

UC Riverside

UC Riverside Previously Published Works

Title

Leaping lizards landing on leaves: escape-induced jumps in the rainforest canopy challenge the adhesive limits of geckos.

Permalink

<https://escholarship.org/uc/item/01w3304r>

Journal

Journal of the Royal Society Interface, 14(131)

Authors

Higham, Timothy

Russell, Anthony

Niklas, Karl

Publication Date

2017-06-01

DOI

10.1098/rsif.2017.0156

Peer reviewed

Research



Cite this article: Higham TE, Russell AP, Niklas KJ. 2017 Leaping lizards landing on leaves: escape-induced jumps in the rainforest canopy challenge the adhesive limits of geckos. *J. R. Soc. Interface* **14**: 20170156. <http://dx.doi.org/10.1098/rsif.2017.0156>

Received: 2 March 2017

Accepted: 2 June 2017

Subject Category:

Life Sciences—Physics interface

Subject Areas:

biomechanics, biophysics, biomaterials

Keywords:

biomechanics, adhesion, plant, *Thecadactylus*, beam, bending mechanics

Author for correspondence:

Timothy E. Higham

e-mail: thigham@ucr.edu

Leaping lizards landing on leaves: escape-induced jumps in the rainforest canopy challenge the adhesive limits of geckos

Timothy E. Higham¹, Anthony P. Russell² and Karl J. Niklas³

¹Department of Biology, University of California, Riverside, CA 92521, USA

²Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada T2N 1N4

³Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853, USA

TEH, 0000-0003-3538-6671

The remarkable adhesive capabilities of geckos have garnered attention from scientists and the public for centuries. Geckos are known to have an adhesive load-bearing capacity far in excess (by 100-fold or more) of that required to support their body mass or accommodate the loading imparted during maximal locomotor acceleration. Few studies, however, have investigated the ecological contexts in which geckos use their adhesive system and how this may influence its properties. Here we develop a modelling framework to assess whether their prodigious adhesive capacity ever comes under selective challenge. Our investigation is based upon observations of escape-induced aerial descents of canopy-dwelling arboreal geckos that are rapidly arrested by clinging to leaf surfaces in mid-fall. We integrate ecological observations, adhesive force measurements, and body size and shape measurements of museum specimens to conduct simulations. Using predicted bending mechanics of petioles and leaf midribs, we find that the drag coefficient of the gecko, the size of the gecko and the size of the leaf determine impact forces. Regardless of the landing surface, safety factors for geckos range from a maximum of just over 10 to a minimum of well under one, which would be the point at which the adhesive system fails. In contrast to previous research that intimates that gecko frictional adhesive capacity is excessive relative to body mass, we demonstrate that realistic conditions in nature may result in frictional capacity being pushed to its limit. The rapid arrest of the lizard from its falling velocity likely results in the maximal loading to which the adhesive system is exposed during normal activities. We suggest that such activities might be primary determinants in driving their high frictional adhesive capacity.

1. Introduction

The well-developed adhesive system that characterizes the majority of gecko species has been intensely investigated over the past few decades [1–5]. Studies examining the frictional adhesive capabilities of geckos on smooth surfaces (e.g. acrylic glass) reveal safety factors determined from whole animal clinging experiments that exceed 100 [6], and calculated theoretical absolute maxima that are an order of magnitude higher [7]. Such observations intimate that the gekkotan adhesive apparatus has a capacity far in excess of that needed to simply support body mass or accommodate forces of acceleration imparted during routine locomotion on vertical surfaces. Although some consideration has been given to why this might be so, it is possible that studies investigating single setae or setal arrays obtain unrealistically high values of force because they are unable to account for stress concentrations at the whole-pad level [8–12]. Additionally, examination of naturally exploited substrates that display complex topography has revealed that adhesive contact can be drastically diminished, cutting safety factor estimates to modest values [11–13]. Such studies highlight the need to investigate ecologically relevant substrates [14], which represent one component of the

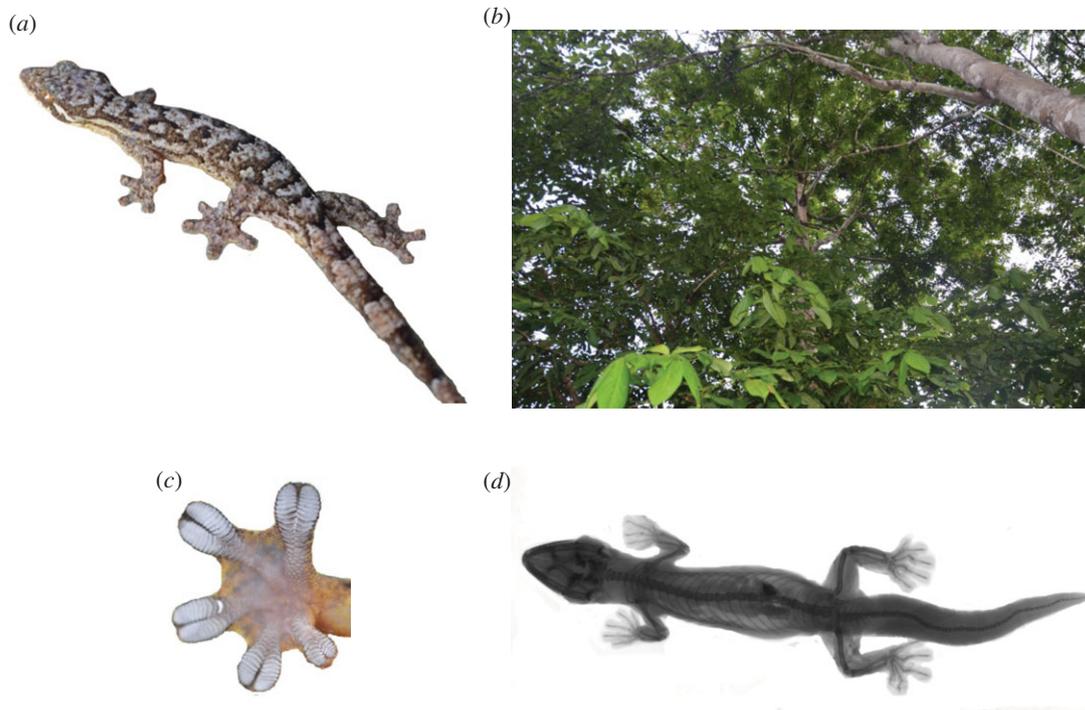


Figure 1. *Thecadactylus rapicauda* and its habitat. (a) An adult of the species; (b) a view of its forest canopy habitat as seen from the ground at Nouragues in French Guiana; (c) an image of the adhesive toepads of *T. rapicauda*; and (d) an X-ray image of *T. rapicauda* in ventral view, approximating the skydiving posture assumed following an escape-induced jump. (Online version in colour.)

organism–substrate interaction. Furthermore, it is evident that there is a paucity of consideration of the dynamic frictional adhesive forces that might be induced through the employment of natural behaviours. Understanding these is key to determining the limits and evolution of the frictional adhesive capabilities of geckos [14,15].

Aerial behaviours are common among arboreal vertebrates, and are important for survival. However, there is a gradient in the level of aerodynamic control following the launch, ranging from simply falling to gliding to parachuting [16,17]. A situation in which the adhesive system of geckos is subjected to high loading (greatly in excess of that experienced in static clinging) is in the arresting of a fall following a jump from a support in response to a perceived threat. Such escape jumps are a common behaviour among geckos [18–27], and are accompanied by the assumption of a ‘skydiving’ posture that is seemingly universally exhibited by geckos ([28] and fig. 1*g,h* in [25]), even those that lack an adhesive system. Given that many geckos are arboreal, often living high in the canopy [29–34], and that they have been documented to jump or fall from trees and land on either leaves or relatively smooth tree trunks [29,35], arrest of the fall will be rapid and result in high deceleration and impact forces. As such, these escape manoeuvres will induce high loadings on the adhesive system and may, therefore, be related to their large frictional adhesive capacity. A key question, therefore, centres upon how the impact and deceleration forces experienced when landing from a fall/jump compare to the maximum force-generating capabilities of pad-bearing geckos.

To explore this we combine observations of geckos in their natural habitat, measurements of frictional adhesive capability in the laboratory, and morphological measurements of an ontogenetic series of individuals. We predicate our study on observations of Vitt & Zani [29] who reported

that an individual of *Thecadactylus rapicauda* (the turnip-tailed gecko; figure 1*a*), upon being startled, launched itself from a perch in the forest canopy at a height of 30 m, assumed the skydiving posture, and arrested its fall by catching onto a leaf with two feet 15 m below its take off site. The turnip-tailed gecko is widespread across the Amazonian region, is often the only nocturnal arboreal lizard in its range [29,36], and often occupies canopy regions (figure 1*b*) of rain-forest habitat (at heights of up to 28 m in French Guiana, Philippe Gaucher 2016, personal communication). It thus occupies a complex three-dimensional habitat that provides a mosaic of potential landing sites within the densely configured canopy foliage [37]. *Thecadactylus rapicauda* has a well-developed adhesive apparatus (figure 1*c*) that is capable of generating significant frictional adhesive force [3,38].

We estimate aerodynamic forces, maximum impact forces, and subsequent loading on the adhesive system upon impact for this species. We model the landing platform, and bending mechanics following impact, as a cantilevered beam that includes the petiole and the midrib of the leaf. We simulated conditions relating to landing on a leaf following a jump-induced fall by using multiple values of leaf area, petiole length and drag coefficient. Based upon ecological observations we predict that the loadings will be very high and potentially push the limits of frictional adhesive capability. We discuss the importance of ecological observations and the quantification of the landing surface, which might mitigate the negative consequences of high impact forces.

2. Methods

2.1. Morphology

Because geckos assume a skydiving posture when falling [25] or in microgravity situations [28], we assumed that the ventral

Table 1. Mass, area and tail condition information for the museum specimens used in this study. Acronyms: AMNH, American Museum of Natural History; KU, Kansas University Biodiversity Institute and Natural History Museum; OMNH, Oklahoma Museum of Natural History; USNM, United States National Museum (Smithsonian).

museum ID	body mass (g)	ventral body area without tail (cm ²)	ventral tail area (cm ²)	original or regenerated tail
AMNH 101936	4.00	7.53	1.86	original
FMNH 168128	13.10	14.80	4.47	original
FMNH 228257	13.20	21.94	4.78	original
KU 194933	38.00	34.95	8.05	regenerate
KU 207765	32.00	34.85	5.87	regenerate
KU 220185	2.00	5.11	1.09	original
KU 229883	17.50	20.52	4.91	original
KU 229884	14.00	17.56	3.93	original
KU 229885	5.00	8.64	1.62	regenerate
KU 229886	2.00	4.90	0.95	original
OMNH 36310	19.00	24.25	5.07	regenerate
OMNH 36751	27.50	28.62	6.99	regenerate
OMNH 36753	19.20	26.57	5.08	regenerate
OMNH 36754	23.70	25.91	5.40	original
OMNH 36755	22.60	28.42	5.48	regenerate
OMNH 36756	20.20	26.65	4.58	regenerate
OMNH 36757	22.00	29.10	4.90	regenerate
OMNH 36759	25.20	28.67	5.53	regenerate
OMNH 37336	6.30	14.77	2.57	regenerate
OMNH 36760	22.80	27.90	5.70	original
UMMZ 83283	2.30	5.64	1.16	original
USNM 208238	30.33	30.91	6.29	regenerate
USNM 247451	11.04	15.70	3.78	original
USNM 269006	9.06	13.40	3.19	original

surface of the gecko is the area presented perpendicular to air flow and, therefore, the source of drag. Thus, we calculated the maximum projected area (with and without tail), based upon ventral X-ray images (figure 1*d*), of 24 individuals ranging from 2 to 38 g (detailed in table 1). For this, we used ImageJ with a ruler in the field of view for scaling. This species frequently autotomizes its tail, and 11 of the individuals in our study had regenerated tails. Thus, we assessed the potential difference in area of original and regenerated tails to determine whether tail condition would materially affect aerial performance.

2.2. Frictional adhesive force measurements

Using nine individuals (5.8–18.3 g) collected in the field in French Guiana [3], we quantified maximum clinging force (F_{adhesion}) using a portable force transducer, as detailed in previous studies [3,39] (table 2). Briefly, a portable load cell (Mark-10 Series 5 force gauge), sensitive to 50 N, was attached to a small rectangular piece of acrylic glass, onto which the gecko's forelimb was placed and the gecko pulled away from the transducer as a slow and steady rate. Maximum tension (N) was recorded for each trial, and maximum F_{adhesion} was measured from a minimum of three trials per individual. From these measurements, we established a scaling relationship between body mass and frictional adhesive force for all four limbs, which allowed us to estimate the frictional adhesive capacity of each of the measured individuals in our study.

Table 2. Mass and frictional adhesive force measurements for *Thecadactylus rapicauda* recorded in French Guiana.

individual	body mass (g)	adhesive force for both forelimbs (N)
1	5.8	3.4
2	6.25	2.68
3	12.25	5.02
4	12.3	5.1
5	12.8	4.48
6	13.8	4.32
7	15.75	6.66
8	17.3	5.48
9	18.3	4.86

2.3. Drag coefficient estimates

The drag coefficient (C_D) was estimated using literature values of other lizards that exhibit aerial behaviour. A recent study of lacertid lizards, including a species capable of directed aerial descents and one that is not specialized for aerial behaviour, revealed that

drag coefficients typically ranged from approximately 1.0 to 3.0 [40]. Like *T. rapicauda*, none of the lacertids exhibits any striking morphological specialization for aerial behaviour [40]. We used values of 1.0 and 3.0 in our simulations to bracket the potential drag coefficients of *T. rapicauda*.

2.4. Leaf and petiole as a cantilever beam

The parameters associated with leaf and petiole bending were estimated from previous studies [41–43]. We modelled the petiole and midrib of the leaf serially as a cantilever beam with uniform diameter [44]. We acknowledge the huge amount of diversity in leaf/petiole mechanical properties [41,42,44–47], but it is not our goal to explore the range of mechanical responses of leaves to falling geckos. Instead, we used a simplified leaf and petiole to explore potential values of impact force. Therefore, we did not take into account any properties of the leaf, other than its midrib. In other words, we modelled the leaf lamina as a midrib, with the understanding that complex interactions can occur between a falling gecko and the lamina on either side of the midrib.

Because petiole bending is critical for determining the displacement of the surface, we estimated petiole length by first using the leaf area reported by Vitt & Zani [29]. Using this, we extracted the length of the petiole from regressions from a recent study correlating leaf surface area and petiole length for 38 tropical tree species [48]. From petiole length, we were able to estimate petiolar flexural stiffness (EI), which is the product of Young's modulus (E) and the second moment of area (I). Because leaf area and petiole length vary within the foliage, we bracketed our simulations using petiole lengths of 0.08 m ($EI = 0.003 \text{ N m}^2$) and 0.16 m ($EI = 0.032 \text{ N m}^2$), with values of EI extracted from the regression equations reported by Niklas [41] for petioles of constant thickness. Given that the stiffness of the leaf midrib is lower than that of the petiole [44], we then multiplied our values of EI by 0.89 to correct for the reduced stiffness of the petiole when combined with the leaf lamina [42]. We simply added the estimated length of the midrib of the leaf (based on leaf area) to the length of the petiole in order to produce an estimate of overall leaf length (L).

2.5. Impact dynamics

To determine the force imparted on the leaf by a falling lizard that contacts it, thus causing bending, we first estimated terminal velocity (V_t) of the geckos using the following equation (figure 2a):

$$V_t = \sqrt{\frac{2mg}{\rho AC_D}} \quad (2.1)$$

where m = mass of the lizard (in kg), g = force due to gravity (9.81 ms^{-2}), ρ = air density (1.2 kg m^{-3}), A = ventral area of the gecko calculated from X-rays (in m^2), and C_D is the coefficient of drag. V_t was calculated for each individual across the size range of our sample. We compared these values to those extracted from the equation for impact velocity:

$$V_i = \sqrt{2 \times g \times h}. \quad (2.2)$$

We used V_t for all calculations after determining that V_t was reached for every combination that we examined, such that $V_t < V_i$. Terminal velocity was used to calculate the impact force (F_i) experienced by the gecko. The initial force exerted on the leaf (P) by the gecko was simply the product of mass and acceleration due to gravity (figure 2b):

$$P = mg. \quad (2.3)$$

2.6. Petiole and leaf midrib bending dynamics

Using the value of P from above, we estimated the tip deflection (δ) of the petiole and leaf lamina by first modelling it as a uniform cantilever beam with the concentrated impact force (P) occurring at the distal tip at length L [41,43,49] (figures 2c and 3).

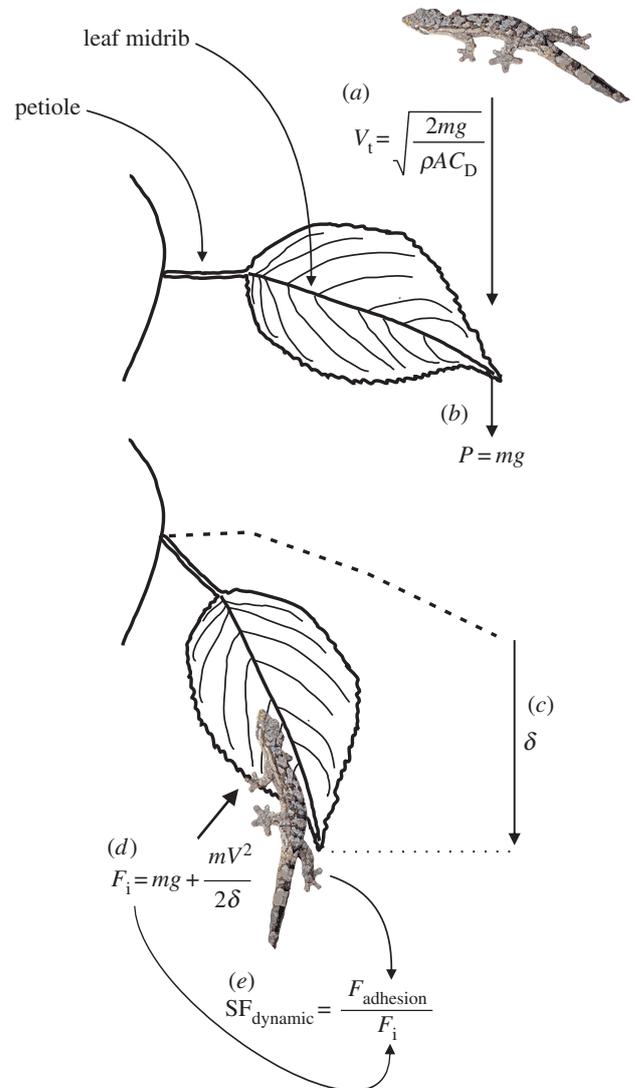


Figure 2. A schematic of a jump and landing, illustrating the calculations used in our study. The gecko reaches terminal velocity (V_t), as it falls towards the leaf surface (a). The distance fallen before V_t is attained depends on the mass of the gecko (m), the acceleration due to gravity (g), the density of the air (ρ), the ventral surface area of the gecko (A), and the drag coefficient of the gecko (C_D). The terminal load on the leaf (P) will result from the m and g of the gecko (b). The deflection of the leaf (δ) is determined using an elliptical integral of the first kind (c). The impact force experienced by the gecko (F_i) will result from P , the kinetic energy of the gecko ($mV_t^2/2$), and δ (d). Finally, the dynamic safety factor (SF_{dynamic}) relates the adhesive capabilities of the geckos to the impact force (e). See the text for further information. (Online version in colour.)

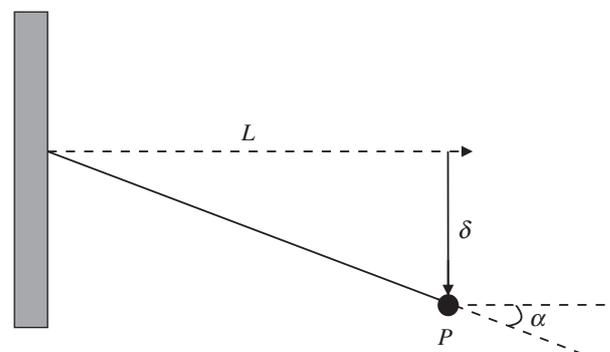


Figure 3. A schematic showing the cantilevered beam modelled in this paper. The beam, which consists of the petiole and midrib (together = L), will begin at right angles to the hypothetical trunk, and will deflect downwards (δ) due to the impact of the gecko (P). This will result in an angular excursion of the beam (α).

We assumed the initial angle of the leaf to be perpendicular to the hypothetical vertical tree trunk, and the deflection angle (α) is estimated relative to the horizontal (figure 3).

Large deflections of cantilevered stems and leaves can be analysed provided that exact expressions of their curvature, K , are known. The exact expression for K is $d\theta/ds$. The bending moment in the y (vertical) direction imposed on the cantilever, $-Py$, is the product of EI and the curvature:

$$EI \left(\frac{d\theta}{ds} \right) = -Py, \quad (2.4)$$

where P is the load applied from above.

Because $d\theta/ds = \sin \theta$, equation (2.4) has a dynamic analogy with the equation governing the oscillatory motion of a pendulum. Solving equation (2.3) by means of this analogy and relating the solution to the length of the column, yields

$$L = \left(\frac{1}{2k} \right) \int_0^\alpha \frac{d\theta}{(\sin^2(\phi/2) - \sin^2(\theta/2))^{1/2}}, \quad (2.5)$$

where $k = (P/EI)^{1/2}$ and α is the deflection angle at the tip of the cantilever (figure 3).

Equation (2.5) is simplified by introducing the new variable such that

$$\sin\left(\frac{\theta}{2}\right) = \sin\left(\frac{\alpha}{2}\right) \sin \phi. \quad (2.6)$$

Differentiation of equation (2.6) yields

$$d\theta = \frac{2p \cos \phi d\phi}{(1 - p^2 \sin^2 \phi)^{1/2}}. \quad (2.7)$$

Combining equations (2.5) and (2.7), yields

$$L = \left(\frac{1}{k} \right) \int_0^{\pi/2} \frac{d\phi}{(1 - p^2 \sin^2 \phi)^{1/2}} = \left(\frac{1}{k} \right) [K(p)]. \quad (2.8)$$

The integral in equation (2.8) has the form of a complete elliptic integral of the first kind, denoted as $K(p)$, the value of which depends solely on α . From the relationship $k = (P/EI)^{1/2}$ and equation (2.7), we obtain

$$P = [K(p)]^2 \frac{EI}{L^2}, \quad (2.9)$$

which indicates that the explicit relationship between P , I , L , E , and $K(p)$ depends exclusively on α . Rearranging equation (2.9) yields the dimensionless load parameter

$$[K(p)]^2 = [K \sin(\alpha/2)]^2 = \frac{PL^2}{EI}. \quad (2.10)$$

The complete integral was then used to determine the value of δ/L , as described in [43]. Multiplying δ/L by L yielded the linear deflection of the petiole and leaf midrib (δ).

2.7. Impact force and safety factor

Finally, F_i experienced by the gecko was calculated using δ as the displacement upon impact (figure 2d). In all simulations, the gecko was assumed to stop immediately without slippage along the lamina of the leaf. Using the work-energy principle, it was calculated as

$$F_i = mg + \frac{mV_t^2}{2\delta}. \quad (2.11)$$

To relate the potential frictional adhesive force to impact force we calculated a dynamic safety factor (SF_{dynamic}) as the ratio of F_{adhesion} (for both forefeet) to F_i (figure 2e):

$$SF_{\text{dynamic}} = \frac{F_{\text{adhesion}}}{F_i}. \quad (2.12)$$

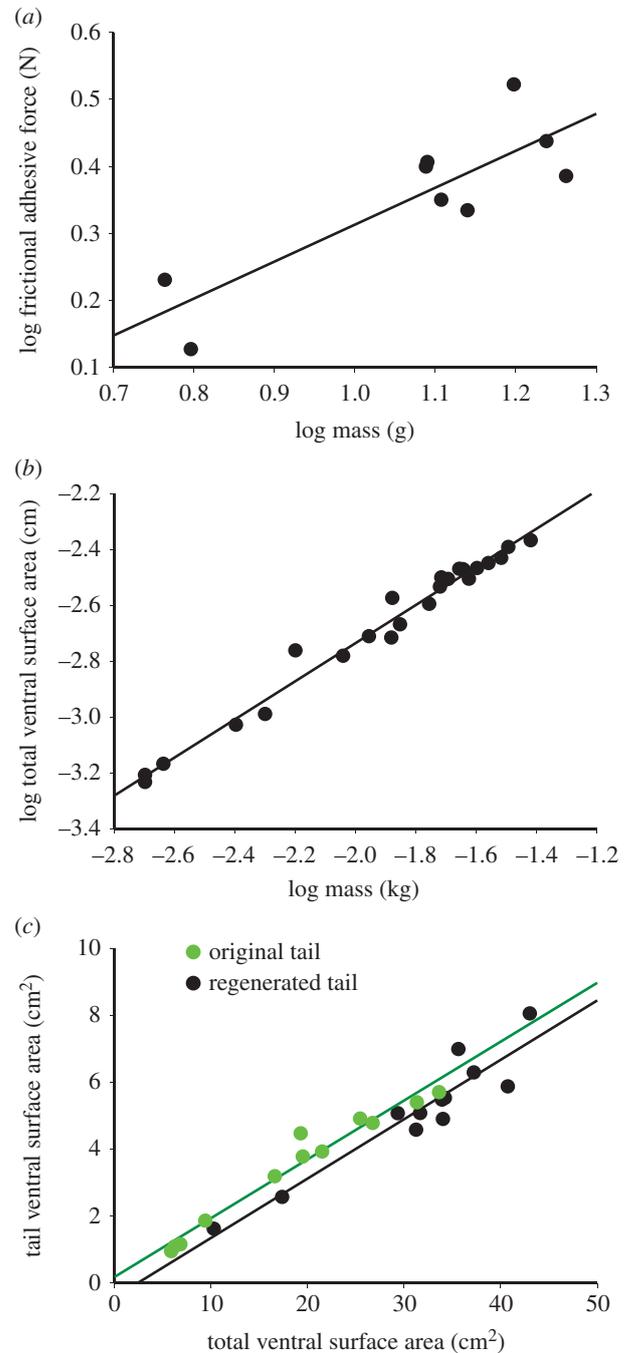


Figure 4. Linear regressions of body mass and frictional adhesive force (a), body mass and total ventral surface area (b), and total ventral surface area and tail ventral surface area (c) of *Thecadactylus rapicauda*. (Online version in colour.)

2.8. Statistics

To determine the relationships between frictional adhesive force and body mass, total ventral surface area and body mass, and tail ventral surface area and total ventral surface area, we used OLS linear regressions in Systat version 13. Body mass and frictional adhesive force were both log-transformed to obtain the scaling exponent and to linearize the data. For the relationships between body mass and petiole/midrib deflection, impact force, and dynamic adhesive safety factor, we applied a second-order polynomial fit to each plot due to the complex curves.

3. Results

Frictional adhesive force for *Thecadactylus rapicauda* is significantly correlated with body mass ($r^2 = 0.72$, scaling exponent = 0.55 ± 0.13 , CI = 0.27, $p < 0.01$; figure 4a), in a

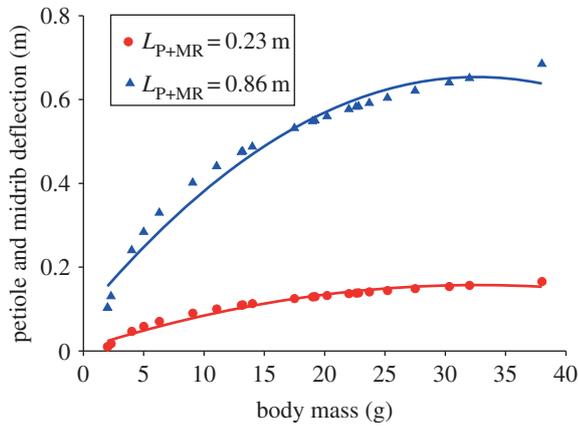


Figure 5. Petiole and leaf midrib (L_{P+MR}) deflection as a function of body size. Triangles (blue) are for the larger leaf and the circles (red) are for the smaller leaf. Note that the maximum deflection, for the largest gecko, was approximately 79% of the combined length of the midrib and petiole, and this was for the larger leaf. Each point on the graph is an individual, for which we measured body mass, maximum projected area and frictional adhesive capability. (Online version in colour.)

negatively allometric fashion. Total ventral surface area (including the tail) is significantly correlated with body mass ($r^2 = 0.98$, $p < 0.001$; figure 4*b*) and scales isometrically (scaling exponent = 0.68 ± 0.02 , CI = 0.04). The ventral surface areas of the original and regenerated tails are both significantly correlated with total ventral surface area ($r^2 = 0.96$ and 0.89 , respectively), and there is no significant difference in the slope of the two regressions (figure 4*c*).

The deflection of the petiole and midrib increased with the mass of the gecko for all simulations (figure 5). In all cases, deflection was greatest for the largest gecko (figure 5). As expected from the mechanical behaviour of a cantilever, petiole and midrib deflection was much greater for the larger leaf, especially for the larger geckos (figure 5).

Gecko impact force (F_i) increases with body mass, this being proportionally greater for a C_D of 1.0 than 3.0 (figure 6*a*). Impact force was greatest for the lowest drag coefficient and the smallest leaf, especially for the larger geckos (figure 6*a*). In almost all cases, adhesive safety factor ($SF_{dynamic}$) increased initially with an increase in body mass (figure 6*b*). However, for body masses above 10–15 g, decreases in $SF_{dynamic}$ often resulted (figure 6*b*). For both drag coefficients, maximum $SF_{dynamic}$ occurs on the larger leaf, especially for the higher drag coefficient (figure 6*b*). Finally, $SF_{dynamic}$ fell below 1.0 when the L_P was 0.08 m and the C_D was 1.0 (figure 6*b*).

4. Discussion

Our simulations reveal that arrests of falls following aerial descents have the capability of pushing geckos to the limits of their frictional adhesive capacity, resulting in adhesive safety factor values from just over 10 to slightly less than one, depending on the situation. This is considerably lower than static safety factors measured under laboratory conditions, which, for whole animal clinging observations, can reach 100 or more for some species of pad-bearing gecko [3]. The three critical variables for a gecko arresting a fall by attaching to a leaf following an escape jump are the compliance of the substrate (dependent on length and flexural stiffness, which will define its displacement upon impact),

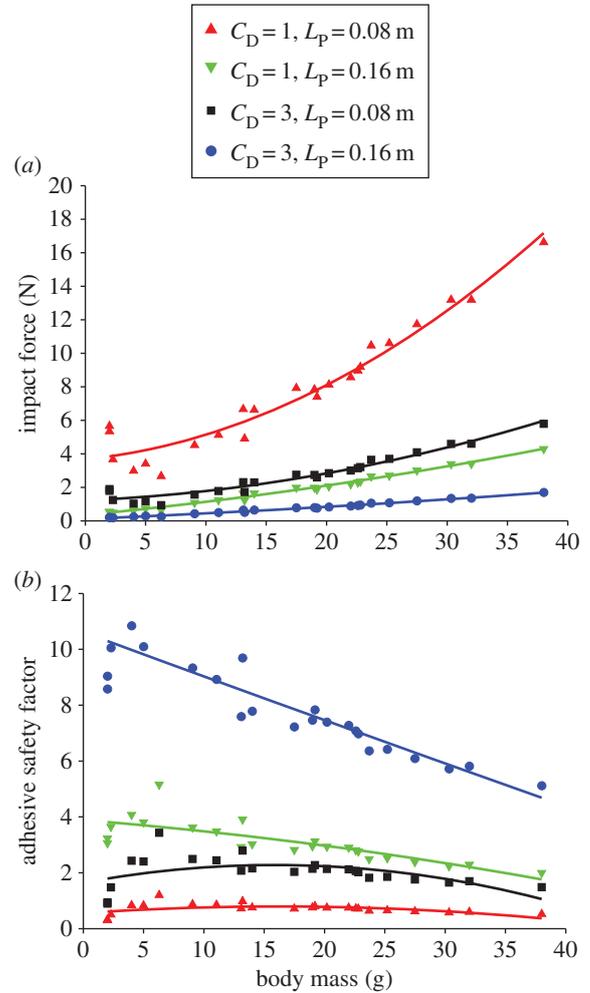


Figure 6. Impact force experienced by the gecko in relation to body mass (*a*) and the frictional adhesive safety factor in relation to body mass (*b*) for uniform beams. Lines denoted by triangles (red and green) are based upon a drag coefficient of 1.0 for 0.08 and 0.16 m petioles, respectively. Lines denoted by squares (black) and circles (blue) are based upon a drag coefficient of 3.0 for 0.08 and 0.16 m, petioles, respectively. Each point on this graph represents an individual, as in figure 5. (Online version in colour.)

the height of the fall (which will define the impact velocity), and the drag coefficient of the gecko during the descent. We show that, in all cases, landing on larger leaves reduces the impact force and maximizes safety factor (figure 6).

Body mass clearly plays a critical role in the ecology of arboreal geckos. Although adhesive force increases with body mass, it does so with a non-isometric allometry if one assumes an expected relationship of 0.66 (based on the relationship between adhesive area and body mass) [50] (figure 4*a*), indicating that the amount of frictional adhesive force is disproportionately lower for progressively larger animals. Regardless, we show that geckos are subjected to impact forces that approach or exceed the safety factor of a single foot, the consequences of which could be dire, possibly resulting in injury or a failed landing attempt. Additionally, larger geckos are disadvantaged by the fact that they are more likely to break a petiole, potentially leading to injury. Thus, selection of an appropriate landing surface, and/or the ability to limit the vertical distance of the descent, could well be critical.

Geckos are often noted for having adhesive capacity that far exceeds (by several orders of magnitude) that required to support body mass on smooth surfaces or to accommodate forces generated by locomotory acceleration as measured in the

laboratory [1,51]. A key aspect of a gecko's ecology, however, is the naturally occurring surface to which it attaches, and the conditions under which this occurs. The relative area that can be contacted by the setae (accounting for adhesive contact) is vastly different among substrates, and is greatly diminished (relative to acrylic and glass) for rock surfaces employed by desert-dwelling geckos [11–13]. An important aspect of gecko adhesive capability that has been largely overlooked is that related to the dynamic forces that may be experienced in nature during locomotion. We show that, even on smooth plant surfaces, safety factors can become critically low when arresting a fall following an aerial descent resulting from an escape response. Such circumstances entail the almost instantaneous stopping of the contacting feet on the leaf surface and the absorption of the loading force induced by deceleration of the body by the adhering feet. These interactions are damped by the compliance of the leaf petiole, which under natural conditions will store the strain energy incurred by the collision and use it to elastically restore its equilibrium condition. Such interactions likely represent the highest loading to which the adhesive system will be naturally exposed. It is possible that the evolution of high adhesive capacity may, at least in part, be related to the arresting of such aerial descents and similar jumps in other environmental circumstances [18,52]. These may be relatively rare events, but the ability to accommodate them when they occur [53] will have major survival value.

Even though our calculations show that safety factors under such circumstances are greatly diminished, they still assume that maximum frictional adhesion can occur, which also assumes that the landing substrate is as smooth as the clean acrylic on which the frictional adhesive forces were measured. It is unclear how smooth such plant surfaces actually are, although likely they are not as smooth as acrylic, with the epicuticle known to be complexly structured and to influence attachment of insects [54–56]. Thus, we likely overestimate the frictional adhesive force and dynamic safety factor. This can be resolved by quantifying the microtopography of natural landing surfaces following field observations. In addition to microtopography, the role of other aspects of plant biology, such as polarizability and hydrophobicity of epicuticular surfaces, requires investigation and documentation.

We made the assumption that the gecko would stop immediately following impact with the leaf surface. However, it is likely that it could slide along the leaf surface following impact, which would reduce the impact force experienced. Multiple factors could play critical roles in these situations. The landing location on the leaf will determine the distance that the gecko could travel. For example, if it landed on the mid-region of the lamina, it could travel distally following impact. However, there is a trade-off. Landing closer to the junction between the leaf lamina and the petiole would result in decreased deflection, thereby increasing the impact force. Whether the gecko can select the location of the landing surface is unknown. Yet another variable of interest is the capacity of the leaf lamina to undergo dynamic side-to-side oscillations, which

would also affect the impact force. Additionally, it is possible that the claws of the gecko could play a part in arresting the fall, but tellingly for *Thecadactylus* the claws are deeply sheathed within a sulcus between the banks of adhesive sensors [57] and it is unlikely that they are deployed in circumstances in which frictional adhesive attachment is relied upon.

At present we are also unable to account for any dynamic mid-air manoeuvres made by geckos. Such consideration is not possible without high-speed videographic observations to enable assessment of this. In addition to the possibility that the drag coefficient might be modulated mid-air by altering the angle of attack, *T. rapicauda* may be able to move horizontally, thereby adjusting its glide path to permit the selection of specific landing surfaces. Geckos [58,59] and other animals [60] have the ability to dynamically execute mid-air manoeuvres.

5. Conclusion

We show that landing on plant surfaces following escape-induced jumps can result in very high impact forces that challenge adhesive capacity, but that these are mitigated by the bending of the leaf and petiole. Thus, aerial descents and the arrest of the fall upon landing provide one avenue for the exploration of the limits to, and potential evolutionary drivers of, frictional adhesive capacity of geckos. Arboreal geckos frequently live high in the canopy, and are often observed falling or jumping in this three-dimensionally complex zone. Increased understanding of how geckos interact with plant surfaces will yield new insights into how innovations facilitate and/or limit extreme behaviours. More generally, we highlight the importance of incorporating ecologically relevant situations when attempting to understand the evolution of a complex system such as the adhesive apparatus of geckos. In addition to the natural surfaces, high velocities of landing are apparent, and it is known that the velocity of the application of adhesion can increase the frictional adhesive force [61].

Ethics. All experiments with geckos were approved by the Centre National de la Recherche Scientifique (CNRS) in France (for French Guiana) and the Institutional Animal Care and Use Committee (IACUC) at the University of California, Riverside. All experiments follow an approved protocol (A20140028) from the IACUC at UC Riverside.

Data accessibility. Raw data are in the included tables.

Authors' contributions. T.E.H. and A.P.R. developed the ideas underlying this paper. T.E.H. collected the adhesive force measurements in French Guiana and carried out the analyses. T.E.H. developed the first draft of the manuscript, and A.P.R. and K.J.N. contributed extensive revisions. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. Funding was provided by a National Science Foundation (NSF) grant (IOS-1147043) to T.E.H.

Acknowledgements. Clint Collins assisted with fieldwork in French Guiana. Philippe Gaucher was of great assistance at Nouragues in French Guiana. We also thank David Labonte and two anonymous reviewers for their valuable suggestions.

References

1. Autumn K, Peattie AM. 2002 Mechanisms of adhesion in geckos. *Integr. Comp. Biol.* **42**, 1081–1090. (doi:10.1093/icb/42.6.1081)
2. Higham TE, Birn-Jeffery AV, Collins CE, Hulseley CD, Russell AP. 2015 Adaptive simplification and the evolution of gecko locomotion: morphological and biomechanical consequences of losing adhesion. *Proc. Natl Acad. Sci. USA* **112**, 809–814. (doi:10.1073/pnas.1418979112)

3. Higham TE, Gamble T, Russell AP. 2017 On the origin of frictional adhesion in geckos: small morphological changes lead to a major biomechanical transition in the genus *Gonatodes*. *Biol. J. Linn. Soc.* **120**, 503–517. (doi:10.1111/bj.12897)
4. Russell AP. 1975 A contribution to the functional analysis of the foot of the Tokay, *Gekko gekko* (Reptilia: Gekkonidae). *J. Zool.* **176**, 437–476. (doi:10.1111/j.1469-7998.1975.tb03215.x)
5. Russell AP. 2002 Integrative functional morphology of the gekkotan adhesive system (Reptilia: Gekkota). *Integr. Comp. Biol.* **42**, 1154–1163. (doi:10.1093/icb/42.6.1154)
6. Irschick DJ, Austin CC, Petren K, Fisher RN, Losos JB, Ellers O. 1996 A comparative analysis of clinging ability among pad-bearing lizards. *Biol. J. Linn. Soc.* **59**, 21–35. (doi:10.1111/j.1095-8312.1996.tb01451.x)
7. Autumn K, Liang YA, Hsieh ST, Zesch W, Chan WP, Kenny TW, Fearing R, Full RJ. 2000 Adhesive force of a single gecko foot-hair. *Nature* **405**, 681–684. (doi:10.1038/35015073)
8. Bullock JMR, Federle W. 2011 Beetle adhesive hairs differ in stiffness and stickiness: in vivo adhesion measurements on individual setae. *Naturwissenschaften* **98**, 381–387. (doi:10.1007/s00114-011-0781-4)
9. Eason EV, Hawkes EW, Windheim M, Christenson DL, Libby T, Cutkosky MR. 2015 Stress distribution and contact area measurements of a gecko toe using a high resolution tactile sensor. *Bioinspir. Biomim.* **10**, 016013. (doi:10.1088/1748-3190/10/1/016013)
10. Russell AP, Johnson MK, Delannoy SM. 2007 Insights from studies of gecko-inspired adhesion and their impact on our understanding of the evolution of the gekkotan adhesive system. *J. Adhes. Sci. Technol.* **21**, 1119–1143. (doi:10.1163/156856107782328371)
11. Johnson MK, Russell AP. 2009 Configuration of the setal fields of *Rhoptropus* (Gekkota: Gekkonidae): functional, evolutionary, ecological and phylogenetic implications of observed pattern. *J. Anat.* **214**, 937–955. (doi:10.1111/j.1469-7580.2009.01075.x)
12. Russell AP, Johnson MK. 2014 Between a rock and a soft place: microtopography of the locomotor substrate and the morphology of setal fields of Namibian day geckos (Gekkota: Gekkonidae: Rhoptropus). *Acta Zool.* **95**, 299–318. (doi:10.1111/azo.12028)
13. Russell AP, Johnson MK. 2007 Real-world challenges to, and capabilities of, the gekkotan adhesive system: contrasting the rough and the smooth. *Can. J. Zool.* **85**, 1228–1238. (doi:10.1139/Z07-103)
14. Niewiarowski PH, Stark AY, Dhinojwala A. 2016 Sticking to the story: outstanding challenges in gecko-inspired adhesives. *J. Exp. Biol.* **219**, 912–919. (doi:10.1242/jeb.080085)
15. Pianka ER, Sweet SS. 2005 Integrative biology of sticky feet in geckos. *Bioessays* **27**, 647–652. (doi:10.1002/bies.20237)
16. Dudley R, Byrnes G, Yanoviak SP, Borrell B, Brown RM, McGuire JA. 2007 Gliding and the functional origins of flight: biomechanical novelty or necessity? *Annu. Rev. Ecol. Evol. Syst.* **38**, 179–201. (doi:10.1146/annurev.ecolsys.37.091305.110014)
17. Dudley R, Yanoviak SP. 2011 Animal aloft: the origins of aerial behavior and flight. *Integr. Comp. Biol.* **51**, 926–936. (doi:10.1093/icb/icr002)
18. Bauer AM. 1990 Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). *Bonn Zool. Monogr.* **30**, 1–220.
19. Anderson JA. 1964 A report on the gecko *Teratolepis fasciata* (Blyth 1853). *J. Bombay Nat. Hist. Soc.* **61**, 161–171.
20. Annandale N. 1905 Notes on some oriental geckos in the Indian Museum, Calcutta, with descriptions of new forms. *Ann. Magazine Nat. Hist.* **15**, 26–32. (doi:10.1080/03745480509443635)
21. Fleming PA, Bateman PW. 2012 Autotomy, tail regeneration and jumping ability in Cape dwarf geckos (*Lygodactylus capensis*) (Gekkonidae). *Afr. Zool.* **47**, 55–59. (doi:10.1080/15627020.2012.11407523)
22. Heyer RW, Pongsapipatana S. 1970 Gliding speeds of *Ptychozoon lionotum* (Reptilia: Gekkonidae) and *Chrysopelea ornata* (Reptilia: Colubridae). *Herpetologica* **26**, 317–319.
23. Loveridge A. 1935 Revision of the African geckos of the genus *Cnemaspis*, with description of a new race. *Proc. Zool. Soc. Lond.* **1935**, 817–822. (doi:10.1111/j.1469-7998.1935.tb06266.x)
24. Minton SA. 1966 A contribution to the herpetology of West Pakistan. *Bull. Am. Mus. Nat. Hist.* **134**, 27–184.
25. Russell AP. 1979 The origin of parachuting locomotion in gekkonid lizards (Reptilia: Gekkonidae). *Zool. J. Linn. Soc.* **65**, 233–249. (doi:10.1111/j.1096-3642.1979.tb01093.x)
26. Oliver JA. 1951 'Gliding' in amphibians and reptiles, with a remark on an arboreal adaptation in the lizard *Anolis carolinensis carolinensis* Voigt. *Am. Nat.* **85**, 171–176. (doi:10.1086/281666)
27. Taylor EH. 1922 *Lizards of the Philippine Islands*. Government of the Philippine Islands Department of Agriculture and Natural Resources Bureau of Science.
28. Wassersug RJ, Roberts L, Gimian J, Hughes E, Saunders R, Devison D, Woodbury J, O'Reilly JC. 2005 The behavioral responses of amphibians and reptiles to microgravity on parabolic flights. *Zoology* **108**, 107–120. (doi:10.1016/j.zool.2005.03.001)
29. Vitt LJ, Zani PA. 1997 Ecology of the nocturnal lizard *Thecadactylus rapicauda* (Sauria: Gekkonidae) in the Amazon region. *Herpetologica* **53**, 165–179.
30. Harmon LJ, Harmon LL, Jones CG. 2007 Competition and community structure in diurnal arboreal geckos (genus *Phelsuma*) in the Indian Ocean. *Oikos* **116**, 1863–1878. (doi:10.1111/j.0030-1299.2007.15958.x)
31. Grismer LL *et al.* 2014 Systematics and natural history of Southeast Asian rock geckos (genus *Cnemaspis* Strauch, 1887) with descriptions of eight new species from Malaysia, Thailand, and Indonesia. *Zootaxa* **3880**, 1–147. (doi:10.11646/zootaxa.3880.1.1)
32. Vitt LJ, Souza RA, Sartorius SS, Avila-Pires TCS, Esposito MC. 2000 Comparative ecology of sympatric *Gonatodes* (Squamata: Gekkonidae) in the western Amazon of Brazil. *Copeia* **2000**, 83–95. (doi:10.1643/0045-8511(2000)2000[0083:CEOSGS]2.0.CO;2)
33. Loveridge A. 1947 Revision of the African lizards of the family Gekkonidae. *Bull. Mus. Comp. Zool. Univ. Harv.* **98**, 1–469.
34. Pianka ER, Vitt LJ. 2003 *Lizards: windows to the evolution of diversity*. Berkeley, CA: University of California Press.
35. Watkins-Colwell GJ. 2003 Gecko hunting in New Caledonia. *Gekko* **3**, 2–8.
36. Bergmann PJ, Russell AP. 2007 Systematics and biogeography of the widespread neotropical gekkonid genus *Thecadactylus* (Squamata), with a description of a new cryptic species. *Zool. J. Linn. Soc.* **149**, 339–370. (doi:10.1111/j.1096-3642.2007.00251.x)
37. Kubo T, Kobayashi T, Kato K, Nishimura S, Uemura S, Ono K, Sumida A, Hara T. 2008 Estimating the three-dimensional structure of canopy foliage based on the light measurements in a *Betula ermanii* stand. *Agric. For. Meteorol.* **148**, 1293–1304. (doi:10.1016/j.agrformet.2008.03.008)
38. Peattie AM, Dirks J-H, Henriques S, Federle W. 2011 Arachnids secrete a fluid over their adhesive pads. *PLoS ONE* **6**, e20485. (doi:10.1371/journal.pone.0020485)
39. Stewart WJ, Higham TE. 2014 Passively stuck: death does not affect gecko adhesion strength. *Biol. Lett.* **10**, 20140701. (doi:10.1098/rsbl.2014.0701)
40. Vanhooydonck B, Meulepas G, Herrel A, Boistel R, Tafforeau P, Fernandez V, Aerts P. 2009 Ecomorphological analysis of aerial performance in a non-specialized lacertid lizard, *Holaspis guentheri*. *J. Exp. Biol.* **212**, 2475–2482. (doi:10.1242/jeb.031856)
41. Niklas KJ. 1999 A mechanical perspective on foliage leaf form and function. *New Phytol.* **143**, 19–31. (doi:10.1046/j.1469-8137.1999.00441.x)
42. Niinemets U, Fleck S. 2002 Petiole mechanics, leaf inclination, morphology, and investment in support in relation to light availability in the canopy of *Liriodendron tulipifera*. *Oecologia* **132**, 21–33. (doi:10.1007/s00442-002-0902-z)
43. Chen L. 2010 An integral approach for large deflection cantilever beams. *Int. J. Non-Linear Mech.* **45**, 301–305. (doi:10.1016/j.ijnonlinmec.2009.12.004)
44. Niklas KJ. 1991 Flexural stiffness allometries of angiosperm and fern petioles and rachises: evidence for biomechanical convergence. *Evolution* **45**, 734–750. (doi:10.1111/j.1558-5646.1991.tb04342.x)
45. Ennos AR, Spatz H-C, Speck T. 2000 The functional morphology of the petioles of the banana, *Musa textilis*. *J. Exp. Bot.* **51**, 2085–2093. (doi:10.1093/jxb/51.353.2085)
46. Niklas KJ, Cobb ED, Niinemets U, Reich PB, Sellin A, Shipley B, Wright IJ. 2007 'Diminishing returns' in the scaling of functional leaf traits across and within

- species groups. *Proc. Natl Acad. Sci. USA* **104**, 8891–8896. (doi:10.1073/pnas.0701135104)
47. Onada Y *et al.* 2011 Global patterns of leaf mechanical properties. *Ecol. Lett.* **14**, 301–312. (doi:10.1111/j.1461-0248.2010.01582.x)
 48. Poorter L, Rozendaal DMA. 2008 Leaf size and leaf display of thirty-eight tropical tree species. *Oecologia* **158**, 35–46. (doi:10.1007/s00442-008-1131-x)
 49. Niklas KJ. 1992 *Plant biomechanics: an engineering approach to plant form and function*. Chicago, IL: University of Chicago Press.
 50. Webster NB, Johnson MK, Russell AP. 2009 Ontogenetic scaling of scansorial surface area and setal dimensions of *Chondrodactylus bibronii* (Gekkota: Gekkonidae): testing predictions derived from cross-species comparisons of gekkotans. *Acta Zool.* **90**, 18–29. (doi:10.1111/j.1463-6395.2008.00324.x)
 51. Autumn K, Hsieh ST, Dudek DM, Chen J, Chitaphan C, Full RJ. 2006 Dynamics of geckos running vertically. *J. Exp. Biol.* **209**, 260–272. (doi:10.1242/jeb.01980)
 52. Fitzsimons VF. 1943 *The lizards of South Africa*. Pretoria, South Africa: Transvaal Museum.
 53. Gans C. 1979 Momentarily excessive construction as the basis for protoadaptation. *Evolution* **33**, 227–233. (doi:10.1111/j.1558-5646.1979.tb04677.x)
 54. Koch K, Bhusan B, Barthlott W. 2009 Multifunctional surface structures of plants: an inspiration for biomimetics. *Prog. Mater. Sci.* **54**, 137–178. (doi:10.1016/j.pmatsci.2008.07.003)
 55. Prüm B, Bohn HF, Seidel R, Rubach S, Speck T. 2013 Plant surfaces with cuticular folds and their replicas: influence of microstructuring and surface chemistry on the attachment of a leaf beetle. *Acta Biomater.* **9**, 6360–6368. (doi:10.1016/j.actbio.2013.01.030)
 56. Prüm B, Seidel R, Bohn HF, Speck T. 2012 Plant surfaces with cuticular folds are slippery for beetles. *J. R. Soc. Interface* **9**, 127–135. (doi:10.1098/rsif.2011.0202)
 57. Bergmann PJ, Russell AP. 2003 Lamella and scansor numbers in *Thecadactylus rapicauda* (Gekkonidae): patterns revealed through correlational analysis and implications for systematic and functional studies. *Amphib.-Reptil.* **24**, 379–385. (doi:10.1163/156853803322440826)
 58. Jusufi A, Goldman DI, Revzen S, Full RJ. 2008 Active tails enhance arboreal acrobatics in geckos. *Proc. Natl Acad. Sci. USA* **105**, 4215–4219. (doi:10.1073/pnas.0711944105)
 59. Jusufi A, Kawano DT, Libby T, Full RJ. 2010 Righting and turning in mid-air using appendage inertia: reptile tails, analytical models and bio-inspired robots. *Bioinspir. Biomim.* **5**, 045001. (doi:10.1088/1748-3182/5/4/045001)
 60. Jafari F, Ross SD, Vlachos P, Socha JJ. 2014 A theoretical analysis of pitch stability during gliding in flying snakes. *Bioinspir. Biomim.* **9**, 025014. (doi:10.1088/1748-3182/9/2/025014)
 61. Puthoff JB, Holbrook M, Wilkinson MJ, Jin K, Pesika NS, Autumn K. 2013 Dynamic friction in natural and synthetic gecko setal arrays. *Soft Matter* **9**, 4855–4863. (doi:10.1039/c3sm50267h)