Sticking like sticky tape: tree frogs use friction forces to enhance attachment on overhanging surfaces

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To live and clamber about in an arboreal habitat, tree frogs have evolved adhesive pads on their toes. In addition, they often have long and slender legs to facilitate not only long jumps, but also to bridge gaps between leaves when climbing. Both adhesive pads and long limbs are used in conjunction, as we will show in this study. Previous research has shown that tree frogs change from a crouched posture (where the limbs are close to the body) to a sprawled posture with extended limbs when clinging on to steeper inclines such as vertical or overhanging slopes. We investigated this change in posture in White’s tree frogs (Litoria caerulea) by challenging the frogs to cling onto a tiltable platform. The platform consisted of an array of 24 three-dimensional force transducers, which allowed us to measure the ground reaction forces of the frogs during a tilt. Starting from a crouched resting position, the normal forces on the forelimbs changed sign and became increasingly negative with increasing slope angle of the platform. At about 106° ± 12°, tilt of the platform the frogs reacted by extending one or two of their limbs outwards. At a steeper angle (131° ± 11°), the frogs spread out all their limbs sideways, with the hindlimbs stretched out to their maximum reach. Although the extension was strongest in the lateral direction, limbs were significantly extended in the fore–aft direction as well. With the extension of the limbs, the lateral forces increased relative to the normal forces. The large contribution of the in-plane forces helped to keep the angle between the force vector and the platform small. The Kendall theory for the peeling of adhesive tape predicts that smaller peel angles lead to higher attachment forces. We compare our data with the predictions of the Kendall model and discuss possible implications of the sliding of the pads on the surface. The forces were indeed much larger for smaller angles and thus can be explained by peeling theory.

1. Introduction

To live in an arboreal habitat, many animals have evolved not only different behavioural strategies but also a variety of attachment organs for climbing. These structures range from hands or feet that can grip around twigs and branches where soft skin can enhance friction to rigid claws that interlock with surface asperities. At the other end of the spectrum are highly specialized pads that have evolved to adhere to relatively smooth substrates, on which gripping limbs and claws would fail.

Despite the great variety of animals that have adhesive pads on their feet, the basic design of the pads can be divided into just two categories: pads can have either a more or less continuous adhesive surface (‘smooth’ pads) or exhibit fine hairs with individual contact points (‘hairy’ pads). Smooth pads always adhere by secreting an adhesive fluid (‘wet’ adhesion), whereas hairy pads can...
work either with or without a fluid. ‘Dry’ adhesion is thought to be present in spiders and geckos [1], but recent studies have also revealed tiny volumes of secretions in these groups [2,3]. The outer layer of smooth pads consists of folds and sub-structures which for tree frogs and some insects is broken up into hexagonally shaped cells partially separated by channels [4–7]. These channels allow for rapid spreading of an adhesive fluid across the pad [8] and for faster drainage of excess fluid [9,10].

Although the basic attachment mechanisms of animal adhesive pads are well understood, the mechanisms behind the control of adhesion, i.e. the quick transition from firm attachment to efficient detachment remains largely unknown. Part of the control seems to be established through the directionality of the adhesive structure itself and accordingly, the direction of the forces acting on the pad. Anisotropic structures on the adhesive pad (i.e. ridges or protrusions) can interlock with surface asperities in one direction, but slip over them in the opposing direction, thus resulting in very different forces, depending on the direction of movement [11]. In hairy pads, the individual hairs have angled tips that provide a default non-sticky state. A short pull on the pad aligns the tips with the substrate for attachment, whereas a release of the pull or a push detaches the hairs [12–16]. In smooth pads, internal fibres running at an angle towards the surface of the outer layer of the pads [17,18] may act in a similar way. Evidence for such directionality has been found across a wide variety of taxa, including flies [19], bush crickets [20], ants [21,22], cockroaches [23], tree frogs [24], spiders [25,26] and geckos [12,27].

Even without any obvious directionality of the adhesive structure itself, the angle between the detachment force vector and the surface can have a strong influence on whether the pad adheres well or detaches easily. Such directionality is known from the peeling behaviour of thin films; for instance, a strip of adhesive tape peeled off from a surface. When the angle to the surface is very small, it is very difficult to detach the strip; however, pulling at a larger angle results in easy detachment. For low peel angles, the force is spread over a large area of the attached strip, so peeling is resisted. With a larger peeling angle, the force is concentrated on a smaller region around the peeling edge that leads to easier removal of the adhesive tape [28]. Transferring this idea of peeling to adhesive pads in animals, it means that if the animal can maintain a shallow angle of the pulling forces, then the pads remain firmly attached to the substrate, thereby preventing peeling. On the other hand, when a quick and easy detachment is required, an increase in the peeling angle (e.g. by increasing the angle of the leg to the substrate) would facilitate detachment by allowing peeling. Peeling theory was established originally by Rivlin [29] and was later modified by Kaelble [30] and Kendall [31]. There is evidence to suggest that many animals use peeling as a mode of detachment; these include ants and bees [21], flies [32], cockroaches [23], geckos [12,33] and frogs [24].

Maintaining a shallow angle of the pulling force vector to the substrate can be achieved by adopting a sprawled posture, placing the adhesive pads as far away from the body as possible. By stretching out and pulling inwards, opposing feet can generate large in-plane forces. Ground reaction force measurements on individual legs in running cockroaches [34] and geckos [35,36] have confirmed this. These large inward forces help to ensure that the angle of the pulling force vector towards the substrate remains small. However, some animals have multi-segmented legs that allow for angle reductions of the last, pad-bearing segment because of the available degrees of freedom in the legs. Consequently, it should not be necessary for them to splay out their feet. Nevertheless, this splaying behaviour has been reported for ants [37], locusts [38] and tree frogs [39,40]. This behaviour not only reduces the torques on each leg joint but also reduces the tendency of a climbing animal to pitch backwards as this splaying behaviour increases the distance between the contact points of fore- and hindlimbs.

Here, we investigate the ground reaction forces generated by White’s tree frogs (Litoria caerulea) when challenged to cling onto substrates of different inclines. Although previous research has shown the frog’s obvious splaying reaction [39], the ground reaction forces involved in this behaviour are still unknown. We asked the following questions: is the splaying behaviour triggered by steeper slopes of the substrates? What are the ground reaction forces involved in the splaying behaviour?

2. Material and methods

2.1. Study animals

Ten individual White’s tree frogs (L. caerulea) obtained from a local supplier were housed in simple plastic containers and fed with water and crickets ad libitum. The boxes were at ambient local temperature that varied between 20°C and 26°C. Prior to the experiments, the frogs were carefully rinsed with tap water in order to remove any debris and shed skin that could alter their adhesive performance, and then blotted dry with tissue paper to remove excess water. The frogs were then weighed to the nearest gram on a digital balance (35 ± 3 g) and their snout-to-vent length (SV-length) was measured to the nearest millimetre using a mechanical calliper (76 ± 3 mm).

2.2. Force measurement set-up

In order to measure ground reaction forces in all three directions (x-, y- and z-directions), a force measurement array (FMA) was used. This array consisted of 24 separate, custom-built three-dimensional force transducers, arranged in three rows and eight columns with each sensor having a plastic square on top (30 × 30 mm with 1 mm clearance gap), resulting in a tiled strip of ca 250 × 90 mm ‘active’ measurement area (for details see Dai et al. [39] and figure 1). The tiles were coated with a white paint, giving a slightly hydrophobic and micro-rough surface (average roughness Ra = 9.7 ± 9.1 μm, measured on 18 squares). We defined the x-axis as the left–right axis in the plane of the platform and parallel to the axis of rotation. The forces along the z-axis were termed here as lateral as the frog was usually positioned in such a way on the platform that its left–right orientation was aligned with this axis. The y-axis was defined perpendicular to the z-axis and was also in the plane of the platform. The forces along the y-axis were termed fore–aft forces. Together, they are termed in-plane forces. When the platform was in a vertical position, the y-axis coincided with the direction of the gravity vector. The z-axis was defined perpendicular to the plane of the platform and termed as normal forces, pushing into the platform (load) or pulling out of the platform (adhesion).

Each of the force transducer units functioned as simple cantilever beams in a metal T-shaped arrangement [35]. Forces were measured from the deflection of the cantilever beams by foil strain gauges glued to the beams. The resolution for each direction was similar (ca 1–2 mN); the fundamental resonance frequency for the x- and y-axis was lower (ca 125–138 Hz) than...
for the z-axis (ca 350 Hz). The data were logged, using a data acquisition platform (PXIe-8130, National Instruments, USA) at a sampling rate of 500 Hz.

The FMA and data acquisition platform were mounted on a horizontal axle within a metal frame in order to rotate the set-up (figure 1a). The rotation was performed manually with a speed of \(4 \pm 2\) \(\text{s}^{-1}\). The rotation of the platform was measured by the turning of a potentiometer mounted onto the axle. The change of resistance was displayed on a multimeter (Föhrch UT52, Germany) and filmed together with the behaviour of the frog using a digital video camera. From a simple calibration curve, we were able to calculate back the tilt angle of the platform from the displayed resistor values of the potentiometer.

2.3. Video recordings

A digital video camera (Olympus i-Speed 3, 1280 \times 1024 pixels, 50 Hz) was synchronized with the force recordings. As the camera could be rotated together with the force platform, the perpendicular angle of the camera view onto the platform (dorsal view of the frog) remained the same, regardless of the tilting angle of the platform. A mirror was mounted at an angle next to the force transducer array, giving a frontal view of the frog. Both the video recordings and data acquisition were initiated by a TTL-pulse using a manual switch.

2.4. Procedure of a measurement trial

After a frog was placed on the platform, we began to rotate the platform starting at a tilt angle of about 80°. We started at this angle as the frogs showed no splaying behaviour between 0° and 80°. The frogs were facing uphill, so that the longitudinal axis of the frog was roughly aligned with the y-axis of the platform (deviating by an average of 9° from this axis; \(n = 67\)). The platform was slowly rotated until the frog completely detached from the platform. The frogs were tested 10 times each in a randomized order and allowed to rest for at least 3 min between trials where the platform was wiped clean using a cloth dampened with water. This resulted in a total of 100 recordings of which only 67 were suitable for further analysis. Recordings were discarded when the frogs climbed outside the FMA area, jumped off or detached before they showed any splaying behaviour of the limbs as the latter was interpreted as a sign of fatigue.

2.5. Analysis of force and video recordings

The force and video recordings were both analysed using custom-built MATLAB scripts (MathWorks Corporation, USA). The positions of the limbs were digitized from individual video frames (figure 2, right-hand image). For each limb, the tip of each toe and the ankle/wrist was manually digitized in order to extract the extension of the limbs and the number of pads that were in contact with the platform. Furthermore, the tip of the snout and the position of the vent of the frog were digitized to extract the size (SV-length), posture and position of the animal’s body on the sensors (figure 2). Sometimes, other body parts, such as the frog’s chin or belly, touched the sensors as well. Whenever a sensor was shared by multiple points of contact (limbs or other body parts), we assigned equal parts of the resultant force to all contributing parts. For cases where different parts of the same limb were touching multiple sensors, a resultant force vector for each direction was calculated. To compare our data with the predictions of the peeling theory, we vectorially summed up the x-, y- and z-vectors to one single resultant force vector for each limb.

2.6. Statistics

A statistical analysis was performed, using the statistical toolbox in MATLAB. The qualitative behaviour of the frogs was separated into three different categories corresponding to different tilting angles of the platform. The Mann–Whitney U-test was used to test between two categories. When the same category was tested more than once, the level of significance was corrected by multiplying the \(p\)-value by the number of repetitions (Bonferroni correction). Results were plotted, using ‘box-whisker’-plots. The median and the 25 per cent and 75 per cent quartiles (‘box’) are indicated. The plotted ‘whiskers’ extend to the most extreme data values that are not outliers. Points are drawn as outliers if they are larger than \(q_3 + w(q_3 - q_1)\) or smaller than \(q_1 - w(q_3 - q_1)\), with \(w = 1.5\) being the whisker length and \(q_1\) and \(q_3\) the 25th and 75th percentiles, respectively. Values given in the text are averages with the standard deviations, unless otherwise stated.

3. Results

3.1. Behaviour of the frogs on different inclines

After a frog was placed on the force platform, the platform was slowly rotated from an initial starting point (slope of about 80°) through a vertical orientation (90°) and then to an upside-down orientation (about 160°). During this rotation, the frog tended to change its posture in a characteristic way (figure 2 and the electronic supplementary material, video S1). Starting from an initial resting position where the limbs were tucked in very close to the body (denoted here as ‘rest’ and digitized at an average platform angle of 80° ± 9°), the frog quickly splayed out one or more limbs...
when the platform was rotated further (106° ± 12°, denoted here as ‘1st spread’). After further rotation, the frogs changed their posture again, with limbs being splayed out much further, sometimes to their maximum extension. This was denoted here as ‘2nd spread’ and was triggered at a platform angle of 131° ± 11°. We often found gradual changes between these two categories, where legs were extended one after the other. The platform was then rotated until the frog completely dislodged from the platform. Very shortly before complete detachment, where one or two limbs were still in contact with the platform, we digitized the remaining pads in contact and put them into the category ‘detachment’. These points were used for the comparisons with the peeling theory (see §3.4 and §§3 and 4).

3.2. Spreading of the limbs
We used the three different postures (‘rest’, ‘1st spread’ and ‘2nd spread’) to extract limb positions. Figure 3 shows the perpendicular distance of the limbs from the longitudinal axis of the frog. During the course of the rotation of the platform, the lateral spread for both the fore- and the hindlimbs increased significantly (details of the statistical results are shown in table 1). The biggest change happened for the hindlimbs when going from the 1st spread to the 2nd spread; often, the feet of the hindlimbs extended as far as the body length of the frogs (figure 3c).

Additionally, the fore–aft distance of each limb from the body centre (snout–vent midpoint) increased. This change was more pronounced in the forelimbs, which reached further forward when the platform passed a vertical position (positive values in figure 3b). The hindlimbs stretched further back, as the slope became steeper (negative values in figure 3b; details of the statistical results are shown in table 1). When the platform reached an overhanging tilt (greater than 130°), we noticed that in a few cases the frogs positioned one hindlimb at the same level as the COM (around the zero position for the 2nd spread in figure 3b). At this tilt level, the pitching moment is reduced, and frogs use their hindlimbs to share the pull-off force.

3.3. Ground reaction forces
Figure 4 illustrates the changes in the lateral, fore–aft and normal forces for the three postures. Each data point represents the relative x-, y- or z-force (force per body weight) generated by a single limb at the appropriate point in time.

The lateral forces (x-forces) for the resting posture and the 1st spread were small and scatter with their average around zero, thus showing no preferred direction. When the frogs were challenged to cling on to an overhanging surface (2nd spread or x2 in figure 4), the frogs used opposing feet to pull inwards to support the mass of the body, visible in a clear directionality of the forces. Also, the magnitude of the lateral forces increased significantly in this situation (details of the statistical results are listed in table 2). Although the lateral forces do not directly contribute to the adhesion of the frog, they play an important role in determining the peeling angle of the limbs (discussed below).

The fore–aft forces (y-direction) did not change much between the three postures. This indicated that the frog was not using its legs to pull against one another as they did in the lateral direction. Instead, the y- and z-forces followed more or less the behaviour predicted of an object resting on an inclined ramp. For such an object, the y- (and z-components) can be calculated from simple trigonometry, where the y-component follows the sine of the platform angle. Consequently, sin 80° and sin 106° are fairly similar in magnitude for the resting posture and the 1st spread, respectively. Although the load on both fore- and hindlimbs did not differ significantly between the resting posture and the 1st spread, the forelimbs took more of the weight of the frog in the 2nd spread, visible in the greater y2 forces for the forelimbs compared with the hindlimbs (figure 4; details of the statistical results are listed in table 2).

The normal forces also mainly followed the predicted forces and changed in their direction when changing from an incline below 90° to an overhanging position, as expected. In the resting position, all limbs were pressing into the surface (positive z-values). When the surface was in a slight overhanging orientation (106°), the forelimbs were pulling outwards, while the hind legs counterbalanced the pitching moment by pressing inwards. On the overhanging platform (2nd spread), all limbs were in a pulling direction (negative z2 values). Summing up all force vectors produced approximately vertical force vectors with magnitudes close to the body weights of the frogs (not shown here). However, we did find in many cases (54% of the trials) that the frogs placed one or more toes outside the force measurement area and thus reduced the total force recorded on the platform. In order to keep as many data points as possible, we did not exclude cases where only one limb was placed outside the measurement area but did exclude cases where more than one limb was.

3.4. Comparison with peeling theory
We modelled the frog’s adhesive pads as pieces of adhesive tape. We used the three force components of each leg
measurement to calculate the magnitude of the resultant force vector and its angle to the plane of the platform where all angles were calculated to fall between 0° and 90°.

The magnitude is equivalent to the pulling force acting on the adhesive tape. Figure 5 shows the magnitude of the resultant force vectors (the vectorial sum of all three force components) over the reconstructed angle for each limb for the three postures and the 'detachment' category. In this analysis, the only data points considered were those where the limbs produced negative normal forces. When the frogs were in their resting position, only the forelimbs occasionally pulled on the force transducer, preventing a pitching moment of the body. The majority of the data points are thus represented by the 1st and 2nd spreading behaviour (green and red data points, respectively), and show a wide range of peeling angles. Despite the scatter, the upper limit of the distribution follows qualitatively the prediction made by the peeling theory; for small peeling angles, the forces were high, whereas those for higher peeling angles were low.

4. Discussion

In this study, we have shown that tree frogs change their posture from a resting posture with flexed limbs to a sprawled posture when trying to cling on to an overhanging surface. By splaying out their limbs and using opposing legs, large

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**Table 1.** Statistical results from pairwise comparisons between postures for the forelimbs (FLs) and hindlimbs (HLs), using the Mann–Whitney test.

<table>
<thead>
<tr>
<th>limb</th>
<th>comparison</th>
<th>z</th>
<th>R</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>lateral extension</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FL</td>
<td>'rest' versus '1st spread'</td>
<td>4.05</td>
<td>4420</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>FL</td>
<td>'1st spread' versus '2nd spread'</td>
<td>2.62</td>
<td>2682</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>HL</td>
<td>'rest' versus '1st spread'</td>
<td>2.95</td>
<td>4242</td>
<td>&lt;0.01</td>
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<tr>
<td>HL</td>
<td>'1st spread' versus '2nd spread'</td>
<td>8.13</td>
<td>3509</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>fore–aft extension</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FL</td>
<td>'rest' versus '1st spread'</td>
<td>−2.42</td>
<td>3154</td>
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</tr>
<tr>
<td>FL</td>
<td>'1st spread' versus '2nd spread'</td>
<td>5.31</td>
<td>3086</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>HL</td>
<td>'rest' versus '1st spread'</td>
<td>−3.59</td>
<td>2948</td>
<td>&lt;0.001</td>
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<tr>
<td>HL</td>
<td>'1st spread' versus '2nd spread'</td>
<td>0.59</td>
<td>2378</td>
<td>&gt;0.05</td>
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in-plane shear forces are generated on their pads that are directed inwards. This behaviour uses frictional adhesion. By keeping the angle of their legs (or at least the resultant force vector acting on the pads) shallow with respect to the substrate, they are able to prevent their pads from peeling off.

This behaviour has been reported before, not only in tree frogs [39,40] but also in locusts [38] when they were challenged to cling on to sloping substrates. However, as the latter study investigated adhesion on rough surfaces, the locusts were splaying out their legs to reduce the approach angle of the claws when interlocking with surface asperities. Ground reaction force measurements on climbing geckos [35,36] and cockroaches [34] have also shown that in-plane forces play an important role. They are thought to promote claw and pad attachment in these fast-running animals.

In order to explain the large lateral forces we measured in this present study, we used the predictions from peeling theory. By reconstructing the angle of the resultant force vectors from the three force components ($x$, $y$, and $z$), we were able to plot a graph of force magnitude $F$ against angle $a$ with respect to the substrate (figure 5). In §4.1, we discuss the widely used Kendall peeling model [31].

### 4.1. Kendall peeling model

The Kendall model was initially established by Rivlin [29] and later adapted by Kendall [31,41]. It consists of a surface energy term owing to the creation of new surfaces, a potential energy term owing to the movement of the applied force and an elastic term owing to the extension of the tape. An energy balance yields an equation with two components, a pure extension component that does not change with the peel angle and a no extension component that does.

#### 4.1.1. No extension component

The Kendall peeling model without the extension component considers a homogeneous tape, infinitely flexible in bending but infinitely stiff in tension, with a constant width $b$ (see the inset of figure 5) and constant adhesive energy $\Delta y$ (the

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Figure 4. Relative forces (force per body weight) generated by individual limbs in the $x$-, $y$- and $z$-directions for the resting posture, 1st and 2nd spread (indexed here with 0, 1 and 2, respectively). The direction of the forces is indicated by the diagram in the centre.

Table 2. Statistical results from pairwise comparisons between postures for the left front (LF), right front (RF), left hind (LH) and right hindlimb (RH) using the Mann–Whitney test.

<table>
<thead>
<tr>
<th>limb</th>
<th>comparison</th>
<th>$z$</th>
<th>$R$</th>
<th>$p$-value</th>
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<td>RF ‘1st spread’ versus ‘2nd spread’</td>
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<td>2344</td>
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<td>LH ‘rest’ versus ‘1st spread’</td>
<td>4.28</td>
<td>3566</td>
<td>&lt;0.001</td>
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<td>RH ‘1st spread’ versus ‘2nd spread’</td>
<td>-4.15</td>
<td>2106</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>fore–aft forces</td>
<td>FL versus ‘rest’ versus ‘1st spread’</td>
<td>-7.0</td>
<td>1150</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>HL ‘1st spread’ versus ‘2nd spread’</td>
<td>-7.0</td>
<td>1150</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
fracture energy or ‘stickiness’ of the tape). The latter is correlated with the surface energy of the newly created surface during crack propagation, but for most tapes the fracture energy is strongly dominated by viscous dissipation. Indeed, as Kendall [31] points out, $\Delta y$ is mostly larger than the work of adhesion and varies with the speed of pull-off. Kendall estimated $\Delta y$ from a peel test at an angle of $90^\circ$ to the surface, because the elastic term was negligible at this angle. For a given value of $\Delta y$, the peeling force required to separate the tape from the substrate at a given fracture energy then only depends on the peeling angle $\alpha$:

$$F_{\text{peel}} = \frac{b\Delta y}{1 - \cos \alpha}. \quad (4.1)$$

Often, the peeling force is normalized for the width $b$ of the tape, giving the peel strength ($P = F/b$):

$$P = \frac{\Delta y}{1 - \cos \alpha}. \quad (4.2)$$

Estimates of the work of adhesion can be obtained from indentation experiments. Such experiments, carried out on *L. caerulea* by Barnes *et al.* [42], provide two estimates for the work of adhesion. The first of these, 0.1 Nm$^{-1}$, was derived from the unload part of the force–distance curve using Johnson, Kendall and Roberts (JKR) contact theory [43]. The second estimate 0.4 Nm$^{-1}$, also based on JKR theory, was derived from the pull-off force $F_{\text{po}}$ using the following equation:

$$F_{\text{po}} = \frac{3}{2} \pi WR, \quad (4.3)$$

where $W$ is the work of adhesion, and $R$ is the composite or effective radius of contact between two bodies. This second, higher estimate of the work of adhesion seemed to us more appropriate for our experimental situation as it is calculated from a pull-off force, and was inserted into equation (4.1) to produce the solid black peeling curve on figure 6, a much better fit to the data.

Another possible way of looking at our own data is to fit a ‘Kendall curve’, using the least-squares method based on the data points in the ‘detachment’ category, because the frog was in the process of falling from the platform at this point. When values for small angles (less than $10^\circ$) are excluded, the best fit to these ‘detachment’ values (not illustrated) is based on a fracture energy of 0.85 Nm$^{-1}$, which is lower than the fracture energy calculated from the peel test experiments.

Because the fracture energy would be predicted to be larger than the work of adhesion, an estimate of the fracture energy of *Litoria* toe pads is obviously desirable. Such an estimate has not been published, but can be calculated from the peeling experiment of Barnes *et al.* [39]. Following the methodology of Kendall [31], the fracture energy can be calculated from the peel strength of a $90^\circ$ pull-off. The resulting value of 1.6 Nm$^{-1}$, which, inserted into equation (4.1), produces the solid red curve in figure 6, a much better fit to the data.

The fracture energy of an adhesive tape itself is influenced, not only by how well the adhesive bonds to the substrate, but also by its viscoelastic properties as energy can dissipate when the soft tape material is stretched during separation from the surface. Unlike the work of adhesion, the fracture energy can be increased due to several parameters, including the separation speed of the pad from the surface that increases energy dissipation for viscoelastic
materials [44–47] and possible crack arresting properties of the pad structure. It is well known that crack propagation on patterned adhesive films can lead to significantly higher energy dissipation compared with the peeling of smooth films [48–51]. Experiments on elastomer films with defined patterns of incisions yielded fracture energies that were more than 20 times higher than those measured on unstructured films of the same material [48]. The structured topology of the tree frog’s toe pad consists of an array of hexagonal cells, separated by channels [4,5,52]. As each of the cells makes intimate contact with the substrate [53], one can expect that this microstructure will continuously enforce crack propagation arrest and re-initiation during toe pad peeling [48,54]. This mechanism of dissipative increase in fracture energy can be seen as a macroscopic analogy to the Lake–Thomas effect [55] occurring for the fracture of rubbery polymer networks where the fracture energy arises from the rupture of single polymer chains during crack propagation.

These arguments explain why the value obtained for the work of adhesion (0.1 or 0.4 N m\(^{-1}\)) is much lower than the value for fracture energy calculated from the peel test (1.6 N m\(^{-1}\)). The latter, by contrast, is clearly within the range predicted from the data, being greater than predicted from the ‘detachment’ data (0.85 N m\(^{-1}\)), but close to the Kendall curve of figure 5 that was fitted by eye to the highest forces produced by the frog’s feet at different attachment angles.

### 4.1.2. Pure extension component

As shown in figure 6, the curve for the inextensible tape becomes physically unrealistic, reaching infinitely high forces for angles converging to zero. The fact that the forces quickly become excessively large at small angles means that under realistic conditions the tape will in fact stretch, depending on the thickness \(h\) of the tape material and its Young’s modulus \(E\). The following analysis accounts for a stretching of the tape by incorporating both parameters into the Kendall model [31], in which peel strength reaches a maximum value of

\[
\frac{p^2}{2Eh} + \frac{P(1 - \cos \alpha)}{\Delta \gamma} + \Delta \gamma = 0.
\]  

With an estimated thickness \(h\) of approximately 1 mm and a Young’s modulus \(E\) of 25 kPa for the adhesive toe pad (indentation experiments of Barnes et al. [42]), the predicted force values (black dashed line in figure 6) give a reasonable fit for large peeling angles (greater than 45°) but seriously underestimate the larger force values at small peeling angles by reaching a maximum at 8.9 N m\(^{-1}\).

As the peel strength depends on the stiffness of the material (i.e. a tape with a stiffer backing will be more difficult to detach as it bends less), it could be that the pad’s real stiffness is higher than our estimate. Indeed, our estimate, based on microindentation, does not account for either the presence of bone or cartilage that extends almost to the end of the digits or the fact that the outer cell layer is relatively stiff because it is highly keratinized. This keratinization gives a Young’s modulus in the range 5–15 MPa, as measured by nanoindentation using an atomic force microscope [56]. Indeed, a much better fit to our force data is produced by using an elastic modulus of \(E = 500\) kPa (see dashed red line in figure 6). Such a value lies between the values obtained from micro- and nanoindentation of the pad. Moreover, it could also be that animals have control over the pad’s stiffness. It was shown by Dirks et al. [17] and Gorb & Scherge [18] that internal fibres found in the adhesive pads of many animals (including tree frogs [57,58]) change from an initial perpendicular orientation, to an angled orientation when subjected to shear or load. Such a change in geometry of the internal fibres could cause stiffening of the pad [17], providing an elegant way to control adhesive force, but further experimental data are needed to test this.

### 4.2. Slippage considerations

Decreasing the angle of the leg towards the surface in order to prevent peeling increases the chance of slipping, as the feet are subjected to a greater shear force. We often observed that the extended legs of the frogs slid slowly inward when the frog was in an inverted position. As a consequence, the leg angle increases and with it, the risk of peeling. In order to compensate for that, the frogs tended to re-position their legs outwards as soon their feet slid too far inwards (visible in video S1 as electronic supplementary material). Pads will only resist sliding if

\[
F_{\text{peel}} \cos \alpha < \pi tL,
\]

or

\[
P < \frac{tL}{\cos \alpha},
\]

where \(t\) is the pad’s static shear stress, and \(L\) is the proximal–distal length of the contact zone (defined here as \(L = 0.75b\)).

The limits of sliding (equation (4.6)) and peeling (equation (4.2)) are plotted together in figure 7, using the estimates of \(\tau = 1\) kPa [53], \(\Delta \gamma = 1.6\) N m\(^{-1}\) and \(L = 3.5\) mm. The limit curves divide the area of the graph into four ‘sections’ (labelled A–D) representing combinations of pulling force and leg angle, which illustrate different conditions for the pads. As in the peeling curve, any data point above the sliding limit curve would result in slipping of the pads. Section (A) represents combinations of force and angle at which the pads would slide but not peel. The area below the sliding curve but above the peeling curve (area (B) in figure 7) represents situations where the pads would only peel but not slide. The area below both curves (area (C)) delineates an area where the pads would withstand both peeling and sliding, with a critical angle \(\alpha_c\), marking the maximum force the pads can withstand without peeling or sliding (from equations (4.2) and (4.6)). \(\alpha_c\) can be calculated as \(\arccos(\tau l/\Delta \gamma + tL)\), giving a value of about 46° for the conditions assumed for figure 7.

Most of the data points fall into area (A), where the frogs’ toe pads are sliding but resist peeling. Thus, frogs seemingly tolerate sliding of their feet, repositioning them if necessary, i.e. when the leg angle becomes too large following sliding towards the body (see the electronic supplementary material, video S1). We suspect that the frogs may use ‘dynamic’ adhesion, i.e. they maintain a low peeling angle in order to prevent their pads from peeling even though this results in sliding. The maximum force achieved in the ‘safe zone’ (which occurs at the critical angle; figure 7) is about 42 g. Figure 7 is based on the peel strength at the critical angle (5 N m\(^{-1}\)) in a toe pad of 4.6 mm width. This gives a force of 0.023 N (5 x 4.6/1000). Because a frog has 18 toes, the total force equals 0.41 N (18 x 0.023) or 41.8 g. This is just enough to hold the animal upside-down (average weight of the frogs \(\approx 35\) g). However, to move actively on overhangs, a larger safety factor is necessary. This can be achieved...
only by reducing the peel angle (by leg extension), which consequently led to slipping.

Slippage was also found for the peeling of polymers [51] and discussed as a possible mechanism for the dissipation of energy owing to frictional work at the interface [47,59]. It would be interesting to test the frogs on surfaces of different roughness, in order to see whether reduced slipping would allow the legs to reach a lower leg angle and thereby stronger adhesion. Such data would also allow a comparison with existing models for the effects of energy dissipation on adhesion [47,51].

5. Conclusions
This study has shown that tree frogs use friction forces in order to generate large adhesive forces which might help prevent the peeling of their pads. The frogs in our experiments showed a very obvious spreading of their limbs in order to redirect the resultant force vector. However, in other animals, even a slight, less noticeable pull of the legs towards the body might achieve a similar result. Our findings are also in agreement with force measurements on individual toe pads of restrained tree frogs by Barnes et al. [39]. When the pull-off direction from an individual toe pad was performed in a perpendicular direction, the forces per area were too small to compensate for the body weight of the frog. By contrast, when smaller pull-off angles were chosen, adhesive forces per area yielded high enough values.

The predictions of the Kendall model with the extension component seem to underestimate the forces found in our experiments as we observed a fairly steep relationship between the peel forces and the peel angle. However, it should be noted that by using the elastic modulus from indentation experiments we probably underestimate the stretching stiffness in the longitudinal direction of the pad. Possible other factors of higher work of adhesion arising from viscoelastic effects and crack arresting properties of the toe pads might not be enough to explain the steep relationship. However, an increasing stiffness of the pad can, as the Kendall model without the extension component, which considers an unstretchable material does result in a steeper relationship between peel strength and peel angle.

In our experiments, we also observed that adhesive pads tend to slip on smooth surfaces, leading to an increase in the peeling angle. In order to compensate for this, the frogs showed a repetitive repositioning of their feet. The combination of peeling and slipping has barely been addressed in the peeling behaviour of thin films, as slipping is mostly negligible. By contrast, slipping can be a problem for the adhesive pads of animals, especially when they adhere by using a secreted adhesive fluid. Therefore, animals provide very interesting systems through which to study the trade-offs between peeling and sliding.

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Figure 7. The predictions for peeling and sliding intersect and create four areas (A – D) where the pads slide without peeling (A), peel without sliding (B), resist both (C) or slide and peel at the same time (D). The maximum of area (C) represents a critical angle \( \alpha_c \) where the maximum force can be held in a stable position. Blue markers denote the ‘rest’ position, green and red the 1st spread and 2nd spread, respectively; black markers show points just before detachment.


