REVIEW

Geckos running with dynamic adhesion: towards integration of ecology, energetics and biomechanics

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ABSTRACT

Morphological specializations often enable animals to deal with challenges in nature, a prime example being the adhesive system of geckos. With this, geckos can access smooth and vertical (and even inverted) areas of the habitat that most other animals cannot. However, what is known about how geckos cling stems primarily from laboratory studies of static adhesion, with an emphasis on the integumentary component of the adhesive apparatus. In reality, the system is hierarchical, with complex musculotendinous, vascular and sensory systems that are crucial for achieving attachment, modulation of attachment strength and ultimately, detachment. Experiments examining these additional components are virtually non-existent. Additionally, there is a paucity of information about the surfaces on which geckos move, how geckos move in their natural habitat and how the adhesive system is controlled during running over complex surfaces. It is unclear whether having an adhesive system reduces the energetic costs of running compared with lizards that lack the system. We propose a complimentary set of laboratory and field studies to fill major gaps in our understanding of gecko adhesion and locomotion. Key outstanding questions are: (1) How does surface structure influence locomotion? (2) How might geckos modulate adhesion through physiological mechanisms? (3) How do geckos locomote in complex natural habitats that vary in structural properties? (4) What are the underlying energetic costs of moving dynamically in nature with an adhesive system? We address these questions and generate a roadmap for future work, including the framing of testable hypotheses. The results of such studies will help us to understand the evolution of fast locomotion in small ectothermic vertebrates and the energetic costs of moving in complex habitats. In addition, they may inform the development of small adhesive robots.

KEY WORDS: Sensory, Accelerometry, Oxygen consumption, Roughness, Locomotion, Lizard

Introduction to gecko form and function

Geckos constitute an extensive and diverse radiation of lizards that Inhabit the majority of the temperate and tropical regions of the globe (Bauer, 2019). It is the adhesive system of geckos that clearly sets them apart from more generalized lizards (even though *Anolis* lizards also have a similar system, it is not as specialized as that of geckos; Russell and Garner, 2023). The details of the gekkotan system, both internal and external, have been reviewed by several authors (Russell and Johnson, 2009; Autumn et al., 2014; Higham

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et al., 2019; Russell and Gamble, 2019; Russell et al., 2019). From extensive work, it is clear that structural differences in the ankle (Higham et al., 2021b), vascular system of the digits (Russell, 1981), muscles and tendons of the digits (Russell and Bauer, 1989) and external anatomical form (Russell and Gamble, 2019) all contribute to the complex adhesive apparatus. Unsurprisingly, the complexity of the system has long been noted. Indeed, Home (1816), in the early years of the 19th century stated (under the assumption that vacuua were responsible for attachment):

'where the [gecko] *mechanism is to be employed in air, under greater disadvantages with respect to gravity, and is to last for very short periods, and then immediately afterwards be renewed, a more delicate structure of parts, a greater proportional depth of cavities, and a more complex muscular structure becomes necessary'*

Home (1816).

This, in part, alludes to the challenges of relating this complexity to real-world situations.

Gecko digits are relatively shorter than those of other lizards (Russell et al., 1997; Zhuang et al., 2019). Although beneficial for adhesion, this limits the out lever of the foot, thereby decreasing the propulsive force (Collins and Higham, 2017). The digits of pad-bearing geckos tend to radiate around a broad arc, providing them with a symmetrical, fan-like arrangement (Russell et al., 1997; Fig. 1), as opposed to the ancestral saurian arrangement in which they are aligned essentially parallel to one another. This configuration increases the spacing between digits, with the expanded toepads intruding into the interstices between them, allowing pad-bearing geckos to adopt a variety of body orientations on vertical surfaces while always having some of the toepads aligned with gravitational loading. When geckos engage and disengage their adhesive system, they impart varying normal and shear forces to the setae, the integumentary agents of attachment. With reference to the limbs, placing proximally directed tension on the fields of setae engages the system and increases friction, whereas relaxing this tension enables easy detachment (Federle and Labonte, 2019). The outcome of this is the deployment of a very strong adhesive that can be released easily, with minimal energetic cost (Autumn et al., 2006a), providing an effective way of moving and adhering simultaneously. The aforementioned shear forces can be imposed by gravitational loading when on a vertical surface but are also predicted to be able to be generated actively, thereby effecting adhesive attachment beyond the vertical (including inverted locomotion). This is achieved through contraction of muscles that tense the lateral digital tendon network (Russell, 1986; Fig. 2), pulling on the plates of the adhesive toepads and acting as gravity would if the gecko were on a vertical surface (Hiller, 1968).

Controlling application and release of adhesion involves active hyperextension of the toepads, resulting in unique patterns of digital movement upon their placement and release (Higham et al., 2017a).
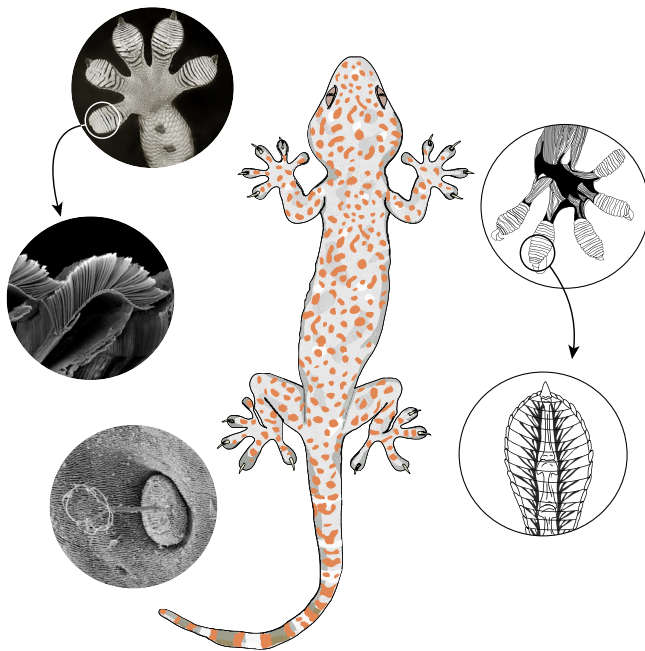
Fig. 1. The structural components that contribute to the overall functioning of the adhesive apparatus of geckos. The toepads (top left), the individual setae (middle left), a sensory receptor on the ventral surface of a digit (bottom left), the muscles and tendons involved in adhesion (top right), and the lateral digital tendons (bottom right).

Active digital hyperextension, ostensibly employed by all geckos with fully developed toepads, is the process by which the digits unfurl or 'peel' from the substrate, starting at their tips (see Fig. 2). This was observed by Schmidt (1904) and Hiller (1968), but was only quantified during locomotion recently (Russell and Higham, 2009). Such geckos do not deploy their adhesive system when moving on a level surface but instead maintain the hyperextended configuration of the digits throughout the limb cycle. When moving on inclined surfaces, however, the adhesive system is engaged at footfall and detached prior to the foot being raised from the substratum. Actively attaching to the substrate in this manner is thought to enhance the perpendicular preload required for setal attachment (Autumn et al., 2000), thereby pressing the setal tips to within nanometers of the substratum, maximizing contact area (Russell et al., 2019). The superimposition of the hyperextension cycle upon the more ancestral limb cycle results, however, in a trade-off. Among individual *Hemidactylus garnotii*, the time taken to attach and detach the adhesive system during locomotion under different circumstances remains constant (20 ms; Autumn et al., 2006b), resulting in stride frequency (and therefore speed) being constrained. This suggests that increases in speed might be driven by stride length rather than stride frequency. Confirming this cost, Russell and Higham (2009) found that trials in which geckos deployed their adhesive system were slower than those where they kept their digits hyperextended.

During locomotion most lizards routinely move quadrupedally, with their femora and humeri directed laterally from the body. This sprawling posture imparts great stability but requires complex three-dimensional movements of the limb segments (Russell and Bels, 2001). Such a kinematic pattern is relatively costly since muscles must resist relatively large joint moments because the contact points (the feet) are situated far from the center of mass (Reilly et al., 2007). In terms of center of mass mechanics, lizards are comparable to other legged vertebrates in that their limbs operate

as inverted pendula at walking speeds but assume a bouncing gait at faster speeds (Farley and Ko, 1997; Higham, 2019). Geckos largely follow the pattern of locomotion exhibited by other climbing lizards but exhibit a few exceptions. First, geckos appear to employ unique (relative to other lizards) patterns of hindlimb function during locomotion on up- and downhill surfaces. For example, the forelimbs and hindlimbs both propel geckos during uphill locomotion, but during downhill locomotion the forelimbs act as brakes while the hindlimbs act as stabilizers (Birn-Jeffery and Higham, 2014, 2016). Mechanically, geckos climbing with the aid of adhesion exhibit only positive fore–aft forces during rapid vertical locomotion, indicating a lack of deceleration forces (Autumn et al., 2006b; Wang et al., 2015b; Schultz et al., 2023). Additionally, the forelimbs appear to generate a greater proportion of total propulsive force (by pulling) than do those of other lizards when moving uphill (Zaaf et al., 2001); all four limbs of Tokay geckos produce similar fore–aft impulses on vertical surfaces (Wang et al., 2015c). This pattern differs considerably from other generalized lizards that rely on the hindlimbs for the majority of propulsion and where braking forces are dominated by the forelimbs (McElroy et al., 2014). How these differences manifest in nature is unclear, but perhaps the adhesive system reduces the energetic cost of vertical locomotion (see below for further discussion).

Much is known about the generalities of how geckos generate frictional adhesion (Autumn et al., 2000, 2006a; Tian et al., 2006), and how adhesion relates to various surface and behavioral variables, such as roughness (Huber et al., 2007; Cobos and Higham, 2022; Gillies et al., 2014), wetness/humidity (Stark et al., 2013, 2016), use of claws and adhesion (Naylor and Higham, 2019; Garner et al., 2021), and digit placement relative to body orientation (Russell and Oetelaar, 2016; Song et al., 2020). Our understanding is, however, far from comprehensive. What is known has been assembled in a somewhat piecemeal fashion, resulting in a rich but disparate compendium of information. Indeed, there are many lineages of geckos, but the information thus far has been limited to very few species. This has led to generalization and inductive reasoning, with all geckos being subsumed under a general umbrella. Some of this stems from the availability of geckos in the pet trade, as well as the size and effectiveness of the adhesive system under laboratory conditions. It is evident that there are grand challenges (Russell et al., 2019) that should be addressed in a systematic and hierarchical manner if our comprehension of this phenomenon is to improve. With over 1800 species (Bauer, 2019), there are likely numerous 'solutions' to how different taxa deal with the environment. Additionally, we still have few data relating to how geckos use their adhesive system in nature. Thus, information gleaned in the lab needs to be enhanced and connected to field data. To date, a plethora of studies have been directed toward biomimetic simulation of the gecko adhesive mechanism, with these far outnumbering fundamental investigations that focus on the operation of this system in nature (Niewiarowski et al., 2016) or under stringently controlled laboratory circumstances. We herein identify these grand challenges and outline an integrated approach to addressing them as they relate to the evolutionary and ecological significance of adhesively assisted gecko locomotion. We then indicate how such an enhanced understanding might provide a more solid foundation upon which biomimetic approaches can be based.

Ecomechanical grand challenges in gecko locomotion research

Russell et al. (2019) outlined five grand challenges to be tackled by those interested in advancing our understanding of gecko adhesion.
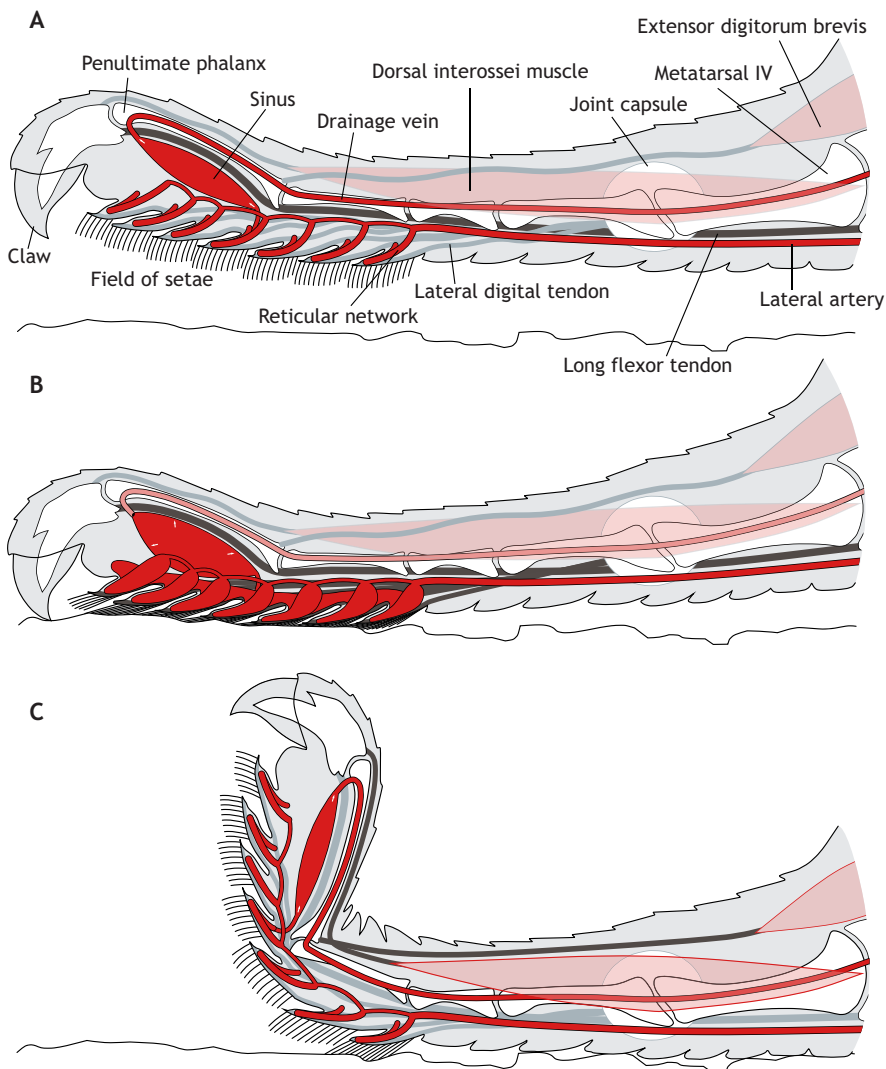
Fig. 2. Position of a gecko toe (digit IV of the pes) before, during and after contact with a surface. (A) Position of the toe before contact. (B) Position of the toe during strong frictional adhesion. (C) Position of the toe following active digital hyperextension at the end of the stance. Shown within are the vascular system (red), the muscles (light red), the distalmost metatarsal and phalanges (white), and the tendons (light gray when not under tension and dark gray when under tension). Undulant (light gray) tendon lines further indicate that these structures are not under tension. Note that when the setae are loaded fully in tension (B), their contact angle with the substrate is less than 30 deg. At this time, the reticular network and the blood sinus are engorged and under pressure, pushing the setae closer to the substrate to maximize contact. The lateral digital tendons provide branches to each scansor, thereby transmitting the tensile force from the flexor muscles. The extensor digitorum brevis and dorsal interossei muscles are involved in active digital hyperextension by pulling on the penultimate phalanx. The long flexor tendon drives the claw towards the substrate. See the text for more details.

Of these, three relate directly to furthering our appreciation of 'running with adhesion' and it is those that we expand upon here. (1) Employ the diversity of geckos to understand how the adhesive system is tuned to environmental challenges. (2) Enhance our understanding of how geckos actually use their adhesive system in nature. (3) Compare, contrast and synthesize the diversity of fibrillar adhesives in the natural world. We re-cast these three grand challenges as ecomechanical grand challenges (EGCs), in that we are proposing ways to understand how geckos move and function under varying ecological conditions. EGC1: understanding the influence of surface topography on gecko locomotion, both in the lab and in nature. EGC2: understanding the sensorimotor control of adhesion under dynamic conditions. EGC3: understanding the energetic costs of locomotion in nature. Below we outline how these ecomechanical grand challenges can be attacked through reciprocally illuminating laboratory and field investigations and we link these to the overarching EGCs listed above. Overall, the findings from these avenues of research will need to be integrated to enhance our comprehension of the intricacies of adhesively assisted locomotion in geckos.

Geckos in the laboratory

We propose that a more rigorous investigation of adhesive and running performance in the laboratory should be pursued. Through the replication of natural surfaces and the visualization of contact during locomotion we can gain a deeper understanding of how surface topography influences adhesive locomotion. In addition, exploring the physiological mechanisms underlying the control of adhesive force is necessary for understanding how adhesion can be modulated. Below we highlight specific areas on which to focus.

EGC1: how does surface structure influence attachment and locomotion? How does what we know about gecko adhesion apply to these lizards during motion? Static friction is possible when a gecko holds station (and is even maintained after death; Stewart and Higham, 2014), but the interactions quickly become more complex when a gecko walks or runs. Sliding friction will occur as the adhesive system translates posteriorly during motion. This is commonly observed in laboratory experiments involving gecko running (T.E.H., personal observation). As a result of such shearing motions, stick–slip friction models become relatively complex (Das et al., 2015) but need to be applied to the analysis of locomoting geckos.

We know that surface roughness and frictional adhesive forces, at least at the level of the seta or spatula, likely display a U-shaped curve, such that intermediate roughness (relative to the size of the attachment structures) will result in the lowest force (Huber et al., 2007). In this case, the roughest surfaces will still have patches that are equal to, or greater than, the area of a setal tip (Fig. 3). That said,

how pull-off forces relate to gecko function during friction-based adhesion is unclear. The actual setal stalk angles at the time when the lateral digital tendons are under tension would be much lower than that used during pull-off force experiments (see Fig. 2B for example). Thus, pull-off forces are good estimates of the strength of spatulate bonds but might be very misleading when applied to the actual operation of the integrated adhesive mechanism. Indeed, at the level of the organism (i.e. whole-foot experiments), increasing the roughness of the surface leads to an approximately linear decline in frictional adhesion (not accounting for the contribution of the claw; Naylor and Higham, 2019; Fig. 3). As outlined below, visualizing the contact of the setae and/or entire toe is necessary for understanding exactly what is making contact. In the only directly relevant study to date, the effects of surface texture on gecko acceleration were found to be fairly linear, with acceleration declining as surface roughness increased (Vanhooydonck et al., 2005). In that study, however, the substrates used resulted in alteration of multiple aspects of the surface simultaneously. For

Fig. 3. Roughness versus adhesive force for a single spatula and the entire toe. The dashed orange plot in the middle panel is loosely based on the data from Naylor and Higham (2019) and the blue line is redrawn from the data in Huber et al. (2007). Note that, at the nano-level (blue line in the middle panel and configuration in the bottom panel), there is a U-shaped curve where adhesive force is minimal at moderate roughness values due to minimal contact between the spatula tip and the substrate (2 in bottom panel). At the micro-level (orange line in the middle panel and configuration in the top panel), frictional adhesive force decreases linearly due to decreasing amount contact between the toe pad and the substrate (1 to 3 in the top panel). Incorporating the involvement of the claw results in attachment force increasing when roughness is high due to the ability to interdigitate with the asperities on the substrate (to the right of point 3 in the orange plot in the middle panel). The schematic in bottom panel is redrawn from Huber et al. (2007).

example, the wire mesh substrate afforded small cylinders that were much narrower than the digits of the geckos. Therefore, additional studies that alter a single aspect (e.g. asperity height – the distance between a peak and the floor of a valley – a measure of roughness), while keeping everything else equal, will reveal which surface structural factors impact gecko running.

Visualizing the adhesive contact between a gecko and a surface is a key requirement for relating surface structure to performance and biomechanics. The first step is the testing of different materials to determine whether force output varies. After selecting the material that permits maximum force generation, the texture of the surface can be manipulated. Replicas of textured surfaces can be made using a two-step moulding process (Kumar et al., 2019). Negative impressions of a surface are created using liquid forms of polyvinylsiloxane (PVS), polydimethylsiloxane (PDMS) or epoxy. The negative replica can then be filled with positive substrate material such as PDMS or epoxy (Kumar et al., 2019). In addition, 3D printing using two-photon polymerization lithography (TPL) permits nanoscale print resolution (Wang et al., 2023b). However, a thorough understanding of the nanotopography of a surface is first needed, and often a replica is required for this analysis.

Why use replicas and 3D prints and not the original surface? First, replicas and 3D prints can be formed in transparent material, allowing for the visualization of contact between the gecko and the surface of interest (especially when lit from below). They can also eliminate numerous abiotic and biotic attributes of a surface, including compliance, chemistry, color and curvature (Kumar et al., 2019). Finally, biotic samples will dry quickly, thereby altering the actual microstructure of the surface. Thus, replicas and 3D prints maintain the integrity of surface topography while minimizing the effects of variation in surface materials. Additionally, there are situations where natural surfaces cannot be removed or collected. Impressions of real surfaces can be obtained in nature (Russell and Johnson, 2007), which then serve as negatives in the replication process. We advocate that trackways employed in locomotor experiments should be fabricated using replicas or 3D-printed facsimiles, thereby eliminating all other confounding factors. The added benefit of 3D printing is that certain attributes of the surface, such as density or shape of asperities, can be controlled and produced with a uniform distribution. Direct replicas of natural surfaces will reproduce the potentially unorganized arrangement of asperities.

Technological advancements for visualizing adhesive contact are relatively recent. Optical systems permit high-resolution differential contrast microscopy based on transmission light microscopy principles: a light beam shines from the probe and propagates through the tested substrate (Kumar et al., 2020; van den Boogaart et al., 2022). Some optic sensors can exploit frustrated total internal reflection (FTIR), which works by trapping a beam of light inside a substrate of high refractive index relative to air, such as glass (Betts et al., 1980; van den Boogaart et al., 2022; Amador et al., 2024; Eason et al., 2015). This technique involves shining a light into the substrate at a shallow angle, which is then reflected internally. When an adhesive contact is made, the relative reflective index drops at the point of contact which allows light to escape. The area in contact will then illuminate. However, there are limitations to these optic procedures, notably the need for a transparent adhesive model that is pushed towards the surface of interest. In addition, the resolution and frame rate of the cameras used must be high. This approach may only be applicable for interactions at the microscopic scale: nanocontacts remain at the limits of the lateral resolution of light (Jacobs and Martini, 2017). Gecko setal tips are approximately
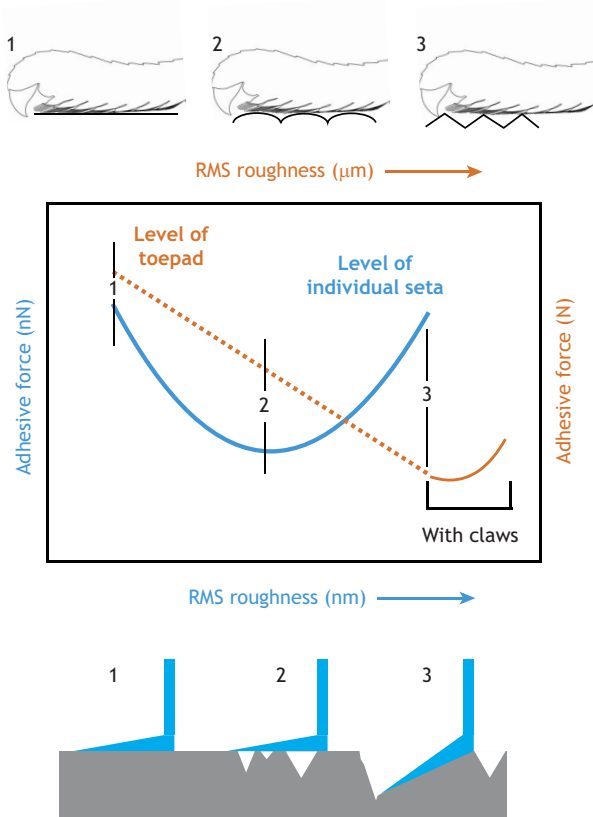
200 nm in diameter, which may be beyond the limits of this technique. Rather than light transmission through a transparent adhesive structure, a recent technique involves reflection interference contact microscopy (RICM). A hybrid approach that combines a non-planar RICM model with an assessment of the entire interferogram might prove to be effective (Contreras-Naranjo and Ugaz, 2013). Because gecko adhesion ultimately occurs at the nanoscale, this makes contact dynamics extremely difficult to visualize. A combination of experimental and simulation techniques is likely necessary for simply understanding the dynamics of contact (Jacobs and Martini, 2017); actually visualizing the contact (including sliding and attachment/detachment) during locomotion presents an additional challenge.

Recent studies have examined adhesion of toes and feet at the macroscale (Song et al., 2021). In this case, adhesive forces of Tokay geckos generally increase with object diameter. Across a range of round rods (diameters from 12.7 to 38 mm), adhesion increased continually to a value of 95.3% of the planar control value. Another recent study examined lamellar and toe shear adhesion of Tokay geckos on macroscopic engineered rough surfaces (Gillies et al., 2014). Shear adhesion dropped by 95% when the amplitudes and wavelengths of the surface structures approached the lamella length and inter-lamella spacing. Ultimately, gecko adhesion could be predicted by the ratio of the lamella dimensions to surface feature dimensions, although it is unclear if this translates to all species of pad-bearing geckos. This constitutes yet another factor for consideration when determining the efficacy of adhesive locomotion. Following the collection of data regarding adhesion across surfaces that vary in nano, micro and macroscale structure, one can then test the ability of geckos to run across trackways constructed of hierarchically different structure. The advancement of force sensor arrays in multisensory electronic skin (to mimic human skin) has led to the ability to measure very small pressures (via deformation) on the surface the material (Qiu et al., 2022). With such a material covering the surface of a trackway, detailed measurements of force could be made across all contact points.

EGC2: what are the roles of muscular and vascular control, and sensory feedback, during adhesively assisted locomotion?

How might a gecko adjust its adhesive system from within when faced with varying demands? Lateral digital tendons, through their muscular connections, may well be able to impart the requisite amount of tension to the setae, allowing them to maintain force generation while at rest, and when moving and the foot is planted, thereby permitting loading of the setae to their optimal degree (Fig. 2). Sliding upon contact of the setae will be induced until the setae are optimally loaded (Autumn et al., 2000), and the tension in the lateral digital tendon system potentially maintains this until released before detachment. The spreading of the digits over a broad arc will require active loading of the setae in tension because their orientation is such that gravitational loading cannot effectively achieve this for all digits. Active loading in this way is also necessary for inverted attachment and locomotion. Severing the lateral digital tendons (surgically) would be a way to test their role in applying the setae and maintaining the appropriate level of loading. Recording the strain (and therefore force applied) directly from the tendons in the digits under *in vivo* conditions, as has been accomplished for larger leg tendons in animals such as birds (Higham and Biewener, 2009), is probably not feasible for geckos owing to the small size of the pertinent tendons. Neuromuscular recordings, through electromyography, of the digital muscles that control the tendons, will reveal whether increased recruitment occurs when greater tension is needed.

The vascular system of the digits includes extensive blood sinuses that are hypothesized to increase the compliance of the toes (Hiller, 1968; Russell, 1981) and is, therefore, another potential source of adhesive control during locomotion. This has been implicated in the function of the adhesive system since originally suggested by Dellit (1934). The current interpretation, based upon morphology, posits that blood flows into the digit via the lateral arteries and fills the reticular networks and digital sinus, ultimately leaving via the drainage vein (Fig. 2). The sphincter connecting the sinus with the drainage vein is closed during surface contact of the setal fields when frictional force is high, thus permitting pressure to build upstream (Fig. 2B). The digital flexor muscles draw the penultimate phalanx down, applying additional pressure to the sinus. Together, these actions push the setal fields into closer contact with the surface on which the gecko is moving. When the digit is about to begin digital hyperextension, the sphincter will open and allow blood to flow out of the digit via the drainage vein, thereby reducing blood pressure in the toe (Fig. 2). Our ability to quantify blood flow at that level and during movement has not heretofore been possible because of technological limitations. A potential way of obtaining such measurements involves the combination of laser Doppler flowmetry (LDF) and photoplethysmography (PPG) in a single optical probe (Bergstrand et al., 2009). Another forthcoming possibility might be the use of wireless miniature soft robots that can locomote throughout the vascular system and detect a number of parameters (Wang et al., 2023a). We hypothesize that geckos will modulate the pressure in the blood sinuses as challenges to the adhesive system change. We predict that higher pressures will occur on rougher surfaces to press the setae closer to the surface and maximize attachment to available points of contact.

A critical aspect of adhesive control relates to sensory feedback, but little is known about how geckos sense their locomotor environment in both tactile and proprioceptive ways. Sensory feedback is likely to be critical for (i) altering the deployment of their adhesive system in response to slight changes in inclines and (ii) modulating adhesive force by increasing the tension on the digital tendons via muscle contractions. Sensing whether they are on an incline may be driven by the vestibular system or shear-sensitive sensilla on their limbs. Recent work has highlighted the range in form (and distribution) of gekkonid sensilla and the bristles that they bear (Fig. 1; Russell et al., 2014; Riedel and Schwarzkopf, 2022; Bauer et al., 2023), but the functional implications of this variation are currently unknown. Future work could explore sensorimotor integration through electrophysiological recordings (Hiller, 1978) coupled with electromyography (Foster and Higham, 2014), or tactile sensitivity experiments (Bradley et al., 2021). Advances in this area will surely benefit the design of dynamic robots that are able to respond to differing environmental conditions.

Geckos in nature

We propose that shifting the focus to geckos in nature should be built upon a deeper understanding of gecko adhesion and locomotion as gleaned from findings obtained under controlled laboratory conditions. Results from studies examining how geckos locomote over replicates of natural surfaces can inform predictions about movement in nature. Below we highlight key challenges for understanding the deployment of gecko adhesion while moving in nature.

EGC1: how do geckos locomote in complex natural habitats that vary in their structural properties?

The habitats in which geckos live vary considerably in structure across many scales (Fig. 4). However, much of what we know about gecko locomotion is derived from a taxonomically and

Fig. 4. Geckos in their natural habitat. (A) *Rhoptropus afer*. (B) *Hemidactylus thayene*. (C) *Gekko smithii*. (D) *Gekko takaoue*. (E) *Gekko gecko*. (F) *Lepidodactylus lugubris*. Photo credits: T.E.H. (A) and Lee Grismer (B–F).

methodologically rather limited array of laboratory studies. At a broad ecological level, the adhesive capabilities of geckos determine the spatial use of their habitat (Wright et al., 2021), suggesting a strong relationship between adhesion, locomotion and habitat use. Higham and Russell (2010) quantified laboratory and field velocities of geckos running in nature. However, these bursts of locomotion occurred following release of the animals from the researcher's hand. More recently, we (Higham, 2025) quantified maximum adhesive force of geckos in the lab and then quantified their escape kinematics and performance in nature. Again, these events were only semi-natural given that the geckos were captured and released to document their escape kinematics on video.

To get closer to an accurate estimate, we need to quantify what geckos do in nature, both in terms of habitat structure, locomotor accelerations and limb coordination. A growing movement in biology is focused on bringing biomechanical investigations into the field (Koehl and Wainwright, 1977; Herrel et al., 2006; Bauer et al., 2020; Higham et al., 2021a; Ferry and Higham, 2022), capitalizing upon the emergence of ecomechanics as a discipline of study (Wainwright, 1976). Geckos constitute a promising candidate for such an endeavor, given their enormous taxonomic and ecological diversity. Studying the ecomechanics of geckos should be embedded within current theoretical/modeling frameworks. For example, Higham et al. (2021a) proposed that gecko adhesion can be represented by an ecomechanical model given the inclusion of traits related to both animal morphology and ecology (habitat):

$$F_C = \sqrt{G_C} \cdot \sqrt{\frac{A}{C}}, \tag{1}$$

where F_C is the adhesive force capacity, G_C is the surface energy as defined by the material to which adhesion occurs [this not being the same as the surface energy definition stated by Hiller (1968)], A is the area of contact (determined by the surface and the animal) and C is the compliance of the adhesive system (Bartlett et al., 2012). By obtaining information about actual contact with surfaces of different topographies and then determining the topography of natural surfaces (using confocal microscopy; Higham et al., 2019), we can begin to model adhesion of geckos in nature. Following the development of approaches for collecting real-world data on gecko movements, we can begin to investigate additional questions regarding geckos in nature. We outline what we consider to be the most critical of these below.

EGC3: what are the underlying energetic costs of moving dynamically in nature with an adhesive system?
Autumn et al. (2006b) determined that mechanical power of geckos climbing is almost exactly equivalent to the product of gravity and velocity (minimum mechanical power production possible). This suggests that energy expenditure might be lower in geckos compared to other lizards when climbing a vertical surface. In addition, previous work has found that nocturnal geckos have a lower cost of locomotion compared with other lizards and their locomotor performance at suboptimal temperatures approaches that of diurnal lizards at high, optimal temperatures (Autumn et al., 1999). Thus, their efficient climbing, coupled with their lower cost of transport, may result in a very low cost of locomotion in nature. However, real-world measurements of accelerometry are needed to estimate oxygen consumption.

Several studies have quantified whole-body acceleration in the laboratory while simultaneously measuring O_2 consumption ($\dot{V}_{O_2}$)

(Wilson et al., 2006; Halsey et al., 2009). Wilson et al. (2006) tested the hypothesis that acceleration can serve as a proxy for energy expenditure in free-living cormorants (*Phalacrocorax carbo*). They did this by quantifying overall dynamic body acceleration (ODBA) with an externally attached three-axis accelerometer while at rest and during walking exercise on a treadmill. After determining that there was a significant positive correlation between ODBA and $\dot{V}_{O_2}$, they measured ODBA in free-living cormorants during foraging trips. Based on expected energy requirements during parts of foraging bouts (e.g. after catching prey or during the descent phase of a dive), ODBA matched expectations. In a comprehensive review, Halsey et al. (2009) examined the relationship between ODBA and $\dot{V}_{O_2}$ among species of birds and mammals (chickens, cormorants, geese, ducks, penguins, coypu, humans, armadillos and skunks) and found that the relationship between ODBA and $\dot{V}_{O_2}$ was consistently significant, with R^2 values ranging from 0.86 to 0.94. Regardless, there were differences among the species in the actual relationship, suggesting that ODBA and $\dot{V}_{O_2}$ should be validated in the lab before extrapolating to movements in nature. For geckos, these measurements should be conducted on level, inclined and inverted surfaces to capture the array of possibilities experienced in nature.

How do we quantify acceleration, and therefore energetics, in undisturbed and natural locomotion? GPS and animal-borne accelerometry have been recently used to study hunting dynamics of lions and cheetahs in Africa (Wilson et al., 2018), as well as movement and attack behaviors of other large mammals (Wang et al., 2015a). Applying this technique to smaller animals has been challenging because of the weight of the instrumentation. However, technological advancements have led to miniaturization of accelerometers and to making them cost effective. Recent studies have employed animal-borne accelerometers to quantify cryptic behavior in small nocturnal animals (Hanscom et al., 2023a,b). These studies recover information that is not accessible from traditional behavioral observations given the complexity of the habitat, the fact that movement occurs at night, and the potential for high-speed movements and rapid accelerations. Thus, studying geckos in nature, especially those that are nocturnal, should incorporate accelerometry.

For diurnal geckos, field-based videography could be used to quantify movement patterns, especially for geckos that occupy a small area in an uncluttered microhabitat. Several limitations are evident with this methodology, including the lack of sufficient battery power to sustain the cameras for long periods of time. Additionally, almost all habitats will have 3D components, which would require multiple cameras and a calibration of the filming volume in 3D. Overall, accurate measurements of velocity and acceleration will be difficult for freely moving geckos using cameras alone. Thus, combining this with accelerometers, or simply using accelerometers alone, is likely to be more fruitful.

We predict that geckos will minimize energetic cost in nature through smooth locomotion that minimizes fluctuations in velocity, as was found by Autumn et al. (2006a,b). Given that the muscles controlling the digital tendons might increase in activity on rougher surfaces, we also predict that total energy used will be lower when moving on smoother surfaces. Inclination is predicted to impact energetics such that moving uphill and in an inverted posture will be more costly when compared to level and downhill locomotion. How geckos move in an inverted posture has long attracted scientific attention. What are the energy requirements for inverted locomotion? When inverted, gravity is no longer available for inducing the shear stress needed to actuate the adhesive system.

Instead, it is likely that increased employment of muscle-based loading of the adhesive system is necessary. This will probably increase the cost of locomotion. It is, of course, evident that inverted clinging and locomotion cannot be sustained for long (see Hiller, 1968) because gravity pulls the entire body away from the surface. Evidence suggests that fatigue sets in relatively rapidly and detachment (falling) results. Thus, inverted posturing and locomotion will likely be more energetically expensive owing to these factors as well. Do geckos employ their limbs as inverted pendula while walking upside down? This seems unlikely given that potential energy likely dips during midstance, rather than increases as in normal walking. Perhaps the limbs act as pendula! These unanswered questions about inclined and inverted locomotion provide multiple avenues for future field-based research.

EGC1: what is the importance of adhesive safety factor for gecko locomotion?

Safety factor is the ratio of failure stress (mechanical strength) to functional stress (Biewener, 2005), and can play a major role in the survival of an individual organism (Higham et al., 2021a). For any structure, a high safety factor indicates that it will be robust to internal/external forces. Safety factors that approach a value of 1 indicate that the structure (or system) will no longer be able to withstand a given force. For the adhesive system of geckos, the safety factor is the ratio of adhesive ability to the actual adhesive force used in nature. Assumptions based upon geckos adhering statically to a perfectly smooth surface yield predicted safety factors of up to an astonishing 3900% (Autumn, 2006). However, it has long been acknowledged that these are extreme overestimates given that geckos neither remain stationary nor move on perfectly smooth surfaces (Autumn et al., 2014). Indeed, safety factors can reach dangerously low levels when considering real life situations, such as landing with high impact forces after a fall (Higham et al., 2017b) or moving on rough surfaces that provide little area for contact with the adhesive system (Russell and Johnson, 2007; Johnson and Russell, 2009; Johnson et al., 2009; Cobos and Higham, 2022). This functional stress in the safety factor equation will be the highest that an animal experiences over its lifetime, which makes it quite challenging to measure.

We (Higham, 2025) quantified the safety factor for *Rhoptropus bradfieldi* during accelerations in nature, although these estimates were based upon single releases and not representative of extended periods of time. This safety factor was quantified by dividing the maximum adhesive force of this species on acrylic (smooth surface) by the locomotor force (body mass×maximum acceleration) during the escape. Depending on the individual, safety factors ranged from 0.4 to 25.4. How do these values change when only voluntary movements are quantified over an extended period? How does safety factor vary among species, individuals, and surface types? These questions can be addressed using long-term animal-borne accelerometry coupled with laboratory measurements of adhesive capacity. We predict that geckos operate close to a safety factor of 1 at times. However, unlike a mechanical failure of a structure such as a bone, the consequences for geckos (e.g. slipping or falling) are not likely to be long-term unless they are injured or consumed by a predator.

EGC1: how and when are claws and adhesive toepads used during locomotion – co-operation or conflict?

Most geckos that have adhesive toepads also carry claws on these digits. Among these, there is a dichotomy in the configuration of these two components (Fig. 5). In some, the adhesive system must
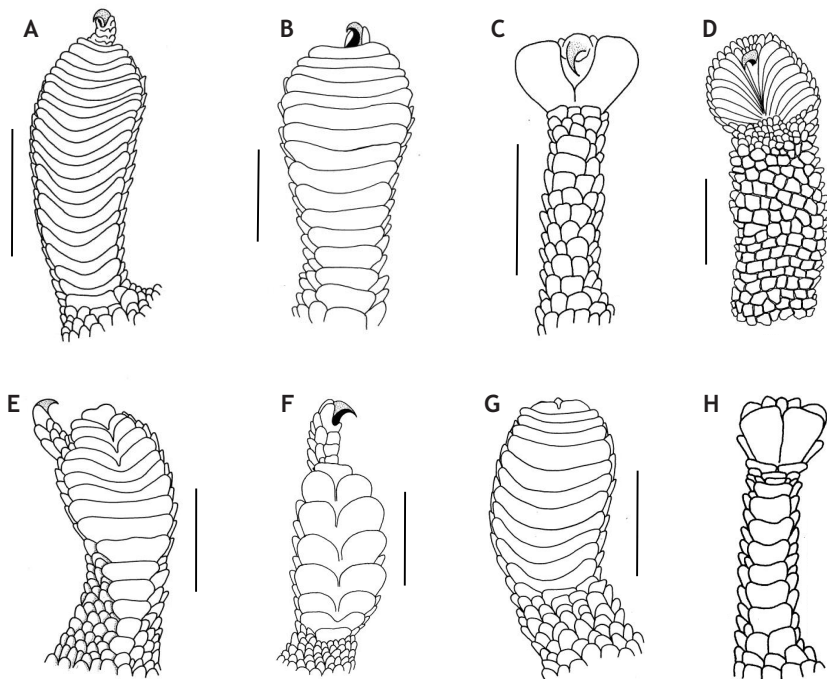
Fig. 5. Illustrations of the different toepad types and pad/claw configurations of geckos. (A,B) Unitary toepad/claw configuration in *Gekko vittatus* (A) and *Tarentola ephippiata* (B). (C,D) Terminal leaf-like toepad with pad/claw independence in *Euleptes europaea* (C) and *Uroplatus ebenaui* (D). (E,F) Cantilevered penultimate phalanx condition with pad/claw independence in *Gehyra australis* (E) and *Hemidactylus mabouia* (F). (G,H) Taxa that have toepads but lack claws. Basal pad in *Chondrodactylus bibronii* (G) and terminal leaf pad in *Ebenavia inunguis* (H). Scale bars: 5 mm (A) and 2 mm (B–H).

be engaged for the claws to be able to interdigitate with the substrate, because the toepad and claw mechanism are ensheathed in a common integumentary envelope (Fig. 5A,B). When such digits are hyperextended, the claws are necessarily disengaged (Fig. 2C). An alternative arrangement is evident in gecko lineages that either sport terminal leaf-like pads (Fig. 5C,D), which are limited to the distal regions of the digits or that have basally situated toepads from which the claw mechanism is cantilevered free of the underlying adhesive mechanism (Fig. 5E,F). In such geckos, the claws and toepads can be independently controlled. The potential benefit of a configuration in which the claws and toepads are independent is nicely illustrated by a recent study of geckos attempting to occupy the same microhabitat on Giraglia Island (Corsica; Russell and Delaugerre, 2017). *Euleptes europaea*, a leaf-toed taxon (Fig. 5C), is widespread on the island and was long-established there before both the erection of buildings and the recent (likely human-mediated) invasion of *Tarentola mauritanica*, a taxon in which the claws and toepads form a unitary configuration (similar to Fig. 5B). The friable, naturally occurring rocky surfaces on which *E. europaea* thrives tend to impede adhesive capabilities but are amenable to claw-induced traction. *E. eurpoaea* overcomes this challenge by furling the toepad leaves towards the median axis of the digits. *T. mauritanica*, in contrast, suffers from fouling of the adhesive apparatus on such surfaces and is unable to use its claws because of reflexive responses that attempt to rid the adhesive plates of the accumulated dust [self-cleaning of the adhesive system (Hansen and Autumn, 2005) being inhibited because of the absence of uncontaminated surfaces upon which to release it], and is therefore restricted solely to the occupation of only the non-friable surfaces of the human-constructed edifices on the island.

For geckos that have both an adhesive apparatus and claws, a benefit can also result, regardless of the arrangement of the two clinging systems. On very smooth surfaces, adhesion is the dominant mechanism for clinging (Fig. 6). However, when the substrate is extremely rough, adhesion is no longer as effective (Fig. 6A). In such cases, the claws become the dominant attachment mechanism and allow the gecko to move effectively (Fig. 6; Naylor

and Higham, 2019). The presence of both claws and toepads appears to result in a U-shaped clinging performance curve (Fig. 3), with one end (smooth) representing strong clinging performance due to adhesive structures and the other end (very rough) having strong clinging performance due to claw engagement. A key question is whether the kinematics and energetics of geckos climbing when relying on claws for attachment differs from these aspects when the adhesive system dominates. Although the same attachment force might be possible in each of these situations, the location along the digit where attachment is made will differ. This may have an impact on how the animal applies propulsive forces to the substrate.

What surfaces would best be suited for geckos with linked claws and toepads, toepads alone, or decoupled claws and toepads (Fig. 5)? The variability of the microhabitat should be considered to address this question. Geckos that frequently move over smooth surfaces and rarely encounter rough ones may benefit from having reduced claws or even from lacking them altogether. Those species that may frequently encounter friable or dusty surfaces would benefit from decoupled claws and toepads. Finally, those species that live on very rough tree bark or rocky surfaces might benefit from fully coupled claws and adhesive structures. Following these initial observations, careful laboratory experiments that control the features of the substrate and the attributes of the animal could tease apart the benefits and costs of claws and adhesion across surfaces. Finally, a phylogenetic framework could be used to assess the evolution (and possible convergent evolution) of claw and adhesive structure in relation to habitat use (Krings et al., 2023).

Selection of appropriate taxa for addressing the ecomechanical grand challenge questions

To address the ecomechanical grand challenge key questions outlined above, we propose that focus should, as much as possible, be placed upon monophyletic radiations that are ecologically, morphologically and ethologically diverse, thereby avoiding some confounding factors that might arise by employing a range of more distantly related taxa. It is not likely that all the aforementioned
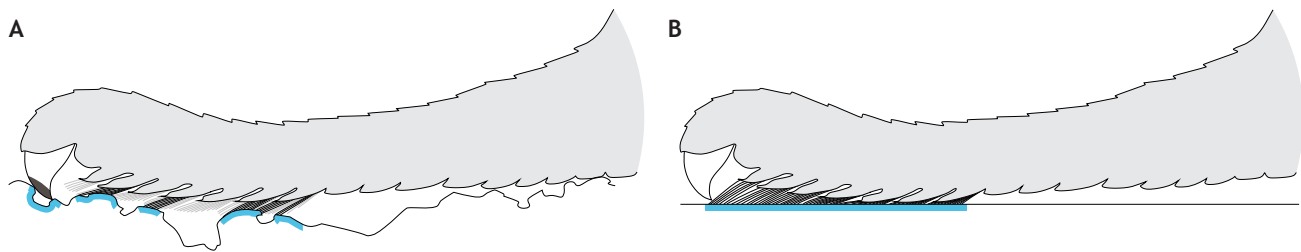
Fig. 6. Illustrations of a digit (with claw) on a rough and smooth surface. (A) On the rough surface, the setae only partially make contact with the surface (blue regions) and the claw fully interdigitates with the surface asperities (black tip of claw). (B) On the smooth surface, the claw is rendered non-functional, but the setae make much more extensive contact with the surface (blue region).

questions will be able to be addressed by employing a single radiation, but the taxa selected for each question should be informed by these criteria.

A prime candidate for an initial foray into this integrative approach is the monophyletic group in southern Africa that includes *Chondrodactylus*, *Pachydactylus*, *Colopus*, *Elasmodactylus*, and *Rhoptropus* (Heinicke et al., 2017). We make this suggestion for the following reasons: (i) its members lack functional claws (Fig. 5G), eliminating the potential for conflict or synergism between claws and the adhesive system (questions relating to the potential synergy or conflict between the adhesive system and claws will require investigation of additional taxa); (ii) the radiation includes species with a range of body sizes (some suitable for accelerometry) and a myriad of morphological specializations associated with the gain and secondary loss of adhesion (Haacke, 1976; Lamb and Bauer, 2006; Higham et al., 2015), making them well-suited for addressing the impacts of morphological diversity on function and movement in nature; (iii) climbing species are often restricted to petrologically different kinds of rocks or boulders (and occasionally trees) that are isolated by large tracts of desert terrain, enabling easy (and repeatable) observations (Johnson et al., 2009; Parrinha et al., 2025); and (iv) they include both diurnal and nocturnal species. Broad predictions based on these initial studies could then be used to make appropriate selections to expand the comparative framework to include species with functional claws, as well as species occupying a range of other habitats (e.g. rainforests). In addition, multiple radiations with comparable ranges in morphology and ecology, but that occupy different regions of the gekkotan phylogenetic tree, should be explored to determine whether groups have converged on common solutions.

Conclusions and broader applications

We have identified a series of ecomechanical grand challenges that build from our understanding of gecko adhesion under relatively static and simple conditions. Key challenges include visualizing the real-time interactions between the adhesive apparatus and the substratum during locomotion, investigating the neuromuscular and vascular control of adhesion, determining the sensory input that assists with this fine control, leveraging technological advancements in animal-borne accelerometry to determine how, and at what cost, geckos move freely in nature, and teasing apart the modulation of adhesion and claw-based clinging under natural conditions.

In addition to gaining an understanding of gecko adhesion, locomotion and energetics, there are broader implications of the research program outlined in this paper. First, the physiological basis of the control of adhesion, including muscle activation patterns and the sensory feedback necessary for fine control, could be applied to gecko-inspired robots to create a more dynamic system

that can respond to changes in the situations in which they are deployed. Second, understanding movement patterns of small animals in complex habitats will contribute to a greater appreciation of the movement ecology of small vertebrates. In fact, a recent study highlighted that, of 1000 randomly selected papers (covering both plants and animals) that focused on movement, only 2.1% focused on reptiles (Holyoak et al., 2008). Thus, geckos could serve as a model system for rapid, and tractable, locomotion in complex habitats. The costs of locomotion in different scenarios, as well as the effectiveness of the adhesive system on different surfaces, could be used to develop predictive models regarding habitat use. These could then be tested using the above-mentioned techniques for tracking and recording data from moving animals in nature.

Competing interests
The authors declare no competing or financial interests.

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