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A Physical Model Approach to Gecko Adhesion Opportunity and Constraint: How Rough Could It Be?

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Synopsis It has been nearly 20 years since Autumn and colleagues established the central role of van der Waals intermolecular forces in how geckos stick. Much has been discovered about the structure and function of fibrillar adhesives in geckos and other taxa, and substantial success has been achieved in translating natural models into bioinspired synthetic adhesives. Nevertheless, synthetics still cannot match the multidimensional performance observed in the natural gecko system that is simultaneously robust to dirt and water, resilient over thousands of cycles, and purportedly competent on surfaces that are rough at drastically different length scales. Apparent insensitivity of adhesion to variability in roughness is particularly interesting from both a theoretical and applied perspective. Progress on understanding the extent to which and the basis of how the gecko adhesive system is robust to variation in roughness is impeded by the complexity of quantifying roughness of natural surfaces *and* a dearth of data on free-ranging gecko substrate use. Here we review the main challenges in characterizing rough surfaces as they relate to collecting relevant estimates of variation in gecko adhesive performance across different substrates in their natural habitats. In response to these challenges, we propose a practical protocol (borrowing from thermal biophysical ecological methods) that will enable researchers to design detailed studies of structure–function relationships of the gecko fibrillar system. Employing such an approach will help provide specific hypotheses about how adhesive pad structure translates into a capacity for robust gecko adhesion across large variation in substrate roughness. Preliminary data we present on this approach suggest its promise in advancing the study of how geckos deal with roughness variation. We argue and outline how such data can help advance development of design parameters to improve bioinspired adhesives based on the gecko fibrillar system.

Introduction

When Autumn et al. (2000) published two new seminal studies measuring the adhesive force of a single gecko seta and establishing van der Waals forces as the dominant source of adhesion (Autumn et al. 2002), they must have known that their work would catalyze a tsunami of basic research and potential applications of the gecko adhesive system. What would have been harder to anticipate at that time is how the focused research efforts of nearly 20 years does not yet enable us to answer basic questions about gecko ecology and evolution, or to create robust gecko-inspired synthetic adhesives (Niewiarowski et al. 2016). What kinds of questions are still beyond our reach? Some examples include: How often do dirt or water compromise the adhesive locomotion or station holding of free-ranging geckos? Is the form/function of the gecko adhesive system (e.g., setal length, modulus, density, and geometry) invariant across all the myriad types of gecko habitats that vary in roughness across many length scales? What are the typical safety factors built into the design of the gecko adhesive system considering the substrates and behavior of free-ranging geckos in their natural environments? This sample of questions is not an exhaustive list of gaps in our knowledge, yet it does capture two major deficiencies of understanding that must be addressed: 1) there exists little if any quantitative information on the habitat usage of free-ranging geckos, much less the characterization of substrates employed for locomotion and station-holding; 2) mechanistic understanding of gecko adhesion is defined by models and theory of contact mechanics for ideal or highly simplified systems which may not be representative of the behavior of fibrillar systems in general or gecko adhesion in particular. In this paper, we develop and present a new approach to help tackle the problem of gecko adhesion as it relates to surface roughness.

Challenges in studying surface roughness effects on adhesion

In considering how surface roughness impacts gecko adhesion, two interrelated problems quickly come into focus. First, as mentioned previously, we have very little quantitative data on the surface roughness characteristics of substrates used by free-ranging geckos (Russell et al. 2007). An obvious response to such a limitation would be to collect data on surface roughness of substrates used by geckos. However, this is a surprisingly non-trivial undertaking, highlighting the second problem: natural surfaces vary in roughness over length scales spanning seven to eight orders of magnitude (Persson 2003). Common statistics used to express roughness (e.g., root mean square [RMS], R_A, Hurst exponent) for comparative purposes tend to collapse variation in the topography of a three-dimensional surface into single parameters that potentially mask variation critical to contact mechanics theory (Jacobs et al. 2017). Therefore, the problem of understanding limits and capabilities of geckos with respect to adhesion on surfaces that vary in roughness requires quantitative data on the surfaces used by free-ranging geckos, as well as tractable methods for characterizing surface roughness in a way that is relevant to gecko adhesive performance.

From a biological perspective, studying the adhesion of geckos on natural surfaces has been mostly overshadowed by research focusing on the mechanics of adhesion under carefully controlled conditions in the laboratory. While the laboratory-based research literally launched the discovery of a new type of adhesive system (fibrillar) with all its attendant interest of biologists and material scientists, that work has not yet substantively informed perspectives about the role of adhesion in gecko ecology and evolution. Specifically, biologists have repeatedly hypothesized or assumed that the gekkotan adhesive system is a key innovation or part of a suite of characters comprising a key innovation in the ecology, evolution, and radiation of geckos (Russell 1979; Losos 1986; Vitt and Pianka 2005; Garcia-Porta and Ord 2013; Stroud and Losos 2016). Geckos are one of the most diverse and widely distributed groups of squamates (Gamble et al. 2008; Pyron et al. 2013), and part of their success (note that about 40% of gekkotan species lack an adhesive system) has been attributed to their ability to traverse a wide array of surfaces that may be smooth, rough, dirty, wet, or dry. Leaves, flower petals, branches and trunks of trees, friable and non-friable rocks, sand, and other terrestrial substrates comprise the surfaces upon which geckos regularly perch on or move across. In contrast, the imagery associated with gecko-inspired adhesive applications includes people scaling the clean windows or metal surfaces of buildings using adhesive gloves and shoes. Proofs of concept like Stanford's StickyBot (Santos et al. 2007) and the DARPA Z-Man project (Hawkes et al. 2015) reinforce the implicit idea that ultra-smooth surfaces represent the ultimate challenge for both geckos and the synthetic mimics they inspire. It is not just a coincidence that most fundamental research on gecko and gecko-inspired adhesion makes use of these same kinds of surfaces (e.g., smooth glass or plastics) to explore limits in the structure and function of how fibrillar adhesive systems like that of the gecko work (Russell and Johnson 2007). Ironically, because the mechanics of such systems are contact area dependent (van der Waals forces of attraction), smooth, clean surfaces that are the basis of such imagery and most gecko adhesion research are actually the least challenging surfaces for adhesion by geckos.

Very few surfaces found in the natural habitats of geckos are smooth at the length scale of typical laboratory test surfaces such as glass and plastic. Because the roughness of a surface is expected to affect the contact area fibrillar adhesives are able to achieve, the effects of roughness have been explored theoretically (Persson and Gorb 2003; Persson 2007; Kovalev et al. 2018) and in the laboratory (Vanhooydonck et al. 2005; Huber et al. 2007; Pugno and Lepore 2008; England et al. 2016; Pepelyshev et al. 2018). More recently, studies of the natural surfaces used by geckos have started to explore the impact of substrate use and the potential ecological and performance consequences (e.g., geckos in the genus *Rhoptropus*) in relation to a variable and unpredictable surface roughness (Russell and Johnson 2007; Russell et al. 2007; Russell and Johnson 2014; Collins et al. 2015). Exactly how fibrillar adhesive systems like those found in geckos enable robust adhesion while accommodating variation in roughness at many length scales is still not well understood (Brodoceanu et al. 2016). Some empirical and theoretical work with synthetic mimics indicates important roles for properties such as hierarchy (Bauer et al. 2015), tip shape (Gorb et al. 2007; Gillies and Fearing 2014), materials (Fischer et al. 2017), and geometry (Filippov and Gorb 2015; Popov et al. 2016). However, surprisingly little is known about variation in these and other parameters within and among individual geckos or among different species, especially as such variation might be related to different habitat preferences or associations. Indeed, analyses of covariation between gecko toe pad and habitat characteristics have only recently (Russell et al. 2007; Johnson and Russell 2009; Russell and Johnson 2014) begun to move beyond simple scaling and performance comparisons such as toe pad size versus body size versus adhesive capacity (Irschick et al. 1996; Vanhooydonck et al. 2005; Peattie and Full 2007), or other coarse-grained relationships that rely on idealized values of toe pad characters (e.g., average setal length, diameter, and density).

The ability of geckos to stick reversibly to rough surfaces is a unique trait of the fibrillar morphology of the gecko adhesive system. The intimate contact of spatula with the surface is essential for van der Waals adhesion (Autumn and Peattie 2002). For contact between two smooth surfaces that have no adhesion, the actual contact area depends on the modulus and the applied pressure (Hertz 1895). For two surfaces that have a finite adhesion, the actual area is much higher than that predicted by the Hertz model and a solution to this problem was provided by Johnson Kendall and Roberts for soft contacts, also known as JKR equation (Johnson et al. 1971). For hard contacts, the actual contact area is provided by Derjaguin–Muller–Toporov (Derjaguin et al. 1975) which takes into account the attractive forces outside of the Hertz contact region. All of these models are for ideal smooth surfaces. The actual force required to separate the two surfaces also depends on the geometry of the contact and some common examples are spherical tips, flat punches, or a peeling tape geometry. In a peeling geometry, the force depends on the peeling angle (Kendall 1975) and the low detachment forces for gecko adhesion are attributed due to high peeling angles.

For contact with rough surfaces, it is expected and intuitive that adhesion would be lower due to reduction in the real contact area. For hard materials, the adhesion is lost very rapidly due to roughness. On the other hand, soft rubbers are used to create good seals, because soft materials can deform and adapt to the surface roughness and increase the real contact area. The real contact area is where the surfaces are close enough for van der Waals interactions to be effective. In experiments, the adhesion energy is plotted as a function of RMS roughness or as the arithmetic mean (Ra) (Fuller and Tabor 1975; Briggs and Briscoe 1977). If a surface is divided in "n" number of points, the RMS roughness is defined as a square root of the summation of (y_i^2/n), where y_i is the difference in height at any point "i" and the mean height. On the other hand the arithmetic mean is summation of y_i/n. The difficulty in using the one simplified parameter-based approach is that surfaces with very different topology can give the same values of Ra or RMS roughness (Halling 1978; Jacobs et al. 2017).

A realistic rough surface has roughness at many length scales superimposed on top of each other. Imagine a sine wave of a particular amplitude and wavelength. If you had many such sine waves superimposed on top of each other with wavelengths ranging from sub-nanometer to millimeter or centimeters, these surfaces can then be mathematically expressed as a surface roughness power spectrum. A typical power spectrum is plotted on a log–log scale with the x-axis that scales as 1/wavelength (q-vector) and the y-axis is a measure of contribution of that wavelength (for simplicity referred here as amplitude). In general, the amplitude decreases with increase in q-vector for surfaces with fractal roughness (Jacobs et al. 2017). A complete characterization of surface roughness requires measurements of roughness at many length scales (atomic scale to macroscopic millimeter or centimeter scale).

There has been some history of theoretical approaches to model the effect of surface roughness on adhesion using simplified versions of surface roughness descriptions (Greenwood and Williamson 1966). Persson has developed a model for adhesion between a deformable smooth surface and a hard rough surface using a complete description of surface roughness using roughness power spectra (Persson and Tosatti 2001). Although this theoretical approach provides quantitative predictions of how adhesion changes with roughness, characterizing roughness at all relevant length scales in and of itself presents a formidable challenge (Gujrati et al. 2018). No single instrument or analysis technique is capable of recovering and expressing roughness profiles over length scales inclusive of tens of nanometers up to millimeters.

Because the roughness of natural surfaces varies at so many different length scales (from the atomistic to the millimeter) relevant to the gecko adhesive system (Persson 2007), it is not obvious how to study the way in which variation in surface roughness impacts the adhesive performance of free-ranging geckos. Some qualitative theory has been developed showing how fibrillar adhesive systems should be affected by surface roughness, especially at length scales corresponding to that of idealized gecko spatulae on the order of 10–100 nm (Persson and Gorb 2003; Huber et al. 2007), and is of enormous heuristic but low predictive value (Levins 1968) when considering how surface roughness may impact the ecology and evolution of the gecko adhesive system. For example, although theory suggests that high roughness at the spatular length scale of 10–100 nm should prohibit good contact necessary for the ideal gecko system, it is not clear how roughness at other length scales might affect those expectations. Are the effects of roughness at different length scales additive, interactive, or in some other way determinative to how the gecko fibrillar system makes contact with surfaces? If we must consider all length scales simultaneously (e.g., through employing quantitative measures such as surface roughness power spectra), models and theory rapidly become intractable. Persson's model can be applied using a simplified compliance of an array of setal hairs. However, this model simplifies the complexity of the compliance of the underlying tissue layer and also the hierarchical structure that results in less stiff spatula. The gradient of compliance may also be important in increasing the adhesion on rough surfaces. Indeed, both challenges must be addressed in order to study the potential effects of surface roughness on gecko adhesion. First, we need models to test hypotheses about how roughness affects the gecko fibrillar adhesive system. Second, we need an approach to characterize surfaces at all relevant length scales that free-ranging geckos do and do not use.

Adapting techniques from thermal ecology: a physical model approach to surface roughness

The complexities of modeling the interaction between the gecko adhesive system and rough surfaces, and the practical difficulties associated with characterizing surface roughness at all the relevant length scales are not unique challenges. Indeed, we argue that temperature is another environmental parameter that presents analogous challenges for prediction and characterization. In reviewing the techniques that thermal ecologists have used to study temperature variation and its effect on the thermal biology of lizards (Angilletta 2009), we believe an analogy can help move the study of roughness effects on gecko adhesion forward. We develop the rationale and offer a preliminary, proof of concept implementation of such an approach below.

When ecologists wanted to study the effects of the thermal environment on the ecology and evolution of lizards, they were confronted with two problems: 1) how to model heat exchange between the environment and the body of a lizard, and 2) how to measure temperature in a way that is relevant to rates of heat exchange. Lizards are ectotherms which mean that their body temperatures are determined by the microhabitats they occupy. Temperature is simply a measure of the heat content of an object, and the physics of heat transfer are well-enough understood that modeling the exchange of heat between a lizard and its microhabitat is, in principle, readily solvable using thermodynamic theory (O'Connor and Spotila 1992). In other words, all that is required is solving for the equilibrium body temperature of the lizard given the known routes and functional relationships of heat exchange (O'Connor and Spotila 1992). Early work on thermoregulation in lizards used mathematical models based on thermodynamic theory to predict the body temperatures of lizards in real environments.

What thermal ecologists quickly realized, however, is that such analytical approaches could not deliver predictions at the resolution necessary to understand how temperature might influence free-ranging individual lizards. There were simply too many required simplifying assumptions about factors such as (but not limited to) system equilibrium, body shape, and the complexity of expected heat loss and gain of real objects in dynamic environments. Moreover, measuring the sources of heat gain and loss in particular microhabitats was not reducible to easily obtained proxies, such as air or ground temperature, but was instead relatively intractable (Angilletta 2009). Faced with these challenges, thermal ecologists developed what has come to be known as a physical model approach (Bakken and Gates 1975). A physical model in thermal ecology is a replica of the organism of interest (a lizard) that matches its shape, size, radiative, conductive, and convective exchange rates. Usually, it is constructed from a hollow metal cast painted to match the reflectivity of the live organism, giving the model an equilibrium temperature that matches that of the live lizard, but which is reached much more rapidly (a comparatively short time constant). For the purposes of predicting the body temperatures of lizards moving around in real environments, physical models solved the two problems which could not be solved using the mathematical approach: (1) the models integrated the complexities of dynamic heat exchange between the organism and the environment, providing an unbiased estimate of body temperature, *and* (2) they made possible the rapid and extensive sampling of real environments with respect to the body temperatures different microhabitats would allow lizards to reach across space and time. We argue that the form of the limitations leading to the development of the thermal physical models, and the solutions that the models provided, can be directly applied to the study of surface roughness and the gecko adhesive system, which we turn to next.

Using the physical model for heat exchange described above as a guide, a physical model of the gecko adhesive system would be constructed such that it interacts with its environment (surfaces) in a way that mimics a live gecko. Ideally, it also should be deployable in real environments used by geckos such that surfaces could be broadly sampled with respect to adhesion potential. The goal of constructing and using such models would include estimating adhesion potential of particular substrates (surfaces) such that hypotheses about the role of specific surface characteristics on the ecology and evolution of gecko adhesion could be tested. Therefore, it is important that the mechanics of how the model interacts with surfaces approximates that which occurs for gecko toe pads. Moreover, if the model can be constructed in large numbers and easily deployed (tested) in real environments, we would be able to examine questions such as: Do free-ranging geckos use surfaces at random with respect to their adhesion potential? Do geckos in different environments experience an availability of surfaces that constrain or enable use based on adhesion potential? Is the toe pad design of geckos from one environment equal to or inferior to the toe pad design of geckos from different environments? In fact, these are just samples of questions. Below we describe a prototype physical model we developed to meet the objectives described above: to test hypotheses about the effects of surface roughness on gecko adhesion. In describing model construction and intended use, we will draw heavily on the previous discussion about thermal physical models with the hope that the potential power of a gecko adhesion physical model will become more clear.

Prototype physical models

Physical model design

Our prototype physical model included a gecko subdigital adhesive pad shed with a soft, compliant backing, designed to replicate the complex compliance hierarchy of the gecko adhesive system (Russell 2002). Toe sheds have been used to study gecko adhesion previously (Badge et al. 2014) and were used as the contact interface for our physical models because replicating their geometry and hierarchy with a synthetic material is not yet feasible. Because the toe shed does not include other components of the gecko system which contribute to the overall compliance of a gecko toe pad, we developed a backing for the sheds based on the work of Bartlett et al. (2012) who established an area-based compliance measurement ($\sqrt{\frac{A}{C}}$, where A is equal to pad area and C is equal to compliance) for live geckos of about 0.43 $\sqrt{Nm}$. Using mean live gecko subdigital pad areas from Stark et al. (2012), we estimated live gecko toe pad compliance at about 0.001 m/N.

$$C = \frac{L}{wtE}. \tag{1}$$

Using Equation (1), where C equals compliance, L is equal to the length, w is equal to the width, t is equal to the thickness, and E equals elastic modulus, we found that Sylgard 184 polydimethylsiloxane (PDMS) with an E of about 1 MPa and dimensions of 10 mm (L) × 5 mm (w) ×2 mm (t) achieves the estimated compliance of a live gecko toe pad. Thus, we used PDMS in the dimensions described above to create the soft, compliant backing of the prototype physical models. Consequently, our physical models are comprised of a toe shed plus a PDMS backing material (Fig. 1). It is important to note that model prototype development should include determination of whether the PDMS backing described above contributes to desired performance of the physical model. That is, as we compare the adhesion estimates provided by the physical model to the adhesion of live geckos on the same surfaces we can adjust the design of the backing to improve the correlation between estimates as necessary. Whether it is possible to develop a physical model using the PDMS design approach to mimic the portions of gecko toe pad not included in the shed is an empirical question.

Physical model construction

Molds composed of polymethylmethacrylate (PMMA) were used to cast the compliant backing of the physical models. The molds were created by removing several 10 mm × 5 mm sections from a 2 mm thick piece of PMMA via laser cutter. This piece of PMMA was then placed on another piece

Fig. 1 Example of a prototype physical model with the fibrillar surface pointing up and attached to a PDMS backing sized to approximate overall effective compliance of a gecko toe pad. Note that the fibrillar surface area is approximately equal to that of a single toe of a Tokay Gecko.

of PMMA using Sylgard 184 PDMS (Dow Corning, Midland, MI, USA), mixed at a 10:1 ratio, as an adhesive. The molds were cured at room temperature for at least 48 h before use.

Sylgard 184 PDMS was prepared as above and poured into the completed molds. A glass microscope slide was scraped across the tops of the molds to level the PDMS. The PDMS was cured for ~16 h and four subdigital adhesive pad sheds from three Tokay geckos (*Gekko gecko*) were placed ventral side up on the semi-cured PDMS. The sheds were gently pressed into the PDMS in between lamellae using a clean probe. The shed-backing complexes were cured for at least an additional 30 h. Shed-backing complexes were removed from their molds via scalpel and forceps and secured on 25 mm × 25 mm pieces of 3 mm thick PMMA using uncured PDMS as an adhesive. Complete physical models were cured for 48 h before use. Subdigital pad area was determined by imaging physical models with a flatbed scanner (HP Scanjet G3100; HP Inc., Palo Alto, CA, USA) and tracing the area around setae-bearing lamellae. Mean subdigital pad area for the physical models was 23.75 ± 2.80 mm^2.

The compliance of the prototype physical models was estimated using shear force data from adhesion testing on an aluminum substrate. Physical model compliance was calculated as the inverse slope of the linear portion of the force–displacement curve.

Table 1 Mean RMS roughness values for the seven different test substrates utilized in this study

Substrate	RMS roughness (μm)
Aluminum	0.207±0.010
Frosted glass	1.521±0.134
Painted drywall	1.733±0.135
P2500 sandpaper	3.303±0.056
P2000 sandpaper	4.294±0.086
P1000 sandpaper	4.873±0.115
Grip tape	31.643

Values represent mean±SE.

Mean physical model compliance was 0.01 ± 0.004 m/N.

Substrate preparation and characterization

Seven different substrates with various levels of surface roughness were used: 80 grit grip tape (Black Diamond Sports, Palo Alto, CA, USA), 3 different sandpapers (P1000, P2000, P2500; 3M, St. Paul, MN, USA), painted drywall, frosted glass, and aluminum. The sandpapers and grip tape were secured to a glass microscope slide via double-sided tape. The other three surfaces were cut to a dimension such that their masses were similar. Mean test substrate mass was 6.15 ± 0.23 g. Six-pound fishing line was secured to each test substrate using adhesive tape and a slip knot was tied in the other end to attach to a motorized force sensor.

Substrate surface roughness was characterized via optical profilometer (Zygo NewView 7300; Zygo Corp., Middlefield, CT, USA). Three scans at 5× magnification were performed for each substrate (with the exception of grip tape, as its long wavelength, high amplitude roughness led to difficulties in scan acquisition) at three different locations per substrate sample. Average RMS surface roughness values were obtained for each surface from these three scans (Table 1).

Physical model and live gecko shear adhesion testing results

Physical model shear adhesion forces were measured utilizing a motorized force rig used to test whole animal gecko adhesion (Niewiarowski et al. 2008) in an environmental chamber with controlled temperature and humidity (35–45% RH, 23°C). Physical models were secured onto a PMMA substrate ventral side up via double-sided tape and test substrates were secured to a motorized force sensor (Fig. 2). Test substrates were gently placed onto the physical models and were pulled along the adhesive axis

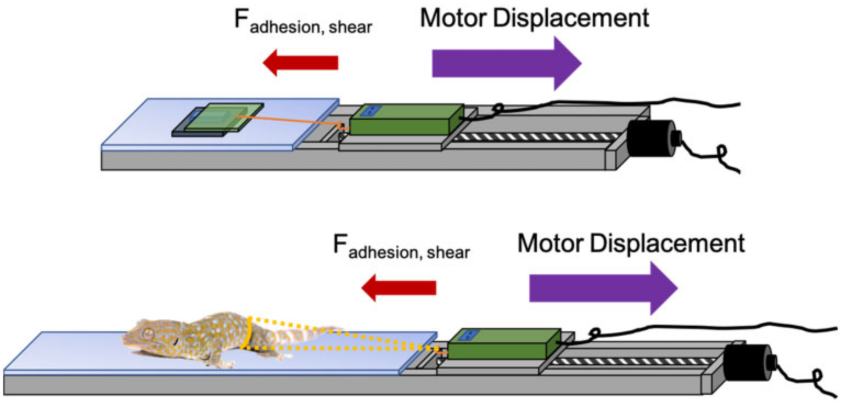

Fig. 2 Diagram showing the horizontal force testing apparatus (Niewiarowski et al. 2008) and setup used to test adhesion of live geckos (bottom panel) and physical models (top panel).

(proximal to distal displacement) of the subdigital adhesive pad shed until maximum force was reached or until 1 cm of substrate displacement occurred. Maximum force was determined by estimating the force per unit area that would be equivalent to 20 Newtons, a force cutoff used in whole animal gecko adhesion trials to prevent damage to the subdigital adhesive pads. Each physical model was tested three times per substrate.

Five Tokay geckos (*G. gecko*) were utilized to obtain live gecko shear adhesion data (*sensu* Niewiarowski et al. 2008). Maximum shear adhesion was measured similar to shear adhesion measurements for physical models, except that each substrate was placed on the force rig and geckos were displaced parallel to the surface via pelvic harnesses attached to the motorized force sensor (Fig. 2). Maximum shear adhesion was determined when all four of the gecko's feet began to slide along the surface. Shear adhesion trials were halted at 20 Newtons (for whole geckos, and normalized to the surface area of the shed comprising the contact face of the physical model), as to not damage their subdigital adhesive pads (Stark et al. 2012). Each gecko was tested three times per substrate. Mean gecko mass and subdigital pad area were 87.6 ± 16.95 g and $481.17 \pm 83.49\ mm^2$, respectively. All substrates were cleaned in between trials with 70% ethanol followed by reverse-osmosis water (with the exception of painted drywall, as application of the liquids would degrade the surface). Live gecko adhesion data for the P2000 and P2500 substrates were obtained from unpublished data (Klittich et al. in preparation).

Preliminary results comparing our prototype physical models with live geckos on seven different types of surfaces are encouraging. Following recommendations developed for thermal biophysical models (Dzialowski 2005; Bakken and Angilletta 2014), we have initiated a comparison of the adhesion of physical models to that of live geckos under the same conditions. Collecting such data enables us to verify that the physical models "behave" similarly to a live gecko from the perspective of adhesion, such that we can use the models to predict gecko adhesion on many kinds of surfaces in the laboratory and in the field. Consistent with the techniques used with thermal physical models (Niewiarowski 2001), when the regression of live gecko adhesion observations against observations of adhesion of the physical model explains a high proportion of variance in live gecko adhesion, the physical models can be used as reliable predictors of gecko adhesion. Such a regression is ideally based on a large sample of matched observations across the range of surfaces of interest to sample. A full "calibration" of the physical models is beyond the scope of this study, but as a first step we compared live gecko and physical model adhesion (Fig. 3) on a small sample of our prototypes in the laboratory on aluminum, four different grits of sandpaper, painted drywall, and frosted glass; some of which are substrates used in previous gecko adhesion studies (King et al. 2014).

Note that in this preliminary analysis (Fig. 3), we used only five Tokay geckos, and four physical models. The following description is qualitative only as the data do not conform to the assumption of independent observations required by inferential statistics. Overall, the prototype physical models estimate adhesive forces for the surfaces that are quite like the forces generated by geckos. One apparent difference between the two sets of estimates seems to be that there is less variance in force measured from repeated observations on any given substrate. The standard deviations in physical model measurements are on average about half as large as

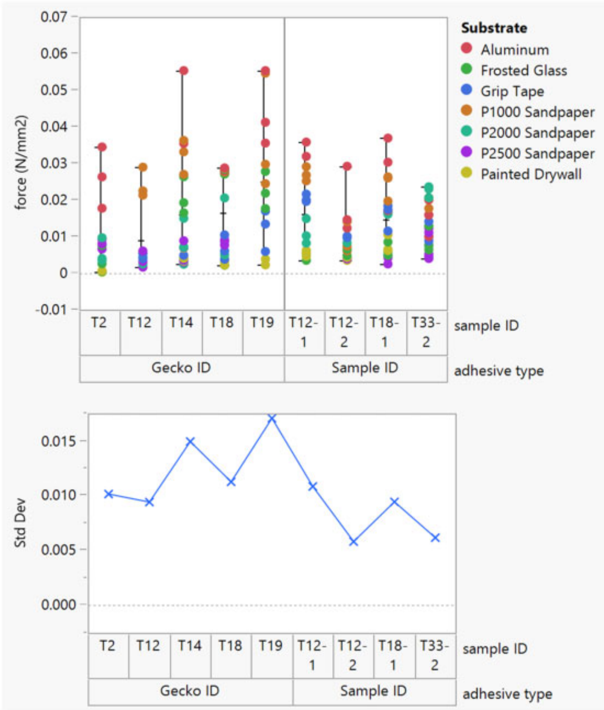

Fig. 3 (Top panel) Variability chart of adhesive force observations of geckos and physical models, color coded by substrate type. Vertical lines show range of observations, cross-hatches show overall mean force across substrate type for each adhesive ID (individual geckos or physical models). (Bottom panel) Standard deviation of observations for each adhesive ID (individual geckos or physical models) lumped across substrate type.

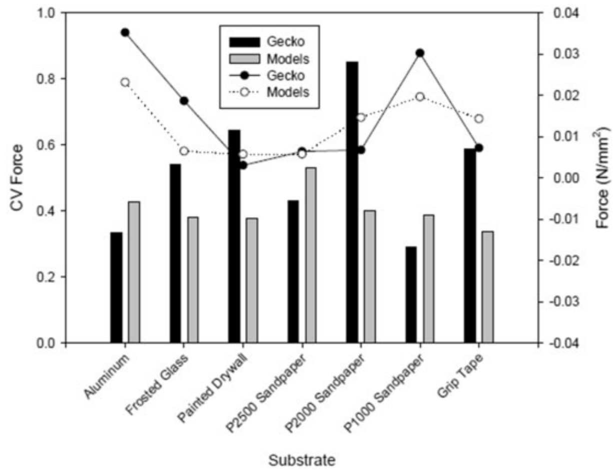

Fig. 4 CV of standardized force for geckos and physical models as a function of substrate type (vertical bars) and standardized mean adhesive force of geckos and models as a function of substrate type (round symbols and lines).

that for live geckos (0.131 vs. 0.0082, gecko and model average SD, respectively).

Because in general, mean and variance are correlated, we calculated coefficients of variation (CV) for both sets of data and overlaid them on a plot of average force estimates from the live gecko and physical model trials, as a function of test substrate (Fig. 4). Note that even after standardizing the variation by scaling it to the mean, variance in model estimates within a test substrate seem to be lower than for live geckos, except for the aluminum, P2500, and P1000 sandpaper. Moreover, qualitatively, the CVs seem to vary less among the physical models compared with the live geckos, when looking across test surfaces. Finally, average force estimates for the geckos and the physical models track one another surprisingly well when looking across substrates (Fig. 4). Although the scatter of points is fairly broad, this is based on a small number of animals and physical models. These preliminary data suggest that the large within and between variability in live geckos will require sample sizes similar to those used in our adhesion experiments to obtain reliable estimates of adhesion for any single set of conditions.

Overall, these pilot data encourage us that the physical model approach, at least under a limited set of laboratory conditions, may be viable. That is, we believe collecting a more thorough set of data that will allow rigorous testing the fit of physical model estimates to live gecko adhesion is warranted and currently in progress. Several observations from the data presented here are informing our next steps. First, it is interesting that the adhesive forces generated by live geckos on any particular substrate appear to be more variable than the physical model estimates (Fig. 3). A conspicuous source of variation in live gecko adhesion performance includes how the behavior of individual geckos impacts how well they stick, consistent with active control of the deployment of the toe pad seen in some studies (Russell and Higham 2009). It is also likely that the multilayered structures (Russell 1973, 2002) that form the "backing" to the setal arrays (including, bone, muscle, fat, connective tissue, and vascular sinuses) could lead to more variable effective compliance from trial to trial with or without active behavioral manipulation by the gecko. Furthermore, the calculated compliance of the physical models is about one order of magnitude higher than anticipated by our design. Future prototypes will be tested with a less stiff PDMS formulation. One consequence of these differences between the live geckos and the models is that the fit of a regression of live gecko estimates against physical models may be limited by such uncontrollable variability in gecko adhesion that is fundamentally different from the thermal models application this technique is based upon. Another source of variation arises from the methods we used to test our prototypes. When thermal physical models are deployed to generate a model calibration, the models are placed into the identical microhabitat previously occupied by a live lizard (in an attempt to match the thermal biophysical environment between live lizard and physical model). In our tests, we could not place our physical model onto a region of the test surface from which we measured the adhesive force of the gecko. Moreover, the total toe pad area of the gecko is from 10 to 20 times the area of our physical model which means that the live gecko adhesion arises from the gecko "sampling" a much larger area of the test surface than the physical models. The implications of these differences are not clear, however there are potential ramifications for both average and variance estimates of force that come from the physical models that must be addressed in sampling designs going forward.

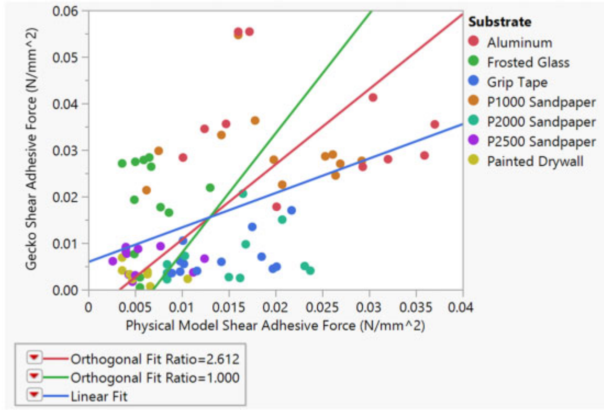

Fig. 5 Three different linear regressions of standardized gecko adhesive force vs. standardized physical model adhesive force. Variance ratios for the three different fits are shown (PC, RMA, and Type I regression listed from top to bottom).

Next steps

The reasonable agreement between model and gecko adhesion in our sample for the chosen substrates needs to be tested more rigorously with a larger sample of geckos and models. Moreover, given the proportion of variation still not explained in the regression, sources of uncontrolled variation must be minimized or eliminated where possible. One conspicuous source has to do with an aspect of our methodology which departed from the fundamental analogy drawn from thermal physical models: our toe pad models were not tested on the identical surface as the live geckos. We are currently exploring techniques to address this and other potential sources of variance and differences between model and gecko adhesion. Ultimately, we will choose a regression model that allows for error variance in both the model and gecko estimates (e.g., PC or RMA regression; Fig. 5) which also suggests that reducing variance in gecko force estimates due to behavior could further improve our calibration of models.

Assuming a reasonable model calibration can be obtained, we plan to use the physical models to develop testable hypotheses in a manner analogous to that used for thermal physical models. For example:

- Compare adhesive forces on substrates selected by free-ranging geckos in their natural habitats to adhesive forces of substrates not selected.
  - Do substrates used by geckos enable higher adhesive performance compared with substrates not selected for use?
  - Is substrate use highly selective when the cost of reduced adhesive performance is high?
- Compare adhesive performance on substrates from habitats of species which are conspicuously different (geckos that use vegetation versus those that are saxicolous).
  - Are gecko adhesive systems specialized for the substrates they live on?
- Compare adhesive performance on substrates used exclusively by geckos that coexist via habitat partitioning.
  - Is gecko adhesive performance reciprocally lower on substrates utilized exclusively by the other species compared with performance on their own substrates.
- Build a comparative database for adhesive performance on different substrates that can be probed with multivariate techniques such as PCA to uncover toe pad parameters (e.g., setal length, density, and modulus) that covary with surface asperity feature parameters.
  - Does variation in toe pad parameters associated with surface roughness variation follow tradeoffs identified for fibrillar adhesives in adhesion design maps (Spolenak et al. 2005; Greiner et al. 2009).

The successful development of a physical model also opens up the possibility of testing fibrillar adhesives on model rough surfaces for which we have accurate measurements of roughness power spectra. The comparison between the physical model and theoretical adhesion models (based on the knowledge of roughness power spectral analysis) will help us judge whether continuum mechanics-based models are able to capture the performance of fibrillar adhesives on rough surfaces. This comparison is critical in addressing the importance of fibrillar adhesives and development of future theoretical models, allowing us to address the role surface roughness of natural surfaces may have played in evolution of specific shape and size of fibrillar adhesives.

Summary and conclusions

Given formidable challenges associated with understanding how surface roughness affects adhesion of the setae-based systems evolved by geckos and other animals, it is easy to forget that just 20 years ago the strategy to create a fibrillar surface to achieve strong and reversible adhesion was completely unknown. Much has been discovered about the contact mechanics of such systems at various length scales, especially through study of isolated system components (e.g., setae and lamellae) under highly controlled laboratory conditions and surfaces. The next step in advancing our understanding, to the point where we can extract new design principles for the fabrication of performance matching bioinspired synthetics, as well as reveal the ecological and evolutionary circumstances that drove the emergence of fibrillar systems, will require new empirical and theoretical approaches. We have described one such approach (physical models), rooted in a successful empirical paradigm used to study thermal biology, which we argue addresses two main challenges in studying the effects of surface roughness: modeling the surface fibrillar interface and characterizing roughness of surfaces.

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