

# Biomechanics of cutting: sharpness, wear sensitivity, and the scaling of cutting forces in leaf-cutter ant mandibles

Frederik Püffel<sup>\*1</sup>, O. K. Walthaus<sup>1</sup>, Victor Kang<sup>1</sup> & David Labonte<sup>1</sup>

<sup>1</sup>Department of Bioengineering, Imperial College London, UK

Herbivores large and small need to mechanically process plant tissue. Their ability to do so is determined by two forces: the maximum force they can generate, and the minimum force required to fracture the plant tissue. The ratio of these forces determines the required relative mechanical effort; how this ratio varies with animal size is challenging to predict. We measured the forces required to cut thin polymer sheets with mandibles from leaf-cutter ant workers which vary by more than one order of magnitude in body mass. Cutting forces were independent of mandible size, but differed by a factor of two between pristine and worn mandibles. Mandibular wear is thus likely a more important determinant of cutting force than mandible size. We rationalise this finding with a biomechanical analysis which suggests that pristine mandibles are ideally ‘sharp’ – cutting forces are close to a theoretical minimum, which is independent of tool size and shape, and instead solely depends on the geometric and mechanical properties of the cut tissue. The increase of cutting force due to mandibular wear may be particularly problematic for small ants, which generate lower absolute bite forces, and thus require a larger fraction of their maximum bite force to cut the same plant.

## Introduction

1 Plant-feeding occurs at vastly different scales, from large bulk-  
2 feeding mammals to tiny cell-ingesting leaf miners [1]. Despite  
3 these differences in scale, all herbivores share the same basic  
4 task: they need to mechanically process the plant tissue; if they  
5 cannot tear, masticate, cut, pierce or drill into the plant, they  
6 cannot feed on it. From a simple mechanical perspective, a nec-  
7 essary condition for plant-feeding is then given by the ratio of  
8 two key forces: the maximum force the animal can generate  
9 needs to exceed the minimum force required to fracture the plant  
10 tissue [1–3]. How do these forces change with animal size?

11 Based on a simple scaling argument, the maximum available  
12 force is expected to increase in proportion to a characteristic  
13 area, or with body mass to the power of two-thirds [4]. How-  
14 ever, the scaling of the fracture force is difficult to predict, be-  
15 cause it depends on plant-mechanical properties [5–9], the mode  
16 of fracture [3, 5], and on the geometry of the cutting, chewing  
17 or piercing ‘tool’ in question [10–15]. In absence of robust the-  
18 oretical frameworks, fracture forces are often determined exper-  
19 imentally instead [e. g. 12, 14, 16, 17]. A key challenge for such  
20 experimental approaches is that studies across a large tool size  
21 range typically require using different species, so that fracture  
22 tools usually differ in both scale and shape [2, 12]. In order to  
23 investigate the influence of tool size alone, we here measured  
24 fracture forces using the cutting tools of a species for which  
25 adults vary substantially in size but only little in shape: *Atta*  
26 *vollenweideri* leaf-cutter ants.

27 Leaf-cutter ant colonies consist of up to several million work-  
28 ers, which cover a large range of body sizes, from less than a  
29 milligram to over 100 mg in some *Atta* species [18–21]. No-  
30 tably, this size range reflects ‘static’ differences among workers  
31 of equivalent developmental stages; workers retain their adult  
32 form after eclosion from the pupa. Fully-matured leaf-cutter ant  
33 foragers cut leaf fragments from plants in the colony surround-  
34 ings; these fragments are then carried back to the colony to feed  
35 them to a subterranean fungus grown as crop [22–25]. To cut  
36 transportable fragments from large leaves, leaf-cutter ants typ-  
37 ically use one of their mandibles as an ‘anchor’ which pierces

through the leaf lamina but remains approximately static; a sin-  
gle cut is then made by drawing the second mandible through  
the leaf lamina like a blade [26, 27, see SI video]. Repeated  
cutting cycles, combined with a ‘pivoting’ of the ant around an  
approximately fixed anchor point for the hind legs, then yields  
leaf fragments with semi-circular shape that can be carried back  
to the nest [e. g. 26, 28]. Interestingly, the tendency to cut and  
carry plant fragments correlates with worker size: larger ants  
cut and carry larger fragments [19, 28–30], at higher speeds  
[27, 30–35], and forage on ‘tougher’ plants than smaller ants  
[23, 24, 28, 31, 33, 36–38].

In contrast to this robust empirical evidence for size-related  
preferences in foraging, the biomechanical factors that underpin  
it remain poorly understood [but see 27, 28, 39]. For example,  
do larger workers cut tougher leaves because smaller workers  
are unable to do so, or because they are more efficient? In order  
to assess how the ability to cut leaves varies with size, we pre-  
viously measured the maximum bite forces of *A. vollenweideri*  
leaf-cutter ants [40]. Peak bite forces increased with strong posi-  
tive allometry,  $F_b \propto m^{0.90}$ , in substantial excess of the isometric  
prediction,  $F_b \propto m^{0.67}$ : A large forager of 40 mg generates peak  
bite forces of about 800 mN, 16 times more than a small forager  
of 2 mg,  $F_b \approx 50$  mN, and about as large as the bite forces of a  
vertebrate 20 times heavier [40]. As a result, large foragers are  
presumably able to cut a considerably larger fraction of tropical  
leaves [8, 40].

However, this conclusion is speculative, because it remains  
unclear how the forces required to cut vary with mandible size.  
For example, one may speculate that cutting forces vary with a  
characteristic length [e. g. 12, 41, 42]; smaller ants would then  
have ‘sharper’ mandibles which demand less force to cut a given  
material. To complicate matters further, mandible ‘sharpness’  
may vary across the lifetime of an ant due to mandibular wear  
[27]. The degree of mandibular wear likely depends on the abra-  
siveness of the cut materials [43, 44], the wear resistance of the  
mandible teeth [45–47], the mandible tooth geometry [2, 12],  
and the forces involved in cutting [12]. To investigate the im-  
pact of mandibular wear on cutting forces and to compare it to  
the impact of size, we performed cutting force experiments us-

77 ing either mandibles from freshly eclosed ants (callows), which  
78 initially remain in the nest and thus have ‘pristine’ mandibles,  
79 or from workers which actively partook in foraging, and thus  
80 are likely to have worn mandibles. We hypothesise (i) that  
81 mandibles of small ants cut with less force because they are  
82 sharper, and (ii) that forager mandibles require the application  
83 of larger forces compared to callow mandibles of the same size,  
84 as they are blunted by wear.

## 85 Materials & methods

### 86 Study animals

87 We sampled *A. vollenweideri* leaf-cutter ants from two colonies,  
88 founded and collected in Uruguay in 2014. The colonies were  
89 kept in a climate chamber (FitoClima 12.000 PH, Aralab, Rio de  
90 Mouro, Portugal) at 25 °C and 50 - 60 % relative humidity, with  
91 a 12/12 h light-dark cycle. They were provided with bramble,  
92 laurel, maize and honey water *ad libitum*, supplied in a foraging  
93 arena that was connected to the main colony via PVC tubes ( $\approx$   
94 30cm to the closest fungus box; 25 mm inner tube diameter).

95 To quantify the force required to cut thin leaf-like sheets with  
96 mandibles of different sizes, we collected two sets of ants across  
97 the worker size-range excluding the smallest workers, which  
98 typically do not cut leaves [body mass <1 mg, see 24, 48].

99 First, we extracted workers from the fungal garden that had  
100 either freshly eclosed, identified by their bright cuticle, or were  
101 still in the pupal stage [ $n = 46, 27, 49$ ]. In the weeks following  
102 eclosion, callows remain inside the nest and abstain from for-  
103 aging activities [24, 50]. The mandibles of callow workers are  
104 thus likely ‘pristine’, which allowed us to test for the effect of  
105 mandible size on cutting force without potentially confounding  
106 effects due to mandibular wear [27]. To ensure that the incor-  
107 poration of zinc into the mandibular teeth was completed, cal-  
108 lows were kept alive for at least 72 h post eclosion, defined as  
109 time point at which the legs had completely unfolded [27, 49].  
110 To monitor pupae and callows, they were placed in centrifuge  
111 tubes, which in turn were kept inside the foraging arena. The  
112 tubes contained small amounts of fungus, and had a 3D-printed  
113 polylactic acid (PLA) lid with holes too small for the collected  
114 workers to pass through, but large enough for minims to enter  
115 for pupal maintenance [27]. This method was thus unsuitable  
116 for smaller ants (<10 mg), which were collected by transfer-  
117 ring late-stage pupae into a separated container with sufficient  
118 amounts of fungus and numerous minims instead. Hatched ants  
119 were marked with a unique colour code [Edding 4000 paint  
120 marker, Edding AG, Ahrensburg, Germany; 51].

121 Second, we collected fully-matured workers from the forag-  
122 ing arena ( $n = 39$ ). Depending on their age, these workers may  
123 have mandibles worn from the repeated cutting of leaves [27].  
124 Quantifying the mandibular cutting forces for active workers al-  
125 lowed us to investigate the effect of mandibular wear and its  
126 interaction with worker size.

### 127 Mandible preparation and wear quantification

128 All ants were sacrificed by freezing, weighed to the nearest  
129 0.1 mg (Explorer Analytical EX124, max. 120 g x 0.1 mg,  
130 OHAUS Corp., Parsippany, NJ, USA; body mass ranged be-  
131 tween 1.8 to 46.4 mg), and decapitated using micro-scissors.  
132 The head capsules were split in half along the sagittal plane us-  
133 ing a scalpel, and only the left head hemisphere was retained

(see Fig. 1A). Leaf-cutter ants show no preference between left  
and right mandible when cutting [26], and their bite apparatus is  
bilaterally symmetric [52]. We hence assume that there are no  
systematic differences between both sides. To facilitate sample  
mounting, insect pins were inserted into the head halves (size  
‘2’ for ants < 10 mg, size ‘4’ for ants of 10-20 mg, and size ‘6’  
for ants > 20 mg; Shigakontyu, Tokyo, Japan). The interface be-  
tween insect pin, head capsule and mandible base was then im-  
mobilised with two-component epoxy to minimise compliance  
of the mandible-head-pin complex (Araldite Rapid, Huntsman  
Corp., The Woodlands, TX, USA; see Fig. 1A).

In order to determine a proxy for the degree of mandibular  
wear, all mandibles were photographed with a camera mounted  
onto a light microscope, such that their dorsal surface was in  
focus (DMC5400 on Z6 Apo, Leica Microsystems GmbH, Wet-  
zlar, Germany; see Fig. 1B). Numerous empirical metrics for  
mandibular wear have been proposed in literature, including  
variation of mandible length [53, 54], shape changes of the  
mandibular cutting edge [55–57], number of lost mandibular  
teeth [58], reduction in profile area of distal mandibular teeth  
[59], and length changes of the mandibular teeth most rele-  
vant for cutting [27, 60]. All of these metrics are proxies with  
no direct established mechanistic relation to cutting force. As  
such, their predictive value can only be assessed in correlation  
to direct cutting force measurements, and selecting any one of  
them is difficult to justify *a priori*. We chose a metric that has  
been demonstrated to correlate significantly with cutting force  
in closely-related *A. cephalotes* ants, so enabling a direct com-  
parison [27]; however, we do not intend to imply that this met-  
ric is more or less predictive than any of the others. Following  
Schofield et al. [27], a mandibular wear index,  $W$ , was thus  
defined as:

$$W = (\Delta T_2 + \alpha \Delta T_1) / 2 \quad (1)$$

Here,  $\Delta T_1$  and  $\Delta T_2$  are the differences between observed and  
pristine tooth length for the most distal and second most distal  
tooth, respectively;  $\alpha$  is a weighting factor, defined as ratio be-  
tween the average length differences,  $\alpha = \overline{\Delta T_2} / \overline{\Delta T_1}$  [for more  
details, 27]. This wear index has dimension length, and may  
be interpreted as the weighted average length change of the two  
distal-most teeth. This wear index definition thus is a proxy for  
absolute rather than relative wear.

To calculate the wear index, the length of the mandible blade  
and the two most distal teeth were measured from each photo-  
graph (see Fig. 1B), and the pristine tooth length as function of  
body mass was estimated via regression analysis on measure-  
ments of callow mandibles (for exact methodology, see SI). The  
wear index could not be extracted for 17 out of 76 mandibles,  
because relevant parts of the mandible were obstructed by the  
head capsule.

### 182 Cutting force setup

Mandibular cutting forces were measured with a custom-built  
setup based on a fibre-optic displacement sensor ( $\mu$ DMS-RC32  
controlled via DMS Control v3.015, Philtec Inc. Annapolis,  
MD, USA; linear range of 2.5 mm, recording at 81.4 Hz at 30°  
and 50 % transmitted optical power). The sensor was held in  
place by a custom-built holder, mounted on two micromanipula-  
tors to control its orientation, and attached to a piezo motor stage  
(M-404.6PD controlled via PIMikroMove v2.33.3.0, Physik In-

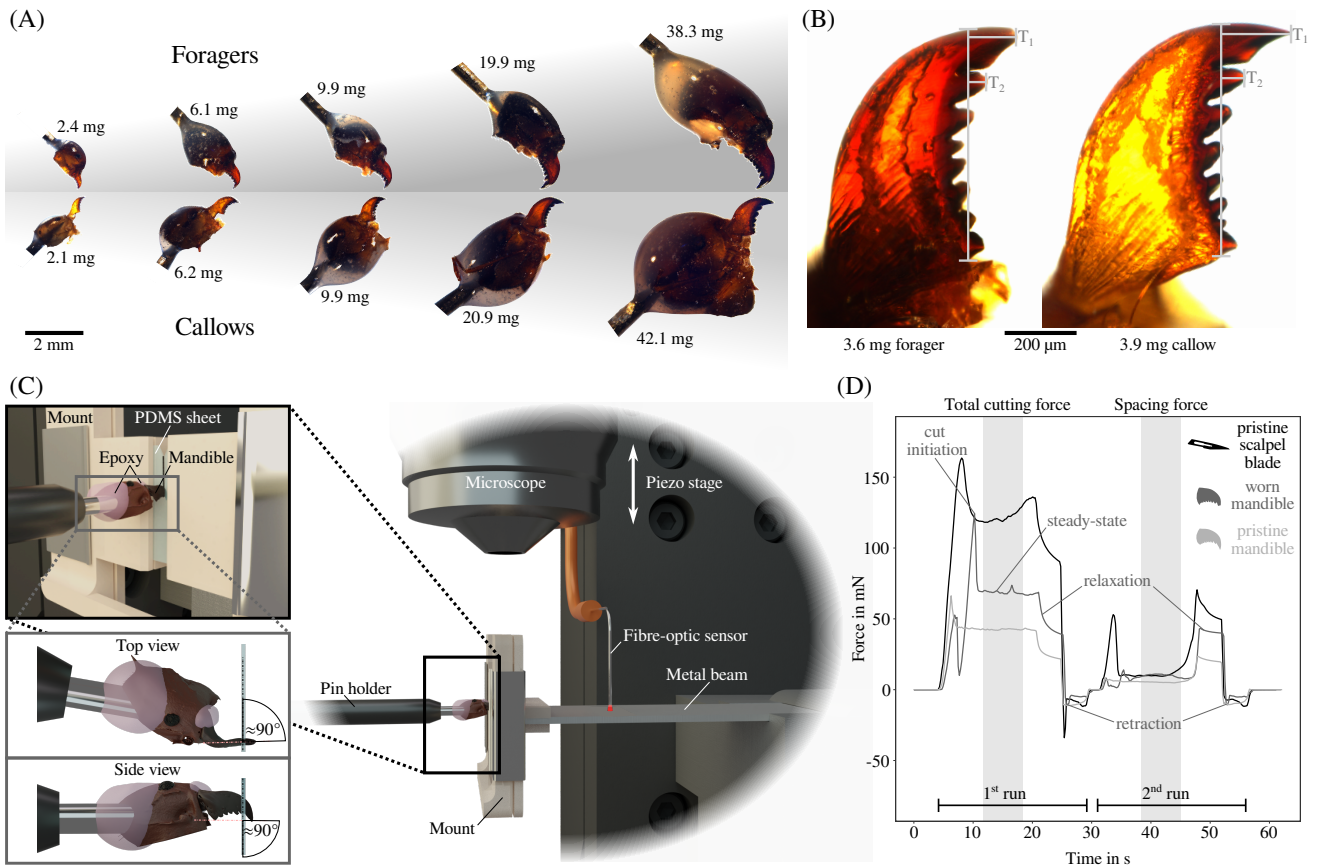


Figure 1 | (A) In order to measure mandibular cutting forces, *Atta vollenweideri* leaf-cutter ants were extracted from the foraging arena and fungal garden of mature colonies (body mass: 1.8-46.4 mg). Both foragers (with worn mandibles) and callows (with pristine mandibles) were used for the experiments to quantify the effects of both worker size and mandibular wear on cutting force. (B) For each mandible, we calculated a wear index based on absolute length changes to the most and second most distal teeth,  $T_1$  and  $T_2$ , respectively [see 27, and SI for more details]. (C) Cutting forces were then measured using a custom-built setup based on a fibre-optic displacement sensor and a bending beam, both connected to a piezo motor stage. A PDMS sheet was fixed in a custom-designed holder, mounted at the free end of the beam, and the mandible was positioned above the sheet such that its cutting edge was perpendicular to the sheet plane. The motor then moved the beam mounting vertically against the mandible, causing the sheet to be cut and the beam to deflect. (D) After an initial loading phase, cutting force peaked at cut initiation, and then dropped to an approximately constant value. At the end of this ‘steady-state’ phase, the forces dropped again when the motor stopped and became negative as the setup was moved back to its original position. A second run through the cut was performed in the same position to extract the spacing force ‘lost’ to sheet bending and friction [e.g. 11, 42]. The drift-corrected average total cutting force and the corresponding spacing force across 2 mm cutting distance (shaded areas) were extracted for further analysis.

191 strumente GmbH & Co. KG, Karlsruhe, Germany; see Fig. 1C).  
 192 The sensor was placed above a stainless steel bending beam  
 193 with a thickness of 0.35 mm, a width of 10.4 mm, and a free  
 194 length of 28.7 mm, such that the sensor tip was about 400  $\mu\text{m}$   
 195 above the beam surface [see 61, for a similar setup]. The beam  
 196 was clamped to the motor stage at one side. At the free end of  
 197 the beam, a 3D printed mount was attached. This mount held  
 198 the cutting substrate during the experiments, clamped in place  
 199 by two metal clips on either side (Supaclip 40, Rapesco Of-  
 200 fice Products PLC, Sevenoaks, UK). At the centre of the mount,  
 201 there was a ‘free’ cutting region (1.5 mm wide and 8 mm long),  
 202 over which mandibles or scalpel blades were positioned for cut-  
 203 ting experiments (see Fig. 1C).

204 The sensor was calibrated with a series of ten calibration  
 205 weights ranging between 10-245 mN (1-25 g, Kern & Sohn  
 206 GmbH, Balingen, Germany), covering the range of observed to-  
 207 tal cutting forces (19 - 172 mN). Weights were suspended from  
 208 the mount in increasing order, and at the lever arm at which  
 209 cutting forces were applied. For each calibration weight, we  
 210 averaged the sensor output across 5 s after initial force fluctu-

211 ations had faded (see SI Fig. 2C). To account for sensor drift,  
 212 the sensor output was extracted for the unloaded beam at the  
 213 beginning and end of the measurement, and a linear drift cor-  
 214 rection was implemented; sensor drift, however, was generally  
 215 small,  $\approx 0.01 \text{ mN s}^{-1}$ , or  $6 \text{ mN min}^{-1}$ , and thus less than 5% of  
 216 the smallest total cutting force over the duration of a typical  
 217 measurement of 60 s. From simple beam theory, the relation-  
 218 ship between applied force and beam deflection should be linear  
 219 for small deflections. We indeed observed linearity for cali-  
 220 bration forces  $< 150 \text{ mN}$ ; for forces exceeding 150 mN, how-  
 221 ever, the sensor distance was systematically ‘sub-linear’, sug-  
 222 gesting deflections sufficiently large to invalidate the use of the  
 223 small angle approximation. We thus used a quadratic regres-  
 224 sion model to characterise the relationship between force and  
 225 distance, which accounted for more than 99% of the variation,  
 226 and yielded a lower Akaike Information Criterion compared to  
 227 a linear or cubic model ( $\text{AIC}_{\text{linear}} = 91.7$ ,  $\text{AIC}_{\text{quadratic}} = 59.6$ ,  
 228  $\text{AIC}_{\text{cubic}} = 61.6$ ; see SI Fig. 2D).

## 229 Polymer sheet production and mechanical 230 testing

231 Previous studies on mandibular cutting forces used leaf lamina  
232 and floral petals as cutting substrates [26, 27]. This choice has  
233 the advantage that it is of direct biological relevance. However,  
234 plant tissues are typically heterogeneous, of uneven thickness,  
235 and have mechanical properties that vary with hydration and  
236 tissue age, so introducing potential for substantial covariation  
237 that is difficult to control [e. g. 9, 62–65]. In order to minimise  
238 variation due to material inhomogeneities, we used well-defined  
239 PDMS sheets as cutting substrate.

240 PDMS sheets were made with a 4:1 (silicon base: curing  
241 agent) mixing ratio (SYLGARD 184, Dow Inc., Midland, MI,  
242 USA). The mixed but uncured PDMS was sandwiched between  
243 two silanised glass plates, separated by feeler gauges (200 $\mu$ m,  
244 Precision Brand, Downers Grove, IL, USA; see SI Fig. 2A),  
245 and pre-cured in an oven at 100°C for two hours (Drying oven,  
246 Sanyo Electric Co., Ltd., Osaka, Japan). The PDMS ‘sandwich’  
247 was then cooled to room temperature, slowly peeled from the  
248 glass plates, placed on aluminium foil, and fully cured at 165°C  
249 for a further 48 hours [66]. Sheet thickness was verified through  
250 measurement at six random locations across the sheet with a  
251 digital micrometer (max. 25 mm x 0.001 mm, Mitutoyo Corp.,  
252 Kawasaki, Japan), and was  $215 \pm 8 \mu\text{m}$  (mean  $\pm$  standard deviation),  
253 or within 10% of the target thickness.

254 To mechanically characterise the PDMS sheets, pure shear  
255 tearing and uniaxial tension tests were conducted with a univer-  
256 sal tension and compression system (Multitest5-xt, Mecmesin  
257 Ltd., Slinfold, UK; 10 N load cell and Mec277 double-action  
258 vice grips with diamond jaws). Two rectangular samples from  
259 each of the eight PDMS sheets were cut and used for pure shear  
260 tearing; in one of the two paired samples, a notch of 3 mm length  
261 was introduced at the centre of the short side (see SI Fig. 2A for  
262 dimensions). Both samples were tested at a small strain rate  
263 of  $0.0067 \text{ s}^{-1}$  (test speed divided by sample height) to approxi-  
264 mate quasi-static loading conditions. The critical displacement  
265 to rupture was then extracted from the notched sample based on  
266 a time-synchronised video recording. The force-distance curve  
267 of the unnotched sample was integrated from zero to this critical  
268 displacement to obtain the work done by the applied load.  
269 Fracture toughness was then calculated as this work divided by  
270 sample width and thickness [for more details, see 67, 68], yield-  
271 ing an average of  $G_c = 98 \pm 7 \text{ J m}^{-2}$  [for comparison, see 68].

272 Next, uniaxial tension tests at  $0.5 \text{ mm s}^{-1}$  motor speed were  
273 conducted with two ‘dog-bone’ samples cut from each of eight  
274 sheets according to ISO standards (ISO37 and ISO5893). The  
275 Young’s modulus was extracted from the loading region of the  
276 stress-strain curve via linear regression between 0–10% strain  
277 [69, 70]; on average, the Young’s modulus was  $E = 4.1 \pm$   
278  $0.3 \text{ MPa}$  [in agreement with published values, 66].

## 279 Cutting experiments

280 Individual ant heads were fixed onto a pin holder, which was  
281 connected to a 3D micromanipulator ( $n = 85$ ; Manipulator MM  
282 33, Märzhäuser Wetzlar GmbH & Co. KG, Wetzlar, Germany).  
283 The mandibles were then positioned using a top-down micro-  
284 scope such that the dorso-ventral head axis was approximately  
285 horizontal, the mandibular teeth were roughly perpendicular to  
286 the PDMS sheet, and the most distal tooth tip just about ex-  
287 tended over the sheet edge [see 27, and Fig. 1C].

288 We cut a small wedge into all PDMS sheets ( $\approx 30^\circ$  and  
289 1.5 mm deep) to facilitate cut initiation by reducing effects of  
290 sheet bending and buckling [27, 68, 71]. The unstretched sheets  
291 were then placed individually between the two components of  
292 the polymer mount, and metal clips were slid onto the mount  
293 using the clip dispenser provided by the manufacturer, such that  
294 both clamps were approximately parallel and 6 mm away from  
295 the mount centre (see Fig. 1C); this procedure ensured that the  
296 clamping conditions were kept approximately constant across  
297 measurements.

298 The beam mount was then moved toward the mandible until  
299 the tip of the pre-cut wedge was about to contact the mandibu-  
300 lar cutting edge. The sensor recording was started, and the beam  
301 mount was moved vertically against the mandible blade, result-  
302 ing in cutting motion somewhat akin to the ‘blade-like’ cutting  
303 behaviour observed in freely cutting leaf-cutter ants [26, 27].  
304 The motor moved at a constant speed of  $0.3 \text{ mm s}^{-1}$ , at the up-  
305 per end of cutting speeds observed during foraging [ $\approx 0.02 -$   
306  $0.30 \text{ mm s}^{-1}$ , 23, 26, 27, 30, 33, 34, 72], and over a total dis-  
307 tance of 5 mm; the beam deflected by around  $100 \mu\text{m}$  for a  
308 medium cutting force of 65 mN, so that the corresponding dis-  
309 placement of the sheet-holding mount was about 4.9 mm (see SI  
310 Fig. 2C & D). The sheet was subsequently retracted to its origi-  
311 nal position, and a second run was initiated in order to extract  
312 the force due to elastic sheet deformation and sidewall friction  
313 [henceforth referred to as spacing force, e. g. 11, 42, 73, 74]. After  
314 a force peak at cut initiation, the total cutting force remained  
315 approximately constant until the motor stopped, and force de-  
316 creased (see Fig. 1D). We extracted the drift-corrected steady-  
317 state total cutting force averaged across 2 mm following the ini-  
318 tial peak; the corresponding spacing forces were extracted from  
319 the second run at the same motor positions, and averaged across  
320 the same distance (see Fig. 1D).

321 Cutting speeds typically vary with forager size; larger ants cut  
322 more quickly than smaller ants [27, 33, 34]. The effects of speed  
323 on cutting force depend on the viscoelastic properties of the ma-  
324 terial, but are typically small for elastomers such as PDMS cut at  
325 low rates [68, 75]. To briefly confirm that the speed-dependency  
326 is indeed small, we performed a series of measurements with  
327 the mandible of a single forager with a body mass of 19.9 mg  
328 at  $0.1 \text{ mm s}^{-1}$ ,  $0.2 \text{ mm s}^{-1}$  and  $0.3 \text{ mm s}^{-1}$  motor speed. Three  
329 repetitions were completed per speed, without remounting the  
330 mandible between measurements to reduce confounding effects  
331 due to small variations in mandible blade orientation. Variation  
332 due to remounting was quantified by measuring cutting forces  
333 of one small (5.4 mg) and one large forager (38.4 mg) at a con-  
334 stant cutting speed of  $0.3 \text{ mm s}^{-1}$ . Both samples were mounted  
335 three times onto the pin holder, and cutting experiments were  
336 performed three times per mount.

337 Mounting had no significant effect on total cutting force  
338 (Analysis of Variance (ANOVA), small worker:  $F_{2,6} = 4.43$ ,  $p =$   
339  $0.07$ ; ANOVA, large worker:  $F_{2,6} = 0.26$ ,  $p = 0.71$ ); we hence  
340 pooled the nine measurements per mandible and calculated the  
341 coefficients of variation,  $CV_{\text{small}} = 0.10$  and  $CV_{\text{large}} = 0.03$  (see  
342 SI Fig. 1). The relative force variation was significantly larger  
343 for the smaller mandible [Asymptotic test for equality of CV:  
344  $D_{AD} = 7.76$ ,  $p < 0.01$ , implemented in the R package ‘cvequal-  
345 ity’, v 0.2.0, 76], suggesting that consistent mandible alignment  
346 is easier for larger mandibles. However, even for the smaller  
347 mandible, the force variation was small in comparison to the  
348 inter-individual variation across all foragers,  $CV_{\text{foragers}} = 0.52$   
349 (see below). We thus performed only a single measurement per

specimen, unless otherwise indicated.

To contextualise our results based on *biological* ant mandibles and *synthetic* PDMS sheets, we performed two additional experiments. First, we measured cutting forces of pristine scalpel blades (Carbon steel, No.11, Swann-Morton Ltd., Sheffield, UK), positioned such that the blade tip just about extended over the sheet edge to reduce the contact area with the PDMS sheet ( $n = 5$ ). Second, we performed cutting experiments with mandibles on a biological substrate, the leaf lamina of Japanese laurel, *Aucuba japonica*; the colonies were regularly fed with these leaves, and the lamina appeared comparatively homogeneous. Laurel leaves were cut from the plant on the day of the experiment, and kept hydrated using wet tissues between collection and measurement. To reduce variation due to material inhomogeneities, we cut all laurel samples from the same plant, from a leaf region close to the mid-vein. Prior to the cutting experiment, we measured lamina thickness and mounted the samples such that the cut ran perpendicular to the mid-vein. We used mandibles of 13 out of the 85 prepared ants, seven foragers (body mass 5.4 - 38.8 mg) and six callows (body mass 6.2 - 46.4 mg), mounted once with 1-3 repetitions per specimen. To account for differences in lamina thickness,  $t_l$ , we corrected the measured total cutting force,  $F_{m,c}$ , as  $F_c = F_{m,c} \bar{t}_l / t_l$ , where  $\bar{t}_l$  was the average lamina thickness ( $256 \pm 29 \mu\text{m}$ ).

Across all experiments, measurements were considered invalid and thus repeated when at least one of the following criteria was met: (i) the head capsule came into contact with the clamp or the cutting substrates; this occurred when the head capsule was initially close to the clamp and the PDMS sheet buckled; (ii) the mandible slipped out of the cut; (iii) the steady-state phase was too short to extract a meaningful cutting force ( $< 2 \text{ mm}$ ); (iv) the epoxy fixation of the joint failed, leading to mandible rotation; in these cases, the samples were re-glued and used again; and (v) the sample slipped out of the pin holder as observed occasionally for measurements involving high cutting force as on laurel (see below).

## Data curation and statistical analysis

We excluded a total of four out of 46 callows and five out of 39 foragers, because optical inspection of the mandible suggested that small amounts of epoxy contaminated the mandibular teeth, and cleaning attempts failed or caused visible damage. Additionally, we excluded one out of seven forager-laurel measurements, because the total cutting force exceeded the calibration range ( $> 245 \text{ mN}$ ).

Extraction of the average total cutting and spacing force from the raw data was done in python [v 3.9.7, 77], and all statistical analyses were conducted in R [v 4.1.1, 78]. To characterise the relationship between the extracted forces, body mass, and the two experimental groups (foragers vs callows), we used Analysis of Covariance (ANCOVA) with Type III sums of squares [79]. In addition, we performed Ordinary Least Squares (OLS) regressions to characterise the scaling relationships within the experimental groups. Unless stated otherwise, we performed these analyses on  $\log_{10}$ -transformed data.

## Results

### Cutting forces are independent of mandible size

Total cutting forces,  $F_c$ , were independent of body mass (ANCOVA:  $F_{1,72} = 0.97$ ,  $p = 0.33$ ), but depended significantly on the experimental group (callows, vs forager,  $F_{1,72} = 21.2$ ,  $p < 0.001$ ; see Fig. 2A). These main effects must be interpreted with caution as the interaction term was significant [ $F_{1,72} = 4.42$ ,  $p < 0.05$ , see 79], suggesting that the relationship between total cutting force and body mass may differ between the experimental groups. Indeed, within callows, total cutting forces tended to increase with body mass, whereas they decreased slightly within foragers. However, neither result was significant ( $p \geq 0.11$ , see Table 1).

Averaged among experimental groups, total cutting forces of foragers exceeded those of callows by a factor of two,  $64 \pm 33 \text{ mN}$  vs  $31 \pm 7 \text{ mN}$ , respectively (see Fig. 2C). Notably, the coefficient of variation also differed significantly by about a factor of two ( $CV_{\text{foragers}} = 0.52$  and  $CV_{\text{callows}} = 0.23$ ; Asymptotic test for equality of CV:  $D_{AD} = 19.1$ ,  $p < 0.001$ ), suggesting that both relative and absolute force variation was larger among foragers. Despite these differences, the magnitude of total cutting force extracted for both groups was small in comparison to that of pristine scalpel blades,  $105 \pm 34 \text{ mN}$ , (see Fig. 2C; Wilcoxon rank sum test, forager mandibles vs scalpel blades:  $W = 29$ ,  $p < 0.05$ ; callow mandibles vs scalpel blades:  $W = 0$ ,  $p < 0.001$ ).

Across all ant mandibles, spacing forces,  $F_s$ , were  $5 \pm 3 \text{ mN}$  with neither significant differences between experimental groups, nor significant size-effects (ANCOVA, experimental group:  $F_{1,72} = 0.34$ ,  $p = 0.56$ ; body mass:  $F_{1,72} = 0.25$ ,  $p = 0.62$ ; see Table 1 and SI figure). Because callow mandibles cut with less force, the relative spacing component was about two times higher ( $15 \pm 8 \%$  vs  $8 \pm 6 \%$  (ANCOVA:  $F_{1,72} = 5.98$ ,  $p < 0.05$ ). Spacing forces of scalpel blades were  $12 \pm 4 \text{ mN}$ , or  $14 \pm 8 \%$  of the cutting forces, significantly larger than for callow and forager mandibles (see Fig. 2C; Wilcoxon rank sum test, forager mandibles vs scalpel blades:  $W = 8$ ,  $p < 0.001$ ; callow mandibles vs scalpel blades:  $W = 10$ ,  $p < 0.001$ ).

Because mandible spacing forces were size-invariant, the scaling of fracture forces,  $F_f = F_c - F_s$ , essentially mirrored the results obtained for the total cutting force (see Fig. 2B). Fracture forces were independent of body mass (ANCOVA:  $F_{1,72} = 1.64$ ,  $p = 0.20$ ), but depended significantly on experimental group ( $F_{1,72} = 22.6$ ,  $p < 0.001$ ), with a significant interaction ( $F_{1,72} = 4.46$ ,  $p < 0.05$ ). Within foragers,  $F_f$  tended to decrease with size, but this trend was not significant ( $p = 0.22$ , see Table 1); on average,  $F_f$  was  $59 \pm 32 \text{ mN}$ , comparable to the minimum force obtained for scalpel blades ( $44 \text{ mN}$ ). Within callows, however,  $F_f$  now increased significantly with worker size ( $p < 0.05$ , see Table 1), at the lower end approaching the minimum cutting forces predicted from tearing experiments ( $21 \text{ mN}$ , see Fig. 2B and discussion).

To test if the observed differences in mandibular cutting force between callow and forager mandibles is also present with biological substrates, we measured cutting forces for a small subset from both experimental groups with laurel leaf lamina. Total cutting forces, corrected for differences in lamina thickness, were  $141 \pm 44 \text{ mN}$  for foragers, exceeding those of callows ( $95 \pm 14 \text{ mN}$ ) by almost  $50 \text{ mN}$  (see Fig. 3A); this difference was not significant (Welch Two Sample t-test:  $t_{5,99} = -$

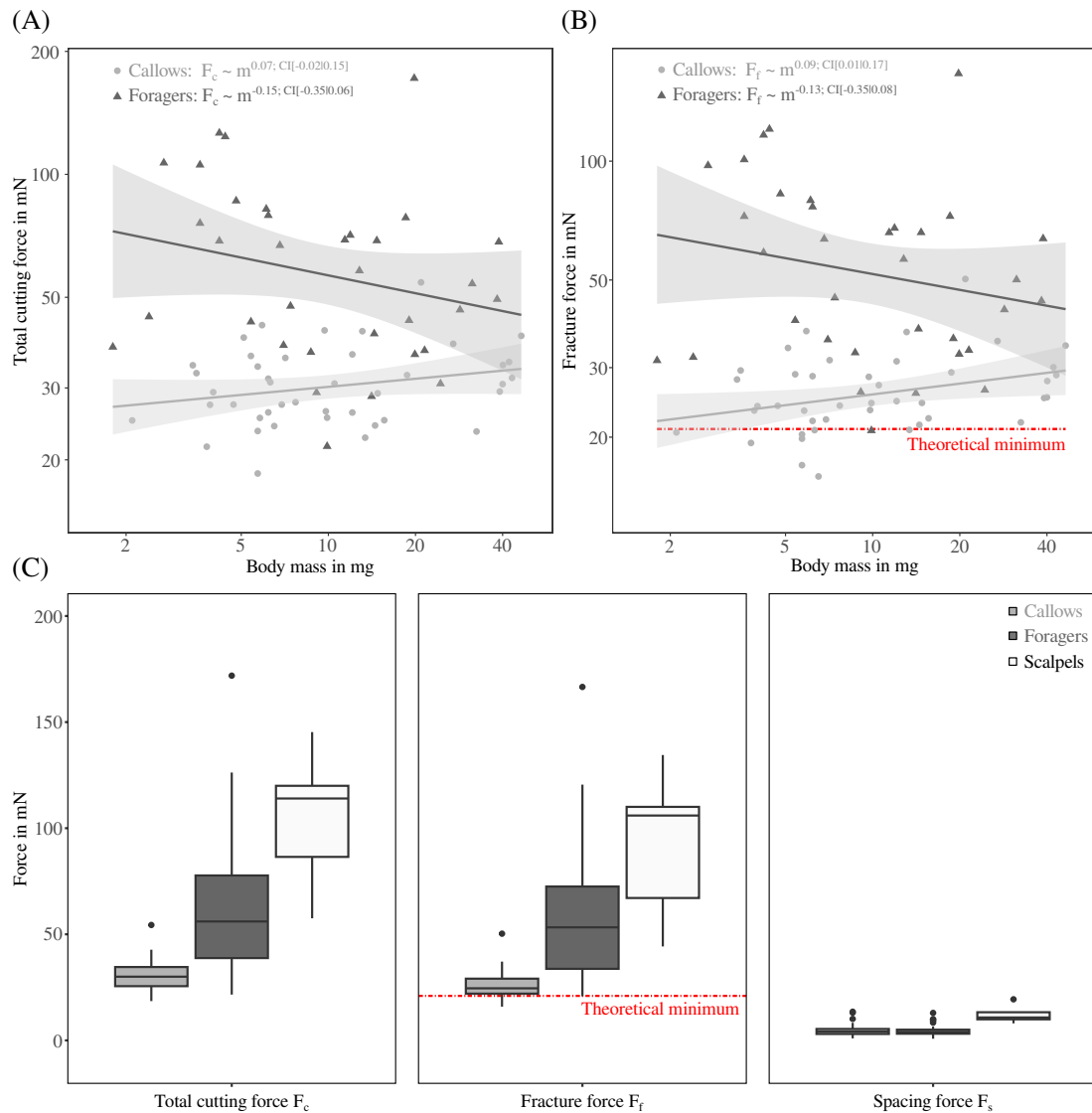


Figure 2 | **(A)** Leaf-cutting is performed by workers spanning approximately one order of magnitude in body mass. To assess how cutting ability is affected by body mass, we measured mandibular cutting forces across almost the entire size-range (body mass,  $m$ , 1.8 to 46.4 mg), and across two experimental groups: callows with pristine mandibles ( $n = 42$ ), and active foragers with mandibles affected to varying degrees by wear ( $n = 34$ ). Total cutting forces,  $F_c$ , were independent of body mass for both experimental groups (see main text for statistics), but twice as high for foragers compared to callows. **(B)** Fracture forces,  $F_f$ , were not significantly affected by body mass in foragers. For callows, however,  $F_f$  increased significantly,  $F_f \propto m^{0.09}$ , from values close to a theoretical minimum based on pure shear tearing tests to values closer to those obtained from foragers. **(C)** On average, total cutting and fracture forces of both groups were significantly smaller than those measured for pristine scalpel blades ( $n = 5$ ,  $F_c = 105 \pm 34$  mN,  $F_f = 92 \pm 36$  mN). Spacing forces,  $F_s$ , were about  $5 \pm 3$  mN for both groups independent of body mass, and significantly smaller than for scalpel blades. Spacing forces contributed around 10% of the total cutting force for mandibles.

Table 1 | Results of Ordinary Least Squares regressions describing the relationship between total cutting force,  $F_c$ , spacing force,  $F_s$ , fracture force,  $F_f$ , absolute and relative mandibular wear index,  $W$  and  $W^*$ , respectively, with body mass in mg. All regressions were performed on  $\log_{10}$ -transformed values, apart from mandibular wear which contained negative values; this regression was done on semi- $\log_{10}$ -transformed data instead. 95 % confidence intervals are provided in parentheses. The low  $R^2$  values underline that body size only had a small influence on all performance metrics.

Quantity / unit	Group	Elevation	Slope	$R^2$
$F_c$ / mN	Foragers	1.90 (1.69, 2.11)	-0.15 (-0.35, 0.06)	0.06
$F_c$ / mN	Callows	1.41 (1.33, 1.50)	0.07 (-0.02, 0.15)	0.06
$F_s$ / mN	Foragers	0.74 (0.51, 0.98)	-0.14 (-0.37, 0.08)	0.05
$F_s$ / mN	Callows	0.65 (0.42, 0.88)	-0.05 (-0.27, 0.16)	0.01
$F_f$ / mN	Foragers	1.85 (1.62, 2.07)	-0.13 (-0.35, 0.08)	0.05
$F_f$ / mN	Callows	1.32 (1.23, 1.41)	0.09 (0.01, 0.17)	0.11
$W$ / $\mu\text{m}$	Foragers	13.43 (1.75, 25.10)	-6.02 (-17.19, 5.16)	0.05
$W^*$ / (-)	Foragers	0.24 (0.07, 0.42)	-0.13 (-0.29, 0.04)	0.10

464 2.40,  $p = 0.054$ ). However, after subtracting spacing forces,  
 465 the difference in fracture force was significant ( $114 \pm 23$  mN vs  
 466  $85 \pm 11$  mN; Two Sample t-test:  $t_{10} = -2.68$ ,  $p < 0.05$ ), with  
 467 an average of 28 mN, similar to the result obtained for PDMS  
 468 (33 mN).

### 469 Cutting speed only has a small effect on 470 cutting force

471 The cutting speeds during natural foraging typically vary with  
 472 both worker size and leaf-mechanical properties; larger ants  
 473 cut faster than smaller ants, and ‘tougher’ leaves are cut more  
 474 slowly than ‘tender’ leaves [27, 33, 34]. We quantified the inter-  
 475 action between speed and total cutting force on synthetic PDMS  
 476 sheets: Total cutting forces increased significantly but modestly  
 477 with speed (ANOVA:  $F_{1,7} = 33.0$ ,  $p < 0.001$ ) from  $29 \pm 2$  mN  
 478 at  $0.1 \text{ mm s}^{-1}$  to  $36 \pm 1$  mN at  $0.3 \text{ mm s}^{-1}$  (see SI Fig. 1). Total  
 479 cutting forces thus increased by 20 % for a threefold increase in  
 480 speed.

### 481 Cutting forces increase significantly with 482 mandibular wear

483 The mean mandibular wear index of foragers was  $8 \pm 10 \mu\text{m}$ ,  
 484 significantly different from zero, defined as the pristine state  
 485 (One-sided Wilcoxon rank sum exact test:  $V = 272$ ,  $p <$   
 486  $0.001$ ), and independent of body mass (ANOVA on semi- $\log_{10}$ -  
 487 transformed data:  $F_{1,22} = 1.25$ ,  $p = 0.28$ ; see Table 1 and  
 488 Fig. 3B). This size-independence suggests that absolute wear  
 489 was the same across sizes, and thus that smaller ants lost a larger  
 490 fraction of their teeth to wear. Although the relative mandibu-  
 491 lar wear index, normalised with the pristine length of the second  
 492 most distal tooth, indeed slightly decreased with size from about  
 493 20 % for a 3 mg forager to 5 % for a 30 mg forager, this decrease  
 494 was not significant (ANOVA on semi- $\log_{10}$ -transformed data:  
 495  $F_{1,22} = 2.43$ ,  $p = 0.13$ ; see Table 1). Total cutting force increased  
 496 significantly with absolute wear at a rate of  $2.09 \text{ mN } \mu\text{m}^{-1}$  (OLS  
 497 regression on untransformed data: 95 % CI of slope (0.76 |  
 498 3.43),  $p < 0.01$ ,  $R^2 = 0.33$ ; see Fig. 3C), comparable to the rate  
 499 of  $3.7 \text{ mN } \mu\text{m}^{-1}$  reported for closely related *A. cephalotes* [27].

## Discussion

501 Leaf-cutter ants are iconic herbivores, with key impact on  
 502 ecosystem ecology throughout the Neotropics [25, 80]. The  
 503 continuous size-variation of their workers has also made them a  
 504 model system for the study of ergonomic benefits of advanced  
 505 polyethism in social insects [e.g. 24, 36, 81–83]. A key task  
 506 faced by any leaf-cutter colony is to cut fragments in the colony  
 507 surroundings, to maintain a fungus used as crop. Workers of  
 508 which size are best suited for this task? Larger workers gener-  
 509 ate larger bite forces, and may thus be able to cut a larger variety  
 510 of leaves [40, 52]. But the ability to cut depends not only on the  
 511 available bite force, but also on the force required to cut the leaf  
 512 with their mandibles – the key determinant is the ratio between  
 513 both forces. Larger mandibles are putatively blunter, and may  
 514 thus require larger bite forces to cut the same material [12–14].  
 515 How do cutting forces vary with mandible size?

516 In this work, we approached this question empirically, and  
 517 measured the forces required to cut homogenous PDMS sheets  
 518 with mandibles of workers of different body sizes. Cutting  
 519 forces varied only weakly with mandible size, but differed con-  
 520 siderably between mandibles taken from callows, which were  
 521 pristine, and mandibles taken from foragers, which were af-  
 522 fected to varying degree by wear. Before we discuss the bio-  
 523 logical implications and mechanical basis of these results, we  
 524 briefly address two key aspects in which our experiments differ  
 525 from natural cutting behaviour.

526 First, one may raise reasonable doubts about the extent to  
 527 which results obtained on a synthetic elastomer can enable  
 528 conclusions about biologically relevant cutting performance on  
 529 leaves. The choice of PDMS as a test substrate was motivated by  
 530 the need to minimise confounding variation in cutting forces due  
 531 to material inhomogeneities, age- and hydration-dependence,  
 532 expected for heterogeneous biological materials such as leaves  
 533 [e.g. 8, 9, 62–65]. However, whether mandibles cut PDMS or  
 534 leaves, the involved forces are amenable to mechanical analysis  
 535 from first principles. We provide such an analysis at the end of  
 536 the discussion, and the results confirm that the main conclusions  
 537 of our study likely port to biological substrates, so enabling an  
 538 initial discussion which focusses on biological implications.

539 Second, we acknowledge that even if experiments with

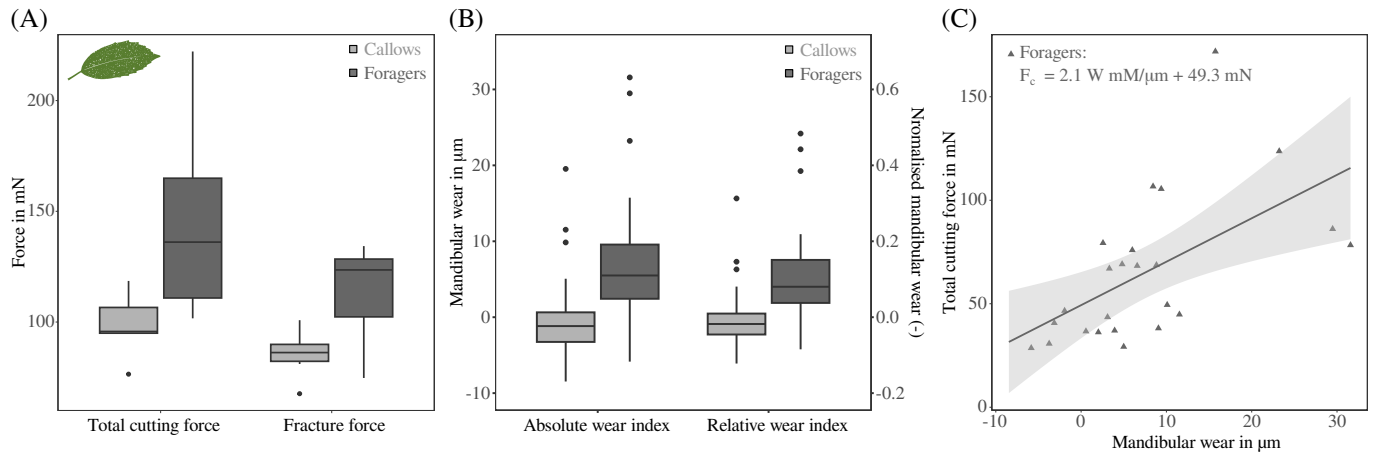


Figure 3 | (A) We tested if the difference in cutting force between callows and foragers persists with biological substrates by performing cutting experiments on *Aucuba japonica* leaf lamina with mandibles from six foragers and six callows across the size-range. The absolute difference in fracture force between callows and foragers was 28 mN, similar to the results obtained for PDMS sheets (33 mN). (B) We calculated a simple mandibular wear index, defined as the weighted average length change of the two most distal teeth [ $n = 66$ , see 27, and Eq. 1]. In foragers, the absolute wear index,  $W$ , was  $8 \pm 10 \mu\text{m}$ , independent of worker size; by definition,  $W$  was centred around zero for callows ( $0 \pm 5 \mu\text{m}$ ). On average, foragers lost approximately 12% of their distal teeth in length, as indicated by the relative wear index,  $W^*$ . (C) Mandibular cutting forces increased significantly with absolute wear index ( $n = 24$ , Ordinary Least Squares regression on forager data: slope = 2.09, 95 % CI (0.76 | 3.43),  $R^2 = 0.33$ ). Although the total variation explained by wear index remains below 50 %, it accounts for six times more variation than body mass.

540 PDMS can provide insights into cutting forces expected for  
 541 leaves, our cutting experiments do not fully mirror the complex-  
 542 ity of cutting behaviour of leaf-cutter ants. For example,  
 543 mandibles rotate instead of translate; neck muscles may be  
 544 used to change head and mandible orientation during cutting,  
 545 and perhaps even directly contribute to cut propagation; and  
 546 the section of the mandible blade used for cutting may be ad-  
 547 justed to account for local differences in mandible ‘sharpness’,  
 548 or to dynamically alter the effective mechanical advantage of  
 549 the mandible lever system. Despite these differences, two argu-  
 550 ments suggest that our experiments are informative: Cutting  
 551 forces of pristine mandibles were close to a theoretical mini-  
 552 mum for PDMS; and although more complex mandible motion  
 553 may decrease cutting forces in some cases [84, 85], out-of-plane  
 554 forces applied to thin sheets likely result in sheet bending in-  
 555 stead of concentrating tensile stresses, leading instead to an in-  
 556 crease in cutting forces. Because leaf-cutter ants already need  
 557 to show exceptional morphological and physiological adapta-  
 558 tions to be able to produce bite forces sufficient to cut leaves  
 559 [40, 86], it is biologically implausible and physically impossi-  
 560 ble that forces during ‘free cutting’ are substantially amplified  
 561 over the minimum force dictated by leaf toughness (see below  
 562 for a detailed quantitative argument).

### 563 Size-invariance of cutting forces puts larger 564 workers at an advantage

565 The weak size-dependence of cutting forces stands in stark con-  
 566 trast to the strong positive allometry of maximum bite forces  
 567 in *A. vollenweideri*, which grow in almost direct proportion  
 568 to body mass,  $F_b \propto m^{0.9}$  [40]. As a result of this difference,  
 569 the fraction of the maximum bite force required to cut the  
 570 same material will decrease almost in direct proportion to mass,  
 571  $F_c/F_b \propto m^{-0.9}$  – a factor of  $30^{0.9} \approx 20$  across the size range con-  
 572 sidered in this study. For materials that could in principle be cut  
 573 by workers across the size range, the differential scaling of bite  
 574 and cutting forces affords considerable behavioural flexibility to

larger workers, bound by two extreme choices.

575

576 First, larger workers may choose to bite with maximum force,  
 577 i. e. fully activate their closer muscles during cutting. The  
 578 excess force  $F_b/F_c$  directly determines the maximum possible  
 579 strain rate of the mandible closer muscle during cutting [87];  
 580 larger ants would then cut with substantially larger speeds. Cut-  
 581 ting speed amplification may be attenuated by viscoelastic ef-  
 582 fects which incur speed-dependent losses that increase the cut-  
 583 ting force. In fracture, viscoelastic losses amplify the critical  
 584 force by some power of the crack speed, and typically,  $F_t \propto \sqrt{v_c}$   
 585 [88–90]. However, cutting forces usually show a much smaller  
 586 speed-dependence, as the characteristic crack dimensions are  
 587 tied to cutting tool geometry instead [e. g. 68, 75]. Indeed, a  
 588 threefold increase in cutting speed resulted in an increase in cut-  
 589 ting force of only 20 %, compared to about  $\sqrt{3} \approx 75\%$  expected  
 590 for tearing [68, and see SI Fig. 1].

591 Second, and alternatively, large workers may choose to bite  
 592 with the same multiple of the required cutting force than small  
 593 workers, i. e. only sub-maximally activate the mandible closer  
 594 muscle during cutting, in which case muscle strain rate would be  
 595 identical [87]. Although the cutting speed of larger ants would  
 596 be sub-maximal as a result, this may be energetically advan-  
 597 tageous, because muscle operates with maximum mechanical  
 598 efficiency – the ratio between metabolic energy expended and  
 599 mechanical energy produced – over a narrow range of interme-  
 600 diate strain rates [91]. On the basis of these arguments, we sur-  
 601 mise that, even where a leaf can in principle be cut by small  
 602 workers, it may be advantageous to assign larger workers to the  
 603 task. In practise, foraging is a complex behaviour, and the be-  
 604 havioural choices of workers and their impact on the scaling of  
 605 cutting speed and mechanical efficiency need to be addressed  
 606 experimentally in future work.



## Cutting force variation is mainly driven by mandibular wear rather than body size

Throughout their life-time, leaf-cutter ant workers may cut a substantial amount of leaf tissue. To give a rough estimate, a mature colony of about one million foragers may cut about 3000 m<sup>2</sup> of leaf area per year [25], and each square meter may require  $\approx 3$  km of cutting [92]. Across the time period where a worker may actively forage [about 4 months, 50], it may thus cut approximately 3 m leaf tissue,  $(4 \cdot 3 \cdot 3 \cdot 10^6)/(12 \cdot 10^6) = 3$ , or about 500 times their body length [ $\approx 6$  mm for a typical *A. vollenweideri* forager, 93]. Such extensive leaf-cutting likely causes substantial mandibular wear [27]. Consistent with this conjecture is the observation that average cutting forces of pristine and forager mandibles differed by about 35 mN, or a factor of about two for PDMS sheets, comparable to results on leaf lamina reported for closely related *A. cephalotes* [27]. The absolute difference may sound small, but it amounts to about 50% of the force required to cut the median tropical leaf, and to about 15% of the maximum bite force of a medium 10 mg forager [8, 40]. In absence of a strong size-effect, it appears that most of the difference between pristine and forager mandibles stems directly from mandible wear, or natural, wear-independent variation in mandible geometry. Indeed, even a simple empirical wear index based on the weighted average length change of the two distal-most teeth captures a remarkable 30% of the variation in cutting force, in striking contrast to the meagre 5-10% of variation explained by body mass (see see Table 1).

The substantial effect of wear on cutting forces is biologically meaningful, for it implies that wear may almost compete with body size in determining the ability of a worker to cut a given substrate: Cutting forces for mandibles from workers with a body mass between 4-6 mg varied by a factor of seven ( $n = 14$ ), equivalent to the difference in maximum bite force between two workers that differ in mass by about a factor of  $7^{1/0.9} \approx 8$  [40]. The effect of wear can thus be as large as the effect of an eight-fold reduction in the effective physiological cross-sectional area of the mandible closer muscle [52]. Both the susceptibility and the exposure to wear may themselves be size-dependent, putting smaller workers at further disadvantage. Mandibles of smaller workers may be more susceptible to wear, because they have to exert similar forces, but have smaller characteristic dimensions [12, 27]; they may be more likely to be worn, because foraging parties tend to be dominated by ants of intermediate size (between 3-10 mg, O.K. Waltheus et al., unpublished data). In support of this hypothesis, three lines of evidence may be presented: First, in large workers (body mass  $> 30$  mg,  $n = 10$ ), cutting forces varied only by a factor of three across pristine and forager mandibles, as opposed to a factor of seven for the mandibles of small workers (body mass  $< 6$  mg,  $n = 24$ , see Fig. 2A). Second, although the scaling coefficients for total cutting forces of both callows and forager mandibles were not significantly different from zero (see Table 1), they were significantly different from each other (see results). Third, both absolute and relative wear index tended to decrease with size, although these trends were not significant (see results and SI figure).

Based on the significant increase of required cutting force with mandibular wear, we may speculate on the effect wear has on the fraction of cuttable leaves for both small and large workers. Previous analysis of leaf-mechanical data, in combination with bite force experiments, suggested that a 30 mg worker may be able to cut almost all species of tropical leaves, and a 3 mg

worker may be able to cut about half of them [8, 40]. Although this analysis neglected the effects of friction and mandible geometry, it may still serve as a reasonable starting point to estimate the effects of wear. We may calculate the reduction in the fraction of cuttable leaves based on the following two assumptions: First, the required cutting force for a pristine mandible,  $W = 0$ , is size-invariant and approximately equal to the product between fracture toughness and leaf lamina thickness (also see below). Second, the increase in cutting force with wear is material-independent and equal to the regression slope extracted for PDMS ( $2.09 \text{ mN } \mu\text{m}^{-1}$ ). For mandibles subjected to considerable wear,  $W = 20 \mu\text{m}$ , the minimum required cutting forces would thus be shifted up by  $\approx 40$  mN for all leaves. For a 30 mg worker, the fraction of cuttable leaves would be virtually unaffected (99.5%), whereas a 3 mg worker could cut from almost 50% of tropical leaves with pristine mandibles to less than 10% with worn mandibles.

The significant increase of required cutting force with wear, and the conjectured reduction in cuttable plant species, likely necessitates behavioural adaptations, and may partially explain ‘age polyethism’, i.e. systematic changes in task preferences with worker age. Indeed, leaf-cutter ants with worn mandibles cut at significantly lower speeds and are more likely to carry rather than cut [27]; the oldest colony workers may cease foraging altogether, and switch to mechanically less demanding tasks such as waste disposal [50, 94]. The role of wear in determining the mechanical performance of leaf-cutter ants in particular and herbivorous insects in general is worthy of considerably more attention than it has received [44, 53, 55, 57, 60, 95–97].

## Biomechanics of cutting – how sharp are ant mandibles?

The size-invariance of cutting forces and their strong sensitivity to wear have biological consequences. From a mechanical perspective, both results may be surprising at first glance, and thus call for a more thorough evaluation. Intuitively, it appears reasonable to expect that mandibles of larger workers require a larger force to cut the same material. Indeed, the force required to fracture thin or thick model ‘targets’ with biological puncture tools increases significantly with characteristic dimensions of the tool, such as the tip diameter [12, 14]. The expectation that tool size influences mechanical performance is closely tied to the notion of tool ‘sharpness’. However, a robust definition of sharpness as such is not a trivial task, as suitably illustrated by the large number of sharpness metrics suggested in the literature [e.g. 13, 14, 17, 42, 74, 98–101].

In order to rationalise our experimental results qualitatively and quantitatively, we first note that even an arbitrarily sharp mandible will not cut with arbitrarily small force. Cutting is akin to fracture, in the sense that it results in the creation of new surface area. Each unit area of new surface incurs an energy cost  $dU_A$ , and the work which provides this energy has to be supplied by the externally applied load, so that, from a simple virtual work argument,  $dU_{ext} = dU_A$ . Thus, and without loss of generality, the force  $F$  required to cut a slab of thickness  $t$  is bound from below by  $F \sim G_c t$ , where  $G_c$  is the energy per unit area of new surface, a characteristic material property [41, 68, 71, 102]. For our experiments with PDMS,  $G_c \sim 100 \text{ J m}^{-2}$  and  $t \sim 200 \mu\text{m}$  (see methods), so that  $F \sim 20 \text{ mN}$ . This simple argument lends itself to a definition of an intuitive, quantitative, and functionally relevant index for sharpness,  $S$ : the required cutting force

is equal to the minimum possible force, and independent of tool geometry, if and if only the dimensionless group  $S = G_c t F^{-1}$  is unity; the cutting tool may then be considered ideally sharp [for a conceptually similar suggestion, see 101]. The fracture forces measured for pristine mandibles of small workers are indeed very close to this theoretical minimum (see Fig. 2B), suggesting that a further reduction in cutting force through changes in mandible morphology may not be possible. Thus, pristine mandibles of small workers appear ideally sharp,  $S \approx 1$ , at least for PDMS (see below for a generalisation of this argument). In contrast, pristine mandibles of larger workers, scalpel blades and the most worn mandibles of foragers have a functional sharpness index  $S$  between  $2/3$  and  $1/5$ ; in other words, cutting (and fracture) forces are between 50-500% larger than the theoretical minimum, hinting at contributions from cutting tool geometry. The next task is thus to rationalise the putative influence of mandible geometry on cutting force.

The energy associated with the creation of new surface is not the only energy the external force has to supply. Friction, plasticity or sheet bending each carry their own energetic demands, so reducing the fraction of the external work available to drive the cut,  $dU_{ext} - dU_l = dU_{cut}$  [102]. Some of these costs, for example due to elastic sheet bending or sidewall friction, can be accounted for by drawing the mandible through the cut again, and are thus removed in the fracture force [see Fig. 3B, 11]; but others, related to the direct interaction between the mandible cutting edge and the material close to the crack-tip, likely remain. The simplest possible assumption is that tool geometry can be characterised by a single characteristic length scale,  $R$  [e. g. 11, 68, 103–105]. From dimensional arguments, this length scale will compete with a characteristic material length scale. In fracture mechanics, the typical length scale is given by the ratio between  $G_c$  and a characteristic stress  $\sigma_c$ , which may be interpreted physically as a critical crack tip opening displacement, or as the size of a crack process zone in which non-linear mechanisms consume additional energy [e. g. 11, 104, 106–108]. Thus, for this simplest case, dimensional arguments suggest that the additional energy term will be of the form  $dU_l \sim C \sigma_c R t dx$ , where  $C$  is a dimensionless constant. The fracture force now reads:

$$F_f = G_c t + C \sigma_c R t \quad (2)$$

from which the functional sharpness index follows as:

$$\frac{1}{S} = 1 + C \frac{\sigma_c R}{G_c} \quad (3)$$

In both equations, the first term represents the unavoidable cost arising from fracture alone; the second term accounts for additional costs linked to tool geometry. For simple geometries such as a cylindrical wire, an exact analysis is possible, and yields  $C = (1 + \mu)$ , where  $\mu$  is the coefficient of friction [41]. For our experiments, we equate  $\sigma_c$  with the ultimate tensile strength of PDMS [about 4 MPa, 70], and assume that the friction coefficient of mandibles on PDMS is similar to values for steel,  $\mu \approx 1$  [109, 110]. The geometry-dependent term  $2\sigma_c R G_c^{-1}$  then accounts for half of the cutting force,  $S = 0.5$ , if the characteristic length is  $R = 1/2 G_c \sigma_c^{-1} = 12.5 \mu\text{m}$ . A typical choice for  $R$  is the radius of the cutting edge [e. g. 11, 12, 14, 68, 98], and indeed, our rather approximate calculation is in remarkable agreement with direct measurements of the cutting edge radius of worn mandibles in *A. cephalotes*,

$R \approx 17 \mu\text{m}$  [27]. Pristine mandibles, in turn, may have a cutting edge radius as small as 50 nm [27], so that  $S = 0.996 \approx 1$ , in seeming agreement with the observation that the pristine mandibles of the smallest workers approach the theoretical minimum cutting force for PDMS (see Fig. 2B). The simple definition of sharpness suggested in Eq. 3 thus has the advantage that it is based on mechanical analysis instead of empirical correlation with observed mechanical performance, that it clearly separates material- and tool-dependent contributions to sharpness, and that its magnitude has a clear physical interpretation.

From this cursory analysis, we may surmise that fracture forces are effectively independent of mandible geometry if  $2\sigma_c R G_c^{-1} \ll 1$ , but grow in proportion to  $R \propto m^{1/3}$  for  $2\sigma_c R G_c^{-1} \gg 1$  [68, 103]. These limits thus delineate two regimes characterised by geometric invariance and length scaling of cutting forces, respectively, and in practise, the scaling of cutting forces with  $R$  may fall anywhere in between. This result may be put to use in two ways.

First, and in combination with our experimental data, it allows an approximate assessment of the parsimonious but unverified hypothesis that the characteristic mandible dimension  $R$  is isometric, i. e.  $R \propto m^{1/3}$ . Plausible alternative hypotheses may be derived. For example, the tip radii of insect claws depart from isometry and scale as  $R \propto m^{1/2}$ , presumably to ensure that tip stresses remain size-invariant [111]. In direct analogy, it is conceivable that pristine mandible cutting edge radii show a scaling shallower than isometry, or are even size-invariant. To test the hypothesis of isometry, we estimate the cutting edge radius  $R$  from the cutting force measured for a pristine mandible of the largest workers (40 mg in body mass), via  $F_c = G_c t + 2\sigma_c R t$ , yielding  $R_{40} \approx 5 \mu\text{m}$ . Next, we use this result to extract a proxy for the proportionality constant  $a$ , invoking the null hypothesis of isometry,  $R = a m^{1/3}$ , and then predict the variation of cutting force across the callow size range from 2.1–46.4 mg, using Eq. 2. An OLS regression on  $\log_{10}$ -transformed predictions yields an intercept of 1.33 and a slope of 0.07, remarkably close to the experimental values of 1.32 and 0.09 (units: mN, mg; see Table 1). Our experimental results are thus consistent with isometry of the mandible cutting edge radius. Although  $R$  may vary by as much as a factor of  $30^{0.33} \approx 3$  across the size range investigated in this study, cutting forces vary only little with size, because even large mandibles satisfy  $2\sigma_c R G_c^{-1} < 1$ . However, the considerable variation in our data even for pristine mandibles limits the statistical power to establishing consistency, and direct experimental assessment, for example via scanning electron microscopy [12, 27], is necessary to firmly establish isometry.

Second, Eq. 2 can be put to work to assess whether the size-invariance of cutting forces observed for a synthetic material such as PDMS may extend to natural materials typically cut by leaf-cutter ants. To this end, we extract proxies for the median  $G_c \approx 400 \text{ N m}^{-1}$ ,  $t = 200 \mu\text{m}$  and  $\sigma_c \approx 3 \text{ N mm}^{-2}$  from an extensive study on the leaf lamina of about 1000 tropical plant species [8], and again use Eq. 2 to predict the expected scaling of cutting forces. We find an intercept of 1.9 and a slope of 0.02. Thus, the size-dependence of the net cutting force in natural materials may be even weaker than for PDMS, because leaves have a higher toughness, but similar ultimate strength, so that  $2\sigma_c R G_c^{-1} < 1$ , and the geometry-independent term in Eq. 2 dominates. We stress that this analysis is approximate, and cutting of plant leaves may for example incur larger bending costs, because they are much stiffer. Preliminary support is however available from cutting force measure-

846 ments with laurel leaves. Based on the median tropical leaf with  
847  $G_c = 400 \text{ N m}^{-1}$ , and  $\sigma_c = 3 \text{ N mm}^{-2}$ , and the lamina thickness  
848 of laurel,  $t \approx 250 \mu\text{m}$ , Eq. 2 predicts cutting forces for a pristine  
849 mandible with  $R = 5 \mu\text{m}$  and a worn mandible with  $R = 12.5 \mu\text{m}$   
850 of 108 and 119 mN, respectively, in reasonable agreement with  
851 our experimental results (see Fig. 3A). Thus, a difference in cutting  
852 edge radius that would increase cutting forces in PDMS  
853 by about 40% increases those for the median leaf by a mere  
854 10%. Although the simple model based on dimensional argu-  
855 ments appears to quantitatively capture salient features of our  
856 experimental data, more thorough experimental validation, in-  
857 cluding cutting measurements with a range of natural materials  
858 and direct measurements of cutting edge radii, are in order.

859 The putatively weak size-dependence of mandible cutting  
860 forces for natural materials has two consequences worthy of  
861 brief discussion. First, it implies that mandible wear needs to  
862 be more severe in order to have an appreciable effect on cutting  
863 forces. As an illustrative example,  $S = 0.5$ , corresponding to a  
864 doubling of the required cutting force, occurs for  $R \approx 12.5 \mu\text{m}$   
865 in PDMS; the equivalent radius for the median tropical leaf is  
866  $R \approx 67 \mu\text{m}$  – about five times larger. However, there is robust ev-  
867 idence that wear affects leaf-cutter ant performance even when  
868 cutting natural materials: the average fracture force required for  
869 forager mandibles to cut laurel leaf lamina was about 30 mN  
870 higher than for callow mandibles (see Fig. 3A), and similar re-  
871 sults were reported by Schofield et al. [27] for *A. cephalotes*  
872 workers and *Prunus lusitanica* leaves; leaf-cutter ants with worn  
873 mandibles cut at significantly lower speeds [27, see also 53  
874 for similar results on leaf beetles]; and leaf-cutter ants with  
875 worn mandibles show changes in task preferences [27, 50, 94].  
876 Clearly, the role of wear in modulating cutting forces of natu-  
877 ral materials requires further experimental investigation. Sec-  
878 ond, and conversely, it suggests that even moderately small cut-  
879 ting edge radii may suffice to achieve  $S \approx 1$ . For example, for  
880  $R = 1 \mu\text{m}$ ,  $S = 0.99 \approx 1$ , and even for  $R = 10 \mu\text{m}$ ,  $S = 0.87$ , still  
881 within 15% of the maximum sharpness for cutting the median  
882 leaf. Thus, selection pressure on materials and edge geometry  
883 for the cutting tools of small animals may be less strong than  
884 previously suggested [12, 47].

## 885 Conclusions and outlook

886 The ability to cut leaves involves complex interactions between  
887 worker size, bite force capacity, wear-dependent cutting forces,  
888 plant-material properties and adaptive cutting behaviour. We  
889 tried to untangle this complexity, by removing the confound-  
890 ing effects of material heterogeneity and non-linear mandible  
891 motion, and studied the effects of worker size across two exper-  
892 imental groups with varying levels of mandibular wear.

893 Although smaller ants may experience a larger increase in  
894 cutting force from pristine to worn mandibles, cutting forces  
895 were still largely size-independent, in contrast to our initial  
896 hypothesis. The ability to cut leaves is thus mostly affected  
897 by size-dependent bite forces, plant-material properties, and  
898 mandibular wear, so that larger ants require a substantially  
899 smaller fraction of their maximum bite force to cut the same  
900 material. In agreement with our second hypothesis, the effects  
901 of wear on cutting force can be substantial, which may strongly  
902 reduce the range of accessible plant tissues for small workers.

903 Pristine mandibles of callow workers are exceedingly ‘sharp’,  
904 and even mandibles with moderate levels of mandibular wear

require similar forces to the ‘sharpest’ pristine scalpel blade;  
these results indicate morphological adaptations of leaf-cutter  
ant mandibles to the high mechanical demands of cutting [27,  
45].

A natural extension to this work would be to use other ma-  
terials as cutting substrate, and to test quantitative predictions  
on cutting force variation and cutting edge geometry for a  
broader selection of biologically relevant substrates. A careful  
inspection of the mandibular cutting blade, in combination with  
mandible abrasion experiments, could yield important insights  
into the mechanisms of wear resistance in insects [43, 45].

We hope that the findings of this study will help to increase  
our understanding of size-specific foraging preferences in leaf-  
cutter ants, and more generally, may provide a framework to dis-  
cuss the relative importance of tool geometry vs material prop-  
erties in biological cutting.

## Acknowledgments

We thank Flavio Roces, who for kindly provided the ant colonies used  
in this study, and Franka Nauert, Aurèlie Levillain and Andrea Attipoe  
for their preliminary work on the fibre-optic setup. This study is part of  
a project that has received funding from the European Research Coun-  
cil (ERC) under the European Union’s Horizon 2020 research and in-  
novation programme (Grant agreement No. 851705) awarded to DL.

## References

- [1] Sanson G. 2006 The biomechanics of browsing and grazing. *American Journal of Botany* **93**: 1531-1545.
- [2] Evans AR, Hunter J, Fortelius M, Sanson GD. 2005 The scaling of tooth sharpness in mammals. In: *Annales Zoologici Fennici*. JSTOR, pp. 603–613.
- [3] Clissold F. 2007 The biomechanics of chewing and plant fracture: Mechanisms and implications. *Advances in Insect Physiology* **34**.
- [4] Alexander RM. 1985 The maximum forces exerted by animals. *Journal of Experimental Biology* **115**: 231–238.
- [5] Vincent JF. 1990 Fracture properties of plants. In: *Advances in Botanical Research*, Elsevier, volume 17. pp. 235–287.
- [6] Lucas PW, Turner IM, Dominy NJ, Yamashita N. 2000 Mechanical defences to herbivory. *Annals of Botany* **86**: 913-920.
- [7] Sanson G, Read J, Aranwela N, Clissold F, Peeters P. 2001 Measurement of leaf biomechanical properties in studies of herbivory: Opportunities, problems and procedures. *Austral Ecology* **26**: 535-546.
- [8] Onoda Y, Westoby M, Adler PB, Choong AMF, Clissold FJ, Cornelissen JHC, Díaz S, Dominy NJ, Elgart A, Enrico L, Fine PVA, Howard JJ, Jalili A, Kitajima K, Kurokawa H, McArthur C, Lucas PW, Markesteijn L, Pérez-Harguindeguy N, Poorter L, Richards L, Santiago LS, Sosinski Jr EE, Van Bael SA, Warton DI, Wright IJ, Joseph Wright S, Yamashita N. 2011 Global patterns of leaf mechanical properties. *Ecology Letters* **14**: 301-312.
- [9] Hua L, He P, Goldstein G, Liu H, Yin D, Zhu S, Ye Q. 2020 Linking vein properties to leaf biomechanics across 58 woody species from a subtropical forest. *Plant Biology* **22**: 212–220.

- 958 [10] Lucas PW. 2004 Dental functional morphology: how teeth  
959 work. Cambridge University Press.
- 960 [11] Atkins T. 2009 The Science and Engineering of Cutting: The  
961 Mechanics and Processes of Separating, Scratching and Punc-  
962 turing Biomaterials, Metals and Non-metals. Oxford, UK:  
963 Butterworth-Heinemann.
- 964 [12] Schofield RM, Choi S, Coon JJ, Goggans MS, Kreisman TF,  
965 Silver DM, Nesson MH. 2016 Is fracture a bigger problem for  
966 smaller animals? force and fracture scaling for a simple model  
967 of cutting, puncture and crushing. *Interface Focus* **6**.
- 968 [13] Anderson PS. 2018 Making a point: shared mechanics underly-  
969 ing the diversity of biological puncture. *Journal of Experimental*  
970 *Biology* **221**: jeb187294.
- 971 [14] Crofts S, Lai Y, Hu Y, Anderson P. 2019 How do morphological  
972 sharpness measures relate to puncture performance in viperid  
973 snake fangs? *Biology Letters* **15**: 20180905.
- 974 [15] Gundiah N, Jaddivada S. 2020 Making the cut: mechanics of  
975 cutting and steering of insect probes. *Current Opinion in Insect*  
976 *Science* **42**: 84–89.
- 977 [16] Anderson PS, LaBarbera M. 2008 Functional consequences of  
978 tooth design: effects of blade shape on energetics of cutting.  
979 *Journal of Experimental Biology* **211**: 3619–3626.
- 980 [17] Crofts S, Anderson P. 2018 The influence of cactus spine surface  
981 structure on puncture performance and anchoring ability is tuned  
982 for ecology. *Proceedings of the Royal Society B* **285**: 20182280.
- 983 [18] Weber NA. 1972 The fungus-culturing behaviour of ants. *Amer-*  
984 *ican Zoologist* **12**: 577-587.
- 985 [19] Wetterer JK. 1994 Forager polymorphism, size-matching, and  
986 load delivery in the leaf-cutting ant, *Atta cephalotes*. *Ecological*  
987 *Entomology* **19**: 57-64.
- 988 [20] Wetterer JK. 1995 Forager polymorphism and foraging ecology  
989 in the leaf-cutting ant, *Atta colombica*. *Psyche* **102**: 131-145.
- 990 [21] Wetterer JK. 1999 The ecology and evolution of worker size-  
991 distribution in leaf-cutting ants (hymenoptera: Formicidae). *So-*  
992 *ciobiology* **34**: 119-144.
- 993 [22] Cherrett JM. 1968 The foraging behaviour of *Atta cephalotes*  
994 I. (Hymenoptera, Formicidae). *Journal of Animal Ecology* **37**:  
995 387-403.
- 996 [23] Cherrett JM. 1972 Some factors involved in the selection of veg-  
997 etable substrate by *Atta cephalotes* (L.) (hymenoptera: Formici-  
998 dae) in tropical rain forest. *Journal of Animal Ecology* **41**: 647-  
999 660.
- 1000 [24] Wilson EO. 1980 Caste and division of labor in leaf-cutter ants  
1001 (Hymenoptera: Formicidae: *Atta*): I. the overall pattern in *A.*  
1002 *Sextens*. *Behavioral Ecology and Sociobiology* **7**: 143-156.
- 1003 [25] Wirth R, Herz H, Ryel RJ, Beyschlag W, Hölldobler B. 2003  
1004 Herbivory of Leaf-Cutting Ants: A Case Study on *Atta colom-*  
1005 *bica* in the Tropical Rainforest of Panama. Berlin, Heidelberg,  
1006 New York: Springer Science & Business Media.
- 1007 [26] Tautz J, Roces F, Hölldobler B. 1995 Use of a sound-based vi-  
1008 bratome by leaf-cutting ants. *Science* **267**: 84.
- 1009 [27] Schofield RM, Emmett KD, Niedbala JC, Nesson M. 2011 Leaf-  
1010 cutter ants with worn mandibles cut half as fast, spend twice the  
1011 energy, and tend to carry instead of cut. *Behavioral Ecology and*  
1012 *Sociobiology* **65**: 969-982.
- [28] Wetterer JK. 1991 Allometry and geometry of leaf-cutting in  
*Atta cephalotes*. *Behavioral Ecology and Sociobiology* **29**: 347-  
351.
- [29] Roces F. 1990 Leaf-cutting ants cut fragment sizes in relation to  
the distance from the nest. *Animal Behaviour* **40**: 1181-1183.
- [30] Burd M. 1996 Foraging performance by *Atta colombica*, a leaf-  
cutter ant. *The American Naturalist* **148**: 597-612.
- [31] Rudolph SG, Loudon C. 1986 Load size selection by foraging  
leaf-cutter ants (*Atta cephalotes*). *Ecological Entomology* **11**:  
401-410.
- [32] Howard JJ. 1988 Leafcutting and diet selection: relative influ-  
ence of leaf chemistry and physical features. *Ecology* **69**: 250-  
260.
- [33] Nichols-Orians CM, Schultz JC. 1989 Leaf toughness affects  
leaf harvesting by the leaf cutter ant, *Atta cephalotes* (L.) (Hy-  
menoptera: Formicidae). *Biotropica* **21**: 80-83.
- [34] Roces F, Hölldobler B. 1994 Leaf density and a trade-off be-  
tween load-size selection and recruitment behaviour in the ant  
*Atta cephalotes*. *Oecologia* **97**: 1-8.
- [35] Röschard J, Roces F. 2002 The effect of load length, width and  
mass on transport rate in the grass-cutting ant *Atta vollenwei-*  
*deri*. *Oecologia* **131**: 319-324.
- [36] Wilson EO. 1980 Caste and division of labor in leaf-cutter ants  
(Hymenoptera: Formicidae: *Atta*): II. the ergonomic optimiza-  
tion of leaf cutting. *Behavioral Ecology and Sociobiology* **7**:  
157-165.
- [37] Nichols-Orians CM, Schultz JC. 1990 Interactions among leaf  
toughness, chemistry, and harvesting by attine ants. *Ecological*  
*Entomology* **15**: 311-320.
- [38] Wetterer JK. 1994 Ontogenetic changes in forager poly-  
morphism and foraging ecology in the leaf-cutting ant *Atta*  
*cephalotes*. *Oecologia* **98**: 235-238.
- [39] Paul J, Gronenberg W. 1999 Optimizing force and velocity:  
Mandible muscle fibre attachments in ants. *The Journal of Ex-*  
*perimental Biology* **202**: 797-808.
- [40] Püffel F, Roces F, Labonte D. 2022 Strong positive allometry of  
bite force in leaf-cutter ants increases the range of cuttable plant  
tissues. *bioRxiv* .
- [41] Kamyab I, Chakrabati S, Williams JG. 1998 Cutting cheese with  
wire. *Journal of Materials Science* **33**: 2763-2770.
- [42] Schuldt S, Arnold G, Kowalewski J, Schneider Y, Rohm H. 2016  
Analysis of the sharpness of blades for food cutting. *Journal of*  
*Food Engineering* **188**: 13–20.
- [43] Reynolds OL, Keeping MG, Meyer JH. 2009 Silicon-augmented  
resistance of plants to herbivorous insects: a review. *Annals of*  
*Applied Biology* **155**: 171-186.
- [44] Depieri RA, Siqueira F, Panizzi AR. 2010 Aging and food  
source effects on mandibular stylets teeth wear of phytophagous  
stink bug (Heteroptera: Pentatomidae). *Neotropical Entomology*  
**39**: 952-956.
- [45] Schofield RM, Nesson MH, Richardson KA. 2002 Tooth hard-  
ness increases with zinc-content in mandibles of young adult  
leaf-cutter ants. *Naturwissenschaften* **89**: 579-583.
- [46] Labonte D, Lenz AK, Oyen ML. 2017 On the relationship be-  
tween indentation hardness and modulus, and the damage resis-  
tance of biological materials. *Acta Biomaterialia* **57**: 373–383.

- 1069 [47] Schofield R, Bailey J, Coon JJ, Devaraj A, Garrett RW, Gog- 1126  
 1070 gans MS, Hebner MG, Lee BS, Lee D, Lovern N, et al. 2021 1127  
 1071 The homogenous alternative to biomineralization: Zn-and mn- 1128  
 1072 rich materials enable sharp organismal “tools” that reduce force 1129  
 1073 requirements. *Scientific Reports* **11**: 1–23. 1130
- 1074 [48] Röschard J, Roces F. 2003 Fragment-size determination and 1131  
 1075 size-matching in the grass-cutting ant *Atta vollenweideri* depend 1132  
 1076 on the distance from the nest. *Journal of Tropical Ecology* **19**: 1133  
 1077 647–653. 1134
- 1078 [49] Schofield RM, Nesson MH, Richardson KA, Wyeth P. 2003 Zinc 1135  
 1079 is incorporated into cuticular “tools” after ecdysis: The time 1136  
 1080 course of the zinc distribution in “tools” and whole bodies of 1137  
 1081 an ant and a scorpion. *Journal of Insect Physiology* **49**: 31–44. 1138
- 1082 [50] Camargo R, Forti LC, Lopes J, Andrade A, Ottati A. 2007 1139  
 1083 Age polyethism in the leaf-cutting ant *Acromyrmex subterra- 1140  
 1084 neus brunneus* forel, 1911 (hym., formicidae). *Journal of Ap- 1141  
 1085 plied Entomology* **131**: 139–145. 1142
- 1086 [51] Pielström S, Roces F. 2013 Sequential soil transport and its in- 1143  
 1087 fluence on the spatial organisation of collective digging in leaf- 1144  
 1088 cutting ants. *Public Library of Science One* **8**: e57040. 1145
- 1089 [52] Püffel F, Pouget A, Liu X, Zuber M, van de Kamp T, Roces 1146  
 1090 F, Labonte D. 2021 Morphological determinants of bite force 1147  
 1091 capacity in insects: a biomechanical analysis of polymorphic 1148  
 1092 leaf-cutter ants. *Journal of the Royal Society Interface* **18**: 1149  
 1093 20210424. 1150
- 1094 [53] Raupp MJ. 1985 Effects of leaf toughness on mandibular wear 1151  
 1095 of the leaf beetle, *Plagioderia versicolora*. *Ecological Entomol- 1152  
 1096 ogy* **10**: 73–79. 1153
- 1097 [54] Dockter DE. 1993 Developmental changes and wear of larval 1154  
 1098 mandibles in *Heterocampa guttivitta* and *H. subrotata* (notodon- 1155  
 1099 tidae). *Journal of the Lepidopterists’ Society* **47**: 32–48. 1156
- 1100 [55] Roitberg BD, Gillespie DR, Quiring DM, Alma CR, Jenner WH, 1157  
 1101 Perry J, Peterson JH, Salomon M, VanLaerhoven S. 2005 The 1158  
 1102 cost of being an omnivore: mandible wear from plant feeding in 1159  
 1103 a true bug. *Naturwissenschaften* **92**: 431–434. 1160
- 1104 [56] Smith M, Kvedaras O, Keeping M. 2007 A novel method to de- 1161  
 1105 termine larval mandibular wear of the african stalk borer, eldana 1162  
 1106 saccharina walker (lepidoptera: Pyralidae). *African Entomology 1163  
 1107* **15**: 204–208. 1164
- 1108 [57] Kvedaras OL, Byrne MJ, Coombes NE, Keeping MG. 2009 In- 1165  
 1109 fluence of plant silicon and sugarcane cultivar on mandibular 1166  
 1110 wear in the stalk borer *Eldana saccharina*. *Agricultural and 1167  
 1111 Forest Entomology* **11**: 301–306. 1168
- 1112 [58] Oettler J, Johnson RA. 2009 The old ladies of the seed harvester 1169  
 1113 ant *Pogonomyrmex rugosus*: foraging performed by two groups 1170  
 1114 of workers. *Journal of Insect Behavior* **22**: 217–226. 1171
- 1115 [59] Kokko EG, Schaber BD, Entz T. 1993 Quantification of 1172  
 1116 mandibular wear of female alfalfa leafcutter bees, *Megachile 1173  
 1117 rotundata* (f.)(hymenoptera: Megachilidae), by image analysis. 1174  
 1118 *The Canadian Entomologist* **125**: 93–99. 1175
- 1119 [60] Kuřavová K, Hajduková L, Kočárek P. 2014 Age-related 1176  
 1120 mandible abrasion in the groundhopper *Tetrix tenuicornis* (tet- 1177  
 1121 rigidae, orthoptera). *Arthropod Structure & Development* **43**: 1178  
 1122 187–192. 1179
- 1123 [61] Labonte D, Federle W. 2015 Rate-dependence of ‘wet’ biolog- 1180  
 1124 ical adhesives and the function of the pad secretion in insects. 1181  
 1125 *Soft Matter* **11**: 8661–8673. 1182
- [62] Choong MF. 1996 What makes a leaf tough and how this affects 1183  
 the pattern of *Castanopsis fissa* leaf consumption by caterpillars. 1184  
*Functional Ecology* **10**: 668–674. 1185
- [63] Spatz H, Kohler L, Niklas K. 1999 Mechanical behaviour of 1186  
 plant tissues: composite materials or structures? *Journal of 1187  
 Experimental Biology* **202**: 3269–3272. 1188
- [64] Hayot CM, Forouzesh E, Goel A, Avramova Z, Turner JA. 2012 1189  
 Viscoelastic properties of cell walls of single living plant cells 1190  
 determined by dynamic nanoindentation. *Journal of Experimen- 1191  
 tal Botany* **63**: 2525–2540. 1192
- [65] Cordoba-Barco G, Casanova F, Ealo JL. 2020 Determination of 1193  
 poro-viscoelastic properties of vegetal tissues as a function of 1194  
 moisture content by means of stress relaxation tests. *Rheologica 1195  
 Acta* **59**: 201–208. 1196
- [66] Seghir R, Arscott S. 2015 Extended pdms stiffness range for 1197  
 flexible systems. *Sensors and Actuators A: Physical* **230**: 33– 1198  
 39. 1199
- [67] Sun JY, Zhao X, Illeperuma WR, Chaudhuri O, Oh KH, Mooney 1200  
 DJ, Vlassak JJ, Suo Z. 2012 Highly stretchable and tough hydro- 1201  
 gels. *Nature* **489**: 133–136. 1202
- [68] Zhang B, Shiang CS, Yang SJ, Hutchens SB. 2019 Y-shaped 1203  
 cutting for the systematic characterization of cutting and tearing. 1204  
*Experimental Mechanics* **59**: 517–529. 1205
- [69] Palchesko RN, Zhang L, Sun Y, Feinberg AW. 2012 Devel- 1206  
 opment of polydimethylsiloxane substrates with tunable elas- 1207  
 tic modulus to study cell mechanobiology in muscle and nerve. 1208  
*PLoS One* **7**: e51499. 1209
- [70] Johnston I, McCluskey D, Tan C, Tracey M. 2014 Mechanical 1210  
 characterization of bulk sylgard 184 for microfluidics and mi- 1211  
 croengineering. *Journal of Micromechanics and Microengineer- 1212  
 ing* **24**: 035017. 1213
- [71] Lake GJ, Yeoh OH. 1978 Measurement of rubber cutting resis- 1214  
 tance in the absence of friction. *International Journal of Frac- 1215  
 ture* **14**: 509–526. 1216
- [72] Roces F, Lighton JR. 1995 Larger bites of leaf-cutting ants. *Na- 1217  
 ture* **373**: 392. 1218
- [73] Atkins AG, Mai YW. 1979 On the guillotining of materials. 1219  
*Journal of Materials Science* **14**: 2747–2754. 1220
- [74] McCarthy CT, Hussey M, Gilchrist MD. 2007 On the sharpness 1221  
 of straight edge blades in cutting soft solids: Part i - indentation 1222  
 experiments. *Engineering Fracture Mechanics* **74**: 2205–2224. 1223
- [75] Gent A. 1996 Adhesion and strength of viscoelastic solids. 1224  
 is there a relationship between adhesion and bulk properties? 1225  
*Langmuir* **12**: 4492–4496. 1226
- [76] Marwick B, Krishnamoorthy K. 2019 cvequality: Tests for the 1227  
 equality of coefficients of variation from multiple groups. *R 1228  
 software package version 0.1 3*. 1229
- [77] Van Rossum G, Drake FL. 2009 Python 3 Reference Manual. 1230  
 Scotts Valley, CA: CreateSpace. 1231
- [78] R Core Team. 2022 R: A Language and Environment for Statis- 1232  
 tical Computing. R Foundation for Statistical Computing, Vi- 1233  
 enna, Austria. URL <https://www.R-project.org/>. 1234
- [79] Field A, Miles J, Field Z. 2012 Discovering statistics using r. 1235  
*Great Britain: Sage Publications, Ltd* . 1236

- 1180 [80] Fowler HG, Pagani MI, Da Silva OA, Forti LC, Vasconelos DL. 1236  
 1181 1989 A pest is a pest is a pest? the dilemma of neotropical leaf- 1237  
 1182 cutting ants keystone taxa of natural ecosystems. *Environmental* 1238  
 1183 *Management* **13**: 671-675.
- 1184 [81] Oster GF, Wilson EO. 1978 Caste and ecology in the social in- 1239  
 1185 sects. Princeton University Press. 1240
- 1186 [82] Wilson EO. 1983 Caste and division of labor in leaf-cutter ants 1241  
 1187 (Hymenoptera: Formicidae: *Atta*): III. ergonomic resiliency in 1242  
 1188 foraging by *A. cephalotes*. *Behavioral Ecology and Sociobiol-* 1243  
 1189 *ogy* **14**: 47-54. 1244
- 1190 [83] Wilson EO. 1983 Caste and division of labor in leaf-cutter ants 1245  
 1191 (Hymenoptera: Formicidae: *Atta*): IV. colony ontogeny of *A.* 1246  
 1192 *cephalotes*. *Behavioral Ecology and Sociobiology* **14**: 55-60.
- 1193 [84] Reyssat E, Tallinen T, Le Merrer M, Mahadevan L. 2012 Slicing 1247  
 1194 softly with shear. *Physical Review Letters* **109**: 244301. 1248
- 1195 [85] Liu Y, Hui CY, Hong W. 2021 A clean cut. *Extreme Mechanics* 1249  
 1196 *Letters* **46**: 101343. 1250
- 1197 [86] Püffel F, Johnston R, Labonte D. 2023 A biomechanical model 1251  
 1198 for the relation between bite force and mandibular opening angle 1252  
 1199 in arthropods. *Royal Society Open Science* **10**: 221066. 1253
- 1200 [87] Labonte D. 2022 A theory of physiological similarity in muscle- 1254  
 1201 driven motion. *bioRxiv* . 1255
- 1202 [88] Barquins M, Maugis D. 1981 Tackiness of elastomers. *The Jour-* 1256  
 1203 *nal of Adhesion* **13**: 53-65. 1257
- 1204 [89] Shull KR. 2002 Contact mechanics and the adhesion of soft 1258  
 1205 solids. *Materials Science and Engineering: R: Reports* **36**: 1- 1259  
 1206 45. 1260
- 1207 [90] Müser H, Martin, Persson BN. 2022 Crack and pull-off dynam- 1261  
 1208 ics of adhesive, viscoelastic solids. *Europhysics Letters* **137**: 1262  
 1209 36004. 1263
- 1210 [91] Hill AV. 1964 The efficiency of mechanical power development 1264  
 1211 during muscular shortening and its relation to load. *Proceedings* 1265  
 1212 *of the Royal Society of London. Series B. Biological Sciences* 1266  
 1213 **159**: 319-324. 1267
- 1214 [92] Garrett RW, Carlson KA, Goggans MS, Nesson MH, Shepard 1268  
 1215 CA, Schofield RM. 2016 Leaf processing behaviour in *Atta* leaf- 1269  
 1216 cutter ants: 90% of leaf cutting takes place inside the nest, and 1270  
 1217 ants select pieces that require less cutting. *Royal Society Open* 1271  
 1218 *Science* **3**: 1-12. 1272
- 1219 [93] Moll K, Federle W, Roces F. 2011 The energetics of running 1273  
 1220 stability: costs of transport in grass-cutting ants depend on frag- 1274  
 1221 ment shape. *The Journal of Experimental Biology* **215**: 161- 1275  
 1222 168. 1276
- 1223 [94] Hart AG, Ratnieks FL. 2001 Task partitioning, division of labour 1277  
 1224 and nest compartmentalisation collectively isolate hazardous 1278  
 1225 waste in the leafcutting ant *Atta cephalotes*. *Behavioral Ecol-* 1279  
 1226 *ogy and Sociobiology* **49**: 387-392. 1280
- 1227 [95] Chapman R. 1964 The structure and wear of the mandibles in 1281  
 1228 some african grasshoppers. *Proceedings of the Zoological Soci-* 1282  
 1229 *ety of London* **142**: 107-122. 1283
- 1230 [96] Arens W. 1990 Wear and tear of mouthparts: a critical problem 1284  
 1231 in stream animals feeding on epilithic algae. *Canadian Journal* 1285  
 1232 *of Zoology* **68**: 1896-1914. 1286
- 1233 [97] Köhler G, Jentsch A, Reinhardt K. 2000 Age related mandible 1287  
 1234 abrasion in three species of short-horned grasshoppers (caelif- 1288  
 1235 era: Acrididae). *Journal of Orthoptera Research* : 81-87. 1289
- [98] Reilly GA, McCormack BA, Taylor D. 2004 Cutting sharpness 1290  
 measurement: a critical review. *Journal of Materials Processing* 1291  
*Technology* **153-154**: 261-267. 1292
- [99] McCarthy CT, Annaidh AN, Gilchrist MD. 2010 On the sharp- 1293  
 ness of straight edge blades in cutting soft solids: Part ii- 1294  
 analysis of blade geometry. *Engineering Fracture Mechanics* 1295  
**77**: 437-451. 1296
- [100] Schuldt S, Arnold G, Roschy J, Schneider Y, Rohm H. 2013 1297  
 Defined abrasion procedures for cutting blades and comparative 1298  
 mechanical and geometrical wear characterization. *Wear* **300**: 1299  
 38-43. 1300
- [101] Zhang B, Anderson PS. 2022 Modelling biological puncture: 1301  
 a mathematical framework for determining the energetics and 1302  
 scaling. *Journal of the Royal Society Interface* **19**: 20220559. 1303
- [102] Williams JG, Patel Y. 2016 Fundamentals of cutting. *Interface* 1304  
*Focus* **6**: 20150108. 1305
- [103] Kountanya RK, Endres WJ. 2004 Flank wear of edge-radiused 1306  
 cutting tools under ideal straight-edged orthogonal conditions. 1307  
*Journal of Manufacturing Science and Engineering* **126**: 496- 1308  
 505. 1309
- [104] Creton C, Ciccotti M. 2016 Fracture and adhesion of soft materi- 1310  
 als: a review. *Reports on Progress in Physics* **79**: 046601. 1311
- [105] Zhang B, Hutchens SB. 2021 On the relationship between cut- 1312  
 ting and tearing in soft elastic solids. *Soft Matter* **17**: 6728- 1313  
 6741. 1314
- [106] Barenblatt GI. 1962 The mathematical theory of equilibrium 1315  
 cracks in brittle fracture. *Advances in applied mechanics* **7**: 55- 1316  
 129. 1317
- [107] Lawn B. 1993 Fracture of Brittle Solids. Cambridge University 1318  
 Press, 2 edition. 1319
- [108] Long R, Hui CY, Gong JP, Bouchbinder E. 2021 The fracture 1320  
 of highly deformable soft materials: A tale of two length scales. 1321  
*Annual Review of Condensed Matter Physics* **12**: 71-94. 1322
- [109] He B, Chen W, Jane Wang Q. 2008 Surface texture effect on 1323  
 friction of a microtextured poly (dimethylsiloxane)(pdms). *Tri-* 1324  
*bology Letters* **31**: 187-197. 1325
- [110] Li J, Zhou F, Wang X. 2011 Modify the friction between steel 1326  
 ball and pdms disk under water lubrication by surface texturing. 1327  
*Meccanica* **46**: 499-507. 1328
- [111] Patrick JG, Labonte D, Federle W. 2018 Scaling of claw sharp- 1329  
 ness: mechanical constraints reduce attachment performance in 1330  
 larger insects. *Journal of Experimental Biology* **221**. 1331