



SYMPOSIUM

Attachment Beyond the Adhesive System: The Contribution of Claws to Gecko Clinging and Locomotion

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Synopsis Attachment is imperative for many biological functions, such as holding position and climbing, but can be challenged by natural conditions. Adhesive toe pads and claws have evolved in multiple terrestrial lineages as important dynamic attachment mechanisms, and some clades (e.g., geckos) exhibit both features. The functional relationship of these features that comprise a complex attachment system is not well-understood, particularly within lizards (i.e., if pads and claws are redundant or multifunctional). Geckos exhibit highly adept frictional adhesive toe pads that continue to fuel biological inquiry and inspiration. However, gecko claws (the ancestral lizard clinging condition) have received little attention in terms of their functional or evolutionary significance. We assessed claw function in *Thecadactylus rapicauda* using assays of clinging performance and locomotor trials on different surfaces (artificial and natural) and inclines with claws intact, then partially removed. Area root mean square height (Sq), a metric of 3D surface roughness, was later quantified for all test surfaces, including acrylic, sandpaper, and two types of leaves (smooth and hairy). Maximum clinging force significantly declined on all non-acrylic surfaces after claw removal, indicating a substantial contribution to static clinging on rough and soft surfaces. With and without claws, clinging force exhibited a negative relationship with Sq. However, claw removal had relatively little impact on locomotor function on surfaces of different roughness at low inclines ($\leq 30^\circ$). High static and dynamic safety factor estimates support these observations and demonstrate the species' robust frictional adhesive system. However, maximum station-holding capacity significantly declined on the rough test surface after partial claw removal, showing that geckos rely on their claws to maintain purchase on rough, steeply inclined surfaces. Our results point to a context-dependent complex attachment system within geckos, in which pads dominate on relatively smooth surfaces and claws on relatively rough surfaces, but also that these features function redundantly, possibly synergistically, on surfaces that allow attachment of both the setae and the claw (as in some insects). Our study provides important novel perspectives on gecko attachment, which we hope will spur future functional studies, new evolutionary hypotheses, and biomimetic innovation, along with collaboration and integration of perspectives across disciplines.

Introduction

Permanent or temporary attachment to a surface can occur within and between animals, and between an animal and a substrate (Nachtigall 1974; Emerson and Diehl 1980; Flammang 1996; Gorb 2008; Bullock and Federle 2009; Kovalev et al. 2014). This attachment often entails overcoming certain challenges of the environment, such as wave action (e.g., Carrington et al. 2009), gravity (e.g., Foster and Higham 2012), and slippery (Clark and Higham

2011), heterogeneous (Gorb and Gorb 2009), or friable (e.g., Russell and Delaugerre 2017) surfaces.

Within terrestrial animals, the ability to successfully attach and detach from surfaces repeatedly, or dynamic attachment, is critical to avoid slipping and falling during rest and during movement on non-horizontal surfaces (Cartmill 1985; Barnes 2006). Two prevalent structures within and across animal groups that confer this ability are adhesive pads and claws (Nachtigall 1974; Gorb 2008; Labonte and Federle 2015).

Adhesive pads, the sites of animal–surface interactions, are classified by their structure and nature of adhesive forces produced (see [Barnes 2007](#); [Gorb 2008](#)). Some insects and arachnids exhibit tiny hair-like structures, or setae, projecting from a glandular ('wet') pad that intimately contact a surface to generate intermolecular forces (i.e., van der Waals) along with fluid-based forces ([Beutel and Gorb 2001](#); [Gorb 2001](#); [Bullock et al. 2008](#); [Wolff and Gorb 2016](#)). Dry adhesion is based only on forces associated with the setae, and is prevalent in spiders (e.g., [Kesel et al. 2003](#)) and lizards ([Ruibal and Ernst 1965](#); [Williams and Peterson 1982](#)). The shearing of densely arranged setae over a surface can yield substantial frictional adhesive forces, best exemplified by geckos (see [Autumn et al. 2000](#); [Autumn and Peattie 2002](#)).

Claws represent another dynamic attachment feature convergent within and between arthropods and tetrapod vertebrates ([Gorb 2001, 2008](#); [Alibardi 2009](#); [Patrick et al. 2018](#)). As the composition and development of these structures vary across clades, we use a simple functional definition of claws: pointed, often recurved projections of the distal aspect of a limb or digit that attach via penetration (soft surfaces) or mechanical interlocking (surface asperities are larger than the claw tip), and/or friction (surface asperities are smaller than the claw tip) (see [Cartmill 1974](#); [Dai et al. 2002](#); [Labonte and Federle 2015](#)). Some clades, including insects, spiders, and lizards, exhibit adhesive pads as well as claws ([Gorb 2008](#); [Labonte and Federle 2015](#)), posing further questions about the evolutionary relationships between and the functional significance of these concurrent attachment morphologies. Do they confer different functions or redundancy?

The combination of adhesive toe pads and claws represents what we consider a 'complex attachment system', with multiple attachment morphologies and/or multiple attachment functions within an individual. We can conceptualize different relationships of form and function within these systems using interspecific perspectives from [Wainwright et al. \(2005\)](#). When multiple features confer one attachment function within an individual (i.e., 'many-to-one mapping'), this can be considered a redundant, possibly synergistic, attachment system. Such a system may enhance performance within a particular context, as well as provide maintenance of overall function if one feature fails. For example, Atelid primates have prehensile tails bearing a friction-enhancing volar pad which, along with the autopodial volar pads, provide grip during suspension and locomotion ([Meldrum 1998](#)). Converse to

this scenario, an organism could exhibit a multifunctional attachment system in which one feature serves multiple functions (i.e., 'one-to-many mapping'), or multiple features may confer different functions within an individual (i.e., 'one-to-one' or 'many-to-many mapping'). Functional partitioning allows structures to become optimized for different roles (e.g., tube feet in some sea cucumbers; [Santos et al. 2009](#)). Although this may lead to vulnerability to a perturbation, it may also allow an organism to effectively perform a variety of tasks, such as running on diverse surfaces. Where do adhesive pads and claws fall with respect to these categories?

Within lizards, anoles and geckos are the only groups with frictional adhesive digital pads ([Ruibal and Ernst 1965](#); [Russell 1972, 1979](#); [Peterson 1983](#)). In geckos, the pads comprise a particularly hierarchical and integrated suite of external and internal structures that finely modulate setal–surface contact and enable strong, repeated attachment on vertical and inverted surfaces ([Russell 1972, 1975, 1979, 1981, 2002, 2016](#); [Autumn et al. 2000](#); [Autumn 2006](#)). Approximately two-thirds of gecko species exhibit this putative evolutionary key innovation, with multiple independent origins of diverse pad forms across the phylogeny ([Russell 1976](#); [Pianka and Sweet 2005](#); [Gamble et al. 2012, 2017](#); [Russell and Gamble 2019](#)). Geckos are thus a rich source of biological interest and inspiration ([Autumn et al. 2014](#); [Patek 2014](#); [Niewiarowski et al. 2016](#)).

Claws are the ancestral clinging condition exhibited by all modern lizard groups ([Pianka and Vitt 2003](#)) but have received relatively little attention within geckos. Interestingly, claws have been lost or reduced (i.e., become vestigial or lost on some digits) within pad-bearing and secondarily padless gecko lineages on multiple occasions ([Khannoon et al. 2015](#)). Much remains to be explored concerning the apparent diversity of autopodia across the clade, including patterns of evolution and the ecological significance of different morphologies. [Figure 1](#) outlines possible selective regimes for phenotypic combinations of toe pads and claws, ignoring potential effects of non-adaptive evolutionary processes (e.g., phylogenetic constraint or pleiotropy).

Within three gecko genera, [Zani \(2000\)](#) reported positive correlations between pad area, claw curvature, and clinging force on smooth surfaces; taller claws were correlated with higher performance on rough surfaces. [Crandell et al. \(2014\)](#) found positive relationships between pad area, claw size, and arboreality in anoles, but a negative relationship of claw curvature that conflicts with other padless lizards (e.g., [Tulli et al. 2009](#); [D'Amore et al. 2018](#)). These

	+ Claws	- Claws
+ Pads	<p>Positive selection for both: <i>Redundancy & synergism</i></p> <ul style="list-style-type: none"> Retain function if one fails Enhance attachment ability <p><i>Division of labor</i></p> <ul style="list-style-type: none"> Cope with different conditions <p><u>Substrate</u></p> <ul style="list-style-type: none"> Varied: rough, smooth, soft, hard Inclines prevalent 	<p>Negative selection against claws:</p> <ul style="list-style-type: none"> Impede placement of pad Constrain pad size Injury risk <p>Relaxed selection on claws:</p> <ul style="list-style-type: none"> Attachment inferior to pads <p><u>Substrate</u></p> <ul style="list-style-type: none"> Specific: smooth, soft Inclines prevalent
- Pads	<p>Negative selection against pads:</p> <ul style="list-style-type: none"> Reduce locomotor speed Fouling/injury risk <p>Relaxed selection on pads:</p> <ul style="list-style-type: none"> Attachment inferior to claws <p><u>Substrate</u></p> <ul style="list-style-type: none"> Specific: rough, hard friable Inclines variable 	<p>Negative selection against both:</p> <ul style="list-style-type: none"> Fouling/injury risk <p>Relaxed selection on both:</p> <ul style="list-style-type: none"> Attachment ability inconsequential <p><u>Substrate</u></p> <ul style="list-style-type: none"> Specific: soft friable Inclines few

Fig. 1 Potential selective regimes, including abiotic factors (i.e., substrate), that could result in the four pad–claw character combinations seen within the Gekkota (non-adaptive evolutionary processes are not considered here). Top left: The presence of both pads and claws may enhance attachment ability or maintain function if one mechanism fails (i.e., redundancy), or it may accommodate various inclined substrates within its environment (i.e., multifunctional). Top right: Claw loss or reduction could reflect relaxed selection (see Lahti et al. 2009) if surfaces are regularly encountered that optimize the adhesive system but not the interlocking of claws. Claws may also pose a risk of becoming caught or a physical impediment to the flush placement of the pads, as previously speculated in anoles (e.g., Garner et al. 2017) and may be selected against. Bottom left: Claws without pads represents the ancestral phenotype. However, relaxed and/or negative selection is hypothesized to have led to the secondary loss of pads and subsequent radiation within some lineages (see Higham et al. 2015). Pads pose a potential fouling and injury risk, as well as a locomotor speed cost (see Autumn et al. 2006; Russell and Higham 2009). Bottom right: Both structures may be lost within lizards occupying surfaces that do not require attachment and/or present an injury risk.

studies suggest that pads and claws have evolved in concert within these clades, potentially driven by functional demands. Experimental studies are rare, but Mahendra (1941) used claw amputation to qualitatively examine clinging and climbing ability within a house gecko, *Hemidactylus flaviviridis*, which appeared to decline on rough, but not smooth surfaces. Garner et al. (2017) instead used partial claw removal (i.e., trimming the distal keratinized aspect to avoid tissue damage; see Bloch and Irschick 2005) and evaluated its effect on clinging performance in *Anolis sagrei*. Clinging force was maintained on smooth artificial surfaces, but performance was not tested on rough or natural surfaces. How do claws contribute to clinging ability and locomotion on different substrates?

In this study, we assessed claw function in *Thecadactylus rapicauda* (turnip-tailed gecko; Houttuyn 1782), an arboreal species that uses a variety of natural surfaces (e.g., tree bark, bromeliad leaves) and humanmade structures throughout neotropical and southern Caribbean island forests (Vitt and Zani 1997; Russell and Bauer 2002). This species exhibits sharp, “sheathed” claws (i.e., recessed in subdigital sulci) between divided lamellae of the toe pad

(Russell and Bauer 1988, 2002; Bergmann and Russell 2003; see Fig. 2), and previous studies have demonstrated strong frictional adhesive capabilities relative to other lizards (Higham et al. 2017a, 2017b). If gecko claws contribute to static and dynamic attachment via mechanical interlocking and friction, then we expect that partial claw removal in *T. rapicauda* will (1) confer lower clinging performance on rough surfaces (but not smooth surfaces) and (2) alter locomotor kinematics on rough surfaces, particularly those that are inclined.

Materials and methods

Study site, individuals, and claw removal

Wild geckos were captured at two camps within the Nouragues Ecological Research Station (Centre National de la Recherche Scientifique, French Guiana), ‘Inselberg’ (4805' N, 52,841' W) and ‘Saut Pararé’ (4802' N, 52,841' W), in February 2018. We obtained the mass of each individual using a Pesola scale, and standard morphological measurements (snout-vent-length and limb element lengths) were taken with calipers or later from photographs in ImageJ (version 1.51j8; National Institutes of

Health, USA; Table 1). Individuals underwent clinging performance and locomotor trials before and after we trimmed the claw tips from all digits (precluding any living tissue; *sensu* Garner et al. 2017); digit I lacks claws (Russell and Bauer 1988).

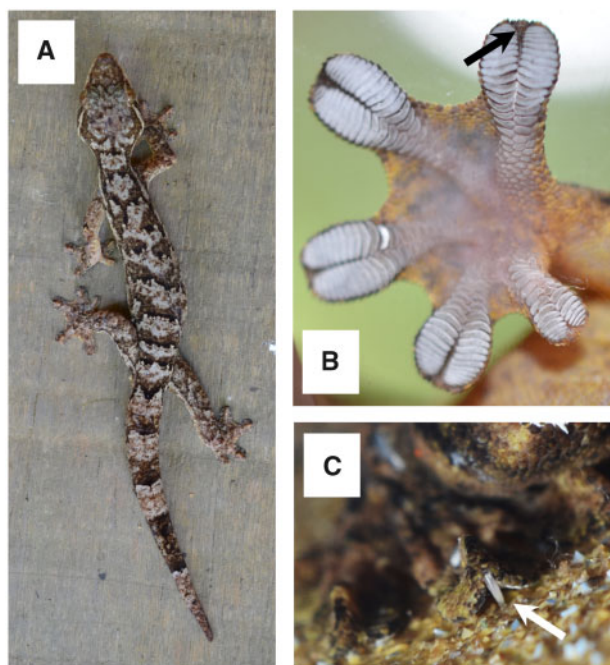


Fig. 2 Images of *T. rapicauda*. (A) Dorsal view of individual on treated wood (field station shelter), (B) Ventral view of manus on acrylic showing divided scanzors of the toe pads with arrow pointing to a “sheathed” claw, (C) Lateral-oblique view of pes on 60-grit sandpaper with arrow pointing to a claw contacting the surface.

Individuals were given several hours to recover before subsequent trials. Ambient temperature and relative humidity were recorded for all trials; body temperature was also determined from digital infrared thermometer readings of the ventral surface for all locomotor trials. Geckos were released at their site of capture after trials were completed. All handling procedures were in accordance with approved IACUC protocols for the University of California, Riverside (AUP 20170039).

Test surfaces

Both natural and artificial surfaces were used in our experiments. Two types of tree leaves, one “smooth” (*Pyschotria* sp.) and the other “rough” (i.e., hairy with trichomes; *Clidemia* sp.) were selected from habitat typical of the species, although we did not observe *T. rapicauda* occupying these specific leaves or tree species. Based on observations of geckos utilizing wooden shelters around both camps, we also included a treated wood sample. Finally, acrylic and 60-grit sandpaper (samples from two manufacturers) were selected as standardized surfaces of extreme smoothness and roughness. All samples were retained for surface analyses “described under ‘Surface microtopography’”

Clinging performance

Maximum clinging force

In the first clinging performance assay, we determined maximum peak tension force from 14 individuals. As conducted in previous field studies (e.g.,

Table 1 *T. rapicauda* morphological data

Individual No.	Body mass (g)	Snout-vent-length (cm)	Forelimb length (cm)	Humerus length (cm)	Hindlimb length (cm)	Femur length (cm)
1	11.2	8.68	1.83	0.96	2.28	1.13
2	16.6	9.43	2.15	1.18	2.46	1.26
3	20	9.64	2.41	1.22	2.37	1.27
4	21.2	9.75	2.40	1.21	2.42	1.27
5	15	8.77	2.00	1.07	2.53	1.24
6	14.5	8.85	2.12	1.12	2.22	1.19
7	23.2	9.67	2.40	1.22	2.67	1.37
8	15.2	9.35	1.95	1.08	2.36	1.26
9	17	9.64	2.19	1.02	2.64	1.34
10	11	8.64	1.76	0.77	2.05	1.06
11	14.4	8.60	1.92	0.96	2.27	1.17
12	20.5	9.83	2.56	1.29	2.74	1.42
13	14	8.87	1.99	1.02	2.43	1.14
14	10.9	7.63	1.83	0.90	2.04	1.05

Higham et al. 2017a), geckos freely placed the right manus onto a test surface affixed to a portable force gauge (Mark-10 Series 5) and were steadily pulled in parallel opposition until slipping occurred. A maximum force value (newtons) was recorded from five trials per individual per test surface before and after partial claw removal; test surface order was randomized. The setae achieved exceptionally high contact and frictional adhesion on acrylic, so we attempted to avoid damaging the toe pads (i.e., separation of the lamellae from the toe pad) for subsequent performance and locomotor trials. Therefore, “true” maximum clinging force on acrylic was not likely obtained in our study (see [Supplementary Table S1](#) for raw force data).

Station-holding capacity

We tested station-holding capacity within a subset of individuals ($n = 5$) by placing a gecko on a horizontal platform and slowly rotating it from 0 to roughly 180° (i.e., level to inverted; *sensu* Huber et al. 2007). From video recordings of three to four trials per individual (before and after partial claw removal), we determined the maximum angle achieved before the gecko began to fall. This assay was conducted only on acrylic and 60-grit ‘sandpaper 2’ (see [Supplementary Table S2](#) for raw fall angle data).

Locomotor behavior

Finally, seven geckos were recorded from lateral view using an Edgertronic SC1 monochrome high-speed camera (250 frames/s) while running on acrylic and sandpaper 2 at level and 30° inclines before and after partial claw removal. These inclines were selected to capture running and climbing behavior; 30° was based on previous gecko locomotor studies (e.g., Russell and Higham 2009; Collins and Higham 2017) and to ensure that geckos would be able to successfully ascend all substrates. Two to four trials were conducted per individual and substrate treatment (four total treatments; random order) with claws intact and removed.

From videos in which the gecko exhibited sequential, straight, and clean (i.e., did not run into trackway walls) strides, we digitized multiple points along the body using the DLTdv5 package (Hedrick 2008) in MATLAB (version R2015b; MathWorks, Inc., USA). These data were then imported into IGOR PRO (version 4.0; Wavemetrics, Inc, USA), where smoothing splines (smoothing factor = 2) were applied. We then extracted multiple variables that encompassed aspects of timing, posture, and forward movement (see [Supplementary Table S3](#) for variable list and definitions).

Analyses

Surface microtopography

Area root mean square height (Sq), a metric of 3D roughness, was determined for each test surface (i.e., acrylic, wood, 60-grit sandpaper samples 1 and 2, and smooth and rough leaves) using a confocal laser scanning microscope (LEXT OLS4000, Olympus Corporation, Japan) and 3D topographical reconstructions in MountainsMap Premium 7.2 software (Digital Surf, France). Unlike 2D metrics of roughness derived from a single transect through the sample, such as mean roughness (Ra) and root mean square, our area roughness values were derived from numerous surface transects (see Higham et al. (2019) for further details).

Clinging performance

We ran linear mixed-effects (LME) models using the lme4 and lmerTest packages (Bates et al. 2015; Kuznetsova et al. 2017) in R Studio (version 1.1.456; RStudio, Inc., USA) to test the contribution of claws to clinging performance (both clinging force and station-holding angle). For each surface model, claw status, body mass, and ambient conditions (i.e., temperature and relative humidity) were coded as fixed effects with maximum performance trials nested within geckos (i.e., random effect). Log transformation was used to normalize performance and body mass data prior to analyses.

We also calculated an average static clinging safety factor for each surface before and after partial claw removal by multiplying an individual’s maximum clinging force on each surface by 4 (representing whole-organism performance) and dividing by body weight. We ran paired samples *t*-tests to compare static clinging safety factor on each surface before and after partial claw removal in SPSS (version 24; IBM Corp., USA).

Locomotor behavior

All locomotor variables were normalized via log transformation prior to analysis; forelimb and hindlimb strides were analyzed separately. To remove the effect of speed, kinematic variables were regressed with average stride velocity; for all significant regressions ($\alpha \leq 0.1$), residuals were obtained and used in subsequent analyses. To test the effect of claws on each of the kinematic variables within each substrate treatment, we ran LME models (see previous section); multiple, unequal numbers of strides (and initial acceleration observations) per individual per test surface (1–4 strides each) were incorporated. Each model had the following structure:

the response variable as predicted by claw status, body size (body mass, snout-vent-length, fore/hindlimb length, or humerus/femur length), body temperature, and ambient conditions (i.e., fixed effects), with strides nested within treatment and treatment nested within individual geckos (i.e., random effects).

Furthermore, we tallied the number of strides (of those analyzed) in which the distal toes appeared to remain a least partially hyperextended (i.e., all or some toes in hyperextended position) throughout the stride.

Locomotor safety factor

Using maximum initial acceleration values and body mass measurements, we estimated the amount of force that geckos exerted in order to move from a stationary position on a level and an inclined surface, or their “locomotor force.” True maximum clinging force values on acrylic were estimated from a regression of body mass and clinging force (per manus, claws intact) with data published for this species captured at the same locality in Higham et al. (2017b). These estimates and the per manus measurements for 60-grit sandpaper were then multiplied by 4 to provide a whole-organism estimate of maximum clinging force. By then dividing clinging force by locomotor force, we calculated an average “locomotor safety factor” for each surface–incline treatment before and after partial claw removal. Because we did not observe a significant difference in clinging performance on acrylic after partial claw removal in our study, we used the maximum clinging performance estimates from the Higham et al. (2017b) data in our calculations for both “claws intact” and “claws removed.” We also ran paired samples *t*-tests in SPSS to compare locomotor safety factors for each substrate treatment before and after partial claw removal.

Results

Roughness of test surfaces and distal toe morphology

The six test surfaces are here listed by their Sq value from smoothest to roughest: acrylic (0.0 μm), smooth leaf (6.4 μm), wood (29.3 μm), 60-grit sandpaper 2 (87.6 μm), rough leaf (94.1 μm), and 60-grit sandpaper 1 (105.2 μm). 3D microtopographical reconstructions for the smooth leaf and sandpaper 2, as well as a micrograph of the rough leaf trichomes can be viewed in Supplementary Fig. S4.

To gain a sense of the scale of interactions between the surfaces and the attachment structures, we measured the fourth pedal digit of a single

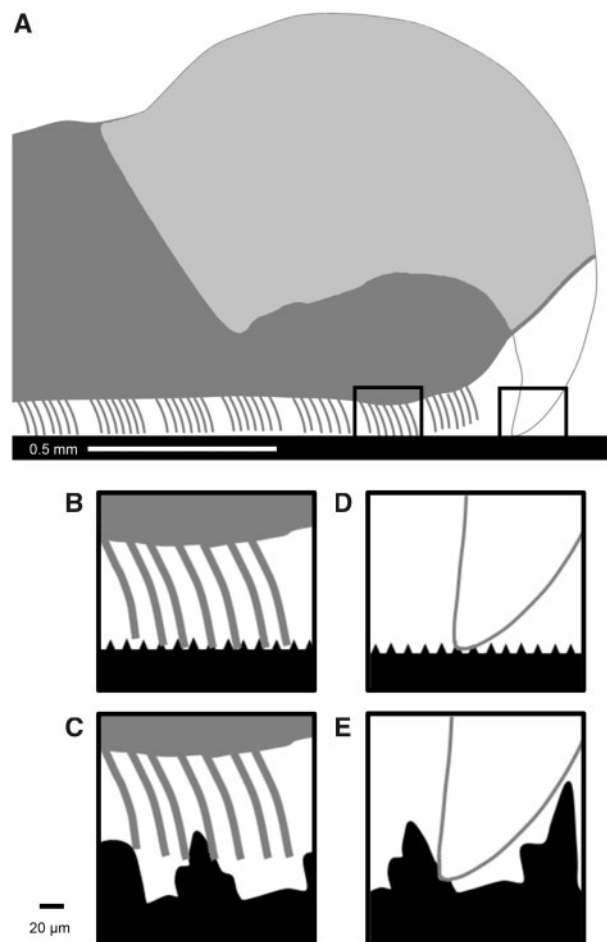


Fig. 3 Schematic drawings of attachment structures and surface interactions to approximate scale. (A) Overview of distal toe with claw tip (white) projecting from sulcus (light gray) and setae projecting from ventral surface of the toe (dark gray) onto a surface (black). (B) and (C) Closer view of setae (length to scale) and a surface with low (top) and high (bottom) roughness. (D) and (E) Closer view of claw tip (diameter to scale) and a surface with a low (top) and high (bottom) roughness. (B) Most setae make contact on a surface with small asperities (as in the smooth leaf); (C) Some setae are precluded from making contact on a surface with large, irregular asperities (as in 60-grit sandpaper); (D) The claw tip slides over the surface, rather than mechanically interlocking with small asperities; (E) The claw tip mechanically interlocks with large surface asperities.

preserved *T. rapicauda* individual (ZFMK 85463) to obtain maximum setal length (109.6 μm ; *sensu* Russell and Johnson 2007), claw length (1.34 mm; *sensu* Zani 2000), and claw tip diameter (13 μm). Figure 3 shows a simple 2D schematic of the distal toe with the setae (length) and claw at approximate scale with one another.

Clinging performance—maximum clinging force

LME models showed that clinging force was maintained on acrylic ($t(9.2) = -1.35$, $P = 0.21$) after

partial claw removal, but was significantly lower on the smooth leaf ($t(13.0) = -3.75$, $P = 2.4 \times 10^{-3}$), wood ($t(14.0) = -2.63$, $P = 0.020$), sandpaper 2 ($t(12.7) = -11.90$, $P = 2.87 \times 10^{-8}$), rough leaf ($t(28) = -4.80$, $P = 4.79 \times 10^{-5}$), and sandpaper 1 ($t(14.8) = -7.77$, $P = 1.37 \times 10^{-6}$) surfaces (Fig. 4); ambient predictors (temperature and relative humidity) found to be nonsignificant in initial models were excluded from final LME models (LME model output summaries can be found in Supplementary Table S5.A).

Average static clinging safety factor estimates (Table 2) were highest on acrylic (claws intact: 67.0 ± 6.05 ; claws removed: 56.5 ± 17.2) and lowest on the rough leaf (claws intact: 5.2 ± 0.9 ; claws removed: 1.1 ± 0.4). Paired samples t -tests of log transformed static clinging safety factor values showed a significant decline after partial claw removal on the smooth leaf ($t(12) = 3.10$, $P = 9.0 \times 10^{-3}$), sandpaper 2 ($t(11) = 7.87$, $P = 8.0 \times 10^{-6}$), rough leaf ($t(13) = 5.40$, $P = 1.2 \times 10^{-4}$), and sandpaper 1 ($t(13) = 5.41$, $P = 1.2 \times 10^{-4}$), with a nonsignificant decline on wood ($t(13) = 2.12$, $P = 0.054$). Safety factor was maintained on acrylic ($t(7) = 1.09$, $P = 0.31$).

When maximum clinging force was mass adjusted, pooled across individuals for each surface, and regressed with Sq values, we observed a significant negative relationship both with claws intact ($R^2 = 0.687$; $P = 0.042$) and after partial claw removal ($R^2 = 0.770$; $P = 0.022$), the latter showing a stronger relationship.

Clinging performance—maximum station-holding angle

LME models showed that station-holding capacity after claw removal was maintained on acrylic ($t(10) = 1.74$, $P = 0.11$), but significantly declined on sandpaper 2 ($t(10) = -4.61$, $P = 9.62 \times 10^{-4}$) (Fig. 5); ambient predictors (temperature and relative humidity) found to be non-significant in initial models were excluded from final LME models (LME model output summaries can be found in Supplementary Table S5.B).

Locomotor behavior—kinematics and initial acceleration

LME models showed that claw status had a significant effect on some kinematic variables under specific substrate treatments within forelimb and hindlimb strides (see Supplementary Table S5.C, D for LME model output summaries). Unless otherwise indicated, the proceeding results describe significant

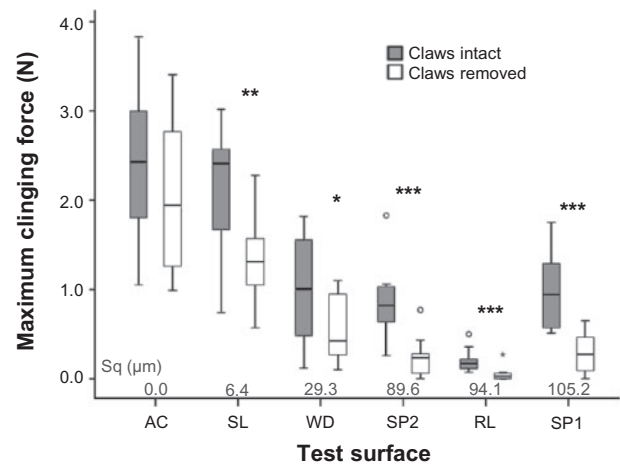


Fig. 4 Maximum clinging force (N) of the right manus averaged across individuals ($n = 14$) on each test surface before and after partial claw removal. Surfaces are arranged by increasing area root mean square height (Sq; μm) values: AC (acrylic), SL (smooth leaf), WD (wood), SP2 (60-grit sandpaper sample 2), RL (rough leaf), SP1 (60-grit sandpaper sample 1). Each plot shows the median (center line), interquartile ranges (box), and the range of values (within whiskers) that are not outliers (open circles and small star). Significant differences from LME models are indicated by asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 2 Average static clinging safety factor estimate on each test surface

Test surface	Average safety factor		Δ
	Claws intact	Claws removed	
Acrylic	67.01 ± 6.51	56.49 ± 17.20	
Smooth leaf	53.89 ± 4.75	36.3 ± 4.57	**
Wood	23.75 ± 3.38	14.46 ± 2.70	
Sandpaper 2	21.44 ± 2.74	5.56 ± 1.01	***
Rough leaf	5.20 ± 0.88	1.09 ± 0.44	***
Sandpaper 1	25.33 ± 2.71	7.56 ± 1.78	***

Δ Significance levels: ** $P < 0.01$, *** $P < 0.001$.

changes that occurred after partial claw removal. Within the forelimb strides, there was a significant increase in duty factor on level sandpaper ($t(19.3) = 2.54$, $P = 0.020$). Time to toe unfurling decreased on inclined sandpaper ($t(13.3) = -2.21$, $P = 0.045$) but increased on level acrylic ($t(29.0) = 2.26$, $P = 0.032$); time to hyperextension increased on level sandpaper ($t(20.3) = 2.53$, $P = 0.020$). In terms of posture, body pitch angle significantly increased on level acrylic ($t(29.0) = 2.89$, $P = 7.28 \times 10^{-3}$); the humerus showed a greater extent of retraction on inclined sandpaper ($t(22.0) = 5.62$, $P = 1.20 \times 10^{-5}$) and greater protraction on level acrylic ($t(29.0) = -2.156$, $P = 0.040$).

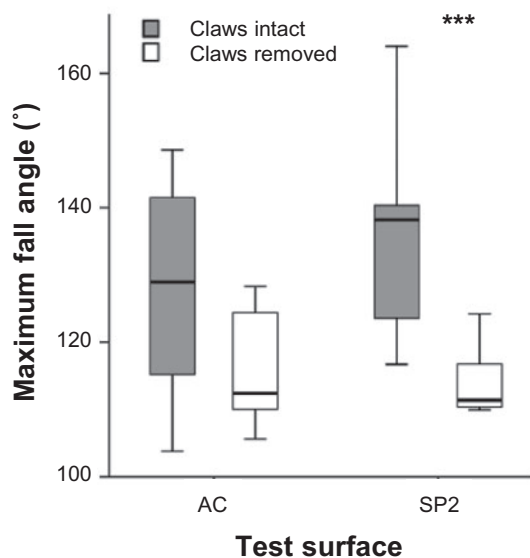


Fig. 5 Maximum fall angle (°) averaged across individuals ($n=5$) on acrylic (AC) and 60-grit sandpaper (SP2) before and after partial claw removal. Each plot shows the median (center line), interquartile ranges (box), and the range of values (within whiskers). Significant differences from LME models are indicated by asterisks: *** $P < 0.001$.

For timing variables of the hindlimb strides, duty factor increased on both inclined ($t(24.0) = 2.44$, $P = 0.024$) and level ($t(7.9) = 4.82$, $P = 1.39 \times 10^{-3}$) acrylic. The duration of toe relaxation ($t(25.9) = 2.17$, $p = .040$) and time to hyperextension ($t(26.0) = 2.63$, $P = 0.014$) increased on level sandpaper, but the duration of hyperextension declined on this surface ($t(26.0) = -2.70$, $P = 0.012$) and on level acrylic ($t(17.5) = -2.52$, $P = 0.022$). Finally, the extent of femur depression increased on level sandpaper ($t(26.0) = 3.01$, $P = 5.81 \times 10^{-3}$); a non-significant trend of greater femur retraction was observed on level acrylic ($t(9.0) = -2.17$, $P = 0.060$). In terms of forward movement, step length decreased on these two surfaces (level sandpaper: ($t(26.0) = -2.80$, $P = 9.54 \times 10^{-3}$; acrylic: ($t(16.2) = -2.58$, $P = 0.020$)). The extent of hind-foot slippage was significantly greater before partial claw removal on level acrylic ($t(7.5) = -5.52$, $P = 6.95 \times 10^{-4}$). Finally, LME models for initial acceleration did not indicate a significant effect of claw status (see [Supplementary Table S5.E](#)).

Of the strides analyzed, a higher percentage of the total forelimb strides (52%) showed at least partial hyperextension of the toes throughout the stride than the total hindlimb strides (25%). The percentage of partially hyperextended forelimb and hindlimb strides declined after partial claw removal (forelimbs: from 74% to 34%; hindlimbs: from

Table 3 Average locomotor safety factor estimates on each substrate treatment

Substrate treatment	Average safety factor		Δ
	Claws intact	Claws removed	
level (0°) acrylic	307.93 \pm 59.25	331.73 \pm 58.84	
inclined (30°) acrylic	96.11 \pm 5.97	94.48 \pm 3.70	
level (0°) sandpaper	78.98 \pm 21.40	44.33 \pm 14.97	
inclined (30°) sandpaper	38.90 \pm 14.80	7.55 \pm 1.31	*

Δ Significance levels: * $P < 0.05$.

37% to 13%); this trend was observed within each substrate treatment (see [Supplementary Table S6](#)).

Locomotor safety factor estimates

Average locomotor safety factor estimates ([Table 3](#)) were highest on level acrylic (claws intact: 307.9 ± 59.3 ; claws removed: 331.7 ± 58.8) and lowest on inclined sandpaper (claws intact: 38.9 ± 14.8 ; claws removed: 7.5 ± 1.31). Paired samples t -tests of log-transformed locomotor safety factor values showed a significant decline on inclined sandpaper after partial claw removal ($t(4) = 3.56$, $P = 0.024$). Locomotor safety factor was maintained for the level ($t(5) = -1.45$, $P = 0.206$) and inclined ($t(5) = 0.26$, $P = 0.80$) acrylic substrates; a nonsignificant decline was observed on level sandpaper ($t(4) = 2.21$, $P = 0.092$) ([Fig. 6](#)).

Discussion

We found that the claws of *T. rapicauda* are critical to maintaining clinging function on non-smooth surfaces but observed limited impacts of claw removal on locomotor dynamics. The latter can likely be attributed to this species' ability to generate sufficient force on experimental surfaces and inclines. More demanding inclines, however, likely limit net frictional adhesive force, thereby placing greater importance on the claws for friction and mechanical interlocking on rough surfaces. Overall, claw and adhesive function in geckos appears context-dependent.

Surface roughness and interactions

A grand challenge in the field of gecko adhesion is to better incorporate and quantify "roughness" in a consistent and meaningful way (see [Russell and Johnson 2007, 2014](#); [Johnson et al. 2009](#); [Drotlef et al. 2019](#); [Higham et al. 2019](#); [Niewiarowski et al. 2019](#)). The artificial and natural test surfaces used in this study showed a wide range of root mean square height values (Sq). As anticipated, acrylic, frequently used to elicit maximum frictional adhesive

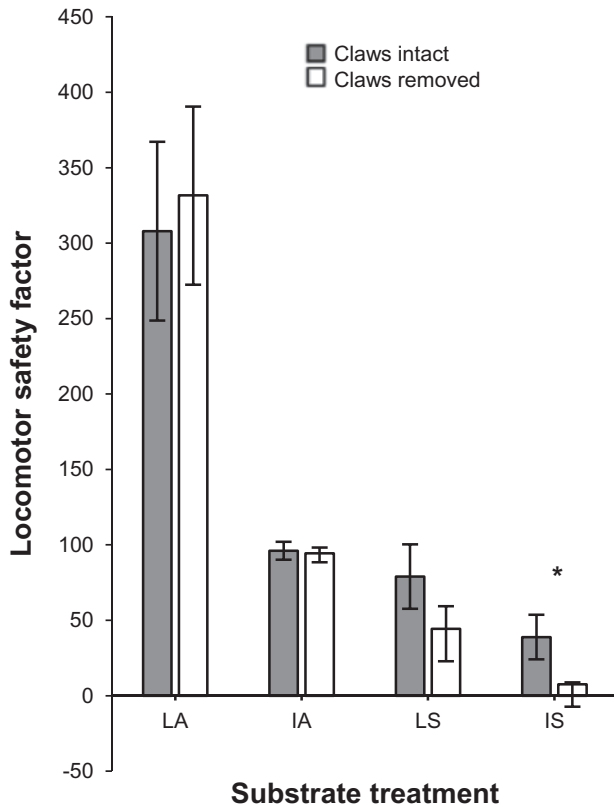


Fig. 6 Average locomotor safety factor estimates with standard error bars before and after partial claw removal for each substrate treatment: LA (level acrylic), IA (inclined acrylic), LS (level sandpaper), IS (inclined sandpaper). Significant differences from paired-samples t-tests are indicated by asterisks: * $P < 0.05$. See values in Table 3.

performance (e.g., Higham et al. 2017a), was completely smooth. Surprisingly, the two samples of 60-grit sandpaper showed a nearly $20\ \mu\text{m}$ difference in S_q . Caution should be exercised when using surfaces from different natural and manufactured sources; analysis and quantification of surface characteristics is advisable to ensure consistency and to contextualize organism–surface interactions.

It appears that the claws could interlock with the asperities of wood and the two sandpaper samples, as well as the trichomes of the rough leaf. The largest asperities of the smooth leaf are similar in size to the claw tip, and therefore friction between the two would be more likely than mechanical interlocking (Dai et al. 2002; Prüm et al. 2013). Estimating contact interactions between surfaces and attachment structures can be useful for establishing an upper bound on clinging capacity (e.g., Russell and Johnson 2014), while performance measurements provide a more realistic representation of clinging function (Irschick et al. 1996; Higham et al. 2019).

Clinging performance

As predicted, maximum clinging force significantly decreased on all non-acrylic surfaces after partial claw removal, with the most dramatic declines occurring on the three roughest surfaces (60-grit sandpapers and rough leaf). We assumed that claw interlocking would be limited on the smooth leaf (supported by low S_q), so we suspect that the significant decline in force after claw removal may reflect surface compliance and penetration by the claws. In-depth study of biological puncturing from a claw–substrate perspective is wanting (see Anderson 2018).

Regardless of claw status, a significant negative relationship between clinging force and roughness was observed. This aligns with previous studies showing that increasing surface heterogeneity diminishes setal contact area and thereby limits frictional adhesive force (e.g., Russell and Johnson 2007, 2014), while claws help to maintain clinging ability on rougher surfaces (e.g., Betz 2002; Bullock and Federle 2011). This was further supported by the decline in station-holding capacity (i.e., maximum fall angle) on 60-grit sandpaper (but not acrylic) after partial claw removal. However, other substrate properties, such as surface chemistry and polarizability, should also be considered in future studies using artificial (Autumn 2006; Badge et al. 2014; Stark and Mitchell 2019) and natural surfaces (Gorb and Gorb 2009; Prüm et al. 2013; Higham et al. 2019).

Locomotion

Deployment of the gekkotan adhesive system can result in a loss of locomotor performance, as each step requires time to unfurl the toe pads, establish and break frictional adhesive bonding, and disto-proximally peel the pads from the substrate via active hyperextension (Russell 1975; Autumn et al. 2006; Russell and Higham 2009). Russell and Higham (2009) found that running speed in *Tarentola mauritanica* (claws intact) was greater in individuals that kept their toes hyperextended on rough inclines but was lesser on smooth inclined surfaces, indicating a trade-off between forward velocity and maintaining purchase. Moreover, unfurling of the toe pads was induced at 10° inclines (30° in all individuals), while toes were held in hyperextension on level surfaces, regardless of surface texture. However, it is unclear if these patterns are representative of all pad-bearing geckos.

Our study examined locomotor behavior before and after partial claw removal on smooth and rough surfaces at level and 30° inclines. We found that

some aspects of footfall (including toe movement) timing, body posture, and forward movement were impacted by claw status on certain substrate treatments, but this was not consistent between the forelimbs and hindlimbs. We observed a substantial difference in the frequency of partial toe hyperextension between analyzed forelimb and hindlimb strides; a reduction in the proportion of hyperextended strides was observed after partial claw removal for both regions across all treatments.

Within forelimb strides, duty factor and time to toe hyperextension from the onset of stance increased on level sandpaper after claw removal. We observed a 38% decrease in the number of partially hyperextended strides for this treatment, meaning that the distal toes overall appeared to be more flexed, and therefore in greater contact with the substrate more frequently after claw removal. Increased duty factor and delayed hyperextension may represent a compensatory response to reduced stability, as might occur if an attachment modality is lost. More rapid initiation of toe unfurling and greater humerus retraction on inclined sandpaper may also relate to a perceived loss of purchase. Although we observed kinematic changes on level acrylic (i.e., increased time to toe unfurling, body pitch angle, and humerus protraction) after partial claw removal, their functional significance is unclear.

The hindlimbs exhibit different responses to claw removal and substrate treatments relative to the forelimbs; only 25% of all strides exhibited partial toe hyperextension. On level sandpaper, the duration of distal toe contact and time to onset of hyperextension increased (as in forelimb strides), with a lower duration of hyperextension. This again may suggest that geckos behaviorally compensate for grip loss after claw removal by increasing distal toe contact. Moreover, greater femur depression on this treatment could coincide with a pedal adjustment, but more detailed mechanical analyses are needed to test this. Step length decreased on level sandpaper after claw removal, again suggesting a reduction in purchase. Increased duty factor on both inclined and level acrylic may correspond with the decreased frequency of hyperextended strides observed after claw removal and potentially increased surface contact (i.e., greater frictional adhesion), with the duration of hyperextension also lower on level acrylic. We are unsure why decreased step length and greater hind-foot slippage were observed on this surface given the apparent reduction of toe hyperextension.

It should be noted that we cannot confirm when and if the pads and claws were actually engaged during locomotion, only when distal toes appeared to

contact the substrate. Many geckos, including *T. rapicauda*, exhibit cartilaginous paraphalanges integrated with other digital features, which confer precise control of pad placement and adhesion (Russell and Bauer 1988; Russell 2002). Moreover, this species appears to be able to withdraw its claws into the digital sulci (personal observation), but the extent of control of this behavior is not known. Future gecko attachment studies should consider ways in which to confirm claw–substrate interaction.

Differences between forelimb and hindlimb characteristics in response to claw removal may point to a division in their function during locomotion on different surfaces and inclines; the latter has been observed in *Chondrodactylus bibronii* when comparing uphill and downhill strides (Birn-Jeffery and Higham 2014). Zaaf et al. (2001) found little difference between fore and hindlimb kinematics during horizontal running or vertical climbing on cork in *Gekko gekko* (claws intact) but noted that the degree of sprawling was greater in the hindlimb on the level substrate and greater in the forelimb on vertical substrate (along with duty factor and step length). Moreover, we know in other quadrupeds that hindlimbs tend to confer propulsion on level surfaces, while forelimbs are dominant on inclines (e.g., Lammers et al. 2006). More distinct adjustments of both fore and hindlimb kinematics within *T. rapicauda* may be observed at steeper inclines. We did not detect a significant effect of claw status on initial acceleration for any substrate treatment, but we did not attempt to elicit maximum sprint speed performance during trials.

Clinging performance and locomotion

High static clinging safety factors for pad-bearing geckos on artificial smooth surfaces in the lab (e.g., Autumn et al. 2000) led to a short-lived notion that geckos are “overbuilt.” However, we now appreciate that application of the adhesive system under non-static and/or suboptimal conditions can substantially depress this margin of safety (Stark et al. 2015; Niewiarowski et al. 2016; Higham, et al. 2017a, b; Higham et al. 2019; Stark and Mitchell 2019). Rougher or more irregular surfaces pose greater challenges to attachment, particularly at greater inclines (Huber et al. 2007). Our study demonstrates that claws enhance static clinging and locomotor safety factor on relatively rough, inclined surfaces in *T. rapicauda*. We observed a significant negative effect of partial claw removal on performance on leaves and sandpaper. However, partial claw removal induced little locomotor alteration on surfaces

orientated at 30° or below. These observations and our high estimates of both clinging and locomotor safety factors suggest that the toe pads are able to maintain function under these conditions. Given that the adept adhesive system of this species is hypothesized to have evolved for the acute and extreme demands of defensive canopy leaping and high impact forces during landing (Higham et al. 2017b), our results are perhaps unsurprising. However, we did observe falling on inverted surfaces, which was exacerbated by roughness and claw removal. Comparisons of locomotor kinematics under more challenging substrate conditions in this species would help to further elucidate the functional and evolutionary significance of gecko claws.

Pads and claws: a functionally redundant or multifunctional attachment system?

As observed in some insects, we saw within a padded gecko a substantial loss of static clinging ability on the roughest surfaces after claw removal that points towards a multifunctional, or division of labor system, in which pads dominate on smooth, solid surfaces and claws dominate on rough and penetrable surfaces (see Betz 2002; Bullock and Federle 2011; Voigt et al. 2012). However, that clinging performance declined with increasing surface roughness when claws were intact also indicates that there is some functional redundancy and potential synergism within this system, where together the pads and claws confer greater attachment on surface topographies that allow both features to attach; such synergism has been reported in beetles (Betz 2000) and an insect mimic (Song et al. 2016).

When we consider the role of gecko claws under dynamic conditions, we see that locomotor behavior is largely conserved after removal across treatments. This again supports functional redundancy between attachment structures at inclines below 30°. However, if claw removal had a larger impact on rough surfaces at greater inclines, it would suggest a division of labor. In another study, Russell and Delaugerre (2017) observed that on horizontal and inclined friable schist substrate, *Euleptes europaea* (European leaf-toed gecko) appeared to engage its claws while holding the pads in hyperextension, presumably to avoid fouling during locomotion (see Hu et al. 2012). On concrete, however, the geckos appeared to fully unfurl the toes while engaging their claws. We surmise that gecko and some insect attachment systems are context-specific; redundant or multifunctional qualities can be exhibited depending on the conditions under which the organism

employs its attachment system. This may also extend to reproductive functions (e.g., egg gluing and positioning in geckos; Bauer 2013).

Implications and future directions

Manipulating the toe pad as to neutralize its function while leaving the claws intact would be an ideal next step to better understand gecko attachment. Although this has been successfully conducted in beetles (see Betz 2002), the complexity and high concentration of sensory structures of the gekkotan adhesive system makes completely isolating functional effects rather difficult. Such experiments using biomimics (as in Song et al. 2016) may prove to be an informative alternative to live animal manipulation, also highlighting how material science research can help advance our understanding of a biological system. As Niewiarowski et al. (2016) articulated, continued advancement of adhesion research fundamentally requires not only data on wild geckos under ecologically relevant conditions, but also the integration of perspectives from multiple disciplines.

Although we recognize the standing diversity of gekkotan autopodial form beyond a few model species (Russell 1972, 1976; Gamble et al. 2012; Bauer 2019; Russell and Gamble 2019; Zhuang et al., manuscript in revision) and are beginning to illuminate the genomic underpinnings of this diversity (e.g., Gamble 2019), we must continue to increase our efforts to investigate how this diversity actually functions under “real-world” conditions (Higham and Russell 2010; Collins et al. 2015; Russell and Delaugerre 2017; Higham et al. 2019; Stark and Mitchell 2019). This study contributes important perspectives toward this goal, including novel perspectives regarding gecko claw function. Moreover, this work serves as a launching point for new hypotheses aimed at understanding the evolution of gecko attachment. For example, the loss and reduction of claws in some species may be driven by selection and modification of the adhesive system and/or habitat conditions, such as substrate availability (Fig. 1). Linking ecology with the extent of correlated morphological evolution between claws and toe pads is an important aim moving forward, as is testing biomechanical properties of particular morphologies. This will also lend itself to understanding complex functional systems and evolutionary key innovations at large.

We highlight an additional attachment feature as a potential source of inspiration for biomimetics and related endeavors. From Favi et al. (2014), “nature has shown, with striking examples, how diverse

strategies can be used to generate adhesion in nearly all environmental extremes.” We posit that looking to “diverse strategies” within an organism may be fruitful for finding solutions to complex problems and dreaming up new technologies. In other words, geckos may have more to offer than just their toe pads. Could combinations of features within synthetic materials or robots, such as claws and adhesive structures, enhance their performance and/or universality? We look forward to both the intellectual and practical rewards of synergism between diverse research groups to come.

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Supplementary data

[Supplementary data](#) are available at *ICB* online.

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