

RESEARCH ARTICLE

The biomechanics of tree frogs climbing curved surfaces: a gripping problem

Iain D. C. Hill¹, Benzhenq Dong², W. Jon P. Barnes^{1,*}, Aihong Ji² and Thomas Endlein³

ABSTRACT

The adhesive mechanisms of climbing animals have become an important research topic because of their biomimetic implications. We examined the climbing abilities of hylid tree frogs on vertical cylinders of differing diameter and surface roughness to investigate the relative roles of adduction forces (gripping) and adhesion. Tree frogs adhere using their toe pads and subarticular tubercles, the adhesive joint being fluid-filled. Our hypothesis was that on an effectively flat surface (adduction forces on the largest 120 mm diameter cylinder were insufficient to allow climbing), adhesion would effectively be the only means by which tree frogs could climb, but on the 44 and 13 mm diameter cylinders, frogs could additionally utilise adduction forces by gripping the cylinder either with their limbs outstretched or by grasping around the cylinder with their digits, respectively. The frogs' performance would also depend on whether the surfaces were smooth (easy to adhere to) or rough (relatively non-adhesive). Our findings showed that climbing performance was highest on the narrowest smooth cylinder. Frogs climbed faster, frequently using a 'walking trot' gait rather than the 'lateral sequence walk' used on other cylinders. Using an optical technique to visualise substrate contact during climbing on smooth surfaces, we also observed an increasing engagement of the subarticular tubercles on the narrower cylinders. Finally, on the rough substrate, frogs were unable to climb the largest diameter cylinder, but were able to climb the narrowest one slowly. These results support our hypotheses and have relevance for the design of climbing robots.

KEY WORDS: Adhesion, Adduction, *Litoria caerulea*, *Osteopilus septentrionalis*

INTRODUCTION

The ability to climb is common in animals, being utilised by amphibians, reptiles, birds and mammals, as well as many arthropods. It offers many advantages, including access to safety from ground-dwelling predators, faster travel in dense vegetation regions and access to food (including prey) (Hildebrand and Goslow, 2001). Arboreal animals possess a wide range of morphological adaptations to assist in the behaviour of climbing. These may include long arms for reaching and pulling, and hind legs adapted for jumping from branch to branch. Additionally, they need some way of remaining attached to substrates they climb. Claws do

this rather well, either by interlocking with surface irregularities or by digging into the surface if it is soft enough. However, several animal groups have developed mechanisms of adhesion (e.g. geckos, tree frogs and many arthropods) for the same purpose (though geckos and insects may possess claws as well). These adhesive mechanisms may be used alone, or in conjunction with the production of adduction forces, which, aided by friction, are used to grip structures such as stems and branches (Cartmill, 1985).

The adhesive mechanisms of climbing animals have been widely studied in recent years, especially those of geckos, insects and tree frogs. This is to a large extent due to their relevance to biomimetics. Firstly, as discussed by Barnes (2007), this is because they have remarkable powers of adhesion to a wide variety of surfaces. Even a large gecko can run across a ceiling (Autumn and Peattie, 2002), and a tree frog jumping from branch to branch does not fall so long as a single toe pad makes good contact with the tree (Bijma et al., 2016). Additionally, ants can carry over 100 times their own weight while walking upside-down (Federle and Endlein, 2004). Secondly, the adhesive mechanisms are reversible (geckos can walk at over 10 steps per second) and detachment is effortless (Autumn, 2007). Thirdly, animal adhesive pads can also have self-cleaning properties and thus do not get fouled (Crawford et al., 2012; Hansen and Autumn, 2005; Hu et al., 2012). It is also appropriate to add that, as gecko feet are non-adhesive in the default state because they have a very low contact fraction (<6.6% of surface), they do not stick to everything they touch (Autumn and Hansen, 2006). Such combinations of properties are not found in more traditional adhesives, but are now being developed in many laboratories, inspired by the natural world (Xia, 2016).

Turning specifically to frogs (Amphibia; Anura), there is extensive work on the biomechanics of frog jumping (e.g. Astley and Roberts, 2014; Astley et al., 2015), but much less on climbing, the speciality of tree frogs. However, two papers are of particular interest (Manzano et al., 2008; Herrel et al., 2013), as they provide strong evidence that the forelimbs of at least some tree frog species can generate gripping forces. These gripping forces are used both in the manipulation of food and in locomotion, particularly horizontal walking and climbing along narrow substrates. The species most adept at these behaviours are members of the Family Phyllomedusidae (Duellman et al., 2016), which are able to traverse rods down to a diameter of 1 mm. Appropriately, these frogs are known as monkey frogs, as they tend to move from place to place by climbing rather than jumping as do most other tree frogs. Manzano et al. (2008) have shown that they are able to employ both power and precision grips, as defined by Napier (1956). Roughly speaking, a power grip describes how one holds a hammer, while an example of a precision grip would be holding a pencil.

Tree frogs adhere by means of a wet adhesive joint, a low-viscosity fluid being secreted by the epithelium of the toe pads, located ventrally on each digit (Federle et al., 2006). The toe pad epithelium consists of squamous epithelial cells, surrounded by

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channels that serve to distribute the pad fluid over the surface of the pad (Green, 1979; Emerson and Diehl, 1980; Smith et al., 2006a). At the nanoscale, these epithelial cells are covered in a dense array of nanopillars (Scholz et al., 2009). The main adhesive force is thought to be capillarity, though a contribution from viscosity-dependent hydrodynamic forces is likely, but as yet unproven (Hanna and Barnes, 1991; Barnes et al., 2006; Persson, 2007; Butt et al., 2010; Drotlef et al., 2012; Endlein et al., 2013). The ability to generate high friction forces is probably more important than the ability to generate adhesive ones (Endlein et al., 2013), as frogs are normally active on surfaces with slopes varying between horizontal and 90 deg, though they can support themselves on overhanging surfaces, and small frogs can hang on when completely upside-down (Barnes et al., 2006; Smith et al., 2006b). Friction forces are higher than should be possible from a fluid joint (Federle et al., 2006), so it is likely that there is actual contact between pad and substrate. Indeed, the tips of the nanopillars appear, from interference reflection microscopy, to be making actual contact with the underlying surface (Federle et al., 2006). Subarticular tubercles, located more proximally on each digit, have a structure similar to that of the toe pads, but are smaller and anatomically less specialised; for example, the channels that separate the cells are both shallower and narrower (Green, 1979; Endlein et al., 2017).

Studies of adhesion have largely been carried out on flat surfaces, specifically because, on such surfaces, there is no possible contribution from adduction forces (Cartmill, 1985). However, the world of tree frogs seldom consists of flat, smooth surfaces, but rather curved ones such as branches and twigs, where, as discussed above, there is good evidence for gripping by adduction. This paper is aimed at bridging this gap, studying the relative roles of adhesion and gripping on surfaces varying in both curvature and roughness, the roughness being chosen to be a surface where the frogs generate minimal adhesive forces. We compared the climbing abilities of two species of hylid frog, *Litoria caerulea* and *Osteopilus septentrionalis*, on cylinders of different diameter, the largest effectively acting like a flat surface in relation to the size of the frogs. The intermediate cylinder was chosen so that it would be possible for frogs to generate adduction forces across the body, i.e. a 'bear hug', whereas the narrowest was such that toes would be able to wrap around the cylinder. Where climbing was observed, we measured the frogs' velocity as well as the gait used. Additionally, as the smooth surfaces were transparent, we used the technique of frustrated total internal reflection (FTIR) (Betts et al., 1980; Endlein et al., 2013; Eason et al., 2015) to observe the structures used in climbing the different cylinders, enabling us to observe when the sub-articular tubercles, located more proximally on each toe, were used in addition to the toe pads.

MATERIALS AND METHODS

Study animals

White's tree frogs [*Litoria caerulea* (White 1790)] and Cuban tree frogs [*Osteopilus septentrionalis* (A.M.C. Duméril & Bibron 1841)] were obtained from commercial suppliers (*L. caerulea* from Partick Aquatics and Reptiles, Glasgow, UK; *O. septentrionalis* from Coast to Coast Exotics, Darlington, UK). *Litoria caerulea* ($n=4$) had snout-vent lengths (SVLs) in the range of 48–60 mm, and SVLs of *O. septentrionalis* ($n=4$) ranged from 48 to 71 mm. All frogs were housed in custom-built vivaria (295×460×765 mm, width×length×height), illuminated with full spectrum terrarium lamps (Repti Glo 2.0 Compact, www.exo-terra.com) on a 12 h:12 h light:dark cycle. Ambient room temperature was controlled and coupled with heat mats to provide a temperature of

23±2°C; additionally, a Honeywell Ultrastar humidifier (Honeywell, Bracknell, Berkshire, UK) provided a relative humidity of approximately 70%. The frogs were provided with houseplants (*Ficus* sp.) to climb on and dishes of Cu-free fresh water. They were fed with house crickets (ca. three per week) dusted with Nutrobal, a calcium balancer and multivitamin supplement (Vetark Professional, Hants, UK). Prior to testing, each individual frog was identified and weighed, and the length of its forelimbs, hindlimbs, front span and SVL was measured to the nearest millimetre using a set of mechanical callipers (see Table S1 for the actual measurements). Before each session of experiments, the frogs involved were removed from the vivaria and checked for any debris or shedding skin that could affect their ability to climb and/or adhere. The use of individual frogs was randomised and, prior to testing, each frog was left in a separate labelled container for 30 min to allow it to be as calm as possible for data collection. All experiments were non-invasive and accorded with current laws on animal experimentation in the UK.

Experimental design

In order to determine the relative roles of adhesion and gripping forces (adduction forces with both frictional and normal components) in climbing, the frogs were video-recorded while climbing three vertical Perspex cylinders of different diameter (120, 44 and 13 mm), as shown in Fig. 1. Measurements made included gait and velocity of climbing. Comparisons were also drawn between climbing smooth surfaces (the Perspex surface of the cylinders) to which the frogs could adhere and a rough surface (the same cylinders covered with fine-grade sandpaper; Grade P320, which is covered in sand particles with an average diameter of 46.2 µm). Crawford et al. (2016) and Endlein et al. (2017) have demonstrated that such surfaces are non-adhesive for frogs (fall angle <90 deg on a flat surface covered with this grade of sandpaper). This is confirmed by our own experiments (see Fig. S1). Additionally, to make quantitative measurements of the different regions of the feet making contact with the surface during these different climbs, we used the technique of FTIR as described below. All climbs were recorded using two Basler A602f (Ahrensburg, Germany) digital cameras at a rate of 15 frames s⁻¹ that were synchronised using Streampix software (Version 3, Norpix Corporation, Montreal, Canada) and positioned to provide the best views of climbs in relation to the different cylinder diameters and whether they were covered with rough sandpaper. The diameters of the cylinders were selected in order to provide a curved surface that the frogs could not grip around (i.e. much like a flat surface in relation to the size of the frogs) (Fig. 1A), a surface they could span with their front limbs to generate adduction forces (Fig. 1B) and a surface they could grip with the digits of one hand and execute a power grip (Fig. 1C).

Video recordings and their analysis

To ensure accurate measurements of features of the frogs' climbing, baseline scale readings were taken each time cameras were repositioned. Measurements of two complete strides were used to determine stride length, while rates of ascent (cm s⁻¹) were determined by measuring the distance a frog's snout tip moved during at least two complete strides. Climbing strategies were also visually analysed to determine which gaits frogs were utilising during ascent. The most common were a 'lateral sequence walk' in which the footfalls of the four legs were approximately equally spaced in time, and a 'walking trot' in which a front limb is moved at approximately the same time as the opposite rear (definitions from Hildebrand, 1985). Both gaits are defined as walks because the duty

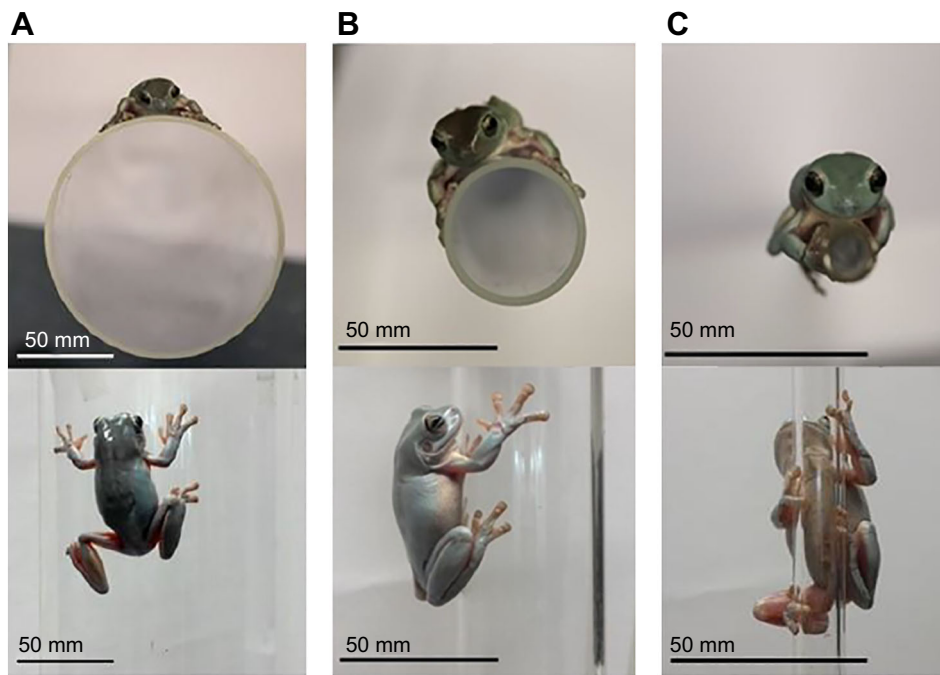


Fig. 1. Images of the same individual *Litoria caerulea* on three diameters of Perspex cylinder viewed from above (top images) and the side (bottom images). Cylinder diameters represented are (A) 120 mm, (B) 44 mm and (C) 13 mm.

factor (relative duration of ‘on-ground’ period) was more than 0.5 (~0.8 in most cases). In addition, a ‘slip’ gait was defined as a climb during which the legs frequently slipped on the surface (ca. 70% of steps), the frog finding stable purchase on the substrate difficult, and ‘other’ as patterns of footfall that were irregular, with few or no slips.

In a random order, assigned at the beginning of each session, individual frogs were encouraged to climb the three different diameters, with a successful climb defined as the animal completing at least two full strides uninterrupted by periods of rest. Frogs were given regular breaks between climbs and experiments were discontinued for the day with individual frogs if they showed any unwillingness to climb. The aim was to obtain a minimum of five successful climbs for each individual frog on each cylinder that the frogs were able to climb.

Measurement of contact area

To visualise the frog’s areas of contact with the substrate, custom-built LED arrays (Tru Opto, ultra-bright, narrow-angle 5 mm, Rapid Electronics, Colchester, Essex, UK) were constructed to fit the top and bottom of each cylinder, arranged so that the light was directed inwards into the Perspex material. Because of total internal reflection, the light was ‘trapped’ within the Perspex and only ‘escaped’, producing a bright spot, when something (e.g. water) with a significantly higher refractive index than air ($n_{\text{water}}=1.33$ compared with $n_{\text{air}}=1.0$) touched the surface. This technique, FTIR, has been developed in our laboratory (see Endlein et al., 2013) from the ‘cat-walk’ of Betts et al. (1980) and is used here to visualise the areas of the toe pads ($n_{\text{fluid}}\approx 1.33$) and other structures that make contact with the cylinders during tree frog climbing. The areas of these bright spots were measured using custom-made MATLAB (MathWorks, Natick, MA, USA) scripts. In this way, the total contact area of individual limbs could be measured and comparisons made between individuals, species and the same frog on the different diameter surfaces. A visual analysis of images generated from these videos was also used to determine the extent to which other limb structures (particularly the subarticular tubercles) were

being used in addition to the toe pads. Although such an analysis was possible for climbs on the two largest diameter cylinders (44 and 120 mm), climbs on the 13 mm cylinder proved impossible to analyse quantitatively, as frogs climb this cylinder by wrapping their digits around it. Thus, the bright spots of contact may be obscured by other limb parts or be located on parts of the cylinder that are edge-on to the camera. Thus, as shown in Fig. S2, the area of a circle of 1 mm diameter, as measured from the video image, will depend on its location on the cylinder. Centrally placed circles can be accurately measured, but more laterally placed ones have areas that progressively decline as you move laterally in either direction. Although this effect is similar for both the 120 and 44 mm cylinders, the figure shows that, taking into account the leg span of the frogs, these measurement errors will occur more commonly on the smaller 44 mm diameter cylinder (and even more so on the smallest 13 mm diameter cylinder; data not shown). Given that the areas of contact were often not circles (or other simple geometric shapes for which a correction factor could be simply calculated), correction factors were not a practical option. Instead, in most cases (e.g. Table 1), relative contacts between different structures (e.g. toe pads and subarticular tubercles) were made on a percentage basis. Pads and tubercles are located close to each other, but the foot may be placed anywhere on the back of the cylinder. Thus, although measurements of the actual area of contact are subject to the errors described above, comparisons of the relative areas of contact of adjoining structures will be much more accurate. One further point is worth making, as many of our experiments compare performance on cylinders of different diameter. As measurements on the smaller diameter cylinders are more likely to underestimate the actual area of contact, our finding that contact is increased on such cylinders occurred in spite of the effects of cylinder curvature described above.

Statistical analysis

In addition to the standard packages provided in R version 3.1.1 (<http://www.R-project.org/>), the following R packages were used: lme4, ggplot2, RVAideMemoire, gridExtra, Rmisc, caret, car and lmerTest.

Table 1. Results of the best-fit linear mixed-effect model for rate of ascent and percentage of contact of *Litoria caerulea* and *Osteopilus septentrionalis*

Model	SS	MS	Numerator d.f.	Denominator d.f.	F	P
Rate of ascent						
Diameter	132.817	66.409	2	135.135	5.419	0.0054*
Surface	289.366	289.366	1	136.253	23.612	<0.0001*
Species	18.336	18.336	1	3.184	1.496	0.304
Weight	54.982	54.982	1	3.13	4.487	0.1206
Species:Weight	49.811	49.811	1	3.195	4.065	0.1316
Percentage of contact						
Diameter	22774.2	22774.2	1	97.208	231.007	<0.0001*
Species	1983	1983	1	6.302	20.114	0.0037*
Diameter:Species	691.3	691.3	1	97.211	7.012	0.0094*

Asterisks indicate $P < 0.05$.

Rate of ascent

The available data were inputted into a linear mixed-effect model (LME) that used rate of ascent (ROA) as the response variable. The explanatory variables were the ‘diameter’ and ‘surface texture’ of the substrate, ‘weight’ and ‘species’ of frog climbing and an interaction between ‘weight’ and ‘species’. The individual frog and trial number were included as ‘random effects’ to compensate for the fact that we ran a small number of frogs repeatedly during the climbs. A stepwise down model selection was used by comparing Akaike information criterion values to determine the model that best fitted the data.

Gait

Gait was determined using successful climbs that had at least two steps, categorized by the following: (1) lateral sequence walk; (2) walking trot; (3) slip; and (4) other (see above for definitions). To determine whether gait varied with diameter on the smooth surface, a Kruskal–Wallis test was used. Owing to a lack of climbs, this was not completed on the rough surface.

Area of contact (subarticular tubercle and other areas of foot contact in relation to toe pad contact)

To standardise the relative contribution of contact areas of subarticular tubercles and other areas of the foot for each step, their proportion of total area (in %) was used as the response variable. Contact was measured once during each step at the point the next limb to move (or set of limbs in the case of ‘trots’) came out of contact with the surface. This enabled the examination of the percentage of contact of tubercles (which could not be separated from other structures of the hands/feet in some instances). An LME with the fixed explanatory variables of the ‘diameter’ of the substrate, the ‘species’ of frog and an interaction between ‘species’ and ‘diameter’ was conducted. This included the individual frog and step as ‘random effects’. The same method of model selection as described previously was applied to determine the model of best fit. General linear models (GLMs) were used to examine changes in the contact area (mm^2) of these areas of the foot in response to diameter of the substrate.

RESULTS

Effects of cylinder size and substrate surface on rates of ascent

To determine the influence of substrate diameter on rate of ascent, both species of tree frog were tested on all three diameters of cylinder on both smooth (adhesive) and rough (non-adhesive) surfaces (Fig. 2). Considering first the smooth surface, ROA was significantly different between cylinder diameters in the whole

model ($P < 0.005$, d.f.=2; Fig. 2, Table 1), with ROA increasing with decreasing diameter. This was the case for both species in the model. Although differences between them were not statistically significant ($P > 0.05$, d.f.=1), the average ROA was higher for *O. septentrionalis* than for *L. caerulea* on all three cylinders.

When effective adhesion was inhibited through the application of the rough surface to the cylinders (see Fig. S1), ROA was significantly lower for both species ($P < 0.0001$, d.f.=1; Fig. 2, Table 1). Indeed, frogs were only able to climb when they could grip around the substrate, exhibiting the greatest number of successful climbs at the highest ROA on the 13 mm diameter cylinder (Fig. 2). Frogs exhibited difficulty climbing the 44 mm diameter cylinder, as movements were slow and laboured, and no frogs were able to climb the 120 mm diameter cylinder. Indeed, on the 120 mm diameter cylinder, only those frogs with the largest limb span were able hold onto to the substrate for more than a few seconds, falling when climbing was attempted. On the 44 mm cylinder, most frogs were able to hold onto the surface by gripping around the cylinder. Indeed, all had a forelimb span that would have enabled them to grip around the 44 mm diameter cylinder from 188 deg (frog with smallest forelimb span) to 246 deg (frog with largest forelimb span). However, they often detached and fell when attempting to move a limb. As a result, there were comparatively few successful climbs on the 44 mm substrate, and all appeared to take a great deal of effort for the frogs to perform.

Effect of cylinder size and substrate surface on gait

In order to determine how climbing gait was affected by substrate diameter and surface, videos were analysed to establish the gait frogs used while ascending. There were differences between gaits employed on the different surfaces and diameters. On the smooth 44 and 120 mm diameter cylinders, the dominant gait employed by both species was a ‘lateral sequence walk’ (Table 2). This changed to a ‘walking trot’ when climbing on the smooth 13 mm diameter cylinder, the changes in the preferred pattern of walking being significantly different for both frog species (Kruskal–Wallis test, $P = 0.003$, d.f.=2; Table 2). Movies 1–5 show examples of climbs on all three diameters and under both surface conditions. The dominant gait on the rough 13 mm substrate was a ‘lateral sequence walk’, indicating the difficulty in climbing on the different surface. There were no successful climbs on the rough 120 mm diameter and too few on the 44 mm diameter surface for a quantitative analysis to be possible.

Visualisation of surface contact

When climbing on a flat surface, contact with the surface in both species was dominated by the toe pads, with subarticular tubercles

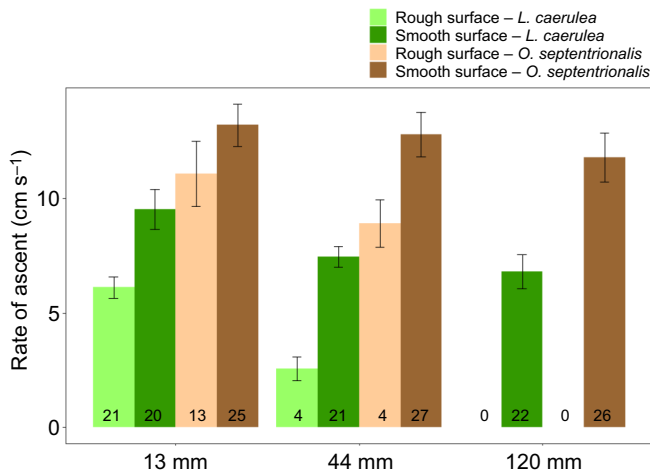


Fig. 2. Average rates of ascent of *Litoria caerulea* and *Osteopilus septentrionalis* on all three diameters of cylinder, including data from both smooth (adhesive) and rough (non-adhesive) surfaces. The bars represent the mean \pm s.e.m. rate of ascent (cm s^{-1}). Values at the base of each bar represent the number of successful climbs. Climbs on the largest diameter cylinder on a rough surface are shown here as zero as frogs were unable to complete climbs under those conditions.

and other, less specialised areas of the toes and feet making up only a small percentage of the total contact. This is illustrated by the FTIR images in Fig. 3, where all but two of the bright spots were produced by toe pads. Contact on the 120 mm substrate is comparable to that of the flat surface. Percentage of contact was significantly affected by ‘diameter’ ($P < 0.0001$, d.f.=1; Table 1) and ‘species’ ($P = 0.0037$, d.f.=1; Table 1), as well as the interaction between the two ($P = 0.0094$, d.f.=1; Table 1). Measurements of the areas of these bright spots indicate that, on this 120 mm diameter cylinder, the toe pads make up 76.7% of the total contact area in *L. caerulea* and 83.7% in *O. septentrionalis* (Fig. 4). When the substrate diameter decreased to 44 mm, toe pad surface contact increased from a mean of 56 to 70 mm^2 in *L. caerulea* and from 50 to 57 mm^2 in *O. septentrionalis* (Table 3), but there was a much greater increase in the contact of other structures, such that the toe

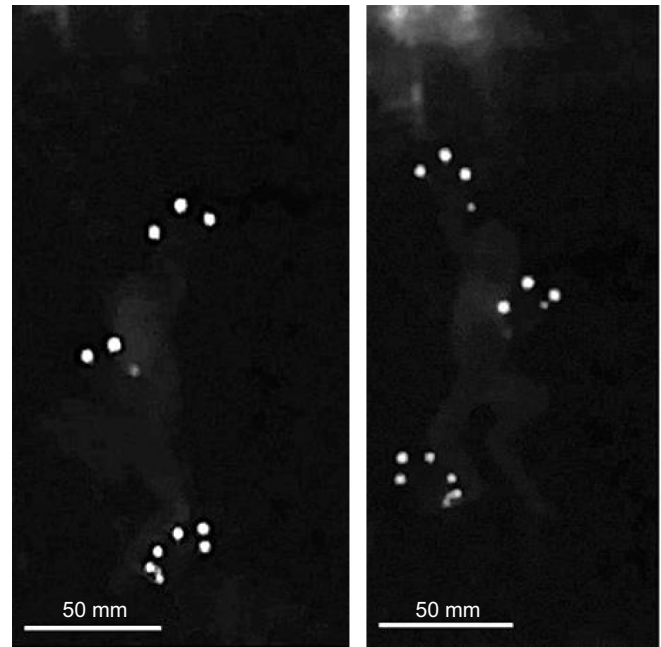


Fig. 3. Frustrated total internal reflection (FTIR) images of *L. caerulea* (left) and *O. septentrionalis* (right) climbing on a flat surface with areas of contact illuminated. These images illustrate that, on a flat surface, most of the contact is made by the toe pads. There are four toes on each forelimb (upper two footprints in each image), five on each hindlimb (lowest footprint in each image), with minimal contact from the subarticular tubercles (seen as a single extra-small bright spot in each hind footprint image).

pad contribution to the total was reduced to only 43.0% in *L. caerulea* and 59.8% in *O. septentrionalis* (Fig. 4). Though not quantifiable on the smallest 13 mm diameter cylinder, contact area images of frogs climbing this cylinder clearly suggest that further increases in contact area occur, with most of the ventral surface of feet appearing to be in contact in some images (Fig. 5A). Overall, these results, illustrated in Figs 5 and 6, indicate that contact with the substrate is inversely related to the substrate diameter, and that the subarticular tubercles have possibly evolved to aid tree frogs in climbing the small diameter structures that make up so much of their arboreal habitat.

The experimental data underlying the above results are available in Datasets 1–3.

Table 2. Numbers of each observed gait/mode of climbing exhibited by each species on each diameter of cylinder on both rough and smooth surfaces

Diameter	Gait	<i>L. caerulea</i>		<i>O. septentrionalis</i>	
		Smooth	Rough	Smooth	Rough
13 mm	Walk	2	15	5	8
	Trot	15	3	18	4
	Slip	3	0	0	0
	Other	0	3	2	1
44 mm	Walk	15	4	11	2
	Trot	0	0	6	0
	Slip	6	0	4	2
	Other	0	0	6	0
120 mm	Walk	17	n.a.	18	n.a.
	Trot	0	n.a.	2	n.a.
	Slip	5	n.a.	2	n.a.
	Other	0	n.a.	4	n.a.

Walk, lateral sequence walk; trot, walking trot; slip, walking gait where the legs frequently slipped on the surface; other, irregular patterns of stepping. Values in bold indicate the highest number of times gaits were employed in each experimental situation. n.a. represents conditions where frogs were not able to climb.

Table 3. Summary of average total contact area (mm^2) made by toe pads and subarticular tubercles or other foot structures at mid-stance for both species on the two largest diameters of cylinder and *P*-values indicating any statistical differences between them (general linear models)

Cylinder diameter (mm)	Contact area (mm^2)			
	<i>O. septentrionalis</i>		<i>L. caerulea</i>	
	Toe pad	Tubercles/other foot structures	Toe pad	Tubercles/other foot structures
120	50	10	56	20
44	57	41	70	98
<i>t</i>	-0.98	-6.28	-2.51	-8.78
<i>P</i>	n.s.	<0.0001	<0.015	<0.0001

The smallest diameter (13 mm) results are not presented owing to complications encountered when attempting to analyse these data quantitatively. n.s., not significant.

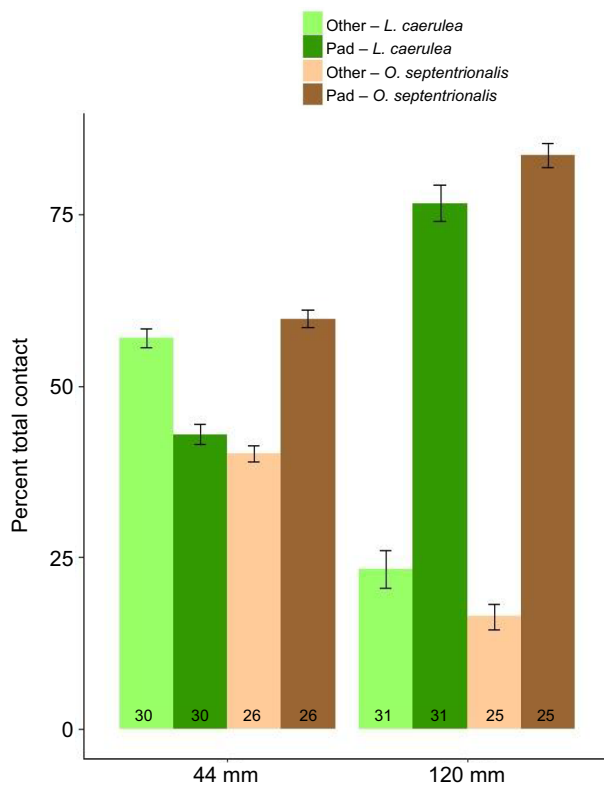


Fig. 4. Percentage contact areas of toe pads and other ventral structures on the digits (mainly subarticular tubercles) presented as means \pm s.e.m. for *L. caerulea* and *O. septentrionalis* on the two larger diameter cylinders. Values at the base of each bar represent the number of individual steps analysed. See Table 1 for statistical comparisons.

DISCUSSION

The most significant findings of this study are that: (1) in situations where both adhesion and adduction are possible, they combine to achieve faster, more-efficient climbing, and (2) on smaller diameter structures, subarticular tubercles are increasingly used in addition to the toe pads.

Grips and ascent

Although tree frog adhesion requires a relatively smooth surface (Crawford et al., 2016), adduction is not so limited, but does require the curvature of the surface to be great enough for limbs and/or digits to be able to grasp it, using a combination of normal and tangential (friction) forces (Cartmill, 1985). Friction forces are also required to counteract the force of gravity because the frogs are climbing a vertical surface.

Tree frogs are specialised for their arboreal way of life by the presence of adhesive toe pads and subarticular tubercles for adhesion and long digits for grasping, which often include an intercalary cartilage between the two most distal phalanges (Noble and Jaekle, 1928). They also possess specialised musculature within the hands and fingers (Burton, 1998), similar to that employed by other arboreal species, including primates (Napier, 1967; Bloch and Boyer, 2002; Manzano et al., 2008; Sustaita et al., 2013). In our experiments, frogs were unable to grip around the largest selected diameter of cylinder and, as a result, climbing was only possible with adhesive forces. ROA increased on the middle diameter cylinder, which was small enough to be gripped using adduction (a ‘bear hug’). The very fastest climbs, however, took place on the smallest diameter cylinder, which was small enough to

be gripped using individual digits. When adhesion was not possible through the application of the rough surface to the same diameters of cylinder, frogs were unable to climb the largest diameter cylinder, but some climbs were achieved on the middle diameter cylinder, but with a visible exertion required to do so. Frogs were able to climb the smallest diameter cylinder, even on the rough, non-adhesive surface. However, climbs were significantly slower than those when the surface was smooth on the same diameter. Thus both adduction and adhesion play a role not just in widening the range of surfaces that tree frogs can climb, but also in increasing climbing speed, where both mechanisms can operate.

Vertical climbing studies such as ours often focus on kinematics rather than ROA (Hanna, 2006; Isler, 2005), and, in primates, demonstrate the presence of both a ‘power grip’ and a ‘precision grip’ (Napier, 1956; Landsmeer, 1962; Cartmill, 1985). Indeed, the evolution of grasping has been linked to the development of arboreality in early primates (Napier, 1967; Sargis, 2001; Bloch and Boyer, 2002). A power grip should occur more commonly in climbing, whereas manipulation of food, which is much better developed in arboreal than in ground-living frogs (Gray et al., 1997), would be more likely to utilise a precision grip (Gray et al., 1997; Sustaita et al., 2013). However, Manzano et al. (2008) and Herrel et al. (2013) demonstrate both types of grip in their studies of tree frogs negotiating narrow substrates. In our experiments, it was a power grip that was used by frogs climbing the narrowest of our cylinders. The second of the above studies (Herrel et al., 2013) is of particular interest as it researches the locomotor ability of a tree frog (*Phyllomedusa azurea*), a member of a family of highly specialised, arboreal frogs well known for their slow but precise limb movements (Blaylock et al., 1976) on narrow substrates. These were 1, 4 and 40 mm in diameter, oriented either horizontally or tilted at 45 deg (Herrel et al., 2013). The results – ‘faster movement on wider substrates’ and ‘faster movement on inclined substrates’ – are somewhat different from ours, but this is almost certainly due to the importance of balance on these narrow, non-vertical substrates, but less important in our experiments on vertical surfaces. Additionally, chameleons have been shown to exhibit greater gripping power on small diameter substrates (Losos et al., 1993; Herrel et al., 2011), and vertical substrates have been shown to increase the variability of grasping hand postures in mouse lemurs (Reghem et al., 2012).

Gaits

During climbing, the stance phase took up 50% or more of each step. In our experiments, we observed both a ‘lateral sequence walk’, where only one limb was moved at a time, and a ‘walking trot’, where diagonal pairs of legs were moved together. Additionally, on surfaces that frogs found difficult to climb, less regular stepping patterns were seen (Table 2), including stepping patterns where slipping on the surface was common. In both *L. caerulea* and *O. septentrionalis*, the ‘walking trot’ was the dominant gait employed on the smallest diameter cylinder under smooth conditions. This is the situation where both adhesion (as explained in the following section) and adduction forces were highest, and where, as discussed above, walking speeds were highest. In all other situations, the ‘lateral sequence walk’ dominated, though it should be added that (1) there were few successful climbs for *O. septentrionalis* on the 44 mm diameter cylinder under rough conditions, a combination that this species found particularly difficult to negotiate, and (2) there were no data for either species on the 120 mm diameter cylinder under rough conditions, a situation in which neither adhesion nor adduction was possible. These results

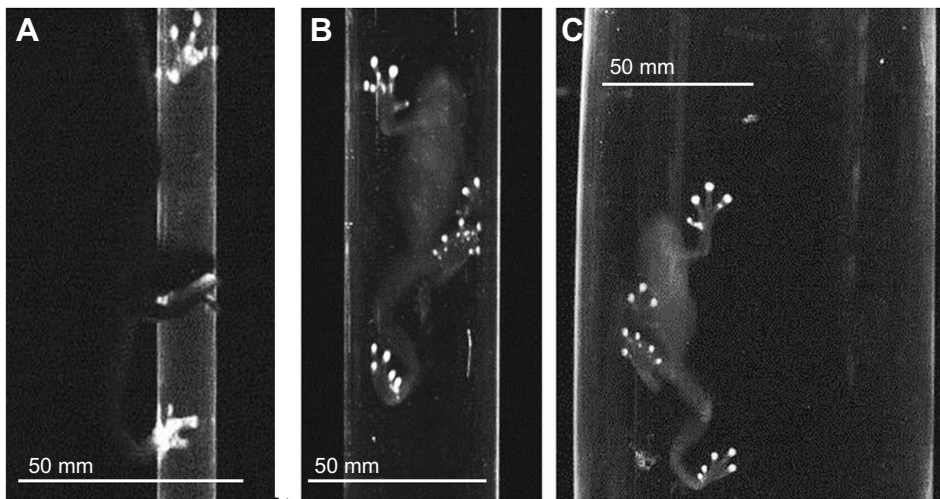


Fig. 5. Illumination of toe pads and other structures using the FTIR technique while *L. caerulea* climbed smooth substrates. Cylinder diameters represented are (A) 13 mm, (B) 44 mm and (C) 120 mm.

thus demonstrate, on the 13 mm diameter smooth surface, a clear correlation between (a) good adhesion combined with good adduction, (b) highest walking speeds (see ‘Grips and ascent’, above) and (c) a ‘walking trot’ gait where the frogs were able to move diagonal pairs of limbs at the same time. Climbing studies focused on arboreal mammals have also examined gait adjustment to substrate diameter including a dominant use of diagonal-sequence footfall patterns when walking on a narrow diameter object (Schmitt and Lemelin, 2004). On flat (as opposed to curved) surfaces, tree frogs (*Rhacophorus omeimontis*) have been recorded using a walking trot on horizontal surfaces (T.E., B.D., Y. Chen, W.J.P.B., A.J. and Z. Dai, unpublished data), but this shifted to a lateral sequence walk when frogs were climbing a vertical surface. Our study demonstrates that under smooth conditions on a vertical, narrow cylinder, contact with the substrate can be more easily maintained through the application of both adhesion and adduction. In turn, this allows frogs to remain attached using just two limbs instead of three, and employ the more efficient walking trot gait that is associated with locomotion on a horizontal surface (Ahn et al., 2004; T.E., B.D., Y. Chen, W.J.P.B., A.J. and Z. Dai, unpublished data).

Contact area

Both species examined in this study are amongst the larger species of tree frog. SVLs of full-grown *O. septentrionalis* lie in the range of

75 to 140 mm, and those of *L. caerulea* in the range of 70 to 115 mm. Both species also possess particularly well-developed subarticular tubercles (Green, 1979). Indeed, Smith (2003) proposed, on the basis of her studies of the tree frogs of Trinidad, that this correlation between size and development of subarticular tubercles was related to a role in climbing. She identified a positive correlation between adult size and degree of arboreality, in that the largest species of Trinidadian tree frogs are often found high in the canopy, while smaller species are commonly found in shrubs only a metre or so above the ground (see also Kenny, 1969). This is in contrast to considerations of allometry, either within or between species, as the mass of tree frogs increases as approximately the cube of their linear dimensions whereas toe pad area only increases as their square (Barnes et al., 2006; Smith et al., 2006b). Larger frogs would thus be expected to have a lower ability to adhere, unless other structures play a role.

On the largest diameter cylinder, most of the contact was made by toe pads, which is comparable to what is seen on a flat surface (Fig. 3), but contact by the subarticular tubercles and other areas of the hands and feet increased on the 44 mm diameter cylinder, exceeding that of the pads in the case of *L. caerulea* (Fig. 4). Although data from the 13 mm cylinder cannot be analysed quantitatively because the toes wrap around the cylinder, interfering with the view of some of the adhering structures, it is

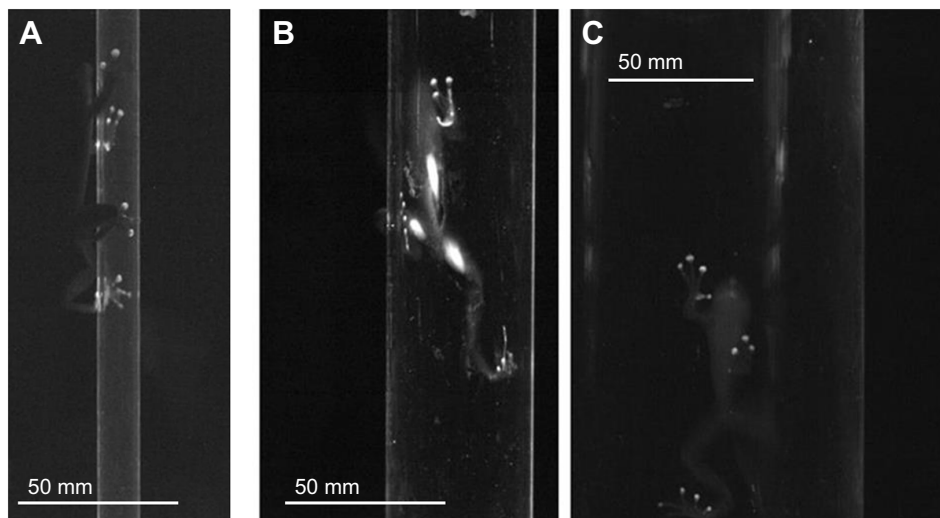


Fig. 6. Illumination of toe pads and other structures using the FTIR technique while *O. septentrionalis* climbed smooth substrates. Cylinder diameters represented are (A) 13 mm, (B) 44 mm and (C) 120 mm.

clear from Figs 5 and 6 that the role of the subarticular tubercles on the 44 mm diameter cylinder was increased even further on the 13 mm diameter cylinder. Indeed, these contact visualisation results clearly show that substrate contact is significantly increased on smaller diameter substrates, this increase being due in part to an increase in pad contact area, but more importantly in the use of subarticular tubercles and other parts of the ventral surface of the fingers and palms. From the viewpoint of anatomy, this change is not unexpected, as the location of the subarticular tubercles means that they will always make contact as the fingers wrap around small diameter structures, but much less on a flat surface. Indeed, on flat surfaces, larger tree frogs do not adhere as well as smaller ones, but they do adhere better than would be predicted on the basis of their toe pad area alone (Barnes et al., 2006). Small diameter substrates will, however, be common in the natural habitats of most tree frogs, where the subarticular tubercles will play an important role during climbing, especially so in large (and therefore heavy) frogs.

Conclusions and further study

In a related study carried out on a different species of tree frog, Endlein et al. (2017) measured forces from frogs climbing a large cylinder comprising 24 separate three-dimensional force platforms (A.J., S. Yuan, T.E., I.D.C.H., W. Wang, H. Wang, Z. Jiang, W.J.P.B. and Z. Dai, unpublished data) and from individual pads and subarticular tubercles. The experimental findings confirm the presence of compressive forces, particularly strong when the frogs were climbing a non-adhesive surface, just as the research described in the present study would predict (performance on 44 mm diameter cylinder). Also, as previous studies have shown (e.g. Smith, 2003 for tree frogs; Drotlef et al., 2015 for torrent/rock frogs), the surface anatomy of the subarticular tubercles is broadly similar to that of the toe pads, though the grooves separating the epithelial cells are, on the whole, shallower than in the toe pads, and the nanopillars covering the surface of these cells are at a lower density in the subarticular tubercles, though there is a fair amount of variation (Endlein et al., 2017). In spite of the differences, measurements of the adhesive and frictional forces of pads and tubercles were broadly similar, with friction forces in each case being substantially greater than adhesive forces (Endlein et al., 2017).

As far as we are aware, this is the first body of work to examine how different adhesive structures function in regard to tree frogs and the application of both adhesion and friction forces during climbing on curved surfaces. Our results demonstrate that, as the diameter of a curved substrate decreases, tree frogs increasingly rely on adduction and gripping to generate friction forces, these forces arising from subarticular tubercles as well as toe pads. This allows them to meet the challenges posed by the complexities of an arboreal lifestyle (Cartmill, 1985; Hildebrand and Goslow, 2001).

The possession of more than one kind of attachment device is relatively common in animals. Most arboreal lizards (Zani, 2000) and a wide variety of insects (Beutel and Gorb, 2001) possess both adhesive pads and claws. The latter are most effective on rough surfaces, failing when the size of the claw tip is greater than the size of the asperities that comprise the surface (Dai et al., 2002). In contrast, adhesive pads function best on smooth surfaces (Zhou et al., 2014; Crawford et al., 2016). In insects, where adhesive pads may be 'hairy' or 'smooth' (Federle, 2006), adhesion may occur in more than one location and serve different functions. For instance, stick insects have 'toe' pads (arolia) for adhesion and 'heel' pads (euplantulae) for friction (Labonte and Federle, 2013), the arolia being the only pads in contact when the insect was hanging upside-

down, whereas when upright in their normal sprawled posture, the insects rested on their euplantulae. A further example, with similarities to the tree frog situation in that the secondary adhesive structures are located more proximally on the leg and are only used in special situations, is the possession by leafhoppers of special tarsal pads (platellae) for jumping from smooth surfaces (Clemente et al., 2017). They generate high friction forces, ensuring that the feet do not slip during take-off. Such a wide variety of adhesive structures are giving rise to the development of new adhesive devices. Materials based on the dry adhesive mechanism of geckos have led the way. Indeed, such gecko-based synthetic adhesives have recently enabled a 70 kg human to scale a vertical glass plate (Hawkes et al., 2015). As far as tree frogs are concerned, possible applications include improved design in wet-weather tyres (Barnes, 1999; Barnes et al., 2002; Persson, 2007), holding devices for surgery (Chen et al., 2015), improved friction in safety razors (Tsipenyuk and Varenberg, 2014) and climbing robots (Haynes et al., 2009). The research described here illustrates how, on cylindrical structures, adhesion could be combined with adduction in climbing robots, increasing both the range of materials that can be climbed and the velocity of climbing.

Previous work examining the ecological implications and evolution of grasping behaviours and limb positioning in arboreal species have identified this development in primates as, potentially, a product of biomechanical accommodations to differing substrate sizes in arboreal environments (Schmitt, 2003). However, such skilled forelimb movements are more common in tetrapod taxa (Iwaniuk and Whishaw, 2000; Sustaita et al., 2013), indicating a common origin in early tetrapods, and may have resulted from food-handling behaviours (Gray et al., 1997; Iwaniuk and Whishaw, 2000). Multiple reptile species have been found to exhibit differing climbing strategies in response to ecological niches, such as partial arborealism and canopy position determining the size and nature of the substrates encountered (Losos and Sinervo, 1989; Losos et al., 1993; Zaaf et al., 2001a; Spezzano and Jayne, 2004; Vanhooydonck et al., 2005, 2006; Renous et al., 2010; Foster and Higham, 2012). Further investigation into how tree frogs make use of their natural environment could yield better insights into how they specifically apply the adaptive climbing qualities indicated by this study. The differences observed here between *L. caerulea* and *O. septentrionalis* were relatively small, but *L. caerulea* has been shown to be significantly less able to negotiate narrow structures compared with *Phyllomedusa* (Manzano et al., 2008). Thus, like reptiles, tree frogs can be expected to show differences in climbing performance that reflect their ecological niche utilisation (Losos and Sinervo, 1989; Losos et al., 1993; Zaaf et al., 2001b; Irschick and Garland, 2001).

Acknowledgements

We thank Tiffany Armstrong for her help and advice during the course of this study.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: W.J.P.B., A.J., T.E.; Methodology: I.D.C.H., B.D., W.J.P.B., A.J., T.E.; Software: I.D.C.H., T.E.; Validation: T.E.; Formal analysis: I.D.C.H.; Investigation: I.D.C.H., B.D., W.J.P.B., A.J.; Resources: W.J.P.B.; Data curation: I.D.C.H.; Writing - original draft: I.D.C.H.; Writing - review & editing: I.D.C.H., W.J.P.B., T.E.; Visualization: I.D.C.H., B.D., A.J.; Supervision: W.J.P.B., A.J.; Project administration: W.J.P.B., A.J.; Funding acquisition: W.J.P.B., A.J., T.E.

Funding

This study was supported by a grant from the Royal Society, London (International Exchange Scheme 2014/R2: reference IE140717) awarded to W.J.P.B. and A.J.,

and by grants from the National Natural Science Foundation of China (grant no. 51375232) and the Natural Science Foundation of Jiangsu Province (grant no. BK20141410) awarded to A.J.

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.168179.supplemental>

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