Extreme positive allometry of animal adhesive pads and the size limits of adhesion-based climbing

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Organismal functions are size-dependent whenever body surfaces supply body volumes. Larger organisms can develop strongly folded internal surfaces for enhanced diffusion, but in many cases areas cannot be folded so that their enlargement is constrained by anatomy, presenting a problem for larger animals. Here, we study the allometry of adhesive pad area in 225 climbing animal species, covering more than seven orders of magnitude in weight. Across all taxa, adhesive pad area showed extreme positive allometry and scaled with weight, implying a 200-fold increase of relative pad area from mites to geckos. However, allometric scaling coefficients for pad area systematically decreased with taxonomic level, and were close to isometry when evolutionary history was accounted for, indicating that the substantial anatomical changes required to achieve increases in relative pad area are limited by phylogenetic constraints. Using a comparative phylogenetic approach, we found that the departure from isometry is almost exclusively caused by large differences in size-corrected pad area between arthropods and vertebrates. To mitigate the expected decrease of weight-specific adhesion within closely related taxa where pad area scaled close to isometry, data for several taxa suggest that the pads’ adhesive strength increased for larger animals. The combination of adjustments in relative pad area for distantly related taxa and changes in adhesive strength for closely related groups helps explain how climbing with adhesive pads has evolved in animals varying over seven orders of magnitude in body weight. Our results illustrate the size limits of adhesion-based climbing, with profound implications for large-scale bio-inspired adhesives.

The evolution of adaptive traits is driven by selective pressures, but can be bound by phylogenetic, developmental and physical constraints [1]. Integrating evolution and biomechanics provides a powerful tool to unravel this complex interaction, as physical constraints can often be predicted easily from first principles [2]. The influence of physical constraints is especially evident in comparative studies across organisms which differ substantially in size [3, 4, 5, 6]. For example, Fick’s laws of diffusion state that diffusive transport becomes increasingly insufficient over large distances, explaining the development of enlarged surfaces for gas and nutrient exchange (e.g. leaves, roots, lungs, gills, guts) and integrated long-distance fluid transport systems (e.g. xylem/phloem, circulatory systems) in larger animals and plants. How these systems change with size is determined by physical constraints [7, 8, 9]. While ‘fractal’ surface enlargements are possible without disrupting other body functions, strong positive allometry can conflict with anatomical constraints. For example, structural stability demands that animals should increase the cross-sectional area of their bones in proportion to their body weight, but excessively thick leg bones can compromise other physiological functions and hamper locomotion [3, 10, 11].

Adhesive pads are another example of an adaptive trait subject to size-dependent physical constraints. These systems allow animals to climb smooth vertical or inverted surfaces, thereby opening up new habitats. Adhesive pads have evolved multiple times independently within arthropods, reptiles, amphibians and mammals, and show impressive performance: they are rapidly controllable, can be used repeatedly without any loss of performance, and function on rough, dirty and flooded surfaces [12]. This performance has inspired a considerable amount of work on technical adhesives that mimic these properties [13]. A key challenge for both biological and bio-inspired adhesive systems is to achieve size-independent performance [14, 15, 16], i.e. the maximum sustainable adhesion force, $F$, should be proportional to the mass to be supported, $m$. For vertically climbing animals, $F$ is the product of the maximum adhesive stress, $\sigma$, and the adhesive pad area, $A$, each of which may change with mass ($A \propto m^a$ and $\sigma \propto m^b$), so that constant size-specific attachment performance requires:

$$m \propto A\sigma \propto m^a m^b \rightarrow a + b \approx 1 \quad (1)$$

where $a$ and $b$ are the scaling coefficients for $\sigma$ and $A$ in relation to body mass, respectively. If animals maintain geometric similarity when increasing in size, $A$ would scale as $m^{2/3}$, so that the adhesion per body weight for large geckos ($m \approx 100 \text{g}$) is expected to be approximately $10^{7/3} \approx 200 \text{ times}$ smaller than for tiny mites ($m \approx 10 \mu\text{g}$) if the pads’ adhesive strength $\sigma$ remained unchanged ($b = 0$). Large animals can only circumvent this problem by (i) developing disproportionately large adhesive pads ($a > 2/3$), and/or (ii) systematically increasing the maximum force per unit pad area ($b > 0$). How do large climbing animals achieve adhesive forces equivalent to their body weight?

Using the simple biomechanics argument outlined above as a framework, we here provide a comparative analysis of the allometry of adhesive pad area across 225 species,
covering more than seven orders of magnitude in weight – almost the entire weight range of animals climbing with adhesive pads — and including representatives from all major groups of adhesion-based climbers.

Results and Discussion

Scaling of adhesive pad area

Across all taxa, adhesive pad area showed extreme positive allometry and scaled as $A \propto m^{1.02}$ (reduced major axis regression (RMA); see fig. 1 and tab. 1 for detailed statistics), an increase sufficient to compensate for the predicted loss of weight-specific adhesion, even if adhesive strength remained unchanged. Thus, adhesive pads occupy a larger fraction of the body surface area in larger animals. Within closely related taxonomic groups, however, pad area grew more slowly with body mass, indicating a strong phylogenetic signal (see fig. 1 and 2).

When evolutionary relationships were accounted for, the observed scaling coefficient decreased dramatically, and was consistent with isometry (fig. 1, 2 and tab. 1). This systematic change of allometric coefficients with taxonomic rank suggests that phylogenetic inertia impedes a disproportionate increase of pad area within closely related groups (fig. 2 and 3 A). Our results thus add to a body of evidence suggesting that the evolutionary flexibility of allometric slopes is low and larger changes in particular traits are mainly achieved by shifts of the allometric elevation [18, 19].

Removal of the influence of body size by analysing the residuals (termed ‘relative pad area’ in the following) of a phylogenetic reduced major axis regression (pRMA) allowed us to further investigate at what taxonomic level major shifts in relative pad area occurred, separating the effects of size and ancestry. Relative pad area differed strongly between vertebrates and arthropods, but comparatively little variation existed within these groups (fig. 3 A). More than 58% of the variation in residual pad area was explained by differences between vertebrates and arthropods (nested ANOVA, $F_{1,175}=845$, $p<0.001$, see tab. 2), so that body weight and phylum alone accounted for more than 90% of the total variation in pad area. Rather than being driven solely by variation in body size, differences in relative pad area appear to be tied to characteristic features of the corresponding phyla, such as, for example, the presence or absence of multiple distal pads (toes) per leg (fig. 3 B, C). However, we also found evidence for differences in relative pad area within lower taxonomic ranks. For example, members of the gekko genus *Sphaerodactylus* had considerably smaller pads than other Gekkotan lizards, whereas *Gekko* lizards had particularly well-developed pads (based on their relative pad area, fig. 3 A). In insects, hemimetabolous orders had smaller relative pad areas than holometabolous orders (see fig. 3 A). Adhesive pads can allow access to arboreal habitats [20, 21, 22], but they may come at the cost of reduced locomotor performance in situations where no adhesion is required [23, 24]. Thus, the multiple independent losses, gains, and reductions of adhesive pads in amphibians, insects, lizards and spiders [25, 26, 27, 28] likely reflect the ecological, behavioural and taxonomic diversity within these groups [29, 30].
adaptations are also present above species or genus level. Here, we extend these studies to investigate whether such ties despite a near-isometric growth of pad area [16, 34].

strong adhesive strength can vary systematically with size, resulting in an almost body size-independent attachment ability. Recent studies on tree frogs and ants revealed that pad ability, or develop alternative strategies to compensate for evolution at least for closely related taxa. Larger animals within closely related taxa must therefore either cope for evolution at least for closely related taxa. Larger animals ranging from 10\(\text{^6}\) to 10\(\text{^4}\) grams requires extraordinary morphological changes: assuming otherwise isometric animals, the proportion of the total body surface area specialised as adhesive pad needs to increase by a factor of 10\(\text{^7/3}\) \(\approx\) 200. This extreme shape change may impose a size limit for adhesion-based climbing.

The size-limits of adhesion-based climbing

Strong positive allometry of non-convoluted body structures in organisms ranging in size over many orders of magnitude is difficult to achieve, owing to simple anatomical constraints. For example, bone mass in terrestrial animals is predicted to increase with mass\(^{4/3}\) to maintain constant bone stress levels, but this would require unrealistic relative bone masses for larger mammals (scaling up an 8-gram shrew with ca 4% bone mass would produce a rather unfortunate 8-tonne elephant with 400% bone mass). The actual scaling coefficient is inevitably smaller (\(\approx 1.1\)) [10, 31], and alternative strategies have evolved to limit bone stresses [11].

Maintaining a pad area proportional to body weight in animals ranging from \(10^{-5}\) to \(10^2\) grams requires extraordinary morphological changes: assuming otherwise isometric animals, the proportion of the total body surface area specialised as adhesive pad needs to increase by a factor of 10\(\text{^7/3}\) \(\approx\) 200. This extreme shape change may impose a size limit for adhesion-based climbing. Scaling up the relative pad area of arthropods and small vertebrates to a human of 180 cm body length and 80 kg body mass would result in an adhesive pad area of \(\approx 106.91 \cdot 80000^{0.02} \approx 0.81 \text{ m}^2\), approximately 2/5 of the total available body surface area (\(\approx 2 \text{ m}^2\), [33]). The required morphological changes, if at all possible, would thus be enormous, and difficult to achieve over short evolutionary timescales. Our results therefore indicate that phylogenetic inertia restricts the ‘design space’ for evolution at least for closely related taxa. Larger animals within closely related taxa must therefore either cope with a size-related decrease in their relative attachment ability, or develop alternative strategies to compensate for it. Recent studies on tree frogs and ants revealed that pad adhesive strength can vary systematically with size, resulting in an almost body size-independent attachment abilities despite a near-isometric growth of pad area [16, 34]. Here, we extend these studies to investigate whether such adaptations are also present above species or genus level.

Figure 4 shows whole-body adhesion per pad area plotted against body weight for 17 frog species from 4 families and 12 genera [35, 36, 37, 38]. All adhesion measurements were conducted using a tilting platform, and are thus comparable across studies. Over two orders of magnitude in body weight, adhesion force per unit area increased with \(m^{0.3}\) (RMA slope 0.3, 95% confidence interval (CI): (0.2, 0.43), generalised least-squares (GLS) slope 0.19, 95% CI: (0.08, 0.31)), sufficient to achieve body size-independent adhesive performance despite an approximately isometric growth of pad area (RMA slope 0.74, 95% CI: (0.62, 0.87), GLS slope 0.70, 95% CI: (0.58, 0.83)). In contrast to our results for the allometry of pad area, this relationship remained virtually unchanged when phylogenetic relationships were accounted for, indicating that pad performance directly responded to selective pressures unconstrained by phylogenetic history (phylogenetic RMA slope 0.28, 95% CI: (0.2, 0.42), phylogenetic GLS slope 0.17, 95% CI: (0.07, 0.27), see fig. 4). Together, our results provide strong evidence that two different strategies have evolved to deal with the physical challenges of a larger body size. These strategies have been adopted at different taxonomic levels, highlighting how phylogenetic and physical constraints can influence the evolution of adaptive traits. Across distantly related groups, leg morphology is sufficiently different to accommodate large differences in relative pad area. Within closely related groups, where anatomical constraints result in a scaling of pad area closer to isometry, some taxa appear to have increased their pads’ adhesive efficiency with size. The mechanisms underlying this increase in adhesive strength are still unclear, but may be of considerable interest for the development of large-scale bio-inspired adhesives. Various hypotheses have been proposed [14, 16, 37], but still remain to be tested.

force scaling and the evolution of ‘hairy’ adhesive pads

Arzt et al (2003) suggested that large animals with hairy adhesive pads have evolved higher hair densities to increase

Table 1: Results for generalised least squares and reduced major axis regressions describing the relationship between log\(_{10}\) (adhesive pad area) (in \(\mu\text{m}^2\)) and log\(_{10}\) (mass) (in g) across all taxa. Covariance in pad area and body mass between related species was either ignored (uncorrected) or accounted for (corrected). Pagel’s lambda is a statistic measuring the strength of phylogenetic signal (\(\lambda=1\) indicates that the trait evolves like Brownian motion along the phylogeny, whereas \(\lambda=0\) indicates that the trait is not correlated with phylogeny [17]). Numbers in brackets give approximate 95% confidence intervals of the estimated parameters where available.

<table>
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<th>Corrected</th>
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<tbody>
<tr>
<td>Reduced major axis</td>
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<tr>
<td>Pad area against mass</td>
<td>6.91 (6.84, 6.98)</td>
<td>6.54 (6.47, 6.62)</td>
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<tr>
<td>Mass against pad area</td>
<td>-6.76 (-7.08, -6.44)</td>
<td>-8.38 (-8.77, -7.99)</td>
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<tr>
<td>Generalised least squares</td>
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<tr>
<td>Pad area against mass</td>
<td>6.88 (6.80, 6.94)</td>
<td>6.44 (6.28, 6.61)</td>
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<tr>
<td>Mass against pad area</td>
<td>-6.29 (-6.61, -5.96)</td>
<td>-7.54 (-7.97, -7.10)</td>
</tr>
<tr>
<td>Elevation</td>
<td>1.02 (0.97, 1.07)</td>
<td>0.78 (0.74, 0.83)</td>
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<tr>
<td>Slope</td>
<td>0.98 (0.93, 1.03)</td>
<td>1.28 (1.21, 1.36)</td>
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<tr>
<td>Pagel’s (\lambda)</td>
<td>0 (fixed)</td>
<td>0.93 (fitted)</td>
</tr>
<tr>
<td>Pagel’s (\lambda)</td>
<td></td>
<td>0.90 (fitted)</td>
</tr>
</tbody>
</table>

CI: (0.2, 0.42), phylogenetic GLS slope 0.17, 95% CI: (0.07, 0.27), see fig. 4). Together, our results provide strong evidence that two different strategies have evolved to deal with the physical challenges of a larger body size. These strategies have been adopted at different taxonomic levels, highlighting how phylogenetic and physical constraints can influence the evolution of adaptive traits. Across distantly related groups, leg morphology is sufficiently different to accommodate large differences in relative pad area. Within closely related groups, where anatomical constraints result in a scaling of pad area closer to isometry, some taxa appear to have increased their pads’ adhesive efficiency with size. The mechanisms underlying this increase in adhesive strength are still unclear, but may be of considerable interest for the development of large-scale bio-inspired adhesives. Various hypotheses have been proposed [14, 16, 37], but still remain to be tested.
their pads’ adhesive strength, an idea derived from the assumption that adhesive forces scale with the width of individual hair tips [39]. Assuming isometric growth of the total pad area, Arzt et al. predicted that hair density would need to increase with $n^{2/3}$ in order to achieve constant mass-specific adhesion, in agreement with the data presented (but see ref. [40] which showed that adhesive hair density increased with body mass only when species were treated as independent data points, but not when phylogeny was considered). However, our data show that total pad area is directly proportional to body mass across distantly related taxa, so that a constant hair density would suffice. In addition, there is no experimental evidence that the adhesive strength of animal adhesive pads increases with decreasing size of individual contacts [16, 41]. Thus, it appears unlikely that ‘force scaling’ has played an important role in the evolution of fibrillar adhesive systems [42].

Adhesive pads constitute a prime model system for studying the link between morphology, performance and fitness [43]. Further mechanistic and comparative studies are needed to elucidate the factors driving the evolution of these structures, and may ultimately allow us to mimic their properties with synthetic adhesives.

Materials and Methods

Data collection

Data were either collected by the authors or extracted from references [16, 29, 35, 36, 37, 38, 41, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86].

Arthropod specimens were collected around Cambridge (UK), Brisbane (Australia), or obtained from the Cambridge Phasmid Study Group. All arthropods were identified [87, 88, 89], and their live weight was recorded (ME5, resolution 1 µg, max 5 g or 1202 MP, resolution 0.01 g, max 300 g, both Sartorius AG, Goettingen, Germany). Attachment pads were photographed either with a Canon EOS (Canon, Tokyo, Japan) mounted on a stereo microscope (MZ16, Leica Microsystems Ltd., Heidelberg, Germany), or by using scanning electron microscopy (SEM) for large and small specimens, respectively. Some pads were imaged whilst in contact with glass, visualised using the stereomicroscope with coaxial illumination. For SEM imaging, individual legs were dried, mounted on stubs, sputter-coated at 65 mA for 10-20 s (K575X turbo-pump sputter, Quorum Technologies, Sussex, UK) and examined with a field emission gun SEM at a beam voltage of 5 kV (Leo Gemini 1530VP, Carl-Zeiss NTS GmbH, Oberkochen, Germany).

Data on toepad-bearing gecko species were collected from live animals kept in the D.J.I. laboratory (under an Institutional Animal Care and Use (IACUC) protocol 2012–0064 from the University of Massachusetts at Amherst to DJ Irschick), and preserved specimens from the American Museum of Natural History and the Museum of Comparative Zoology at Harvard University. For each specimen, photos of one fore foot were obtained by pressing it tightly against the glass plate of an Epson PerfecVision V500 Photo Scanner (Seiko Epson Corp., Owa, Suwa, Nagano, Japan) next to a ruler and taking a digital scan. The total toepad area across all digits was measured using ImageJ v1.49r [90]. We also measured snout-vent-length (SVL, ±1 mm) from each individual using a clear plastic ruler. Where possible, we measured multiple conspecific individuals, and used the mean as the species value.

Literature data were taken from the papers’ text or tables, or were extracted from figures using WebPlotDigitizer 3.3 (WPD, developed by Ankit Rohatgi (http://arohatgi.info/WebPlotDigitizer), or ImageJ v1.49m. We tested the performance of WPD with an x-y plot of 20 random numbers between 1 and 1000 (x) and 0.01 and 10 000 (y) on a log-log scale, and found an accuracy of ≈0.6% for the raw data.

We used live body weights where available, and interpolated live weight from body length where necessary, using established scaling relationships [40]. A list of the included species can be found in the appendix.

<table>
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<th>F</th>
<th>p-value</th>
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Table 2: Results for a nested ANOVA on the residuals of a phylogenetic reduced major axis regression. $\eta^2$ is the variance in residual pad area accounted for by the different taxonomic levels, and most of the variation occurs between phyla.
Figure 3: (A) Overview of the diversity of taxa examined in this study. Branch lengths do not reflect time or base pair substitutions (see methods). Branches are coloured according to a maximum likelihood estimate of the ancestral state of relative pad area (i.e., the residuals from a log-log regression of pad area against body weight), visualising systematic differences in relative pad area between arthropods and vertebrates. All values apart from tip states are only approximate and are not used to support any conclusions (see methods). (B & C) Cartoons depicting footpad morphology for representative groups within the phylogeny shown above with smooth and hairy adhesive pads. Projected pad area is highlighted in orange for each representative (see methods).
Adhesive pad area

Animals attach to smooth surfaces by employing specialised attachment pads on their legs. These pads are either covered with dense arrays of fibrils (‘hairy pads’), or are macroscopically unstructured (‘smooth pads’). In order to compare pad areas across different taxa and pad morphologies, the following assumptions were made:

1. ‘Projected’ pad area is the most meaningful measure of contact area in comparative studies. Projected pad area is the surface area of the foot specialised specifically for generating adhesion and friction [91]. In a fibrillar pad, inevitably only a fraction of this area comes into surface contact, i.e. the ‘real’ contact area is significantly smaller than the projected contact area.

2. All animals employ a similar fraction of their available pad area when maximum performance is required. It is unclear what fraction of the available pad area is employed by animals of different size [16, 92, 93], and systematic studies are lacking. However, the small number of direct contact area observations available strongly suggest that animals often use the entire area of their adhesive pads [91, 94], i.e. that they are not ‘overbuilt’. We thus assume that all climbing pads are designed so that their whole area can be used in critical situations.

3. Adhesive performance is dominated by distal pads. Insects can have several attachment pads per leg. There is strong evidence that these pad types differ in their morphology, as well as in their performance and function during locomotion [16, 44, 65, 70, 91]. Many insects do not employ their distal pads when no adhesion is required [44, 65, 95, 96, 97, 98], whereas during inverted climbing, only distal pads are in surface contact [83]. Accordingly, insects with ablated distal pads cannot cling upside down to smooth surfaces [44, 98]. Distal pads thus appear to be true ‘adhesive pads’ [83]. Proximal pads, in contrast, can be ‘non-sticky’, and may be designed as non-adhesive friction pads [99, 100]. The distal pads are usually part of the pretarsus, but some insects lack a pre-tarsal pad. In these insects, the distal tarsal pad can show similar morphological specialisations [101, 102]. Proximal pads are mainly found in arthropods, but they may also be present in frogs [35, 103]. As the contribution of proximal pads to adhesion is unclear and likely variable, we exclude them for this study. In most insects, the total proximal pad area is between 3-5 times larger than the distal pad area, and pad area is still positively allometric even when proximal pads are included (reduced major axis regression slope between 0.8-0.9).

4. The variation of pad area/adhesive strength between different legs/toes and sexes of the same species, and the variation introduced by the animals’ ecology is independent and randomly distributed with respect to body weight. Several studies have shown that the size, morphology and performance of attachment devices can depend on the ecological niche occupied by the animals [20, 22, 29, 59, 104]. Variation can also occur between sexes [70, 105, 106], different legs or toes [20, 84], or even between populations of the same species occupying different habitats [24]. For this study, we assume that because of the large number of samples and the wide range of body sizes included, any bias introduced by these factors can be ignored.

5. Adhesive performance of ‘wet’ and ‘dry’ pads is comparable. Dynamic adhesive pads are frequently categorised as ‘wet’ or ‘dry’. However, there is no evidence for a functional difference between these two pad types [107], and indeed maximal adhesive stresses are comparable [16].

As some of the data used in this study originate from different groups, we quantified the consistency of pad area measurements among researchers. A selection of SEM images (three hairy, and seven smooth pads) were given to 10 scientists who independently measured nominal pad area. We found an average coefficient of variation of 17±9%, which was independent of the animals’ body weight (ANOVA, F_{1,8}=0.067, p=0.8). Scaling relationships calculated with this dataset did not vary significantly across scientists (slope: likelihood ratio statistic= 0.38; elevation: Wald statistic=1.21, both df=9 and p>0.9).

Phylogenetic and statistical analyses

In order to account for the non-independence of data from related species, we first formed groups within which adhesive pads are likely homologous, based on their position on the leg and their structure (i.e. hairy vs. smooth). These groups are (1) Squamata, (2) Anura, (3) Araneae, (4) mites with smooth pads, (5) mites with hairy pads, (6) insects with tarsal hair fields (e.g. some Coleoptera and Raphidioptera), (6) insects with smooth
pulvillii (e. g. some Hemiptera), (7) insects with hairy pul-
villii (e. g. some Diptera), (8) insects with unfoldable arolia
(some Hymenoptera), (8) insects with non-versible arolia
(e. g. some Polyneoptera, Hemiptera and Lepidoptera),
(9) insects with specialised distal euplantula (some Poly-
neoptera), (10) insects with tibial pads (e. g. some aphids).
These groups were all connected directly to the root of
the tree, so that analogous structures share no branch,
and thus the respective elements in the error covariance
matrix of our linear models are zero [108]. Within this
groups, we assembled a tree topology from phylogenies
published for the constituent groups (Anura [109], Squa-
mata [110], Aranae [28], Insecta [111], Blattodea [112],
Coleoptera [113], Diptera [114], Hemiptera [115, 116], Hy-
menoptera [117, 118]. As statistically supported branch
lengths were not available, comparative phylogenetic pro-
cedures which allow for more complex evolutionary mod-
els, such as Ornstein-Uhlenbeck models [119, 120], were
not feasible. Instead, we performed phylogenetic gener-
alised least squares on 10,000 trees with randomised branch
lengths that were rendered ultrametric via a correlated rate
model [121]. In order to account for the uncertainty of
the phylogenetic error covariance structure, Pagel's λ was
estimated simultaneously via a maximum likelihood optimi-
isation [17, 122]. The fitted coefficients were normally
distributed, with a coefficient of variation below 1% (see
fig. S1 in Supplementary Information). For simplicity, we
report results for an ultrametric tree calculated from a tree
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distributed, with a coefficient of variation below 1% (see
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model [121]. In order to account for the uncertainty of
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estimated simultaneously via a maximum likelihood optimi-
isation [17, 122]. The fitted coefficients were normally
distributed, with a coefficient of variation below 1% (see
fig. S1 in Supplementary Information). For simplicity, we
report results for an ultrametric tree calculated from a tree

Scaling of pad performance in tree frogs
All data are from whole-animal force measurements, con-
ducted using a tilting platform. In total, we extracted data
for pad area and body weight for 17 species belonging to 4
families from references [35, 36, 37, 38]. The phylogenetic
tree underlying the phylogenetic regressions was extracted
from the detailed phylogeny in [109], and is shown in fig. S2
in the Supplementary Information.

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WF, the Denman Baynes Senior Research Fellowship to DL and
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Appendix
The following species were included:

**Amphibia:** Anura. Dendrobatidae: *Mannophryne trini-
tatis* (Garman, 1887), Hemiphractidae: *Flectonotus fitgeraldi*
(Parker, 1933), Hylidae: *Dendropsophus microcephalus* (Cope,
1886); *Dendropsophus minusculus* (Rivero, 1971); *Dendrops-
ofhus minutus* (Peters, 1872); *Hyla cinerea* (Schneider,
1799); *Hyla versicolor LeConte*, 1825; *Hyphiboa boaens* (Lin-
aeus, 1758); *Hyphiboa crepitans* (Wied-Newied, 1824);*Hyph-
iboa geographicus* (Spix, 1824); *Hyphiboa punctatus* (Schneider,
1799); *Litocra caerulea* (White, 1790); *Osteopilus septen-
trionalis* (Duméril & Bibron, 1841); *Phyllodytes au-
ratus* (Boulenger, 1917); *Phyllomedusa trinitatis* Mertens,
1926; *Scinax ruber* (Laurenti, 1768); *Smilisca phaeota* (Cope,
1862); *Sphaenorhynchus lacteus* (Daullin, 1801); *Trachy-
cephalus venulosus* (Laurenti, 1768), Craugastoridae: *Pristi-
manthus euphronides* (Schwart, 1967), Ranidae: *Staurois gal-
tatus* ( Günther, 1858), Rhacophoridae: *Rhacophorus pardalis* G ünther, 1858

**Arachnida:** Araneae. Ctenidae: *Clenas curvipes* (Key-
sel, 1881); *Ctenus sinuatipes* Pickard-Cambridge, 1897;
*Clenus sp.* 3 Walckenaer, 1805; *Cupiennius coccineus* Pickard-Cambridge, 1901; *Cupiennius getazi* Simon, 1891;
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Cambridge, 1897), Thomisidae: *Misumenops* spec.

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Hymenoptera, Formicidae: Atta cephalotes (Linnaeus, 1758); Atta colombica (Guérin-Méneville, 1844); Camponotus schmitzi Stärcke, 1933; Myrmica scabrinodis Nylander, 1846; Oecophylla smaragdina Fabricius, 1775; Polyhachis dives Smith, 1857, Vespidae: Vespa crabo Linnaeus, 1758

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Mantodea, Mantidae: Stagmomantis theophila Rehn, 1904

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