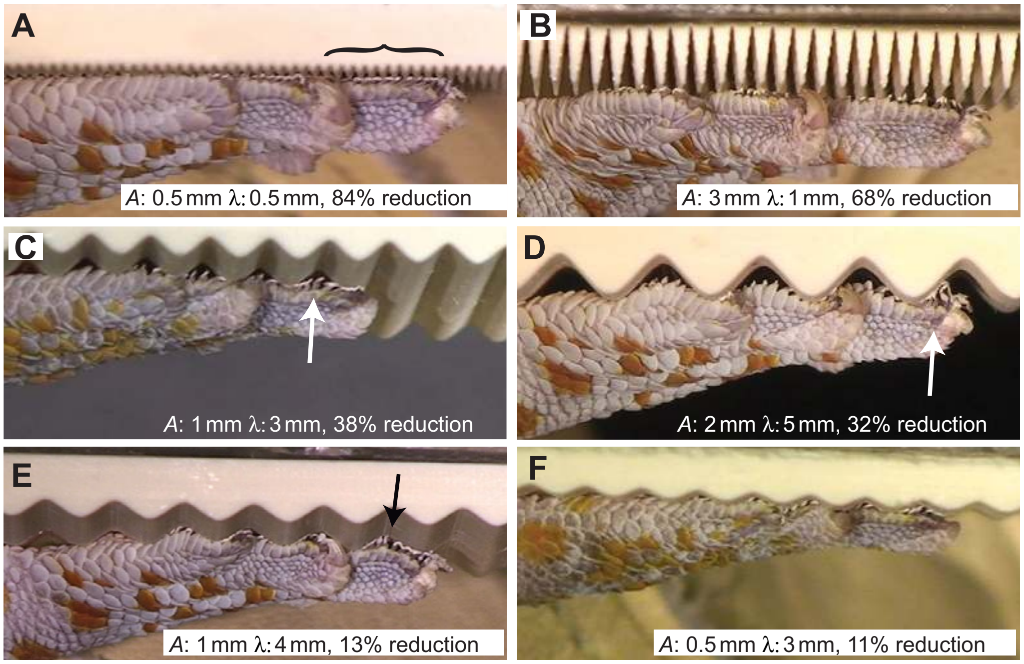

Fig. 3. Photos taken from a video of load-drag-pull trials on several, engineered rough surfaces. At wavelengths below the lamella dimensions (A,B) the roughness is too large for the toes and lamella to conform (black bracket showing lamellae only contacting tips of ridges). The intermediate surface dimensions (C,D) approximately correspond to the point at which a significant loss in adhesion is measured, where lamella can slightly conform, but the toes cannot (white arrows). At larger surface dimensions (E,F), the lamella and toes can conform to the surface, and there is no significant loss in shear adhesion (black arrow).

safety factor of the gecko adhesive system, which is in some cases stated to be several hundredfold (Autumn et al., 2006b). This was pointed to by Vanhooydonck et al., but lack of strong data prevented a stronger conclusion (Vanhooydonck et al., 2005). Our data may be used to explain how evolutionary forces shaped lamellar traits by allowing a more rigorous comparison between surface features found in the species' natural environment and the dimensions and fidelity of the toe structures found on various lizards' feet. More data will need to be collected from a wider variety of species as well as characterization of substrates found in the natural environment to allow further conclusions.

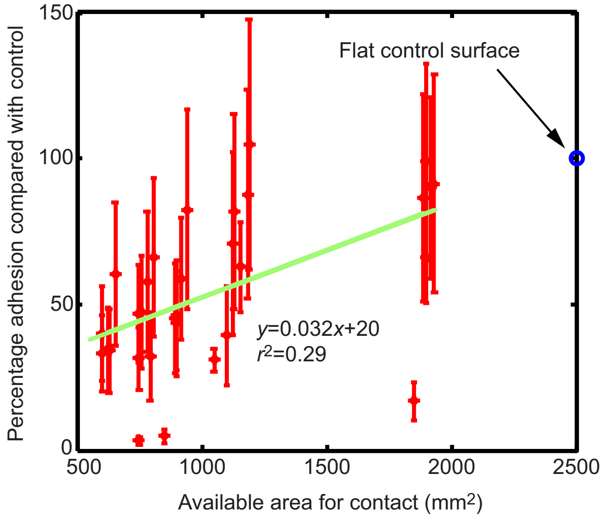

Fig. 4. Percent reduction in maximum shear force from a flat control surface versus available area for contact in the top 0.87 mm of the sinusoidal surface. Russell and Johnson (Russell and Johnson, 2013) suggested that increased available area for contact may predict an increase in adhesion; however, we found this was not significant (r^2=0.29), showing that a more complex metric is needed to predict surface adhesive forces (error bars are 95% confidence intervals).

These results also hold strong implications for the design of synthetic gecko adhesives: a new controllable adhesive inspired by the gecko. Current synthetic gecko-inspired adhesives incorporate only micro- and nano-structures that adhere ideally to smooth surfaces, but few synthetic adhesives have incorporated macroscale structures similar to those found on gecko feet that would allow for adhesion on macroscopically rough surfaces (Ge et al., 2007). In one case, Lee et al. fabricated nanofiber arrays on lamellae analogues from a hard polymer and demonstrated that adhesion on non-planar surfaces was five times greater than arrays without lamellar support structures (Lee et al., 2009). Our results suggest that adhesion to rough surfaces of these gecko-inspired adhesives may be improved if the relative size between the adhesive geometry and surface geometry is carefully considered. Further understanding of the mechanisms of adhesion on a macroscale level may enable adhesion on non-planar surfaces: one of the ultimate engineering goals required for wide-scale application of synthetic gecko-inspired adhesives.

MATERIALS AND METHODS

Species selection

Live Tokay geckos [*Gekko gecko* (Linnaeus 1758)] (106±13 g, mean ± s.d.; *N*=4) were used for our experiments because: (1) they have been used extensively in adhesion research, and protocols are well established, (2) the fabrication process for the engineered rough surfaces made possible surface features that are similar in size to the intermediate structures of the Tokay gecko foot and (3) the Tokay gecko has one of the most well-developed lamellar structures of the lizards that exhibit dry adhesion.

Gecko lamellae dimensions

Dimensions of the lamellae were determined by taking photographs with a camera mounted on a microscope, and measuring structures using image analysis software (ImageJ, NIH, Bethesda, MD, USA). The lamellar wavelength was defined to be the average distance between lamellae, and the lamellar amplitude was defined as the average proximal to distal length directed along the length of the lamella, as indicated in Fig. 5. Lamellae had a mean (±s.d.) amplitude of 0.87±0.13 mm (*N*=10) and wavelength of 0.7±0.16 mm (*N*=10).

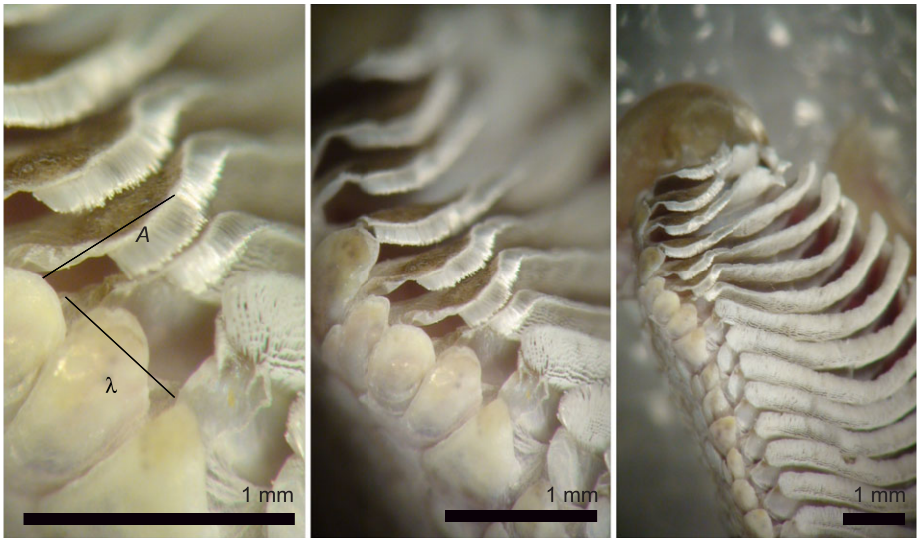

Fig. 5. Lamellae observed on the toe of a live Tokay gecko, showing example measurements of the lamellar wavelength (λ) and amplitude (*A*).

Engineered surface fabrication

We used computer-aided design software (SolidWorks, Dassault Systemes, Lowell, MA, USA) to create designs of sinusoidal surfaces with various combinations of amplitudes (*A*) and wavelengths (λ; Fig. 6). We made these designs into wax molds using a 3D printer (Thermojet, 3D Systems, Rock Hill, SC, USA). PU was cast into the wax molds and de-molded once cured. Each PU surface was 50 mm long by 50 mm wide. Sinusoidal surfaces were selected because they are easy to characterize and because the rounded edges prevented claw engagement, which would interfere with the surface–lamella interaction. Amplitudes and wavelengths were chosen to be the same order of magnitude as the lamellae to toe dimensions, with 35 surfaces being created in total, with amplitudes of 0.5 to 3 mm (±0.08 mm) and wavelengths of 0.5 to 6 mm (±0.08 mm). The flat control surfaces were made of PU, cast into molds made in the same 3D printer as the sinusoidal surfaces to minimize differences in microscale roughness.

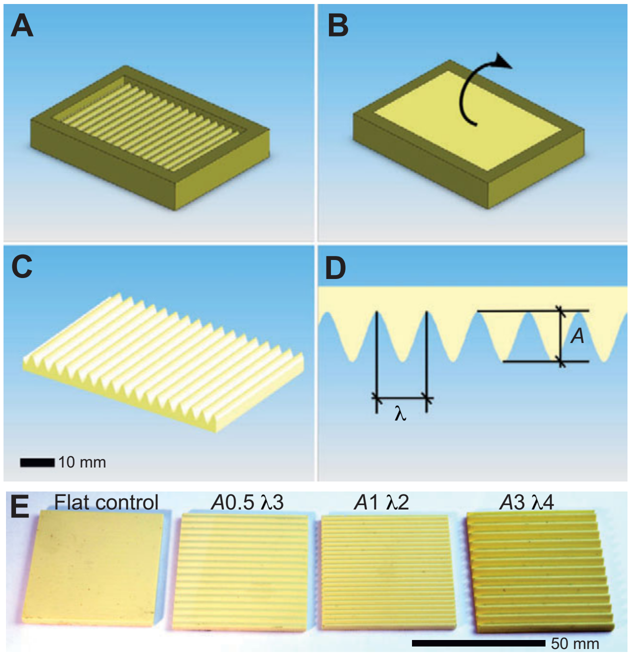

Fig. 6. Creation of the surfaces. (A) A 3D wax mold was printed. (B) Polyurethane (PU) was then cast into the mold and allowed to cure. (C) The PU surface was then removed from the mold. (D) Cross-section of the surface showing amplitude *A* and wavelength λ. (E) The flat PU control surface as well as three example surfaces used in the various conditions.

Experimental apparatus and testing methodology

We mounted the sinusoidal surfaces on a 6-axis force transducer (Nano17, ATI-Industrial Automation, Apex, NC, USA), which were then attached vertically to the edge of a rigid table. Data acquisition software (MATLAB, MathWorks, Natick, MA, USA) was used to collect and analyze the forces in the *x*-, *y*- and *z*-axes. Additionally, a side view video camera was set up to record the behavior of gecko feet, toes, lamella and claws.

Simulated steps were performed by manually moving a gecko foot in a load-drag-pull path that allows measurement of the peak engagement forces (Fig. 7). Tokay geckos were held vertically, with their head up, and a back foot was used to engage the bottom of the sinusoidal surface. A pre-load normal force of ~1–2 N was applied to the entire gecko foot for ~1 s by pressing with a gloved hand, and then released. When the normal force returned to 0 N, the gecko was dragged upwards vertically along the surface at a steady speed of 2–5 mm^{-1}, being careful not to apply additional normal or lateral forces. Gravish et al. (Gravish et al., 2010) have determined this to be a reasonable drag velocity range, because 1 mm s^{-1} is the transition velocity above which there is a power law increase in force. Following this power law, we calculated that we should expect to see less than a 1% difference in measured adhesion due to velocity effects across the range of allowable velocities. Small errors in velocity in our range should not have a large effect on measured forces. As the foot approached the upper edge of the surface, we pulled the foot off in the normal direction.

Trial selection criteria

Before and after each trial, we tested the gecko on the flat PU control surface to ensure that the gecko was adhering consistently. If geckos could not attain a benchmark force of 9 N on the control surface before and after the surface trial, we discarded the trial. Trials were also excluded if any claw engagement, foot disengagement, significant lateral or normal forces were above 1 N, or if dragging speeds were out of our set range, as calculated by measuring the time of the drag phase across a set distance with a stopwatch. In addition, individuals were not used during periods when their setae were molting. Two hundred and twenty-four trials yielded acceptable data from four individuals. We attempted to have each animal serve as its own control by testing the same rear foot of each gecko on all surfaces at least twice. However, due to variations in animal behavior and the criterion used to accept or reject trials, not every gecko is represented equally in every condition. The vast majority of conditions (30/35) had at least six acceptable trials from at least two geckos across the range of conditions. Our data set represents an attempt to balance the challenge of collecting data from live animals with gathering sufficient data across the large number of conditions.

The shear force for each trial was taken as the maximum generated during the steady-state drag period, as seen in Fig. 1. We used maximum

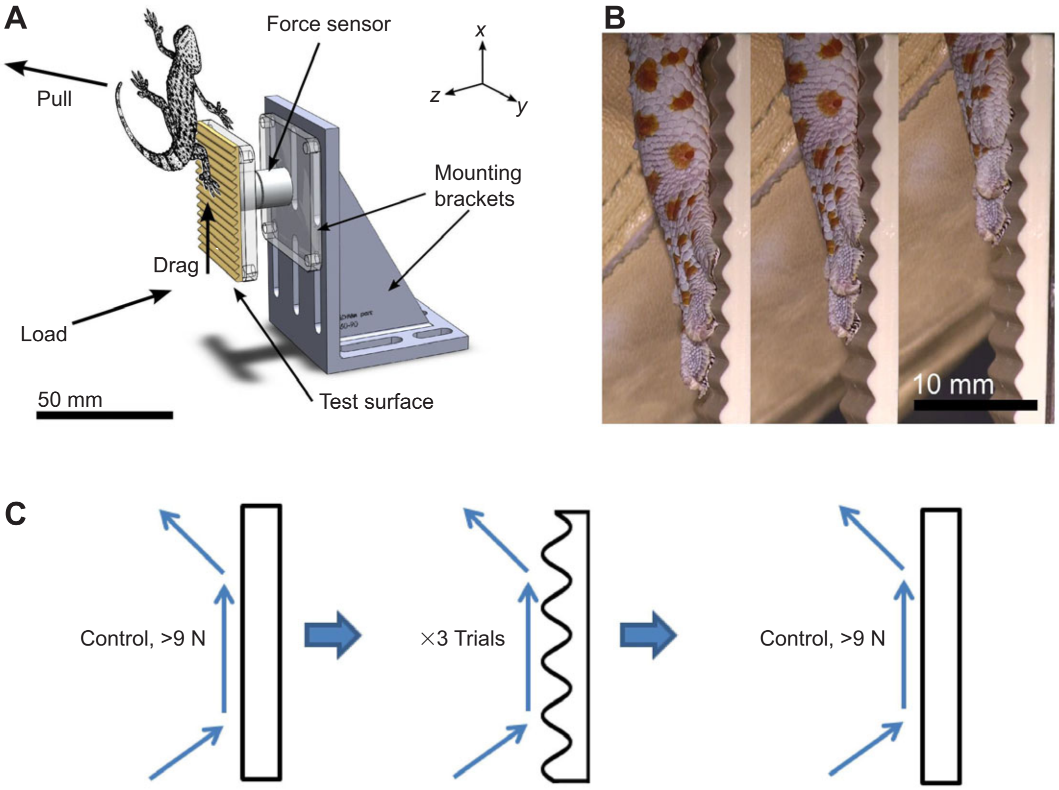

Fig. 7. The load-drag-pull methodology used for this study. (A) The experimental apparatus showing how the simulated steps were performed with the Tokay geckos. (B) A sequence of stills taken from video of a foot drag on a surface with amplitude 3 mm and wavelength 5 mm. (C) The testing methodology in which the rear foot is tested on the PU flat control surface, then three trials are performed on the condition being tested, and finally, the foot is again tested on the flat PU control surface afterwards.

shear force values for each surface to determine the change in maximum performance between the control surface and the sinusoidal, engineered surfaces.

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Competing interests

The authors declare no competing financial interests.

Author contributions

A.G.G. conceived the study. A.G.G., A.H., H.L., A.R. and K.S. were involved in the design and execution of the experiment. H.L., R.S.F. and R.J.F. interpreted the results. A.G.G. wrote the manuscript, and R.S.F. and R.J.F. drafted and revised the manuscript.

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Supplementary material

Supplementary material available online at http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.092015/-/DC1

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